TAXONOMY, DEVELOPMENT AND MORPHOLOGY OF THE IMMATURE STAGES OF CICADELLIDAE (HOMOPTERA)

by

Jeyaraney Kathirithamby

Being a thesis submitted in part fulfilment of the requirements of the University of London for the degree of Doctor of Philosophy.

Imperial College of Science and Technology,
Field Station,
Silwood Park,
Sunninghill,
Ascot,
Berkshire.

September, 1971

ABSTRACT

This thesis is concerned with the external morphology of the larval and adult stages of some British Cicadellidae (Homoptera) and a key is presented to fifth instar larvae of twenty-two species.

Detailed descriptions of the external morphology of six species have been made, and the development of the external male and female genitalia has been traced through the immature stages to the adult. The development of the chaetotaxy in successive instars of eight Cicadellid species was investigated and a key to the separation of the larval instars of British Cicadellidae of acid grasslands is provided.

Further, growth in five species was analysed by the multiple discriminant analysis which was applied to seven measured structural features. The analyses used are described and the results discussed.

Some numerical methods were applied to fifty-one characters of fifth instar larvae of twenty-two species. The results of these analyses are described and compared with the existing taxonomy of the adult stages. An attempt is made at providing a key to the fifth instar larvae of the twenty-two species of British Cicadellidae.

Further, the detailed morphology and taxonomy of various parts of the abnormal genitalia of parasitized individuals of Cicadellidae are presented in the appendix.

TABLE OF CONTENTS

Page

(vii) Chaetotaxy

SECTION B: Multivariate Analysis of Growth in Five Species of Cicadellidae

III. MULTIPLE DISCRIMINANT ANALYSIS

SECTION C: The Application of Multivariate Analysis to the Taxonomy of the Fifty Instar Larvae of Twenty-two British Cicadellidae

Page

(ii) Multiple Discriminant Analysis

(iii) Principal Co-ordinate Analysis

SECTION D: Key to Fifth Instar Larvae of Twenty-two British Cicadellidae

GENERAL INTRODUCTION

The British members of the family Cicadellidae fall into thirteen subfamilies, ninety-eight genera and two hundred and sixty-seven species. These Cicadellids dwell in grasses, low vegetation or on shrubs and trees. Characteristically of Auchenorhyncha they have sucking mouth parts and are plant feeders.

The first section of this thesis is concerned with the detailed taxonomy, development and external morphology of the larval and adult stages of six species, namely of *Ulopa reticulata* (Fabricius), *Doratura stylata* (Boheman), *Cicadula persimilis* (Edwards), *Mocydiopsis parvicauda* Ribaut, *Balclutha punctata* (Thunberg) and *Zygina scutellaris* (Herrich-Schaeffer).

There are very few descriptions of Cicadellid larvae in literature, although considerable work has been performed on the adult stage. One of the early accounts of the larval stage is by Leonard (1915) who described the immature stages of *Idiocerus provancheri* Van Duzee. Osborn (1916) gave a short description of the larval stages of *Cicadula sexnotata*, which Jurisoo (1964) later called a "species group" which embraced several closely related species, which can be distinguished only by the external male genitalia (Wagner, 1941); this group comprises *Macrosteles laevis* Ribaut, *M. cristatus* Ribaut and *M. sexnotatus* (Fallén). Bollow (1950) in his paper concerning the reappearance of *M. laevis* in Bavaria included a short description of the larval stages. Misra (1920), Hackman (1922) and MacGill (1932) in their studies on *Nephotettix bipunctatus* (Fabricius) and *N. apicalis* (Motsch), *Cicadella hieroglyphica* Say and *Erythroneura pallidifrons* Edwards also included short descriptions of the larval stages.

Multivariate analysis of growth was carried out on five species, namely *U. reticulata*, *M. parvicauda*, *C. persimilis*, *Errastunus ocellaris* (Fallén) and *B. punctata*. This is the first time such an analysis was applied to a group of five species of insects which belong to the same family but to different subfamilies and tribes. Similar analyses have been applied by Blackith, Davies & Moy (1963) to the development of *Dysdercus fasciatus* (Sign.), by Blackith & Blackith (1969) to Morabine grasshoppers and by Brown (1969) to two species of *Ectobius*.

Several numerical methods were applied to fifty-one characters of fifth instar Cicadellid larvae of twenty-two species. As there is no key to the European larval members of this family, an attempt is made at contriving one for twenty-two common species.

General Material and Methods

All the species studied were collected at the Imperial College Field Station, Silwood Park. The various larval instars of Cicadellidae were obtained mainly by rearing. Although it is fairly easy to find the fourth and fifth instars in the field, the first three instars are extremely difficult to collect. This is mainly because the earlier instars are small and tend to remain near the soil. The adults were caught in the field at the appropriate times of the year. The grass dwelling species were collected by means of a sweep net and the tree dwelling species on a black beating tray.

The adults were paired, placed on their apparent natural plant hosts which were planted in flower pots of 8 cm in diameter, and caged within cylinders of dimensions of 7 cm in diameter and 14 cm in height. These cylinders were made of cellulose acetate fitted with muslin windows. Mass cultures in larger cages were kept during the winter months.

Macrosteles sexnotatus (Fallén) was reared on oats 'Condor' at 20°C and 16 light hours. Cultures in 25°C were unsuccessful.

U. reticulata was reared on *Calluna vulgaris* (L.) in 20°C and 16 light hours, but cultures in 25°C again proved unsuccessful.

D. stylata was reared on *Holcus mollis* L. at 20°C and 16 light hours.

M. parvicauda was reared on *Agrostis* spp. at 25°C. Cultures in 20°C were not successful.

C. persimilis and *Z. scutellaris* were reared on *Dactylis glormerata* L. in 25°C. Again cultures of both species kept in 20°C were unsuccessful.

B. punctata was reared on *Deschampsia flexuosa* (L.)in 20°C and 16 light hours.

The rearing technique was simple but the actual rearing of the larvae was difficult and tedious, as the plants were often attacked by fungi and although the adults were found in a mixture of grasses in the field, they usually laid eggs on one species of grass.

All the first instar larvae were preserved in a mixture of 40% alcohol and 10% glycerol. Other instars were preserved in 70% alcohol except *Z. scutellaris*, which was preserved in a mixture of 40% alcohol and 10% glycerol in all instars as the body contents readily dissolved in 70% alcohol.

The external male and female genitalia of the adults were dissected after softening the terminalia in cold 10% potassium hydroxide for about an hour. They were then washed in 90% and 100% alcohol and finally passed through xylene for a few seconds. Preparations were made on 3 X 1 inch micro -cavity slides and the specimens were mounted in canada balsam.

All drawings were made with the aid of a Binocular Dissecting Microscope using an eye piece graticule.

Section A THE TAXONOMY AND EXTERNAL MORPHOLOGY OF THE LARVAL AND ADULT STAGES OF CICADELLIDAE

I. EXTERNAL MORPHOLOGY

(i) HEAD

(a) Introduction and Review of Literature

There are no records on the detailed descriptions of the external morphology of larval stages of Cicadellidae, although the taxonomy and morphology of the adult stage has been quite thoroughly studied.

Muir & Kershaw (1911) studied the mouth parts of Hemiptera and Muir (1926) reconsidered some of the points in the morphology of the head of Homoptera. Evans (1939) gave a concise account of the morphology of the head of Homoptera. Later (1946) he compared the structure of the head of Leafhoppers with that in all other orders of insects. Recently he pointed out the structure which developed in recent Homoptera, but is absent in the extinct ones (1957).

Spooner (1938) drew up the phylogeny of Hemiptera, based on an account of the comparative study of the mouth parts of Hemiptera-Homoptera. Kramer (1950) gave a detailed comparative account of the morphology of Auchenorhynchous Homoptera which included a detailed description of the Cicadellid *Aulacizes irrorata* (Fabricius).

One of the many papers Snodgrass wrote was on the loral plates and hypopharynx of Hemiptera (1938). Duporte (1946, 1957) performed a thorough study of the insect head and one of his recent works was on the anterior tentorial arms and their significance in interpreting the morphology of the Cicadas (1962).

Quite recently Ali (1958) studied the external morphology of several Cicadellidae and gave descriptions of the head.

Parsons (1964) gave an account of the origin and development of the Hemipteran cranium.

The external morphology and the characters used in the taxonomy of the head in Cicadellidae are examined in this section.

(b) Definitions of the Accepted Morphological Terms, and Terminology and Descriptions used by Previous Authors

Before attempting to present the external morphology of the head in Cicadellidae, a list of definitions of the accepted morphological terms and those which have been used somewhat loosely are summarized below.

Terms	Definitions
Vertex or crown	Dorsal aspect of the head lying between the compound eyes.

Terms	Definitions
Face	Anterior region of the head.
Frons	Facial region between the compound eyes.
Postclypeus	Median swollen region on the face lying ventral to the frons.
Anteclypeus	Triangular sclerite lying below the postclypeus.
Frontogenal sulcus	Lateral sulcus which extends from anterior margin of vertex to antennal socket.
Clypeogenal sulcus	Ventral extension of the frontogenal sulcus which unites the clypeal region to the gena laterally.
Clypeoloral sulcus	That part of the lateral sulcus which unites the clypeus to the lorae.
Coronal sulcus	A sulcus extending half way up the vertex in the adults.
Ecdysial cleavage line	An unpigmented line of weakness which extends along the mid-dorsal line, forking either on the anterior margin of the vertex or the dorsal facial region in the larval stages.
Lorae	Mandibular plates lying on either side of the anteclypeus.
Maxillary plates	Region lateral to the lorae and below the compound eyes.

As the terminology and descriptions used by previous authors is variable a table of comparative terminology was drawn up and is given in Table 1.

Table 1 Comparative Terminology and Descriptions of the External Morphology of the Head used by Previous Authors

	Parsons	Snodgrass
Frons	(1964) The anterior median blastocephalon gives rise to the frons, clypeus and labrum	(1963) Facial region between the compound eyes and crown
Vertex	-	(1963) The top of the head
Ecdysial Cleavage Line	-	(1960) The so-called "epicranial suture" is a preformed line of weakness where the cuticle splits at ecdysis and is more properly the ecdysial cleavage line. Characteristic in immature insects and retained only in a few adults. (1947) Forks lie between two sets of head muscles, but variable in different insects.
Coronal Sulcus	-	-
Postfrontal Sulcus	-	(1947) One arm of ecdysial line following a different course.
Frontal Sulcus	-	(1947) One arm of ecdysial line. Agrees with Duporte that there is no constancy in the position of the suture.

Duporte	Kramer	Evans
(1957) Median postoral lobe lying dorsal to clypeus and bounded laterally by the frontogenal sulcus. It is very variable and, except in larval insects, indeterminate.	(1950) The postclypeus merges with the frons. It is not possible to determine the exact extent of it.	(1946) The unpaired median sclerite, which is bounded posteriorly by the postfrontal suture, laterally by the frontal suture and anteriorly by the epistomal fold. (1957) Is a distinct cephalic sclerite.
-	-	-
(1946) Ecdysial cleavage line is an unpigmented exocuticle, and the epicranial suture is a groove marking the position of an internal ridge. The latter term should not be used and should be substituted by the frontal and coronal sutures, forming the stem and arms of the ecdysial line.	-	-
(1957) Stem of ecdysial cleavage line.	-	(1946) Coronal suture divides the vertex longitudinally.
-	-	(1946) Coronal suture diverges into postfrontal suture.
(1957) Arms of ecdysial line. No morphological significance according to Ferris, and not a cleavage line - difficult to explain its presence in immature insects.	-	(1946) Postfrontal suture is continuous to antennae as frontal suture. One or other may be absent in some species.

Table 1 (continued)

	Parsons	Snodgrass
Epistomal Fold	(1964) Frontoclypeal sulcus; absent in Hemiptera	(1963) Frontoclypeal or epistomal sulcus. It separates the clypeus from the frons. May be absent, or if present forms an internal ridge. (1960) Arched upwards in some insects into facial region, or may be incomplete or absent even in those with strong jaw-like mandibles when the frontal and clypeal regions are continuous.
Postclypeus	-	(1947) Cibarial dilators originate in clypeus. (1935) Anterior-most largest plate - clypeus. (1963) Region below the frons.
Frontogenal Sulcus	-	-
Clypeogenal Sulcus	(1964) The clypeoloral and lorogenal sulci join to form this sulcus	-

Duporte	Kramer	Evans
(1946) No constancy in position. Bounds the frons laterally and dorsally; often absent in adults.		
(1957) A transverse ridge in the median facial region - the frontoclypeal inflection. Unites the frontogenal inflections between the anterior tentorial arms with anterior mandibular condyle. Probably developed as a strengthening ridge to reinforce cranial wall when secondary mandibular articulation was established. Divides the postoral frons and the preoral clypeus.	-	(1947) Anterior tentorial pits lie in this region. (1946) A secondary fold developed for additional strength to anterior part of the head capsule of biting insects; lost in Homoptera due to acquisition of piercing mandibles and change in their position of attachment.
(1957) The origin of the cibarial dilators do not identify the clypeus. Bounded laterally and dorsally by U-shaped epistomal suture. (1962) Large bulging median sclerite in cicadas. Cibarial dilator muscles may primarily be attached to the clypeus but may shift to frons or vertex. (1957) Partly fused with genae	-	(1946) Is the part immediately anterior to antennae. The whole frontal region is called the frontoclypeus, as frons and clypeus are fused.
(1946) Frons are bounded laterally by this sulcus.	-	-
(1957) A ventral continuation of frontogenal sulcus. (1962) In Hemiptera formed from the entire lateral sulcus.		

Table 1 (continued)

	Parsons	Snodgrass
Anteclypeus	-	(1963) Region below the clypeus.
Transclypeal Sulcus	-	-
Lorae	(1964) The exposed outer parts of the hypopharyngeal expansion become incorporated into the cranium as the loral plate. Agrees with Snodgrass (1938) in its hypopharyngeal origin and that it is not derived from clypeus as proposed by Muir & Kershaw (1911) and Spooner (1938). The absence of clypeoloral cleft cleft is an advanced character. Lorogenal sulcus present in many Homoptera.	(1938) Hypopharyngeal origin.
Genae	-	(1963) At the sides of the head.
Subgenal Sulcus	-	(1935) When epistomal suture absent, anterior tentorial pits are present in this sulcus. (1960) Mandibles and maxillae articulate on the lower margins of the genae and are reinforced. (1963) Genal area with an internal ridge which strengthens the genal margin for support of mandibles and maxillae.

Duporte	Kramer	Evans
(1946) Clypeus divided usually into sclerotized anteclypeus and postclypeus.	-	-
-	-	(1947) May be absent due to secondary loss.
-	(1950) Agrees with Snodgrass that outer parts of lora have been differentiated from clypeus.	(1938) May be lateral outgrowths of the clypeus. (1946) Disagrees with Snodgrass (1938) and Butt (1943) in its hypopharyngeal origin.
-	-	(1947) Secondary development; could not have been included in ancestral capsule.
(1957) Narrow reinforcing fold along the lateral margins of the cranial wall.	-	(1947) A transverse suture in the maxillary plate - a primitive feature. Genae separated from maxillae by this suture. Marks the position of the attachment of the maxillary plates and is not homologous with subgenae as proposed by Snodgrass (1935).

Table 1 (continued)

	Parsons	Snodgrass
Antennal ledge	-	-
Maxillary plate	(1964) May be derived from the outer wall of the descended parietal lobe; not appendicular in origin. Its origin from fusion of outer lobe of maxillary appendage with lateral cranium should be discarded on Pesson's (1944) histological evidence.	-

Duporte	Kramer	Evans
-	-	(1946) A constant feature in Homoptera.
-	-	-

Fig. 1 Dorsal View of Head -- *U. reticulata*

a. Adult

b. Fifth Instar

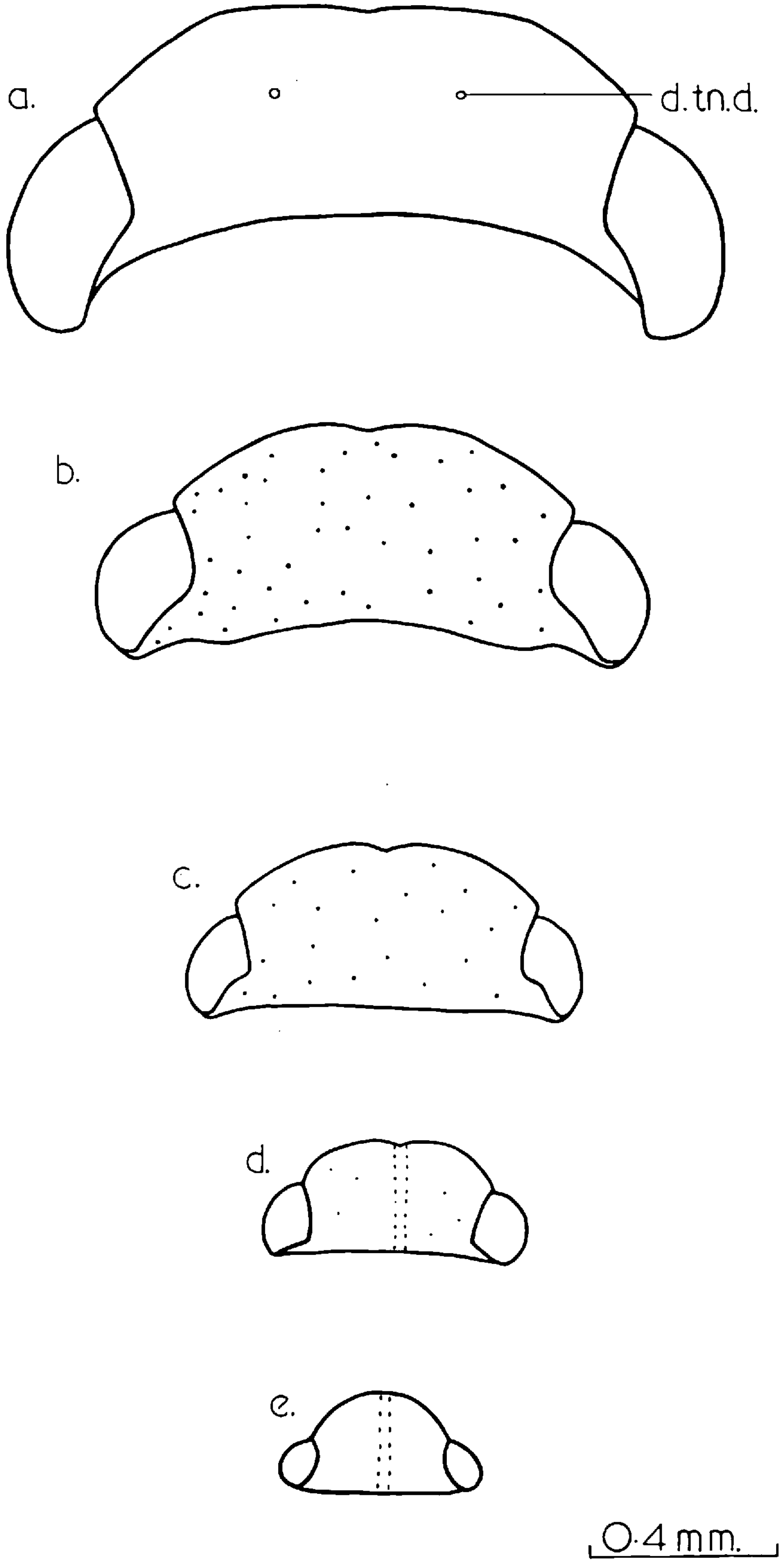
c. Third Instar

d. Second Instar

e. First Instar

d.tn.d. dorsal tentorial depression

FIG I



The vertex in Cicadellidae is the whole dorsal region of the head between the compound eyes. Snodgrass (1960) defines it as the recurved top of the head.

The frons is the ventral-most facial region. Snodgrass' (1960) definition that it lies between the compound eyes and antennae, is clear. He explains that it was defined as the region that lies between the ecdysial cleavage line, but points out that this indicated the inconstancy of its position as the positions of the latter are variable in different immature insects. Kramer (1950) says that the frons merges with the postclypeus which is true for Cicadellidae.

Snodgrass (1960) explains that the ecdysial cleavage line is a line of weakness with no internal ridges, and that it may be Y-shaped or straight. The course taken by the arms and the point at which they terminate is variable, but the arms always lie between two distinct sets of head muscles (Snodgrass (1947)). They are present in all immature insects but only in a few adults such as Dermaptera and Orthoptera. Further he explains their presence in these adults as ancestral adults periodically underwent ecdysis, as do present day Thysanura and most other anthropods. Among winged insects only adult Ephemeroptera shed their cuticle, and this is at a very early stage. Duporte (1957) gives the same explanation as Snodgrass but he refers to the stem and arms as the coronal and frontal sutures. The cleavage line used to be called the epicranial suture, but as this term caused confusion Duporte suggested that it be dropped. In an earlier paper Snodgrass (1947) agreed with Duporte and called the stem and arms of the cleavage line, the coronal and frontal sutures, but later he called the whole Y-shaped line the ecdysial cleavage line.

In the Cicadellidae examined the cleavage line is a line of weakness with no internal ridges, and is usually Y-shaped except in Eupelix cuspidata (Fabricius) where it is straight. The arms and their terminal points vary in position from species to species. As the cleavage line has no sulci or grooves in its inner margin, the stem and arms cannot be called the coronal and frontal sulci.

There is no such unpigmented line retained in the adults of Cicadellidae. However, a sulcus runs half way up the vertex in all the adults examined, except in U. reticulata. This sulcus has internal ridges and is called the coronal sulcus. The arms of the ecdysial cleavage line are not represented by any sulci in the adult Cicadellidae. Evans (1946) says that the coronal sulcus diverges into the post frontal sulcus, but this is absent in the members of the family Cicadellidae examined in this thesis.

The epistomal fold was also called the frontoclypeal sulcus, which according to Parsons (1964) is absent in Hemiptera. Snodgrass (1963) says that this sulcus separates the clypeus from the frons, and according to Duporte (1957) it is a transverse ridge that unites the frontogenal inflections between the anterior tentorial arms. He thinks that it was developed to strengthen the coronal wall when the mandibular articulation was established. Snodgrass (1960) however says that it is absent even in insects with strong jaw-like mandibles where the frontal and clypeal regions are continuous. Evans (1946) considers that it is absent in Homoptera and that the absence is linked with the acquisition of piercing mandibles. In the Cicadellidae studied only the adult of U. reticulata has the epistomal fold which is incomplete and partially separates the frons and the clypeus.

The lateral sulci are also present in all the species studied but their nomenclature is also variable. Evans (1946) calls the dorsal-most sulcus that leads to the antennal socket, the frontal sulcus, as does Ali (1958). However, Duporte (1957) calls this the frontogenal sulcus and says that laterally it binds the frons (1946). According to him, in Anosolabis (Dermaptera), the frontogenal sulcus is continuous with the frontal sulcus although the first is a line suture and the latter a groove. The "line suture" to which he refers is equivalent to the arm of the ecdysial cleavage line. Parsons (1964) also refers to the lateral boundaries of the frons as the frontogenal sulci. The frontogenal sulcus is present in all the subfamilies of Cicadellidae, except the Ulopinae, Jassinae, Macropsinae and Eupelicinae. In these, the frons has no lateral sulci. When present the length of this sulcus varies from species to species. As Duporte mentioned, in the larvae the arms of the ecdysial cleavage line usually meet the frontogenal sulcus and ecdysis takes place along this line. The frontogenal sulcus extends to the antennal socket.

The sulcus that continues ventrally from the antennal socket has also been referred to by various terms. Evans (1946) calls the whole of this sulcus the clypeal sulcus, while Duporte (1957) refers to it as the clypeogenal sulcus. Parsons (1964) refers to that portion of it that is fused to the genae as the clypeogenal sulcus, and the ventral-most portion that is fused to the lorae as the clypoloral sulcus. Parsons' terminology is clear and distinct and has been adopted in this thesis.

Snodgrass (1963) defines the clypeal region as being below the frons, whereas Evans (1947) calls the whole facial region the frontoclypeus, since the epistomal fold is seldom present in Cicadellidae and the frons and clypeus are fused into a single sclerite. Duporte (1962) calls the large bulging sclerite in the Cicadas, the postclypeus.

In the Cicadellidae, this large convex sclerite is generally referred to as the postclypeus, to differentiate it from the triangular anteclypeus lying below it. The ante and postclypeus are usually divided by a transverse transclypeal sulcus. The dorsal region of the postclypeus is united to the genae and the ventral region of it is united to the lorae whereas the anteclypeus hangs freely. The transclypeal sulcus is absent in only one subfamily studied, and that is the Macropsinae. In this subfamily the frons, anteclypeus and postclypeus form one sclerite. Evans (1947) thinks it is a secondary loss, though it is present in Psocoptera which are close to primitive Homoptera.

Snodgrass (1947) says that the cibarial dilators originate in the clypeus, but Duporte (1957, 1962) thinks that the dilators need not necessarily be identified with the clypeus as they may also be attached to either the frons or vertex. In the Cicadellidae, the cibarial dilators arise beneath the clypeus and are marked externally by transverse striations.

The lorae lying on either side of the anteclypeus were considered by Spooner (1938) to have been cut off by progressive development of the clypeoloral cleft. He also considered that the absence of the clypeoloral boundary is a primitive condition. In contrast, Parsons (1964) puts forward a theory that the clypeoloral boundary is progressively lost in evolution and the absence of it is an advanced condition. She says that the loral wall and the lamina maxillaries, unite to form a medio-lateral fold, whose location will vary and is more ventral in Heteroptera than in Homoptera. The median end of this fold is formed by the loral wall and the anterior tentorial pit. The lorogenal cleft is closed and may persist as the lorogenal sulcus externally as in many Homoptera, whereas it is lost in most Heteroptera. She points out that the lorogenal sulcus is absent in most Cicadellidae illustrated by Spooner (1938). In the Cicadellidae examined in this thesis, the lorogenal sulcus is absent but the cleft is present from the first instar onwards, its dorsal limit varying from species to species.

The hypopharyngeal origin of the lorae has been much disputed since this theory was put forward by Snodgrass (1938) and Butt (1943). Muir (1926) earlier said that the lorae were part of the genae, and Spooner (1938) and Evans (1938) said that they are part of the clypeus. But Muir and Kershaw (1911) pointed out that they were not derived from the clypeus and Ferris (1943) said that they belonged to the antennal segment.

Parsons (1964) agreed with Snodgrass and Butt on their hypopharyngeal origin and explains that the exposed parts of the hypopharyngeal expansion become incorporated into the cranium as the loral plate. However Kramer (1950) agrees with Snodgrass that the outer parts of the lorae have been differentiated from the clypeus. In the Cicadellidae studied the lorae are continuous beneath the anteclypeus and this was confirmed by Ali (1958) who agreed with Snodgrass on their hypopharyngeal origin.

According to Parsons (1964) the maxillary plate is derived from the outer wall of the descended parietal lobe. She considers the term "maxillary plate" as misleading, since the origin of genae and subgenae from the maxillary somite is questionable. Parsons' arguments are based on Pesson's (1944) histological evidence which leads her to discard the theory that the maxillary plate arose from the fusion of the outer lobe of the maxillary appendage with the lateral cranium.

Snodgrass (1960) has pointed out that the maxillary and the mandibular plates articulate on the lower margins of the genae and are reinforced by an internal ridge - the subgenal sulcus. Evans (1947) says that the sulcus is a transverse suture in the maxillary plate and that it marks the attachment of the plate to the head capsule, and hence cannot be homologous with the subgenae as was suggested by Snodgrass (1935). According to Duporte (1957) it is a narrow reinforcing fold in the lateral margin of the cranial wall.

In the Cicadellidae studied, only *U. reticulata* has the subgenal sulcus. It separates the anterior maxillary plate from the posterior genae as mentioned by Duporte.

The labrum and labium are present in all the species and have no special modifications.

(c) Detailed Description of the Head of *U. reticulata* and Comparison with the other Species Studied

The following is a description of the head region of *U. reticulata*. Rather than giving detailed descriptions of all the species studied, a general account is given of one species, which is then contrasted with the other five. The descriptions are applicable to all the five larval instars, and any differences between them are pointed out.

In the first instar the vertex is elongated and its anterior margin is rounded. In the later instars the head broadens out (Fig. 1).

The curvature between the crown and facial region in the first instar has a slight ridge, which becomes prominent in the later instars (Fig. 5a, b).

The ecdysial cleavage line which runs along the mid-dorsal line, forks on top of the face and terminates on the antennal ledge. This line is not represented in the adult where it loses its functional value. It is a clear pale unpigmented line present in the first five instars (Fig. 13).

The coronal sulcus is absent in U. reticulata adults (Fig. 1).

A pair of dorsal tentorial depressions are present on the vertex of the adult. No such prominent depression is visible in the larval instars.

A pair of prominent compound eyes are at the sides of the head. Ocelli are absent in the larval and adult stages.

A pair of frontogenal sulci on the face, which in other species usually form the lateral margins of the frons, is absent in U. reticulata. In the larvae the arms of the ecdysial cleavage line form the lateral and dorsal margins of the frons but as the cleavage line is absent in the adult, the frons has no lateral or dorsal margins (Fig. 13).

The postclypeus is represented by the large median sclerite. Laterally it is separated from the genae by the infolded clypeogenal sulcus. This sulcus begins in the antennal socket and is prominent from the first instar onwards. The ventral part of this sulcus is the clypeoloral sulcus, formed between the clypeal region and the lorae.

The almost pear-shaped sclerite below the postclypeus is the anteclypeus. It is almost as large as the postclypeus in the first and the second instars, but the relative proportions change in the third instar, and finally in the adult the anteclypeus is about a third of the area of the postclypeus.

The post- and anteclypeus are separated by an infolded transclypeal sulcus which is prominent from the first instar onwards.

The anteclypeus hangs freely, as opposed to the postclypeus which is attached to the genae and the lorae.

The labrum is a triangular flap suspended from the lower margin of the anteclypeus and is present from the first instar onwards.

The three segmented labium which is tucked between the coxae is very long in the first three instars, reaching to the third coxae. In the later instars it reaches to the second coxae.

The lorae are lateral to the anteclypeus, being attached to the postclypeus by the clypeoloral sulcus, and are continuous beneath the anteclypeus. The lorogenal cleft is present from the first instar but the lorogenal sulcus is absent.

The maxillary plate is divided by a subgenal sulcus into posterior genae lying beneath the compound eyes and an anterior, narrow, maxillary plate which lies beneath the lorae.

The antennae each have a short stumpy flagellum, and are situated right on the posterior margin of the compound eyes. A ledge overhanging the antennae is present from the first instar onwards.

There is a depression which moves laterally from the antennal socket. This depression becomes visible in the second instar and is prominent in the later instars.

The sclerites of the head, thorax and abdominal terga are pitted in all the larval stages, except the first. The number of pits increases in successive instars. The cuticle in the adults is reticulately ridged and bears blunt whitish hairs (Ali, 1958). These hairs are also present in the larval stages.

A comparative account of the external morphology of the head in the other species studied is given in Table 2.

In all the species studied the basic shape of the head changes with its growth from instar to instar. The first two instars tend to have an elongated head which broadens out in the late instars.

In the first instar the compound eyes are large with respect to the rest of the head. The curvature between the crown and the facial regions changes from one instar to the next. The details of the change are given in Table 2.

Table 2 Comparative Account of the External Morphology of the Head in Six Species of Cicadellidae

	U. reticulata	D. stylata	C. persimilis
1. Vertex (dorsal view)	Elongated in instar I, broadens out in later instars.	As U. reticulata	As U. reticulata
2. The curvature between the crown and facial region	A slight ridge in instar I which becomes prominent in later instars.	Broadly obtuse in instar I, a ledge is formed in instar III.	Acute in all larval instars and becomes obtuse in the adult.
3. Ecdysial cleavage line	Runs along the mid-dorsal line, forks on top of the face and terminates on the antennal ledge, from instar I.	Runs along the mid-dorsal line, forks at the anterior margin of the vertex and meets the fronto-genal sulcus, from instar I.	As D. stylata
4. Coronal sulcus	Absent.	Present only in adults, and is a sulcus which runs halfway up the vertex.	As D. stylata
5. Crescent-shaped sulcus	Absent.	Absent.	Absent.
6. Fronto-genal sulcus	Absent.	Prominent from instar I and extends from the anterior margin of the vertex to the antennal socket.	As D. stylata

M. parvicauda	*B. punctata*	*Z. scutellaris*
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *C. persimilis*	As *C. persimilis*	Acute with ledge in larval instars but becomes obtuse in adults.
As *D. stylata*	As *D. stylata*	Runs along the mid-dorsal line, forks on top of the facial region and meets the frontogenal sulcus from instar I.
As *D. stylata*	As *D. stylata*	As *D. stylata*
Absent.	Absent.	A pair present in adults, in the region between the crown and face.
As *D. stylata*	As *D. stylata*	Faint in instars I and II, but prominent in the rest and extends from halfway up the frons to antennal socket.

Table 2 (continued)

	U. reticulata	*D. stylata*	*C. persimilis*
7. Epistomal fold	Present only in adults.	Absent	Absent
8. Postclypeus	Swollen from instar I onwards.	Flat with markings from instar I onwards. Frons fused to clypeus.	Mildly convex with markings from instar III onwards Frons fused to clypeus.
9. Clypeogenal and clypeoloral sulci	Begins in the antennal socket, is infolded and prominent from instar I onwards.	Ventral continuation of the frontogenal sulci. Not infolded and prominent from instar I onwards.	Faint in instar I but prominent in all other instars.
10. Anteclypeus	Triangular sclerite lying below the postclypeus. Is as big as the latter in instars I and II, but relative proportions change in instar III and in the adults the anteclypeus is a third of the area of the postclypeus.	As *U. reticulata*	As *U. reticulata*
11. Transclypeal sulcus	Infolded and prominent from instar I onwards.	Not infolded but prominent from instar I onwards.	Faint in instars I and II but prominent in later instars.
12. Labium	Very long from instars I to III reaching to the third coxae, and in later instars reaches to second coxae.	Medium length	As *D. stylata*

M. parvicauda	*B. punctata*	*Z. scutellaris*
Absent	Absent	Absent
As *C. persimilis*	Mildly convex with markings from instar I onwards. Frons fused to clypeus.	Mildly convex with markings from instar IV onwards.
As *C. persimilis*	Prominent from instar I onwards.	As *B. punctata*
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *C. persimilis*	As *C. persimilis*	Faint in instars I to IV but prominent in instar V and adults.
As *D. stylata*	As *D. stylata*	Reaches up to second coxae.

Table 2 (continued)

	U. reticulata	*D. stylata*	*C. persimilis*
13. Subgenal sulcus.	Begins to appear in instar I, prominent in instar V.	Absent	Absent
14. Ocelli	Absent	Present from instar III onwards.	As *D. stylata*
15. Antennae	Short and stumpy, flagellum.	Medium length flagellum.	Long flagellum
16. Position of antennae	Right on posterior margin of the compound eyes.	Just below the posterior margin of the compound eyes.	As *D. stylata*
17. Antennal ledge	Present from instar I onwards.	Absent	Absent
18. Cuticular outgrowths on ledge	Absent	Absent	Absent
19. Antennal depression	Present from instar II onwards.	Absent	Absent

M. parvicauda	*B. punctata*	*Z. scutellaris*
Absent	Absent	Absent
As *D. stylata*	As *D. stylata*	Absent
As *C. persimilis*	As *D. stylata*	As *C. persimilis*
As *D. stylata*	As *D. stylata*	As *D. stylata*
Absent	Absent	As *U. reticulata*
Absent	Absent	A pair present from instar I onwards.
Absent	Absent	Absent

The ecdysial cleavage line is found only in the larval stages. It runs along the mid-dorsal line and forks at the anterior margin of the vertex in *D. stylata* (Fig. 10), *C. persimilis*, *M. parvicauda* and *B. punctata*. In *Z. scutellaris* it forks on top of the facial region, terminating at the frontogenal sulcus (Fig. 11c), whereas in *U. reticulata* it terminates on the antennal ledge, since the frontogenal sulcus is absent (Fig. 13). In those species where the cleavage line meets the frontogenal sulcus, the latter also splits during ecdysis although it is not a line of weakness.

The frontogenal sulcus reaches to the antennal socket and is absent in *U. reticulata* (Fig. 12b). In *Z. scutellaris* it extends from the mid point of the frons to the antennal socket (Fig. 12a). In all the other species examined it extends from the anterior margin of the vertex to the antennal socket. This sulcus is prominent from the first instar in all the species except *Z. scutellaris*, where it is faintly marked in the first and second instars (Fig. 11a). It forms the lateral boundaries of the frons.

In all the adults studied, except *U. reticulata*, the coronal sulcus reaches half way up the vertex and bisects it longitudinally (Fig. 1). This sulcus is absent in all the

Fig. 2 Dorsal View of Head - *D. stylata*

a. Adult

b. Fifth Instar

c. Third Instar

d. First Instar

oc. ocellus

FIG 2

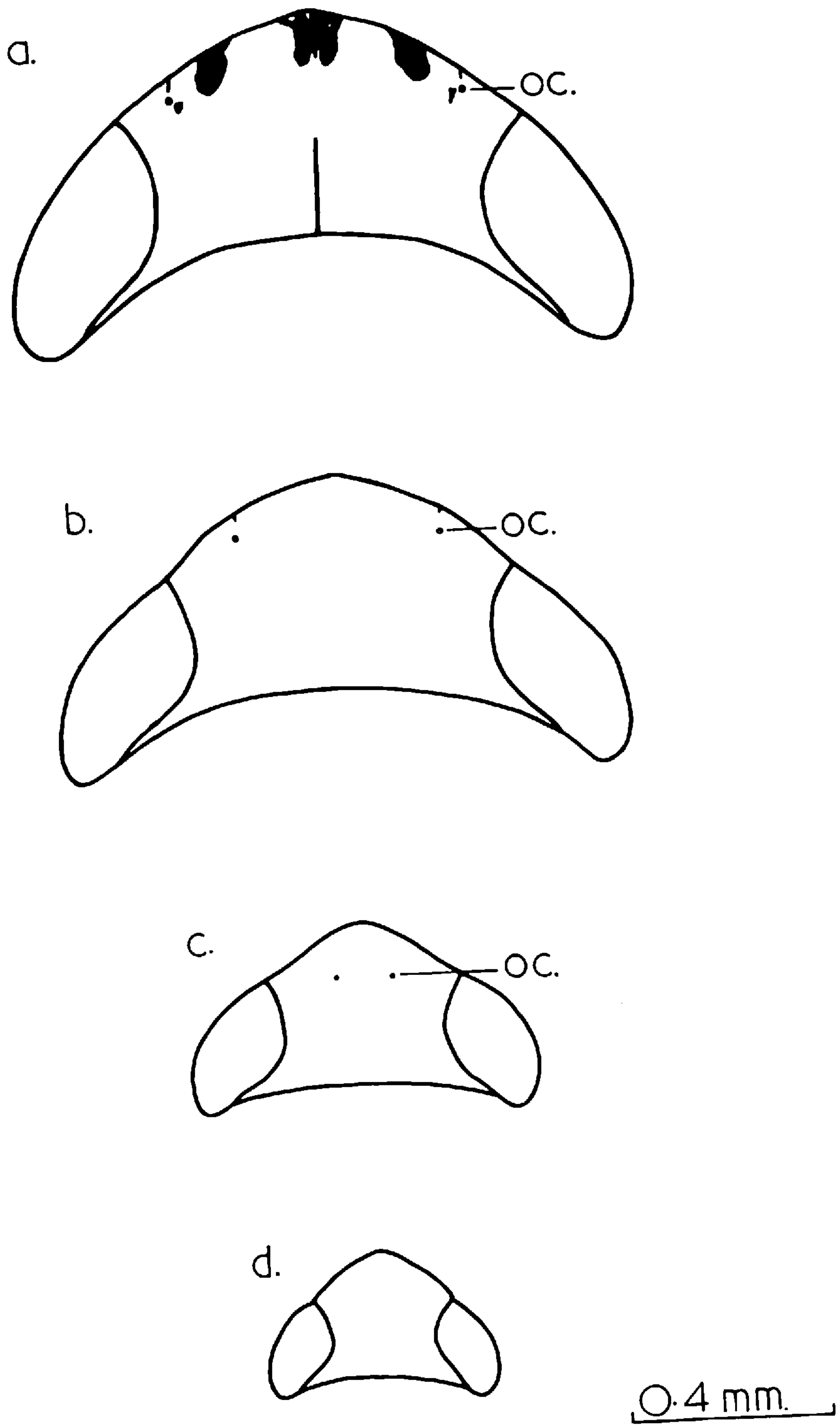


Fig. 3 Dorsal View of Head - *Z. scutellaris*

a. Adult

b. Fifth Instar

c. Fourth Instar

d. Second Instar

e. First Instar

co.s.	coronal sulcus
cr.s.	crescent shaped sulcus

FIG 3

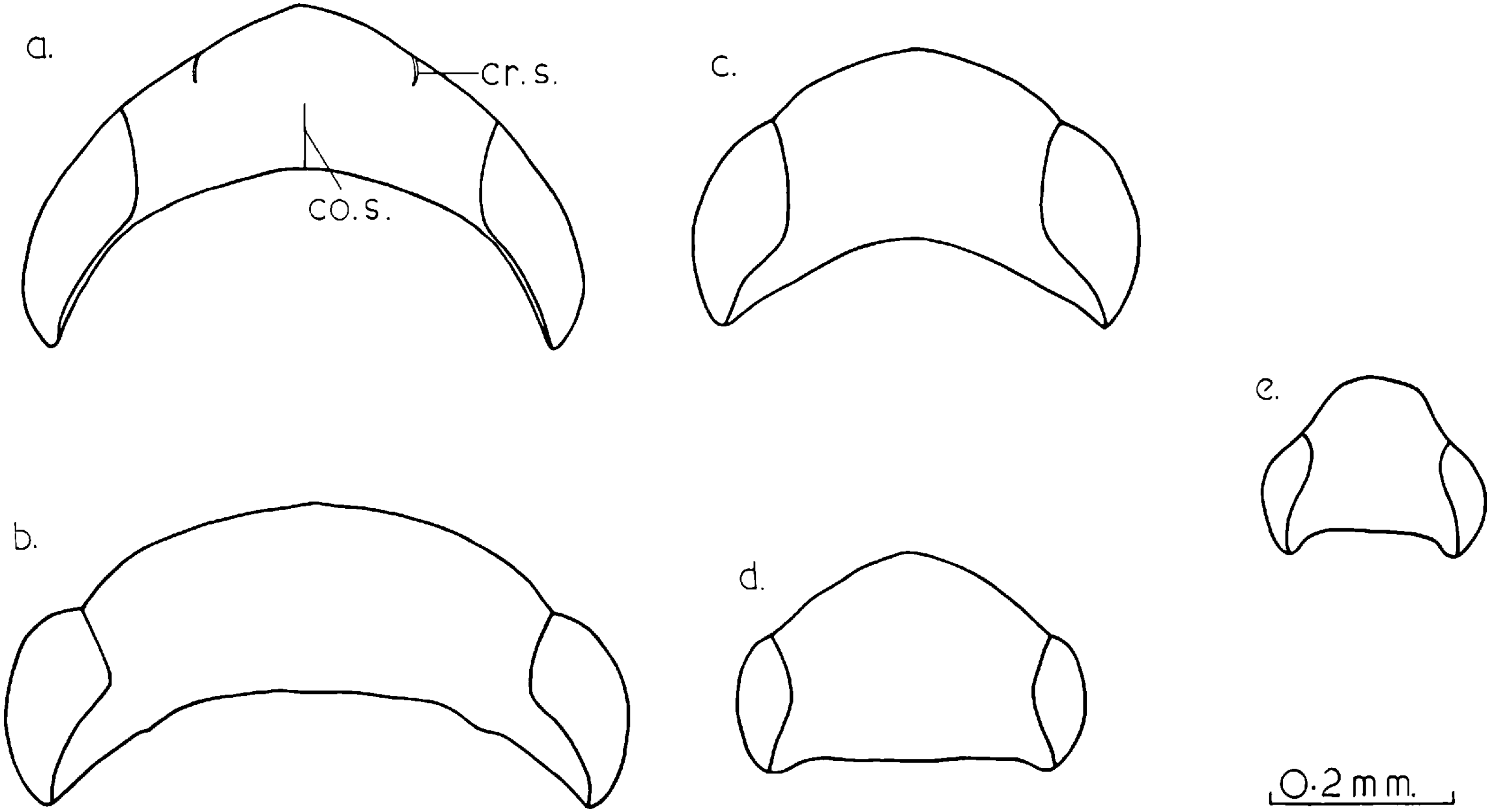


Fig. 4 Dorsal View of Head.

C. persimilis		*M. parvicauda*	
a.	Adult	d.	Adult
b.	Fifth Instar	e.	Fifth Instar
c.	First Instar		

co.s.	coronal sulcus
fr.s.	frontal sulcus

FIG 4

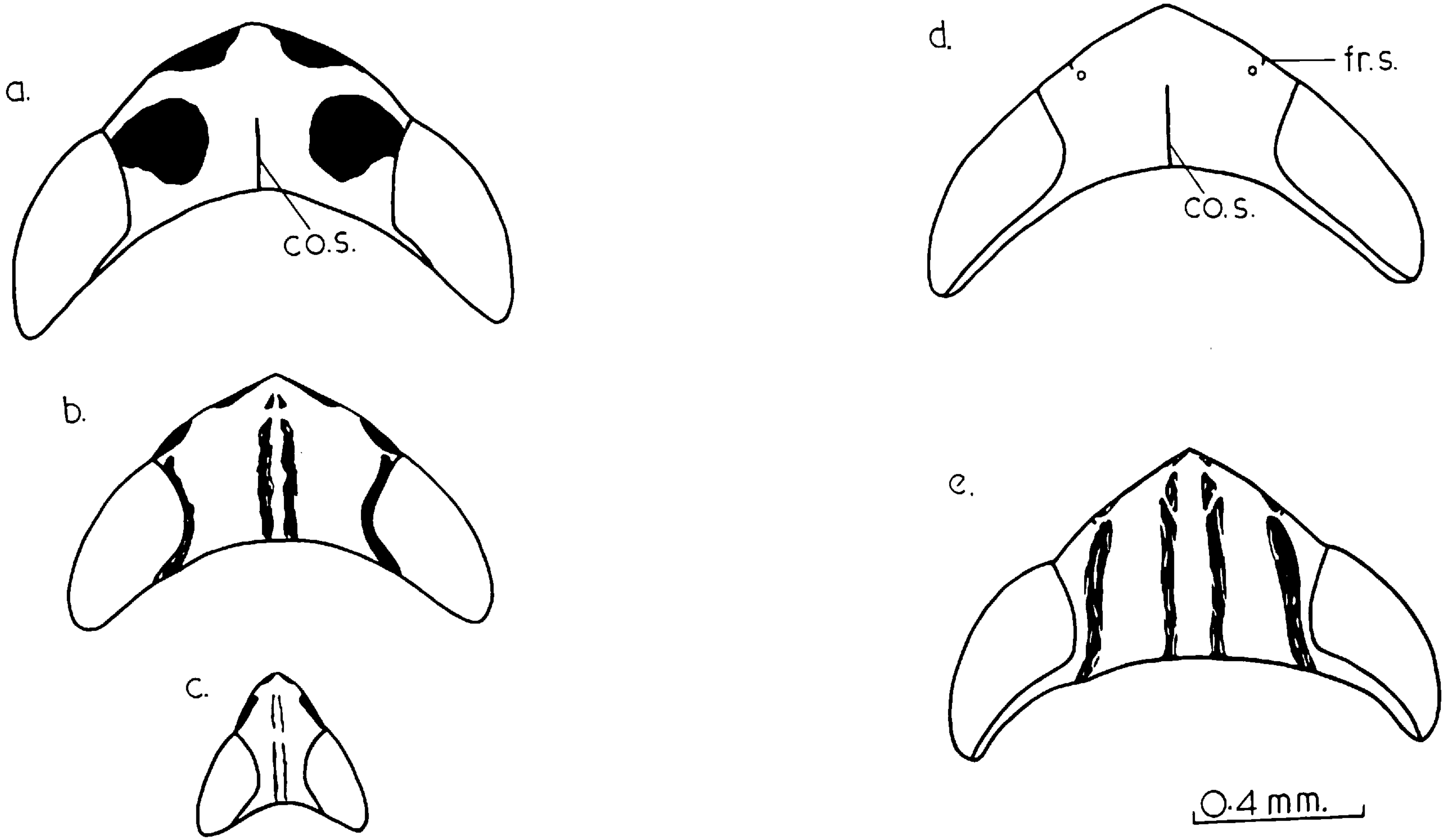


Fig. 5 Lateral View of Head.

U. reticulata

a. Fifth Instar

b. First Instar

D. stylata

c. Adult

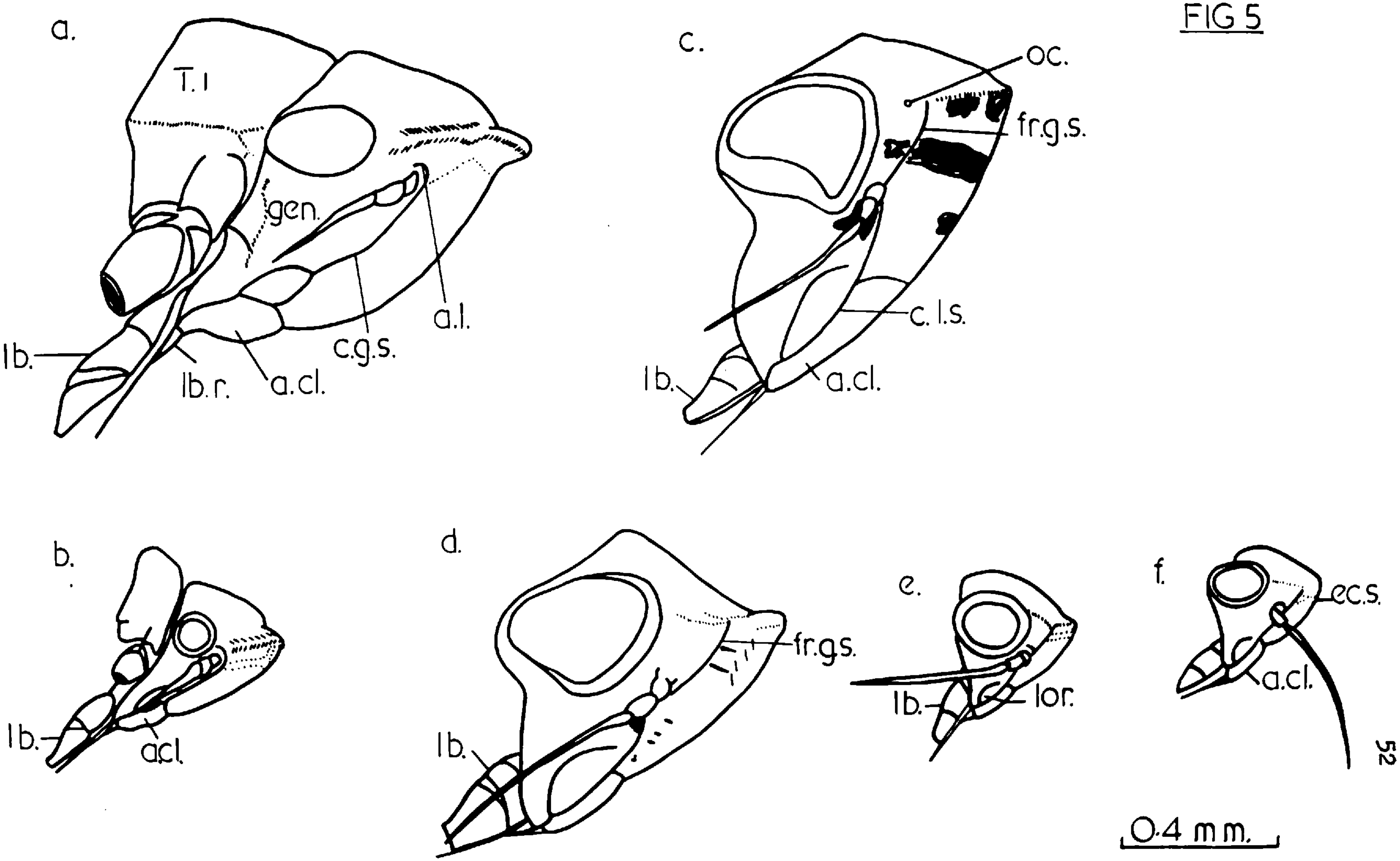
d. Fifth Instar

e. Second Instar

f. First Instar

a.cl.	anteclypeus
a.l.	antennal ledge
c.g.s.	clypeogenal sulcus
c.l.s.	clypeoloral sulcus
ec.s.	ecdysial cleavage line
fr.g.s.	frontogenal sulcus
gen.	gena
lb.	labium
lbr.	labrum
oc.	ocellus
T.1	first thoracic tergum

FIG 5


a.
T. 1
gen.
lb.
lb. r.
a. cl.
c.g.s.
a. l.
b.
lb.
a.cl.
c.
oc.
fr.g.s.
c. l.s.
lb.
a.cl.
d.
lb.
fr.g.s.
e.
lb.
lor.
f.
ec.s.
a.cl.
0·4 mm.

larval instars. Unlike the ecdysial cleavage line, this sulcus has internal ridges. The cleavage line in the larvae is replaced by the coronal sulcus in the adult (Fig. 2, 3, 4).

A pair of crescent shaped sulci are present on the curvature of the crown and facial regions, in the adults of *Z. scutellaris*. The frontogenal sulcus extends up to this crescent-shaped sulcus. The mode and function of this sulcus is unknown (Fig. 7a, 12a).

In all the species studied except *U. reticulata* adult, the dorsal frons and the large median clypeus are fused. In *U. reticulata* adult they are partially separated by the epistomal fold (Fig. 12b).

The large median sclerite is the postclypeus. The external transverse striations on it are due to the cibarial dilators which are attached internally. These striations are prominent in the early instars.

The clypeogenal and clypeoloral sulci which border the postclypeus laterally are present from the first instar onwards in all the species. The postclypeus is therefore fused to the genae and lorae.

The pear-shaped sclerite lying below the postclypeus is the anteclypeus, which is separated from the former by a transclypeal sulcus. This sulcus is present in all the species

Fig. 6 Lateral View of Head - *C. persimilis*

a. Adult

b. Fifth Instar

c. First Instar

a.cl.	anteclypeus
c.l.s.	clypeolabral sulcus
fr.g.s.	frontogenal sulcus
lb.	labium
oc.	ocellus
T.1	first thoracic tergum

FIG 6

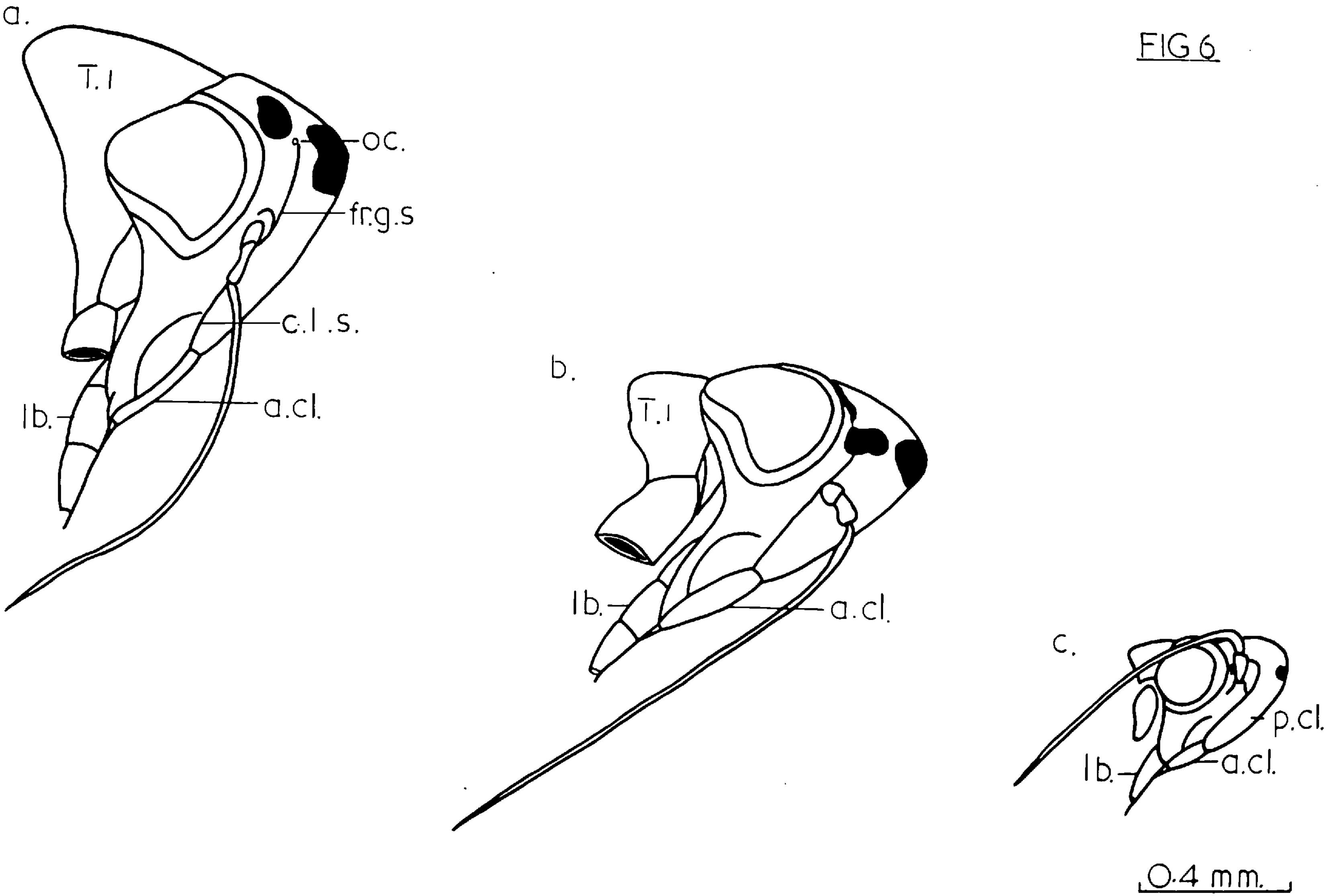


Fig. 7 Lateral View of Head - Z. scutellaris

a. Adult

b. Fifth Instar

a.cl.	anteclypeus
c.g.s.	clypeogenal sulcus
c.l.s.	clypeoloral sulcus
cr.s.	crescent shaped sulcus
cu.og.	cuticular outgrowths
fr.g.s.	frontogenal sulcus
lb.	labium
lbr.	labrum
p.cl.	postclypeus
T.1	first thoracic tergum

FIG 7

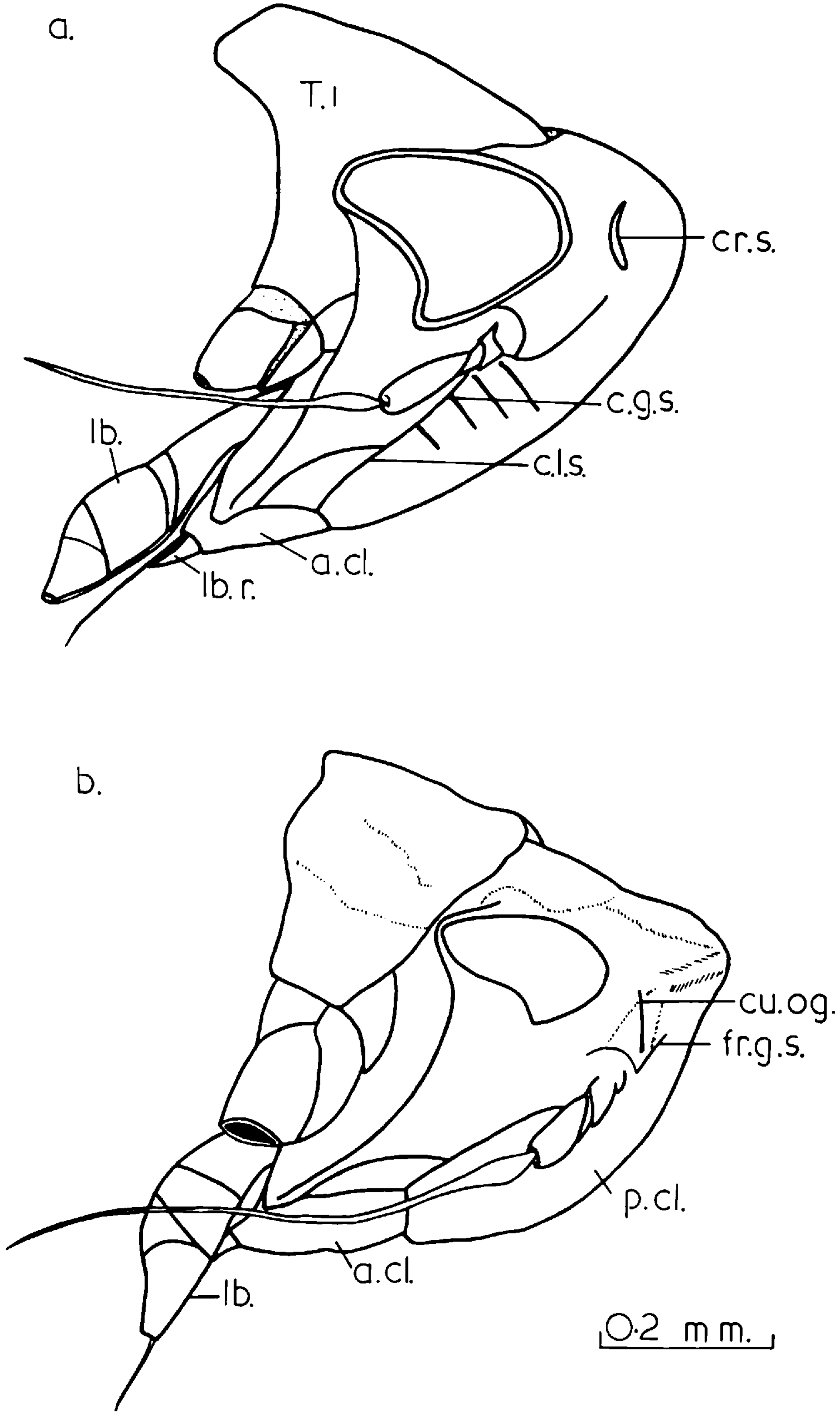


Fig. 8 Facial View of Head - _C. persimilis_

a. First Instar

b. Fifth Instar

c.g.s.	clypeogenal sulcus
fr.g.s.	frontogenal sulcus
max.pl.	maxillary plate

FIG 8

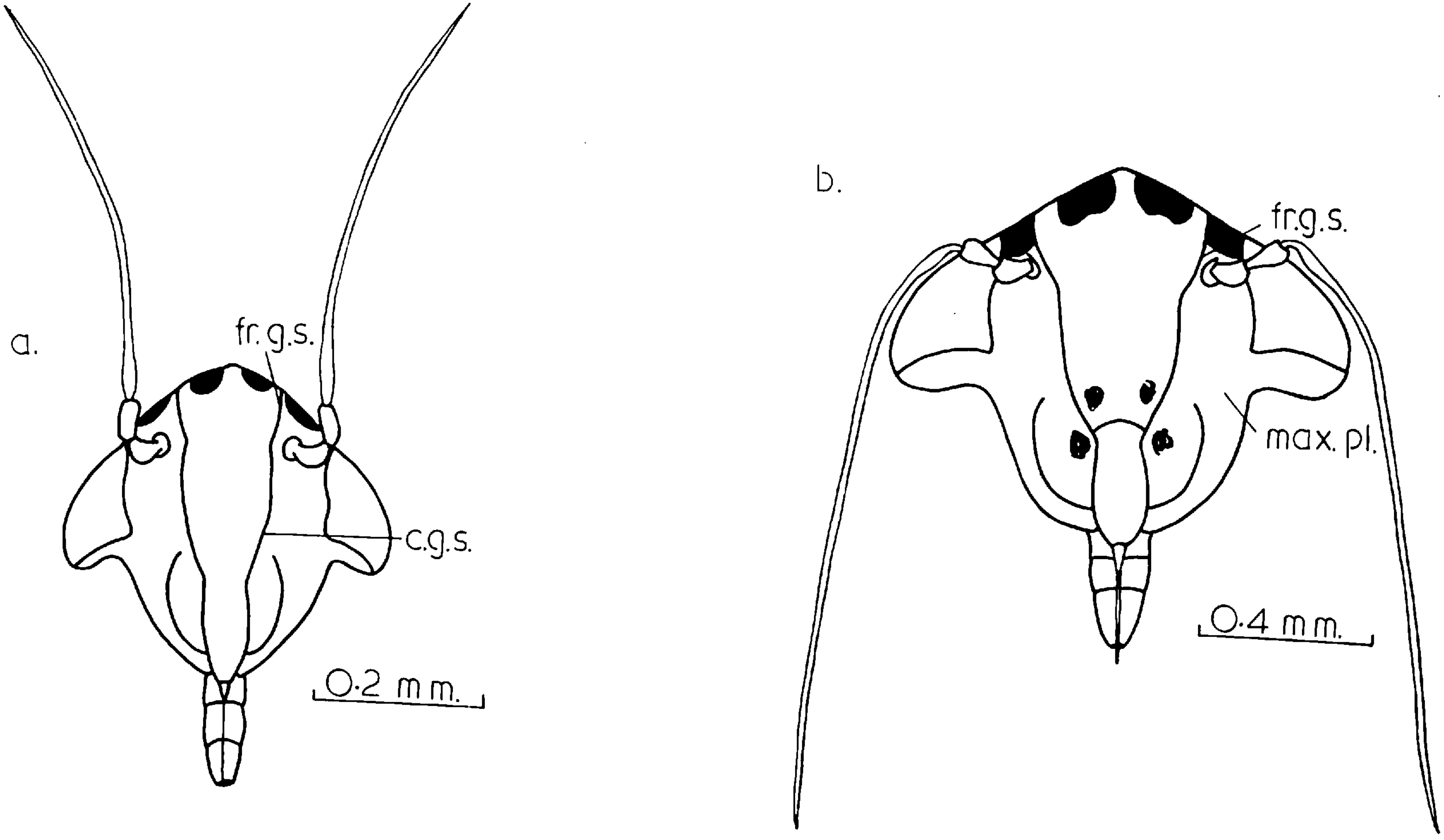


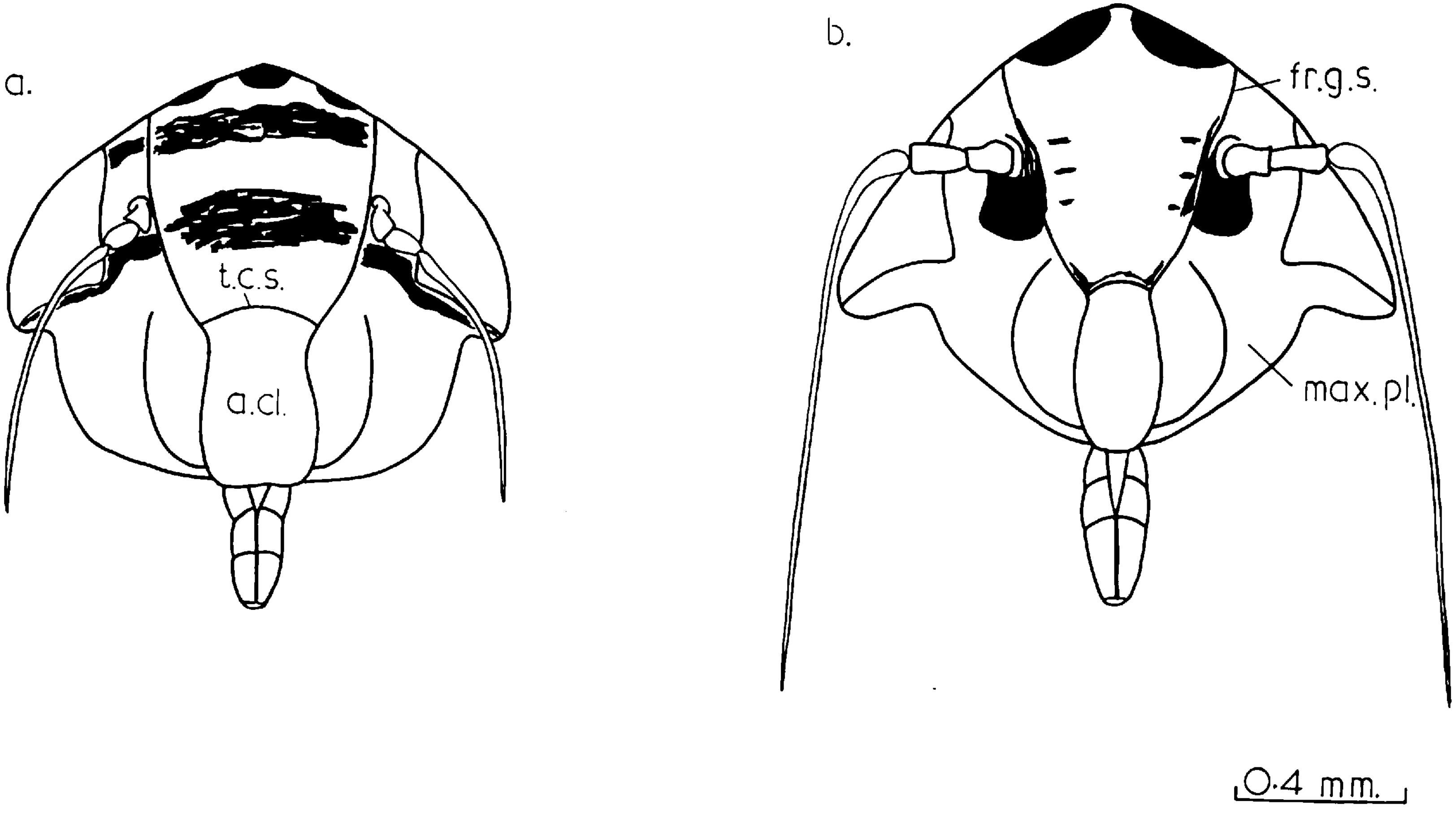
Fig. 9 Facial View of Head.

a. *D. stylata* Adult

b. *C. persimilis* Adult

a.cl.	anteclypeus
fr.g.s.	frontogenal sulcus
max.pl.	maxillary plate
t.c.s.	transclypeal sulcus

FIG 9



studied, but is faint in the first and the second instars of *C. persimilis* (Fig. 8a), *M. parvicauda* and *B. punctata*, and from the first to the fourth instars of *Z. scutellaris* (Fig. 11). In *U. reticulata* it is infolded (Fig. 13).

The small triangular labrum is present in all the species examined and has no particular modifications.

The three segmented labium varies in length in the different species. It is very long in *U. reticulata*, reaching to the third coxae in the early instars (Fig. 13), and reaches to well below the second coxae in the later instars. It is of medium length in *Z. scutellaris* (Fig. 11) where it reaches to the second coxae, and it is short in *C. persimilis* (Fig. 8), *D. stylata*, *M. parvicauda* and *B. punctata*, where it reaches to the first coxae.

The lorae are lateral to the anteclypeus, and the lorogenal cleft is present from the first instar in all the species studied. The lorae are continuous beneath the anteclypeus and the anteclypeus is free.

The maxillary plate lies lateral to the lorae and in all the species examined except in *U. reticulata*, it is an undivided plate.

The antennae are situated well below the posterior margin of the compound eyes in all the species (Fig. 9, 10) except

Fig. 10 Facial View of Head - *D. stylata*

a. First Instar

b. Fifth Instar

c.g.s.	clypeogenal sulcus
c.l.s.	clypeoloral sulcus
ec.l.	ecdysial cleavage line
fr.g.s.	frontogenal sulcus

FIG 10

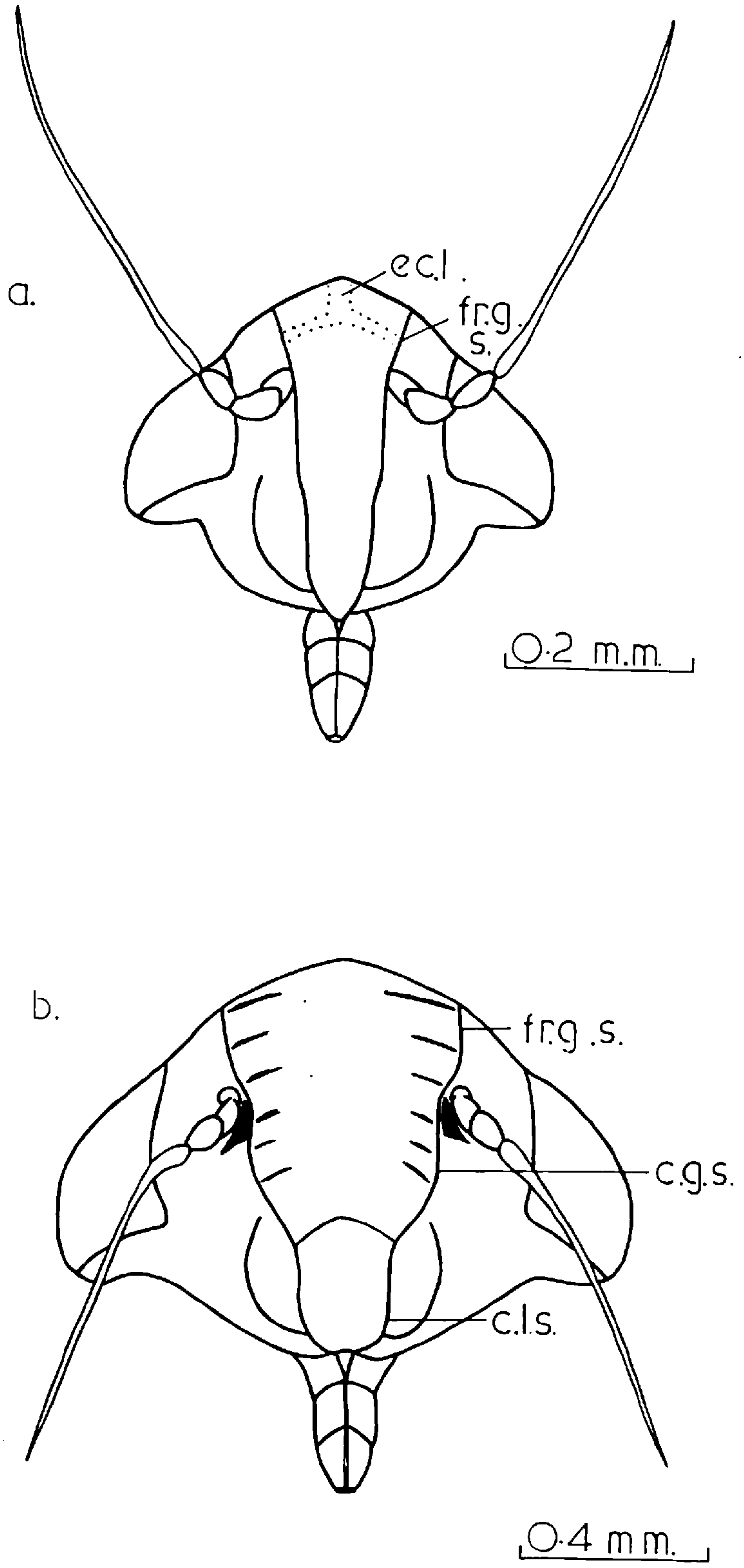


Fig. 11 Facial View of Head - *Z. scutellaris*

a. First Instar

b. Third Instar

c. Fifth Instar

a.cl.	anteclypeus
cu.og.	cuticular outgrowths
ec.l.	ecdysial cleavage line
lb.	labium
lbr.	labrum
lor.	lorum
p.cl.	postclypeus

FIG II

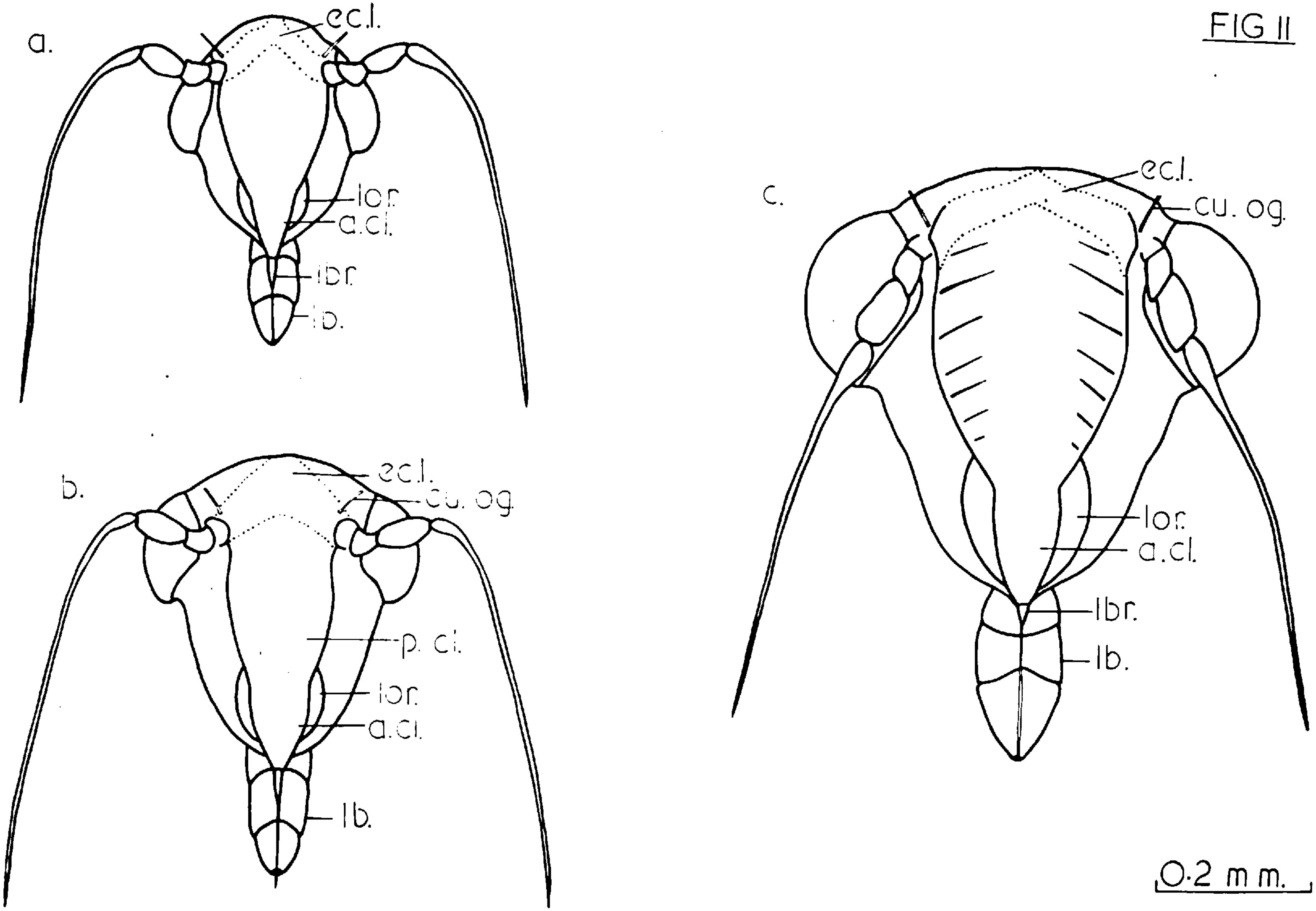

a.
ec.l.
lor.
a.cl.
lbr.
lb.
b.
ec.l.
cu. og.
p. cl.
lor.
a.cl.
lb.
c.
ec.l.
cu. og.
lor.
a.cl.
lbr.
lb.
0·2 mm.

Fig. 12 Facial View of Head.

a. Z. scutellaris Adult

b. U. reticulata Adult

ant.dep.	antennal depression
cr.s.	crescent shaped sulcus
epi.s.	epistomal sulcus
fr.g.s.	frontogenal sulcus
gen.	gena
lb.	labium
lbr.	labrum
lor.	lorum
max.pl.	maxillary plate
sg.s.	subgenal sulcus
t.c.s.	transclypeal sulcus

FIG 12

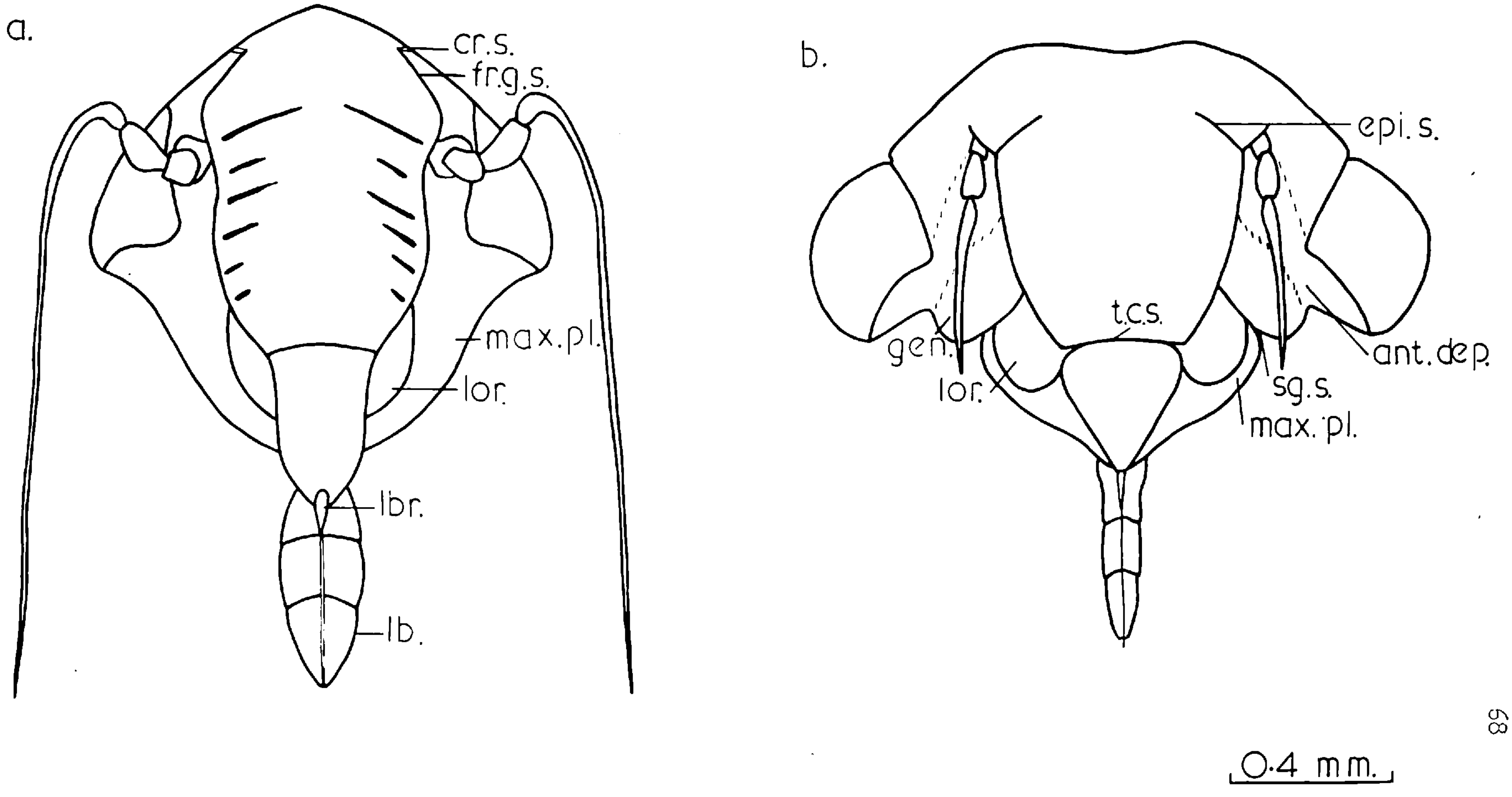

a.
cr.s.
fr.g.s.
max.pl.
lor.
lbr.
lb.
b.
epi.s.
t.c.s.
gen.
ant.dep.
lor.
sg.s.
max.pl.
0·4 mm.

Fig. 13 Facial View of Head - *U. reticulata*

a. First Instar

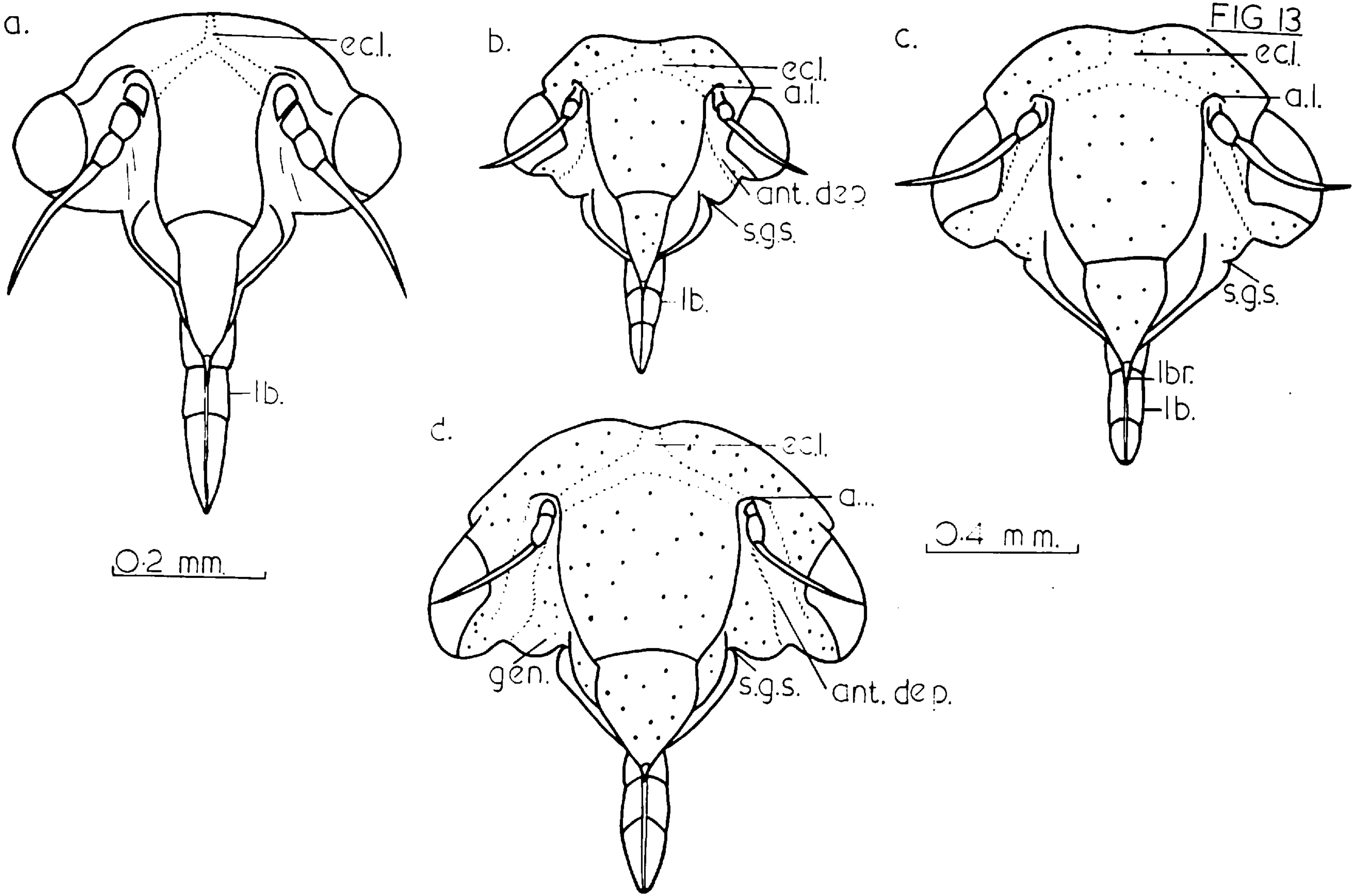
b. Third Instar

c. Fourth Instar

d. Fifth Instar

a.l.	antennal ledge
ant.dep.	antennal depression
ec.l.	ecdysial cleavage line
gen.	gena
lb.	labium
lbr.	labrum
s.g.s.	subgenal sulcus

FIG 13



a.
ec.l.
lb.
0·2 mm
b.
ec.l.
a.l.
ant. dep.
s.g.s.
lb.
c.
ec.l.
a.l.
s.g.s.
lbr.
lb.
0·4 mm.
d.
ec.l.
a.l.
gen.
s.g.s.
ant. dep.

U. reticulata (Fig. 13) where they are located on the posterior margin. The flagellum is short and stumpy in *U. reticulata*, of medium length in *B. punctata* and long in *D. stylata*, *C. persimilis*, *M. parvicauda* and *Z. scutellaris*.

The antennal ledge is prominent in *U. reticulata* and *Z. scutellaris* from the first instar onwards (Figs. 11, 12, 13). A pair of blunt cuticular outgrowths on the antennal ledge are present from the first instar onwards in *Z. scutellaris* (Fig. 11).

Longitudinal markings in the crown are present only in the larval stages of *M. parvicauda* and *C. persimilis* (Fig. 4). In *C. persimilis* adults the longitudinal markings disappear but the spots on the facial regions remain together with a pair of newly acquired black spots on the crown (Fig. 4a, b, c).

The cuticle of the larval stages of *U. reticulata* is pitted and that of the adult is reticulated (Fig. 13). No such pits are present in the larval stages of the other species examined and the cuticle of the adult is also plain.

(ii) THORAX

(a) Introduction and Review of Literature

There are no published articles on the external morphology of the thorax of the Cicadellid larvae, but the thorax of the adult has been looked at by many workers.

The varying shape of the pronotum in the different species was used by Evans (1947) in his classification, as Ribaut (1952) used the presence or absence of the epipleurite in the mesothorax.

Ossianilsson (1949) having studied the sound producing organs, said that the mesonotum can vary in shape from group to group, though the taxonomic value of it was not examined.

Kramer (1950) included the description of the thorax of the Cicadellid A. irronata in his study of the Auchenorhynchous Homoptera.

Ali (1958) in his work on the taxonomy of some Cicadellidae, pointed out the importance of the furcal suture in the mesothorax, as Ross (1957) did later in his study on the evolution in leafhoppers.

(b) Definitions of the Accepted Morphological Terms, and Terminology and Descriptions Used by Previous Authors

As in all insects, the thorax is made up of the pro-, meso- and metathorax. Each segment bears a pair of legs, and the meso- and metathoracic segments each bear a pair of wings.

In the larvae the wings are differentiated as wing pads which increase in length from instar to instar. The wing pads are not functional and the sclerites found on the terga of the adult are absent in the larval stages. The legs of the larvae are used for walking and jumping and hence the sternum is fully developed from the larval stages.

A list of definitions of the accepted morphological terms and those which have been used somewhat loosely are summarized below:

Terms	Definitions
Pronotum	Enlarged dorsal plate of prothorax
Notopleural sulcus	A sulcus separating the dorsal pronotum from the ventral epimeron.
Pleural sulcus	A vertical sulcus dividing the pleuron.
Episternum	Region anterior to the pleural sulcus.
Epimeron	Region posterior to the pleural sulcus.
Episternal sulcus	The sulcus that divides the episternum transversely in the adult.
Basisternum	A ventral sclerite lying anterior to the furcasternum.

Furcasternum	A sclerite found between the coxae, which bears the sternal apodemes.
Antecoxal sclerite	The sclerite formed when the apodemal structures join the katepisternum.
Phragma	A plate-like structure hanging within the thoracic cavity arising from the postnotum.

As in the head, different terminology has been used by the previous authors in their studies of the thorax. Thus it was again found useful to draw up a table of comparative terminology as well as descriptions given by the various authors (Table 3).

The dorsal enlarged plate of the prothorax is the pronotum. According to Snodgrass (1935) its enlargement into a plate is found in Orthoptera, Hemiptera and Coleoptera, and it serves no function except to give attachment to the dorsal muscles of the leg. Evans (1947) explains that in two subfamilies of Cicadellidae, Ledrinae and Macropsinae the pronotum departs from its usual shape. In the former it bears "raised flanges" and is produced laterally, as in the species Tituria planata (Fabricius). In Macropsinae it is either humped or "declivous", the extreme form occurring in Stenopsoides turneri (Evans).

Table 3 Comparative Terminology and Descriptions of the External Morphology of the Thorax used by Previous Authors

	Snodgrass	Matsuda
Pleural sulcus and ridge	(1927) A groove extending upwards from the base of the coxae, forming a pleural ridge internally. It extends inwards and ventrally as the pleural coxal process, which forms the dorsal articulation of the coxa with the body. (1958) Primarily a support for the leg, showing secondary modifications in the alate segments to accommodate the wing and wing muscles.	(1960) A suture dividing the pleuron and extending vertically from the base of the coxa, forming the pleural ridge internally.
Episternum	(1927) Cut off anteriorly from the pleuron by the pleural suture. Its anterior ventral angle extends to the sternum. Undergoes variations in form. (1963) This sclerite may be variously divided.	(1960) An area of the pleuron anterior to the pleural sulcus.
Anepisternum and katepisternum	-	(1960) The dorsal part of the episternum which is defined ventrally by the anapleural membrane or suture, is the anepisternum; and the ventral area of the episternum bounded dorsally by the precoxal suture, is the katepisternum.
Epimeron	(1927) The pleural suture divides the pleuron posteriorly into an epimeron whose anterior ventral angle extends to the sternum forming the postcoxal bridge; behind the leg it is continuous with furca sternum.	(1960) An area of the pleuron posterior to pleural suture.

Kramer	Evans
(1950) A suture separating the episternum and epimeron.	-
-	-
(1950) The sclerite is divided into an anepisternum and katepisternum.	(1946) The mesothoracic episternum is divided into the anepisternum and pre-episternum.
-	(1946) The undivided metathoracic epimeron is concealed by the coxa.

Table 3 (continued)

	Snodgrass	Matsuda
Anepimeron and katepimeron	-	(1960) The dorsal part of the epimeron defined ventrally by precoxal suture is the anepimeron. The ventral part of the epimeron bounded dorsally by precoxal suture is the katepimeron.
Precoxal suture	-	(1960) The suture subdivides the ana- and katepleural rings and primitively extends through the episternal and epimeral regions, and ventrally between the coxa and sternum.
Anapleural suture	-	(1960) The anapleural region is divided into the anepisternum and ventrally into the pre-episternum.
Trochantin	(1927) Lies above the base of leg and behind the precoxal bridge; triangular, elongated dorso-ventrally and the upper end touching the episternum or fused with lower part of the episternum. Lower end of the trochantinal coxal process articulates with the anterior margin of the coxal base. (1929) Remnant of the primitive supra coxal sclerotisation carrying the dorsal articulation of the coxa. (1963) Triangular plate below the episternum formed by the lower angle of the 'point of articulation' of the coxa.	(1960) Is often divided into anterior and posterior trochantins - the former articulates with the coxal margin.

Kramer	Evans
-	-
-	-
-	-
(1950) A large sclerite united with the episternum.	(1946) The whole sclerite is enormously enlarged for jumping.

Table 3 (continued)

	Snodgrass	Matsuda
Basisternum	(1927) Has been called the sternum and sternellum. Basisternum and furcasternum proposed by Crampton (1909) is used, although the first is not basal.	(1960) Anterior region of the primary sternum, which lies anterior to the base of the sternal apophysis.
Furcasternum	(1929) This is a forked endoskeletal structure lying between the coxa. The sterna in higher insects approach one another in each segment and unite upon a common base, produced by a median inflection of the sternal wall - which is the furcasternum.	(1960) Posterior region of the primary sternum.
Furcal sulcus	(1929) This suture is sometimes produced forward, branched laterally, or curved posteriorly, thus giving a variety of structures to its apodemal ridge and often obscuring the primary lines of the sternal division.	-
Sternal apodemes	(1927) A structure typical of the thoracic sternum. The apodemes are a pair of endosternal arms arising either independently from the region between the bases of the coxae or from a common base. The second condition frequently seen in higher insects while the presence of two independent processes is the more primitive condition. (1958) Two apodemes which approach one another and are carried forward on the median inflection of the sternum to form the furca. The arms are	-

Kramer	Evans
(1950) Sternum is divided into prebasisternite, basisternite, and furcasternite. The basisternite is divided by a median suture.	-
-	-
-	-
-	-

Table 3 (continued)

	Snodgrass	Matsuda
	connected by muscles to the pleural apodemes; are intrasegmental, not intersegmental as in Crustacea.	
Phragma	(1927) Is an extension of the postnotum into the thoracic cavity to give increased surface for the attachment of the dorsal longitudinal muscles. When the fore-wings are highly developed phragma is found in the mesotergum. (1958) Each wing segment has notal and postnotal plate. Accommodation for enlarged dorsal muscles is provided by antecostal sclerotic folds. When the fore wings are the primary organs of flight the second phragma become partially or wholly detached from the metatergum. Both the phragma and postnotal plate establish a close association with the mesotergum while extremities of the postnotum unite for security with the postdorsal angle of the mesothoracic epimeron.	(1960) On acquisition of wings the intersegmental phragma is developed more or less strongly in Pterygota, to support the dorsal longitudinal muscles.

Kramer	Evans
(1950) Arises from the postnotum through the invagination of its posterior margin. Closely allied with mesothorax functionally. Differs from the intersegmental phragma between meso- and metathorax of Cercopids where the structure is closely fused with the metathorax.	-

In the species studied, the shape of the pronotum varied especially in its length relative to width. In the tribe Balcluthini, the length of the head is about one sixth the length of the pronotum. The size and the shape of the anterior and posterior margins of it also varied from species to species.

Laterally on the pleuron of each segment lies the pleural sulcus. Snodgrass (1958) states that the pleural sulcus is primarily constructed to support the leg ventrally and the wing and wing muscles dorsally. According to Matsuda (1960) it is a sulcus dividing the pleuron vertically and extending from the base of the coxa to the base of the wing, internally forming the pleural ridge. In the Cicadellidae studied the pleural sulcus is present from the first instar and internally forms a ridge.

Kramer (1950), Snodgrass (1927) and Matsuda (1960) define the episternal and epimeral regions as being anterior and posterior to the pleural sulcus. The episternal regions in the meso- and metathorax are continuous with the basisternum II and sternum III in all the Cicadellidae studied, as was stated by Snodgrass (1927).

The sulcus dividing the episternal region into the dorsal anepisternum and ventral katepisternum, is called the precoxal sulcus by Matsuda (1960), and episternal sulcus by Ali (1958). Ali's term is used in this text, as it causes less confusion.

Grandi (1950) who studied the development of Plecoptera from larva to adult noticed that the chitinization of the epimeral region is secondary, that is, it occurs only in the adult, and is not found in the larva. This is also true of the Cicadellidae examined. Snodgrass (1927) pointed out that the pterygote thorax becomes more heavily sclerotized with the acquisition of wings.

Further, Kramer (1950) considers that in Cicadellidae the trochantin is united with the episternum, and Evans (1946) thinks that in this family it is enlarged to aid jumping. It was noted that in the species studied the trochantin is united to the episternum and is enlarged.

The term basisternum suggested by Crampton (1909) was found unsuitable by Snodgrass, as the sclerite is not truly 'basal' in position. However, he did not suggest any new term for this area. Matsuda (1960) defines it as the anterior region of the primary sternum and Kramer (1950) divides the sternal region into the pre- basi- and furcasternum.

Ali (1958) in his studies on some Cicadellidae called the region within the furcal sulcus, the basisternum, and the region outside it the katepisternum; whereas Kramer (1950) called the region within the furcal sulcus the prebasisternum, the region outside it the basisternum, and the latero-ventral parts of the meso-episterna the katepisternum.

The basisternal pits lie in the region within the furcal sulcus in the species studied, as in those examined by Ali (1958). This region will be called the basisternum in this text.

According to Snodgrass (1929) the furcal sulcus has a variety of shapes, and this was also found in the Cicadellidae studied.

I agree with Snodgrass (1927), Kramer (1950) and Matsuda (1960) that the furcasternum bearing the sternal apodemes in the Cicadellidae is the posterior region of the sternum, at least in the species examined in this thesis. Ali (1958) refers to these apodemes as the sternal apodemes and Kramer (1950) calls them the furcal apodemes. Snodgrass refers to them as the sternal apodemes as well as the "arms of the furca" (1963). Since they arise from the furcasternum I have referred to them as the sternal apodemes. According to Snodgrass (1927) these apodemes which form the endoskeleton of the insect, arise independently or may form a common base; the second condition being seen in the higher insects. He considers that they are intrasegmental and not intersegmental as in Crustacea (1958). In the Cicadellid species examined the sternal apodemes arise from a common base and are intrasegmental.

The phragma according to Snodgrass (1960, 1963) and Matsuda (1960) are deep ridges developed to give increased surfaces for the attachment of wing muscles. Snodgrass (1958) says that when the fore wings are the primary organs of flight the phragma become detached from the metatergum, and both the phragma and the postnotal plate establish a close association with the mesotergum, while the extremities of the postnotum unite with the post-dorsal angle of the mesothoracic epimeron thus giving greater security to the skelotal structures. In the Cicadellidae studied the size of the phragma varied from species to species and the second phragma is more highly developed than the first. As Snodgrass (1927, 1958) said, this may be associated with greater activity of the fore wings but this suggestion needs investigation. As Snodgrass explains, the phragma in the Cicadellidae is given off as an internal plate by the postnotum but the posterior layer of it is closely attached to the metathorax and the anterior to the mesopostnotum.

(c) Detailed Description of the Thorax of *U. reticulata* and Comparison with the Other Species

Prothorax

The pronotum in *U. reticulata* does not have any distinctive shape. The anterior and posterior margins of it are the same width, both in the larval and adult stages. Its length is shorter than that of the head in the larval instars, but is equal to it in the adult. Laterally, prominent ledges are present in the larval stages (Fig. 15).

The pronotum extends ventrally and is separated from the epimeron by the notopleural sulcus, which is present from the first instar onwards (Fig. 16e).

Lying anteriorly to the epimeron is the episternal plate which is separated from the epimeron by a prominent pleural sulcus which ventrally provides the first coxal articulation.

The prothoracic sternum is narrow and is connected to the episternum by a precoxal bridge.

Mesothorax

The terga of the mesothorax in the larvae have a pair of mesothoracic wing pads which appear in instar two and increase in length from instar to instar. As these wing pads do not function, the sclerites on the terga are not developed. In the adult the tergum is made up of three sclerites, the prescutum,

Fig. 14 Dorsal View of Head - *B. punctata*.

a. First Instar
b. Second Instar
c. Third Instar
d. Fourth Instar
e. Fifth Instar
f. Adult

Antennae.

g. *U. reticulata* - First Instar
h. *U. reticulata* - Second Instar
i. *B. punctata* - First Instar
j. *D. stylata* - Second Instar

ec.l.	ecdysial cleavage line
co.s.	coronal sulcus
fl.	flagellum
oc.	ocellus
ped.	pedicel
scp.	scape

FIG 14

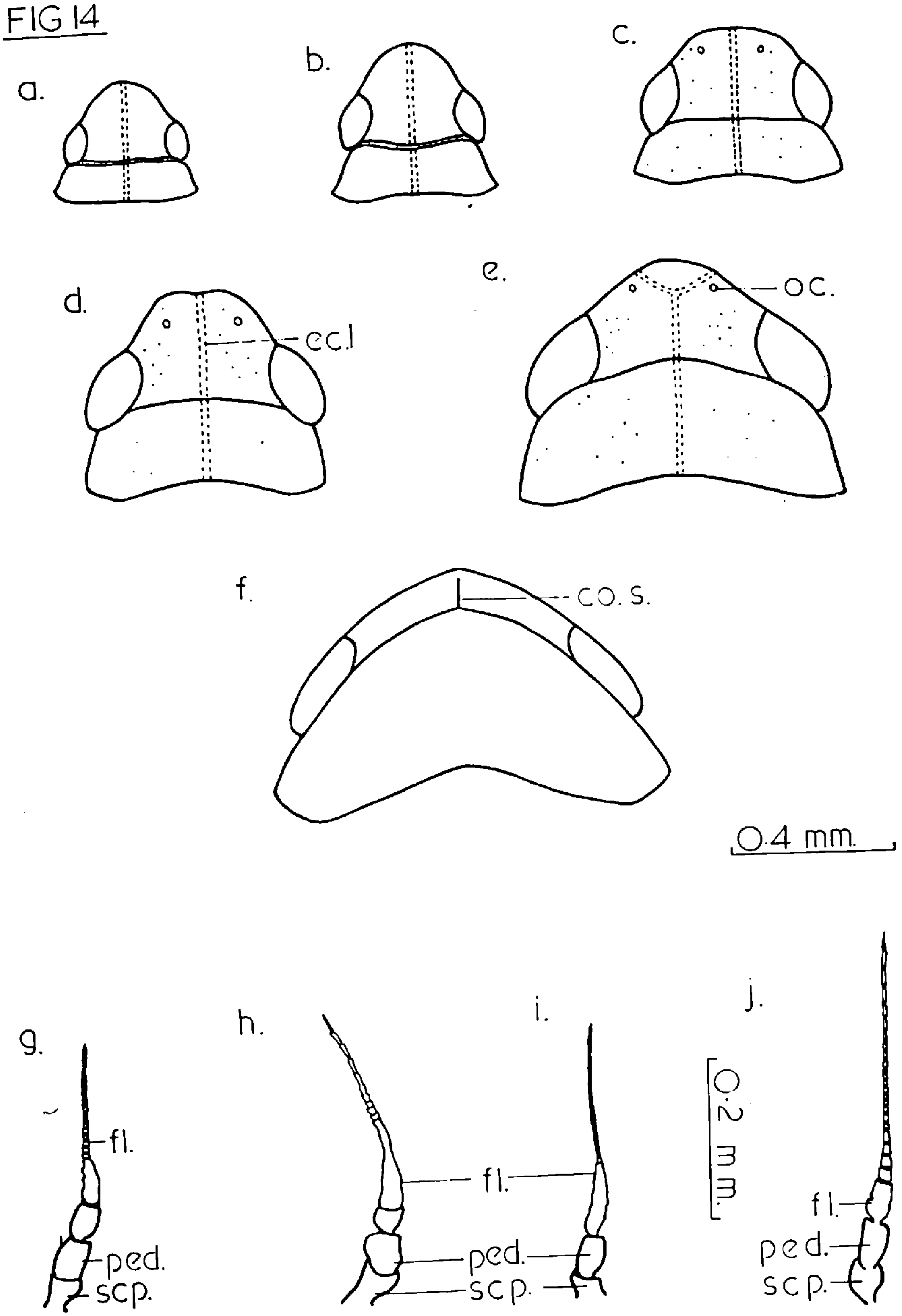

a.
b.
c.
d.
ec.l
e.
oc.
f.
co. s.
0·4 mm.
g.
fl.
ped.
scp.
h.
fl.
ped.
scp.
i.
j.
0·2 mm.
fl.
ped.
scp.

Fig. 15 Dorsal View of Head - *U. reticulata*

a. Fifth Instar
b. Fourth Instar
c. Third Instar
d. Second Instar
e. First Instar
f. Adult

d.tn.d. dorsal tentorial depression

FIG 15

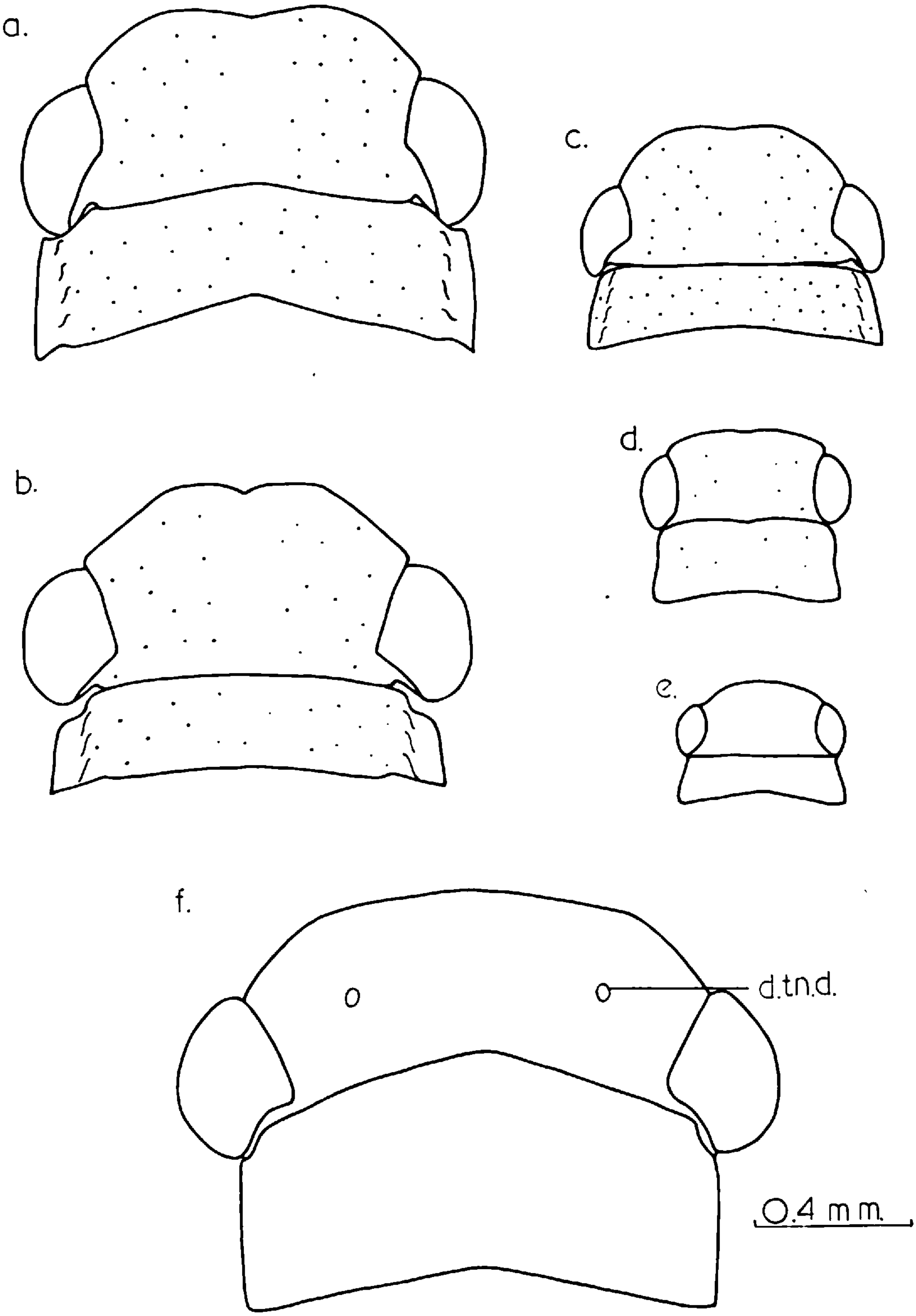


Fig. 16 Lateral View of Thorax - *Z. scutellaris*

a. Adult
b. Fifth Instar

Ventral View of Thorax - *U. reticulata*

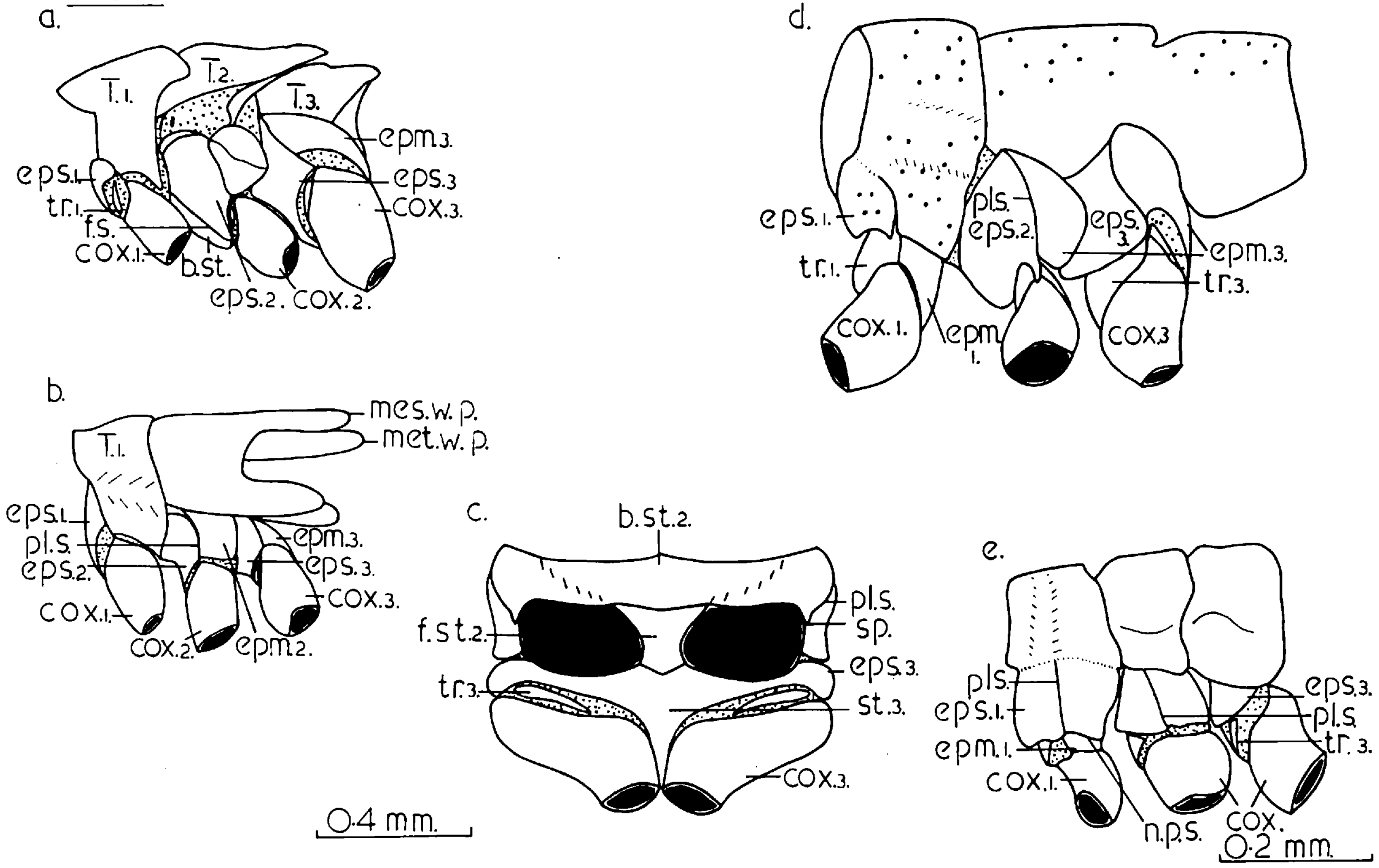
c. Fifth Instar

Lateral View of Thorax - *U. reticulata*

d. Fifth Instar
e. First Instar

b.st.2.	second basisternum
cox.1.	first coxa
cox.2.	second coxa
cox.3.	third coxa
cox.	coxae
epm.1.	first epimeron
epm.2.	second epimeron
epm.3.	third epimeron
eps.1.	first episternum
eps.2.	second episternum
eps.3.	third episternum
f.s.	furcal sulcus
f.st.2.	second furcasternum
mes.w.p.	meso-thoracic wing pads
met.w.p.	meta-thoracic wing pads
n.p.s.	notopleural sulcus
st.3.	third sternum
T.1.	first thoracic tergum
T.2.	second thoracic tergum
T.3.	third thoracic tergum
sp.	spine
tr.1.	first trochantin
tr.3.	third trochantin
pl.s.	pleural sulcus

FIG 16


a.
T.1.
T.2.
T.3.
epm.3.
eps.1.
eps.3
tr.1.
cox.3.
f.s.
cox.1.
b.st.
eps.2.
cox.2.
b.
mes.w.p.
met.w.p.
T.1.
eps.1.
epm.3.
pl.s.
eps.2.
eps.3.
cox.3.
cox.1.
cox.2.
epm.2.
c.
b.st.2.
pl.s.
f.st.2.
sp.
eps.3.
tr.3.
st.3.
cox.3.
0.4 mm.
d.
eps.1.
pl.s.
eps.2.
eps.3.
epm.3.
tr.1.
tr.3.
cox.1.
epm.1.
cox.3
e.
pl.s.
eps.3.
eps.1.
pl.s
epm.1.
tr.3.
cox.1.
n.p.s.
cox.
0.2 mm.

the scutum and the scutellum.

Laterally the pleuron is divided by a prominent pleural sulcus which is present from the first instar. The episternum lies anteriorly. This is an undivided plate in the larvae but in the adult it is divided into the lateral anepisternum and the ventral katepisternum. Posterior to the pleural sulcus is the epimeron which is also undivided in the larvae, but is divided by a deep groove into an anepimeron and a katepimeron in the adult (Fig. 16d, e).

The pleural sulcus which ends beneath the mesothoracic wing pads in the larva provides the pleural wing process in the adult. Ventrally it provides the site of the coxal articulation.

In U. reticulata the epimeron is chitinized only in the adult.

The anepisternum is directed ventrally and is fused to the basisternum, to form a single plate. There is no sulcus dividing this plate into two regions even in the adult (Fig. 16c). The basisternal pits, however, are visible from the first instar onwards, together with a median ridge.

The episternal sulcus which separates the anepisternum from the katepisternum is ventral in position. The furcal sulcus which is absent in the larvae, joins this episternal sulcus in the adult, to form the furca-episternal sulcus. This furca-episternal sulcus separates the katepisternum from the fused anepisternum and basisternum. Laterally on the katepisternum there is a spine which overhangs the coxal cavity and is present from the third instar onwards.

The furcasternum is found between the coxal cavities. The antecoxal sclerite is absent in this species. The anterior region of the furcasternum remains exposed as the katepisternum and does not meet behind the basisternum. The furcasternum gives off the sternal apodemes which arise from a common base and are attached to the pleural apodemes laterally by muscle fibres. These apodemes are visible from the first instar onwards.

Dorsally, the postnotum of the adult is covered by the scutellum, but internally it gives off a plate-like structure called the phragma. The phragma hangs down into the cavity but is small. In the larvae the phragma is present, although the postnotum and scutellum are not differentiated.

Metathorax

The pleural sulcus is very prominent in the larval and adult stages. Ventrally it provides the coxal articulation for the enlarged hind coxae which are used for jumping. This sulcus, as in the mesothorax, divides the pleuron into anterior episternal and posterior epimeral regions.

The episternum is continuous with the sternum ventrally. In the adult it is separated from the sternum by a sulcus which is absent in the larvae.

The epimeral chitinization is secondary, that is, it appears in the adult, as in the mesothorax. The stem of the T-shaped sternum is connected to the epimeron by the postcoxal bridge.

The sternum and the pleural sulcus give off apodemes, but these are not specially modified as in the mesothorax.

The external morphology of the thorax of the other species examined is compared with that of U. reticulata below and also summarised in Table 4.

Prothorax

The anterior and posterior margins of the pronotum in the first and second instars are of the same width in all the species studied. But from the third to the fifth instar the anterior margin becomes much narrower than the posterior in some species such as B. punctata, slightly narrower than the posterior margin in C. persimilis, M. parvicauda, D. stylata and Z. scutellaris, and remains the same width in U. reticulata.

In the first, second and third instars, the pronotum is much shorter than the head. It is as long as the head in the fourth instar, but in the fifth instar larvae and the adult,

Table 4 Comparative Account of the External Morphology of the Thorax in Six Species of Cicadellidae

	U. reticulata	*D. stylata*	*C. persimilis*
1. Anterior and posterior margins of pronotum.	Margins of equal width in larvae and adults.	Margins of equal width in larvae, but the anterior margin slightly narrower in the adults.	As *D. stylata*
2. Proportions of the pronotum to the head.	Pronotum shorter than the head in larvae, but is as long in the adults.	As *U. reticulata*	As *U. reticulata*
3. Ledges at the sides of the pronotum.	Present in larvae	Absent.	Absent.
4. Notopleural sulcus.	Present from instar I.	Absent.	Absent.
5. Prothoracic pleural sulcus	Prominent from instar I.	As *U. reticulata*	As *U. reticulata*
6. Mesothoracic pleural sulcus.	Prominent from instar I.	As *U. reticulata*	As *U. reticulata*
7. Episternal sulcus separating anepisternum and katepisternum.	Present only in adults.	As *U. reticulata*	As *U. reticulata*
8. Epipleuron	Absent	Absent	Present only in adults.

M. parvicauda	B. punctata	Z. scutellaris
As D. stylata	Anterior margin slightly narrower than the posterior in the larvae, but in adults it is very much narrower.	As D. stylata
As U. reticulata	Shorter than the head in instars I to III, of equal length in instar IV and longer than the head in instar V. In the adult the pronotum is much longer and broader than the head.	Pronotum shorter than head from instars I to IV, is as long as the head in instar V and much longer than head in adults.
Absent.	Absent.	Absent.
Absent.	Absent.	Absent.
As U. reticulata	As U. reticulata	As U. reticulata
As U. reticulata	As U. reticulata	As U. reticulata
As U. reticulata	As U. reticulata	As U. reticulata
As C. persimilis	Absent.	Present only in adults.

Table 4 (continued)

	U. reticulata	D. stylata	C. persimilis
9. Obliquely set groove separating katepimeron from anepimeron.	Present only in adults.	As U. reticulata	As U. reticulata
10. Furcal sulcus.	Absent in larvae, joins the episternal sulcus in adults.	Only base of Y-stem present in larvae. An incomplete Y in adults.	As D. stylata, but arms of Y longer than D. stylata.
11. Furca-episternal sulcus.	Present only in adults.	Absent.	Absent.
12. Basisternum.	Not differentiated from episternal region in larvae. Completely separated from katepisternum by furca-episternal sulcus but not differentiated from anepisternum in adults. Pits present from instar I.	Not differentiated from episternal region in larvae. Only partially separated from katepisternum by the furcal sulcus in adults, as the latter is an incomplete Y-shape. Pits present from instar I.	As D. stylata
13. Antecoxal sclerite.	Absent.	Present only in adults.	As D. stylata
14. Furcasternum.	Present between coxae from instar I.	As U. reticulata	As U. reticulata
15. apodeme.	Present from instar I.	As U. reticulata	As U. reticulata

M. parvicauda	*B. punctata*	*Z. scutellaris*
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *C. persimilis*	As *C. persimilis*	Absent in larvae, complete Y-shape arising from the posterior margin of segment in adults.
Absent.	Absent.	Absent.
As *D. stylata*	As *D. stylata*	Not differentiated from episternal region in larvae, but completely separated from it by furcal sulcus in adults. Pits present from instar I.
As *D. stylata*	As *D. stylata*	As *D. stylata*
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*

Table 4 (continued)

	U. reticulata	*D. stylata*	*C. persimilis*
16. Phragma	Small and present from instar I onwards.	Small and present from instar I onwards. Does not hang in cavity but lies horizontally under the scutellum in brachypterous adults, and is large and plate-like hanging in cavity, in macropterous adults.	Present from instar I but small. Large, plate-like bearing a deep median notch, hanging into the cavity in adults
17. Metathoracic pleural sulcus	Present from instar I.	As *U. reticulata*	As *U. reticulata*
18. Metathoracic episternum.	Chitinised in larvae and adults.	As *U. reticulata*	As *U. reticulata*
19. Metathoracic epimeron.	Less chitinised than episternum in larvae; highly chitinised in adults.	As *U. reticulata*	As *U. reticulata*
20. Sternum III.	T-shaped with no marked division between sternum and episternum in larvae. A division is present in adults. Posteriorly joined to epimeron.		

M. parvicauda	B. punctata	Z. scutellaris
As C. persimilis	As C. persimilis	As C. persimilis
As U. reticulata	As U. reticulata	As U. reticulata
As U. reticulata	As U. reticulata	As U. reticulata
As U. reticulata	As U. reticulata	As U. reticulata
As U. reticulata	As U. reticulata	As U. reticulata

it may be slightly longer than the head as in C. persimilis, M. parvicauda and D. stylata. However in Z. scutellaris and in B. punctata, the pronotum is very much longer than the head.

Ledges at the sides of the pronotum are absent in all the species studied except in the larvae of U. reticulata.

Laterally the pronotum and the epimeron are fused to form a single plate in all the species studied except in U. reticulata, where a notopleural sulcus is present. Anterior to this is the episternal plate, which is distinct in all the species examined (Fig. 16a, b; Fig. 17).

A prominent pleural sulcus present on the pleuron separates the epimeron from the episternum. Ventrally it provides the coxal process, but dorsally it ends on the lateral sides of the pronotum.

The prothoracic sternum is narrow in all the species and presents no special modifications.

Mesothorax

Special sclerites have been developed on the meso- and metathoracic segments to aid flight. In the larval stages these sclerites are undeveloped as the wing pads are non-functional. The whole of the tergum of the mesothorax in the larvae is covered with the wing pads, whereas in the adult the tergum is divided into an anterior prescutum, a middle scutum and a

Fig. 17 Lateral View of Thorax - *M. parvicauda*

a. Adult

b. Fifth Instar

Lateral View of Thorax - *C. persimilis*

c. Adult

d. Fifth Instar

a.2.	second anepimeron
as.2.	second anepisternum
cox.1.	first coxa
cox.2.	second coxa
cox.3.	third coxa
epm.3.	third epimeron
eps.1.	first episternum
eps.2.	second episternum
eps.3.	third episternum
eps.s.	episternal sulcus
k.2	second katepimeron
ks.2	second katepisternum
mes.w.p.	meso-thoracic wing pads
pl.s.	pleural sulcus
T.1.	first thoracic tergum
T.2.	second thoracic tergum
T.3.	third thoracic tergum
tr.1.	first trochantin
tr.3.	third trochantin

FIG 17

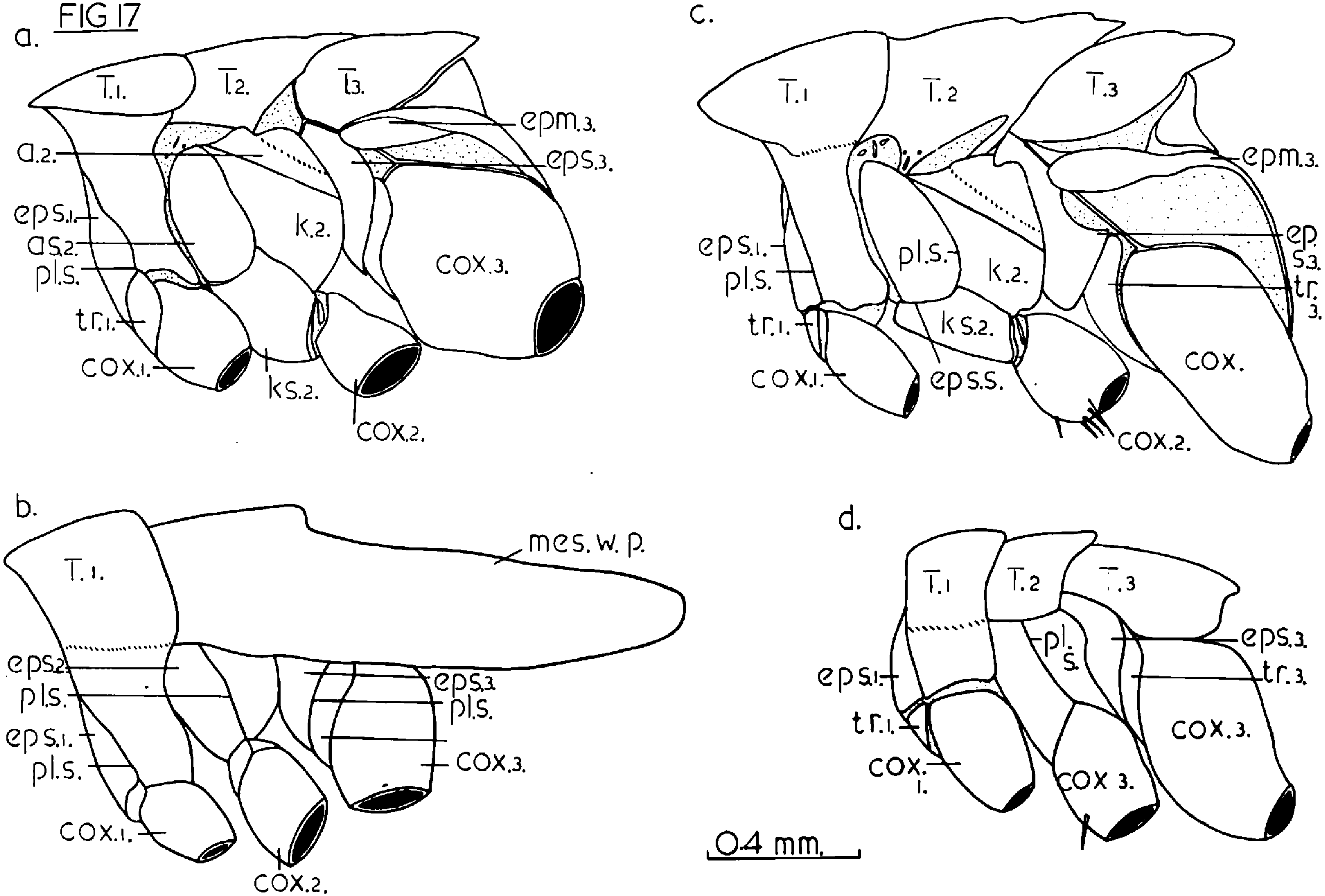

a.
T.1.
T.2.
T.3.
epm.3.
eps.3.
a.2.
k.2.
eps.1.
as.2.
pl.s.
cox.3.
tr.1.
cox.1.
ks.2.
cox.2.
b.
T.1.
mes. w. p.
eps.2
pl.s.
eps.1.
pl.s.
eps.3
pl.s.
cox.3.
cox.1.
cox.2.
c.
T.1
T.2
T.3
epm.3.
ep. s.3.
eps.1.
pl.s.
pl.s.
k.2.
tr. 3.
tr.1.
ks.2.
cox.
cox.1.
eps.s.
cox.2.
d.
T.1
T.2
T.3
eps.3.
pl. s.
tr.3.
eps.1.
tr.1.
cox. 1.
cox 3.
cox.3.
0.4 mm.

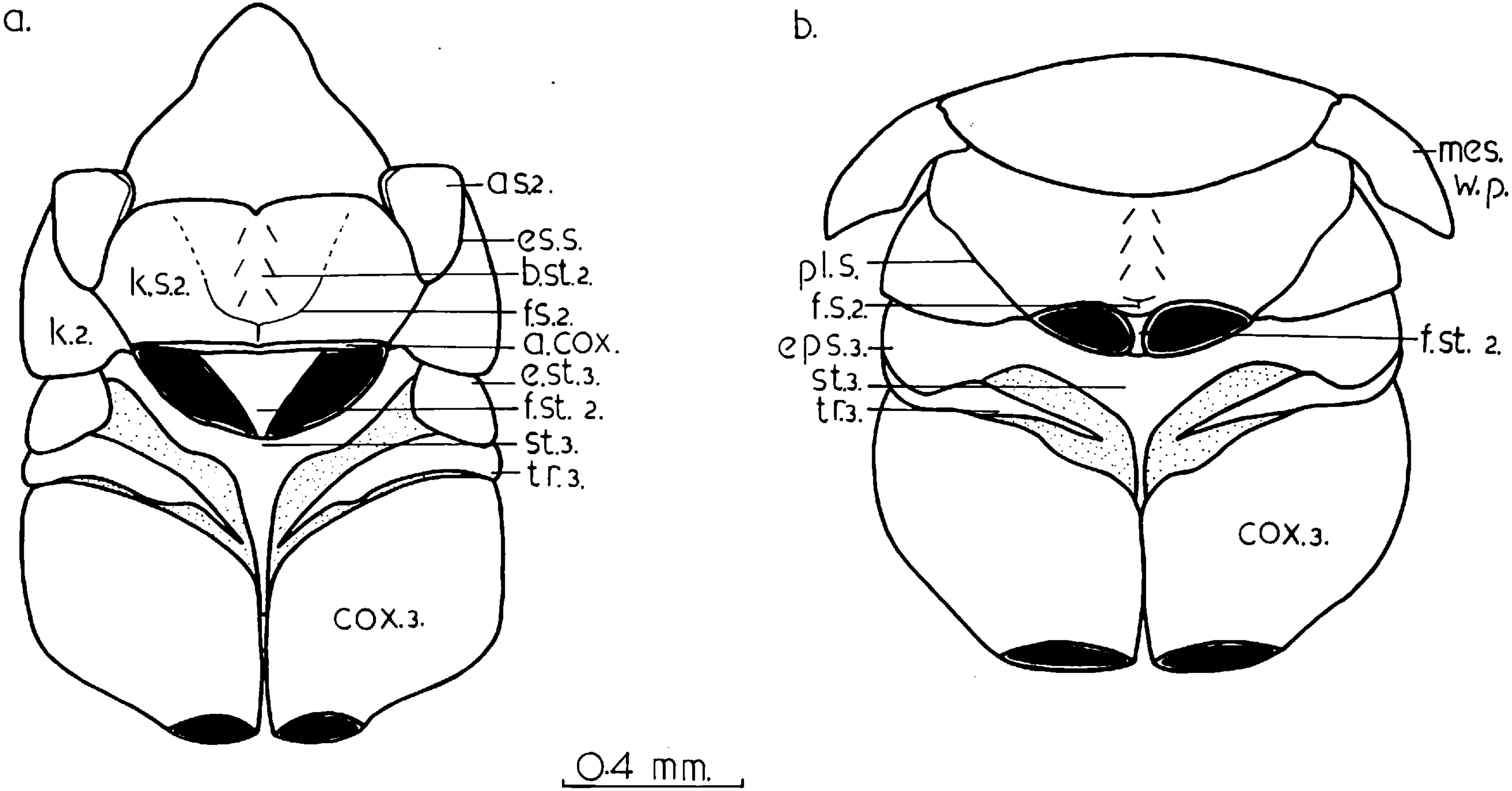
Fig. 18 Ventral View of Meso- and Meta-Thorax -
M. parvicauda

a. Adult

b. Fifth Instar

a.cox.	antecoxal sclerite
b.st.2.	second basisternum
cox.3.	third coxa
eps.3.	third episternum
es.s.	episternal sulcus
e.st.3.	third episternum
f.s.	furcal sulcus
f.st.2.	second furcasternum
k.2.	second katepimeron
k.s.2.	second katepisternum
mes.w.p.	meso-thoracic wing pads
pl.s.	pleural sulcus
st.3.	third sternum
tr.3.	third trochantin

FIG 18



a.
a.s.2.
es.s.
b.st.2.
f.s.2.
k.s.2.
k.2.
a.cox.
e.st.3.
f.st. 2.
st.3.
t.r.3.
cox.3.
b.
mes.
w.p.
pl.s.
f.s.2.
f.st. 2.
eps.3.
st.3.
t.r.3.
cox.3.
0.4 mm.

posterior scutellum. The postnotum is covered over by the scutellum but internally gives off the plate-like phragma. The size and shape of this phragma varies from species to species. It is very large, bifid and hangs down the cavity in the macropterous adults of *C. persimilis*, *M. parvicauda*, *B. punctata* (Fig. 21c), *Z. scutellaris* (Fig. 22a, b), and *D. stylata* (Fig. 20c). In the brachypterous form of *D. stylata* the phragma is tucked horizontally beneath the scutellum (Fig.20a) whereas in *U. reticulata* it is very small (Fig. 21a). The latter two species do not fly and the hind wings are absent in *U. reticulata* adults and are reduced in brachypterous *D. stylata* adults. The phragma which is small in the larval stages (Fig. 20b, 21b, d) is present, though the postnotum and scutellum are not differentiated.

The mesothoracic pleuron, as in the prothorax is divided by a pleural sulcus into anterior episternal and posterior epimeral regions. This sulcus is prominent from the first instar onwards. In the adults the anterior episternal region is divided by an episternal sulcus into a dorsal anepisternum and ventral katepisternum, except in *Z. scutellaris* (Fig. 16a, b). In this species the episternum is an undivided plate, which is a feature of the subfamily Typhlocybinae. In the larval stages of all the species studied, the episternum is an undivided plate.

Fig. 19 Ventral View of Meso- and Meta-Thorax - *D. stylata*

a. Adult

b. Fifth Instar

a.s.2.	second anepisternum
b.st.2.	second basisternum
cox.3.	third coxa
eps.3.	third episternum
f.s.	furcal sulcus
f.st.2.	second furcasternum
k.2.	second katepimeron
k.s.2.	second katepisternum
pl.s.	**pleural sulcus**
st.3.	third sternum
tr.3.	third trochantin

FIG 19

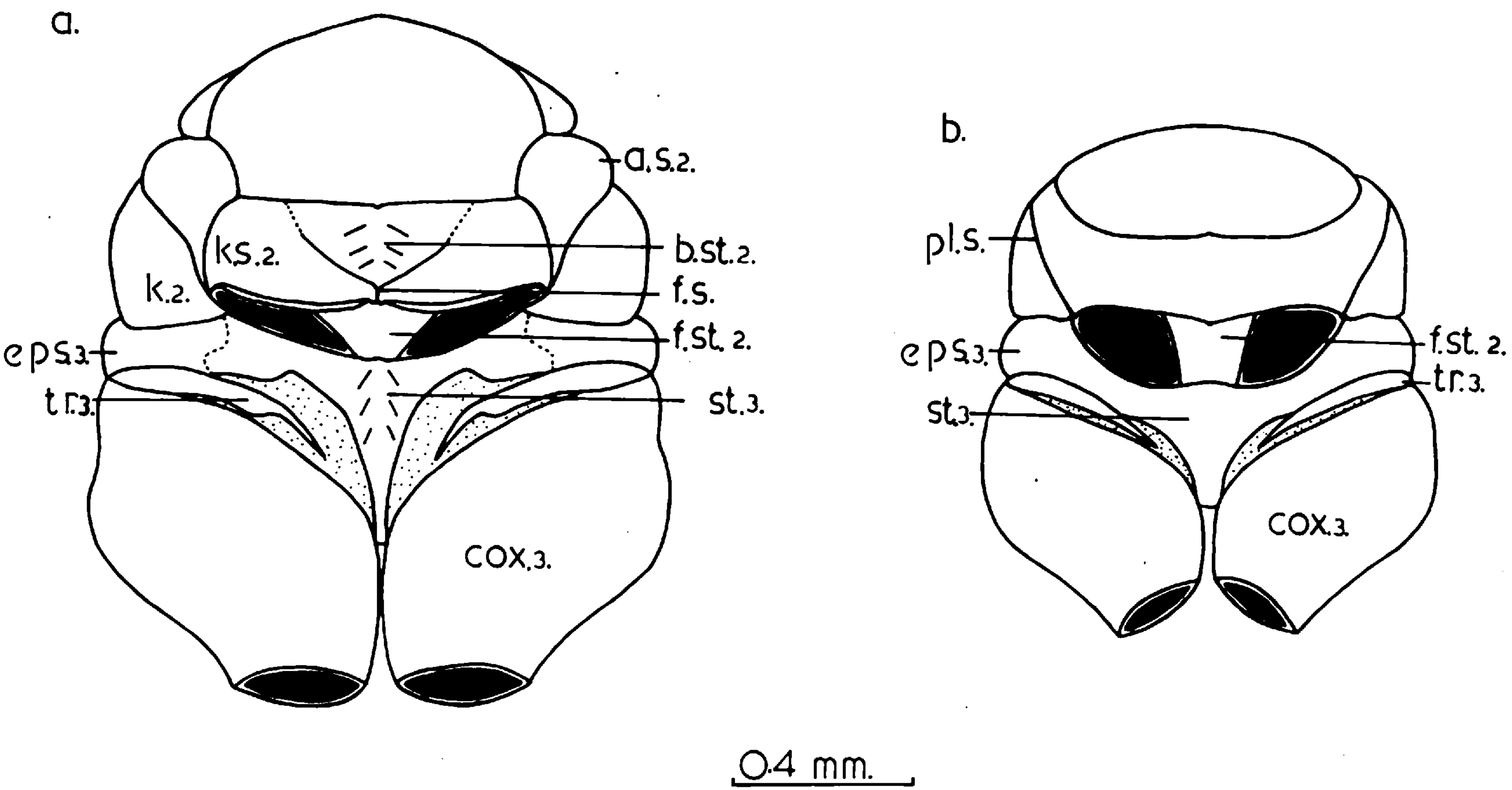

a.
a.s.2.
ks.2.
b.st.2.
k.2.
f.s.
f.st. 2.
eps.3.
tr.3.
st.3.
cox.3.
b.
pl.s.
f.st. 2.
eps.3.
tr.3.
st.3.
cox.3.
0.4 mm.

Fig. 20 Posterior View Through Meso-Thorax - *D. stylata*

a. Brachypterous Adult

b. Fifth Instar

c. Macropterous Adult

cox.2.	second coxa
eps.s.	episternal sulcus
f.s.	furcal sulcus
mes.w.p.	mesothoracic wing pads
met.w.p.	metathoracic wing pads
phr.2.	second phragma
pl.ap.	pleural apodemes
scu.2.	second scutellum
st.ap.	sternal apodemes

FIG 20

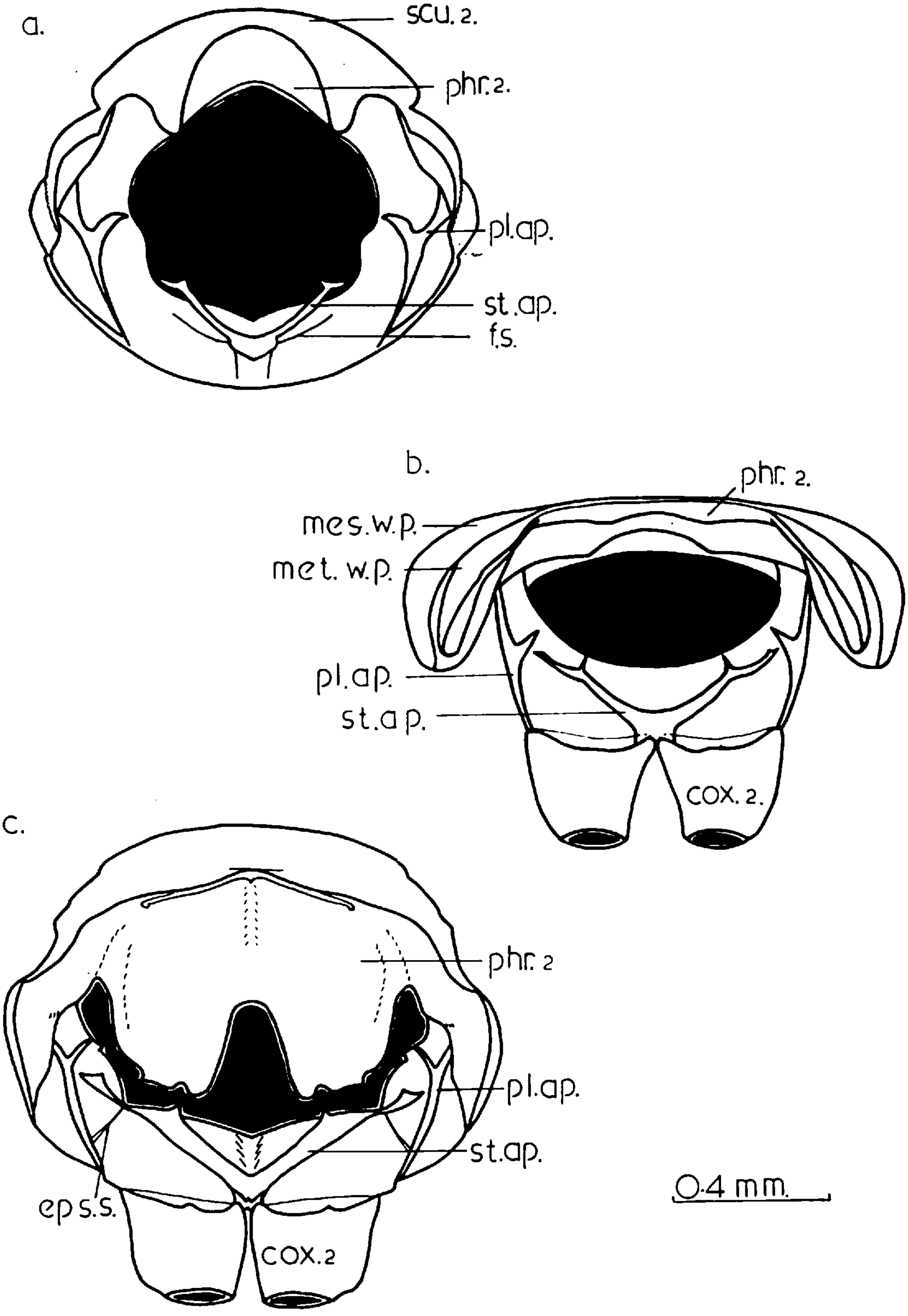

a.
scu. 2.
phr. 2.
pl.ap.
st.ap.
f.s.
b.
phr. 2.
mes.w.p.
met. w.p.
pl.ap.
st.ap.
cox. 2.
c.
phr. 2
pl.ap.
st.ap.
ep s.s.
cox. 2
0·4 mm.

Fig. 21 Posterior View Through Meso-Thorax

a. *U. reticulata* (Adult)

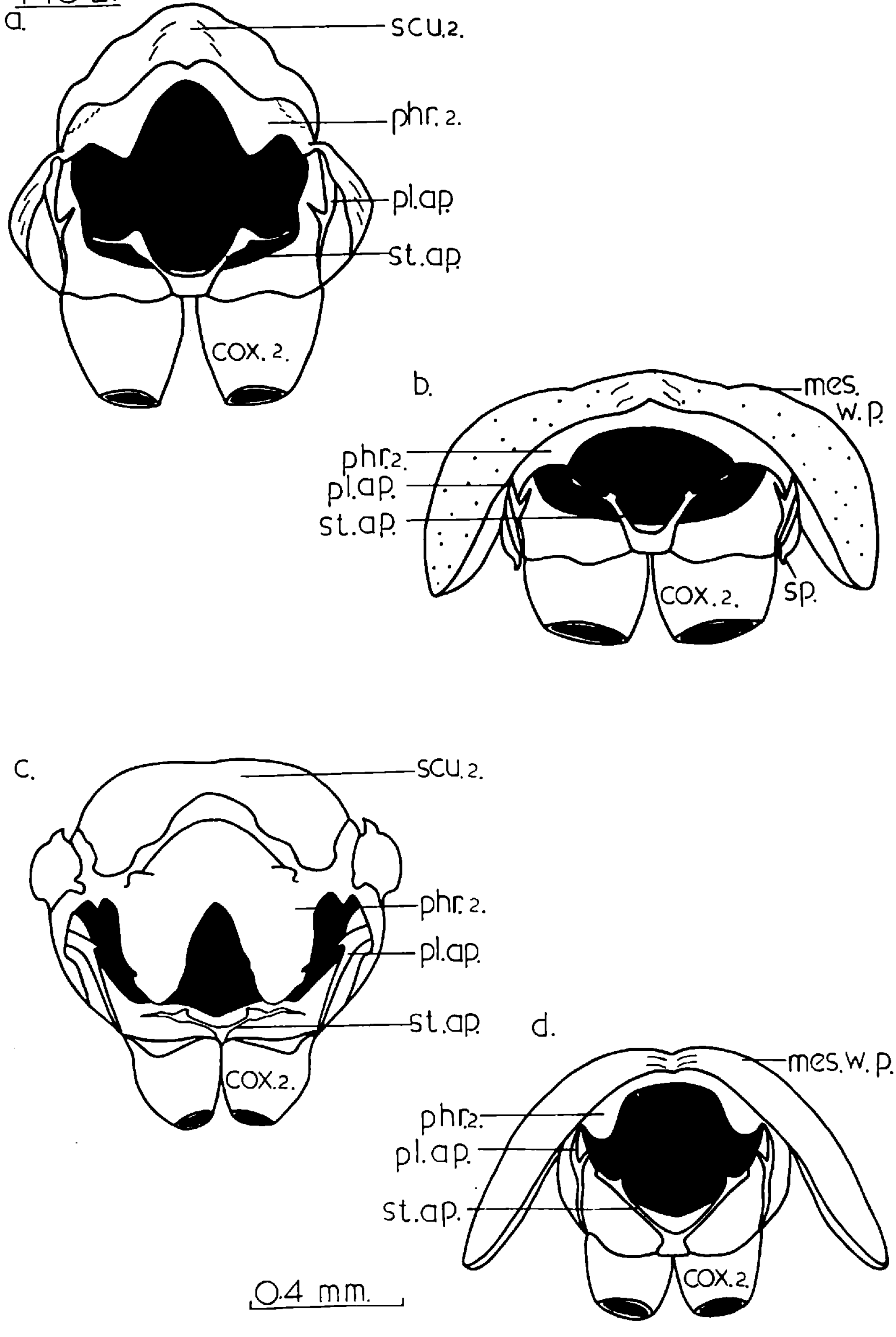
b. *U. reticulata* (Fifth Instar)

c. *B. punctata* (Adult)

d. *B. punctata* (Fifth Instar)

cox.2.	second coxa
mes.w.p.	mesothoracic wing pads
phr.2.	second phragma
pl.ap.	pleural apodemes
scu.2.	second scutellum
sp.	spir
st.ap.	sternal apodemes

FIG 21


a.
scu.2.
phr. 2.
pl.ap.
st.ap.
cox. 2.
b.
mes. w. p.
phr.2.
pl.ap.
st.ap.
cox. 2.
sp.
c.
scu. 2.
phr. 2.
pl.ap.
st.ap.
cox. 2.
d.
mes. w. p.
phr.2.
pl.ap.
st.ap.
cox. 2.
0.4 mm.

The epipleuron is present in the adults of *C. persimilis*, *M. parvicauda* and *Z. scutellaris*.

The epimeral region in all the adults is divided by an oblique groove into a katepimeron and an anepimeron. This groove is absent in the larval stages. The chitinization of the epimeron is secondary in all the species studied.

The pleuron in the larvae bears the coxal articulatory processes but has no special features in relation to the wings. The furcal sulcus in the adult separates the katepisternum, or the episternal region from the basisternum. The shape and position of the sulcus varies from species to species. In *C. persimilis*, *D. stylata* (Fig. 19), *M. parvicauda* (Fig. 18) and *B. punctata* it is an incomplete Y-shape, where the katepisternum and basisternum are separated by the stem of the Y posteriorly, but anteriorly the katepisternum approaches the basisternum. In *U. reticulata* the furcal sulcus joins the episternal sulcus forming the furca-episternal sulcus, which separates the anterior anepisternum and basisternum from the posterior katepisternum. In *Z. scutellaris* the furcal sulcus is complete and not Y-shaped but arises from the posterior margin of the basisternum on either side of it, thus separating the episternal region from the basisternum. In the larval stages only the posterior portion of the stem of the Y is visible, but the basisternal pits and central ridge are present.

Fig. 22 a. Posterior View Through Meso-Thorax - *Z. scutellaris* (Adult)

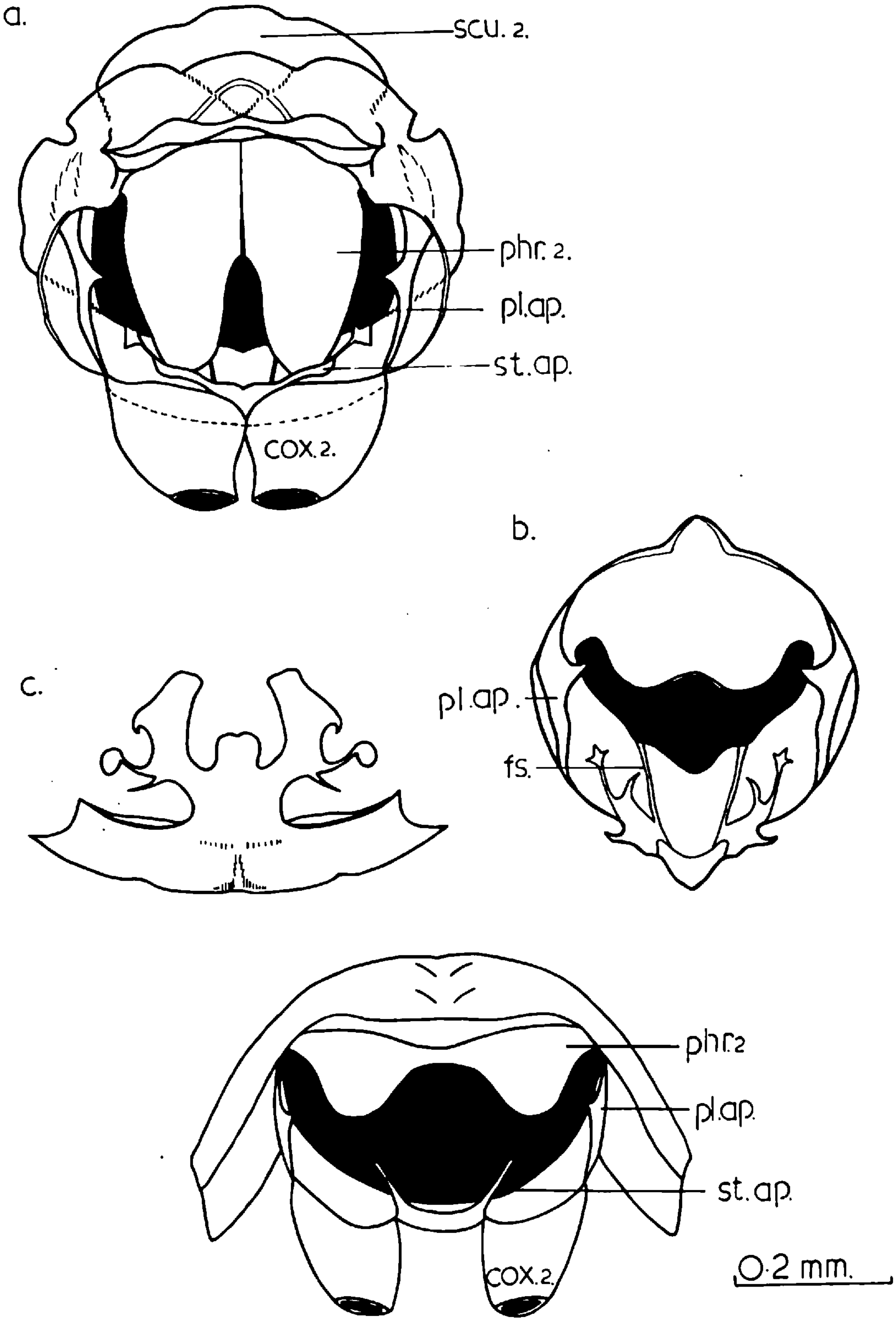
b. Posterio-Dorsal View Through Meso-Thorax - *Z. scutellaris* (Adult)

c. Sternal Apodemes - *Z. scutellaris* (Adult)

d. Posterior View Through Meso-Thorax - *Z. scutellaris* (Fifth Instar)

cox.2.	second coxa
phr.2.	second phragma
pl.ap.	pleural apodemes
scu.2.	second scutellum
st.ap.	sternal apodemes
f.s.	furcal sulcus

FIG 22



The narrow furcasternum is present between the coxae in the larvae and adults. It gives off the sternal apodemes internally which are Y-shaped and arise from a common base in all the species. The sternal apodemes in Z. scutellaris are very large and give off two processes and a median finger-like projection (Fig. 22c). In the larval stages the apodeme is also present, but is smaller in size. The pleural and sternal apodemes are joined by muscle fibres and form part of the endoskeleton of this wing bearing segment.

The antecoxal sclerite is present in all the species studied except U. reticulata.

The trochantin is united to the episternum in all the species.

Metathorax

The tergal region in the larvae is covered by the metathoracic wing pads. In the adults it is formed of the scutum and scutellum.

The pleuron is divided by a prominent pleural sulcus which ventrally provides the coxal process for the enlarged hind coxa. Dorsally in the larvae it ends underneath the wing pads, but in the adult it provides the wing process.

The anterior episternum is fused to the arms of the T-shaped sternum in the larvae. These arms are separated by a sulcus in the adult.

The posterior epimeron is again secondarily chitinized and is joined to the stem of the T-shaped sternum by the postcoxal bridge.

The sternal and pleural apodemes are present but are small and are not specially modified as in the mesothorax.

(iii) LEGS

(a) Introduction and Review of Literature

Imms (1964) while describing the family Cicadellidae, says that the hind tibia is angular with a double row of spines.

Evans (1938) in his work on Cicadellidae commented that although the definition by Imms separated this family from the Membracidae and Cercopidae, the hind tibia may also be circular and have more than two rows of spines. He points out that the hind tibia may be of subsidiary taxonomic value in separating out the primitive Cicadellid groups. In 1947 he added that the structure of the hind tibia is of limited value for taxonomic purposes although it may be useful for indicating relationships.

Kramer (1950) pointed out the presence of apical spines fringing the tarsal segments in Cicadellidae, Cercopidae and Fulgoridae. Ribaut (1952) used the number and position of the spines on the hind femur, in his classification of the Cicadellidae. Le Quesne (1965) separates the family Cicadellidae from other Cicadomorpha by the distinctly keeled posterior tibia bearing spines along or on keels, some of which are mounted on enlarged bases. He adds that the genus *Ulopa* has poorly developed spines.

(b) Definitions of the Accepted Morphological Terms

The six-segmented leg in the family Cicadellidae is made up of the coxa, trochanter, femur, tibia, tarsus and pretarsus, the basic structure of which is similar in all the species studied from the first instar onwards.

The following is a list of definitions of the accepted morphological terms used in this text.

Terms	Definitions
Coxa	Enlarged basal segment of the leg
Trochanter	Triangular second segment between the coxa and femur.
Femur	Third segment of the leg between the trochanter and tibia.
Tibia	The fourth and longest segment of the Cicadellid leg.
Tarsus	The fifth segment of the leg being subdivided into two in the larvae and three in the adult

A table of comparative terminology and descriptions used by previous authors, as in the previous sections, was not drawn up, as the terminology used by the few people who described the insect leg was identical.

(c) Detailed Description of the Legs of *U. reticulata* and Comparison with the Other Species

Fore Leg

Spines are absent on the dorsal anterior region of the femur of the fore leg in *U. reticulata*. The tibia have scattered blunt whitish hairs which are present from the first instar onwards. There are two tarsal segments in instars one to five and three in the adults.

Mid Leg

The tibia and femur as in the fore leg have scattered hairs. The number of tarsi in the larval and adult stages are as in the fore leg.

Hind Leg

Spines are absent on the femur. There are scattered hairs on the angular tibia, along with a few short scattered prominent spines (Fig. 23d, e, f). A crown of spines at the tip of the tibia is absent. The division of the second tarsal segment into a third is visible in instar five. The finger-like projections at the tip of the tarsi are absent in *U. reticulata*.

Table 5 contains a comparative account of the external morphology of the legs in the six species of Cicadellidae examined.

Fig. 23 Tarsal Segments of Hind Leg -
M. parvicauda

a. First Instar

b. Fifth Instar

c. Adult

Hind Legs - *U. reticulata*

d. First Instar

e. Fifth Instar

f. Adult

cox.	coxa
fe.	femur
tar.	tarsal segments
tib.	tibia
tr.	trochanter

FIG 23

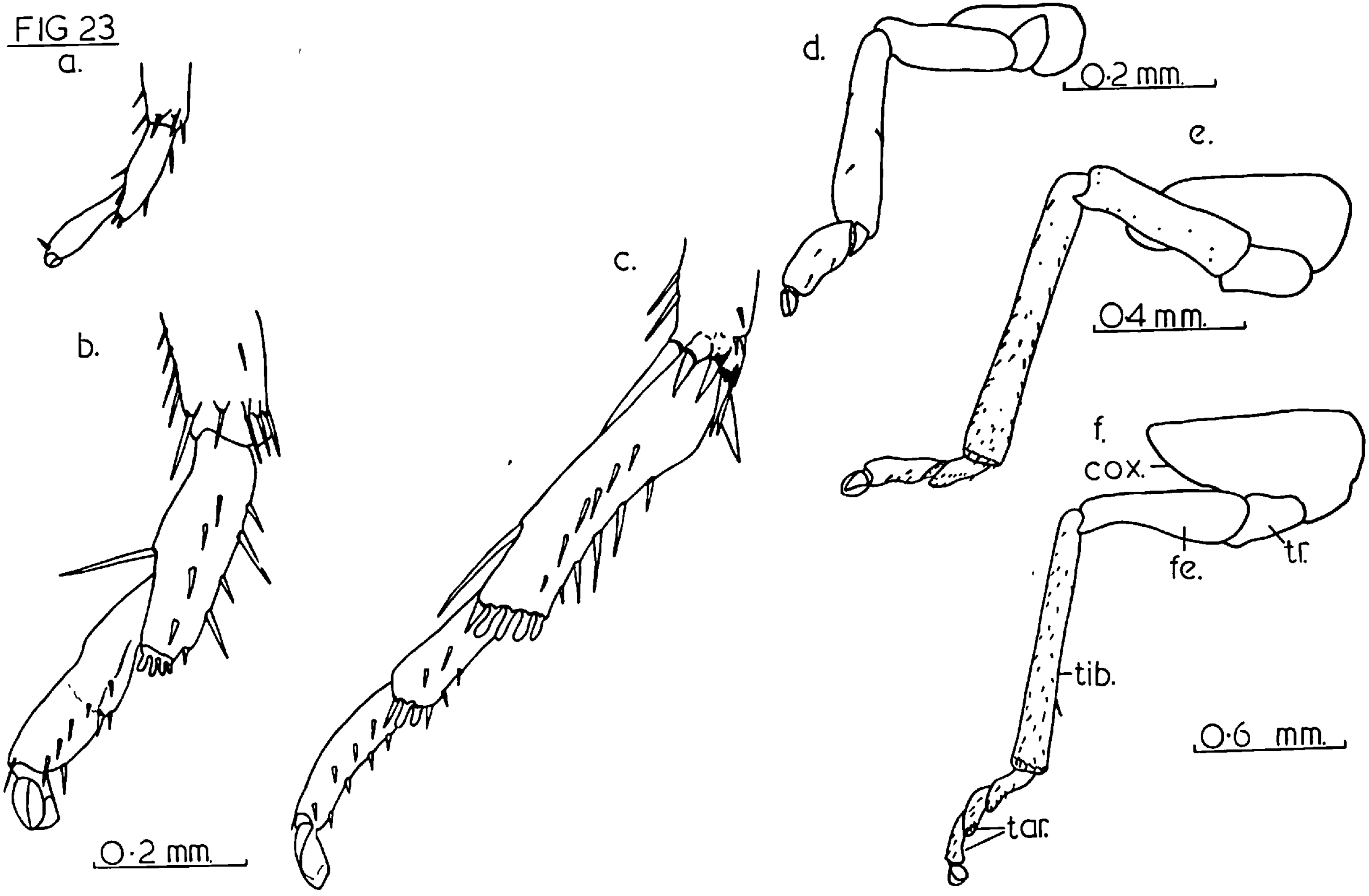


Table 5. Comparative Account of the External Morphology of the Legs in Six Species of Cicadellidae

	U. reticulata	*D. stylata*	*C. persimilis*
Fore leg			
1. Spines on the anterior dorsal surface of the femur.	Absent.	Two in instars I to IV Four in instar V and adults.	As *D. stylata*
2. Spines on tibia.	Absent. Few whitish hairs present.	A few prominent spines present on the dorsal and ventral surfaces in all the larval stages and adults.	As *D. stylata*
3. Tarsus	Two segmented from instars I to V and three segmented in adults.	As *U. reticulata*	As *U. reticulata*
Mid leg			
1. Spines on the anterior dorsal surface of the femur.	Absent	Two in instars I to IV. Three in instar V and adults.	As *D. stylata*
2. Spines on tibia.	Absent. Few whitish hairs present.	A few prominent spines present on the dorsal and ventral surfaces in all the larval stages and adults.	As *D. stylata*
3. Tarsus	Two in instars I to V. Three in adults.	As *U. reticulata*	As *U. reticulata*

M. parvicauda	*B. punctata*	*Z. scutellaris*
As *D. stylata*	As *D. stylata*	Absent
As *D. stylata*	As *D. stylata*	Absent. Few whitish hairs present.
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *D. stylata*	As *D. stylata*	Absent
As *D. stylata*	As *D. stylata*	Absent. Few whitish hairs present.
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*

Table 5 (continued)

	U. reticulata	*D. stylata*	*C. persimilis*
Hind leg			
1. Spines on the anterior dorsal surface of the femur.	Absent. Few whitish hairs present.	Two in instars I to III. Five in instars IV, V and the adults.	As *D. stylata*
2. Spines on tibia.	Absent in larval stages except for the whitish hairs. A few scattered spines present in adults.	Two dorsal and two ventral rows present from instar one onwards. The number increases from instar to instar. Spines have very prominent bases.	As *D. stylata*
	Crown of spines at the tip of tibia is absent.	A crown of spines present at the tip of the tibia from instar I onwards.	As *D. stylata*
3. Tarsus	Two in instars I to V. Three in adults.	As *U. reticulata*	As *U. reticulata*
4. Finger-like projections fringing the tarsi.	Absent	Two in instars I and II. Three in instar III. Four in instar IV. Four in first tarsus and two in second tarsus in instar V. Five in first tarsus, and two in second tarsus in adults.	As *D. stylata*

M. parvicauda	*B. punctata*	*Z. scutellaris*
As *D. stylata*	As *D. stylata*	Absent in all larval stages. Four spines present in adults.
As *D. stylata*	As *D. stylata*	Absent in larval stages except for whitish hairs. Adults have prominent spines.
		Crown of spines at the tip of tibia is not prominent.
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *D. stylata*	As *D. stylata*	Absent

The dorsal anterior surface of the fore, mid and hind femur bears spines in all the species studied except in U. reticulata and the larval stages of Z. scutellaris. The fore and mid femur in M. parvicauda, C. persimilis, D. stylata and B. punctata have a pair each from instars one to five, and the mid femur has two spines from instars one to three, and five in instars four, five and adults. All the stages in U. reticulata and the larval stages in Z. scutellaris have small scattered hairs instead.

The prominent spines on the hind tibia are a useful character for the separation of the family Cicadellidae from other Homoptera. This is true in most species although U. reticulata and Z. scutellaris have no regular spines (Fig. 23d, e, f). The larval stages in these species have scattered hairs, although few spines are present in the adult stage. The spines in D. stylata (Fig. 24a-c), C. persimilis M. parvicauda and B. punctata are present from the first instar onwards. They fall into two dorsal and two ventral rows from the third instar onwards. The exact number of spines on the hind tibia in each species does not provide a useful guide for the identification of the species or instars, and hence is not recorded in this thesis. The shape of the hind tibia is circular in all the species studied, except U. reticulata where it is angular.

Fig. 24 Hind Legs - D. stylata

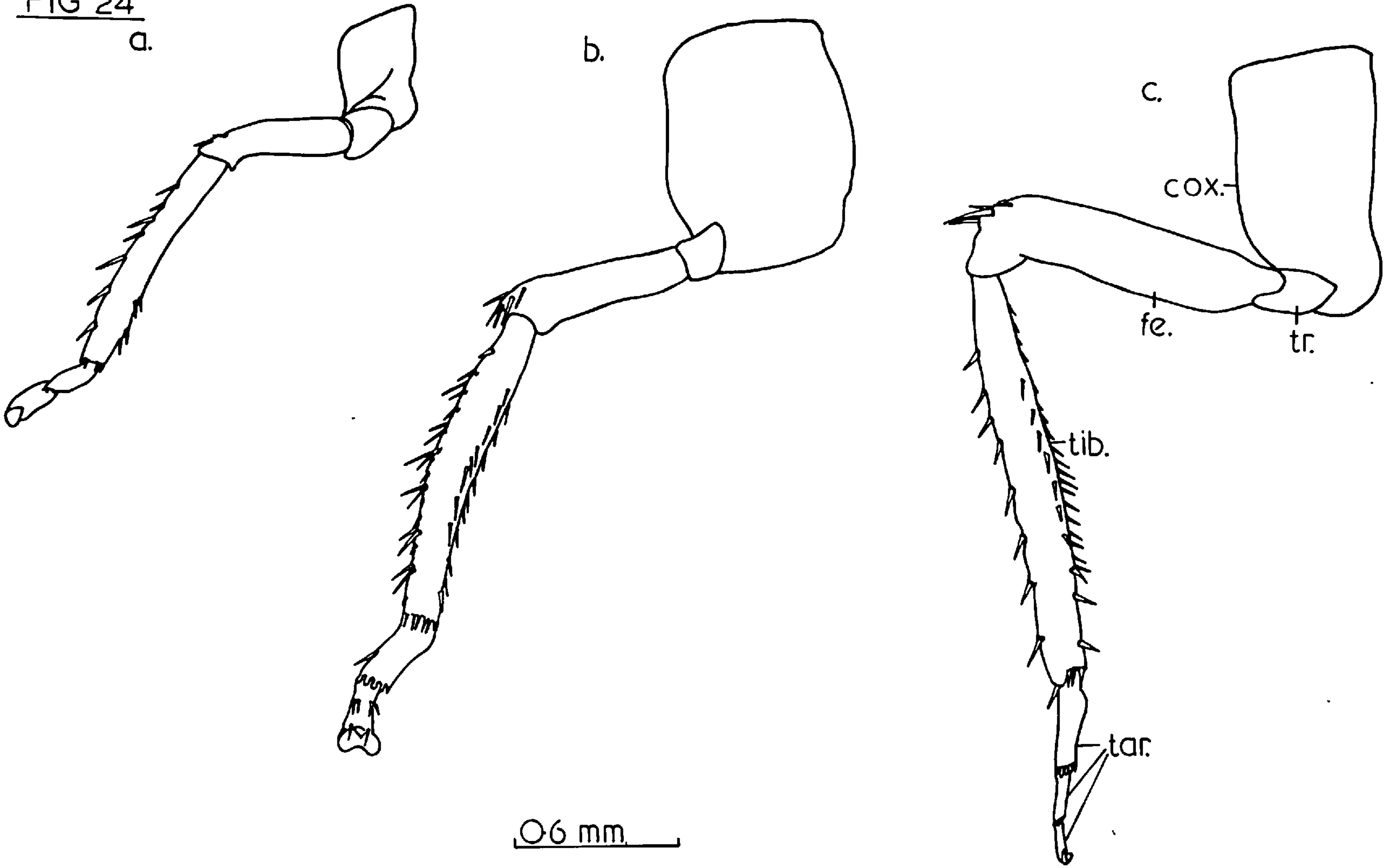
a. First Instar

b. Fifth Instar

c. Adult

cox.	coxa
fe.	femur
tar.	tarsal segments
tib.	tibia
tr.	trochanter

FIG 24



All the five larval instars have two tarsal segments, and the adults have three. The division of the second tarsus into a third is visible in the fifth instar (Fig. 23a, b, c).

Finger-like projections at the apex of the tarsi are present from the first instar in *D. stylata* (Fig. 24a, b, c), *C. persimilis*, *M. parvicauda* (Fig. 23a, b, c) and *B. punctata*. These projections are prominent in the tarsi of the hind leg, and are absent in *U. reticulata* (Fig, 23d, e, f) and *Z. scutellaris*.

As the hind legs are used for jumping, the coxae and tibiae are swollen and long. This is so in all the species studied except *U. reticulata* where the legs are short.

(iv) WING PADS

(a) Introduction

The fore and hing wings in the adult Cicadellidae are developed from the meso- and metathoracic wing pads which are present in the larval stages.

Medler (1942), Oman (1949), Ribaut (1952) and Le Quesne (1965, 1969) used wing venation as one of the taxonomic characters in the adult classifications of Cicadellidae. In the larvae, it was found that the length of the wing pads in the various stages is a useful guide for the identification of instars. A detailed study of this is made in this section.

(b) Development of the Wing Pads in the Larval Instars of Some Species

Snodgrass (1927) says that the wings appear in the second or third instar as hollow flattened outgrowths of the lateral parts of the dorsum, in the meso- and metathorax. He explains that they appear externally as any other appendicular outgrowths in insects which go through incomplete metamorphosis, whereas they appear beneath the cuticle in insects which go through complete metamorphosis.

In the larvae of Cicadellidae the wing pads develop externally. In each instar the meso- and metathoracic wing pads grow to a certain length which is an indication of the particular larval stage.

Table 6 Comparative Account of the Development of the Wing Pads in Six Species of Cicadellidae

	U. reticulata	*D. stylata*
Instar I Mesothoracic wing pads	Not differentiated but the posterior margin is slightly curved.	As *U. reticulata*
Metathoracic wing pads	Rudiments differentiated. A small notch is present in the centre of the posterior margin.	Rudimentary. A pair of bristles are present on either side of the posterior margin.
Instar II Mesothoracic wing pads	Not differentiated but the posterior margin is straight.	Not differentiated but the posterior margin of mesothorax is curved.
Metathoracic wing pads	Rudiments are more pronounced, reaching down the anterior margin of the second abdominal segment. A prominent notch on the centre of the posterior margin is present.	As *U. reticulata*. Bristles present as in first instar.
Instar III Mesothoracic wing pads	Extend to the anterior margin of the first abdominal segment.	As *U. reticulata*
Metathoracic wing pads	Extend to the anterior margin of the second abdominal segment. The notch in the posterior margin is prominent.	Extend to the posterior margin of the third abdominal segment. The pair of bristles on the posterior margin are present.
Instar IV Mesothoracic wing pads	Extend to the posterior margin of the first abdominal segment. The posterior margin of the mesothorax is straight.	As *U. reticulata*

C. persimilis	*M. parvicauda*	*B. punctata*	*Z. scutellaris*
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
As *D. stylata*	As *D. stylata*	As *D. stylata* but bristles absent.	As *D. stylata* but bristles absent.
As *D. stylata*	As *D. stylata*	As *D. stylata*	As *D. stylata*
As *D. stylata*	As *D. stylata*	As *D. stylata* but bristles absent.	As *D. stylata* but bristles absent.
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*	As *U. reticulata*
Extend to the anterior margin of the second abdominal segment. The pair of bristles are present.	As *C. persimilis*	As *C. persimilis* but bristles absent.	As *C. persimilis* but bristles absent .
As *U. reticulata*	As *U. reticulata*	As *U. reticulata*	As *U. reticulata*

Table 6 (continued)

	U. reticulata	*D. stylata*
Metathoracic wing pads	Extend half way down to the second abdominal segment. The mesothoracic wing pads are slightly shorter than the metathoracic ones.	Extend to the posterior margin of the third abdominal segment. Pair of bristles on posterior margin absent.
Instar V Mesothoracic wing pads	Extend half way down to the third abdominal segment.	Extend to the anterior margin of the third abdominal segment.
Metathoracic wing pads	Extend half way down to the second abdominal segment, hence being shorter than the mesothoracic wing pads.	Extend half way down to the third abdominal segment, being slightly longer than the mesothoracic wing pads.

C. persimilis	*M. parvicauda*	*B. punctata*	*Z. scutellaris*
Extend to the anterior margin of the second abdominal segment.	As *C. persimilis*	Extend half way down to the third abdominal segment.	As *C. persimilis*
Extend to the posterior margin of the third abdominal segment.	As *C. persimilis*	Extend half way down to the fifth abdominal segment.	Extend half way down to the fourth abdominal segment.
The same length as the mesothoracic wing pads.	As *C. persimilis*	The same length as the mesothoracic wing pads.	The same length as the mesothoracic wing pads.

A comparative account of the development of the wing pads in the six species studied, is given in Table 6.

In all the first instars examined, the mesothoracic wing pads are not differentiated but the rudiments of the metathoracic ones are differentiated. A notch is present in the centre along the posterior margin of the metathoracic wing pads in *U. reticulata* (Fig. 25a), and a pair of bristles are present on either side of the posterior margin in all the other species, except in *U. reticulata* and *B. punctata*. These bristles are present in the species that have prominent abdominal bristles and tibial spines.

In the second instar the mesothoracic wing pads are not differentiated, but the metathoracic ones reach down to the anterior margin of the first abdominal segment in all the species examined (Fig. 25b, 26b).

In the third instar the mesothoracic wing pads extend down to the anterior margin of the first abdominal segment, in all the species examined (Fig. 25c, 26c). The metathoracic ones extend down to the anterior margin of the second abdominal segment in all the species examined except *D. stylata*, where they extend to the posterior margin of the third abdominal segment. The pair of bristles on each side of the posterior margin is present in the third instar as in the first and second instars.

Fig. 25 Dorsal View of Head and Thorax - *U. reticulata*

a. First Instar

b. Second Instar

c. Third Instar

d. Fourth Instar

e. Fifth Instar

FIG 25

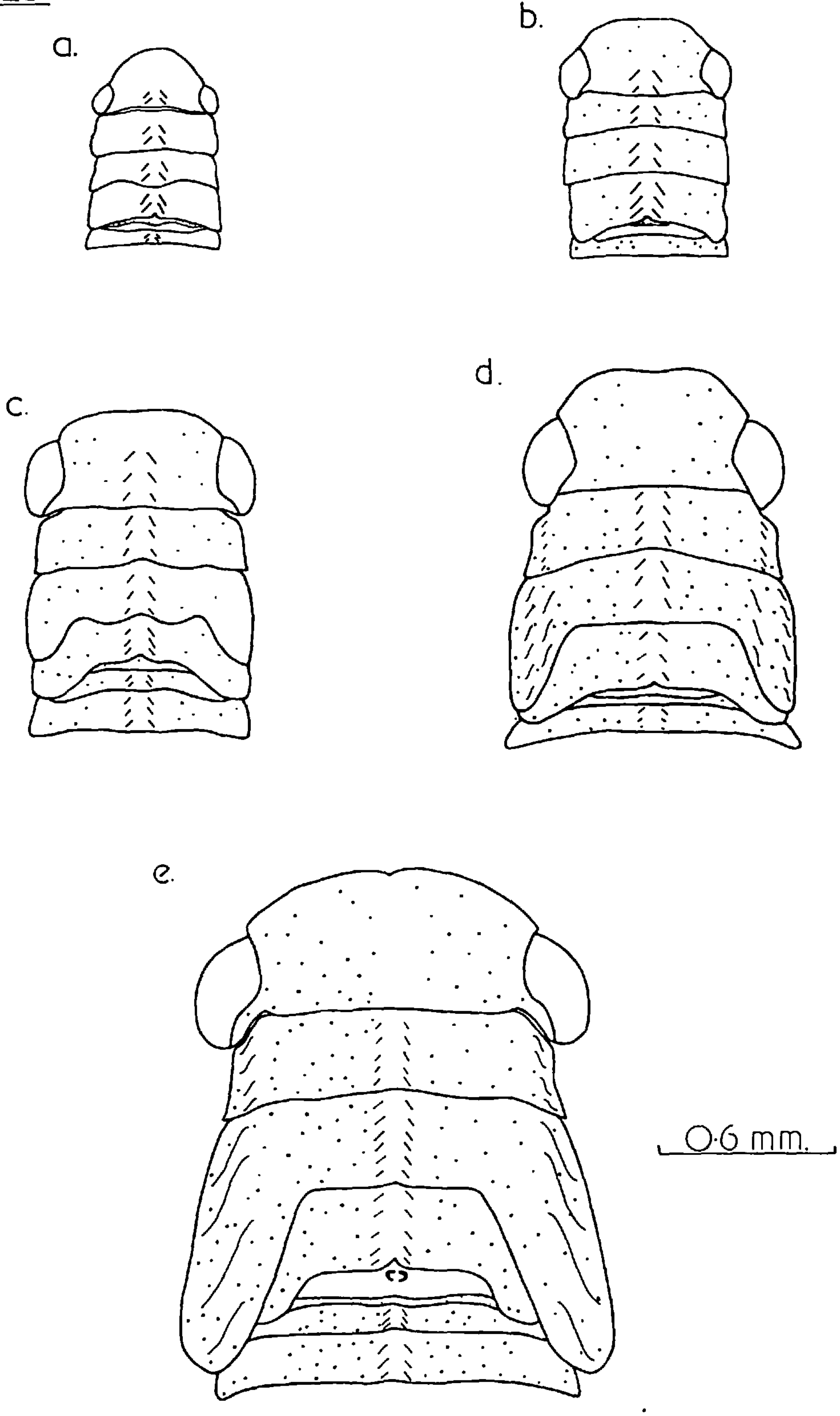


Fig. 26 Dorsal View of Head and Thorax -

M. parvicauda

a. First Instar

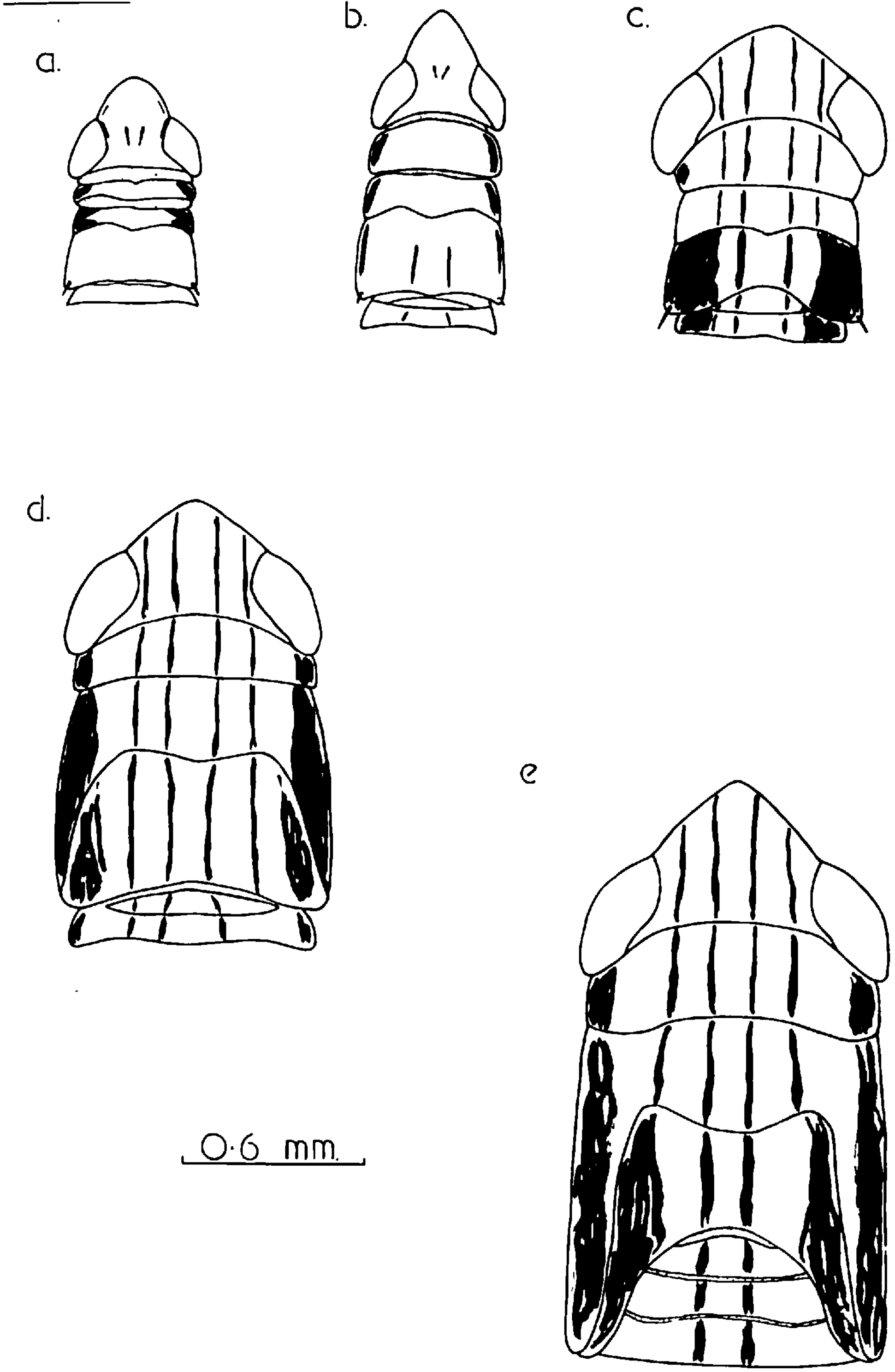
b. Second Instar

c. Third Instar

d. Fourth Instar

e. Fifth Instar

FIG 26



In the fourth instar the mesothoracic wing pads extend down to the posterior margin of the first abdominal segment in all the species examined. The metathoracic wing pads extend half way down to the second abdominal segment in *U. reticulata* (Fig. 25d), to the posterior margin of the third abdominal segment in *D. stylata*, to the anterior margin of the second abdominal segment in *C. persimilis*, *M. parvicauda* (Fig. 26d), and *Z. scutellaris*, and half way down to the third abdominal segment in *B. punctata*. Hence in the fourth instars the mesothoracic wing pads are slightly shorter than the metathoracic ones in all the species examined.

As it can be seen on Table 6, the metathoracic wing pads in the fifth instars of *U. reticulata* are much shorter than the mesothoracic ones (Fig. 25e), whereas they are both almost of the same length in all the other species examined (Fig. 26e). Both pairs of wing pads are very long in *B. punctata*, extending down to the fifth abdominal segment, and are short in *D. stylata*, where they extend down to the anterior margin of the third abdominal segment. In all the other species examined they are of medium length. *D. stylata* adults, of course, are normally brachypterous.

(v) EXTERNAL MALE GENITALIA

(a) Introduction and Review of Literature

The development of the external male genitalia in the Cicadellid *Idiocerus*, was studied by Singh-Pruthi (1924) and the development in *Cicadella hieroglyphica* Say, by Hackman (1922).

Kershaw & Muir (1922) examined the genitalia of the Auchenorhynchous Homoptera. Muir (1925) studied the status of the anterior processes of the male genitalia in Homoptera while George (1929) worked out the morphology and development of the external genitalia and genital ducts of Homoptera and Zygoptera, with reference to *Philaenus* and *Agrion*. The origin and development of the external genitalia of male insects was studied by Dupuis (1950). Kramer (1950) described the male genitalia of *A. irronata* in his studies of the Auchenorhynchous Homoptera. The external male genitalia of Auchenorhyncha is also described by Ossiannilsson, Russell & Weber, in Tuxen (1970).

The varying shape of the external male genitalia in Cicadellidae has been used in the separation of species in the classifications by Medler (1942), Oman (1949), Ribaut (1952), Bierne (1956) and Le Quesne (1965, 1969).

Scudder (1971) gives a comparative account of the morphology of the insect genitalia, which includes the male genitalia.

(b) Definitions of the Accepted Morphological Terms and Terminology, and Descriptions Used by Previous Authors

The size and length of the rudiments of the genitalia in the larval stages, clearly indicates the sex and the particular stage of the larvae from the third instar onwards. A detailed study of this is made and the development of the genitalia is traced through the immature stages to the adult, in this section.

The following is a list of definitions of the accepted morphological terms.

Terms	Definitions
Subgenital plate	Posterior ventral plate which is united to the ninth sternum in the larvae.
Genital plates	Posterior ventral paired plates found in the ninth segment of the adult.
Genital valve	A triangular plate lying in front of the genital plates in the adult, which is also the ninth sternum.
Aedeagus	Distal portion of the median sclerotized intromittent organ.
Parameres	Paired structures lying on either side of the aedeagus.
Phallobase	Basal portion of the intromittent organ

As the terminology used by the previous authors was variable, a table of comparative terminology, as well as descriptions was drawn up and is given in Table 7.

The origin of the subgenital plates has been much disputed. Kershaw & Muir (1922) think that they are derived from the coxites of the eighth segment which become fused to the ninth sternum in the last instar, and Muir (1925) says that they arise from the inner membrane posterior to the eighth sternite. Singh-Pruthi (1924), George (1929), Snodgrass (1957), and Ossiannilsson, Russell & Weber (1970) say that they are outgrowths of the ninth sternum. The origin of these plates is best observed in the larval stages, as described by Singh-Pruthi (1924). Scudder (1971) says that in Orthopteroids and many Homoptera (Membracidae, Cercopidae and Cicadellidae) the genitalia are protected by a distinct subgenital plate.

In the Cicadellidae studied the subgenital plates are outgrowths of the ninth sternum, visible from the third instar onwards.

The primary phallic organs are made up of the aedeagus and parameres. According to Snodgrass (1957) they arise behind the ninth sternum, and this is so in the Cicadellidae studied. Singh-Pruthi (1924) observed in the species I. atkinsoni , that the external male genitalia are derived from these phallic

Table 7 Comparative Terminology and Descriptions of the External Male Genitalia used by Previous Authors

	Snodgrass	Singh-Pruthi	Ossiannilsson, Russell, Weber	Dupuis
Subgenital plate	(1957) The ninth abdominal sternum which bears a pair of lobes of various length is called the subgenital plate.	(1924) The plate is an outgrowth of the ninth abdominal sternum and is developed from a pair of primary lobes. It is flexibly attached to the ventral arch of the ninth sternum	(1970) The genital capsule in the ninth sternum is made up of the genital valve and plate. The genital plates are two horizontal plates of varying shape.	-
Phallic organs	(1957) The phallic rudiments arise on the apparent posterior part of the ninth sternum of the larva, and are found behind the sternal plates. These organs serve intromission and copulation. (1963) The primary genital lobes are the phallic rudiments.	(1924) The development of the genitalia in I. *atkinsoni* are formed from the phallic rudiments.	-	-

George	Kershaw & Muir	Smith	Matsuda	Muir
(1929) The plates are situated on the ninth sternum.	(1922) The anterior gonopods or subgenital plates are derived from the coxite of the eighth sternum. In the last instar it becomes fused to the ninth sternum.	(1969) The gonocoxites of the pterygota may unite secondarily with the derived coxosternites to form the subgenital plates or the gonosternite.	-	(1925) The anterior or genital plates arise from the inner membrane posterior to the eighth sternite.
-	-	-	-	-

Table 7 (continued)

	Snodgrass	Singh-Pruthi	Ossiannilsson, Russell, Weber	Dupuis
Aedeagus, and parameres	(1957) These are developed from a single pair of primary genital lobes, or phallic rudiments. (1963) Each primary lobe divides into two secondary lobes - a median mesomere and a lateral paramere.	(1924) In *Idiocerus* the inner pair of appendages of the ninth sternum split forming the parameres and aedeagus. The lobes are called the paramere lobes.	-	(1950) In superior insects the endophallic outline splits into the lateral exterior part which gives rise to the parameres and a median interior part which forms the aedeagus or the phallus
Aedeagus	(1957) The secondary lobes of the median pair of mesomeres unite with each other to form the aedeagus. (1963) In Hemiptera the mesomeres of the primary genital rudiments unite to form the median aedeagus.	-	(1970) The intromittent copulatory organ consists of the basal phallobase and distal aedeagus, the innerlying or endophallus is a continuation of the ductus ejaculatorius, with the gonopore as the terminal opening.	-

George	Kershaw & Muir	Smith	Matsuda	Muir
(1929) The primitive paramere lobes divide into the parameres and aedeagus. The paramere lobes are also called the penis lobes.	-	-	(1958) The gonapophysis or the ventral reproductive tubicle, forms the phallic organs in the male, which includes the parameres and phallus.	-
(1929) It arises from the ninth segment, and is paired in the earlier stages but in later stages fuses to form the copulatory organs.	(1922) The median gonapophysis is the aedeagus.	(1969) The intromittent organ is the aedeagus.	-	-

Table 7 (continued)

	Snodgrass	Singh-Pruthi	Ossiannilsson, Russell, Weber	Dupuis
Parameres	(1935) In Homoptera these are the periphallic structures; and are referred to as the movable claspers or harpagones. (1957) In the adult they are elongate and are the principal genital claspers. A narrow basal connection is retained with the aedeagus. (1963) In Hemiptera the parameres are simple lobes. When united at the bases with the aedeagus, a phallic unit is formed.	-	-	(1950) The parameres are the copulatory hooks.

George	Kershaw & Muir	Smith	Matsuda	Muir
(1929) In Homoptera the parameres are the outgrowths of the aedeagus. They are present in primitive groups and originate as processes on the aedeagus to serve as claspers.	(1922) The parameres are the posterior gonapophyses.	-	-	-

rudiments, which split into three. Snodgrass (1957) agrees with Sing-Pruthi and says that in Homoptera the primary genital lobes are derived from these rudiments.

Dupuis (1950) explains that in superior insects the primary phallic lobes split into two lateral exterior parts and a median interior part. The lateral parts give rise to the parameres, whereas the median part forms the aedeagus. George (1929) points out that the aedeagus arises from the ninth segment as a paired structure but in the later stages these paired structures fuse to form the copulatory organs. Scudder (1971) says that in Hemipteroids and Endopterygota the primary phallic lobes give rise to the whole male genitalia, that is, the aedeagus and parameres.

The parameres are also referred to as the movable claspers by Snodgrass (1933) and as the copulatory hooks by Dupuis (1950). Snodgrass (1963) explains that the parameres and aedeagus are often not separated at their bases and the three parts form a common phallic unit. George (1929) says that the parameres in Homoptera are outgrowths of the aedeagus, and originate as processes of the aedeagus to serve as claspers.

In the Cicadellidae studied the phallic rudiments split into three, forming the aedeagus and parameres.

(c) Development of the External Male Genitalia

The following is the development of the male genitalia which refers to all the species studied. A comparative account of the development in the six species examined was not drawn up, as the development is very similar in all the species. Hence a general account is presented which is applicable to all the species, and any peculiarities within the species are mentioned.

In the larval stages the rudiments of the external male genitalia are visible from the third instar onwards (Fig. 27a, 28a). Fused to the ninth sternum is a triangular plate-like structure produced posteriorly called the subgenital plate. The length of the split along the centre of the plate varies from species to species. The basic shape of this plate in the larval instars is similar in most of the species, although variations in the shape along the posterior margin may occur. It is pointed in C. persimilis and M. parvicauda (Fig. 30d, f), whereas it is rounded in all the other species studied (Fig. 30b, h, j).

When viewed ventrally the primary phallic rudiments lie hidden behind the subgenital plate, in all the third instars.

In the fourth instar the subgenital plate and the phallic rudiments increase in size but the basic structure remains the same in all the species (Fig. 27b, 28b).

Fig. 27 Ventral View of Last Two Abdominal Segments - U. reticulata (Male)

a. Third Instar

b. Fourth Instar

c. Fifth Instar

d. Lateral View of Adult

e. Adult

aed.	aedeagus
g.p.	genital plate
pa.	parameres
pr.ph.ru.	primary phallic rudiments
s.g.p.	subgenital plate
st.X.	tenth sternite
t.VIII.	eighth tergite
t.IX.	ninth tergite

FIG 27

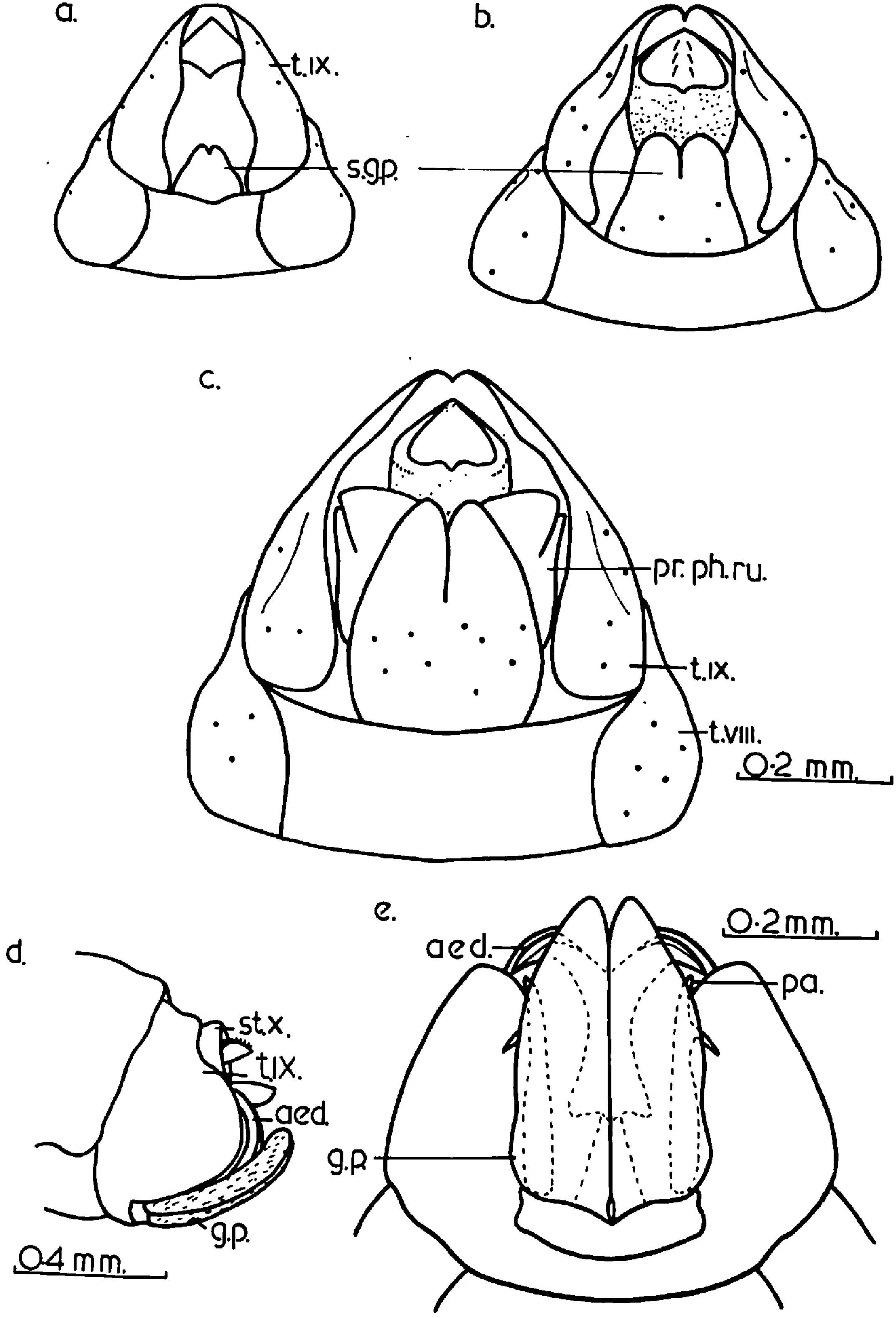

a.
t.ix.
s.g.p.
b.
c.
pr. ph. ru.
t.ix.
t.viii.
0·2 mm.
d.
st.x.
t.ix.
aed.
g.p.
0·4 mm.
e.
0·2mm.
aed.
pa.
g.p.

Fig. 28 Ventral View of Last Abdominal Segment - *M. parvicauda* (Male)

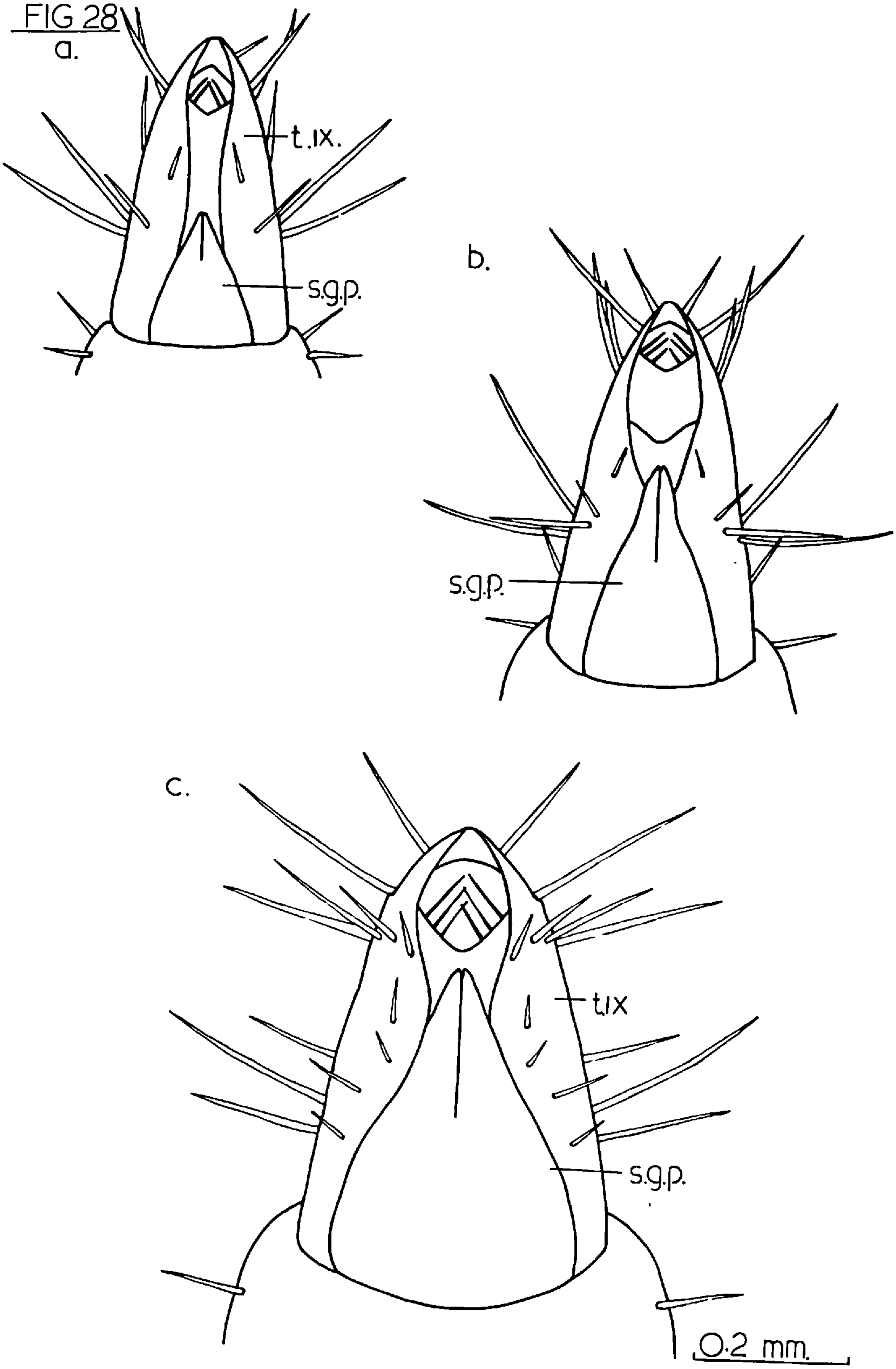
a. Third Instar

b. Fourth Instar

c. Fifth Instar

s.g.p.	subgenital plate
t.IX.	ninth tergite

FIG 28



Both the plates increase in size in the fifth instar, but the primary phallic rudiments in *U. reticulata* are prominent and are produced laterally on either side of the subgenital plate (Fig. 27c), whereas they are not visible laterally in all the other species examined (Fig. 28c).

In the adults the subgenital plate becomes differentiated to form the ninth sternum and the paired genital plates. The ninth sternum is a valve-like structure and is also referred to as the genital valve. All the species examined have this genital valve, except *U. reticulata*. In this species the ninth sternum and tergum are fused (Fig. 27d, e). The paired genital plates lie posterior to the genital valve, the size and shape of which varies from species to species. They bear prominent spines along the posterior margin in *C. persimilis*, *M. parvicauda*, *Z. scutellaris* and *B. punctata* (Fig. 30c, e, g, i). The genital plates in *D. stylata* and *U. reticulata* have short white hairs only (Fig. 27d, 30a).

The primary phallic rudiments present in the larval stages, split into three parts in the adult. When a pharate adult (Hinton, 1946) is dissected from the cuticle of a fifth instar and is then cleared in potassium hydroxide, this division is visible as seen in *D. stylata* (Fig. 29a). The lateral parts form the parameres and the median part forms a two-layered

Fig. 29 Ventral View of Last Abdominal Segment - *D. stylata* (Male)

a. Pharate Adult

b. Adult

aed.	aedeagus
co.	connective
g.p.	genital plate
g.v.	genital valve
pa.	parameres
ph.b.	phallobase
t.IX.	ninth tergite

FIG 29

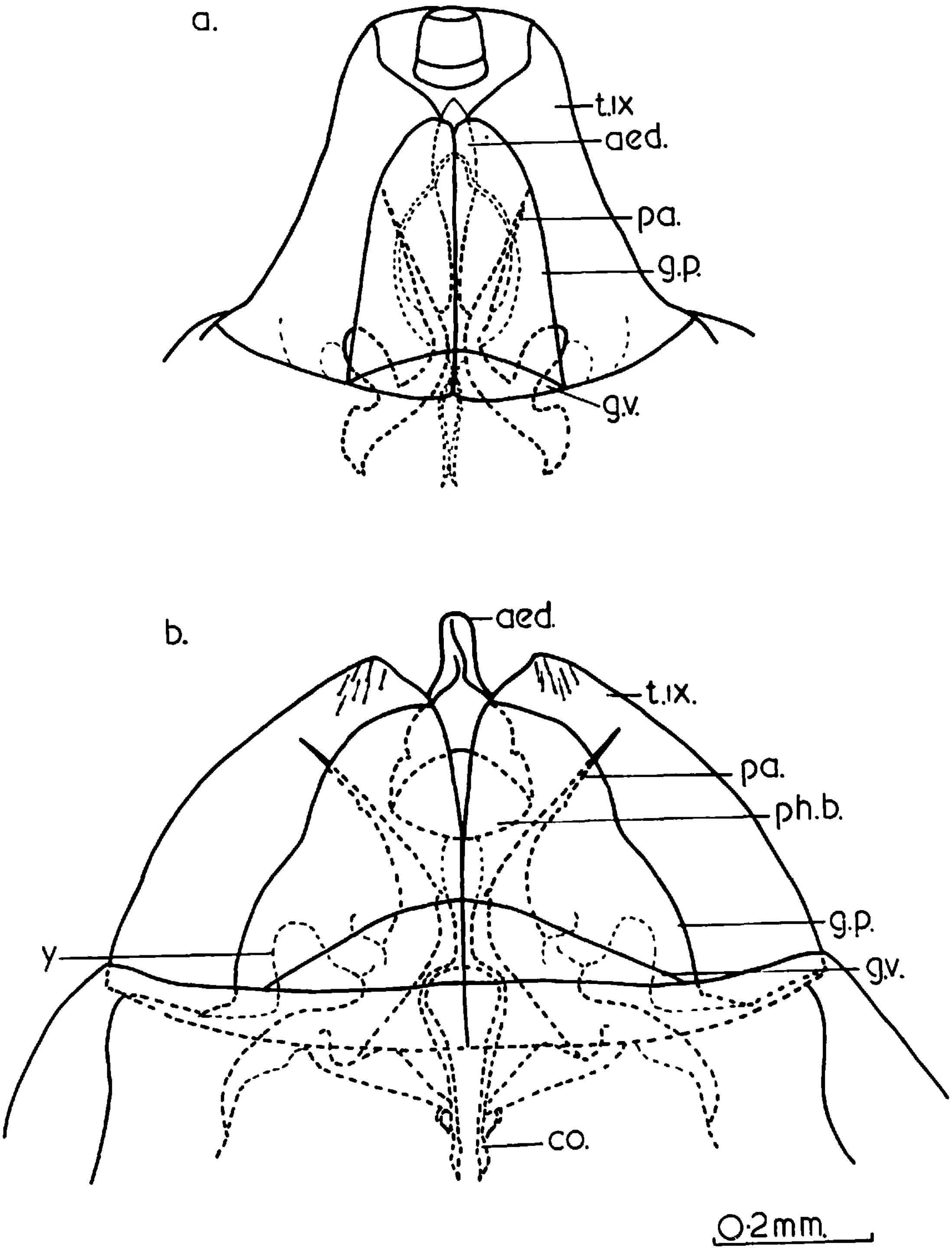
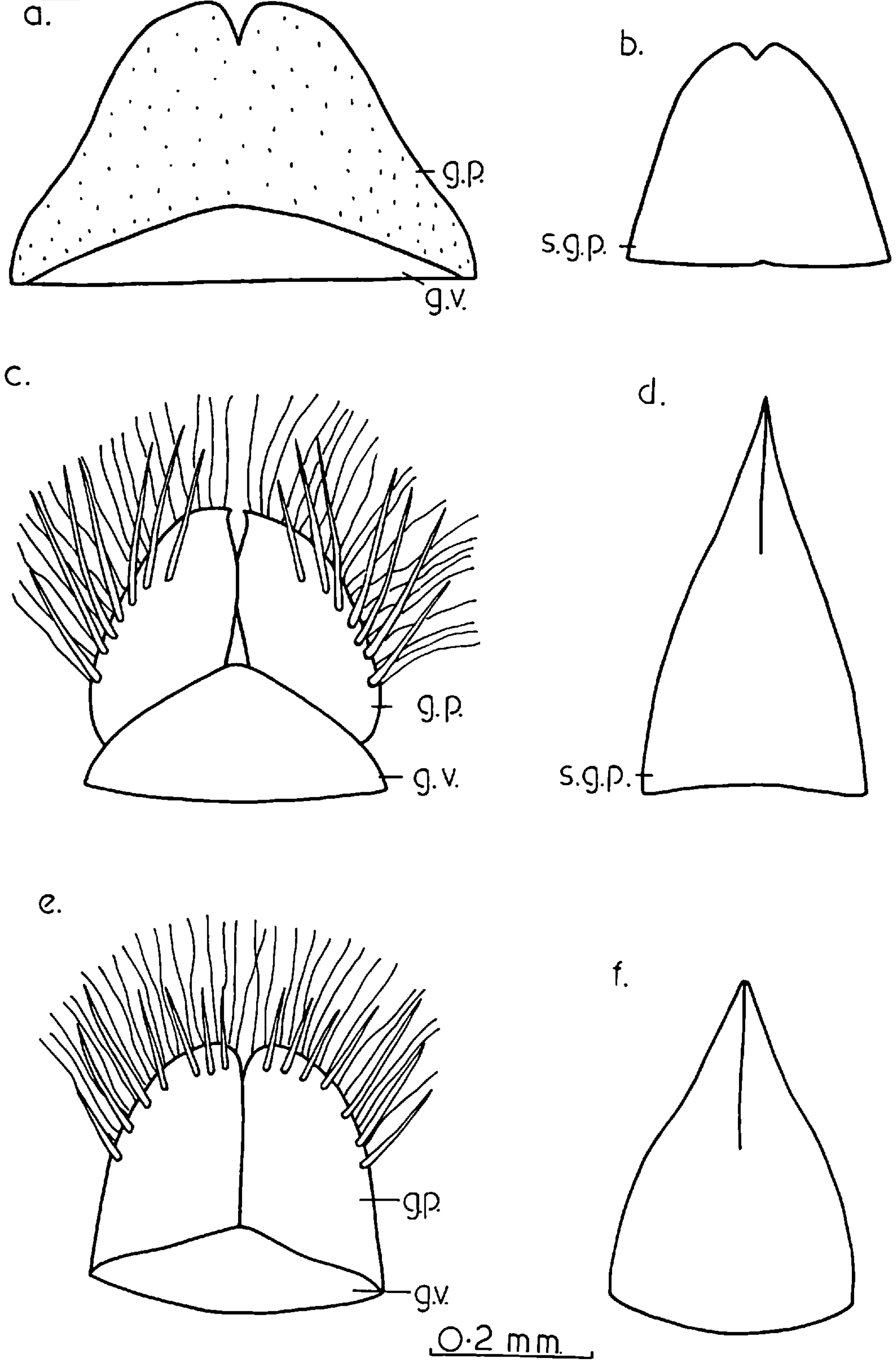


Fig. 30 Ventral View of Genital and Subgenital Plates

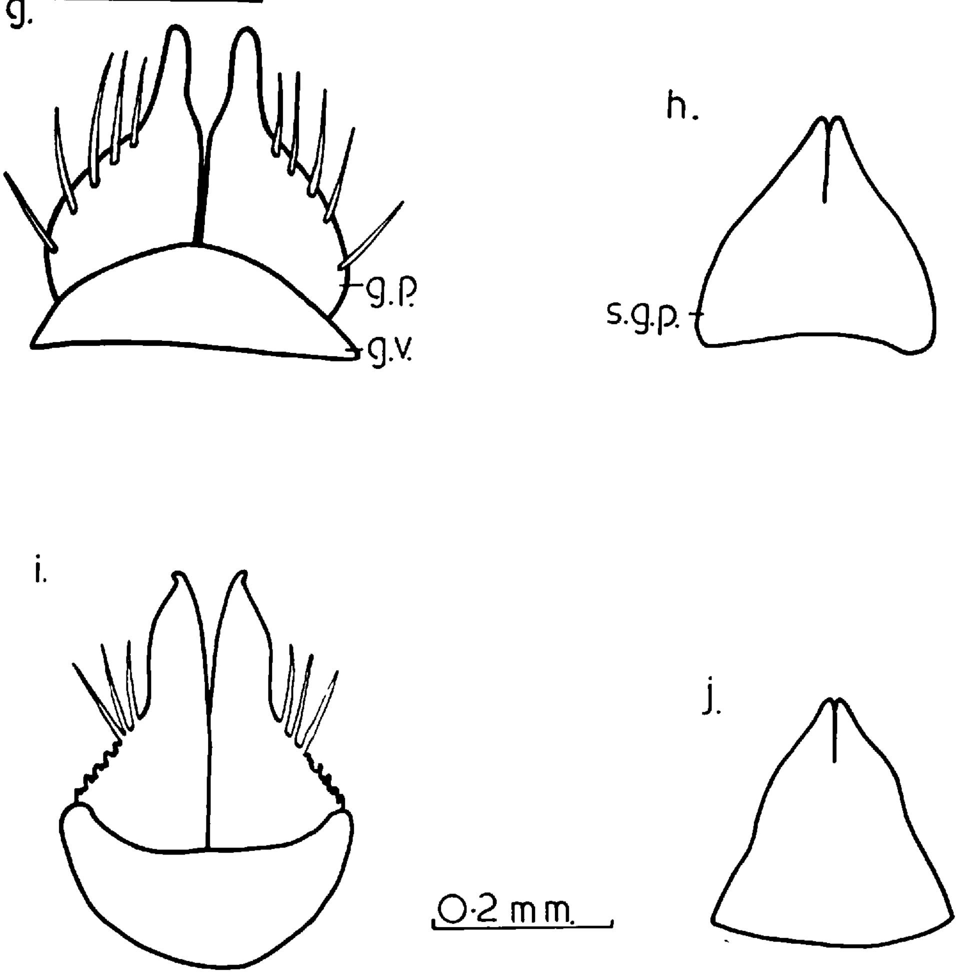
a. *D. stylata* (Adult)
b. *D. stylata* (Fifth Instar)
c. *C. persimilis* (Adult)
d. *C. persimilis* (Fifth Instar)
e. *M. parvicauda* (Adult)
f. *M. parvicauda* (Fifth Instar)
g. *B. punctata* (Adult)
h. *B. punctata* (Fifth Instar)
i. *Z. scutellaris* (Adult)
j. *Z. scutellaris* (Fifth Instar)

g.p.	genital plate
g.v.	genital valve
s.g.p.	subgenital plate

FIG 30



cont. FIG. 30



copulatory organ. It is a very simple structure in a pharate adult but is large and curved posteriorly in the adult forming the aedeagus (Fig. 29b). The phallobase is prominent and large, forming a basal structure supporting the aedeagus. The connective below the phallobase articulates with the parameres laterally. The parameres are in turn united to the genital plates, marked Y in Fig. 29a and b. The inner lining of the aedeagus is the endophallus which is the continuation of the ductus ejaculatorius, with the gonopore as its terminal opening. The shape of the aedeagus is one of the main characters used in the separation of species in the classifications of adult Cicadellidae. It is bifid, curved posteriorly and bent in *U. reticulata*, whereas it is bifid only at the tip in *C. persimilis*, and trifid in *M. parvicauda*. In *B. punctata* it is plain and curved, and is short and thick in *D. stylata* and broad and curved in *Z. scutellaris*.

(vi) EXTERNAL FEMALE GENITALIA

(a) Introduction and Review of Literature

The development of the external female genitalia in Cicadellidae was studied by Hackman (1922) in *C. hieroglyphica*.

Scudder (1957, 1961, 1964, 1971) has carried out a thorough study of the adult ovipositor which included in its description the species *Cicadella* (= *Tettigella*) *viridis* (Linnaeus).

Kramer (1950) while studying the Auchenorhynchous Homoptera, gave a description of the ovipositor of the Cicadellid *A. irronata*. Readio (1922) studied the ovipositors of Cicadellidae with an aim to classify them. He examined forty-eight genera and ninety species, but concluded that the characteristics of ovipositors are not separable at the subfamily level, although related genera may have similar ovipositors. Ali (1958) described the ovipositors of Cicadellidae in his work on the external morphology of some of the species.

(b) Definitions of the Accepted Morphological Terms and Terminology and Descriptions Used by Previous Authors

The rudiments of the external female genitalia, as in the male, are visible from the third instar onwards. Their development is traced from the immature stages to the adult, in this section.

The terminology used for describing the ovipositor is largely after Scudder (1961), and is as follows.

Terms	Definitions
First gonocoxa	The coxa of the abdominal segment VIII.
Second gonocoxa	The coxa of the abdominal segment IX.
First gonapophysis	The median process of the abdominal segment VIII.
Second gonapophysis	The median process of the abdominal segment IX.
Gonangulum	A sclerite attached ventrally to the base of the first gonapophysis articulating dorsally with the second gonocoxa and tergum IX.
Gonoplac	Posterior outgrowth of the coxa of the abdominal segment IX, forming part of or a sheath for the ovipositor.
Gonostyle	Stylus of the genital segment.

As the terminology used by authors previous to Scudder was variable, the following table of comparative terminology and descriptions was drawn up (Table 8).

Scudder (1961) studied the Cicadellid C. viridis, and this species was also examined in this thesis together with six others.

Table 8 Comparative Terminology and Descriptions of the External Female Genitalia used by Previous Authors

	Scudder	Snodgrass
First Gonocoxa	(1961) Is the coxa of abdominal segment VIII, and is an area of sclerotization which appears laterally to the base of the first gonapophysis and is connected to it.	(1963) The first valvifers are small plates which articulate on the anterior ends of the second valvifers. They are the supporting plates of the valvulae.
Second Gonocoxa	(1961) Is the coxa of the ninth abdominal segment and is smaller and more slender than the first.	-
Gonangulum	(1957) It is a sclerite which can be traced in all higher orders of insects, and is developed on the abdominal segments VIII and IX. (1961) This sclerite is prominent in species which use the gonapophysis for sawing, and is developed from the sternal region of the ninth segment and later articulates with the ninth tergum and the second gonocoxa. In Hemiptera it is a sclerite appearing on or between segments VIII and IX, and is triangular or inverted V-shaped. The ventral part of the anterior edge of this sclerite is attached to the anterior end of the first ramus and the ventral part of the posterior end articulates with the second gonocoxa, about a mid-point, forming a fulcrum. The whole posterior side of the sclerite is fused to the anterior ventral edge of tergum IX.	

Kramer	Smith
(1950) The first valvifers bear the first valvulae.	(1969) The first valvifers bear the first gonapophyses.
(1950) The second valvifers bear the second valvulae.	(1969) The second valvifers bear the second gonapophyses.
(1950) The ramal plate is broadly united with the anterolateral region of the tegal plate of the ninth segment.	-

Table 8 (continued)

	Scudder	Snodgrass
First gonapophysis	(1961) This is the median process of the eighth abdominal segment. The dorsal edge of the gonapophyses in *C. viridis* is heavily sclerotized forming the first ramus.	(1963) The prongs of the ovipositor are called the valvulae. The first valvulae slide back and forth on the second valvulae, by interlocking ridges and grooves. The valvulae arise from the anterior ventral angles of the respective valvifers.
Second gonapophysis	(1961) It is the median process of the ninth abdominal segment, the whole ventral edge of which is heavily sclerotized and forms the grooved second ramus in *C. viridis*. In Hemiptera the whole dorsal edge of both gonapophyses is united.	-
Gonoplac	(1961) In *C. viridis* it is attached to the second gonocoxa.	(1963) When present, the third valvula is usually a slender stylus-like process projecting from the rear ends of the second valvifers, or are flat lobes that ensheath the distal end of the ovipositor shaft.

Kramer	Smith
(1950) A thickened rod of sclerite along the ventral edge in the first valvulae. is called the outer ramus	(1969) The gonapophysis VIII bears a groove along the dorsal ramus, and a tongue along the ventral ramus. It is the mesal appendage borne by the gonocoxite VIII.
(1950) The second valvulae are membranous ventrally and bear strong teeth apically. The outer ramus runs along the ventral edge of the valvulae.	(1969) The dorsal rami of the ninth gonapophysis are fused to form a reinforcing bridge between the gonapophyses. It is borne by the gonocoxite IX.
(1950) The third valvulae sheaths the first and second valvulae.	(1969) Referred to as the valvula III, lateral valvula, sheath or gonoplac. It is the lateral appendage of the abdomen and retained in the ninth segment. It acts as a protective sensory sheath of the ovipositor.

The first valvifers referred to by Snodgrass (1963), Kramer (1950) and Smith (1969) are called the first gonocoxae by Scudder (1957), as they are coxal in origin and arise from the eighth segment. Scudder (1964) studied the development of the ovipositor in Gryllus veletis (Alexander and Bigelow) which is almost similar to that of the Cicadellidae examined here. The first gonocoxa arises from the eighth sternum, as explained by Scudder (1957), and gives off the first gonapophysis, which is the median process of the eighth abdominal segment. The first gonapophysis is referred to as the first valvula by Snodgrass (1963) and Kramer (1950).

The second gonocoxa according to Scudder (1957) is the coxa of the ninth segment and gives off the second gonapophysis. The origin of the second gonocoxa from the ninth segment is seen in the larval stages of Cicadellidae. Snodgrass (1963), Kramer (1950) and Smith (1969) refer to the second gonocoxa as the second valvifers, and the second gonapophysis as the second valvula.

The presence of the first and second rami in the first and second gonapophyses is mentioned by Snodgrass (1963), Scudder (1961), Kramer (1950) and Smith (1969). Both the rami are present in all the species studied. Scudder (1961) points out that in Hemiptera the dorsal edge of the second gonapophysis is usually united. This is so in all the species examined.

An important sclerite mentioned by Scudder (1957) is the gonangulum, which is variously modified and can be traced in all higher orders of insects possessing an ovipositor developed from the eighth and ninth abdominal segments. He says that in Hymenoptera, the gonangulum which was previously interpreted as the first gonocoxa, retains its triangular shape and attachments. In Orthopteroid orders the first gonocoxa and gonangulum form a single structure. In Odonata both structures remain distinct, and in Hemiptera the gonangulum is fused to tergum IX and the second gonocoxa articulates at its ventro-posterior angle. Scudder points out that it is well formed in insects which oviposit in plant tissues and hence use the saw-like motions of the gonapophyses. Previously Snodgrass (1935) considered that in Thysanura the gonangulum was part of the second gonocoxa whereas in some orders it was partly composed of a process of tergum IX and in other orders it was homologous with the first gonocoxa. Scudder (1961) explains that from descriptions by Snodgrass (1935), Quadri (1940), Gupta (1950) and his own work, the gonangulum is developed from the sternal region of the ninth segment, which later develops an articulation with the ninth tergum and the second gonocoxa. He adds that the Hemipteroid orders have a similar origin of the gonangulum. In his description of the ovipositor of C. viridis, Scudder (1961) says that the gonangulum is triangular or often inverted V-shaped. I have examined this species and have found that the gonangulum is an irregular five-sided structure (Fig. 34b).

The articulation of the gonangulum with the second gonocoxa forms a fulcrum which Scudder (1961) calls the "pivot p". This fulcrum is seen in all the species studied. At the fulcrum where the gonocoxa and gonangulum articulate, a group of short sharp spines with prominent bases are present on the second gonocoxa. These spines may be sensory or may act as a gripping mechanism when the second gonocoxa and gonangulum move. The whole posterior side of the gonangulum in all the species examined, is fused to the antero-ventral edge of the tergum IX, as was found by Scudder (1961).

The large spoon-shaped third valvula of Snodgrass (1963), Kramer (1950) and Smith (1969), is called the gonoplac by Scudder (1957). He thinks it is a better term than gonostyle, third valvula, third gonapophysis, dorsal or lateral valvula. Michener (1944) believed that the gonoplac is homologous with the second gonostylus of Thysanura, but Scudder (1971) says that developmental studies by Ramsay (1965), Rawat (1939), Ross (1966), d'Rozario (1942) and Snodgrass (1933) show that the gonoplacs arise as outgrowths of the second gonocoxa. In the Cicadellidae studied, it is attached to the second gonocoxa as explained by Scudder (1961).

(c) Development of the External Female Genitalia

As in the males, it was found that the development of the external female genitalia is similar in all the species examined. Hence a general account is presented and any peculiarities within the six species studied are mentioned.

The rudiments of the external female genitalia begin to appear from the third instar onwards, when a pair of outgrowths are visible on the posterior margin of the eighth and ninth sternites (Fig. 31a, 33a). These outgrowths are referred to as 1 and 2 in the diagrams on Figures 31 and 33.

In the fourth instar the ventral-most outgrowth on sternum VIII is longer and on sternum IX two pairs of outgrowths are visible, referred to as 2 and 3 in the diagrams b and c, in Figures 31 and 33. The third pair of outgrowths (3) are lateral in position, unlike the second pair.

In the fifth instar, the pair of outgrowths on sternum VIII is long and covers the second pair (2). Only the apices of the latter are visible. The third pair is broad and concave (Fig. 31c, 33c).

Eight sternites are visible ventrally on the abdomen of the female larvae, as in the male (Fig. 32a). However, in the female adults only seven sternites are visible (Fig. 32b). The seventh sternum in the female adult is very large, whereas the eighth is reduced and divided, being covered by the seventh.

Fig. 31 Ventral View of Last Two Abdominal Segments - U. reticulata (Female)

a. Third Instar

b. Fourth Instar

c. Fifth Instar

st.VIII.	eighth sternite
t.VIII.	eighth tergite
t.IX.	ninth tergite
1.	first pair of outgrowths (future gonapophyses)
2.	second pair of outgrowths (future gonapophyses)
3.	third pair of outgrowths (future gonoplacs)

FIG 31

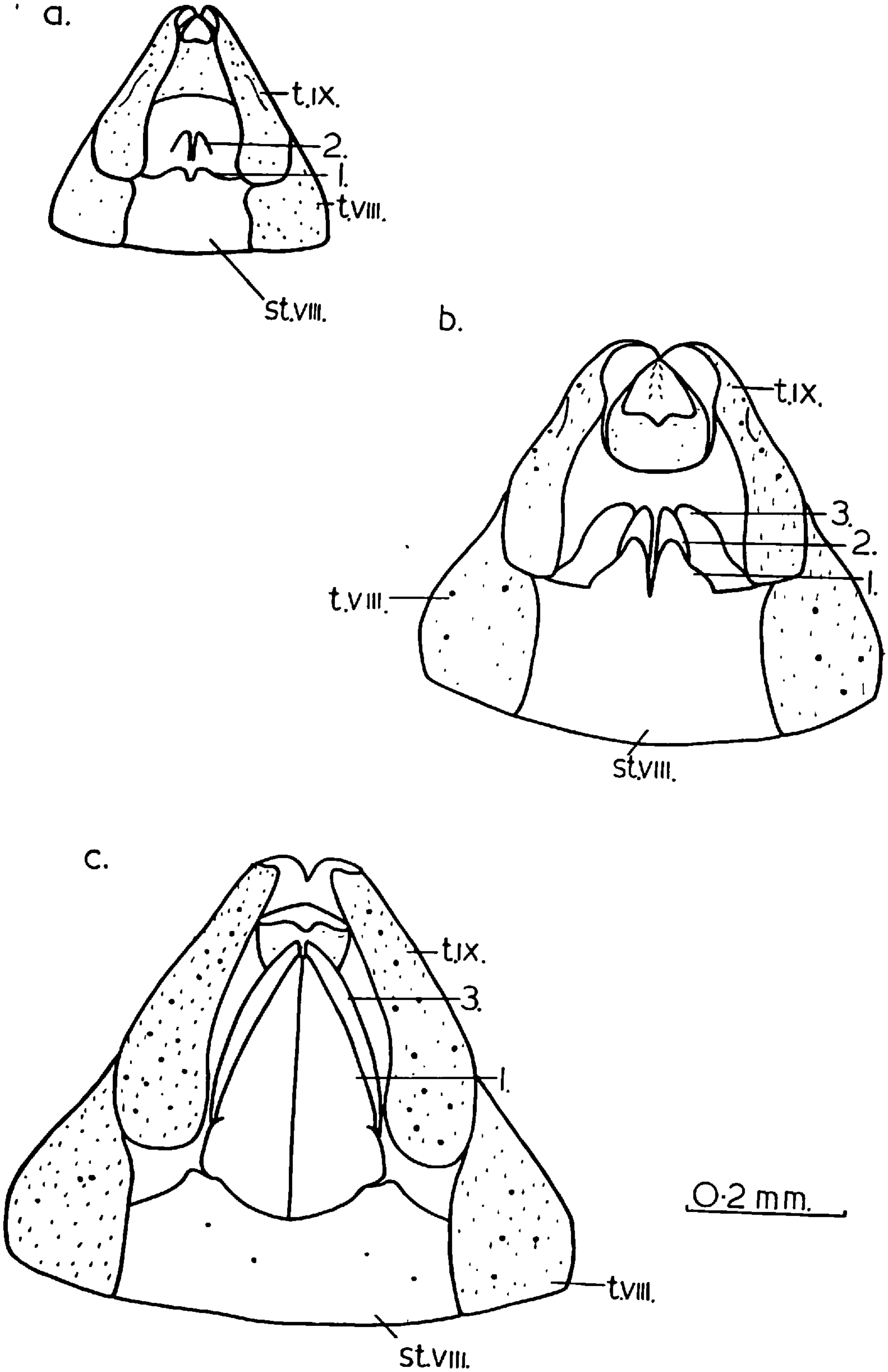

a.
t.IX.
2.
1.
t.VIII.
st.VIII.
b.
t.IX.
3.
2.
1.
t.VIII.
st.VIII.
c.
t.IX.
3.
1.
0·2 mm.
t.VIII.
st.VIII.

Fig. 32 Lateral View of Abdominal Segments -

U. reticulata (Female)

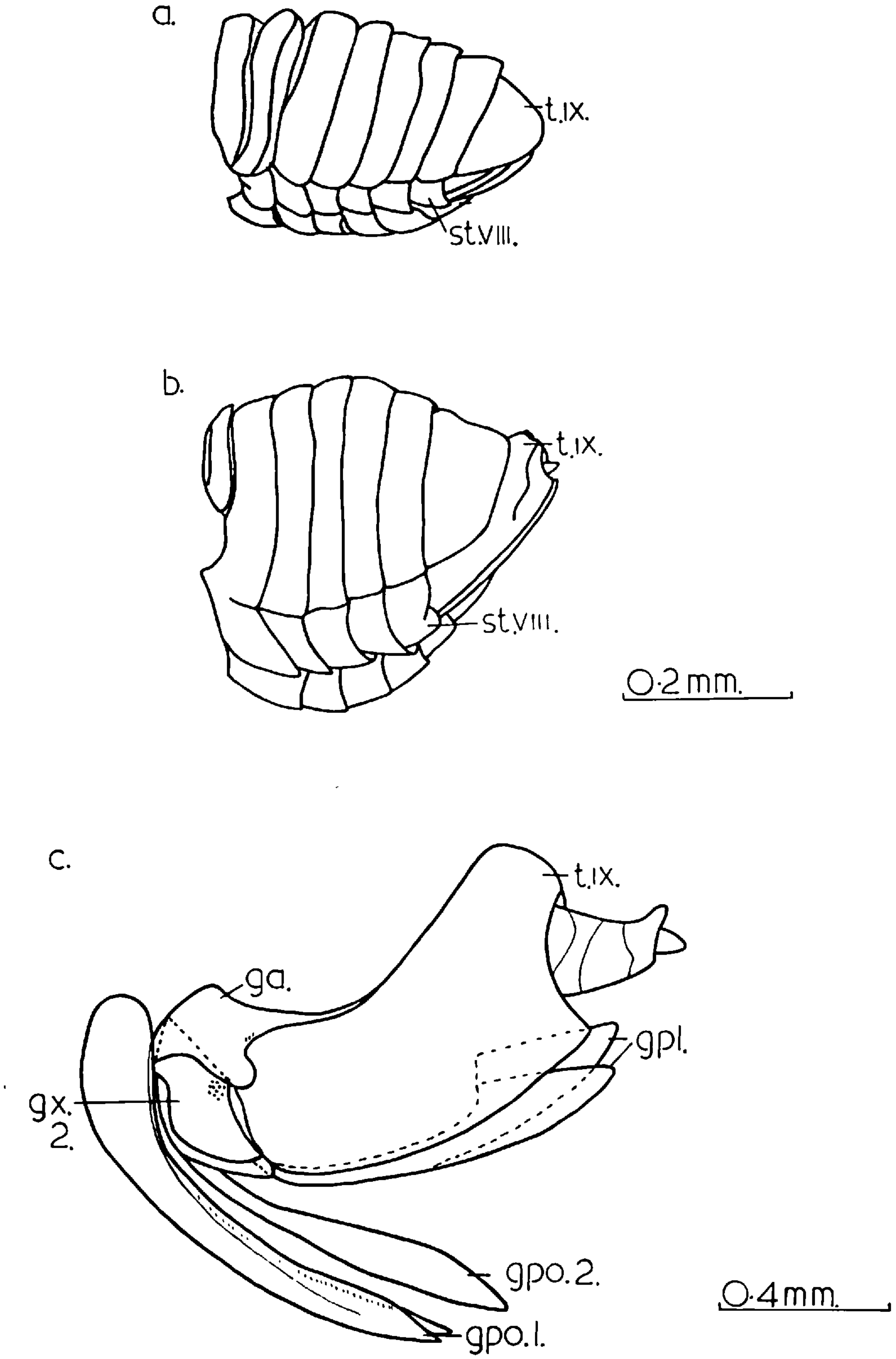
a. Fifth Instar

b. Adult

c. Adult Ovipositor

ga.	gonangulum
gpl.	gonoplac
gpo.1.	first gonapophysis
gpo.2.	second gonapophysis
gx.2.	second gonocoxa
st.VIII.	eighth sternite
t.IX.	ninth tergite

FIG 32



When the seventh sternum is lifted, the eighth sternum is seen lying next to the ventral margin of the eighth tergum and the dorsal margin of the first gonocoxa (Fig. 34a, 35).

The ventral-most pair of lobes in the larval stages, labelled 1 in Figures 31 and 33, develop into the first gonapophyses in the adult. The first gonocoxa is attached anteriorly, and the dorsal edge of the first gonapophyses forms a grooved first ramus. Similarly, the second pair of outgrowths labelled 2, develop into the second gonapophyses, with the second gonocoxa lying anteriorly. The dorsal edge of the second gonapophyses forms a tooth-like edge which is used for slitting the tissue for egg laying. The ventral edge of the second gonapophyses is heavily sclerotised forming the second ramus, and the gonapophyses on both sides unite dorsally along their length.

Lying on top of the second gonocoxa is a heavily sclerotised irregular five-sided sclerite called the gonangulum (Fig. 34b, 35). It is attached to the anterior end of the first ramus, the dorsal posterior region being fused to the ninth tergum and the ventral posterior end articulating with the second gonocoxa about its mid-point. A group of spines are present on the second gonocoxa around this region (Fig. 35 and Plate 1), and as mentioned before they may be sensory or may act as a gripping

Plate 3.

Group of spines on the pivot between the second gonocoxa and gonangulum of female (adult) genitalia - *C. viridis*. (X 390)

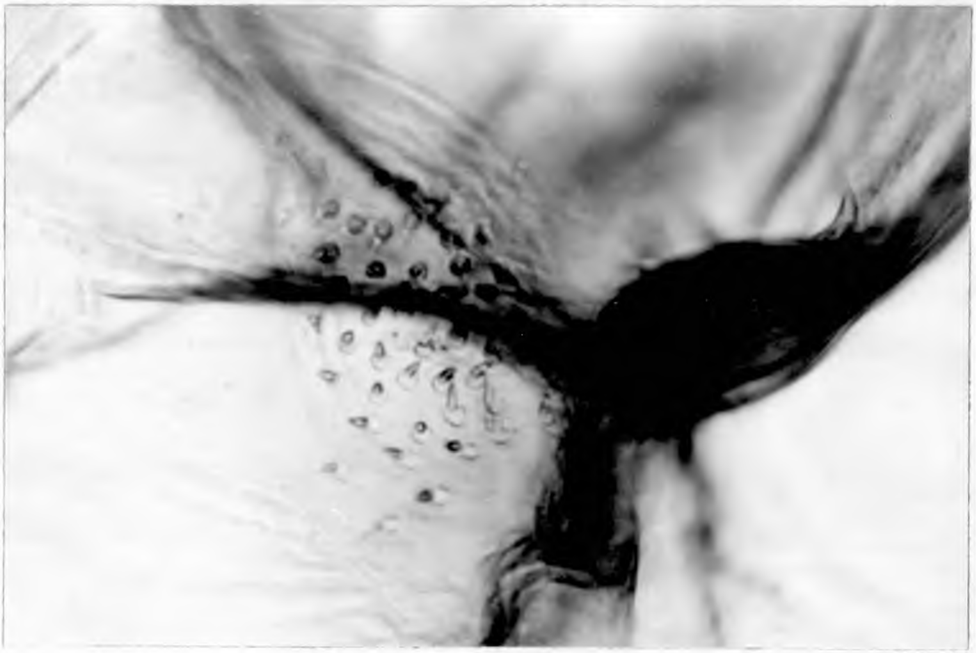


Fig. 33 Ventral View of Last Abdominal Segment - *M. parvicauda* (Female)

a. Third Instar

b. Fourth Instar

c. Fifth Instar

t.IX.	ninth tergite
1.	first pair of outgrowths (future gonapophyses)
2.	second pair of outgrowths (future gonapophyses)
3.	third pair of outgrowths (future gonoplacs)

FIG 33

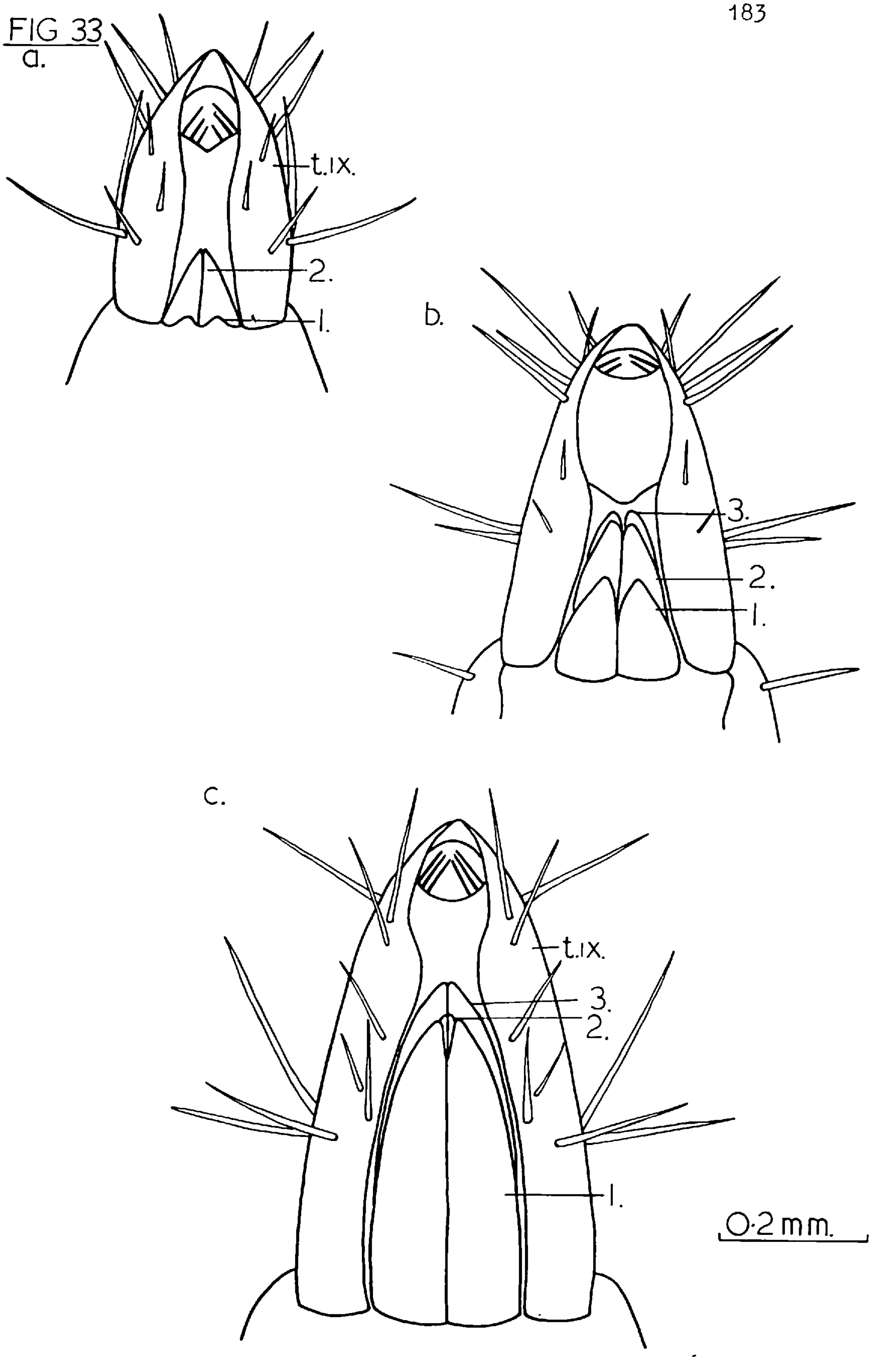


Fig. 34

a. Lateral View of Ovipositor with the Eighth Sternite - *C. viridis*

b. Lateral View of Ovipositor without the Eighth Sternite - *C. viridis*

ga.	gonangulum
gpl.	gonoplac
gpo.1.	first gonapophysis
gpo.2.	second gonapophysis
gx.1.	first gonocoxa
gx.2.	second gonocoxa
r.1.	first ramus
r.2.	second ramus
st.VIII.	eighth sternite
t.IX.	ninth tergite

FIG 34

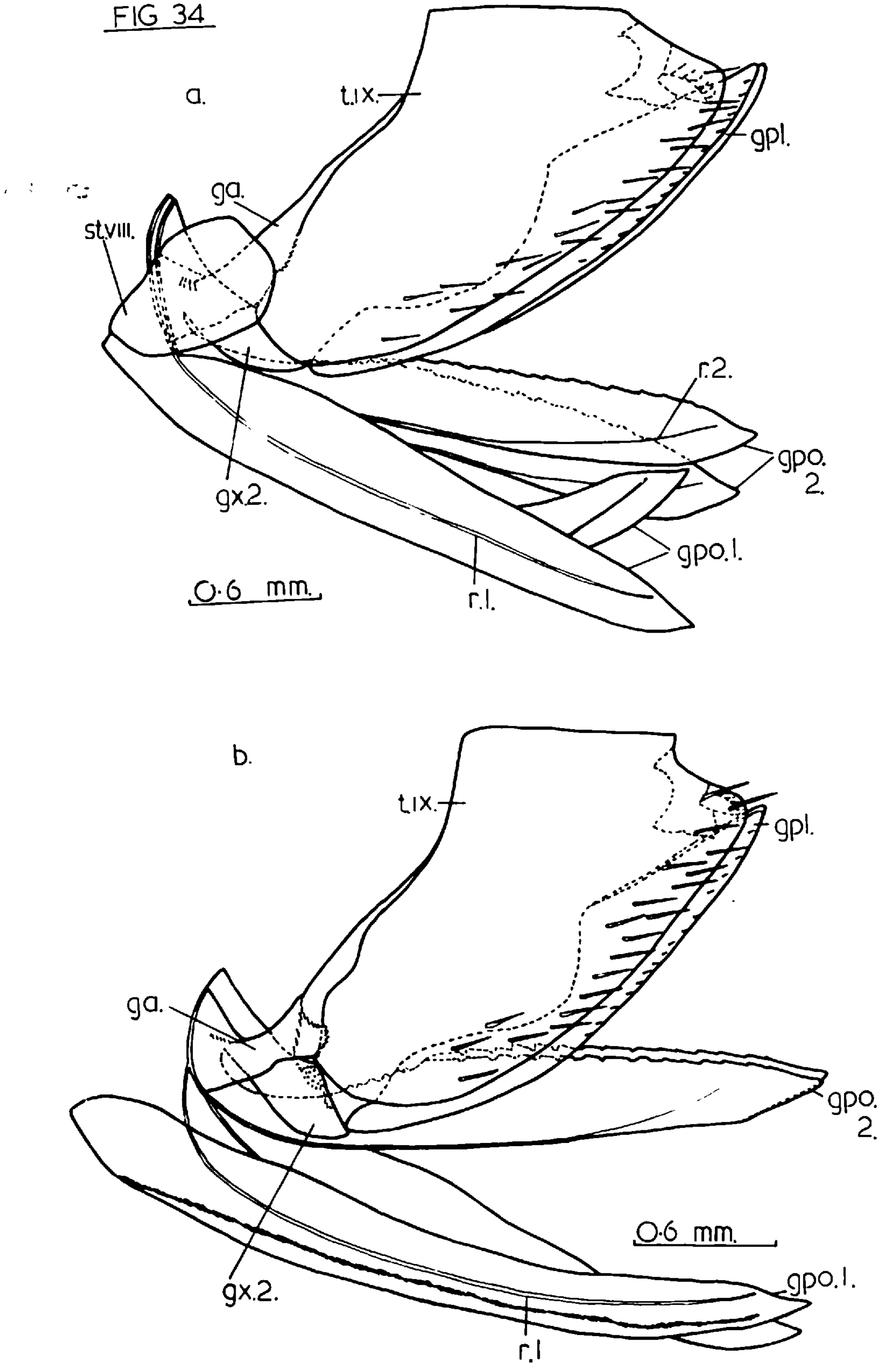
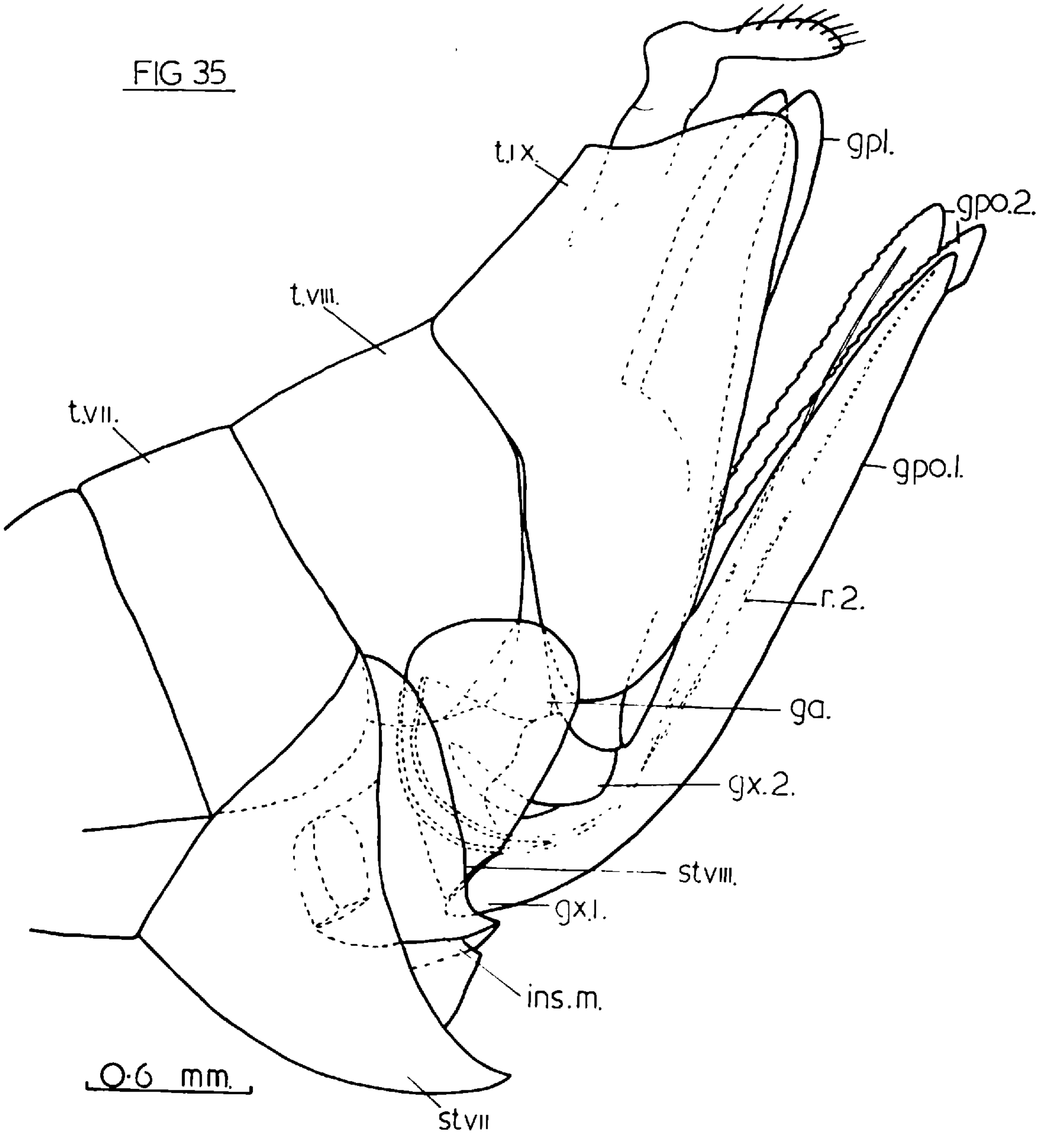

a.
t.IX.
ga.
st.VIII.
gpl.
r.2.
gpo. 2.
gx.2.
gpo.1.
r.1.
0·6 mm.
b.
t.IX.
gpl.
ga.
gpo. 2.
0·6 mm.
gx.2.
gpo.1.
r.1

Fig. 35 Lateral View of the Position of the Ovipositor during Copulation - *G. coccinea*

ga.	gonangulum
gpl.	gonoplac
gpo.1.	first gonapophysis
gpo.2.	second gonapophysis
gx.1.	first gonocoxa
gx.2.	second gonocoxa
ins.m.	intersegmental membrane
r.2.	second ramus
st.VI.	sixth sternite
st.VII.	seventh sternite
t.VI.	sixth tergite
t.VII.	seventh tergite
t.VIII.	eighth tergite
t.IX.	ninth tergite

FIG 35


t.IX.
gpl.
gpo.2.
t.VIII.
t.VII.
gpo.1.
r.2.
ga.
gx.2.
st.VIII.
gx.1.
ins.m.
0·6 mm.
st.VII

mechanism. Similar typesof spines are also scattered along the first and second gonapophyses which may also be sensory in function.

The posterior end of the second gonocoxa is attached to the gonoplac, the anterior limb being attached to the second ramus. The gonoplac is spoon-shaped and ensheaths the first and second gonapophyses when they are not in use.

During copulation, as seen in *Graphocephala coccinea* (Forster) (Fig. 35), the ninth tergum together with the gonoplac move dorsally through almost ninety degrees. The enlarged seventh sternum in *G. coccinea* opens out ventrally, enabling the aedeagus to transfer sperm. A feature of interest is the intersegmental membrane between segments VII and VIII which is partly sclerotized and forms an enclosure for the first gonocoxa, gonangulum and second gonocoxa (Fig. 35). The gonopore is seen to be located between segments VII and VIII in *G. coccinea*.

(vii) CHAETOTAXY

(a) Introduction

Prominent bristles which fall into a definite pattern are present on the dorsal surface of the abdomen, the development of which is described in this section. The species examined were *D. stylata*, *Errastunus ocellaris* (Fallén), *Graphocraerus ventralis* (Fallén), *Euscelis incisus* (Kirschbaum), *M. parvicauda*, *C. persimilis*, *Arthaldeus pascuellus* (Fallén), and *Macrosteles sexuotatus* (Fallén). All the species were examined from the first instar onwards, except *G. ventralis* where first instar larvae were not obtained. Some of the species such as *U. reticulata*, *B. punctata* and *Z. scutellaris*, examined in earlier sections for taxonomy and morphology have small scattered hairs or scattered, blunt cuticular outgrowths, hence they are not included in this section.

(b) Development of the Chaetotaxy Throughout the Larval Instars

The prominent bristles on the dorsal abdominal surface fall into a regular pattern in the various instars. The development of these bristles was traced from the first to the fifth instar. In the adult stage only bristles on abdominal segment IX remain, all the rest disappear.

Abdominal segments III to VIII were examined in the larval stages. Segment IX was excluded in the study, as the exact number and position of these numerous bristles in the later instars on this segment were difficult to record.

It was observed that the size and colour of the bristles in the different species varied, and this is summarized in Table 9.

Table 9

Species	Description of bristles
D. stylata	Sharp, stiff, small and darker brown than colouration of abdominal segment.
E. ocellaris	Long, flexible and of the same colour as abdomen. White patch present on abdominal segment at base of bristle.
A. pascuellus	Long, flexible and pale brown colour as that of the abdomen.
G. ventralis	Short, moderately pointed and pale brown colour unlike the abdomen which is bright green.
E. incisus	Medium size, flexible and pale brown; same colour as the abdomen.
M. parvicauda	Long, flexible and pale yellow colour like the abdomen in the first three instars; becomes pale brown in the last two instars.
C. persimilis	As above (M. parvicauda).
M. sexnotatus	Medium size, pointed and pale brown like the abdomen.

The number and pattern of the bristles on abdominal segments III to VIII in the first three instars of all the species examined, is summarized in Table 10. The number and pattern of the bristles in the fourth and fifth instars are identical to those of the third instar.

The following is the key to Table 10 which is a diagrammatic representation of theright half of the abdomen.

X	presence of one bristle
-	absence of bristle
I	Internal (position)
M	Middle (position)
E	External (position)

Blank space indicates species and instar not observed.

In all the first instars examined bristles are absent from the third to the sixth abdominal segments. On segment VII, six bristles are present in *D. stylata*, *E. ocellaris* and *A. pascuellus*; two in *E. incisus* and *M. sexnotatus*, and four in *C. persimilis* and *M. parvicauda*. On segment VIII all the species examined except *M. sexnotatus* have six bristles. On segment IX all the species have four bristles, and this was a good way of identifying the instar.

In the second instar all the species examined except

Table 10 Development of the Number and Pattern of Bristles on Abdominal Segments III to VIII in the Larval Stages of Eight Cicadellidae

	Abdominal Segment III			Abdominal Segment IV			Abdominal Segment V		
Instar	I	II	III	I	II	III	I	II	III
Position	I M E	I M E	I M E	I M E	I M E	I M E	I M E	I M E	I M E
Species									
D. stylata	- - -	x x -	x x -	- - -	x x -	x x -	- - -	x x -	x x -
E. ocellaris	- - -	x x -	x x -	- - -	x x -	x x -	- - -	x x -	x x -
A. pascuellus	- - -	x x -	x x -	- - -	x x -	x x -	- - -	x x -	x x -
G. ventralis		x x -	x x -		x x -	x x -		x x -	x x -
E. incisus	- - -	x x -	x x -	- - -	x x -	x x -	- - -	x x -	x x -
C. persimilis	- - -	x x -	x x -	- - -	x x -	x x -	- - -	x x -	x x -
M. parvicauda	- - -	x x -	x x -	- - -	x x -	x x -	- - -	x x -	x x -
M. sexnotatus	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -

Abdominal Segment VI									Abdominal Segment VII									Abdominal Segment VIII								
I			II			III			I			II			III			I			II			III		
I	M	E	I	M	E	I	M	E	I	M	E	I	M	E	I	M	E	I	M	E	I	M	E	I	M	E
-	-	-	x	x	-	x	x	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
-	-	-	x	x	-	x	x	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
-	-	-	x	x	-	x	x	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
			x	x	-	x	x	-				x	x	-	x	x	-				x	x	x	x	x	x
-	-	-	x	x	-	x	x	-	-	x	-	x	x	-	x	x	-	x	x	x	x	x	x	x	x	x
-	-	-	x	x	-	x	x	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
-	-	-	x	x	-	x	x	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-	x	-	-	x	x	-	x	x	-	x	x

M. sexuotatus have four bristles on segments III to VI. On segment VII, six bristles are present in all the species except G. ventralis, E. incisus and M. sexuotatus. G. ventralis and E. incisus have four and M. sexuotatus has two. On segment VIII all the species examined except M. sexuotatus have six bristles, the latter has four.

The third, fourth and fifth instars have the similar number and pattern of bristles, as instar two, hence the change in the number and pattern of bristles is found only between instar one and two in the Cicadellid larvae.

II. KEY TO THE SEPARATION OF THE LARVAL INSTARS OF CICADELLIDAE

The following is a key to the separation of the larval instars and sexes (from the third instar onwards) in Cicadellidae. A key to the fifth instar larvae of twenty-two British Cicadellidae is given in Section D.

Key to the Instars of some British Cicadellidae of Acid Grasslands

1. Metathoracic wing pads rudimentary. Mesothoracic
   ones not differentiated. Head elongated .... Instar I
   -Metathoracic wing pads pronounced (later stages) 2

2. Mesothoracic wing pads rudimentary and metathoracic ones
   extend to anterior margin of second abdominal
   segment .... Instar II
   -Meso and metathoracic wing pads clearly
   differentiated 3

3. Mesothoracic wing pads extend to anterior margin of
   first abdomonal segment .... Instar III
   Triangular plate-like structure on sternum IX
   .... Instar III male
   Paired outgrowths on sternum VIII and sternum IX
   .... Instar III female

-Mesothoracic wing pads extend to or beyond posterior margin of first abdominal segment. Metathoracic ones extend beyond half-way down the second abdominal segment 4

4. Mesothoracic wing pads extend to posterior margin of first abdominal segment. Metathoracic ones projecting slightly beyond mesothoracic ones .... Instar IV

Triangular plate-like structure on sternum IX larger. Small primary phallic rudiments visible behind plate-like structure .... Instar IV male

One pair of outgrowths on sternum VIII and two pairs on sternum IX. The third pair is lateral in position .... Instar IV female

-Mesothoracic wing pads extend beyond third abdominal segment 5

5. Mesothoracic wing pads extend to or beyond third abdominal segment. Metathoracic ones extend to or beyond the second abdominal segment ...... Instar V

Triangular plate-like structure very large and rudiments of the primary phallic organs behind this structure are prominent .... Instar V male

First pair of outgrowths on sternum VIII covers second
pair on sternum IX. The third pair is broad,
concave and lateral in position ... Instar V female

III. GENERAL DISCUSSION

The primary taxonomic subdivisions of winged insects are based on the differential development of wings which develop either externally or in the integument which are referred to as the Exopterygota and Endopterygota (Hinton & Mackerras (1967)). Wigglesworth (1964) says that in winged insects or the Pterygota the young resemble the Apterygota in that they are wingless. There is an enlargement of the wing pads in the successive moults and in the last moult the sexual reproductive organs assume their adult form and fully developed wings appear. Once these organs are developed they do not moult except in the Ephemeroptera or may flies which give rise to a subimago which moults to produce the true adult. However, Pesson (1959) says that the absence of wings is not the only character which distinguishes the nymph from the adults. Characters are either particular to the nymph and disappear, or some other character such as wing buds gradually increase at each moult. When they live in the same habitat the difference between the stages decreases at each moult. The general shape, colour, mouth parts, antennae and eyes are the same in the young and adult. He further says that there are as many larval forms distinguishable by size, colour or ornamentation, as there are growth stages. Any species has to be studied closely before these can be distinguished. This is true of the larval forms of the family Cicadellidae, which are Exopterygota and Hemimetabolous.

There are five larval instars in Cicadellidae although Severin (1949, 1950) recorded four and six instars in his study. The Cicadellid larvae and adult share the same habitat although there are exceptions to this, as for instance in the overwintering forms of B. punctata and larval and adult forms of Allygus mixtus (Fabricius), and Macustus grisescens (Zetterstedt) (see Le Quesne, 1969).

In the Cicadellidae examined there are certain morphological features present from the first instar onwards which are carried on to the adult stage, others are characteristic only of the larval or of the adult stage, and yet others are gradually differentiated in the successive instars. Exceptions to this may be found in parasitised individuals (see Appendix I).

1. Morphological Features present both in the Larval and the Adult Stages.

In the facial region of the head the frontogenal sulcus is present from the first instar onwards in all the subfamilies examined except Ulopinae, Jassinae, Macropsinae and Eupelicinae. During ecdysis in the larvae this sulcus also splits, although it is not a 'line of weakness'.

The clypeogenal and clypeoloral sulci that continue ventrally from the frontogenal sulcus are also present from the first instar onwards. Evans (1946) calls this whole sulcus the clypeal sulcus and Duporte (1957) the clypoogenal sulcus, but the terminology adopted in this thesis is after Parsons (1964).

The large median postclypeus and the triangular free anteclypeus are prominent from the first instar. The transclypeal sulcus which separates the post- and anteclypeus is present in all the subfamilies examined, except Macropsinae. The cibarial dilators arise beneath the postclypeus and the transclypeal markings from the first instar, indicate their presence, though Duporte (1957) thinks that as the dilators are purely functional they may be attached to the frons or vertex.

As Parsons (1964) points out, the lorogenal cleft is present from the first instar onwards. The continuation of the lorae beneath the anteclypeus confirms its hypopharyngeal origin suggested by Snodgrass (1938) and later agreed to by Butt (1943) and Parsons (1964).

The subgenal sulcus present only in _U. reticulata_ begins to appear in the first instar but is prominent only in the fifth instar and adult.

The position of the antennae, well below the posterior margin of the compound eyes, is constant in all the species from the first instar onwards except in *U. reticulata* where it is right on the posterior margin. The antennal ledge present only in *U. reticulata* and *Z. scutellaris* is prominent from the first instar onwards.

In the thoracic region, the prominent pleural sulcus which Snodgrass (1958) states is primarily constructed to support the leg ventrally and wing and wing muscles dorsally, is present together with an internal ridge (as pointed out by Matsuda, 1960), in the pro-, meso- and metathorax from the first instar onwards in all the species examined. In the larval stages it ends dorsally underneath the pronotum or wing pads but in the adult it provides the wing process. The pleuron is thus divided by the pleural sulcus into an anterior episternum and posterior epimeron from the first instar onwards.

The notopleural sulcus present only in *U. reticulata* is prominent from the first instar. It separates the pronotum from the epimeral region.

The basisternum is identified by the presence of pits and the central ridge, from the first instar onwards. Snodgrass (1927) found the term basisternum unsuitable, as the sclerite is not truly basal, but he did not suggest any new term.

The furcasternum bearing the sternal apodemes lies posterior to the basisternum from the first instar onwards in all the species examined.

Although the tergum in the larvae is not differentiated, the phragma is present from the first instar onwards in all the species examined.

The legs were of limited taxonomic value as Evans (1947) said, but the prominent spines on the hind tibia of the larva and adult are useful in the separation of this family from other Homoptera. The structure of the legs in the larvae and adults is similar, except that there are two tarsal segments in the larval stages and three in the adult.

2. Morphological Features present only in the Larval Stage

The ecdysial cleavage line or the line of weakness through which the newly moulted larvae appear, is present only in the larval stages in Cicadellidae. Snodgrass (1947) says that adults of Dermaptera and Orthoptera retain the cleavage line; it is postulated that ancestral adults periodically underwent ecdysis as do the present day Thysanura and Collembola and most other anthropods. Among the winged insects only adult Ephemeroptera shed their cuticle and this is at a very early stage. In Cicadellidae, as the cleavage line has no internal ridges its stem and arms will not be referred to as the coronal and frontal sulci, as was done by Duporte (1957). The whole line of weakness is called the ecdysial cleavage line.

A pair of cuticular outgrowths are present on the antennal ledge in the larval instars of *Z. scutellaris*.

The episternal regions of the meso- and metathorax are continuous with the basisternum in all the Cicadellid larvae as stated by Snodgrass (1927).

On the dorsal abdominal surface of some Cicadellid larvae there are prominent bristles which fall into a definite pattern. The number and pattern of the bristles change between the first and second instars only. The third, fourth and fifth instars have identical numbers and patterns of bristles as the second instar. However in the adult stage, the bristles are absent on segments three to eight.

3. Morphological Features present only in the Adult Stage

The coronal sulcus extends half way up the vertex in all the adults examined, except in *U. reticulata*. It has internal ridges and, as was mentioned previously, the stem of the ecdysial cleavage line in the larvae is replaced by the coronal sulcus in the adult. Evans (1946) mentions that the coronal sulcus diverges into the postfrontal sulcus but this latter sulcus is absent in Cicadellidae. Hence, the arms of the cleavage line are not represented by a sulcus in the adult.

The epistomal fold which is also called the frontoclypeal sulcus according to Parsons (1964) is absent in the Hemiptera. However this sulcus is present in the adults of U. reticulata and it partially separates the frons from the clypeus.

A pair of crescent shaped sulci are present on the border of the crown and face in Z. scutellaris adults and a pair of dorsal tentorial pits are present in the adults of U. reticulata.

The dorsal surface of the meso- and metathorax of the adult have special sclerites developed to aid flight. The tergum is divided into an anterior prescutum, a middle scutum and a posterior scutellum.

The phragma in the adult is large and varies in shape from species to species. An interesting observation was that in the bractypterous adults of D. stylata, where the hind wings are very much smaller than the fore wings, the phragma is tucked horizontally underneath the scutellum, whereas in the macropterous adults of this species it is large, bifid and hangs in the cavity. The latter arrangement is also found in all the macropterous adults of C. persimilis, M. parvicauda, B. punctata, and Z. scutellaris. In U. reticulata adults where the hind wings are lost the phragma is very small. Both U. reticulata and the brachypterous forms of D. stylata do not fly. In Cicadellidae the second phragma is highly developed.

Snodgrass (1927, 1958) says that when the fore wings are highly developed, the phragma is found in the mesotergum, and becomes partially or wholly detached from the metatergum. Whether greater development of the second phragma is associated with the greater activity of the fore wings needs experimental investigation.

The meso-episternum lying anterior to the pleural sulcus is divided by the episternal sulcus, in all the adults examined, except *Z. scutellaris*. This undivided episternum is a feature of the subfamily Typhlocybinae. The episternal sulcus divides the episternum into a dorsal anepisternum and ventral katepisternum.

In the adults examined the meso-epimeron is also divided by a deep groove into a katepimeron and anepimeron. The chitinization of the epimeron is secondary as was observed by Grandi (1950) in his study of the development of Plecoptera.

Another feature of the Cicadellid adults is the furcal sulcus which separates the basisternum partially or completely from the katepisternum.

Although the sternal apodemes are present in the larvae, they are small, whereas in the adults they are large, as in *Z. scutellaris*, where the apodemes are peculiarly shaped with two processes and a median finger-like projection. The shape of the apodemes varies in the different forms and species of the adult. In the brachypterous adults of *D. stylata* it is small whereas in the macropterous forms of this species it is enlarged. The pleural and sternal apodemes are joined by muscle fibres forming part of the wing-bearing segment.

In the adults the meta-episternum and sternum III are separated by a sulcus. Further three tarsal segments are present in the legs of the adults whereas the larvae have only two.

4. Morphological Features present in the Larvae which assume their Fully Developed Form in the Adult

a. Wings.

Wings are represented by pads in the larval instars of Cicadellidae and the length of the wing pads increases from instar to instar. This provides a useful guide for the identification of a particular instar.

b. External Genitalia.

The size, shape and length of the rudiments of the external genitalia in the larval stages from the third instar onwards indicates the sex and the particular stage of the larvae. The rudiments assume their fully developed form in the adult.

The subgenital plate in the larval stages of the male differentiates into the genital valve and the paired genital plates in the adult, the primary phallic rudiments dividing into a median aedeagus and lateral parameres.

The first, second and third pair of outgrowths on sternum VIII and IX in the females form the first and second gonapophyses and gonoplacs of the adult. The gonocoxae and gonangulum are formed in the adult stage, the first gonocoxa being derived from the eighth sternum and the second gonocoxa and gonangulum from the ninth sternum.

SECTION B

Multivariate Analysis of Growth in Five Species of Cicadellidae

I. Introduction

Growth in size and change in form during the development of insects have been studied quantitatively by many authors. Dyar (1890) for example, proposed a well-known formula (later extended by Richards (1949)). On a larger scale the study of allometric growth, initiated by Huxley (1932), has been applied to the development of many structures in different insects (e.g. Gould, 1966). These analyses were limited to changes in one or two structures only. On the other hand, modern methods of multivariate analysis (e.g. Hope, 1968) are capable of expressing quantitatively the development of insects defined by measurements on any practicable number of characters. Of such methods principal component analysis, factor analysis, and multiple discriminant analysis (canonical analysis) seem to offer considerable advantages, though they have as yet hardly been exploited. Blackith, Davies & Moy (1963) applied multiple discriminant analysis to the development of _Dysdercus fasciatus_ (Sign.), using sixteen characters in all instars and in both sexes of the last three. Blackith & Blackith (1969) used canonical analysis on twelve characters made over 1450 adults and over 100 male and female six-instar and female seven-instar nymphs of the Morabine grasshoppers. The lengths of the subgenital plates of the adult males and the ovariole numbers of the adult females were analysed separately from the other ten characters. Brown (1969) also carried out a principal component analysis and a multiple discriminant analysis on seventy-four characters in both sexes and all instars in two species of Ectobius.

It seemed a useful enterprise to extend this kind of analysis to a group of species which belong to the same family and hence are sufficiently close to allow common patterns of growth and development to be perceived, but sufficiently distinct to allow comparative treatment as they belong to different subfamilies or tribes. The availability of several species of Cicadellidae suggested they could form the basis of such an analysis. It is, of course, offered as a tentative attempt at the biological interpretation of a relatively sophisticated method of multivariate statistical analysis. How far such interpretations will eventually prove acceptable must depend on the success with which analyses of this kind can be made on a much wider range of animals.

In this analysis of growth there are six developmental stages; the first two instars could not be sexed, the last four were sexed and two types of adult forms in one species were also included; hence there are fifty-two developmental stages in all, with seven measured structural features.

When any two developmental stages of this sort are compared, the overall difference between them is best expressed by calculation of the discriminant function (Fisher, 1938), which in effect is a vector expressing the contrast of the growth patterns. The closely related statistic, D^2 or generalised distance (Mahalanobis, 1936), expressed the extent to which the discriminant function separates the two stages in one or two dimensions depending on the number of characters and stages involved in the analysis. When more than two stages are involved the discriminant functions that link the stages have vector properties and may differ in direction, thus revealing the distinctions between dissimilar changes in shape (Blackith, 1960). The generalised distance can be used as a measure of the extent to which the stages differ from each other. The construction of a system of discriminant axes, on which the growth stages are displayed in terms of canonical variates, is an extension of the method of generalised distances and is described by Rao (1952), Seal (1964), Hope (1968) and others. The mean position of each stage can then be located in relation to this frame of reference (Blackith, 1960).

It is best to assess the differences in growth patterns in terms of vectors associated with the largest roots, of the matrix $W^{-1}B$ where W^{-1} is the inverse of the pooled within-groups dispersion matrix, and B is the between-groups dispersion matrix. In effect, therefore, the latent roots provide one with a set of discriminant weights (each associated with one of the characters measured). The canonical variates therefore form a set of discriminant functions of the pattern $D_1 = a_1x_1 + a_2x_2 + a_3x_3 \dots + a_px_p$ where D_1 etc. are the canonical variates (or multiple discriminant scores) for each growth stage, a_1, a_2 etc. are the weights provided by each element of the corresponding latent vector, and x_1, x_2 etc. are the original measurements on the first, second, etc. of the p structures being studied. One might hope that each vector can then be given a biological meaning (Blackith, 1960). The relative size of each latent root indicates the percentage of the total discriminant power accounted with each axis. The discriminant scores on any two or more axes, for the various developmental stage of both sexes in each species will, when plotted, indicate the extent and nature of greatest possible discrimination between the stages, subject to the data conforming to certain basic assumptions. These are briefly referred to at a later point in the discussion.

II. Materials and Methods

Five species, namely *U. reticulata*, *M. parvicauda*, *C. persimilis*, *E. ocellaris* and *B. punctata*, were used in the multiple discriminant analysis of growth. The first three instars were obtained from cultures, the rearing details of which are given in the general section on material and methods. The last three developmental stages were collected from the field. The specimens were preserved in 70% alcohol and measurements were made with a micrometer eye piece fitted to a compound microscope. The means and standard deviations of the characters measured are given in Appendix II, where all dimensions are in mm. All lengths were recorded in the mid-line and breadths were the maximum values.

The first two instars cannot be sexed by external examination but the measurements of the later instars were recorded for the sexes separately. The two adult forms named as Form I and Form II of *B. punctata* are both macropterous forms which show differences in the abdominal length. The abdomen in Form I is about two-thirds the length of the wings, and the abdomen in Form II is as long as the wings. As this was observed later on in this study no experimental work was done to prove the taxonomic validity of the forms.

But in this analysis of growth the two forms were measured separately. The number of replicates of each species, instar and sex could not be kept constant, as some of the instars were difficult to obtain. This however is not important as the statistical analysis does not require equal numbers of replicates. The following table gives the details of the material measured.

Table 11

Number of Replicates for Each Species, Instar and Sex

Species	Instar and Sex	Replicates
U. reticulata	1st Instar Unsexed	12
	2nd Instar Unsexed	12
	3rd Instar Male	12
	3rd Instar Female	7
	4th Instar Male	9
	4th Instar Female	12
	5th Instar Male	12
	5th Instar Female	12
	Adult Male	4
	Adult Female	12
M. parvicauda	1st Instar Unsexed	12
	2nd Instar Unsexed	12
	3rd Instar Male	5
	3rd Instar Female	12
	4th Instar Male	12
	4th Instar Female	12
	5th Instar Male	12
	5th Instar Female	12
	Adult Male	5
	Adult Female	5

Species	Instar and Sex	Replicates
C. persimilis	1st Instar Unsexed	12
	2nd Instar Unsexed	10
	3rd Instar Male	12
	3rd Instar Female	11
	4th Instar Male	12
	4th Instar Female	12
	5th Instar Male	12
	5th Instar Female	12
	Adult Male	11
	Adult Female	12
E. ocellaris	1st Instar Unsexed	10
	2nd Instar Unsexed	10
	3rd Instar Male	12
	3rd Instar Female	12
	4th Instar Male	12
	4th Instar Female	12
	5th Instar Male	12
	5th Instar Female	12
	Adult Male	10
	Adult Female	10
B. punctata	1st Instar Unsexed	12
	2nd Instar Unsexed	12
	3rd Instar Male	12
	3rd Instar Female	12
	4th Instar Male	12
	4th Instar Female	12
	5th Instar Male	12
	5th Instar Female	12
	Adult Male (Form I)	5
	Adult Female (Form I)	6
	Adult Male (Form II)	7
	Adult Female (Form II)	5

The characters measured are listed below and the reference number assigned to each character remains unchanged throughout the analysis.

1. Head width (including eyes)
2. Head length
3. Pronotal width
4. Pronotal length
5. Hind tibia length
6. Hind femur length
7. Total body length

The Fortran IV Computer Program which carried out the multiple discriminant analysis was written by Mr. R.G. Davies and was executed on the CDC 6600 computer of the University of London Computer Centre. For reasons indicated later the analysis was carried out first on the untransformed primary data and then repeated after a logarithmic transformation of all measurements.

III. Multiple Discriminant Analysis

(i) Untransformed Data

The seven latent roots and percentage discrimination are listed in the following table.

The seven latent roots account for 100% of the discrimination as must be the case on theoretical grounds. A large proportion of it (over 90%) is attributable to the first three, especially the first. In a similar analysis

Table 12 Latent Roots and Percentage Discrimination - Untransformed Data

Latent Roots		Percentage Discrimination
I	216.722	71.917
II	61.651	20.458
III	17.284	5.736
IV	2.830	0.939
V	1.977	0.656
VI	0.697	0.231
VII	0.189	0.063

of the development of Dysdercus fasciatus (Blackith, Davies & Moy (1963)) the second and third canonical variates accounted for relatively larger proportions of the total variance than were noted here, and in the analysis of development of three species of Ectobius (Brown, 1969) a relatively larger proportion of the total variance was attributable to the second latent root.

In the present analysis, as the first three vectors or canonical variates account for 98.12% of the total discriminate power, they seem capable of providing a virtually complete biological interpretation. The other vectors are ignored as they account for very small proportions of the total discrimination. Brown took the first five vectors, which accounted for 95% and Blackith, Davies & Moy took the first three which accounted for 98% of the total variance.

The elements of the latent vectors are given in the following table. These have been normalised so that the sum of the squared elements is equal to unity.

Table 13 Elements of Latent Vectors - Untransformed Data

Variable	Canonical Variate		
	I	II	III
Head width (1)	0.320	0.746	0.146
Head length (2)	-0.187	0.117	0.770
Pronotal width (3)	0.255	0.445	-0.159
Pronotal length (4)	0.643	0.032	-0.597
Hind tibia length (5)	0.478	-0.413	0.045
Hind femur length (6)	0.390	-0.244	0.052
Total body length (7)	0.058	0.055	-0.001

By examination of these vector elements it is possible to indicate the variables making the largest and smallest positive and negative contributions to each canonical axis

Along the first canonical axis, pronotal length has the largest positive weight (0.643), and total body length has the smallest positive weight (0.058), hardly differing from a zero contribution.

Along the second canonical axis, head width has the largest positive weight and total body length again has the smallest positive weight. Hind tibial length has the largest negative weight (-0.413).

Along the third canonical axis, head length has the largest positive weight (0.770) and contrasts strongly with pronotal length which has the largest negative weight (-0.597). Total body length once more has the smallest absolute weight (-0.001).

Characters with large positive or negative weights are of interest for their importance in separating sexes, growth-stages or species. Blackith, Davies & Moy (1963) draw attention to three types of variables:

(a) A single variable associated mainly with one axis and contributing only a little to the others. In the present analysis head width, head length and to a much lesser extent pronotal length behave in this way.

(b) Two or more variables associated similarly and to an appreciable extent with a single axis and referred to as symbatic variables by Blackith & Albrecht (1959). (Pronotal length, hind tibia length and hind femur length along canonical variate I or head width and pronotal width on II).

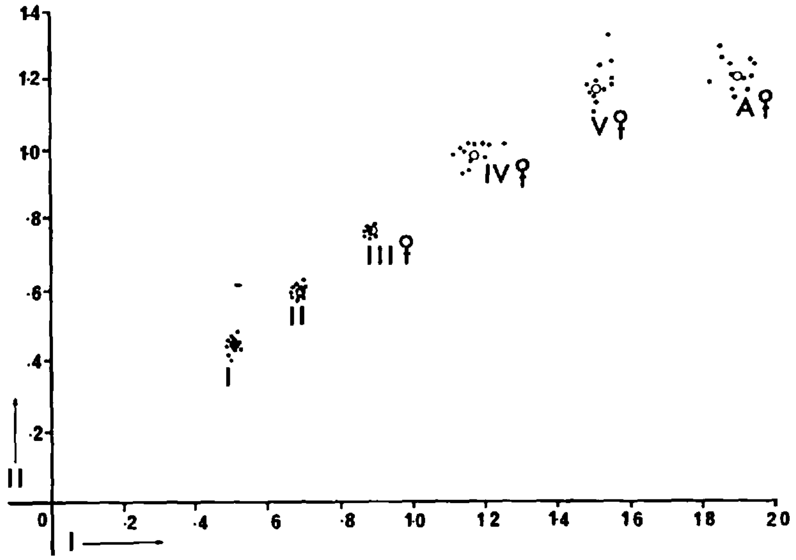
(c) A single variable associated with several axes to a somewhat similar degree. (Head width is the only one approaching this condition).

The significance of each discriminant axis may be assessed through X^2 tests (Hope, 1968), the results of which are given in Table 14. The first six latent roots are all significant.

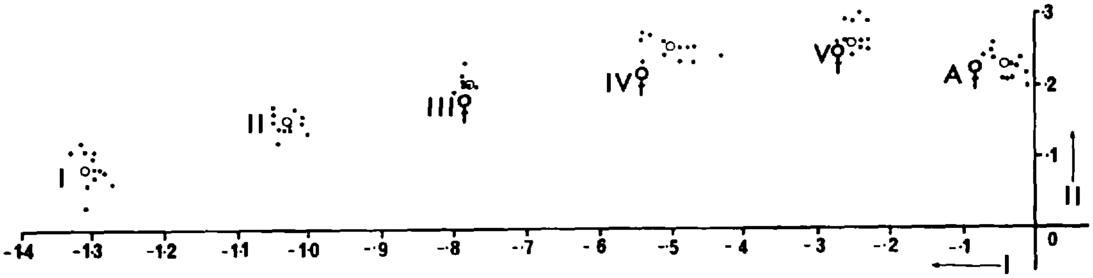
Table 14 Significance of Latent Roots - Untransformed Data

	Latent Roots						
	I	II	III	IV	V	VI	VII
X^2	2801.965	2153.610	1512.593	699.000	567.904	275.173	90.314
D.F.	57	55	53	51	49	47	45
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

The discriminant scores (canonical variates) characterise the particular stage, sex and species from which the original measurements were taken. The values assigned to each individual are clustered around the centroid, i.e. the



a. Untransformed Data



b. Transformed Data

FIG 36 Discriminant Scores and Group Centroids for U. reticulata.

average score for each stage taken from a group of individuals. An example of the close cluster around the centroid is given in the following Table 15 and shown in Fig. 36a; it indicates the relatively small variation between individual specimens.

Table 15 Discriminant Scores and Centroids on First Three Canonical Axes for *U. reticulata* 1st Instar Unsexed - Untransformed Data (12 individuals)

Individual	Canonical Variate		
	I	II	III
1	0.515	0.447	0.162
2	0.533	0.436	0.134
3	0.527	0.448	0.129
4	0.507	0.418	0.140
5	0.500	0.400	0.142
6	0.518	0.435	0.137
7	0.498	0.444	0.114
8	0.499	0.460	0.148
9	0.517	0.462	0.133
10	0.515	0.448	0.158
11	0.521	0.458	0.136
12	0.508	0.468	0.148
First Instar Centroid	0.513	0.444	0.140

The group centroids for all five species, all stages and both sexes are given in Table 16.

The group centroids for only the first three canonical variates are reported as they account for all the

Table 16 Canonical Variates (Group Centroids) - Untransformed Data. First Three Canonical Axes Only

Species, Stage and Instar	Canonical Variate		
	I	II	III
U. reticulata			
1st Instar Unsexed	0.513	0.444	0.140
2nd Instar Unsexed	0.692	0.591	0.168
3rd Instar Male	0.870	0.740	0.193
3rd Instar Female	0.893	0.766	0.204
4th Instar Male	1.164	0.905	0.211
4th Instar Female	1.193	0.979	0.223
5th Instar Male	1.469	.116	0.215
5th Instar Female	1.534	1.165	0.248
Adult Male	1.812	1.146	0.063
Adult Female	1.912	1.194	0.110
M. parvicauda			
1st Instar Unsexed	0.690	0.194	0.196
2nd Instar Unsexed	0.933	0.246	0.192
3rd Instar Male	1.234	0.302	0.210
3rd Instar Female	1.277	0.280	0.221
4th Instar Male	1.637	0.362	0.254
4th Instar Female	..740	0.355	0.268
5th Instar Male	2.059	0.393	0.246
5th Instar Female	2.208	0.436	0.264
Adult Male	2.442	0.318	0.124
Adult Female	2.615	0.340	0.149
C. persimilis			
1st Instar Unsexed	0.685	0.161	0.200
2nd Instar Unsexed	0.941	0.182	0.202
3rd Instar Male	1.287	0.210	0.227
3rd Instar Female	1.322	0.200	0.225
4th Instar Male	1.592	0.211	0.224
4th Instar Female	1.676	0.225	0.229
5th Instar Male	2.068	0.296	0.252
5th Instar Female	2.224	0.289	0.268
Adult Male	2.487	0.270	0.105
Adult Female	2.783	0.256	0.154

Table 16 (continued)

Species, Instar and Sex	Canonical Variate		
	I	II	III
E. ocellaris			
1st Instar Unsexed	0.606	0.220	0.176
2nd Instar Unsexed	0.792	0.232	0.205
3rd Instar Male	1.068	0.303	0.223
3rd Instar Female	1.144	0.294	0.225
4th Instar Male	1.443	0.348	0.265
4th Instar Female	1.496	0.374	0.269
5th Instar Male	1.749	0.352	0.278
5th Instar Female	1.896	0.367	0.302
Adult Male	2.147	0.277	0.226
Adult Female	2.366	0.292	0.260
B. punctata			
1st Instar Unsexed	0.403	0.250	0.118
2nd Instar Unsexed	0.580	0.310	0.136
3rd Instar Male	0.793	0.371	0.137
3rd Instar Female	0.837	0.396	0.139
4th Instar Male	1.143	0.409	0.116
4th Instar Female	1.154	0.428	0.118
5th Instar Male	1.575	0.454	0.071
5th Instar Female	1.607	0.449	0.062
Adult Male (Form I)	2.016	0.227	-0.097
Adult Female (Form I)	2.084	0.279	-0.110
Adult Male (Form II)	2.030	0.274	-0.101
Adult Female (Form II)	2.113	0.278	-0.097

discriminatory power of the system (98.12%). The centroids for any two canonical variates can conveniently be plotted and the growth patterns can be interpreted biologically.

Canonical Axis I. This is mainly concerned with general growth and ranks, at almost equal intervals, the various instars of both sexes in all the species analysed.

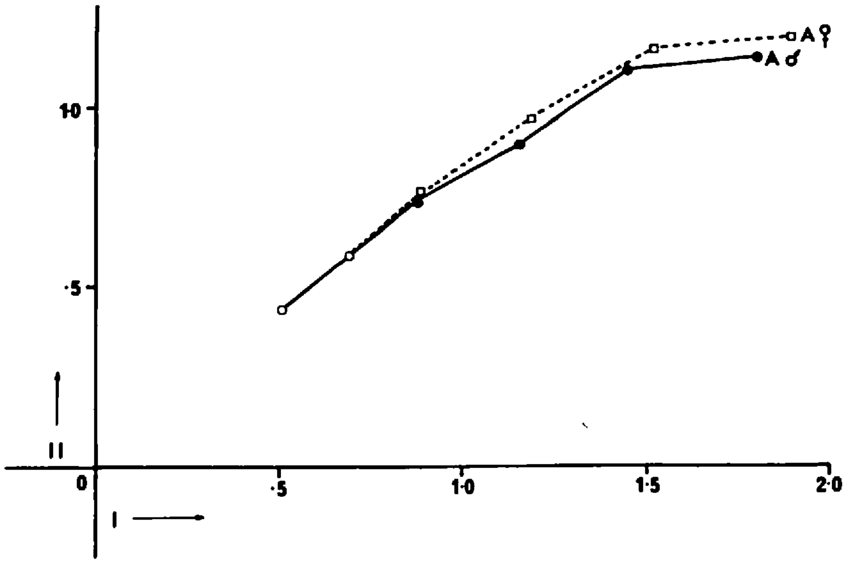
Canonical Axis II does not show any marked discrimination between sexes or instars though it differs between the species and hence is an interspecific growth component.

Canonical Axis III is concerned with maturation or metamorphosis and is the only variable to show a marked discontinuity at the transition to the adult stage.

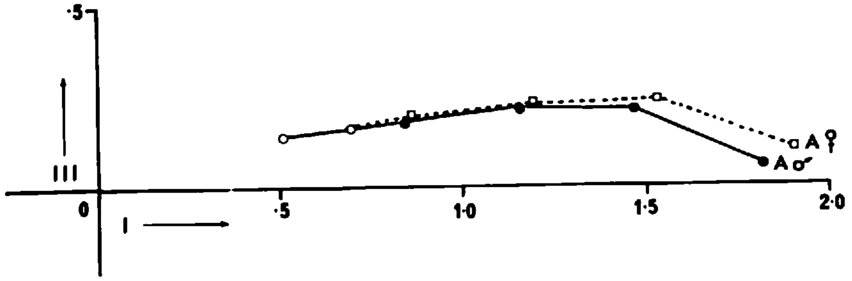
All the three components account for practically all the variation measured in terms of the canonical axes. Of these the first is by far the most important accounting for 71.92% of the total variance and the third is the least important accounting for only 5.74% of the total variance. The second accounts for 20.46% of the total variance.

There is a very close similarity between the growth patterns of all the five investigated species, though *U. reticulata* stands somewhat apart from the others as explained below.

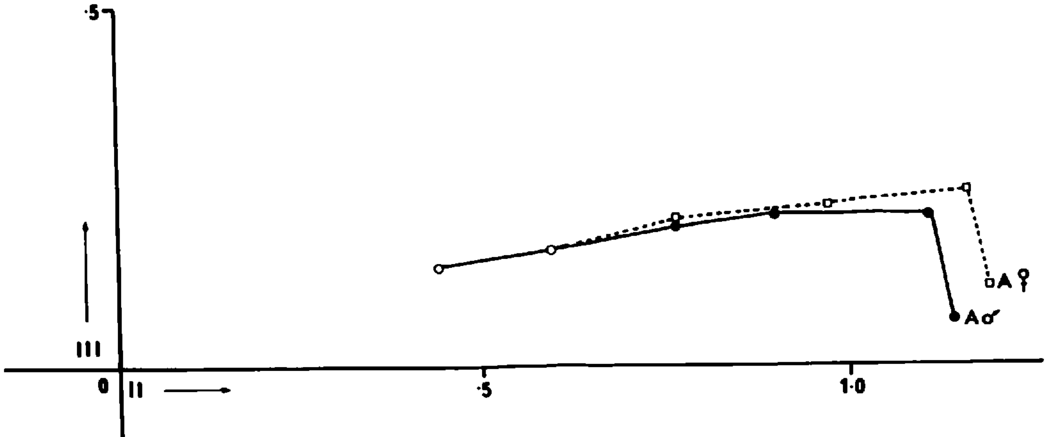
The dominant feature of post embryonic development



a. Canonical Variate I against II

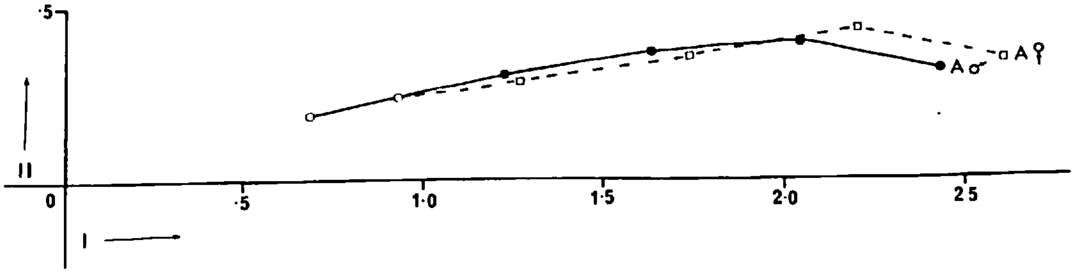


b. Canonical Variate I against III

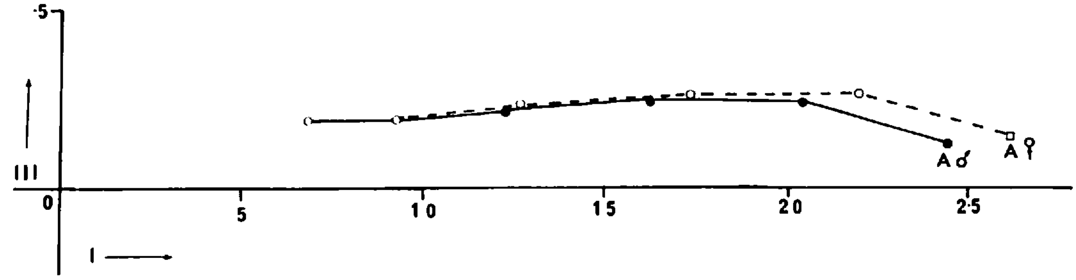


c. Canonical Variate II against III

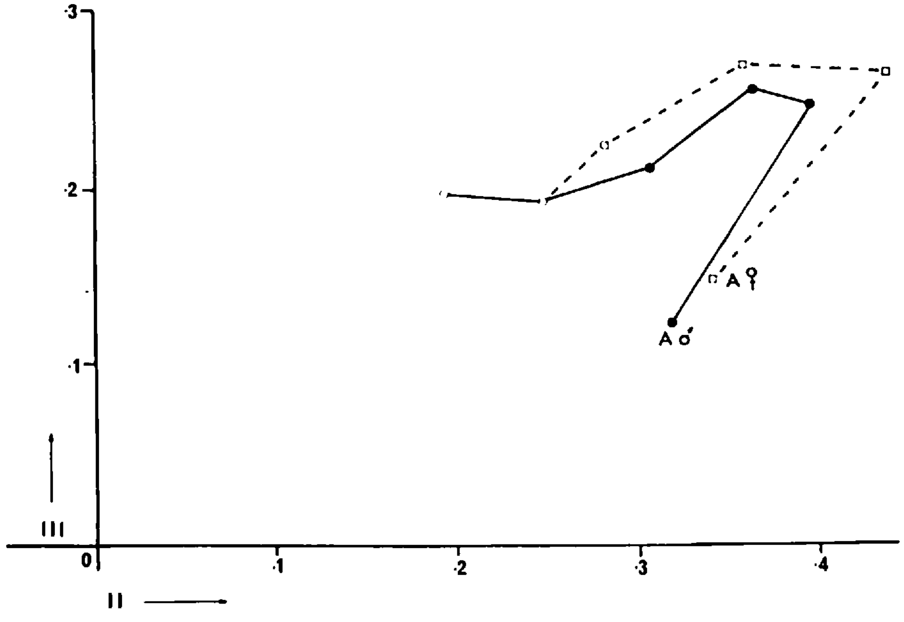
FIG 37 Growth Patterns of U. *reticulata* (Untransformed Data).



a. Canonical Variate I against II



b. Canonical Variate I against III

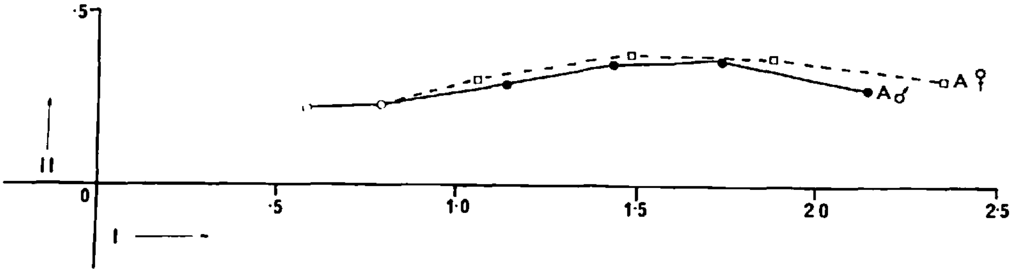


c. Canonical Variate II against III

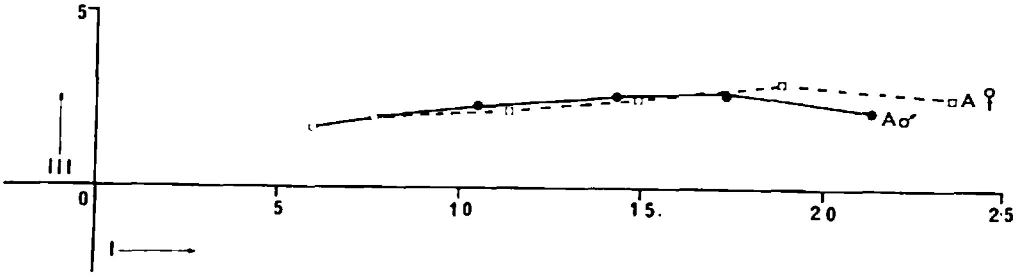
FIG 38 Growth Patterns of *M. parvicauda* (Untransformed Data).

associated with the first axis may be described as a general growth component for two reasons. Firstly it ranks the successive instars of all the species at almost equal intervals (Fig. 37a, 38a, 39a, 40a) and it also involves a substantial weighting from most of the structures measured (Table 13). The overall body length is however not represented in it, an apparent paradox that is explained by the relatively unreliable nature of this dimension, due to the distension and contraction of the abdomen. The head length also contrasts with the other five structural features in determining this component.

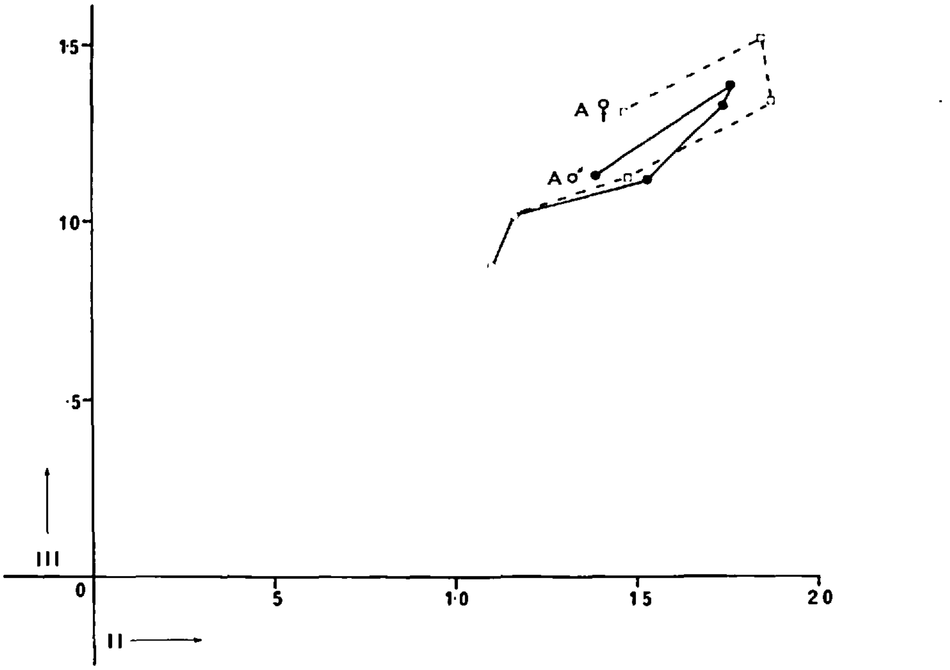
The next component in the overall growth pattern is associated with the second canonical axis, which within most of the species seems to be of relatively little importance as it does not show any pronounced discrimination between the various instars or the two sexes. But it does differ between the species and hence may be considered as an interspecific growth component. This is strikingly so in *U. reticulata* (Fig. 37a) which differs considerably from the other four species studied. In *U. reticulata* this component is also associated with general growth of the species, such as seen in Fig. 37a where the instars are ranked at almost equal intervals on axis II, whereas in the other species (Fig. 38a, 39a, 40a) the instars are not ranked at equal intervals.



a. Canonical Variate I against II

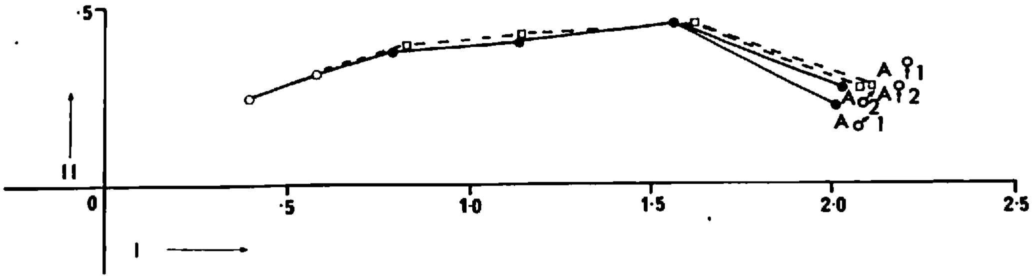


b. Canonical Variate I against III

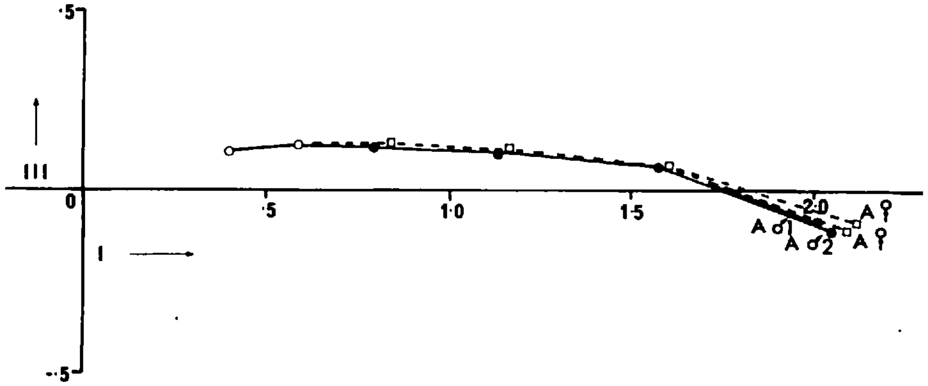


c. Canonical Variate II against III

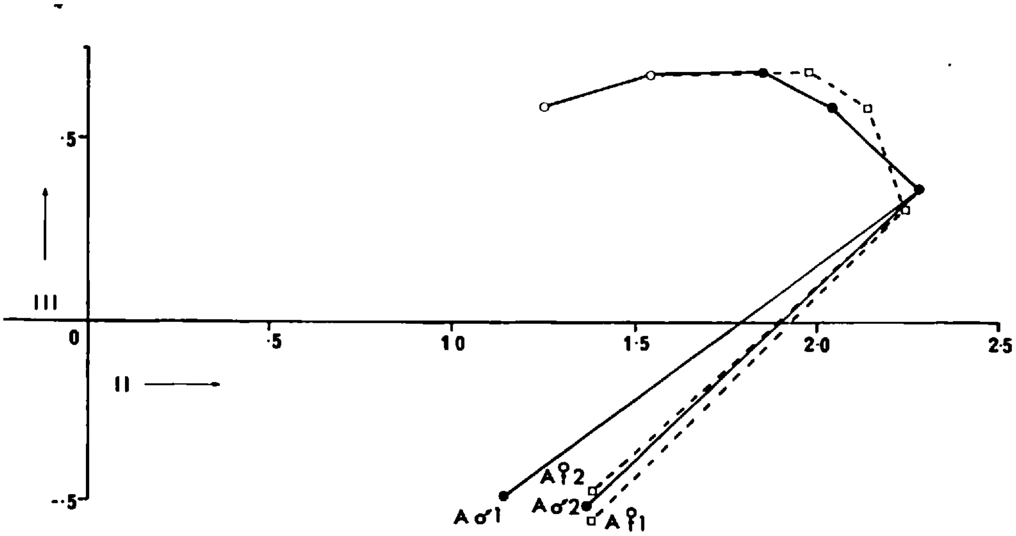
FIG 39 Growth Patterns of *E. ocellaris* (Untransformed Data).



a. Canonical Variate I against II



b. Canonical Variate I against III



c. Canonical Variate II against III

FIG 40 Growth Patterns of *B. punctata* (Untransformed Data).

Table 13 shows that interspecific differences in growth patterns depend on the contrasts between the increase in head and pronotal widths and the lengths of the hind femur and hind tibia. Pronotal length and total body length are not involved nor is there a large contribution from the head length.

The third canonical axis represents a mode of growth particularly associated with the abrupt changes occurring at metamorphosis, i.e. between the fifth instar and the adult stage. The effect is clearly seen in those diagrams where the second and third canonical variates are plotted (Fig. 38c, 39c, 40c) and where there is an abrupt change between the fifth instar and adult. This is mainly attributable to the change in the third axis, though there are indications that the second mode of growth also shows similar relationships and both may be implicated in the difference between the sexes. This is less obvious in U. reticulata (Fig. 37c) and this is yet another way in which its growth-pattern differs from the rest of the species studied. The principal feature of this pattern of growth is the contrast between the dimensions of the lengths of the head and pronotum.

(ii) Transformed Data

Multiple discriminant analysis assumes that all within group covariance matrices are homogenous. If the covariance matrices are equal then the discriminant functions calculated from the untransformed data are the best possible ones. If, however, the covariance matrices are not homogenous a quadratic discriminant function will be more efficient, and this can be obtained by transforming the original data logarithmically. The homogenity of covariance matrices can be tested by Bartlett's test (Seal, 1964), but this test requires the natural logarithm of the determinants of the within-group covariance matrices. In the present analysis one or more of these determinants were zero, so that the test cannot be applied. Although it is sometimes argued that the method of multiple discriminant analysis is robust to heterogeneity of covariance matrices, thus justifying the results obtained with untransformed data, it seemed preferable to repeat the computations with logarithmically transformed data so that the linear and quadratic discriminants could be compared qualitatively.

The latent roots and percentage discrimination ohtained after logarithmic transformation are listed in the following table.

Table 17 Latent Roots and Percentage Discrimination - Transformed Data

Latent Roots		Percentage Discrimination
I	230.314	74.058
II	52.533	16.892
III	22.775	7.323
IV	3.203	1.032
V	1.210	0.389
VI	0.754	0.242
VII	0.206	0.066

As comparison with Table 12 shows, the transformation has not altered one's ability to recognise three major aspects of growth. A large part of the total variance is attributable to the first three latent roots amounting to 98.27% which is virtually identical to the first three latent roots of the untransformed data.

The elements of the latent vectors of the transformed data are given below and should be compared with those of Table 13.

Table 18 Elements of the Latent Vectors - Transformed Data

Variable	Canonical Variate		
	I	II	III
Head width (1)	0.509	0.717	0.217
Head length (2)	0.002	0.028	0.854
Pronotal width (3)	0.349	0.468	-0.414
Pronotal length (4)	0.292	-0.001	-0.196
Hind tibia length (5)	0.535	-0.376	-0.024
Hind femur length (6)	0.487	0.352	0.113
Total body length (7)	0.099	-0.020	-0.009

Along the first canonical axis, hind tibia length has the largest positive weight (0.535) and head length has the smallest positive weight (0.002). This is unlike the untransformed data where lengths of the pronotum and that of the overall body are the largest and smallest positive weights respectively though the latter has relatively small weighting even in the transformed data. In general, however, the two analyses are similar in that all variables except head length and total body length make appreciable positive contributions.

The largest positive and negative weights along the second canonical axis are similar to that of the untransformed data (i.e. head width and hind tibia length).

Along the third canonical axis the largest positive weight is as that in the untransformed data (head length) and the largest negative weight is the pronotal width, unlike the untransformed data. Total body length has the smallest negative weight like the untransformed data.

The three types of variables are as follows:

(a) Hind tibia and hind femur lengths are important on the first axis, and head length on the third axis, contributing little to the other axes. Head width, head length and pronotal length act in a similar way in the untransformed data.

(b) Head width, hind tibia length and hind femur length are associated similarly with the first canonical axis. In the untransformed data pronotal length, hind tibia length and hind femur length act in a similar way along the first axis.

(c) Head width is a single variable associated with several axes to a similar degree.

The significance of each axis is given in the following table. As in the untransformed data, the first six canonical axes are significant.

Table 19 Significance of Each Latent Root - Transformed Data

	Latent Roots						
	I	II	III	IV	V	VI	VII
X^2	2833.485	2071.749	1699.275	747.281	412.639	292.475	97.358
D.F.	57	55	53	51	49	47	45
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

The discriminant scores given to each individual are closely clustered around the centroid which is the average score for each stage taken from a group of individuals. An example of this close cluster around the centroid is given in Table 20 and Figure 36b.

Table 20 Discriminant Scores and Centroids on First Three Canonical Axes for *U. reticulata* 1st Instar Unsexed - Transformed Data

Individual	Canonical Variate		
	I	II	III
1	-1.300	0.085	-0.295
2	-1.273	0.061	-0.348
3	-1.289	0.087	-0.360
4	-1.317	0.061	-0.333
5	-1.319	0.038	-0.328
6	-1.309	0.078	-0.346
7	-1.360	0.112	-0.396
8	-1.332	0.117	-0.319
9	-1.302	0.118	-0.353
10	-1.299	0.089	-0.304
11	-1.301	0.100	-0.347
12	-1.326	0.122	-0.325
First Instar Centroid	-1.311	0.089	-0.338

The group centroids for the first three canonical axes of each species, sex and stage are given in Table 21. The group centroids for any two canonical variates can be plotted and growth patterns can be interpreted biologically.

Canonical Axis I is concerned with general growth and as in the untransformed data it ranks the various instars at more or less equal intervals.

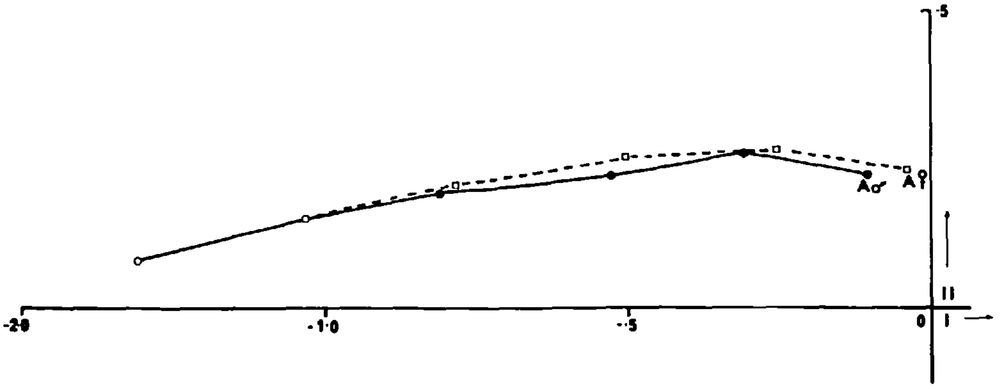
Canonical Axis II shows little importance within a species but as in the untransformed data it differs between

Table 21 Canonical Variates (Group Centroids) - Transformed Data. First Three Canonical Axes Only

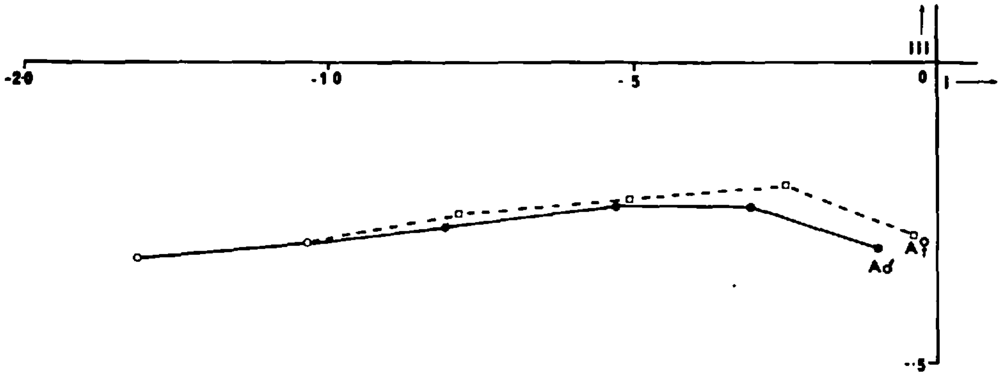
Species, Stage and Sex	Canonical Variate		
	I	II	III
U. reticulata			
1st Instar Unsexed	-1.311	0.089	0.338
2nd Instar Unsexed	-1.035	0.152	-0.302
3rd Instar Male	-0.809	0.199	-0.275
3rd Instar Female	-0.789	0.209	-0.256
4th Instar Male	-0.529	0.222	-0.246
4th Instar Female	-0.508	0.254	-0.234
5th Instar Male	-0.305	0.264	-0.241
5th Instar Female	-0.251	0.265	-0.207
Adult Male	-0.102	0.227	-0.319
Adult Female	-0.044	0.233	-0.297
M. parvicauda			
1st Instar Unsexed	-1.080	-0.243	-0.227
2nd Instar Unsexed	-0.752	-0.195	-0.249
3rd Instar Male	-0.472	-0.155	-0.234
3rd Instar Female	-0.445	-0.166	-0.226
4th Instar Male	-0.205	-0.115	-0.200
4th Instar Female	-0.148	-0.115	-0.187
5th Instar Male	0.014	-0.090	-0.213
5th Instar Female	0.085	-0.072	-0.189
Adult Male	0.171	-0.095	-0.312
Adult Female	0.246	-0.091	-0.272
C. persimilis			
1st Instar Unsexed	-1.084	-0.278	-0.218
2nd Instar Unsexed	-0.743	-0.240	-0.245
3rd Instar Male	-0.445	-0.208	-0.227
3rd Instar Female	-0.422	-0.212	-0.231
4th Instar Male	-0.247	-0.184	-0.238
4th Instar Female	-0.199	-0.176	-0.236
5th Instar Male	0.013	-0.121	-0.215
5th Instar Female	0.082	-0.121	-0.197
Adult Male	0.182	-0.114	-0.348
Adult Female	0.286	-0.144	-0.281

Table 21 (continued)

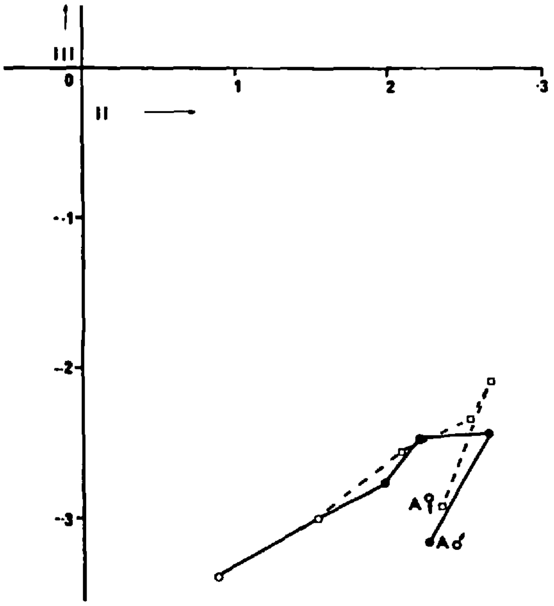
Species, Stage and Sex	Canonical Variate		
	I	II	III
E. ocellaris			
1st Instar Unsexed	-1.192	-0.212	-0.257
2nd Instar Unsexed	-0.909	-0.206	-0.231
3rd Instar Male	-0.598	-0.146	-0.227
3rd Instar Female	-0.538	-0.151	-0.227
4th Instar Male	-0.309	-0.119	-0.187
4th Instar Female	-0.272	-0.102	-0.186
5th Instar Male	-0.132	-0.106	-0.184
5th Instar Female	-0.053	-0.097	-0.167
Adult Male	-0.053	-0.127	-0.228
Adult Female	0.144	-0.114	-0.119
B. punctata			
1st Instar Unsexed	-1.555	-0.109	-0.366
2nd Instar Unsexed	-1.197	-0.090	-0.340
3rd Instar Male	-0.884	-0.072	-0.345
3rd Instar Female	-0.835	-0.057	-0.342
4th Instar Male	-0.544	-0.073	-0.379
4th Instar Female	-0.532	-0.059	-0.373
5th Instar Male	-0.238	-0.062	-0.427
5th Instar Female	-0.221	-0.062	-0.447
Adult Male (Form I)	-0.029	-0.140	-0.761
Adult Female (Form I)	0.006	-0.138	-0.727
Adult Male (Form II)	-0.036	-0.146	-0.798
Adult Female (Form II)	0.002	-0.142	-0.784



a. Canonical Variate I against II



b. Canonical Variate I against III



c. Canonical Variate II against III

FIG41 Growth Patterns of U. reticulata (Log Transformed Data).

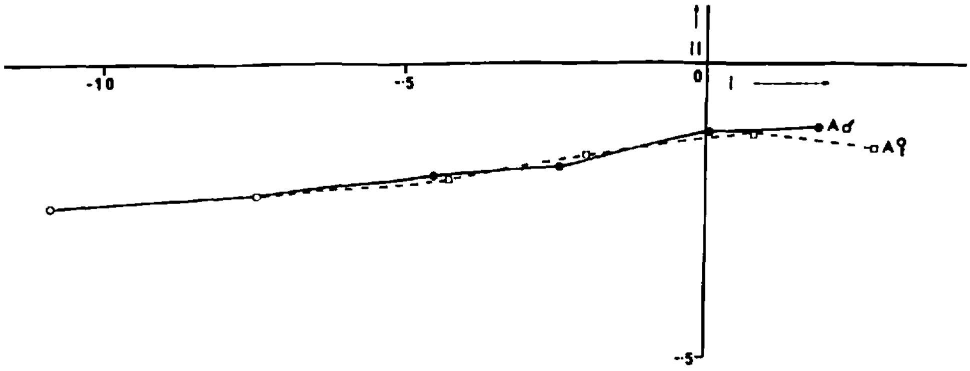
the species and is hence an interspecific growth component.

Canonical Axis III is concerned with maturation or metamorphosis and is the only axis that marks a sharp discontinuity to the adult stage.

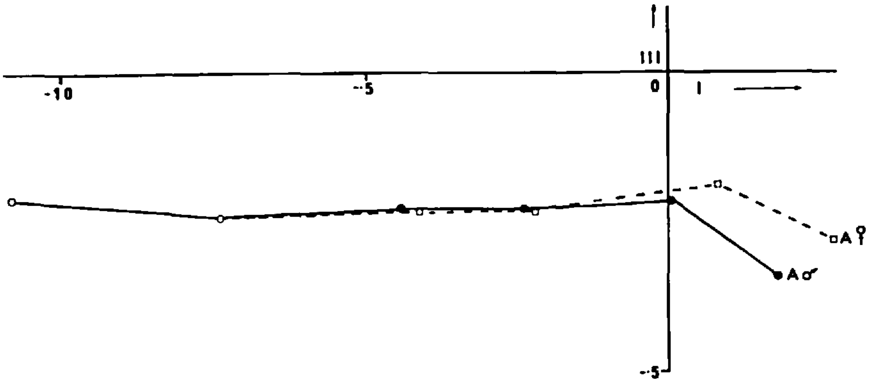
The biological interpretation of the first three axes are similar in the untransformed and transformed data. The first canonical axis is concerned with the general growth component and it is interesting to note that as in the untransformed data most of the structures measured have substantial weighting except for head length and the total body length which is not represented in any of the three axes, hence again pointing out the unreliable nature of that variable. The general growth component in *U. reticulata* is more like the other species analysed in this analysis than it is in the untransformed data (Fig. 41a).

The second canonical axis is, as mentioned before, an interspecific growth component and in this analysis *U. reticulata* is more like the other four species than in the untransformed data. Head width and pronotal width, and lengths of hind femur and tibia act in contrast just as in the untransformed data.

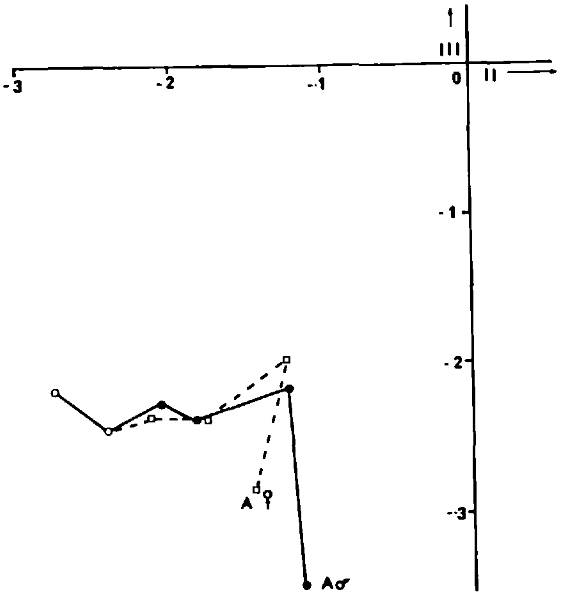
The third canonical axis is associated with metamorphosis. The striking difference between the sexes and the abrupt changes



a. Canonical Variate I against II

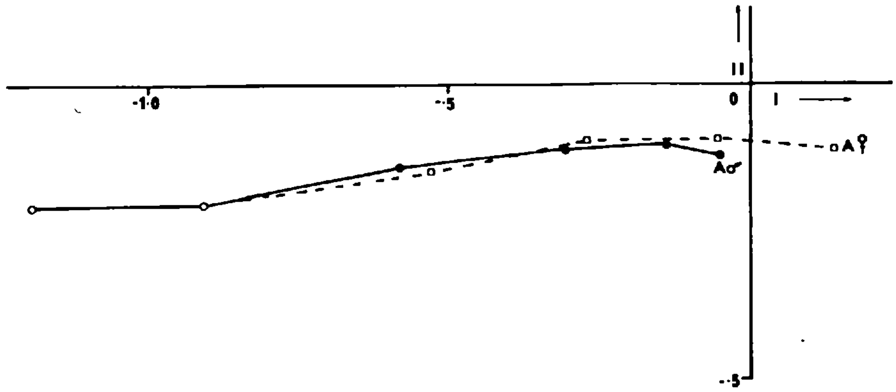


b. Canonical Variate I against III

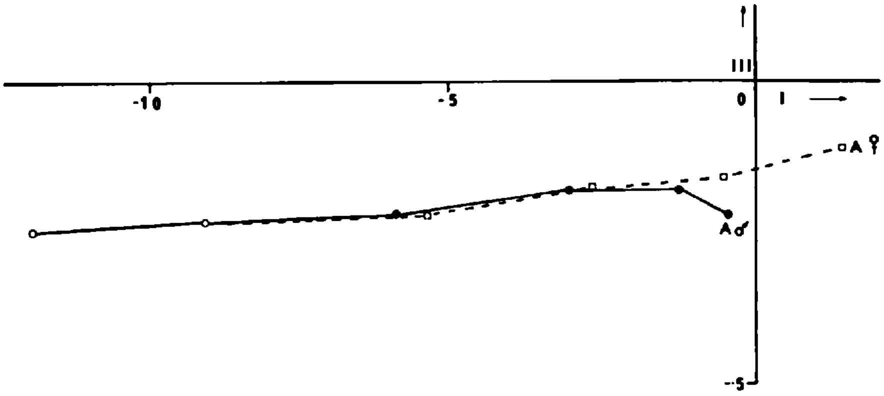


c. Canonical Variate II against III

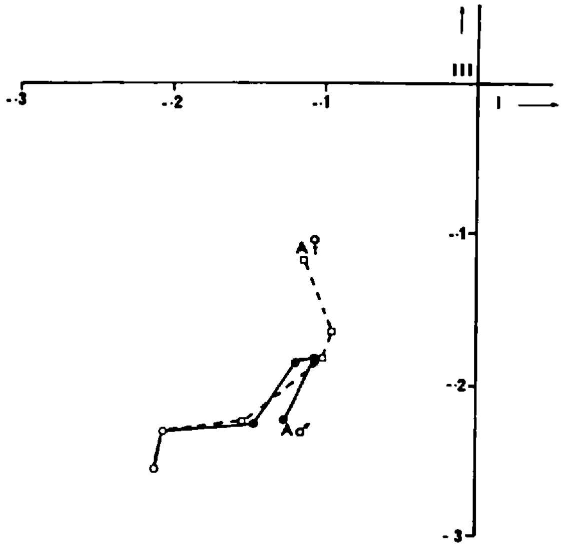
FIG 42 Growth Patterns of C. persimilis (Log Transformed Data)



a. Canonical Variate I against II



b. Canonical Variate I against III



c. Canonical Variate II against III

FIG 43 Growth Patterns of E. ocellaris (Log Transformed Data).

in metamorphosis observed in all the five species except *U. reticulata* in the untransformed data, is however seen here (Fig. 41c). The contrast between head length and pronotal width are the principal features of this pattern of growth and it is a little different from the untransformed data where the contrast was between the lengths of the head and that of the pronotum.

In general, however, the effects of the transformation are not such as to produce a great qualitative difference in the interpretation except perhaps in the case of *U. reticulata*, which tends to resemble the other species more than it did when the untransformed data were used. This implies that the quadratic discriminant function is less efficient and justifies the attention paid to the analysis of the untransformed data.

IV. General Discussion

Except for a few more points most of the aspects have been discussed earlier.

(a) The angles between any pair of discriminant axes can be computed from the normalised vectors given in Table 13 and 18. For any two axes with vectors a and b, the angle is given by

$$\text{Cos } \theta = a.b = a_1b_1 + a_2b_2 \;....\; a_yb_y$$

Considering the three axes used, the following table gives the angles between each of the three pairs of axes.

Table 22 Angles for Three Pairs of Axes of Untransformed and Transformed Data

	Axes	Angles
Untransformed Data	I & II	86.6°
	I & III	118.7°
	II & III	85.6°
Transformed Data	I & II	80.9°
	I & III	92.8°
	II & III	92.4°

While these systems of discriminant axes yield the maximum distinctions between species, instars and sexes, they do not necessarily lend themselves well to an interpretation of growth patterns in terms of uncorrelated growth components. It would seem to be a considerable advantage to define the patterns in these terms but in the present example the axes are in fact close to orthogonality. In this respect, therefore, an alternative analysis in terms of orthogonal principal components would not seem to offer any special advantages. In passing, one may note the statement made by Blackith, Davies & Moy (1963) that discriminant axes are orthogonal is not true in general.

(b) As was pointed out in Section A, the larvae belonging to the family Cicadellidae develop gradually with no striking morphological changes during the five instars. During the last moult, however, a large number of adult characters appear such as the acquisition of wings which were pads in the larval stage, external and internal genitalia which were rudimentary, the formation of the coronal sulcus on the crown, the episternal and furcal sulci on the thorax, sclerotisation of the epimeron, the enlargement of the phragma and sternal apodemes in macropterous forms, and the modification of the seventh, eighth and ninth sternites for the functioning of the male and female genitalia.

This discontinuity in passing into the adult stage is clearly indicated in the growth patterns revealed by multiple discriminant analysis, although the tergites, which develop into external genitalia and similar visible differentiating structures were not included in the analysis. The seven characters measured were chosen without reference to their possible alteration at metamorphosis and thus the choice illustrates well how metamorphosis may influence patterns of growth which are only indirectly concerned with the functional requirements of the adult.

Wigglesworth (1954) pointed out that Hemimetabolous development involves a discontinuity between the adult and proceding instar. In the multiple discriminant analysis in *Dysdercus* by Blackith, Davies & Moy a similar situation was revealed. Moy (unpublished) said that a large number of morphological changes take place during the last moult of *Dysdercus* and this is also now seen in Cicadellidae. It is interesting that the change in growth pattern during the post-embryonic development of *Dysdercus* and of the Cicadellidae is more abrupt than in the development of the one species of Morabine grasshopper (form P24) studied by Blackith & Blackith (1969), and two species of *Ectobius* studied by Brown (1969). In this sense the Hemiptera seem to show a more pronounced metamorphosis than do the Dictyoptera and Orthoptera.

SECTION C

The Application of Multivariate Analyses to the Taxonomy of Fifth Instar Larvae of Twenty-Two British Cicadellidae

I. Introduction

The existing keys to the Cicadellidae concern only the adult members of this family. The earliest of such keys to the British species was by Edwards (1896), which was later revised by Evans (1947). Very recently Le Quesne (1965, 1969) revised keys to two hundred and sixty-seven British species. Ribaut (1935, 1952) worked on the taxonomy of the French members of this family and Oman (1946), Beirue (1956) and De Long (1923) are among the few who classified the American species. The taxonomy of the German species was worked on by Haupt (1935).

The adult classification however, has undergone considerable change especially where the subfamily Deltocephalinae (Euscelini) is concerned. Very few taxonomic studies have been carried out on the larvae. However, a few workers, while describing a particular species which damaged agricultural crops, gave brief descriptions of the immature stages. Hence, various numerical methods were investigated here using forty-two multistate and nine quantitative characters of the fifth instar larvae of twenty-two British Cicadellidae. The results obtained were evaluated and then compared with the orthodox classification of the adults in the hope of obtaining some guidance on the suitability of various numerical methods or their concordance with the results obtained by traditional means. Despite claims by Sokal and Sneath (1963) numerical methods cannot be called objective, although they tend to be robust, in the sense that when based on many characters, the precise method of forming clusters does not affect the results generally.

Only eight of the thirteen subfamilies and twenty-two of the two hundred and sixty-seven recorded species in Britain were studied. The Deltocephalinae is the largest of the subfamilies with eight tribes, of which six have been included here. An attempt was also made to include species from different habitats. Many live on different grasses, but the species dwelling in low vegetation and on trees were also included. Characters of only the fifth instar larvae were analysed as the first two instars are extremely difficult to obtain in the field while the third and the fourth instars are almost identical to the fifth except for their smaller size.

II. Material and Methods

Initially, the different species of larvae were identified by pairing the adults and obtaining the eggs which hatched into larvae, or larvae obtained in the field were reared to the adult stage. The latter method was used in all tree dwelling species which were reared on young seedlings.

(i) List of Species

Table 23 gives the details of the twenty-two species used in the analyses, arranged according to Le Quesne's classification (1965, 1969) based on adult characters.

Table 23

Ulopinae

U. reticulata

Cicadellinae

C. viridis

G. coccinea

Idiocerinae

Idiocerus distinguendus Kirschbaum

Jassinae

Iassus lanio (Linnaeus)

Macropsinae

Oncopsis flavicollis (Linnaeus)

Euplecinae

E. cuspidata

Deltocephalinae

Doraturini

D. stylata

Deltocephalini

  Recilia coronifera (Marshall)

  E. ocellaris

Athysanini

  Rhytistylus proceps (Kirschbaum)

  A. mixtus

  M. grisescens

  M. parvicauda

  C. persimilis

  C. aurantipes (Edwards)

  Elymana sulphurella (Zetterstedt)

Grypotini

  Grypotes puncticollis (Herrich-Schaeffer)

Macrostelini

  M. sexnotatus

Balcluthini

  B. punctata

Typhlocybinae

Erythroneurini

  Z. scutellaris

The list of species with the number accompanying each species used in the analyses is as below and remains the same throughout this account.

1. *U. reticulata*
2. *C. viridis*
3. *G. coccinea*
4. *I. distinguendus*
5. *O. flavicollis*
6. *E. cuspidata*
7. *D. stylata*
8. *R. coronifera*
9. *E. ocellaris*
10. *R. proceps*
11. *G. ventralis*
12. *A. mixtus*
13. *M. grisescens*
14. *M. parvicauda*
15. *C. persimilis*
16. *C. aurantipes*
17. *E. sulphurella*
18. *G. puncticollis*
19. *M. sexnotatus*
20. *B. punctata*
21. *Z. scutellaris*
22. *I. lanio*

(ii) List of Characters

Forty-two multistate and nine quantitative characters were used in the analysis, i.e. fifty-one characters in all. The list of characters and character-states are given in Table 24. The following is the list of quantitative characters, the means and standard deviations of which are given in Appendix III. All dimensions were expressed in mm.

1. Head width (including eyes)
2. Head length
3. Pronotal width
4. Pronotal length
5. Hind femur length
6. Hind tibia length
7. Total body length
8. Length of tergite VIII (along mid-dorsal line)
9. Length of tergite IX (along mid-dorsal line)

Table 24 List of Characters and Character-States of the Fifth Instar Larvae of Cicadellidae

1. Shape of vertex	1. Longer in middle than sides 2. Almost equal length throughout
2. Anterior margin of vertex	1. Round 2. Flat (round at sides) 3. Bluntly pointed 4. Sharply pointed 5. Straight
3. Sides of anterior margin of vertex	1. Coming above eyes 2. Meeting with eyes 3. Meeting with eyes but raised above them

4. Ocelli	1. Absent 2. On vertex very near anterior margin 3. On vertex just above anterior margin of eyes and slightly nearer posterior margin than anterior margin 4. On face just above or beside ecdysial cleavage line or just on crown-face border 5. On face about 2/3 the distance from antennal ridge to posterior margin
5. Frontogenal sulcus	1. Absent 2. Reaching to crown-face border 3. Reaching up to Y-shaped ecdysial cleavage line on face
6. Ante- and post-clypeus	1. Flat 2. Mildly convex 3. Swollen
7. Extent of clypeoloral and clypeogenal sulci	1. To frontogenal sulcus 2. To ridge above antennae 3. To half-way up face above eyes 4. To antennae
8. Angle between crown and face	1. Round 2. Acute 3. Acute with ledge
9. Sharp median keel on face	1. Present 2. Absent
10. Cuticular outgrowths on antennal ledge	1. Present 2. Absent
11. Genae	1. Sharp with oblique angles at sides 2. Round angles at sides

12. Transclypeal sulcus	1. Absent 2. Faint 3. Well defined 4. Infolded
13. Subgenal sulcus	1. Present 2. Absent
14. Antennae	1. Long, reaching to meso- and metathorax 2. Medium 3. Short and stumpy
15. Ridge above antennae	1. Absent 2. Forms an arch 3. In line with clypeogenal sulcus 4. Forms an angle with clypeogenal sulcus
16. Antennal depression	1. Present 2. Absent
17. Anteclypeus	1. Bulbous in appearance 2. Almost rectangular with parallel sides 3. Very narrow
18. Keels at the sides of pronotum	1. Present 2. Absent
19. Finger-like projection on posterior margin of mesoepisternum	1. Present 2. Absent
20. Posterior portion of furcal sulcus on mesothorax	1. Visible 2. Invisible
21. Raised median line on thorax and abdomen	1. Present 2. Absent
22. Length of eighth abdominal tergite	1. Half that of ninth abdominal tergite or almost same length 2. Twice that of ninth abdominal tergite

23. Size of subgenital plate in male	1. 2/3 or 1/2 that of ninth abdominal tergite 2. Extends beyond ninth abdominal tergite
24. Rudiments of the first gonapophyses in female	1. Extends to tip of ninth abdominal tergite 2. Does not extend to tip of ninth abdominal tergite
25. Spines on the rudiments of the gonoplacs in female	1. Present 2. Absent
26. The length of the rudiments of the gonoplacs to the rudiments of the first and second gonapophyses in female	1. Similar length to first and second pairs 2. Slightly longer than first pair 3. Very much longer than first pair
27. Cleft on the rudiments of the first pair of gonapophyses in female	1. Present 2. Absent
28. Subgenital plate in male	1. Hairs present 2. Hairs and pits present 3. Hairs and pits absent
29. Cleft in the centre of the posterior end of subgenital plate in male	1. 1/9 the way down 2. 1/3 the way down 3. 1/2 the way down 4. 2/3 the way down
30. Posterior end of subgenital plate in male	1. Very pointed, narrow and close together 2. Fairly pointed, moderately broad and fairly close together 3. Pointed, close together with narrow lobes 4. Round, broad and close together 5. Round, broad and fairly far apart

	6. Round, moderately broad and close together
	7. Round, narrow and close together
	8. Blunt, moderately broad and fairly close together
31. Sides of subgenital plate in male	1. With concavity
	2. Without concavity
32. Dorsal surface of abdominal segments	1. Covered with bristles with prominent bases
	2. Covered with hairs
33. Bristles with prominent bases	1. Follow a regular pattern
	2. Do not follow a regular pattern
	3. Falls into category 32(2)
34. Number of bristles on abdominal segments III to VI	1. Four in internal and middle rows
	2. None
	3. Falls into category 32(2)
	4. Falls into category 32(1) and 33(2)
35. Number of bristles on abdominal segment VII	1. Six in internal, middle and external rows
	2. Four in internal and middle rows
	3. Two in external row
	4. Two in middle row
	5. Falls into category 34(3)
	6. Falls into category 34(4)
36. Number of bristles on abdominal segment VIII	1. Six in internal and middle rows
	2. Four in middle and external rows
	3. Falls into category 34(3)
	4. Falls into category 34(4)
37. Length of wing pads	1. Metathoracic wing pads very slightly longer than mesothoracic ones

	2. Metathoracic wing pads very much shorter than mesothoracic ones. The earlier reaching down to second abdominal segment, the later to the fourth
38. Apex of anterior and median femora	1. With spines 2. Without spines
39. Apex of hind femora	1. With spines 2. Without spines
40. Spines on hind tibiae	1. Poorly developed 2. Prominent with bases 3. Poorly developed ones on dorsal surface and well developed ones on ventral surface
41. Prominent crown of spines on hind tibiae	1. Present 2. Absent
42. Finger-like projections at the tip of hind tarsus	1. Present 2. Absent

Characters 33 to 36 are not always present, and it might have been more satisfactory to code certain states of these characters as "non-applicable". The method in fact used will necessarily weight some characters a little more heavily than others, but it is not likely to have serious effects when 42 characters, each with several states, are taken into account.

Not all the fifty-one characters were used in all the analyses; forty-two multistate characters were used in some,

Table 25 **Distribution of Character-States in Fifth Instar Larvae of Twenty-Two Cicadellidae**

Species	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	2	5	3	1	1	3	2	3	2	2	2	4	1	3	2	1	1	1	1	2	1
2	1	1	2	3	2	3	1	1	2	2	2	2	2	2	1	2	1	2	2	1	2
3	1	4	2	3	2	3	1	2	2	2	2	2	2	2	1	2	1	2	2	1	2
4	2	5	2	4	3	2	1	1	2	2	2	3	2	2	1	2	2	2	2	1	2
5	1	1	2	4	1	3	2	1	2	2	2	1	2	3	3	2	1	2	2	1	2
6	1	4	1	2	1	1	3	2	1	2	1	3	2	3	1	2	2	1	2	1	2
7	1	3	2	2	2	2	1	3	2	2	2	3	2	2	1	2	2	2	2	1	2
8	1	3	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
9	1	3	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
10	1	3	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
11	1	3	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
12	1	3	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
13	1	3	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
14	1	3	2	2	2	2	1	2	2	2	2	3	2	1	1	2	2	2	2	1	2
15	1	3	2	2	2	2	1	2	2	2	2	3	2	1	1	2	2	2	2	1	2
16	1	3	2	2	2	2	1	2	2	2	2	3	2	1	1	2	2	2	2	1	2
17	1	3	2	2	2	2	1	2	2	2	2	3	2	1	1	2	2	2	2	1	2
18	2	5	2	4	1	1	4	1	2	2	2	3	2	1	1	2	3	2	2	1	2
19	1	3	2	2	2	2	1	1	2	2	2	3	2	1	1	2	2	2	2	1	2
20	1	2	2	2	2	2	1	2	2	2	2	3	2	2	1	2	2	2	2	1	2
21	2	5	2	1	3	2	1	3	2	1	2	2	2	2	1	2	2	2	2	2	2
22	2	5	2	5	1	2	2	1	2	2	2	3	2	3	4	2	2	2	2	1	2

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	1	2	2	2	1	2	3	5	2	2	3	3	5	3	2	2	2	1	2	2
1	1	2	2	1	2	3	2	6	2	1	2	4	6	4	1	1	1	2	1	1
1	1	2	2	2	2	3	3	6	2	1	2	4	6	4	1	1	1	2	1	1
2	2	1	2	2	2	3	4	8	1	1	2	4	6	4	1	2	1	3	1	2
1	1	2	2	2	2	3	3	3	2	2	3	3	5	3	1	2	1	1	2	2
1	1	2	2	1	2	3	4	3	2	2	3	3	5	3	1	2	1	2	1	1
1	1	2	1	3	2	3	3	4	2	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	2	3	2	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	3	7	2	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	2	2	3	3	3	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	2	2	3	3	6	2	1	1	1	2	1	1	1	1	2	1	1
1	1	2	2	2	2	3	3	3	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	3	5	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	2	2	3	3	3	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	3	1	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	3	1	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	3	3	1	1	1	1	1	1	1	1	1	2	1	1
1	1	2	2	1	2	3	2	2	1	1	1	2	3	1	1	1	1	2	1	1
1	1	2	2	1	2	3	1	3	2	1	1	2	4	2	1	1	1	2	1	1
1	1	2	2	1	2	3	3	3	1	2	3	3	5	3	1	1	1	2	1	1
1	1	2	2	2	2	3	2	3	1	1	2	4	6	4	1	2	1	1	2	2
1	1	2	2	2	2	3	3	5	2	2	3	3	5	3	1	1	1	2	1	1

Table 26 **Distribution of the Bristles in the Fifth Instar Larvae of Cicadellidae**

Species	Abdominal Segment																	
	III			IV			V			VI			VII			VIII		
	I	M	E	I	M	E	I	M	E	I	M	E	I	M	E	I	M	E
D. stylata	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
R. coronifera	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
E. ocellaris	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
R. proceps	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
G. ventralis	x	x	-	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x
A. mixtus	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
M. grisescens	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
M. parvicauda	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
C. persimilis	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
C. aurantipes	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
E. sulphurella	x	x	-	x	x	-	x	x	-	x	x	-	x	x	x	x	x	x
G. puncticollis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x
M. sexnotatus	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	x

Key to Table 26:

x	Bristle present
-	Bristle absent.
I	Internal row
M	Middle Row
E	External row

only nine quantitative characters in others, and in still others all fifty-one were used. The distribution of the forty-two multistate characters in the fifth instar Cicadellid larvae are given in Table 25, and Table 26 gives the distribution of the bristles in the right half of the abdomen, in some fifth instar larvae of Cicadellidae.

The data were analysed by a single linkage cluster analysis, a multiple discriminant analysis (= canonical analysis), a principal co-ordinate analysis and a principal component analysis. The Fortran Computer programs for these analyses were written by Mr. R.G. Davies and executed on the CDC 6600 of the University of London Computer Centre.

III. Numerical Methods

The details of the nine numerical methods used are listed below and an outline of each is then discussed separately. This does not involve any detailed statistical explanation as the main aim of this study is the taxonomic interpretation of the analysis.

1. Single linkage cluster analysis of a simple matching coefficient matrix. Forty-two multistate characters. Data not standardised.

2. Single linkage cluster analysis of a correlation matrix. Forty-two multistate characters. Data not standardised.

3. Single linkage cluster analysis of a correlation matrix. Fifty-one characters (forty-two multistate and nine numerical). Data not standardised.

4. Multiple discriminant analysis (canonical analysis). Nine quantitative characters. Untransformed data.

5. Multiple discriminant analysis. Nine quantitative characters. Logarithmically transformed data.

6. Principal co-ordinate analysis of a simple matching coefficient matrix - after transformation by Gower's method. Forty-two multistate characters. Data not standardised.

7. Principal component analysis of a correlation matrix. Nine quantitative characters. Data not standardised.

8. Principal component analysis of correlation matrix. Forty-two multistate characters. Data not standardised.

9. Principal component analysis of a correlation matrix. Fifty-one characters (forty-two multistate and nine quantitative characters). Data not standardised.

(i) Single Linkage Cluster Analysis

Clustering by single linkage was devised by Sneath (1957). Essentially it depends on the admission of new clusters to an existing cluster if any one member of either cluster is linked to a member of the other cluster above a certain level of similarity. The latter is therefore first set at 1.0 (the maximum possible) and progressively lowered in steps of, say, 0.01. At each level the nucleus of a new cluster is sought or the admission of new members to existing clusters. The method has not been favourably received as it leads to the formation of long rather straggling clusters, a process known as "chaining". However, in recent years Jardine & Sibson (1968) regard chaining as a characteristic of the method but not as a defect. Single-linkage cluster analysis is used in the Rothamstead CLASP program for numerical taxonomy and has the further advantage that it is closely related to the method of minimum spanning trees of linking individuals (Gower & Ross, 1969).

(a) Simple Matching Coefficient (Forty-Two Multistate Characters) Data not Standardised

Forty-two multistate characters were used in this analysis. The similarity half matrix gives the similarity coefficient S_{SM} between any two species on a match-mismatch basis. When species match $S = 1$, but when they do not $S = 0$, so that $S_{SM} = \frac{\sum S}{n}$ where n is the number of comparisons.

Species with the highest similarity are _R. proceps_ (10) and _A. mixtus_ (12), and _C. persimilis_ (15) and _C. aurantipes_ (16), with a similarity coefficient of 1 (Fig. 44). _C. persimilis_ and _C. aurantipes_ belong to the same genus

Cicadula, and their larvae are identical in respect of the characters used, except that *C. aurantipes* is larger than *C. persimilis*. The colour and colour markings in both are similar but darker in *C. aurantipes* than *C. persimilis*. *R. proceps* and *A. mixtus* are also similar in respect of the characters used except that *A. mixtus* is larger than *R. proceps*, and the former species is green whilst the latter one is brown with a prominent V-shaped marking extending from the postclypeus to the mesothorax. It must be noted that colour and colour markings were not used as characters in the analysis and quantitative characters were also omitted from this particular analysis, hence these four species have a similarity coefficient of 1.

Species with the lowest similarity coefficient are *U. reticulata*, *C. persimilis*, *C. aurantipes*, *R. coronifera* and *E. sulphurella* (0.190). *U. reticulata* joins the main cluster at the lowest similarity level of 0.57 (Fig. 44), and this is an interesting feature. Perhaps Evans (1947) and Ribaut's (1952) point of placing this species in a separate family by itself is justified here.

The subfamily Deltocephalinae join above the 0.8 level (Fig. 44), but it is difficult to subdivide this subfamily further into tribes except perhaps for Macrostelini and Balcluthini which join at 0.85 and 0.83 levels respectively.

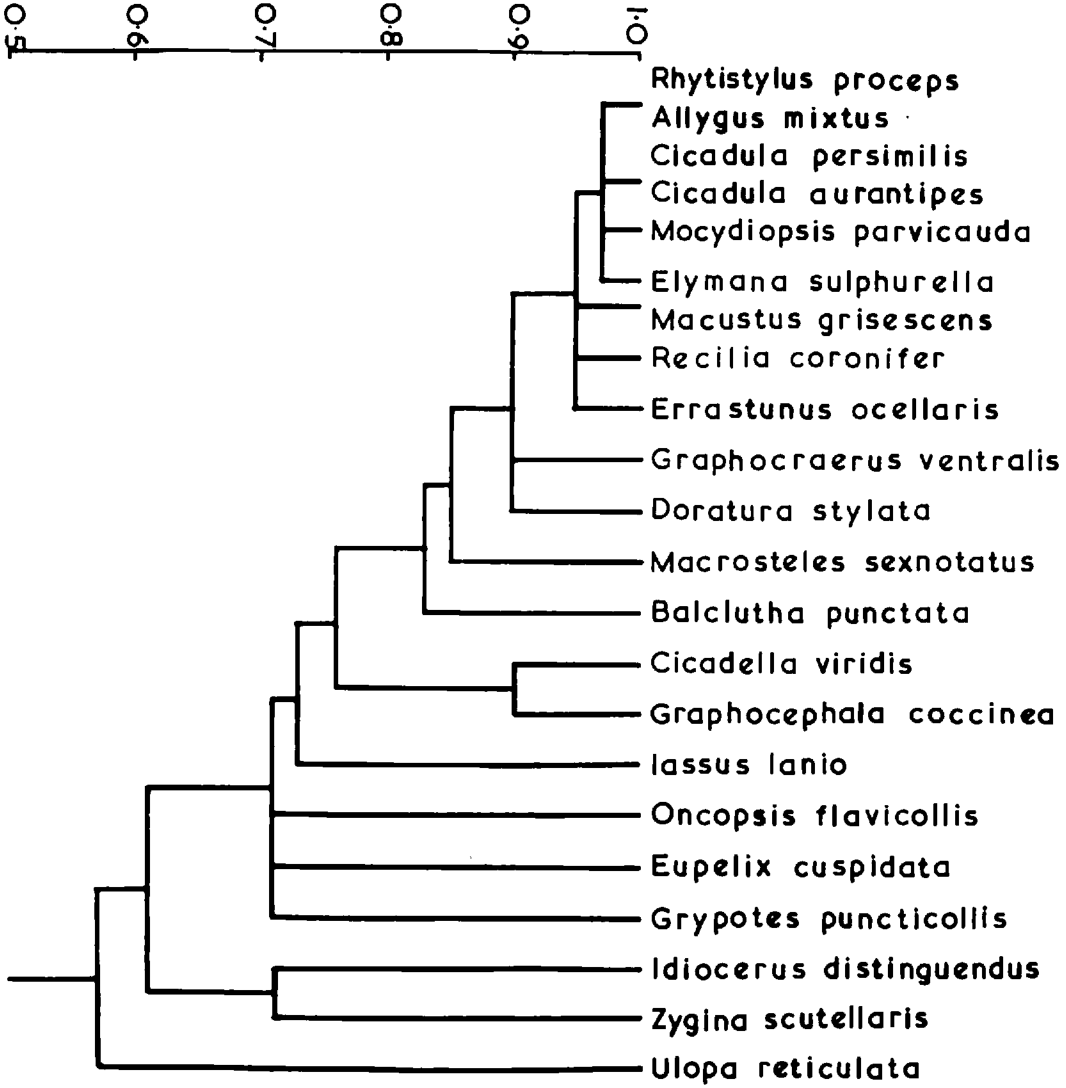


FIG44 Single Linkage Cluster Analysis (42 Multistate Characters)

One species which is usually put under this subfamily appears further down the phenon level. This species, *G. puncticollis*, forms a tribe by itself in the subfamily Deltocephalinae according to Le Quesne (1969), but Evans (1947) and Ribaut (1952) put it in the common tribe of Euscelini. In this analysis it appears with *O. flavicollis* and *E. cuspidata* at the 0.71 level, as does *I. distinguendus* and *Z. scutellaris*. These latter groupings are not in concordance with the orthodox classification of the adults.

C. viridis and *G. coccinea* come together here at the 0.9 level, and *I. lanio* which is in a subfamily in the adult classification appears by itself at the 0.73 level.

Hence this particular analysis groups the Deltocephalinae together except for *G. puncticollis*; the Cicadellinae together, and places *I. lanio* and *U. reticulata* separately, although *O. flavicollis*, *E. cuspidata* and *G. puncticollis*, and *I. distinguendus* and *Z. scutellaris* are placed together in one unit. This is unusual as *Z. scutellaris* has always been put in a family or subfamily Typhlocybinae by all the previous authors. Analysis of more species of Typhlocybids is needed to clarify this.

(b) Correlation Matrix (Forty-Two Multistate Characters). Data not Standardised.

In this analysis the association matrix is first computed from the correlation coefficients between taxa. This may be criticized on theoretical grounds (e.g. Boratyński & Davies, 1971), though in many cases the results are not greatly different from those obtained from alternative measures of association.

Here again *C. persimilis*, and *C. aurantipes*, and *R. proceps* and *A. mixtus* have a correlation level of 1, the lowest correlation being between *U. reticulata*, *C. persimilis* and *C. aurantipes* (0.022). *C. persimilis* and *C. aurantipes*, and *R. proceps* and *A. mixtus* have similar correlation levels for reasons given in the previous analysis.

In this analysis (Fig. 45) most of the species belonging to the Deltocephalinae come as a group except for *B. punctata*, *M. sexnotatus* and *G. puncticollis*. Although none of the previous authors have paid particular attention to *G. puncticollis*, it comes on the lowest similarity level, away from the rest of the Deltocephalinae in this analysis. *U. reticulata* again joins the rest of the species at a low similarity level. The rest of the groupings, except for *C. viridis* and *G. coccinea* which again come together, are not in concordance with the orthodox classification of the adults.

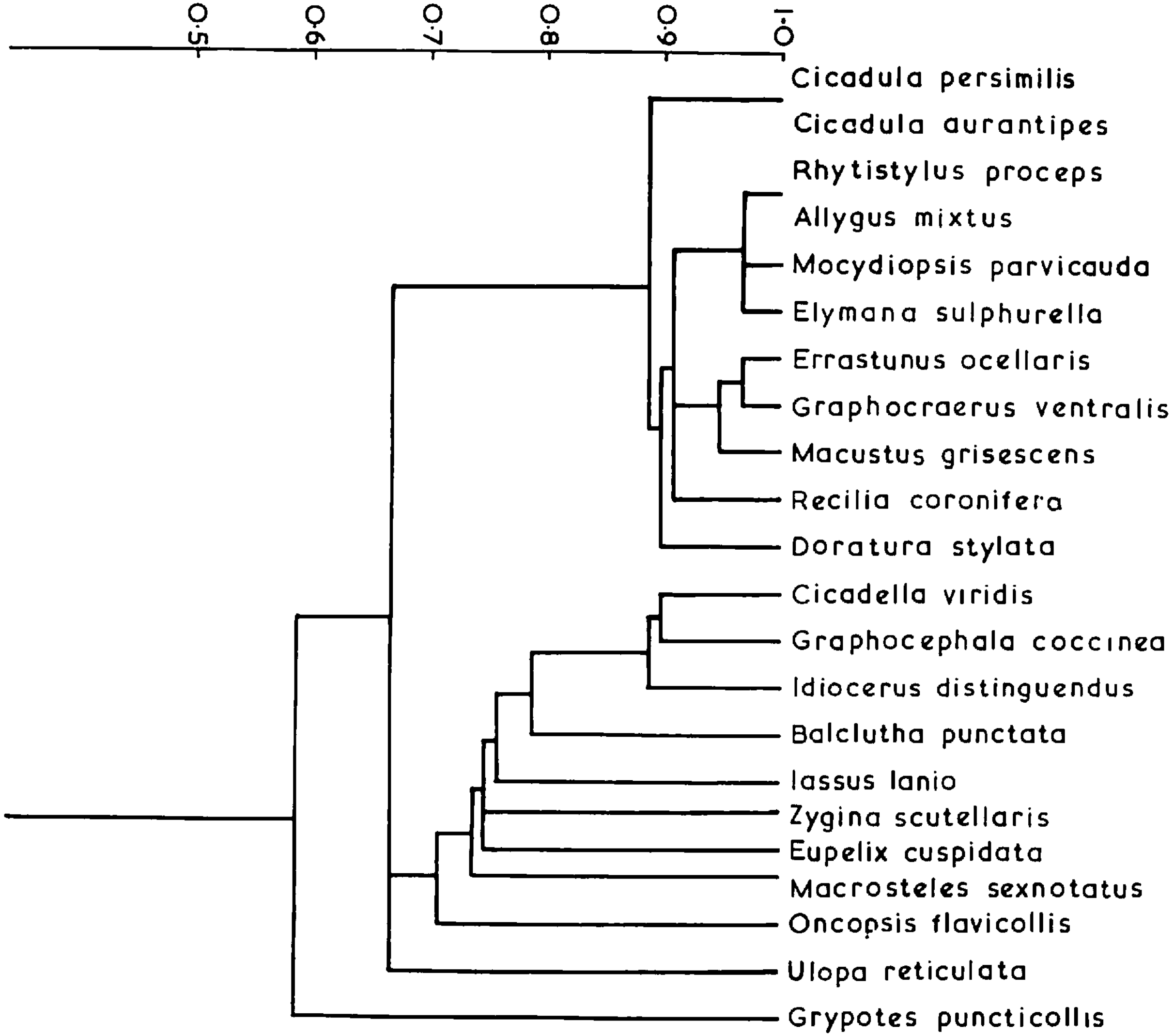


FIG 45 Single Linkage Cluster Analysis — Correlation Matrix
(42 Multistate Characters)

(c) Correlation Matrix (Fifty-One Characters - Forty-Two Multistate and Nine Quantitative). Data not Standardised.

This is a similar analysis to the previous one except that fifty-one characters were used. C. persimilis and C. aurantipes have the highest correlation of 0.991, whilst R. proceps and A. mixtus have a correlation of 0.978. As the nine quantitative characters were used in this particular analysis, these above-mentioned species do not have an association of 1.

Species that join above the 0.9 level form a homogeneous group and they belong to the subfamily Deltocephalinae (Fig. 46), although G. puncticollis, M. sexnotatus and B. punctata, which also belong to this subfamily but to different tribes, join the cluster at the 0.71 and 0.81 levels, M. sexnotatus and B. punctata being at one level. Ribaut (1952) puts both these genera under one tribe of Macrostelini.

The status of G. puncticollis has not changed in this analysis, and Z. scutellaris and E. cuspidata which are normally placed in separate subfamilies join the cluster singly. C. viridis and G. coccinea again come together although U. reticulata which joins the cluster at a low similarity level is with O. flavicollis. D. stylata which belongs to a separate tribe Doraturini, in the subfamily Deltpcephalinae (according

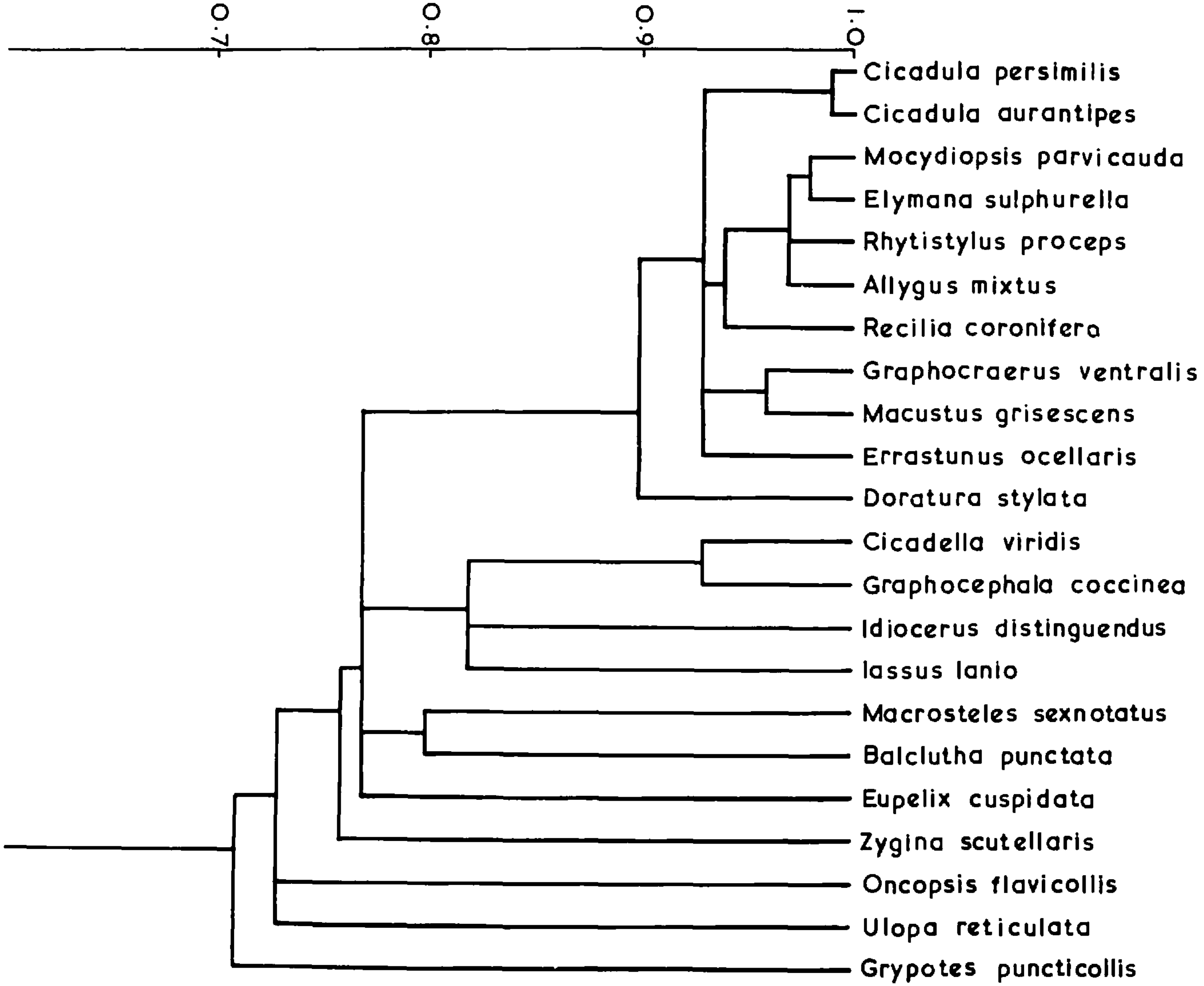


FIG 46 Single Linkage Cluster Analysis — Correlation Matrix (51 Characters).

to Le Quesne, 1969), shows this feature.

The similarities among the three single linkage analyses are as follows:-

a. *C. viridis* and *G. coccinea* form one cluster.

b. The Deltocephalinae, i.e. the group of tribes Doraturini, Athysanini and Deltocephalini form one cluster.

c. *U. reticulata* joins the cluster at a low similarity level.

The differences as shown by the analyses are as follows:

a. Only in the clustering by simple matching coefficient do *M. sexnotatus* and *B. punctata* come close to the rest of the Deltocephalinae. In the other two analyses they appear at low similarity levels.

b. In the analyses on the correlation matrix of forty-two and fifty-one characters, *G. puncticollis* joins the cluster at the lowest similarity level.

Hence these clustering techniques emphasize the close affinities of the species belonging to the subfamilies Cicadellinae and most of the Deltocephalinae, (i.e. the tribes Doraturini, Athysanini and Deltocephalini) and the remoteness of *U. reticulata* to the family Cicadellidae.

On the other hand, the analysis raises doubts on the status of the other species.

(iii) Multiple Discriminant Analyses. Untransformed Data (Nine Quantitative Characters)

This method of analysis has been described in Section B. The means and standard deviations computed for each species are given in Appendix III.

The six latent roots and percentage discrimination are given in Table 27.

Table 27 Latent Roots and Percentage Discrimination - Untransformed Data

Latent Root		Percentage Discrimination
I	169.734	76.531
II	29.239	13.183
III	10.400	4.689
IV	5.187	2.339
V	3.129	1.411
VI	2.094	0.944

A large proportion of the total variance is attributable to the first three latent roots (94.4%), especially to the first.

The elements of the latent vectors indicate the weight given to each variable along a particular canonical axis. Table 28 gives the elements of only the first three vectors; the remaining axes were not included in the analyses as they account for very small proportions of the total variation.

Table 28 Elements of the Latent Vectors - Untransformed Data

Variable	Canonical Variate		
	I	II	III
Head width (1)	0.659	0.512	-0.084
Head length (2)	-0.039	-0.054	-0.529
Pronotal width (3)	0.133	0.213	-0.006
Pronotal length (4)	0.160	0.178	0.660
Hind femur length (5)	0.304	-0.217	0.114
Hind tibia length (6)	0.150	-0.247	-0.068
Total body length (7)	0.002	-0.023	-0.035
Length of VIII tergite (8)	0.439	0.315	-0.043
Length of IX tergite (9)	0.461	-0.617	0.506

Along the first discriminant axis all the variables have almost equal weight, except head width, which contrasts with head length, the former having the largest weight and total body length having the smallest weight.

Along the second discriminant axis head width and head length again form a contrast and total body length has the smallest weight.

It is to be noted that total body length has very small weighting along all the three axes (0.002, -0.023 and -0.035 respectively), and this was also seen in the analysis of growth in Section B, again emphasizing the negligible value of this character in discrimination.

The following chi-squared tests show that each of the six canonical axes are statistically significant.

Table 29 Significance of Latent Roots - - Untransformed Data

	Latent Roots					
	I	II	III	IV	V	VI
X^2	943.210	625.576	446.571	334.408	260.228	207.268
D.F.	29	27	25	23	21	19
P.	0.001	0.001	0.001	0.001	0.001	0.001

The discriminant scores (canonical variates) characterize the particular species from which the original measurements were taken.

The group centroids, i.e. the average scores for each species taken from the group of individuals are given for all the twenty-two species in Table 30. The centroids for any two canonical variates can be plotted and the groupings of the species which are obtained may be interpreted, on theoretical grounds.

Table 30 Canonical Variates (Group Centroids) - Untransformed Data. First Three Canonical Axes Only.

Species	Canonical Variate		
	I	II	III
U. reticulata	1.502	0.496	-0.133
C. viridis	3.166	0.002	-0.223
G. coccinea	2.960	-0.300	-0.183
I. distinguendus	2.066	0.591	-0.032

Table 30 (continued)

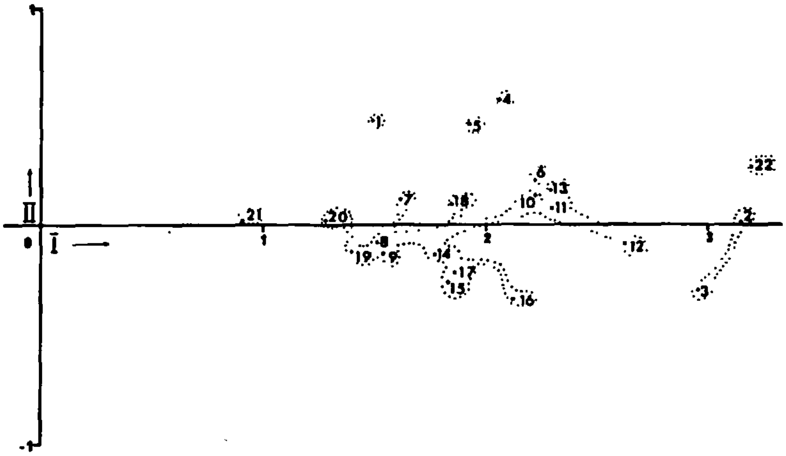
Species	Canonical Variate		
	I	II	III
O. flavicollis	1.932	0.467	0.253
E. cuspidata	2.222	0.215	-0.593
D. stylata	1.620	0.114	-0.078
R. coronifera	1.515	-0.084	-0.038
E. ocellaris	1.549	-0.161	-0.022
R. proceps	2.222	0.179	-0.041
G. ventralis	2.397	0.095	-0.021
A. mixtus	2.579	-0.071	0.109
M. grisescens	2.273	0.167	-0.062
M. parvicauda	1.770	-0.149	-0.043
C. persimilis	1.830	-0.286	0.082
C. aurantipes	2.116	-0.340	0.119
E. sulphurella	1.846	-0.238	0.033
G. puncticollis	1.843	0.100	0.010
M. sexnotatus	1.424	-0.113	-0.071
B. punctata	1.299	0.024	0.036
Z. scutellaris	0.919	0.031	0.009
I. lanio	3.204	0.282	0.303

The species are mainly scattered along the first axis as may be seen in Fig. 47a, b. The Deltocephalinae form a cluster at the centre with the rest of the species scattered around. *G. coccinea* and *C. viridis* lie fairly close together and they belong to one subfamily.

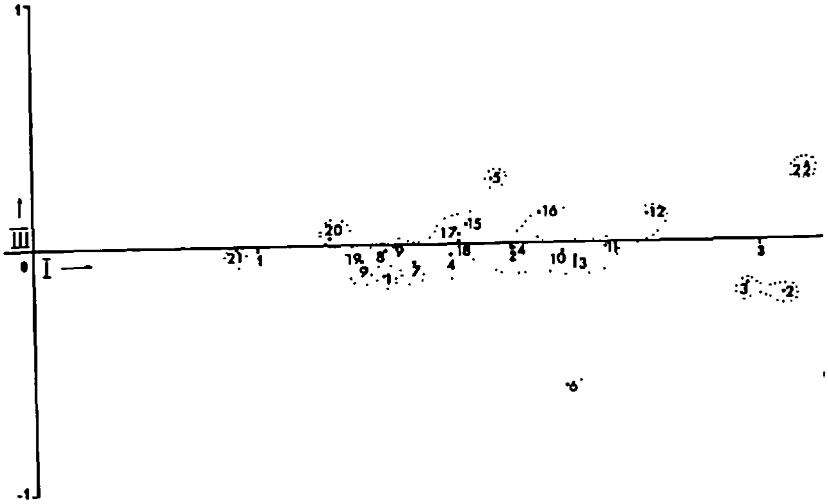
In groupings of the species obtained from canonical variates I-II (Fig. 47b), and II-III (Fig. 47c) the Deltocephalinae are together in the centre with the rest of the species scattered around.

The contrast of the weights of the two variables, the head width and the head length, is emphasized by *E. cuspidata* being

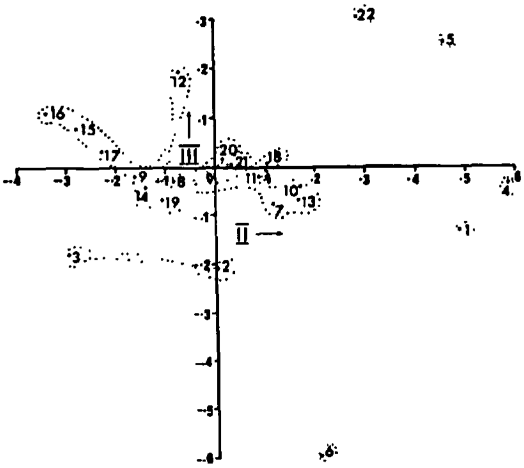
FIG 47 Multiple Discriminant Analysis (9 Quantitative Characters).



a. Canonical Variate I against II



b. Canonical Variate I against III



c. Canonical Variate II against III

placed furthest away from the main group of species.

Hence a rather poor separation of species is seen in this analysis on the nine quantitative characters. Perhaps it can be concluded that a small number of quantitative characters will not form good taxonomic groupings of species.

(ii) Logarithmically Transformed Data

In a multiple discriminant analysis, if the covariance matrices are not homogenous a quadratic discriminant function will be more efficient. This can be constructed by transforming the values of the original data into logarithms. In this analysis, however, the pooled within-group dispersion matrix was singular or ill-conditioned (the determinant being less than 0.001) and no inverse can be obtained. Therefore it is impossible in principle to obtain a meaningful discriminant function for this logarithmically transformed data.

(iii) Principal Co-ordinate Analysis (a) Simple Matching Coefficient Matrix (Forty-Two Multistate Characters). Data not Standardised

The method of principal co-ordinate analysis was devised by Gower (1966) and starts from a comparison of individuals - a Q matrix - which in this case is based on the distance between every pair of individuals. These were computed from the simple matching coefficients S_{SM} of Sokal and Sneath (1963) using the relation $D = (1-S_{SM})^{\frac{1}{2}}$. S_{SM} is not restricted to a 2-state character in this analysis.

Essentially, principal co-ordinate analysis is allied to the better known method of principal components, but differs from the latter in that it will utilise discrete variables measured on a norminal or ordinal scale. The Q-mode distance matrix must first be transformed in a manner specified by Gower (1966) so that distances are preserved in the orthogonal system of principal axes given by the latent vectors of the transformed matrix.

This method of analysis has been applied by Sims (1966) to Oligochaete systematics and in a less developed form by Sheals (1964) to Acarine taxonomy. Wilkinson (1970) used it in the taxonomy of Drepanidae (Lepidoptera), and Boratyński & Davies (1971) used a principal co-ordinate analysis to examine the taxonomy of male Coccoidea (Homoptera). They concluded that the principal co-ordinate methods are best suited to analyse coded, multistate taxonomic data and preferred this method in this particular study.

In the present analysis of twenty-two Cicadellidae, forty-two multistate characters were used. Twenty-two of the characters are 2-state and the rest (20) are multistate, but the employment of the simple matching coefficient does not enable full use to be made of the latter characters.

A between-taxa match-mismatch distance matrix was first computed and the 'distance' between any two pairs of species obtained from the relation given above. This distance lies between 0 and 1, so that species identical to one another have a similarity of 0.0.

C. persimilis and *C. aurantipes*, and *R. proceps* and *A. mixtus* have distance values of zero. The reason for this has been explained in the single linkage cluster analysis, where the same forty-two multistate characters were used. *U. reticulata* also has very low distance coefficients with the rest of the twenty-two species, showing the closest affinity to *I. lanio* (0.707).

The latent roots indicate the proportion of the total variance accounted by each component. Ten such axes were computed and they account for 90.70% of the total variance, the first five accounting for 70.80%. In the analysis by Boratyński & Davies (1971) the first five accounted for 69.45% of the total variance. The latent roots and percentage variance of the ten axes computed are given in Table 31.

Table 31 Latent Roots and Percentage Variance - Principal Co-ordinate Analysis

Latent Root		Percentage Variance
I	1.1033	31.8970
II	0.4924	14.2360
III	0.3266	9.4413
IV	0.2966	8.5747
V	0.2308	6.6731
VI	0.1866	5.3947
VII	0.1517	4.3846
VIII	0.1265	3.6578
IX	0.1197	3.4594
X	0.1043	3.0145

According to Boratyński & Davies, in taxonomic work the first three vectors rarely account for more than 75% of the total variance, although some of the total variance is not of great taxonomic interest. Sheals (1964) says that a vector corresponding to a small latent root would contribute little to the original matrix, and that it was sufficient to calculate the first three latent vectors, a meaningful grouping usually being obtained if latent vectors II and III are used as co-ordinates. In this analysis the first three latent roots account for only 55.5% of the total variance, hence the first five were taken.

As this is a Q-matrix, the principal co-ordinates of each are given by the elements of the corresponding vector. When these are plotted against each other, groupings of the species are obtained which may be meaningful taxonomically. The normalised latent vectors for the first five axes are given in Table 32.

Table 32 Normalised Latent Vectors (= Principal Co-ordinates) for First Five Axes

Species	Latent Vector				
	I	II	III	IV	V
U. *reticulata*	0.5775	-0.2981	0.5024	-0.2037	0.2622
C̄. *viridis*	0.0815	0.3404	-0.3814	-0.3818	0.2246
Ḡ. *coccinea*	0.0677	0.2826	-0.2382	-0.4891	0.0156
Ī. *distinguendus*	0.1724	0.4995	0.0728	0.4138	-0.2870
Ō. *flavicollis*	0.3784	-0.1445	-0.1250	-0.0922	-0.0756
Ē. *cuspidata*	0.1874	-0.3488	-0.4431	0.1604	-0.4010
D̄. *stylata*	-0.1452	-0.0322	0.1114	-0.1352	0.0366
R̄. *coronifera*	-0.1662	-0.0256	-0.0198	-0.0544	-0.0017
Ē. *ocellaris*	-0.1735	-0.0621	0.0273	-0.1109	0.1019

Table 32 (continued)

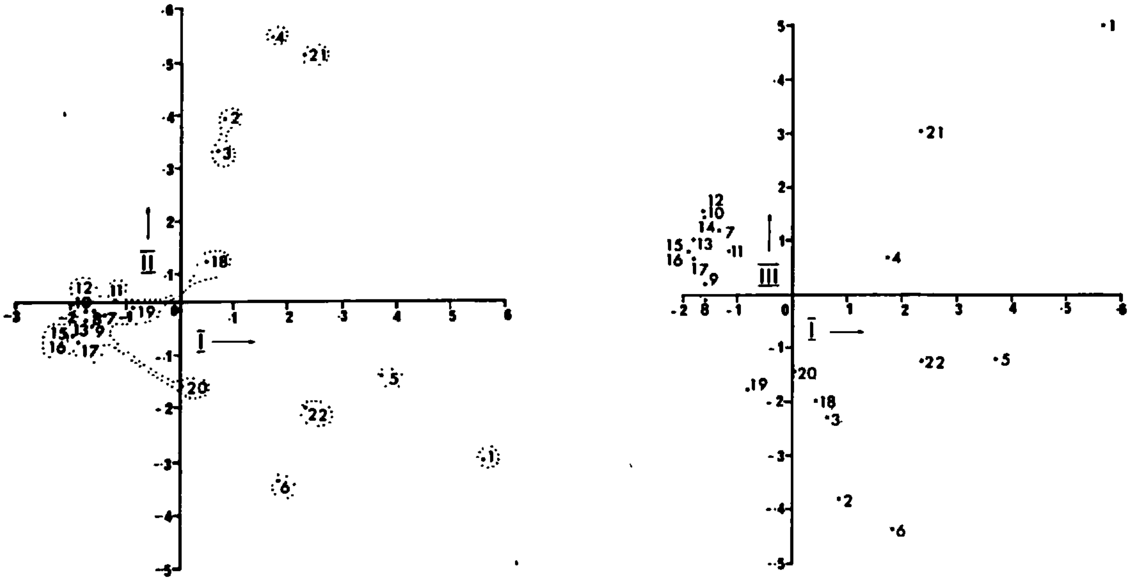
Species	Latent Vector				
	I	II	III	IV	V
R. proceps	-0.1708	-0.0224	0.1519	-0.0232	-0.1258
G. ventralis	-0.1209	0.0033	0.0799	-0.1848	-0.0641
A. mixtus	-0.1708	-0.0224	0.1519	-0.0232	-0.1258
M. grisescens	-0.1828	-0.0495	0.1024	-0.1018	0.0353
M. parvicauda	-0.1734	-0.0574	0.1438	0.0444	-0.0327
C. persimilis	-0.1962	-0.0747	0.0833	0.0641	0.0907
C. aurantipes	-0.1962	-0.0747	0.0834	0.0641	0.0907
E. sulphurella	-0.1937	-0.0811	0.0736	0.0717	0.0270
G. puncticollis	0.0495	0.0739	-0.2080	0.4804	0.6378
M. sexnotatus	-0.0895	-0.0165	-0.1861	0.0975	0.1854
B. punctata	-0.0009	-0.1602	0.1493	0.0273	-0.2979
Z. scutellaris	0.2340	0.4687	0.3042	0.1096	-0.1954
I. lanio	0.2336	-0.2036	-0.1372	0.1754	-0.0313

The first co-ordinate here is principally concerned with the separation of the species on subfamily levels.

The second co-ordinate is concerned with the separation of species at tribal levels, as is the third co-ordinate.

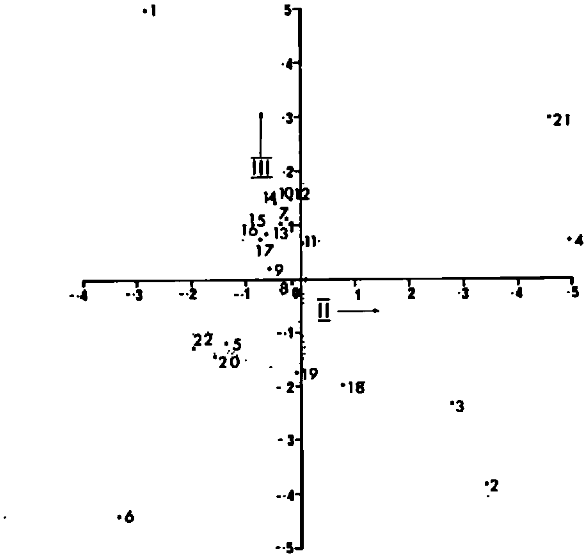
In the groupings of the species obtained by the combination of the first and second co-ordinates (Fig. 48), a tight cluster is formed of species belonging to the subfamily Deltocephalinae. The other species are scattered except for *C. viridis* (2) and *G. coccinea* (3) which belong to one subfamily Cicadellinae. *G. puncticollis* (18), *M. sexnotatus* (19), and *B. punctata* (20) lie a little outside the big Deltocephalinae cluster as they belong to separate tribes Grypotini, Macrostelini and Balcluthini respectively. The separation of the Deltocephalinae into tribes is seen in the combination of the first and third co-ordinates. Here, the

FIG48 Principal Co-ordinate Analysis (42 Multistate Characters).



a.Coordinates I and II

b.Coordinates I and III



c.Coordinates II and III

species belonging to tribe Athysanini are clustered together (species 10 to 17) and species belongong to tribe Deltocephalini *R. coronifera* (18) and *E. ocellaris* (9) are together. However, *G. puncticollis* (18), *M. sexnotatus* (19) and *B. punctata* (20) which belong to separate tribes lie separately. *D. stylata* (7) which belongs to a separate tribe, Doraturini, according to Le Quesne (1969), lies within the Athysanini group of species in this analysis. Similar groupings of species are seen in the combinations of the second and third co-ordinates (Fig. 48c).

It can therefore be concluded that the taxonomic groupings obtained in the principal co-ordinate analysis are similar to the orthodox adult classification as used by Le Quesne, except for *D. stylata*, which here lies within the Athysanini, whereas it is placed in a separate tribe in Le Quesne's classification of the adults. Ribaut (1952) puts it within the common tribe Euscelini.

Finally the single linkage cluster analyses and the principal component analysis have certain similarities and differences. The following are the similarities:-

a. *C. viridis* and *G. coccinea* which belong to one subfamily form a cluster in both analyses, thus showing the close affinity of the two species.

b. The Deltocephalinae form another cluster in both analyses, although in two of the single linkage analyses *G. puncticollis*, *M. sexnotatus* and *B. punctata* join the cluster lower down the similarity level.

c. U. reticulata lies away from the rest of the Cicadellidae in both analyses. This species is placed in a separate family by Evans (1947) and by Ribaut (1952).

However, there are differences in the clustering or the scatter of I. distinguendus, O. flavicollis, E. cuspidata, I. lanio and Z. scutellaris. In the principal co-ordinate analysis they are scattered singly whereas in the single linkage analyses they are clustered. G. puncticollis lies closer to the rest of the Deltocephalinae in the principal co-ordinate analysis than in the single linkage cluster analyses.

(iv) Principal Component Analysis

The three separate principal component analyses used here were all of a correlation matrix, but three separate analyses were made using (a) nine quantitative characters, (b) forty-two multistate characters, and (c) nine quantitative and forty-two multistate, i.e. fifty-one characters in all. All the three analyses were of a R-mode type which begins from the correlations between characters.

From a correlation matrix a set of latent roots and latent vectors are extracted, the latent vectors of which are orthogonal. The latent roots indicate the percentage of the total variance absorbed by each component. The elements of the latent vector indicate the weights attached to each variable in determining the corresponding principal component.

(a) Correlation Matrix (Nine Quantitative Characters). Primary Data not Transformed.

This is an orthodox R-mode analysis which forms a correlation between nine quantitative characters. The nine latent roots and percentage variance were extracted and the first five account for 97.33% of the total variance. The nine latent roots and percentage variance are given in Table 33.

Table 33 Latent Roots and Percentage Variance - Principal Component Analysis (Nine Quantitative Characters)

Latent Root		Percentage Variance
I	7.041	78.232
II	0.723	8.033
III	0.591	6.565
IV	0.237	2.634
V	0.168	1.869
VI	0.114	1.262
VII	0.070	0.773
VIII	0.037	0.408
IX	0.020	0.220

Of these nine vectors only the first three are considered here, accounting for 92.8% of the total variance.

Table 34 gives the elements of the latent vectors for the first three axes only.

Table 34 Elements of the Latent Vectors (Three Axes)

Variable	Latent Vector		
	I	II	III
Head width (1)	0.342	-0.373	0.264
Head length (2)	0.252	-0.560	0.737
Pronotal width (3)	0.349	-0.352	0.140
Pronotal length (4)	0.335	-0.411	0.002
Hind femur length (5)	0.339	0.227	-0.383
Hind tibia length (6)	0.340	0.324	-0.338
Total body length (7)	0.361	0.076	0.107
Length of VIII tergite (8)	0.347	-0.153	0.025
Length of IX tergite (9)	0.323	0.264	-0.344

Along the first axis all the variables have virtually equal weighting with the total body length having the highest weight (0.361). This situation of the variables having equal weighting is characteristic of the first vector in most principal component analyses.

Along the second axis there is a contrast between head length and pronotal length, and total body length has the smallest weight.

Along the third axis there is a contrast of the head length having the largest weight and pronotal length having the smallest weight.

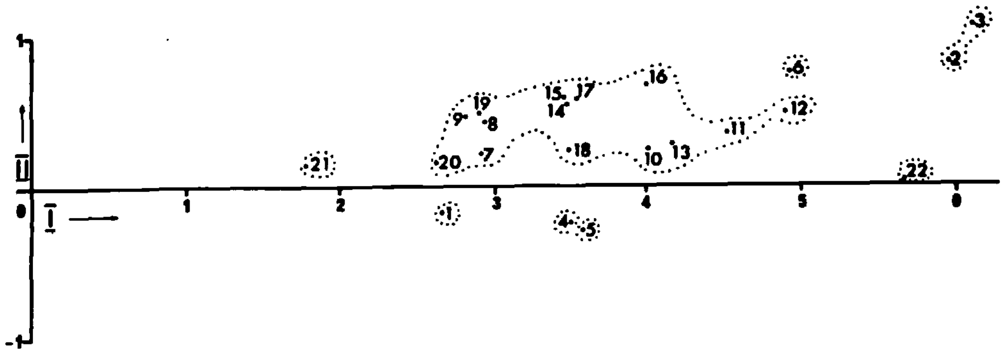
The latent vectors extracted from a correlation matrix are used to compute the principal components. In this particular analysis the principal components computed for each specimen measured and the means for each species were calculated and are given in Table 35.

Table 35 Principal Components on First Three Axes

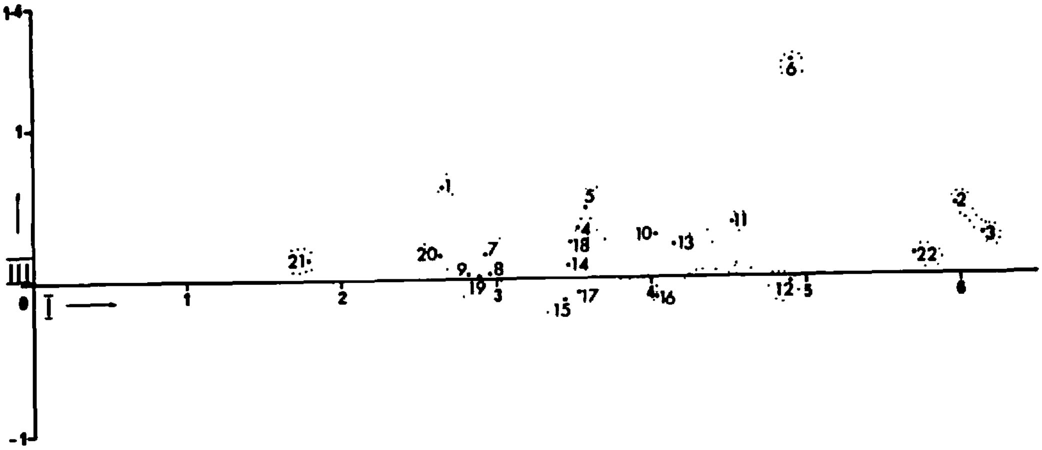
Species	Principal Components		
	I	II	III
U. reticulata	2.662	-0.182	0.605
C. viridis	5.987	0.806	0.349
G. coccinea	6.118	1.067	0.291
I. distinguendus	3.522	-0.216	0.316
O. flavicollis	3.568	-0.278	0.432
E. cuspidata	4.910	0.770	1.418
D. stylata	2.967	0.217	0.193
R. coronifera	2.968	0.412	0.048
E. ocellaris	2.814	0.467	0.030
R. proceps	4.102	0.246	0.296
G. ventralis	4.513	0.349	0.186
A. mixtus	4.902	0.484	-0.021
M. grisescens	4.156	0.286	0.204
M. parvicauda	3.478	0.544	0.093
C. persimilis	3.442	0.573	-0.111
C. aurantipes	4.106	0.653	-0.120
E. sulphurella	3.516	0.560	-0.090
G. puncticollis	3.490	0.235	0.225
M. sexnotatus	2.928	0.473	0.051
B. punctata	2.613	0.183	0.079
Z. scutellaris	1.799	0.143	0.145
I. lanio	5.681	0.017	0.113

The components on any two axes for each species can be plotted against each other and groupings of the species may be interpreted taxonomically. All possible combinations of the first three axes were plotted and are given in Fig. 49.

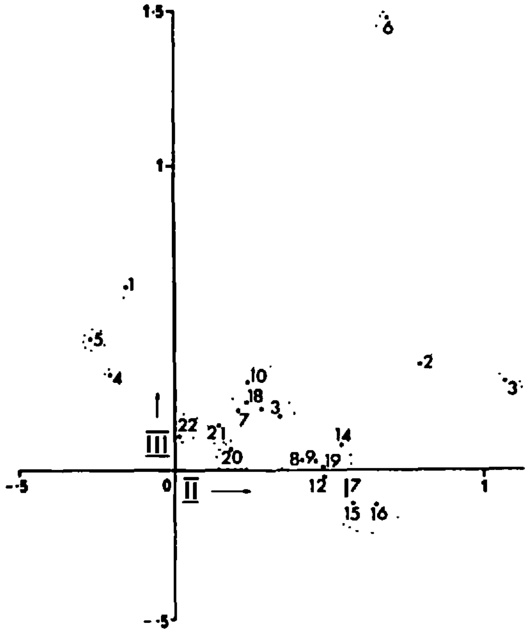
FIG 49 Principal Component Analysis (9 Quantitative Characters).



a. Components I and II



b. Components I and III



c. Components II and III

The groupings of the species obtained from combinations of the first axis with the second and third respectively (Fig. 49a, b, c), show that species are scattered largely along the first axis only. Total body length has the largest weight along this axis and no meaningful groupings were obtained. Even the combinations of the second and third axes do not show any meaningful groupings, although it is quite obvious that head length has the largest weight along both these axes. This is displayed by E. cuspidata (6) being well away from the main group of species. This particular species has an extremely long head and this feature was also brought out in the multiple discriminant analysis on the same nine quantitative characters.

The following are the similarities between the multiple discriminant analysis and the principal component analysis on the same nine quantitative characters.

a. The species are scattered largely along the first axis (Fig. 47a, b; 49a, b).

b. The Deltocephalinae are clustered in the center in both analyses.

c. E. cuspidata lies away from the main group of species and this is more so in the groupings obtained from axes I and III, II and III, in both analyses. In the multiple discriminant analysis head length has a large weight along the third axis, and in the present analysis it has large weights along both the second and the third axes.

d. C. viridis and G. coccinea are clustered together in both analyses.

Hence as both the multiple discriminant analysis and the principal component analysis did not yield taxonomically useful conclusions it can be said that the nine quantitative characters used in both analyses are either too few and/or are of restricted classificatory value.

(b) Correlation Matrix (Forty-Two Multistate Characters). Primary Data not Standardised.

This is also an R-mode matrix like the previous analysis, but here forty-two multistate characters were used in a single analysis.

The largest ten latent roots and percentage variances were computed and this amounted to 9[illegible].79% of the total variance. These are given in Table 36.

Table 36 Latent Roots and Percentage Variance - Principal Component Analysis (Forty-Two Multistate Characters

Latent Root		Percentage Variance
I	13.489	32.116
II	6.658	15.853
III	5.087	12.113
IV	4.376	10.418
V	3.426	8.157
VI	2.686	6.394
VII	1.951	4.646
VIII	1.400	3.334
IX	0.898	2.134
X	0.712	1.696

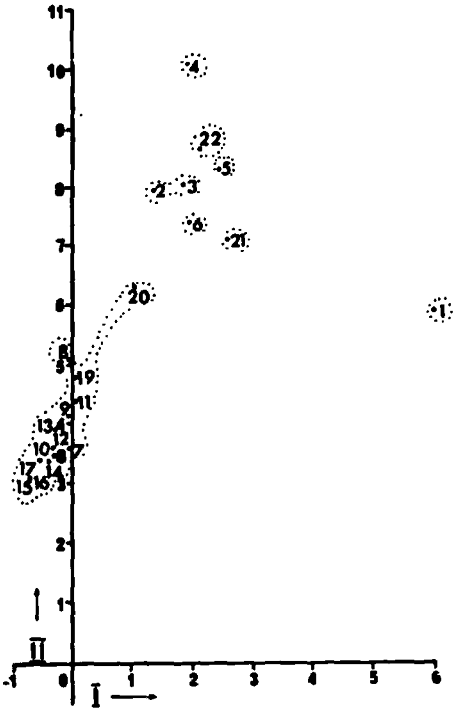
The first five latent roots amount to 78.59% of the total variance. This table, when compared to Table 31, shows that the latent roots and percentage variance are almost similar in the principal co-ordinate analysis and the present analysis, both of which are based on forty-two multistate characters.

The tables in Appendix IV give the variables with above average positive and negative weights for the first five axes, the mean value of the elements being 1/ 42 = 0.1543.

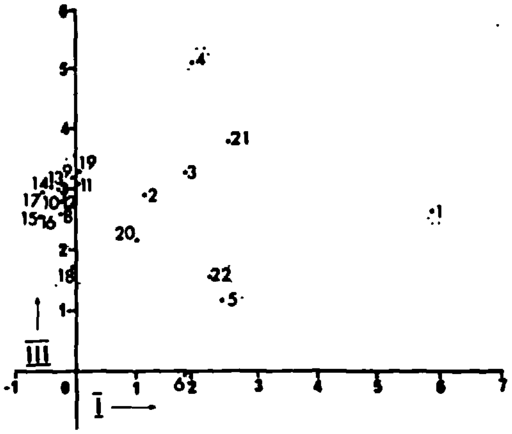
Some of the characters carry large positive and negative weights along many axes. The characters that separate U. reticulata from the rest of the species carry most of the large positive and negative weights along the first axis. The number and position of the bristles on the abdominal segments which can be used for the separation of the Deltocephalinae into tribes, carry large positive weights along the second axis. The characters that separate E. cuspidata from the rest of the species carry the largest weights along the third axis. The fourth and fifth axes are dominated by some general characters.

When the principal components are plotted, groupings of the various species are obtained and it may be possible to give these some taxonomic meaning. Table 37 gives the principal components for the first five axes, all combinations of which were plotted, although only the combinations of the first three axes are given in Fig. 50.

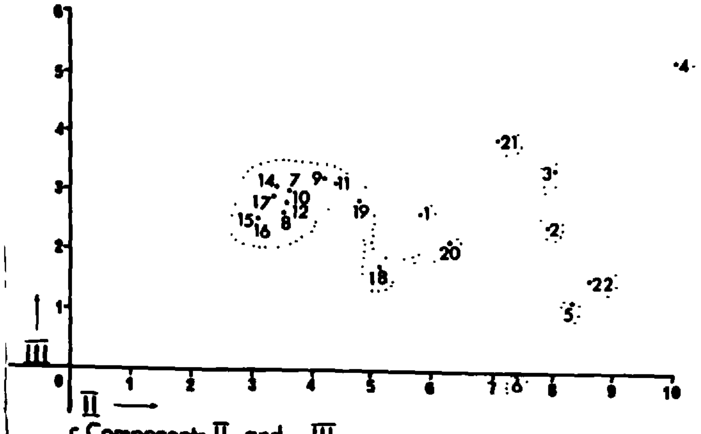
FIG 50 Principal Component Analysis (42 Multistate Characters).



a. Components I and II



b. Components I and III



c. Components II and III

Table 37 Principal Components for the First Five Axes - Principal Component Analysis (42 Multistate Characters)

Species	Principal Components				
	I	II	III	IV	V
U. reticulata	5.961	5.847	2.672	-0.055	1.372
C. viridis	1.353	7.676	2.948	2.522	2.759
G. coccinea	1.841	8.091	3.316	1.518	2.143
I. distinguendus	1.910	10.056	5.137	-1.160	2.349
O. flavicollis	2.430	8.328	1.157	3.217	2.469
E. cuspidata	1.905	7.478	-0.109	-1.191	0.548
D. stylata	-0.031	3.614	3.084	-0.251	1.640
R. coronifera	-0.338	3.519	2.642	-0.076	1.559
E. ocellaris	-0.083	4.269	3.230	-0.404	2.521
R. proceps	-0.315	3.636	2.891	-0.369	1.459
G. ventralis	0.073	4.439	3.191	-0.222	2.268
A. mixtus	-0.315	6.363	2.891	-0.369	1.459
M. grisescens	-0.280	3.907	3.078	-0.489	1.887
M. parvicauda	-0.477	3.477	3.044	-0.424	1.392
C. persimilis	-0.666	3.114	2.597	-0.433	0.942
C. aurantipes	-0.666	3.114	2.597	-0.433	0.942
E. sulphurella	-0.554	3.431	2.914	-0.488	1.381
G. puncticollis	-0.035	5.114	1.733	-1.658	1.036
M. sexnotatus	0.043	4.872	2.819	0.591	1.411
B. punctata	1.073	6.365	2.184	0.756	1.292
Z. scutellaris	2.595	7.168	3.885	1.228	-1.886
I. lanio	2.231	8.630	1.591	0.322	3.200

Corresponding columns of this table could be compared with Table 32 by a method such as Spearman's rank-correlation coefficients, in order to see objectively how far the two methods of classification agree.

The first component ranks the species at subfamily levels and the second and third components are concerned with the separation of the species on tribal levels.

A tight cluster of the subfamily Deltocephalinae is present with G. punccticollis (18), M. sexnotatus (19) and B. punctata (20) lying a little away from the main cluster. Usually they are placed into different tribes, Grypotini, Macrostelini and Balcluthini respectively. Tribes Athysanini, Doraturini and Deltocephalini, which also belong to the same subfamily, lie together with no real scatter or grouping among them (Fig. 50a). R. proceps (10) and A. mixtus (12), and C. persimilis and C. aurantipes (16) are on one point as seen in previous analyses, where the nine quantitative characters were omitted. The Doraturini, Deltocephalini and Athysanini form one cluster even in the groupings obtained with the second and the third axes, which are both concerned with the separation of species at tribal levels. However, if Table 2 (Appendix IV) is examined, the largest positive weights along the second axis are those of the pattern of the bristles on the abdominal surface. All species numbered 7 to 17 have a similar pattern of bristles, whereas G. puncticollis (18), M. sexnotatus (19) and B. punctata (20) have either different patterns, or no prominent bristles.

The rest of the species lie singly except for C. viridis and and G. coccinea which lie in a cluster (they belong to one subfamily, Cicadellinae).

As compared to the single linkage cluster analyses where some of the Deltocephalinae (G. puncticollis, M. sexnotatus and

B. punctata) were not clustered with the rest of the species belonging to the same subfamily, here these three species are slightly outside the main group indicating that they belong to different tribes. In both the single linkage cluster analyses and the present analysis, *U. reticulata* is away from the other Cicadellidae, and *C. viridis* and *G. coccinea* lie close together.

However, when this analysis is compared to the principal co-ordinate analysis several similarities are seen, and these are as follows:-

G. puncticollis, *M. sexnotatus* and *B. punctata* are slightly outside the main group of Deltocephalinae, indicating that they belong to separate tribes. The rest of the subfamily lies in a tight cluster, although the separation of the Athysanini and Deltocephalini into groups which occurs in the principal co-ordinate analysis is absent in the principal component analysis. However, *D. stylata* (7), which is placed in a tribe by itself by Le Quesne, is within the Athysanini cluster in the principal co-ordinate analysis, and within the group of Deltocephalinae in this analysis.

C. viridis and *G. coccinea* are in one group in both analyses, and *U. reticulata* is away from the rest of the Cicadellidae. The rest of the species are scattered singly in both analyses.

Although the principal co-ordinate analysis was a Q-mode analysis and the principal component analysis an R-mode type, similar taxonomic groupings of species were obtained from both.

(c) Correlation Matrix (Fifty-One Characters - Forty-Two Multistate and Nine Quantitative). Primary Data not Standardised.

As in the previous analysis this is a correlation matrix but here fifty-one characters have been used.

The correlation matrix provides a series of latent roots and vectors. The largest ten latent roots extracted account for 95.04% of the total variance. The first five which account for 75.50% of the total variance were used in the analysis. The following table gives the latent roots and percentage variance of the ten axes.

Table 38 Latent Roots and Percentage Variance - Principal Component Analysis (51 Characters)

Latent Root		Percentage Variance
I	14.209	27.861
II	9.708	19.035
III	6.171	12.101
IV	5.050	9.902
V	4.366	8.561
VI	3.005	5.892
VII	2.252	4.416
VIII	1.942	3.807
IX	1.386	2.718
X	0.892	1.748

When compared to Tables 31 and 36 the first five axes in all the three analyses amount to almost similar percentages.

Variables with positive and negative weights greater than the mean value 1/ 51 = 0.141 are of interest. Tables 6 to 10 in Appendix IV give the variables with above-average positive and negative weights along the first five axes.

The first axis which absorbs 27.86% of the total variance has exactly the same variables with weights larger than the mean value as the previous analysis (Table 1, Appendix IV), of forty-two multistate characters. Moreover, these variables have almost similar weights in both analyses (Tables 1 and 6, Appendix IV).

The variables with above-average positive and negative weights along the second axis are given in Table 7 (Appendix IV). The second axis in the analysis of forty-two multistate characters, however, was influenced by characters concerned with the chaetotaxy (Table 2, Appendix IV).

The third axis in both analyses show only a few characters with above-average positive weights that are common to both axes (Tables 3 and 8, Appendix IV). However, the pattern of the bristles which has some large weights along the third axis in this analysis is of lesser importance in the analysis of forty-two multistate characters.

Table 9 (Appendix IV) which gives the variables with above-average positive and negative weights along the fourth axis shows that variables 6, 9, 11 and 18 also carry above-average positive weights along the fourth axis in the analysis on forty-two characters, (Table 4, Appendix IV).

Table 10 (Appendix IV) shows that variables 10 and 40 with above-average positive weights, and variable 41 with above-average negative weight, are common variables along the fifth axis in the same analysis on forty-two multistate characters, and of fifty-one characters (Tables 5 & 10, Appendix IV).

Table 39 gives the principal component scores for the first five axes. All five axes were plotted, although only the combinations of the first three are given here (Fig. 51).

Table 39 Principal Component Scores for the First Five Axes - Principal Component Analysis (51 Characters)

Species	Principal Components				
	I	II	III	IV	V
U. reticulata	4.751	6.398	3.991	2.009	1.003
C. viridis	-0.861	9.293	4.423	3.668	-0.522
G. coccinea	-0.416	9.305	4.730	3.306	0.248
I. distinguendus	-0.416	8.065	8.332	2.531	2.447
O. flavicollis	0.895	8.339	4.647	2.037	-2.297
E. cuspidata	0.212	8.327	3.475	-1.274	1.086
D. stylata	-0.966	3.835	3.059	2.495	1.475
R. coronifera	-1.297	3.707	2.799	2.241	1.151
E. ocellaris	-1.130	4.313	3.391	2.756	1.904
R. proceps	-1.492	4.485	2.760	2.421	1.596
G. ventralis	-1.369	5.558	3.064	3.001	1.876
A. mixtus	-1.776	5.062	2.486	2.674	1.701
M. grisescens	-1.548	4.806	2.906	2.690	1.922
M. parvicauda	-1.537	3.862	2.901	2.409	1.557

Table 39 (continued)

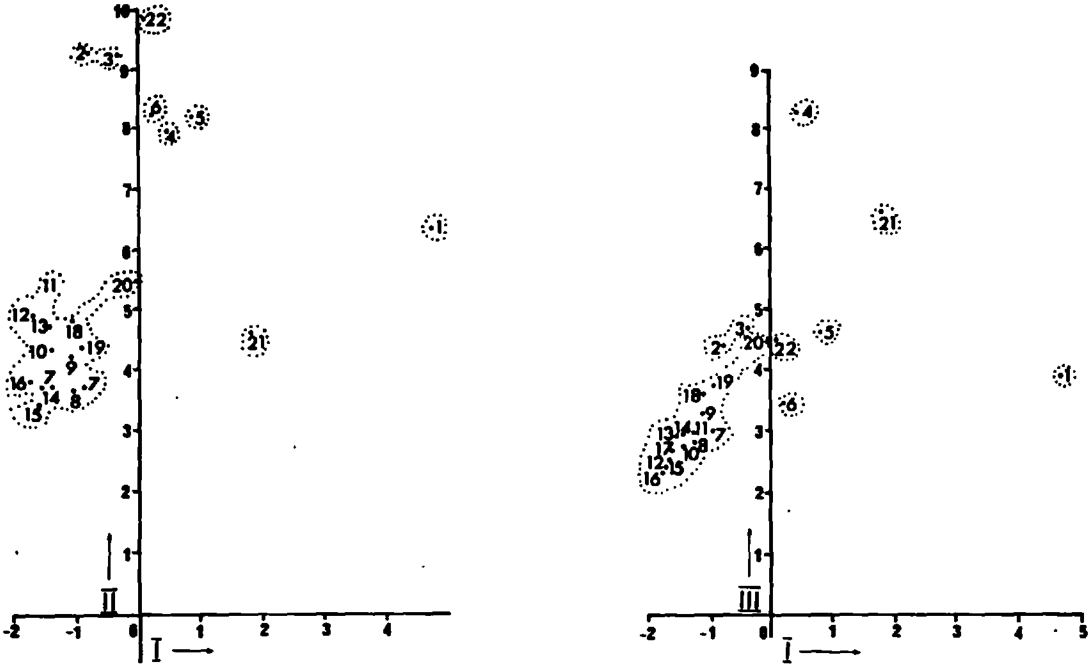
Species	Principal Components				
	I	II	III	IV	V
C. persimilis	-1.693	3.509	2.540	1.998	1.288
C. aurantipes	-1.847	3.910	2.361	2.111	1.367
E. sulphurella	-1.639	3.837	2.736	2.331	1.587
G. puncticollis	-1.148	4.990	3.648	0.573	1.908
M. sexnotatus	-1.013	4.473	3.785	2.262	1.397
B. punctata	-0.013	5.536	4.502	1.473	-0.111
Z. scutellaris	1.814	4.659	6.646	1.209	-1.404
I. lanio	0.072	9.906	4.515	2.148	0.956

As mentioned before, corresponding columns of this table could be compared with Tables 32 and 37 by Spearman's rank correlation coefficients so as to see objectively how far the three methods of classification agree.

As has been said before, the first component is concerned with the separation of the species at the subfamily levels, the second and third are concerned with the separation at tribal levels.

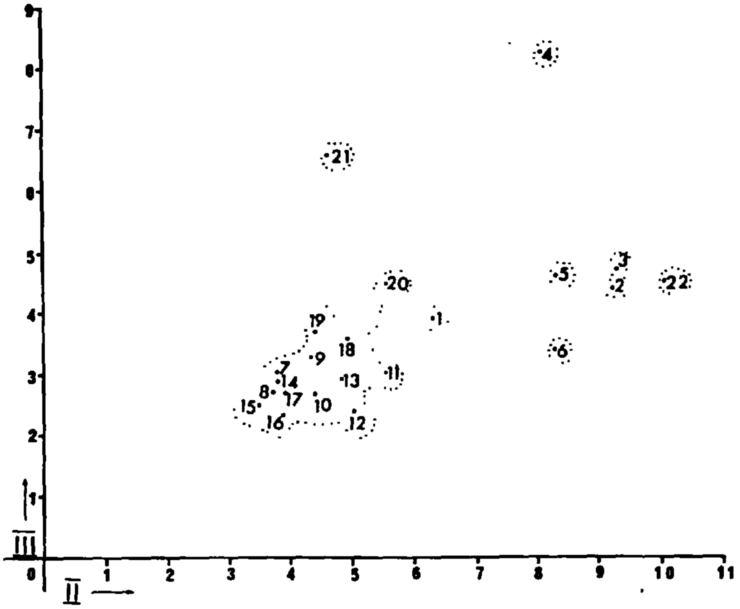
The variables with the largest weights along the first axis are those which separate *U. reticulata* from the rest of the species. Fig. 51 shows that the Deltocephalinae form a cluster, with the rest of the species lying scattered. As in the previous analysis and the principal co-ordinate analysis, both on forty-two characters, *G. puncticollis* (18), *M. sexnotatus* (19) and *B. punctata* (20) are a little outside the big group of Deltocephalinae, especially along axes II and III. The other

FIG 51 Principal Component Analysis (51 Characters).



a. Components I and II

b. Components I and III



c. Components II and III

tribes within this subfamily are not separately grouped and this was so in the previous analysis. The rest of the species are scattered except for C. viridis and G. coccinea which are together.

There is very little change in the scatter or the groupings of the species between this analysis of fifty-one characters and the previous one of forty-two characters. Hence it can be concluded that the nine quantitative characters did not make a great change in the taxonomic grouping of the species in this analysis. The principal co-ordinate analysis on forty-two multistate characters also gave groupings of the species similar to this analysis.

IV. General Discussion

The purpose of applying the various numerical analyses to larval characters was to determine whether a classification based on them agreed or disagreed with the existing taxonomy, which is based on adult characters.

On the whole, the analyses support and complement the existing classification of Cicadellidae, although they raise a number of questions.

The principal co-ordinate and the principal component analyses, both of which were carried out on forty-two multistate characters, as well as the principal component analysis on fifty-one characters, are the methods yielding results in best general agreement with the current orthodox views on Cicadellid classification. The three single linkage cluster analyses were less close to the traditional classification, except that they clustered C. viridis and G. coccinea together, and united most or all of the Deltocephalinae (tribes Doraturini, Athysanini and Deltocephalini). One other aspect revealed by the cluster analysis is that U. reticulata joins the cluster at low levels of similarity, and in the principal co-ordinate and principal component analyses this same species lies away from all others (Fig. 48, 49, 50). The multiple discriminant analysis and the principal component analysis revealed poor taxonomic grouping of the species when they were based on nine quantitative characters.

The principal component analysis on fifty-one characters and forty-two characters give simila' groupings, hence the nine quantitative characters added to the earlier analysis made no change in the pattern of the groupings. This together with the results obtained from the multiple discriminant analysis and principal component analysis on none quantitative characters indicate that these latter characters are either too few to counterbalance the other features, or that they are capable only of various forms of non-taxonomic discrimination, e.g. separating species with very long heads from the rest (e.g. E. cuspidata).

The three successful methods mentioned agree in all the groupings of the species, except that the principal co-ordinate analysis is more satisfactory and groups the two species belonging to the tribe Deltocephalini together (R. coronifera and E. ocellaris) (Fig. 48b, c). It also clusters the species belonging to the Athysanini in one group whereas this is not so in the principal component analyses. The Deltocephalini and Athysanini are grouped together in both these analyses. The clustering of Athysanini and Deltocephalini separately are the natural positions of these tribes (after Le Quesne, 1969) although Ribaut (1952) puts them in a common tribe Euscelini. In the present analysis with only forty-two multistate characters it is difficult to separate such closely related groups. Le Quesne (1969) uses wing venation and to a certain extent shape of aedeagus for the separation of the tribes in the subfamily Deltocephalinae, in the adults. Both these characters cannot of course be applied to fifth instar larvae. If more characters were available the position of these tribes would be clearer.

In the principal component analyses on forty-two and fifty-one characters, both of which were R-type analyses, the characters with positive and negative weights above the mean value are similar for the first, third, fourth and fifth axes. The second axis in the analysis on fifty-one characters is mainly influenced by the quantitative characters, though this hardly changed the groupings of the species.

The following is a summary of the main conclusions:

1. Multiple discriminant and principal component analyses of nine quantitative characters did not yield taxonomically useful data, presumably because the characters were too few and of restricted classificatory value.

2. Broadly speaking, the single linkage clustering methods and the multidimensional methods (principal components and co-ordinate) yielded generally similar conclusions when applied to forty-two multistate characters, with or without the additional nine quantitative characters.

3. However, the principal component and principal co-ordinate methods gave results more closely resembling the orthodox classification of the adult Cicadellidae.

4. However, on points of detailed resemblance the principal co-ordinate analysis of larval characters was closer to the orthodox classification of the adults than was the principal component analysis.

5. If Le Quesne's classification is taken as a standard, then the best method of numerical classification is the principal co-ordinate analysis. There is some theoretical justification for favouring this method (Boratyński & Davies, 1971) and it is therefore probably interesting that its application to previously unanalysed larval characters yields an arrangement most concordant with a widely accepted adult classification.

SECTION D

Key to the Fifth Instar Larvae of Twenty-Two British Cicadellidae

I. Introduction

This section is concerned with the key to the subfamilies and tribes of the fifth instar larvae of twenty-two British Cicadellidae. The description of each species is also included.

II. Key

a. Key to Subfamilies

1. Subgenal sulcus present. Antennal depression prominent.
Apex of hind femora without prominent spines
.... Ulopinae

\- Subgenal sulcus and antennal depression absent. Apex
of hind femora with prominent spines 2

2. Blunt cuticular outgrowths present on antennal ledge and
on dorsal abdominal surface .... Typhlocybinae

\- Blunt cuticular outgrowths absent on antennal ledge
and dorsal abdominal surface 3

3. Vertex as long or longer than width of head, and about
five times longer than pronotal length. Sharp
median keel present on face .... Eupelicinae

- Vertex shorter than width of head and as long or shorter than pronotal length. Sharp median keel on face absent 4

4. Ocelli on face 5

- Ocelli on vertex, or on or near to crown-face border 8

5. Transclypeal sulcus absent. Ridge above antennae in line with clypeogenal sulcus ..... Macropsinae

- Transclypeal sulcus present 6

6. Ridge above antennae forms an angle with clypeogenal sulcus. Ocelli about 2/3 the distance from antennal ridge to posterior margin ... Jassinae

- Ridge above antennae absent 7

7. Length of abdominal tergite VIII about twice the length of abdominal tergite IX. Subgenital plate in male extends beyond abdominal tergite IX, and rudiments of the first pair of gonapophyses in female extends to tip of abdominal tergite IX .... Idiocerinae

- Length of abdominal tergite VIII varies from half to almost the same length as abdominal tergite IX. Subgenital plate in male about 1/2 or 2/3 the length of abdominal tergite IX.

Rudiments of the first pair of gonapophyses in female do not extend to tip of abdominal tergite IX 8

8. Ocelli on vertex just above anterior margin of eyes and slightly nearer to posterior than anterior margin .... Cicadellinae

\- Ocelli nearer anterior margin of vertex or on crown-face border .... Deltocephalinae

b. Key to Tribes of Subfamily Deltocephalinae

1. Prominent bristles that follow a regular pattern present on dorsal abdominal surface 2

\- Prominent bristles absent 4

2. Anteclypeus narrow with width less than half its length .... Grypotini

\- Anteclypeus broad with width half or more than half its length 3

3. Bristles present on abdominal segments III to VIII .... Deltocephalini

\- Bristles absent on abdominal segments III to VI and present on segments VII and VIII ... Macrostelini

4. Prominent bristles absent. Only scattered abdominal hairs present .... Balcluthini

III. Descriptions of Species

Subfamily Ulopinae

Genus Ulopa Fallén

Brown with darker brown pits and small whitish hairs. Ocelli absent. Clypeogenal, clypeoloral and transclypeal sulci infolded. Frontogenal sulcus absent. Subgenal sulcus prominent. Anterior margin of vertex meeting with eyes but raised above them. Ridge above antennae forms an arch. Antennal depression prominent (Fig. 13d). Keels present at the sides of pronotum. Finger-like projection overhands meso-episternum. In male, subgenital plate pitted with short whitish hairs; in female rudiments of the first pair of gonapophyses have cleft at sides (Fig. 31c). Raised median line on thorax and abdomen. Total body length ♂ ♀ 2.7-3.2 mm. .... reticulata (Fabricius). Common in heather.

Subfamily Cicadellinae

Genus Cicadella Latreille

Yellow with longitudinal dark brown lines on body. Anterior margin of vertex largely rounded. Ocelli on vertex, nearer posterior than anterior margin. Ante- and postclypeus light brown and swollen. Labium dark brown. Two black spots on vertex nearer posterior margin and on genae. Scattered dark hairs present on abdomen with scattered bristles on tergite IX. Ventral abdominal surface pale yellow with no markings. Total body length ♂ 5.9-6.3 mm. ♀ 6.2-7.4 mm. .... viridis (Linnaeus) Common in Juncus

Genus Graphocraerus Van Duzee

Milky white with sharply pointed vertex. Ocelli nearer posterior than anterior margin of vertex. Ante- and post-clypeus swollen. Angle between crown and face acute. Total body length ♂ 6.5-7.2 mm. ♀ 6.7-7.4 mm. .... coccinea (Forster) Common on rhododendron

Subfamily Idiocerinae

Genus Idiocerus Lewis

Velvety pale white-green in colour with black strip across crown-face border. Vertex equal length throughout with straight anterior margin. Frontogenal sulcus reaches up to ecdysial cleavage line halfway up the frons (Fig. 52c). Hind tibia with poorly developed spines on dorsal surface and well developed ones on ventral surface. Length of abdominal tergite VIII twice that of abdominal tergite IX (Fig. 53e, f). Sub-genital plate in male extends beyond abdominal tergite IX, and first pair of outgrowths in female extends to tip of

Fig. 52

Facial View of the Fifth Instar Larvae of

a. *O. flavicollis*

b. *G. puncticollis*

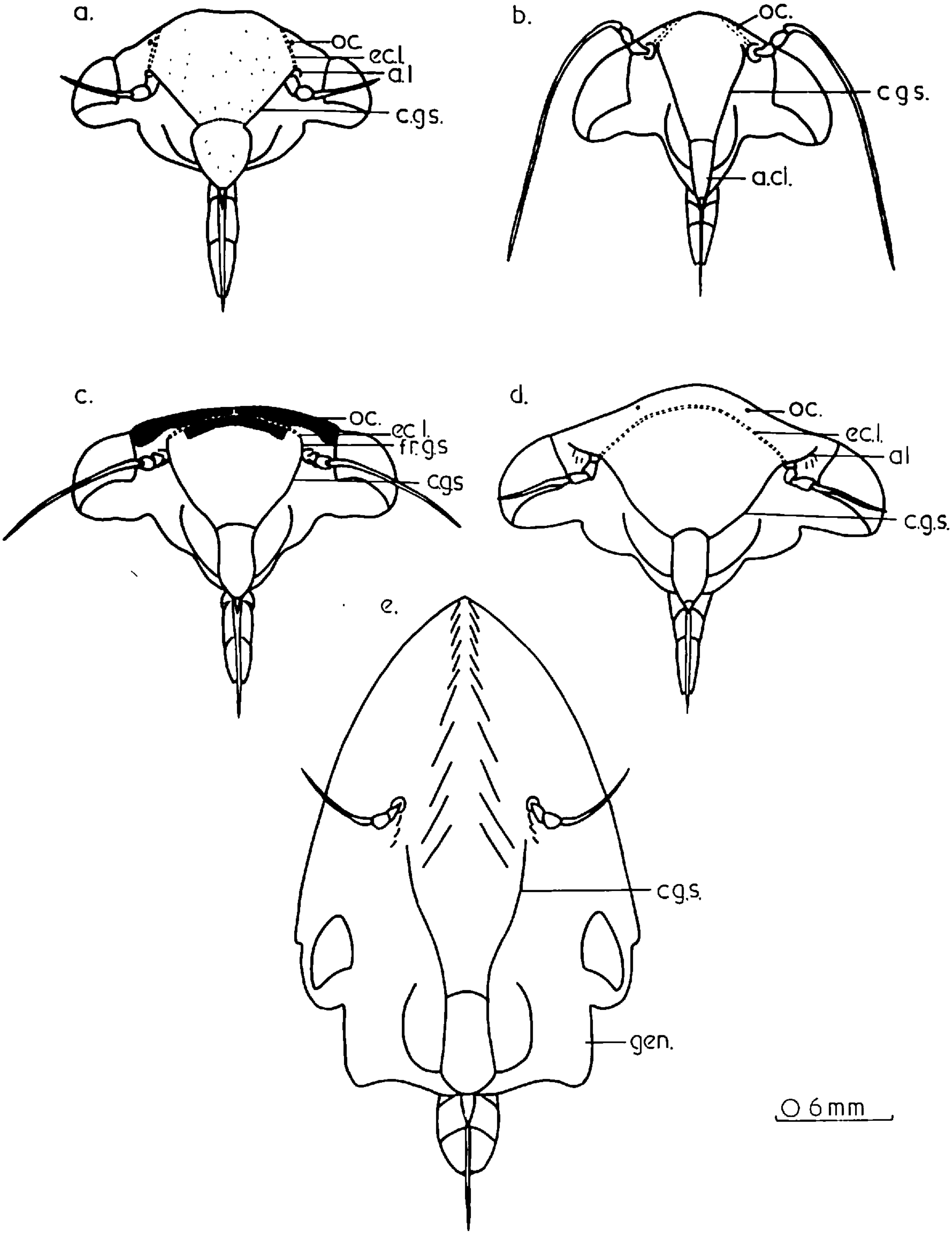
c. *I. distinguendus*

d. *I. lanio*

e. *E. cuspidata*

a.cl.	anteclypeus
a.l.	antennal ledge
c.g.s.	clypeogenal sulcus
ec.l.	ecdysial cleavage line
fr.g.s.	frontogenal sulcus
oc.	ocellus

FIG 52


a.
oc.
ec.l.
a.l
c.g.s.
b.
oc.
c.g.s.
a.cl.
c.
oc.
ec.l.
fr.g.s
c.g.s
d.
oc.
ec.l.
a.l
c.g.s.
e.
c.g.s.
gen.
0 6 mm

abdominal tergite IX (Fig. 53c, d). Scattered abdominal bristles present. Total body length ♂ 4.3-4.8 mm. ♀ 4.6-4.9 mm. .... distinguendus Kirschbaum. Common on white poplar.

Subfamily Macropsinae

Genus Oncopsis Burmeister

Brown with ocelli set in pits on face beside ecdysial cleavage line (Fig. 52a). Frontogenal and transclypeal sulci absent. Clypeogenal sulcus in line with ridge above antennae. No bristles, abdominal hairs only. Total body length ♂ 3.4-3.5 mm. ♀ 3.4-3.6 mm. .... flavicollis (Linnaeus) Common on birch.

Subfamily Eupelicinae

Genus Eupelix Germar

Sandy-coloured with vertex about five times longer than pronotum. Angle between crown and face acute. A sharp median keel present on face. Frontogenal sulcus absent. Clypeogenal sulcus up to just below antennae (Fig. 523). Compound eyes set at sides and well below short stumpy antennae. Genae with oblique angles. Bristles absent, whitish abdominal hairs present. Total body length ♂ 5.0-5.6 mm. ♀ 6.3-7.1 mm. .... cuspidata (Fabricius). Common in grass, mainly Holcus and Agrostis.

Fig. 53

Ventral View of Ninth Abdominal Segment.

a. *I. lanio* (Male Fifth Instar)

b. *I. lanio* (Female Fifth Instar)

c. *I. distinguendus* (Male Fifth Instar)

d. *I. distinguendus* (Female Fifth Instar)

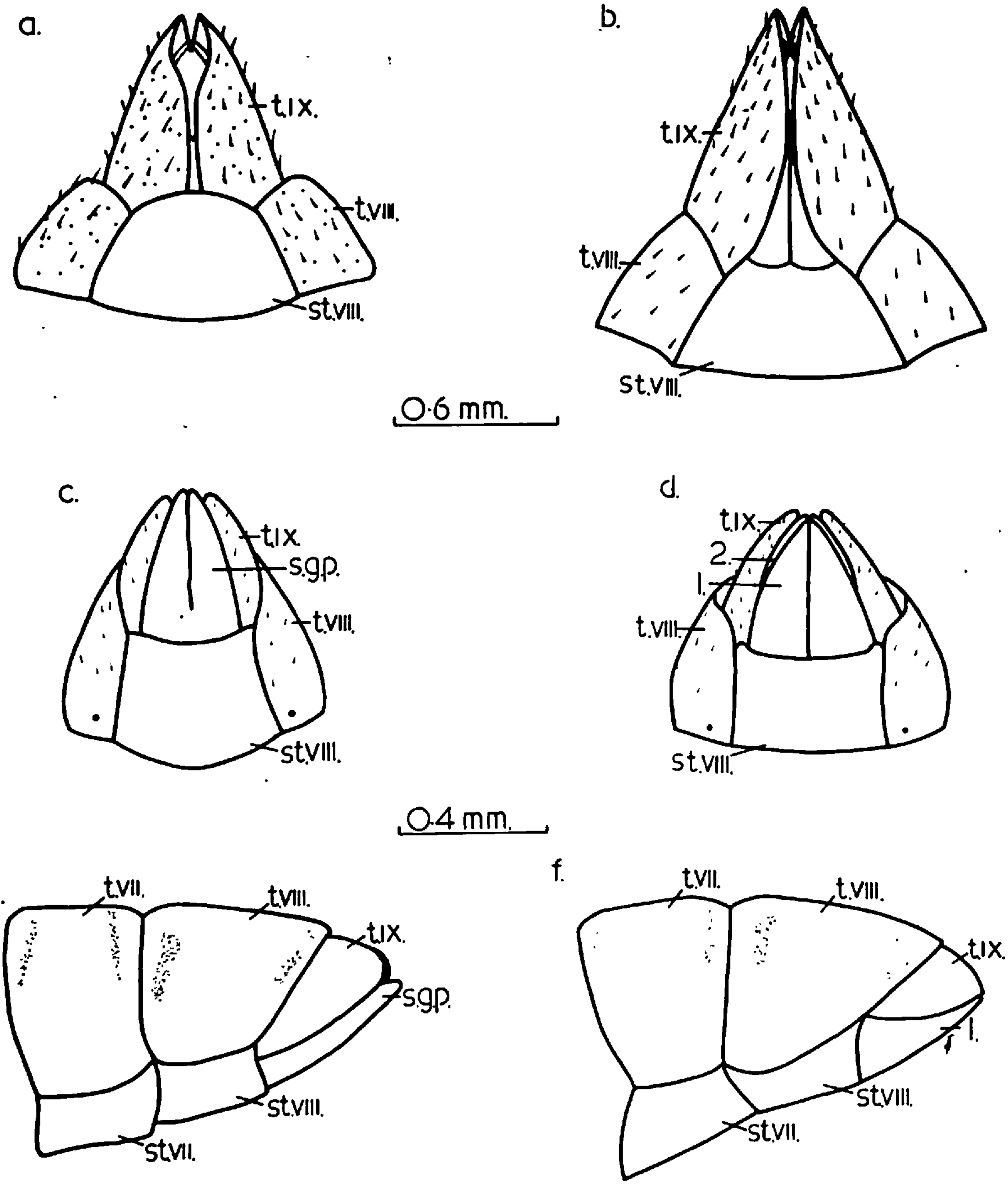
Lateral View of Eighth and Ninth Abdominal Segments.

e. *I. distinguendus* (Male Fifth Instar)

f. *I. distinguendus* (Female Fifth Instar)

s.g.p.	subgenital plate
st.VII.	seventh sternite
st.VIII.	eighth sternite
t.VIII.	eighth tergite
t.IX.	ninth tergite
1.	first pair of outgrowths (future 1st gonapophyses)
2.	second pair of outgrowths (future 2nd gonapophyses)

FIG 53


a.
t.IX.
t.VIII.
st.VIII.
b.
t.IX.
t.VIII.
st.VIII.
0·6 mm.
c.
t.IX.
s.g.p.
t.VIII.
st.VIII.
d.
t.IX.
2.
1.
t.VIII.
st.VIII.
0·4 mm.
e.
t.VII.
t.VIII.
t.IX.
s.g.p.
st.VIII.
st.VII.
f.
t.VII.
t.VIII.
t.IX.
1.
st.VIII.
st.VII.

Subfamily Jassinae

Genus Iassus Fabricius

Grass green or brown (with dark brown pits) in colour. Frontogenal sulcus absent. Ocelli on face about 2/3 the distance from antennal ridge to anterior margin. Antennae short and stumpy. Ridge above antennae forms an angle with clypeogenal sulcus (Fig. 52d). Prominent bristles absent, only scattered abdominal hairs present. Abdominal sternites flat and ninth abdominal tergite covers the rudiments of the external genitalia ventrally (Fig. 53a, b). Total body length ♂ 5.2-6.1 mm. ♀ 6.2-6.6 mm. .... lanio (Linnaeus). Common on Oak.

Subfamily Deltocephalinae

Tribe Deltocephalini

Genus Doratura Sahlberg

Brown with pale brown V-shaped band on dorsal abdominal surface. Angle between crown and face acute with ledge. Wing pads usually short reaching down to anterior margin of third abdominal segment. Bristles on abdomen short and sharp. Spines present on rudiments of gonoplacs in females. Subgenital plate in male broad with a rounded posterior margin, and short whitish hairs. Total body length ♂ 2.7-2.9 mm. ♀ 3.0-3.4 mm. .... stylata (Boheman) Common in grass, mainly Holcus.

Genus Recilia Edwards

Creamy white with brown markings on ante- and postclypeus, and dorsal abdominal surface. Legs with circular brown markings. Total body length ♂ 2.5-2.7 mm. ♀ 2.9-3.1 mm. .... coronifera (Marshall). Common in grass, mainly Holcus.

Genus Errastunus Ribaut

Dark brown with white tipped anterior wing pads. Bases of abdominal bristles with circular white patch. Reddish streak on posterior margin of abdominal segments. Subgenital plate in male and rudiments of the gonapophyses in female dark brown. Total body length ♂ 2.8-3.4 mm. ♀ 3.3-3.9 mm. .... ocellaris (Fallén). Common in grass, mainly Holcus.

Genus Macustus Ribaut

Light brown with darker brown transverse markings on ante- and postclypeus, and vertex. Two dark longitudinal lines on ventral abdominal surface.

Total body length ♂ 3.8-4.1 mm. ♀ 4.2-4.5 mm. .... grisescens (Zetterstedt). Common in grass.

Genus Graphocraerus Thomson

Grass green with white-green eyes and grey-green legs. Short brown bristles on abdomen. Four bristles on segments III-VII and six on segment VIII. Medium length antennae.

Total body length ♂ 4.5-4.6 mm. ♀ 4.6-4.8 mm.

.... ventralis (Fallén)

Common in grass.

Genus Rhytistylus Fieber

Light brown with prominent V-shaped marking on post-clypeus, genae, episternum and epimeron of pro- and meso-thorax.

Total body length ♂ 4.0-4.8 mm. ♀ 4.1-4.9 mm.

.... proceps (Kirschbaum)

Common in grass, mainly Holcus.

Genus Cicadula Zetterstedt

Yellow with four black spots on crown-face border. Two brown longitudinal lines, closely spaced on either side of the mid-dorsal line on vertex. Four such longitudinal lines on thorax and abdomen (two closely spaced on either side of mid-dorsal line and two broad ones on either side) (Plate 2a). Markings absent on ventral abdominal surface. Bristles long, yellow and follow a regular pattern.

Plate 2

a. Fifth instar larvae - C. persimilis
(X 10)

b. Fifth instar larvae - M. parvicauda
(X 10)

Total body length ♂ 3.5-3.7 mm. ♀ 3.5-3.9 mm.

.... persimilis (Edwards)

Common in Dactylis glomerata L.

Genus Cicadula Zetterstedt

Black spots on crown-face border and longitudinal lines on dorsal surface of body as C. persimilis, but is darker yellow and longitudinal lines are very dark brown. Markings present on vertex along margin of compound eyes. Thorax has six clear longitudinal lines (two very closely spaced on either side of mid-dorsal line and four at the sides). Abdomen with four clear lines (two closely placed on either side of mid-dorsal line and two at the sides). Markings present on ventral abdominal surface especially on segment VIII and on subgenital plate in male or rudiments of the first gonapophyses in female. Dark long bristles present which follow a regular pattern.

Total body length ♂ 3.7-3.9 mm. ♀ 4.3-4.5 mm.

.... aurantipes (Edwards)

Common in Juncus

Genus Mocydiopsis Ribaut

Yellow with four longitudinal lines equally spaced on vertex. Six on thorax (two further apart on either side of mid-dorsal line and two each at the sides). Four on abdomen (two on either side of mid-dorsal line and one broad one on either side) (Plate 2b). Red streaks present on posterior margin of abdominal segments. Markings absent on ventral abdominal surface.

Total body length ♂ 3.3-3.7 mm. ♀ 3.8-3.9 mm.

.... parvicauda Ribaut

Common in grass. Reared on Agrostis.

Genus Allygus Fieber

Grass green with green legs. Long bristles, four on segments III to VI and six on segments VII and VIII.

Total body length ♂ 4.8-5.1 mm. ♀ 5.0-5.4 mm.

.... mixtus (Fabricius)

Common in grass.

Genus Elymana DeLong

Pale yellow with pale brown band down thorax and abdomen on dorsal sufface.

Total body length ♂ 3.7-3.9 mm. ♀ 4.5-4.6 mm.

.... sulphurella (Zetterstedt)

Common in grass, mainly Holcus.

Tribe Grypotini

Genus *Grypotes* Fieber

Pale brown with streaks on ante- and postclypeus which are sometimes brown with no markings. Ante- and postclypeus flat and anteclypeus is very narrow with width about a quarter of its length (Fig. 52b). Vertex almost equal length throughout with a straight anterior margin. Bristles present only on segments VII and VIII. Two on segment VII and six on segment VIII.

Total body length ♂ 4.3-4.4 mm. ♀ 4.4-4.5 mm.

.... *puncticollis* (Herrich-Schaeffer)

Common on pine.

Tribe Macrostelini

Genus *Macrosteles* Fieber

Yellow with two black streaks and spots on vertex. Bristles present on segments VII and VIII. Two on segment VII and four on segment VIII.

Total body length ♂ 2.5-2.8 mm. ♀ 3.1-3.3 mm.

.... *sexnotatus* (Fallén)

Common in grass. Reared on Oats 'Condor'.

Tribe Balcluthini

Genus *Balclutha* Kirkaldy

Vertex with rounded sides and blunt anterior margin

(Fig. 14e). Pale brown with no prominent bristles, only abdominal hairs.

Total body length ♂ 3.5-3.9 mm. ♀ 3.6-4.1 mm.

.... punctata (Thunberg)

Common on Deschampsia flexuosa (L.)

Subfamily Typhlocybinae

Tribe Erythroneurini

Genus Zygina Fieber

Whitish grey with a transparent cuticle. Anterior margin of vertex straight. Ocelli absent. Blunt cuticular outgrowths present on antennal ledge and also on dorsal abdominal surface. Eyes grey-green. Apex of anterior and median femora without spines. Hind tibia with poorly developed spines.

Total body length ♂ 2.0-2.2 mm. ♀ 2.2-2.7 mm.

.... scutellaris (Herrich-Schaeffer)

Common in Dactylis glomerata L.

Discussion

There have been various changes in the classification of adult Cicadellidae over the years. Le Quesne's key to the British Cicadellidae is the most recent for the separation of species at subfamily, tribal and genus levels. De Long (1923), Haupt (1935), Ribaut (1936, 1952), Medler (1942), Oman (1949), Evans (1947) and Le Quesne (1965, 1969) used position of ocelli, wing venation, shape of crown, shape of male valve, position of ridge above antennae and shape of aedeagus as main characters for the separation of the species at the subfamily, tribe, genus and species levels. However, except for position of ocelli, shape of crown and position of the ridge above antennae, characters such as wing venation and shape of male aedeagus which were the two main characters for the separation of adult Cicadellidae could not be used in the larval classification. The key to the fifth instar larvae is largely based on characters which are absent in the adults, although characters such as position of ocelli and shape of crown are also included.

SUMMARY

1. A detailed study of the external morphology of the larval and adult stages of six species of British Cicadellidae was made and revealed that a great deal of morphological change occurs at the last moult (i.e. between the fifth instar and adult stage), and to a lesser extent between the first and second instars. Some structures are mainly larval in character and some appear only in the adult stage.

2. One of the most important taxonomic characters of Cicadellid larvae is chaetotaxy. This was studied in eight British species and it was shown that the number and pattern of bristles increase between the first and second instars only. The third, fourth and fifth instars have similar numbers and patterns of bristles as the second instar. In the adult stage, however, only the bristles on the ninth abdominal segment are retained.

3. The development and homology of the external male and female genitalia were studied from the third instar (i.e. when they become visible) to the adult stage. The female third instar has three pairs of outgrowths, one pair arising from the eighth sternite and one pair from the ninth. The female fourth and fifth instars, however, have three pairs of outgrowths, the ventral-most pair arising from the eighth sternite and the other two pairs arising from the ninth. The first and second pairs form the first and second gonapophyses in the adult, and the

third pair develops into the gonoplacs.

The male third, fourth and fifth instars have two pairs of outgrowths arising from sternum nine, namely a prominent triangular plate-like structure called the subgenital plate which overlies a smaller outgrowth behind it; these are the rudiments of the primary phallic organs, the subgenital plate differentiating into the paired genital plates posteriorly and into a triangular genital valve anteriorly, the latter being absent in adults of some species. The rudiments of the primary phallic organs split into three, forming a median aedeagus and the paired parameres.

4. The wings which are pads in the larval stages increase in length from instar to instar. In the macropterous forms of D. stylata the phragma is large and hangs down the mesothoracic cavity, whereas in the brachypterous forms of the same species the phragma is tucked horizontally beneath the scutellum. In all the other species studied which were macropterous forms, the phragma is large, except in U. reticulata where the hind wings are absent and the phragma is small.

5. A key is presented to the five larval instars (of both sexes in the last three instars) of British Cicadellidae. The instars are separable by the length of the wing pads and the progressive development of the rudiments of the external genitalia.

6. Next, growth in five species of Cicadellidae was studied and analysed by multiple discriminant analysis on untransformed and

logarithmically transformed data. Seven measured structural features of six developmental stages (sexes of the last four being treated separately) were considered. This analysis revealed the following:-

a. When the untransformed data were used, U. reticulata showed a different pattern of growth from the other four species. However, when the primary data were logarithmically transformed, the growth pattern in U. reticulata resembled that in the other four species.

b. The greatest discontinuity in the growth was found between the fifth instar and the adult stage, although visible differentiating structures were not included in the analysis; this indicates that metamorphosis may influence patterns of growth of structures which are only indirectly concerned with the functional requirements of the adult. Comparing the growth pattern of Dysdercus and the five species of Cicadellidae studied, with that of Ectobius and the Morabine grasshoppers, it appears that Hemiptera have a more pronounced metamorphosis at the last moult.

7. Further studies included the numerical analysis of forty-two multistate and nine quantitative characters of twenty-two fifth instar larvae of British Cicadellidae, in an attempt at a comparison of classification based on larval characters with the existing taxonomy based on adult characters. The characters studied were analysed by nine numerical methods, the results of which were

evaluated and compared with the existing orthodox classification based on adult characters and revealed the following points:-

a. Although the single linkage analyses gave conclusions which resembled those derived from the principal co-ordinate and the principal component analyses, the two latter analyses yielded data which more closely resembled the orthodox classification based on adult characters.

b. In small details, however, the principal co-ordinate analyses yielded results which fitted the classification of adults (after Le Quesne, 1965, 1969) which is based on the British members of this family.

c. There was no significant change in the groupings of species when fifty-one instead of forty-two characters were used in the principal component analyses. In other words, the nine quantitative characters were either too few, or of restricted classificatory value.

8. Following these studies of the fifth instar larvae of twenty-two species of British Cicadellidae, tentative keys to the subfamilies, tribes and to the species examined were constructed and are here presented.

9. In an appendix the genitalia of parasitized adults are described and the homology of the modified parts is discussed.

ACKNOWLEDGMENTS

I would like to thank Professor T.R.E. Southwood for the facilities offered to me at the Imperial College Field Station, Silwood Park.

My grateful thanks are due to my supervisor, Dr. N. Waloff, for her constant guidance, suggestions and encouragement in the work. I am indebted to Mr. R.G. Davies for his help in the numerical analyses and also for reading the manuscripts and giving valuable criticism.

My thanks are due to Professor O.W. Richards for suggestions, to Dr. N. Waloff, Mr. M.G. Soloman and Miss S. McCarthy for providing me with specimens, and Dr. W.J. Le Quesne who kindly gave me specimens of abnormal *E. urticae*. My thanks are also due to Mrs. Van Emden for translating some German literature, to Mrs. M. Smith for typing the thesis, to Mr. H. Devitt and Mr. J. Smith for the photography and Miss S. McCarthy for help with the dendrograms.

Finally I wish to thank the Lee Foundation of the States of Malaya for the part grant offered to me throughout the three years and to the Trustees of the Edwina Mountbatten Grants for Commonwealth students for meeting the cost of the thesis.

REFERENCES

Ali, A.A. 1958. *The external anatomy of some Jessoidea with a provisional annotated check list of the African Jessidea.* University of London Thesis: 220 pp.

Beirue, B.B. 1956. Leafhoppers (Homoptera: Cicadellidae) of Canada and Alaska. *Can. Ent.* *88*: 180 pp.

Blackith, R.E. 1960. A synthesis of multivariate techniques to distinguish patterns of growth in grasshoppers. *Biometrics* *16*: 28-40.

Blackith, R.E. & Albrecht, F.O. 1959. Morphometric difference between the eye stripe polymorphs of the red locust. *Scient. Jl R. Coll. Sci.* *27*: 13-27.

Blackith, R.E. & Blackith, R.M. 1969. Variation of shape and of discrete anatomical characters in the Morabine grasshoppers. *Aust. J. Zool.* *17*: 697-718.

Blackith, R.E., Davies, R.G. & Moy, E.A. 1963. A biometric analysis of development in *Dysdercus fasciatus* (Sign.) (Hemiptera: Pyrrhocoridae) *Growth* *27*: 317-334.

Bollow, H. 1950. Uber die zwegzikade und ihr wiederauftreten in Bayen. *Pflanzenschutz* *2*: 102-104.

Boratynski, K. & Davies, R.G. 1971. The taxonomic value of male Coccoidea (Homoptera) with an evaluation of some numerical techniques. *Biol. J. Linnean Soc. Lond.* *3*: 57-102.

Brown, V.K. 1969. *Aspects of the Biology and Growth in Three Species of Ectobius (Dictypotera: Blattidea).* University of London Thesis: 397 pp.

Butt, F.H. 1943. Comparative study of mouth parts of representative Hemiptera-Homoptera. *Mem. Cornell Univ. agric. Exp. Stn.* *254*: 20 pp.

Crampton, G.C. 1909. A contribution of the comparative morphology of the thoracic sclerites of insects. *Proc. Acad. nat. Sci. Philad.* *61*: 3-54.

De Long, D.W. 1923. Cicadellidae in *The Hemiptera or Sucking Insects of Connecticut,* Part IV (Ed. Britton, E.B.), pp. 53-163. State Geological and Natural History Survey Bulletin No.34: 807 pp.

d'Razario, A.M. 1942. On the development and homologies of the genitalia and their ducts in Hymenoptera. *Trans. R. ent. Soc. Lond.* *92*: 363-415.

Duporte, E.M. 1946. Observations on the morphology of the face in insects. *J. Morph.* *79*: 371-418.

Duporte, E.M. 1957. The comparative morphology of the insect head. *A. Rev. Ent.* *2*: 55-71.

Duporte, E.M. 1962. The anterior tentorial arms in insects and their significance in interpreting the morphology of the cranium of the Cicadas. *Can. J. Zool.* *137*: 144.

Dupuis, C. 1950. Origine et developpement des organes genitaux externes des mâles d'insects. *Annee biol.* *26*: 21-36.

Dyar, H.G. 1890. The number of moults of Lepidopterous larvae. *Psyche* *5*: 420-422.

Edwards, J.W. 1896. *The Hemiptera-Homoptera* (Cicadina and Psyllina) *of the British Islands.* Reeve & Co. London: 271 pp.

Evans, J.W. 1938. The morphology of the head of Homoptera. *Pap. Proc. R. Soc. Tasm.* 1-20.

Evans, J.W. 1939. A contribution to the study of the Jassoidea. *Pap. Proc. R. Soc. Tasm.* 19-56.

Evans, J.W. 1946. A natural classification of leafhoppers (Jessoidea) Homoptera. Part I. External morphology and systematic position.
Trans. R. ent. Soc. Lond. 96: 47-60.

Evans, J.W. 1947. A natural classification of leafhoppers (Jessoidea), Part III. Jessoidea.
Trans. R. ent. Soc. Lond. 98: 105-271.

Evans, J.W. 1957. Morphology and inter-relationships of extinct and recent Homoptera.
Trans. R. ent. Soc. Lond. 109: 275-294.

Ferris, G.F. 1943. The basic material of the insect cranium.
Microentomology 8: 8-24.

Fisher, R.A. 1938. The statistical utilization of multiple measurements.
Ann. Eugen. 8: 376-386.

George, C.J. 1929. The morphology and development of the genitalia and genital ducts of Homoptera and Zygoptera as shown in the life histories of Philaenus and Agrion.
Q. Jl microsc. Sci. 72: 447-485.

Gould, S.J. 1966. Allometry and size in otogeny and phylogeny.
Biol. Rev. 41: 48', 640.

Gower, J.C. 1966. Some distance properties of latent roots and vector methods used in multivariate analysis.
Biometrika 53: 325-338.

Gower, J.C. 1967. Multivariate analysis and multidimensional geometry.
The Statistician 17: 13-28.

Gower, J.C. & Ross, G.J.S. 1969. Minimum spanning trees and single linkage cluster analysis.
App. Statist. 18: 54-64.

Grandi, M. 1950. Contribute allo studio dei Plecotleri. II. Morphologia comparata.
Boll. Ist. Ent. Univ. Bologna 18: 30-57.

Gupta, P.D. 1950. On the structure, development and homology of the female reproductive organs in Orthopteroid insects.
Indian J. Ent. *10*: 75-123.

Hackman, L.M. 1922. Studies of *Cicadella hieroglyphica* Say. (Homoptera Cicadellidae).
Kans. Univ. Sci. Bull. *14*: 189-209.

Haupt, H. 1935. Homoptera Cicadellina
in *Die Tierwelt Mitteleuropas, Insekten* 4: 115-221.

Hinton, H.E. 1946. Concealed phases in the metamorphosis of insects.
Nature *157*: 552-553.

Hinton, H.E. & Mackerras, I.M. 1967. Reproduction and Metamorphosis
in *The Insects of Australia*
Melbourne Univ. Press: 1029 pp.

Hope, K. 1968. *Methods of Multivariate Analysis*
University of London Press: 288 pp.

Huxley, J.S. 1932. *Problems of Relative Growth*
Methuen, London: 276 pp.

Imms, A.D. 1964. *A General Textbook of Entomology*, 9th Edn. (revised by Richards, O.W. & Davies, R.G.)
Methuen, London: 885 pp.

Jardine, N. & Sibson, R. 1968. The construction of hierarchic and non-hierarchic classifications.
Computer J. *11*: 177-184.

Jürisoo, V. 1964. Agro-ecological studies on leaf hoppers (Anchenorhyncha: Homoptera) and bugs at Ekensgard farm in the province of Halsingland, Sweden.
Meddn. St. VaxtskAust. *13*: 147 pp.

Kershaw, J.C. & Muir, F. 1922. The genitalia of Auchenorhyncha Homoptera.
Ann. ent. Soc. Am. *15*: 201-202.

Kramer, S. 1950. The morphology and phylogeny of Anchenorhynchaus Homoptera (Insecta)
Illinois biol. Monogr. **20**: 78 pp.

Leonard, M.D. 1915. The immature stages of black apple leafhopper (*Ichiocerus provancheri* Van Duzee)
J. econ. Ent. **8**: 414-419.

Le Quesne, W.J. 1965. *Handbook for the Identification of British Insects.* Hemiptera: Cicadomorpha (excluding Deltocephalinae and Typhlocybinae)
Vol. II, part 2(a): 64 pp.

Le Quesne, W.J. 1969. *Handbook for the Identification of British Insects.* Hemiptera: Cicadormorpha, Deltocephalinae.
Vol. II, part 2(b): 140 pp.

MacGill, E.I. 1932. The biology of *Erythroneura* (*Zygina*) *pallidifrons* Edwards.
Bull. ent. Res. **23**: 33-43.

Mahalanobis, P.C. 1936. On the generalized distance in statistics.
Proc. natn. Inst. Sci. India **2**: 49-55.

Matsuda, R. 1958. On the external genitalia of insects.
Ann. ent. Soc. Am. **51**: 84-94.

Matsuda, R. 1960. Morphology of the pleurosternal region of pterothorax in insects.
Ann. ent. Soc. Am. **53**: 712-731.

Medler, J.T. 1942. The leafhoppers of Minnesota, Homoptera, Cicadellidae.
Tech. Bull. Minn. agric. Exp. Stn. **155**: 1-196.

Michener, C.D. 1944. A comparative study of the appendages of the eighth and ninth abdominal segments of insects.
Ann. ent. Soc. Am. **37**: 336-351.

Misra, C.S. 1920. The rice leafhoppers *Nephotethix bipunctatus* Fab. and *Nephotettix apicalis* Motsch.
Mem. Dep. Agric. India ent. Ser. **7**: 207-239.

Muir, F. 1925. On the status of the anterior processes of the male genitalia in Homoptera.
Proc. Hawaii ent. Soc. 6: 41-45.

Muir, F. 1926. Reconsideration of some points on the morphology of the head of Homoptera.
Ann. Ent. Soc. Am. 19: 67-73.

Muir, F. & Kershaw, J.C. 1911. On the homologies and mechanism of the mouthparts of Hemiptera.
Psyche 18: 1-12.

Oman, P.W. 1949. The neartic leafhoppers (Homoptera Cicadellidae). A generic classification and check-list.
Mem. ent. Soc. Wash. 3: 253 pp.

Osborn, H. 1916. Life histories of leafhoppers of Maine.
Bull. Me. agric. Exp. Stn. 248: 53-80.

Ossiannilsson, F. 1949. Insect drummers. A study on the morphology and function of the sound producing organs of Swedish Homoptera Anchenorhyncha with notes on their sound production.
Opusc. ent., Lund. Suppl. 10: 1-145.

Parsons, M.C. 1964. The origin and development of the Hemipteran cranium.
Can. J. Zool. 42: 409-432.

Pesson, P. 1944. Contribution a l'etude morphologique et fonctionelle de la tete, de l'appareil buccal et du tube digestif des femelles de Coccides.
Monographies publ. par les Stations et Lab. de Recherches Agronomiques, Paris: 266 pp.

Pesson, P. 1959. The World of Insects
(Translated by Freeman, R.B.).
George G. Harrape & Co: 204 pp.

Quadri, M.A.H. 1940. On the development of the genitalia and their ducts of Orthopteroid insects.
Trans. R. ent. Soc. Lond. 90: 121-175.

Ramsay, G.W. 1965. Development of the ovipositor of *Deinacrida rugosa* Buller (Orthoptera: Gryllacridoidea: Henicidae) and a brief review of the orthogeny and homology of the ovipositor with particular reference to the Orthopera.
Proc. R. ent. Soc. Lond. (A) *40*: 41-50.

Rao, C.R. 1952. *Advanced Statistical Methods in Biometric Research.*
Wiley, New York: 390 pp.

Rawat, B.L. 1939. On the habits of metamorphosis and reproductive organs of *Naucoris cimicoides* (L.) (Hemiptera-Heteroptera)
Trans. R. ent. Soc. Lond. *88*: 119-138.

Readio, P.A. 1922. The ovipositor of the Cicadellidae (Homoptera)
Kans. Univ. Sci. Bull. *14*: 217-265.

Ribaut, H. 1936. *Faune de France*, 31.
Homopteres Auchénorhynques I (Typhocybidae)
Paris: 228 pp.

Ribaut, H. 1952. *Faune de France*, 57.
Homopteres Auchénorhynques. II. (Jessidae)
Paris: 474 pp.

Richards, O.W. 1949. The relations between measurements of the successive instars of insects.
Proc. R. ent. Soc. Lond. (A) *24*: 8-10.

Ross, H.H. 1957. Evolutionary developments in the leafhoppers, the insect family Cicadellidae.
Syst. Zool. *6*: 87-97.

Ross, M.H. 1966. Notched sternite: A mutant of *Blattella germanica*, with possible implications for the homology and evolution of the ventral abdominal structures.
Ann. ent. Soc. Am. *59*: 473-484.

Scudder, G.G.E. 1957. Reinterpretation of some basal structures in the insect ovipositor.
Nature *180*: 340-341.

Scudder, G.G.E. 1961. The functional morphology and interpretation of the insect ovipositor.
Can. ent. 93: 268-272.

Scudder, G.G.E. 1961. The comparative morphology of the insect ovipositor.
Trans. R. ent. Soc. Lond. 113: 25-40.

Scudder, G.G.E. 1964. Further problems in the interpretation and homology of the insect ovipositor.
Can. ent. 96: 406-417.

Scudder, G.G.E. 1971. Comparative morphology of the insect genitalia.
A. Rev. Ent. 16: 379-406.

Seal, H. 1964. Multivariate Statistical Analysis for Biologists.
Methuen, London: 207 pp.

Severin, H.H.P. 1949. Life history of the blue green sharpshooter Heokolla cirellata.
Hilgardia 19: 187-189.

Severin, H.H.P. 1950. Texanamus incurvatus III. Life history on virus infected and healthy plants.
Hilgardia 19: 546-548.

Sheals, J.G. 1964. The application of computer techniques to Acarine taxonomy - a preliminary examination with species Hypoaspis-Androlaelaps-complex (Acarina).
Proc. Linn. Soc. Lond. 176: 11-21.

Sims, R. 1966. The classification of the Megascolecoid earthworks: an investigation of oligochaete systematics by computer techniques.
Proc. Linn. Soc. Lond. 177: 125-141.

Singh-Pruthi, H. 1924. The development of male genitalia of Homoptera with preliminary remarks on the nature of these organs in other insects.
Q. Jl microsc. Sci. 69: 59-96.

Smith, E.L. 1969. Evolutionary morphology of external male genitalia. 1. Origin and relationships of other appendages.
Ann. ent. Soc. Am. 62: 1051-1079.

Sneath, P.H.A. 1957. Some thoughts of bacterial classification.
J. gen. Microbiol. *17*: 184-200.

Sneath, P.H.A. 1957. The application of computers to taxonomy.
J. gen. Microbiol. *17*: 201-226.

Snodgrass, R.E. 1927. Morphology and mechanism of the insect thorax.
Smithson. misc. Collns. *80*: 1-108.

Snodgrass, R.E. 1929. The thoracic mechanism of a grasshopper and its antecedents.
Smithson. misc. Collns. *82*: 1-111.

Snodgrass, R.E. 1933. The morphology of the insect abdomen. Part II. The genital ducts and ovipositor.
Smithson. misc. Collns. *89*: 1-149.

Snodgrass, R.E. 1935. *Principals of Insect Morphology.*
New York and London McGraw Hill: 667 pp.

Snodgrass, R.E. 1935. The abdominal mechanism of a grasshopper.
Smithson. misc. Collns. *94*: 1-89.

Snodgrass, R.E. 1938. The loral plates and hypopharynx in Hemiptera.
Proc. ent. Soc. Wash. *40*: 228-236.

Snodgrass, R.E. 1947. The insect cranium and epicranial suture.
Smithson. misc. Collns. *107*: 55 pp.

Snodgrass, R.E. 1957. A revised interpretation of external reproductive organs of male insects.
Smithson. misc. Collns. *135*: 60 pp.

Snodgrass, R.E. 1958. Evolution of arthropod mechanism.
Smithson. misc. Collns. *138*: 1-77.

Snodgrass, R.E. 1960. Facts and theories concerning the insect head.
Smithson. misc. Collns. *142*: 1-60.

Snodgrass, R.E. 1963. A contribution toward an encyclopedia of insect anatomy.
Smithson. misc. Collns. 146: 48 pp.

Sokal, R. & Sneath, P.H.A. 1963. Principals of Numerical Taxonomy.
Freeman & Co. San Francisco and London: 359 pp.

Spooner, C.S. 1938. The phylogeny of the Hemiptera based on the study of the head capsule.
Illinois biol. Monogr. 16: 102 pp.

Tuxen, S.L. ed. 1970. Taxonomist Glossary of Genitalia in Insects.
2nd ed. Copenhagen: Munksgaard: 284 pp.

Wigglesworth, V.B. 1954. The Physiology of Insect Metamorphosis.
Cambridge: 154 pp.

Wigglesworth, V.B. 1964. The Life of Insects.
Weidenfield and Niscolson, London: 359 pp.

Wilkinson, C. 1970. Adding a point to a principal co-ordinate analysis.
Syst. Zool. 19: 258-263.

APPENDIX I

Genital Abnormalities in Some Cicadellid Adults

Introduction and Review of Literature

Genital abnormalities are frequently the result of some form of parasitism. According to Wigglesworth (1954) a Strepsipteran or a Dryinid parasite may alter the course of development of a Hymenopteran or Homopteran. Delong (1918) describes the first case of a gynandromorph in the Cicadellid Chlorotettix unicolor (Fh.), although he does not give the cause of this abnormality.

Muir (1918), while reporting on Pipunculid and Strepsipteran parasites, says that in the Delphacidae arrested development of the genitalia can occur, particularly in the aedeagus, the armature of the anal segment, in the genital styles and the connecting rods. Ribaut (1936) adds that parasitism can not only affect the form of the styles, aedeagus and pygophore, but also the abdominal apodemes and the characteristic pigmentation of the males. The pigmentation is most frequently affected and the larvae of Dryinidae or Pipunculidae can make the appearance of a male similar to that of a female. Esaki and Hashimoto (1934, 1935, 1936, 1938) report that a high percentage of the male rice Leaf-hopper of the Japanese Nephotettix bipunctatus cincticeps Uhler , parasitized by Pipunculus species assume female colouration. Parasitization by Strepsiptera according to Oman (1949) usually results in some modification of genital structures depending on how early partial or complete castration has occurred. He says that observed modification in the Leafhopper genital structures range from slight changes in shape to complete absence of development of normal structures which, as both he and Ribaut (1936) state, often lead to misidentification of species. Ribaut gives an example that *G. puncticollis* when parasitized by Pipunculidae, had aedeagus with modified lobes and these were considered as a distinct species, *G. falax* (Kbm.). Lindberg (1946) described in detail the abnormal morphological structures in *Chloriona* species (namely *C. glaucescens* (Fieb.) - Delphacidae) which when parasitized by *Pipunculus chlorionae* (Frey), had not only abnormal external and internal genitalia but these abnormalities were observed in certain other structures such as the wings. Ribaut (1936) also observed in *C. glaucescens* that nothing in this deformation recalled its normal state, and that the styles and the aedeagus were absent.

Abnormalities occur not only in the male but also in the female genitalia. Fenton (1918) in describing the effect of parasitism on the host, quoted Giard (1889) who wrote that the female ovipositor of *Erythroneura hippocastani* Edwards and of Erythroneura (Typhlocyba) douglasi (Edwards) parasitized by Aphelopus melalencus Dalm are greatly reduced and functionless. There was little change in the parasitized males of E. douglasi but the eight-branched aedeagus of parasitized E. hippocastani was reduced to a six or a three-branched structure.

Balazuc (1951) in his paper on the study of abnormality in Hemiptera and of its neighbouring groups gave a short review of the various reported parasites in Homoptera. Scudder (1956) while describing the gynandromorph of Ishnodemus subuleti (Fall.) (Lygaeidae) also noted that genital abnormalities frequently result from parasitism, although he did not notice any external injury and dissection failed to reveal parasites.

During the present study on the family Cicadellidae, specimens with abnormal genitalia were kindly given to me by Dr. N. Waloff and Dr. W.J. Le Quesne. There are only a few papers on detailed morphological studies of the abnormal genitalia, and their homologies and comparisons with the normal larvae and adults of Cicadellidae. For this reason the present observations on three species are included here.

Dr. N. Waloff gave me specimens of E. ocellaris and A. pascuellus which were collected in Silwood Park in 1969. There were large numbers of abnormal males and females of

E. ocellaris although there was only one abnormal specimen of *A. pascuellus*. According to Dr. Waloff (personal communication) *E. ocellaris* can be heavily parasitized by Pipunculids and three species of *Eudorylas*, namely *E. subfascipes* Collins, *E. jenkinsoni* Coe and *E. subterminalis* Collins have been bred out of this host in Silwood, a large number of parasitized adults usually occurring in the second generation. All the abnormal males and females examined here were parasitized by Pipunculidae. *A. pascuellus* is also parasitized by Pipunculidae, *E. jenkinsoni* and *Alloneura sylatica* Meigen (personal communication from Dr. Waloff).

Eupteryx urticae (Fabricius) abnormal adults which were given to me by Dr. W.J. Le Quesne, are usually found on *Urtica dioica* L. and are bivoltine, the abnormal specimens occurring in both generations. Dr. Le Quesne's samples were from Chesham, Buckinghamshire, and a smaller sample was also obtained in Silwood Park. No internal or external parasites were noticed in this species although the abnormality is probably caused by some form of parasitism. Oman (1946) reports that in America, Strepsiptera, Dryinidae and Pipunculidae all parasitize the subfamily Typhlooybinae (then known as Cicadellinae). *Aphelopus* (Dryinidae) frequently parasitizes Typhlocybinae (Imms, 1964) but no genital abnormalities were observed in *E. urticae* individuals parasitized by Dryinidae in the present study.

(a) (i) The External Morphology of Abnormal Genitalia in Some Adults of *E. urticae*

The following is a detailed description of abnormal genitalia in some adults of *E. urticae* which is later compared with the genitalia of normal male and female adults.

The seventh sternite in the abnormal adult (determination of sex, see page 352) is enlarged and highly pigmented. The eighth which is undivided and smaller is partly hidden beneath the sternite VII. A pair of completely separated outgrowths is given off posteriorly by sternite VIII (Fig. 2).

Lying behind the first pair of outgrowths is a second pair which is given off by the ninth sternite. These are separated until half-way down, pointed and narrow with a serrated dorsal margin (Fig. 2b).

A pair of spoon-shaped outgrowths lie behind the second pair. These arise laterally from the ninth sternite and ensheath the first and second pairs of outgrowths. The first, second and third pairs of outgrowths bear no connection with each other.

On dorsal and lateral views the pigmentation of the tergites and sternites (except sternite VIII) is very similar to that of a normal female (Fig. 1).

Fig. 1

Dorsal View of Last Three Abdominal
Tergites - *E. urticae* (Adult)

a. Normal Male
b. Normal Female
c. Abnormal Female

Lateral View of Last Three Abdominal
Tergites and Sternites - *E. urticae* (Adult)

d. Normal Male
e. Normal Female
f. Abnormal Female

g.p.	genital plate
g.pl.	gonoplac
st.VII.	seventh sternite
st.VIII.	eighth sternite
st.IX.	ninth sternite
t.VII.	seventh tergite
t.VIII.	eighth tergite
t.IX.	ninth tergite

FIG. 1

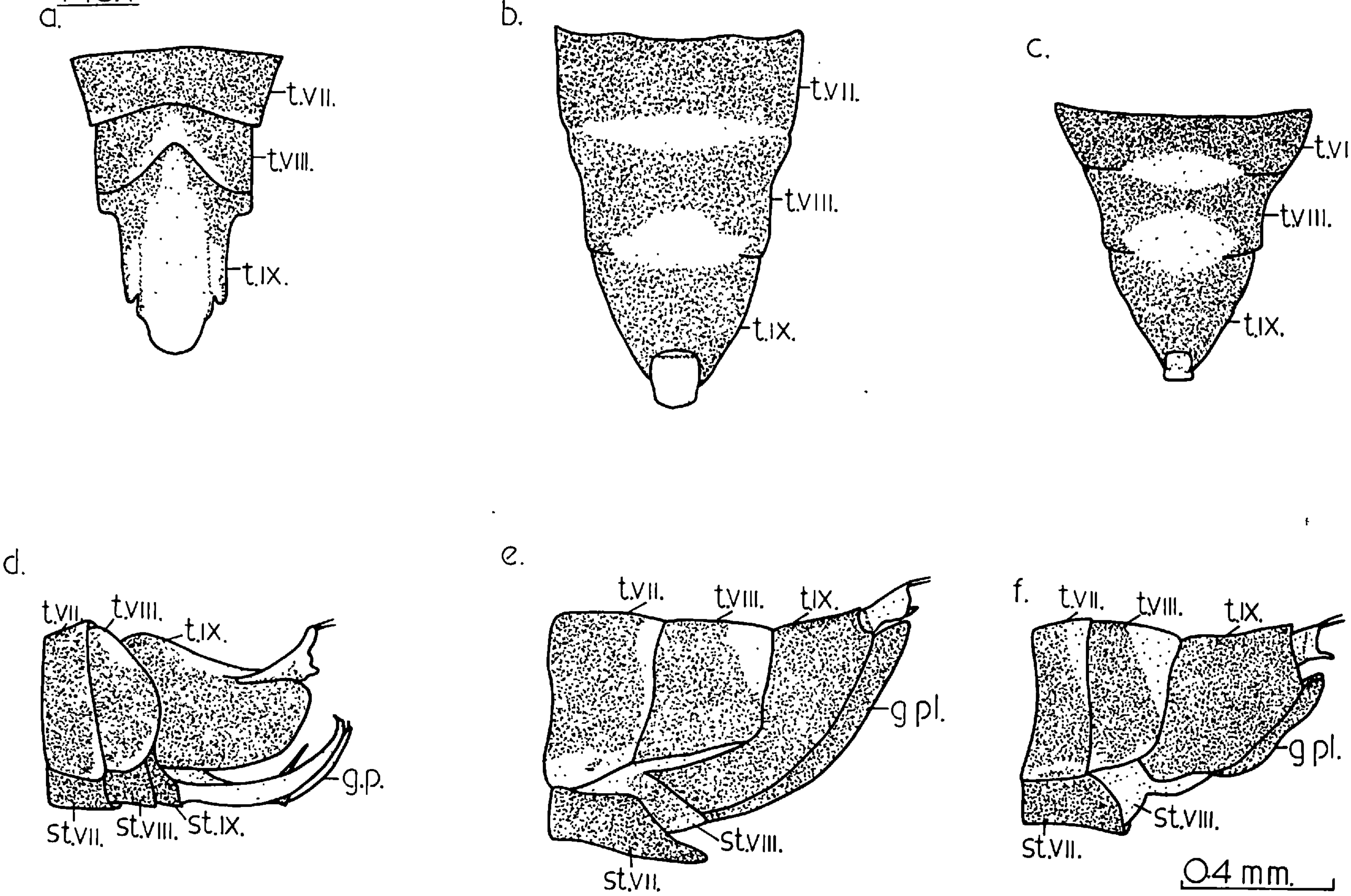

a.
t.VII.
t.VIII.
t.IX.
b.
t.VII.
t.VIII.
t.IX.
c.
t.VII.
t.VIII.
t.IX.
d.
t.VII.
t.VIII.
t.IX.
g.p.
st.VII.
st.VIII.
st.IX.
e.
t.VII.
t.VIII.
t.IX.
g pl.
st.VIII.
st.VII.
f.
t.VII.
t.VIII.
t.IX.
g pl.
st.VIII.
st.VII.
0.4 mm.

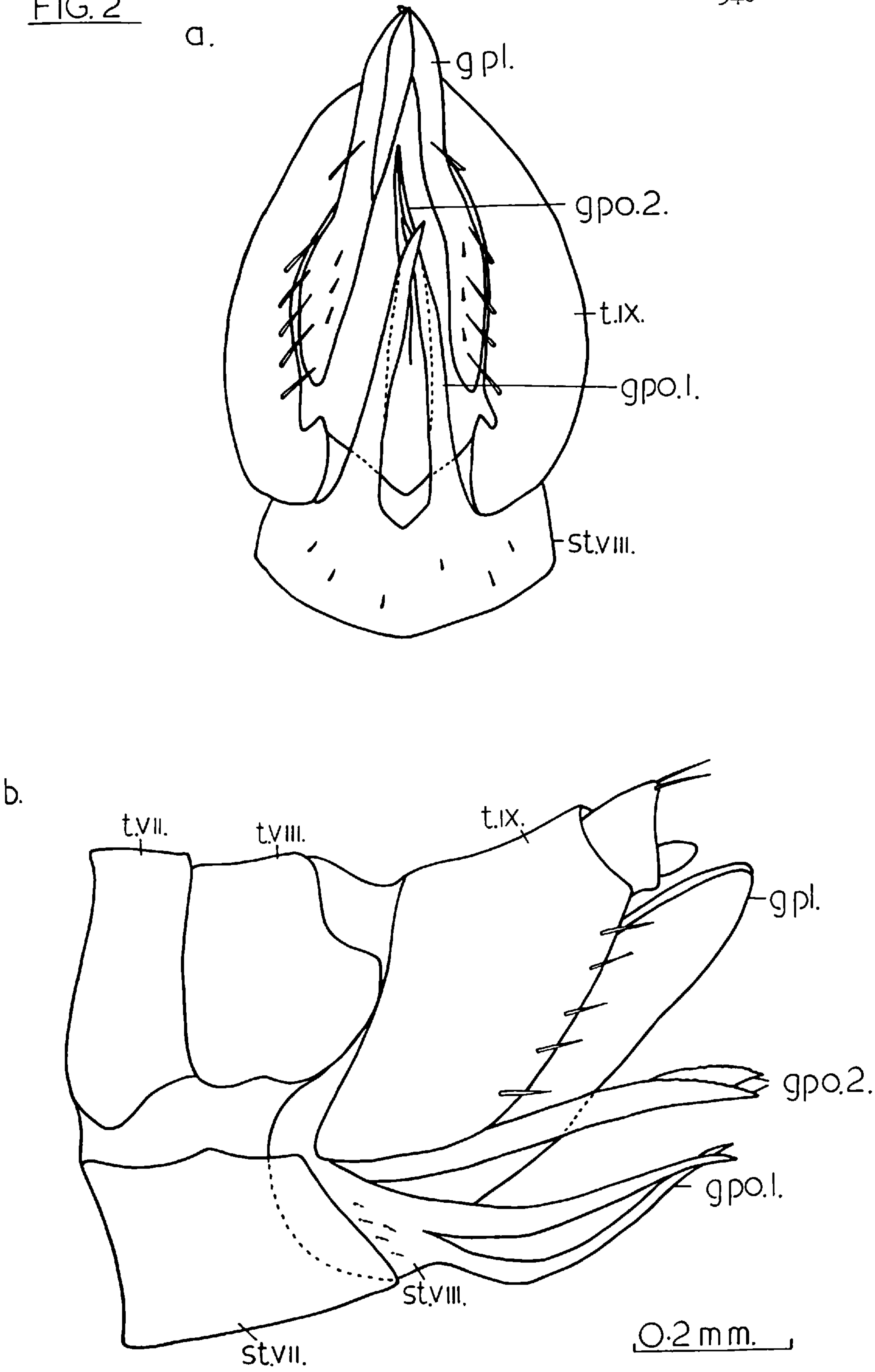
Fig. 2

a. Ventral View of Last Two Abdominal Segments
- *E. urticae* (Abnormal Female)

b. Lateral View of Last Two Abdominal Segments
- *E. urticae* (Abnormal Female)

gpl.	gonoplac
gpo.1.	first gonapophysis
gpo.2.	second gonapophysis
st.VII.	seventh sternite
st.VIII.	eighth sternite
t.VII.	seventh tergite
t.VIII.	eighth tergite
t.IX.	ninth tergite

FIG. 2


a.
g pl.
gpo.2.
t.IX.
gpo.1.
st.VIII.
b.
t.VII.
t.VIII.
t.IX.
g pl.
gpo.2.
gpo.1.
st.VIII.
st.VII.
0·2 mm.

(ii) Comparison of the Abnormal Genitalia with a Normal Male and Female of *E. urticae*

The pigmentation and shape of the last three abdominal tergites from the dorsal aspect are identical in abnormal and normal female adults. The pigmentation in a normal male, however, is different (Fig. 1).

In a normal female adult as in an abnormal adult, tergites VII, VIII and IX along with the enlarged seventh and reduced eighth sternites are present (Fig. 3b). The enlarged seventh sternite in a normal female and an abnormal adult are similar in shape (Fig. 1e, f). Lying posterior to the seventh sternite is the eighth sternite which in a normal female is greatly reduced and divided, being concealed by the enlarged seventh sternite. In a normal female fifth instar larvae, however, the eighth sternite is undivided and fully exposed, whereas in an abnormal adult the eighth sternite is undivided and only partly concealed by the enlarged seventh sternite (Fig. 1f, 2b). This latter condition seen in abnormal adults is a feature of pharate adults. In a normal male adult, however, the tergites and sternites VII and VIII are of regular sise and the paired genital plates lie posterior to sternum IX (Fig. 3a).

A pair of separated outgrowths given off by the eighth sternite in an abnormal adult is similar in origin and shape

Fig. 3

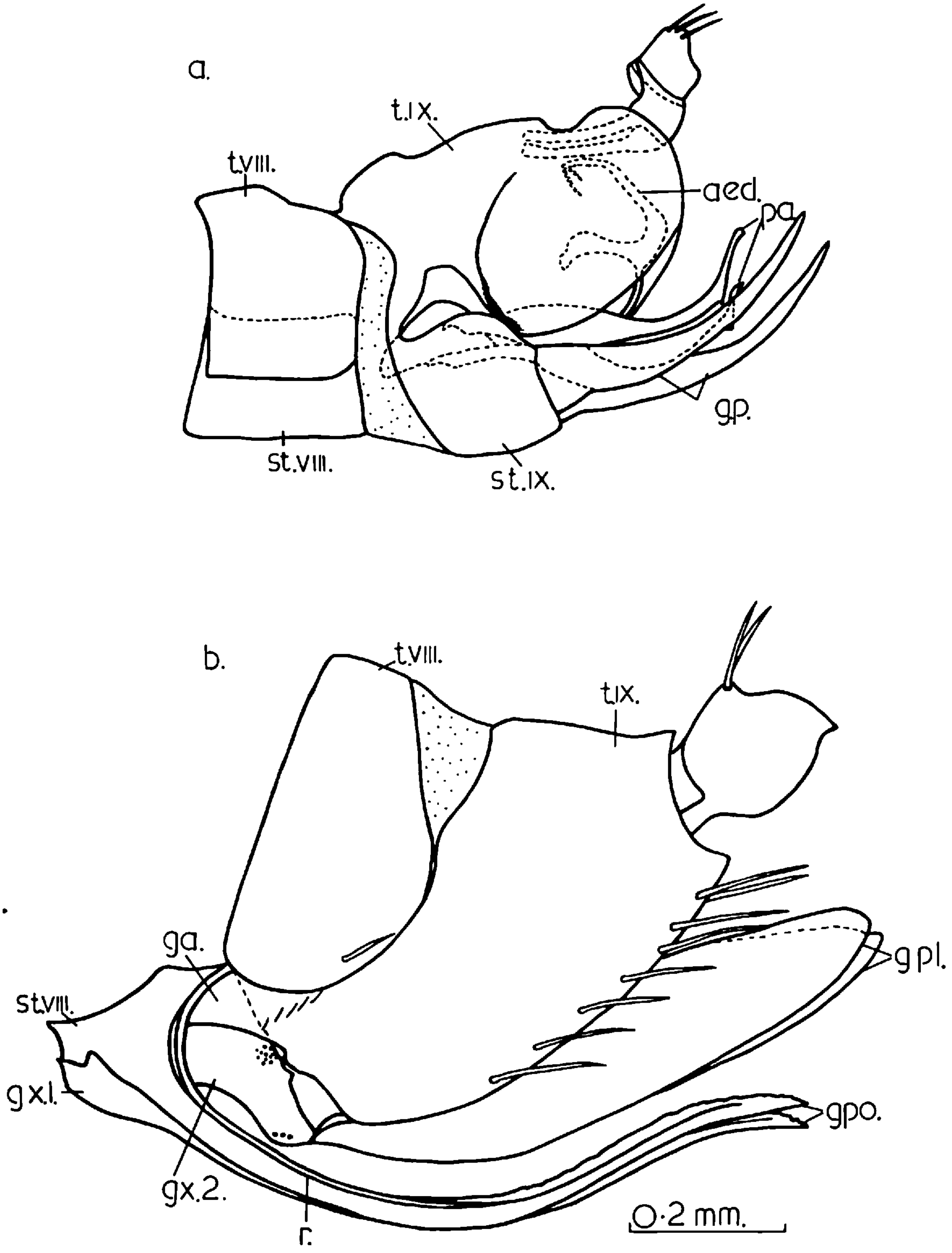
Lateral View of Last Two Abdominal Segments - *E. urticae*

a. Normal Male Adult

b. Normal Female Adult

aed.	aedeagus
ga.	gonangulum
g.p.	genital plate
gpl.	gonoplac
gpo.	gonapophyses
gx.1.	first gonocoxa
gx.2.	second gonocoxa
r.	rami
st.VIII.	eighth sternite
st.IX.	ninth sternite
t.VIII.	eighth tergite
t.IX.	ninth tergite

FIG. 3


a.
t.IX.
t.VIII.
aed.
pa.
gp.
st.VIII.
st.IX.
b.
t.VIII.
t.IX.
ga.
gpl.
st.VIII.
gx.1.
gpo.
gx.2.
r.
0·2 mm.

to the first gonapophysis of a normal female adult. The first ramus and gonocoxa present in the normal female are however absent in an abnormal one (Fig. 2). Hence this first pair of outgrowths is fused to the eighth sternite whereas in normal adult females the first gonapophysis articulates with the eighth sternite by means of the first gonocoxa. In normal male adults the genital plates arise from the ninth segment, as do the parameres and the aedeagus. A genital valve or distinct ninth sternite is absent in this species (Fig. 3a), the ninth tergum and sternum being fused. Hence the first pair of outgrowths in an abnormal adult is homologous to the first gonapophysis of normal female adults.

The second pair of outgrowths on sternum IX in abnormal adults is narrow with a serrated dorsal margin and is identical in origin and shape to the second gonapophysis of normal female adults. This pair, unlike the first, is separated only to halfway down. Ramus II and the second gonocoxa are absent, whereas they are present in normal female adults (Fig. 3b). Hence the second pair of outgrowths like the first pair in abnormal adults, is fused to sternum IX, whereas in normal female adults the ramus II is attached to the second gonocoxa which in turn articulates on a pivot with the gonangulum which is attached to ramus I of the first gonapophysis. Although the anterior region (namely sternum IX) of the second pair of outgrowths in abnormal adults is simple and unmodified, due to its origin and shape the second pair of outgrowths is homologous to the second gonapophysis of normal female adults.

The third pair of spoon-shaped outgrowths which arise laterally on sternum IX is identical in origin and shape to the gonoplacs of normal female adults (Fig. 2a, b). The anterior region of this pair of outgrowths in abnormal adults is simply fused to sternum IX, whereas in normal female adults it is attached to the second gonocoxa (Fig. 3b). However, the posterior spoon-shaped region of this pair of outgrowths in abnormal adults is identical to the gonoplacs and it ensheaths the first and the second pairs like the gonoplacs in normal female adults. Hence in its origin and shape it is homologous to the gonoplacs of normal female adults.

The posterior distal regions of these three pairs of outgrowths are identical to the first and second gonapophyses and gonoplacs of normal female adults, whereas the anterior regions are simple and unmodified, the enlarged seventh sternite being identical to that in normal female adults.

When abnormal adults were dissected a pair of immature ovaries and spermatheca were revealed, whereas dissection of normal female adults of the same sample revealed mature ovaries.

Hence it is concluded that such abnormality as is seen in E. urticae, results from suppression of development of female genitalia, and the so-called 'intersexes' exhibit some modified adult as well as larval characters.

(b) External Morphology of Abnormal Genitalia in Male and Female Adults of E. ocellaris

Unlike the abnormality seen in E. urticae, E. ocellaris has both abnormal males and females. The abnormal genitalia in both sexes are described in detail and are then compared with those in the normal adults of the same species.

(i) Abnormal Male

The pigmentation of the tergites and sternites of abnormal males is pale. Sternites III to VIII are very broad (Fig. 4b). The genital valve or the ninth sternite is differentiated from the paired genital plates, the tergite IX being broader and about two-thirds the size of the genital plates. Bristles are present on tergite IX and along the edge of the paired genital plates.

Lying behind the genital plates and the valve is the aedeagus which has two processes posteriorly. The phallobase at the base of the intromittent organ is small with rounded sides (Fig. 4d). The connectives below the phallobase which are connected to the parameres laterally, vary in shape and size

Fig. 4

Ventral View of Last Four Abdominal Segments
- *E. ocellaris*

a. Normal Male Adult
b. Abnormal Male Adult

Posterior View of Aedeagus and Parameres -
E. ocellaris

a. Normal Male Adult
b. Abnormal Male Adult

aed.	aedeagus
co.	connectives
g.p.	genital plate
g.v.	genital valve
pa.	parameres
ph.b.	phallobase
st.VII.	seventh sternite
st.VIII.	eighth sternite
t.IX.	ninth tergite

FIG. 4

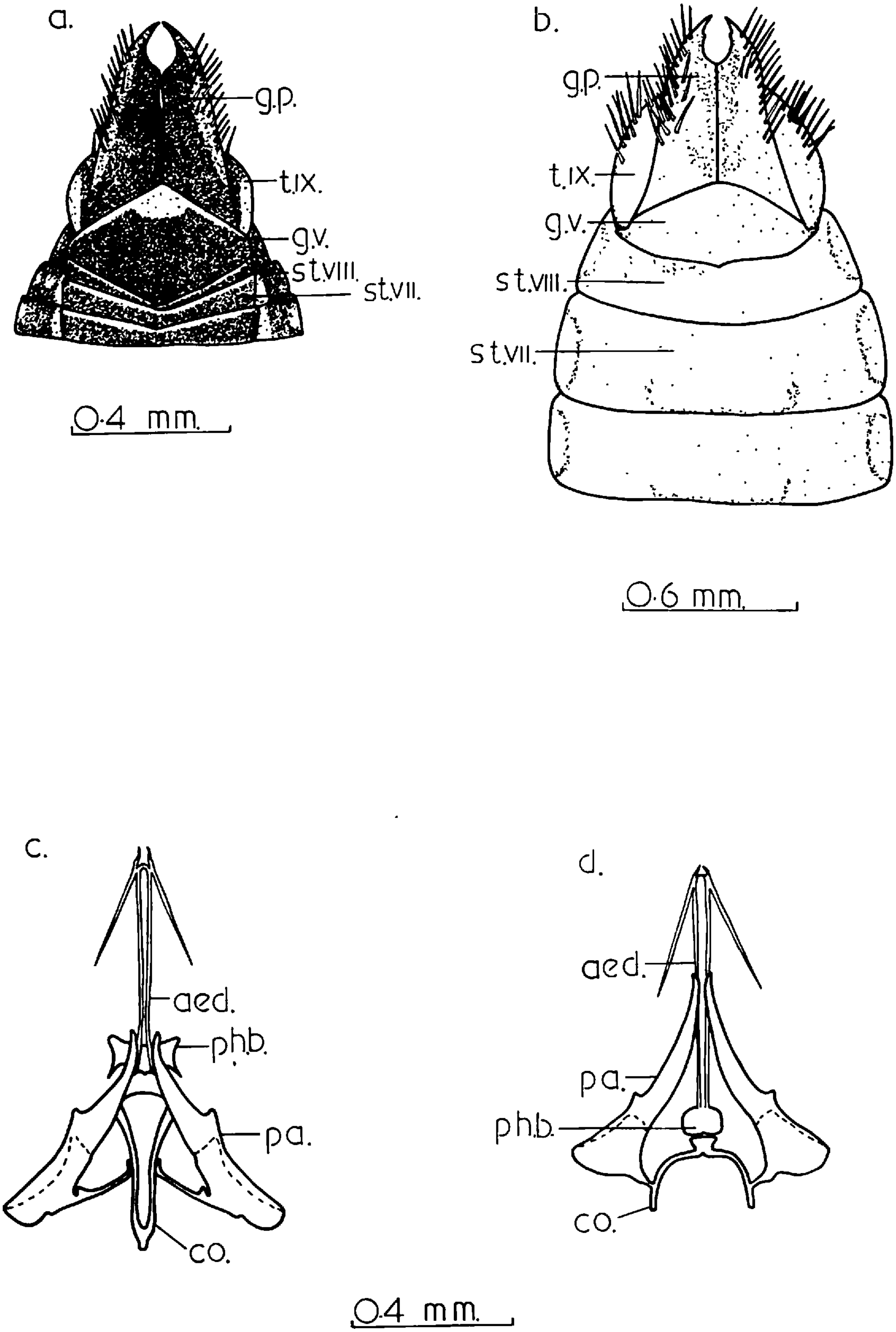

a.
g.p.
t.IX.
g.v.
st.VIII.
st.VII.
0·4 mm.
b.
g.p.
t.IX.
g.v.
st.VIII.
st.VII.
0·6 mm.
c.
aed.
ph.b.
pa.
co.
d.
aed.
pa.
ph.b.
co.
0·4 mm.

Plate 1

Abnormal male genitalia of adult parasitized *E. ocellaris* showing simple spindle-shaped connective. (X 193)

Plate 2

Abnormal male genitalia of adult parasitized *E. ocellaris* showing horse-shoe shaped connective. (X 174)

from abnormal male to male. In some specimens it is a simple horse-shoe shaped structure (Fig. 4d, Plate 2.) while in others it is a simple spindle shaped structure with a plain outer margin (Plate 1). The limbs of the parameres which connect it to the connectives are short. The ends of the connectives anteriorly are either wide apart or fused (Fig. 4d).

(ii) Abnormal Female

The pigmentation of the tergites and sternites in an abnormal female is also pale and sternite VII is enlarged with straight anterior and posterior margins. Sternite VIII is reduced and divided lying beneath the enlarged seventh sternite. The ventral side of each divided eighth sternite is attached to the first gonocoxa.

The first gonapophysis is blade-like with a grooved first ramus which is continued anteriorly and is attached to the reduced gonangulum on its anterior limb. The second gonapophysis is also blade-like with a serrated dorsal margin, the second ramus being attached to a reduced second gonocoxa. The spoon-shaped gonoplac is attached to the posterior end of the second gonocoxa (Fig. 5b).

The shape and size of the gonangulum varies from specimen to specimen. In some individuals it is a small triangular

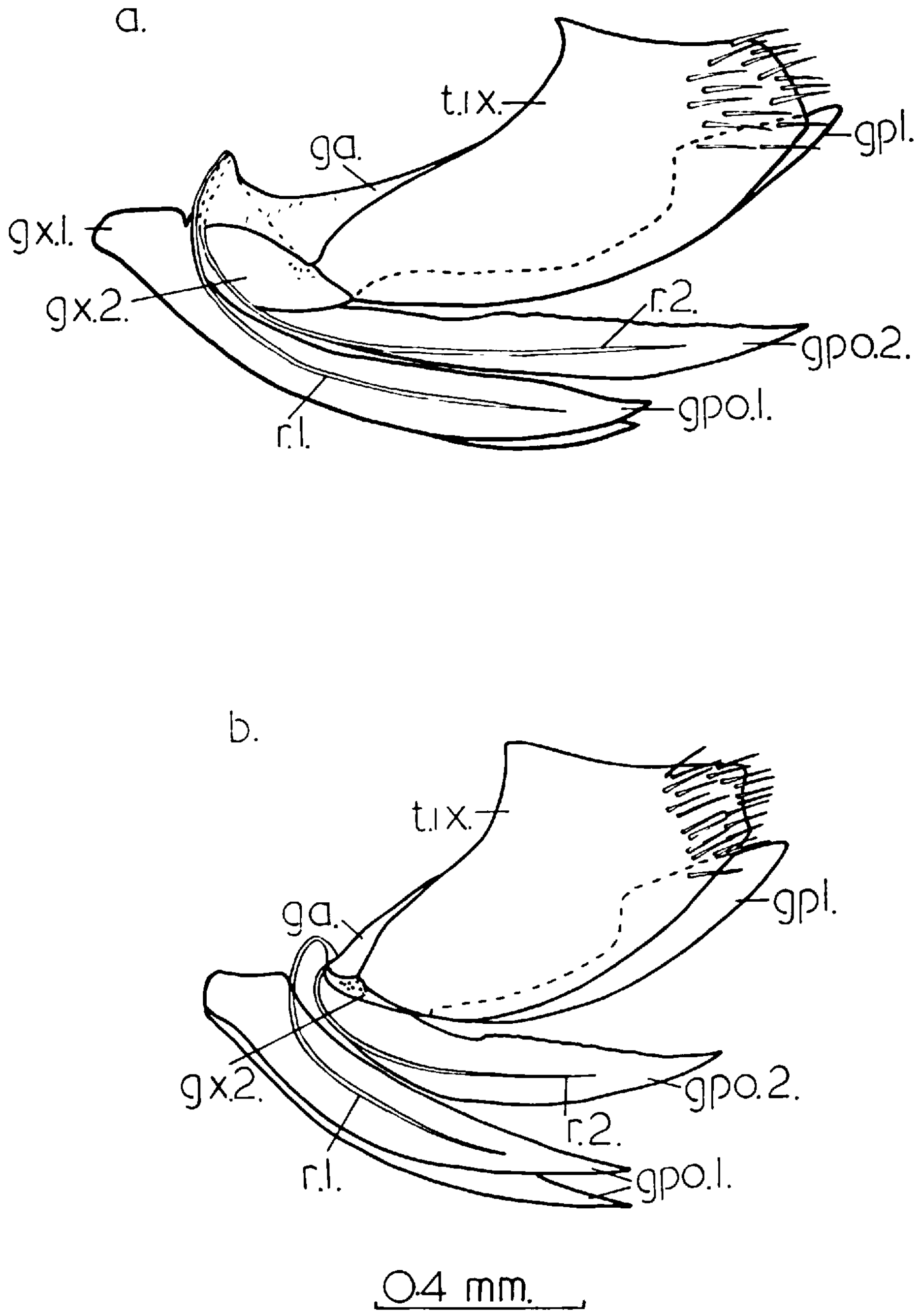
Fig. 5

Lateral View of Last Two Abdominal Segments
- *E. ocellaris*

a. Normal Female Adult
b. Abnormal Female Adult

ga.	gonangulum
gpl.	gonoplac
gpo.1.	first gonapophysis
gpo.2.	second gonapophysis
gx.1.	first gonocoxa
gx.2.	second gonocoxa
r.1.	first ramus
r.2.	second ramus
t.IX.	ninth tergite

FIG. 5


a.
t.ix.
ga.
gpl.
gx.l.
gx.2.
r.2.
gpo.2.
gpo.l.
r.l.
b.
t.ix.
ga.
gpl.
gx.2.
gpo.2.
r.2.
r.l.
gpo.l.
0.4 mm.

shaped structure being completely separated from the second gonocoxa and articulates with it on a pivot (Fig. 5b). In others it is highly chitinized but is in a rudimentary stage of its division from the second gonocoxa. In yet others, it is a small chitinized five-sided structure being completely separated from the second gonocoxa and articulating with it on a pivot. The whole posterior side of the gonangulum in all abnormal females is fused to the ventral edge of tergum IX.

The size of the second gonocoxa is also very much reduced but a group of sharp spines are present in the area where a pivot between it and the gonangulum is formed (Fig. 5b).

(iii) Comparison of Genitalia of Abnormal and Normal Male Adults

The pigmentation in normal male adults is very dark unlike that in abnormal males where it is pale (Fig. 4a, b). Sternites VI, VII and VIII are narrow in normal males whereas they are broad in abnormal ones (Fig. 4a, b). Sternites VII and VIII which are V-shaped in normal males are straight in abnormal males.

The genital valve is broader and bigger in normal males than in abnormal ones, though the paired genital plates are similar in shape and size in both forms. The ninth tergite is only a third of the size of the genital plates in parasitized individuals (Fig. 4a, b).

Plate 3

Normal male genitalia of adult *E. ocellaris* showing spindle-shaped connective. (X 177)

The aedeagus is similar in shape in both forms, but its length varies in abnormal males. The phallobase is broad with pointed edges in normal males whereas it is smaller with rounded edges in abnormal ones. The connective is specially modified, spindle-shaped structure in normal males (Fig. 4c, Plate 3), whereas the shape and size of it varies from a simple horse-shoe shape (Fig. 4d, Plate 2), to a simple spindle-shaped structure in abnormal males (Plate 1). The ends of the connective anteriorly are fused in normal males (Plate 3) whereas in abnormal specimens they end far apart (Plate 2) or may be fused (Plate 1).

The limbs of the parameres, which connect the parameres to the connective, are long in normal males, whereas they are short in abnormal males (Fig. 4c, d, Plate 1&2). The paired parameres are of the same shape and size in both normal and abnormal males.

(iv) Comparison of the Genitalia of Abnormal and Normal Female Adults

The seventh sternite which is enlarged in both forms has a pair of pointed processes at the middle of the posterior margin in the normal females whereas the posterior margin is straight in abnormal females. The pigmentation of the tergites and sternites is dark in normal females and is pale in abnormal ones.

The eighth sternite is similarly divided in both forms and is attached to the first gonocoxa.

The shape of the first gonocoxa and gonapophysis is similar in both forms except that the length of the latter is longer in normal females (Fig. 5a, b). The first ramus which is present in both forms is attached to the anterior limb of the gonangulum.

The gonangulum is a highly sclerotized five-sided structure in normal females, whereas in abnormal ones its size and shape varies. Sometimes it is very much reduced and is a five-sided, or is a triangular shaped structure which is separated from the second gonocoxa, articulating with it on a pivot. In some specimens its separation from the second gonocoxa is at a very rudimentary stage. The origin of the gonangulum from the ninth sternite is seen in these specimens, as Scudder (1961) had postulated after gathering information from descriptions made by Snodgrass (1935), Quadri (1940), Gupta (1950) and his own work. The posterior side of the gonangulum is fused to the anterior-ventral edge of tergum IX in both forms.

The shape of the second gonapophysis is identical in both forms with a serrated dorsal margin and a second ramus which is attached to the second gonocoxa. The length of the second gonapophysis is longer in normal females (Fig. 5a).

The spoon-shaped gonoplacs are attached to the posterior end of the second gonocoxa in both forms.

The second gonocoxa is greatly reduced in abnormal females as compared to that in the normal females (Fig. 5a, b), although the group of short sharp spines are present in the area where a pivot with the gonangulum is present.

Hence these abnormalities in the males and females of *E. ocellaris* adults exhibit varying degrees of reduction of external male or female genitalia.

(d) External Morphology of Abnormal Genitalia in an *A. pascuellus* Adult

On dorsal view the pigmentation and shape of the tergites in the abnormal specimen is simila· to that of normal males (Fig. 6c, d, e), except that the parasitized specimen is broader than the normal males.

On ventral view, the seventh sternite is enlarged with a notch in the centre of the posterior margin, as seen in normal female adults. Sternite VIII is narrow and has two notches at the sides (Fig. 7a). A pair of blade-like outgrowths is given off by sternum VIII. Due to its origin and shape it is homologous to the first gonapophyses of normal female adults, as all male genital structures arise from sternum IX.

Fig. 6

Ventral View of Last Two Abdominal Segments
- *A. pascuellus*

a. Fifth Instar Male
b. Fifth Instar Female

Dorsal View of Last Two Abdominal Tergites
- *A. pascuellus*

c. Normal Male Adult
d. Normal Female Adult
e. Abnormal Adult

g.v.	genital valve
s.g.p.	subgenital plate
st.VII.	seventh sternite
st.VIII.	eighth sternite
t.VIII.	eighth tergite
t.IX.	ninth tergite

FIG. 6

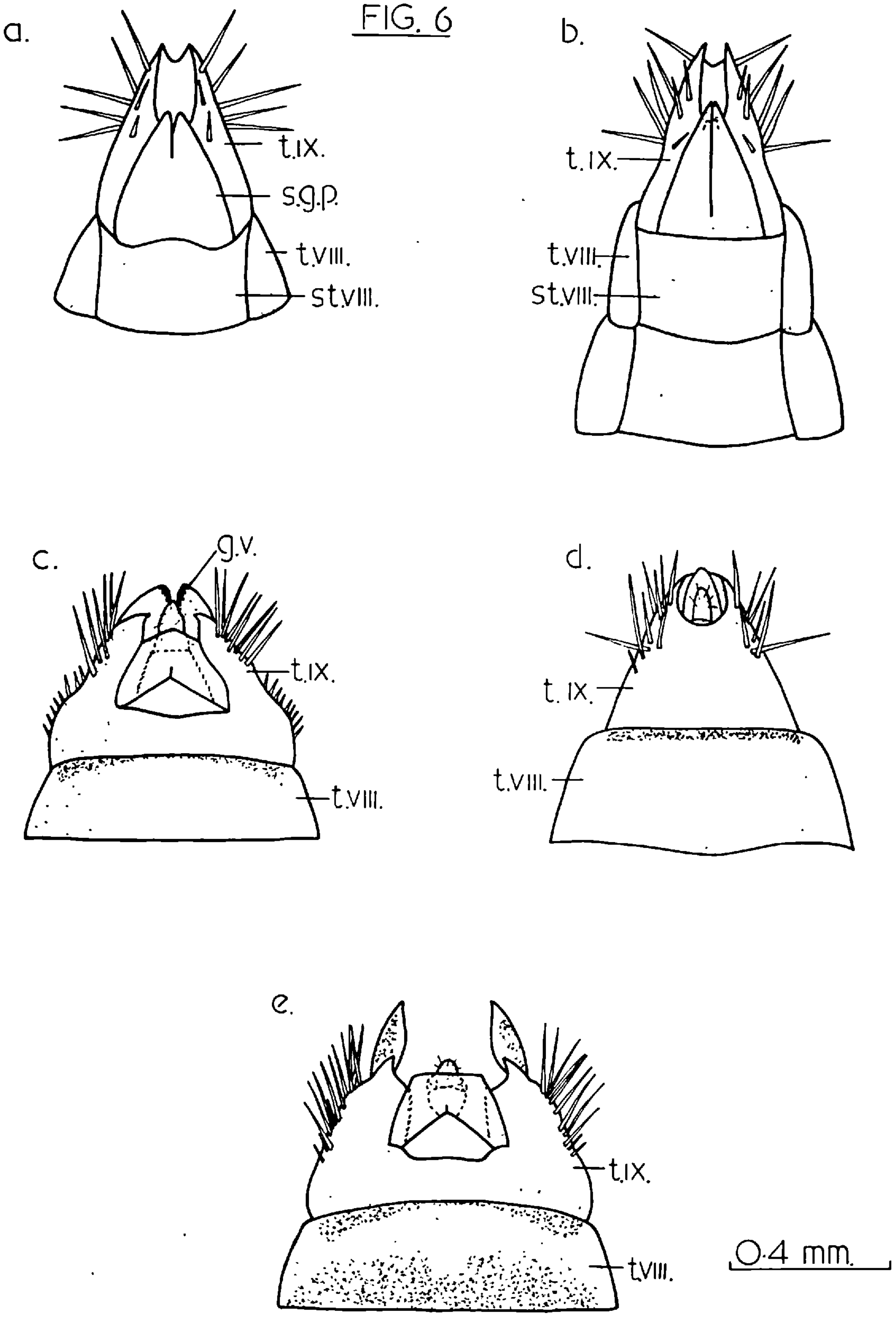

a.
t.IX.
s.g.p.
t.VIII.
st.VIII.
b.
t.IX.
t.VIII.
st.VIII.
c.
g.v.
t.IX.
t.VIII.
d.
t. IX.
t.VIII.
e.
t.IX.
t.VIII.
0·4 mm.

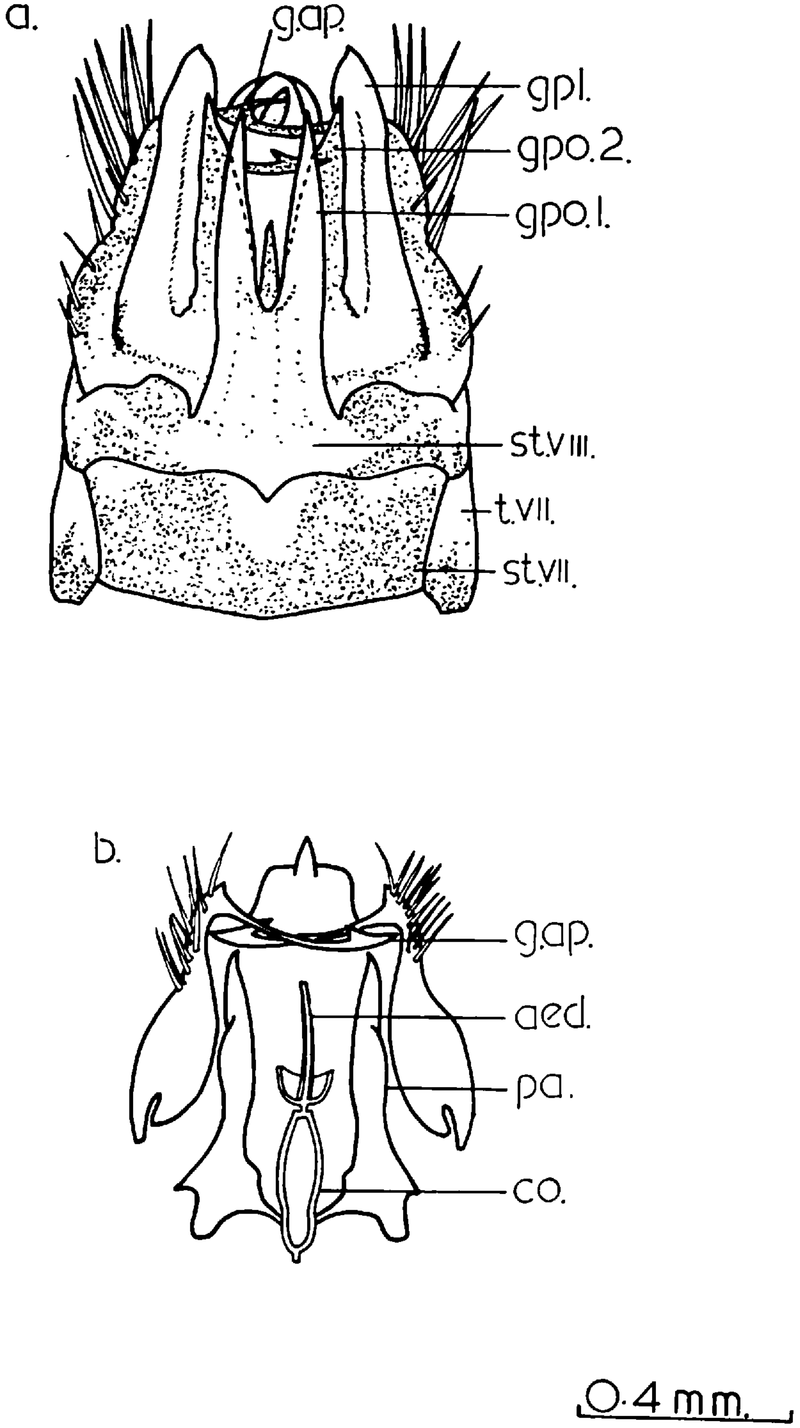
Fig. 7

a. Ventral View of Last Two Abdominal Segments
- *A. pascuellus* (Abnormal Adult)

b. Ventral View of Genital Segment - *A. pascuellus*
(Normal Male Adult)

aed.	aedeagus
co.	connectives
g.ap.	genital appendage
gpl.	gonoplac
gpo.1.	first gonapophysis
gpo.2.	second gonapophysis
pa.	parameres
st.VII.	seventh sternite
st.VIII.	eighth sternite
t.VII.	seventh tergite

FIG. 7



This pair of outgrowths is simply fused to the eighth sternum as in *E. urticae* abnormal females.

The simple unmodified ninth sternum has two pairs of outgrowths, the first being blade-like and is fused one-third of the way up. This is homologous to the second gonapophyses (Fig. 7a). The second gonocoxa and ramus are however absent in this specimen.

The third pair of spoon-shaped outgrowths is fused laterally to sternum IX and in its origin and shape it is homologous to the gonoplacs of the normal females.

Posteriorly on sternum IX a pair of genital appendages are present and these are identical to the ones in normal males (Fig. 7b).

A short unpaired process is present on sternum IX and basally it bears a connective-like structure. This is, due to its origin and shape, homologous to the aedeagus of normal males (Fig. 7). The parameres present in normal male adults are absent in this specimen.

Hence this abnormal specimen of *A. pascuellus* is an intersex, bearing some male and some female external genitalia.

Discussion

Three kinds of abnormality have been identified in three species of parasitized Cicadellidae.

One form is a suppression of the external female genitalia as in E. urticae, where the genitalia exhibit some adult and some larval characters.

The other type of suppression is present in some males and females of E. ocellaris where the external genitalia exhibit varying degrees of suppression of their development.

Thirdly, an intersex was identified in a specimen of A. pascuellus, where some male and some female external genital characters were present simultaneously.

It would be interesting to investigate the reason for the varying degrees of suppression of development exhibited in both abnormal males and females. The external male and female genitalia are obviously differentiated from the third instar onwards, and hence the particular instar of the Cicadellid parasitized may be important. It is possible that when a larva is parasitized early, i.e. in its first or second instar, it will develop into an intersex, whereas larvae parasitized in the third, fourth or fifth instars may exhibit different degrees of suppression of either the male or the female external genitalia, by the time they reach the adult stage. Alternatively, different species may react differently to parasitism.

REFERENCES

Balazuc, J. 1951. La teratologie des Hemipteres et groupes voisins.
Annals. Soc. ent. Fr. 120: 17-66.

Clausen, C.P. 1940. Entomophagous Insects.
MacGraw-Hill Book Co. 688 pp.

Delong, W.D. 1918. The occurrence of probable gynandromorph in the Homoptera.
Ohio J. Sci. 18: 226-227.

Esaki, T. & Hashimoto, S. 1934. Report on the leafhopper injurious to the rice plant and their natural enemies (in Japanese). Publs. ent. lab. Dep. Agric. Kynshu Imp. lab. Univ. (for the year 1933), 40 pp.
Rev. appl. Ent. 22: pp. 375.

Esaki, T. & Hashimoto, S. 1935. Ibid. (f the year 1934) 41 pp.
Ibid. 23: pp. 264.

Esaki, T. & Hashimoto, S. 1936. Ibid. (for the year 1935).
Ibid. 24: pp. 465.

Esaki, T. & Hashimoto, S. 1938. Ibid. (for the year 1937).
Ibid. 26: pp. 439.

Fenton, F.A. 1918. The parasites of leafhoppers with special reference to the biology of the Anteoninae.
Ohio J. Sci. 28: 177-212, 243-278, 285-296.

Imms, A.D. 1964. A General Text Book of Entomology. 9th 9th Edn. revised by Richards, O.W. & Davies, R.G. Methuen, London: 885 pp.

Linderg, H. 1946. Die biologie von Pipunculus chlorionae Frey und die einwirkung von dessen paratismus auf Chloriona - Arten.
Acta Zool. Fenn. 45: 1-50.

Muir, F. 1918. Pipunculidae and Stylopidae in Homoptera. Entomologist's mon. Mag. 54: 137.

Oman, P.W. 1949. The neartic leafhoppers (Homoptera Cicadellidae). A generic classification and check list.
Mem. ent. Soc. Wash. 253 pp.

Ribaut, H. 1936. Faune de France, 31. Homopteres Auchénorhynques (Typhlocybidae). Paris: 228 pp.

Scudder, G.G.E. 1956. Abnormal genitalia in Ishnodemus subuteli (Fall.) (Hemiptera-Lygaeidae)
Entomologist's mon. Mag. 92: 377-379.

Wigglesworth, V.B. 1954. The Physiology of Insect Metamorphosis.
University Press, Cambridge: 152 pp.

APPENDIX II

Species and Instar	Var.	Mean	S.D.
U.reticulata			
1st Instar Unsexed	1	0.468	0.020
	2	0.228	0.015
	3	0.449	0.026
	4	0.089	0.005
	5	0.237	0.011
	6	0.173	0.014
	7	0.943	0.056
2nd Instar Unsexed	1	0.630	0.017
	2	0.277	0.006
	3	0.586	0.020
	4	0.115	0.012
	5	0.314	0.014
	6	0.220	0.006
	7	1.418	0.052
3rd Instar Male	1	0.792	0.026
	2	0.328	0.018
	3	0.741	0.017
	4	0.146	0.007
	5	0.401	0.017
	6	0.271	0.014
	7	1.662	0.109
3rd Instar Female	1	0.818	0.010
	2	0.347	0.016
	3	0.739	0.040
	4	0.159	0.014
	5	0.390	0.007
	6	0.276	0.009
	7	1.900	0.140
4th Instar Male	1	1.002	0.033
	2	0.400	0.016
	3	0.895	0.044
	4	0.236	0.011
	5	0.539	0.023
	6	0.349	0.030
	7	2.478	0.122
4th Instar Female	1	1.058	0.032
	2	0.419	0.011
	3	0.951	0.024
	4	0.239	0.022
	5	0.524	0.031
	6	0.357	0.027
	7	2.509	0.197
5th Instar Male	1	1.248	0.036
	2	0.446	0.027
	3	1.119	0.045
	4	0.305	0.021
	5	0.692	0.021
	6	0.427	0.031
	7	2.968	0.214
5th Instar Female	1	1.311	0.035
	2	0.489	0.020
	3	1.166	0.041
	4	0.315	0.091
	5	0.726	0.027
	6	0.471	0.017
	7	3.002	0.206
Adult Male	1	1.397	0.075
	2	0.391	0.024
	3	1.136	0.072
	4	0.543	0.040
	5	0.834	0.052
	6	0.561	0.022
	7	3.091	0.281
Adult Female	1	1.480	0.043
	2	0.418	0.037
	3	1.221	0.049
	4	0.508	0.024
	5	0.956	0.052
	6	0.581	0.039
	7	3.344	0.194

Species and Instar	Var.	Mean	S.D.
<u>M.parvicauda</u>			
1st Instar Unsexed	1	0.406	0.011
	2	0.242	0.009
	3	0.352	0.013
	4	0.056	0.010
	5	0.538	0.056
	6	0.344	0.031
	7	1.488	0.126
2nd Instar Unsexed	1	0.515	0.015
	2	0.293	0.019
	3	0.455	0.025
	4	0.148	0.032
	5	0.676	0.136
	6	0.454	0.061
	7	1.912	0.107
3rd Instar Male	1	0.654	0.013
	2	0.352	0.025
	3	0.595	0.031
	4	0.217	0.023
	5	0.901	0.023
	6	0.571	0.031
	7	2.483	0.155
3rd Instar Female	1	0.658	0.031
	2	0.361	0.022
	3	0.607	0.022
	4	0.213	0.018
	5	0.963	0.023
	6	0.595	0.045
	7	2.558	0.168
4th Instar Male	1	0.853	0.044
	2	0.419	0.031
	3	0.759	0.025
	4	0.273	0.015
	5	1.222	0.054
	6	0.749	0.028
	7	3.363	0.112
4th Instar Female	1	0.883	0.019
	2	0.444	0.025
	3	0.801	0.027
	4	0.290	0.017
	5	1.317	0.037
	6	0.802	0.026
	7	3.546	0.131
5th Instar Male	1	1.023	0.033
	2	0.445	0.022
	3	0.945	0.027
	4	0.353	0.014
	5	1.559	0.033
	6	0.946	0.056
	7	3.976	0.162
5th Instar Female	1	1.096	0.039
	2	0.493	0.026
	3	1.019	0.029
	4	0.394	0.026
	5	1.649	0.061
	6	1.013	0.024
	7	4.317	0.371
Adult Male	1	1.132	0.032
	2	0.375	0.040
	3	1.042	0.035
	4	0.510	0.037
	5	1.955	0.064
	6	1.070	0.023
	7	3.490	0.172
Adult Female	1	1.204	0.012
	2	0.421	0.015
	3	1.106	0.014
	4	0.548	0.024
	5	2.022	0.070
	6	1.238	0.019
	7	3.848	0.055

Species and Instar	Var.	Mean	S.D.
C.persimilis			
1st Instar Unsexed	1	0.385	0.024
	2	0.248	0.019
	3	0.338	0.013
	4	0.059	0.008
	5	0.560	0.026
	6	0.344	0.017
	7	1.400	0.152
2nd Instar Unsexed	1	0.486	0.017
	2	0.297	0.026
	3	0.450	0.021
	4	0.138	0.013
	5	0.768	0.030
	6	0.452	0.028
	7	1.600	0.101
3rd Instar Male	1	0.640	0.029
	2	0.340	0.021
	3	0.577	0.023
	4	0.191	0.015
	5	1.026	0.035
	6	0.649	0.022
	7	2.269	0.118
3rd Instar Female	1	0.644	0.026
	2	0.341	0.026
	3	0.586	0.033
	4	0.197	0.016
	5	1.060	0.041
	6	0.665	0.025
	7	2.352	0.149
4th Instar Male	1	0.745	0.044
	2	0.372	0.029
	3	0.712	0.028
	4	0.258	0.012
	5	1.300	0.044
	6	0.770	0.039
	7	2.584	0.746
4th Instar Female	1	0.779	0.033
	2	0.378	0.041
	3	0.740	0.022
	4	0.264	0.021
	5	1.347	0.069
	6	0.811	0.061
	7	3.057	0.137
5th Instar Male	1	0.992	0.030
	2	0.436	0.046
	3	0.909	0.027
	4	0.344	0.016
	5	1.677	0.058
	6	0.966	0.073
	7	3.432	0.139
5th Instar Female	1	1.052	0.062
	2	0.462	0.024
	3	0.947	0.034
	4	0.374	0.015
	5	1.798	0.106
	6	1.065	0.107
	7	3.708	0.200
Adult Male	1	1.124	0.041
	2	0.334	0.028
	3	1.027	0.066
	4	0.498	0.022
	5	1.993	0.080
	6	1.132	0.054
	7	3.656	0.097
Adult Female	1	1.220	0.049
	2	0.407	0.026
	3	1.092	0.038
	4	0.547	0.031
	5	2.207	0.069
	6	1.304	0.050
	7	4.704	0.060

Species and Instar	Var.	Mean	S.D.
E. ocellaris			
1st Instar Unsexed	1	0.378	0.031
	2	0.228	0.019
	3	0.346	0.034
	4	0.054	0.006
	5	0.444	0.010
	6	0.280	0.019
	7	1.422	0.153
2nd Instar Unsexed	1	0.463	0.015
	2	0.280	0.023
	3	0.411	0.013
	4	0.095	0.008
	5	0.601	0.034
	6	0.378	0.023
	7	1.634	0.222
3rd Instar Male	1	0.614	0.027
	2	0.337	0.029
	3	0.567	0.020
	4	0.164	0.010
	5	0.817	0.055
	6	0.496	0.034
	7	1.748	0.055
3rd Instar Female	1	0.633	0.021
	2	0.345	0.025
	3	0.587	0.015
	4	0.177	0.017
	5	0.884	0.032
	6	0.533	0.024
	7	1.906	0.175
4th Instar Male	1	0.779	0.036
	2	0.419	0.008
	3	0.725	0.031
	4	0.232	0.011
	5	1.109	0.029
	6	0.683	0.026
	7	2.410	0.184
4th Instar Female	1	0.821	0.022
	2	0.429	0.021
	3	0.757	0.020
	4	0.245	0.009
	5	1.159	0.028
	6	1.688	0.031
	7	2.402	0.154
5th Instar Male	1	0.901	0.041
	2	0.455	0.024
	3	0.846	0.031
	4	0.287	0.017
	5	1.395	0.040
	6	0.809	0.039
	7	2.790	0.236
5th Instar Female	1	0.966	0.018
	2	0.486	0.026
	3	0.919	0.038
	4	0.300	0.014
	5	1.513	0.035
	6	0.902	0.032
	7	3.006	0.155
Adult Male	1	1.008	0.037
	2	0.430	0.030
	3	0.926	0.029
	4	0.390	0.022
	5	1.735	0.061
	6	1.027	0.064
	7	3.209	0.130
Adult Female	1	1.102	0.043
	2	0.477	0.038
	3	1.006	0.028
	4	0.417	0.039
	5	1.911	0.058
	6	1.135	0.061
	7	3.777	0.132

Species and Instar	Var.	Mean	S.D.
<u>B. punctata</u>			
<u>1st Instar</u> Unsexed	1	0.282	0.018
	2	0.198	0.014
	3	0.306	0.030
	4	0.073	0.006
	5	0.226	0.021
	6	0.140	0.012
	7	1.067	0.112
2nd Instar Unsexed	1	0.388	0.023
	2	0.232	0.016
	3	0.405	0.018
	4	0.101	0.008
	5	0.350	0.026
	6	0.214	0.011
	7	1.369	0.136
3rd Instar Male	1	0.504	0.019
	2	0.253	0.017
	3	0.529	0.021
	4	0.142	0.011
	5	0.499	0.016
	6	0.316	0.019
	7	1.552	0.042
3rd Instar Female	1	0.533	0.030
	2	0.260	0.012
	3	0.559	0.022
	4	0.149	0.011
	5	0.519	0.027
	6	0.331	0.020
	7	1.705	0.034
4th Instar Male	1	0.651	0.016
	2	0.258	0.021
	3	0.680	0.022
	4	0.210	0.010
	5	0.759	0.024
	6	0.468	0.025
	7	2.201	0.162
4th Instar Female	1	0.661	0.019
	2	0.269	0.023
	3	0.709	0.021
	4	0.216	0.016
	5	0.768	0.040
	6	0.461	0.025
	7	2.146	0.159
5th Instar Male	1	0.821	0.022
	2	0.256	0.021
	3	0.881	0.038
	4	0.310	0.020
	5	1.065	0.031
	6	0.674	0.050
	7	2.805	0.150
5th Instar Female	1	0.833	0.018
	2	0.243	0.011
	3	0.893	0.020
	4	0.314	0.015
	5	1.107	0.037
	6	0.678	0.030
	7	2.781	0.158
Adult Male (Form I)	1	0.859	0.015
	2	0.113	0.013
	3	0.959	0.042
	4	0.448	0.041
	5	1.482	0.044
	6	0.906	0.017
	7	2.868	0.164
Adult Female (Form I)	1	0.885	0.020
	2	0.126	0.018
	3	0.962	0.020
	4	0.499	0.022
	5	1.512	0.084
	6	0.944	0.034
	7	2.869	0.109

Species and Instar	Var.	Mean	S.D.	
Adult Male (Form II)	1	0.850	0.026	
	2	0.101	0.004	
	3	0.931	0.025	
	4	0.440	0.020	
	5	1.463	0.035	
	6	0.882	0.040	
	7	3.648	0.162	
Adult Female (Form II)	1	0.880	0.026	
	2	0.106	0.002	
	3	0.970	0.023	
	4	0.445	0.053	
	5	1.523	0.051	
	6	0.934	0.036	
	7	3.854	0.229	

APPENDIX III

Species	Var.	Mean	S.D.	Species	Var.	Mean	S.D.
U. reticulata	1	1.300	0.038	*O. flavicollis*	1	1.408	0.045
	2	0.460	0.028		2	0.366	0.048
	3	1.095	0.045		3	1.394	0.052
	4	0.307	0.029		4	0.782	0.138
	5	0.461	0.028		5	0.656	0.081
	6	0.670	0.030		6	1.096	0.121
	7	2.962	0.172		7	3.884	0.225
	8	0.232	0.020		8	0.332	0.022
	9	0.256	0.020		9	0.406	0.043
C. viridis	1	2.067	0.073	*E. cuspidata*	1	1.646	0.022
	2	1.079	0.086		2	1.632	0.196
	3	1.763	0.243		3	1.464	0.068
	4	0.641	0.054		4	0.514	0.047
	5	1.605	0.129		5	0.856	0.078
	6	2.839	0.261		6	1.382	0.081
	7	6.202	0.469		7	6.002	0.702
	8	0.574	0.050		8	0.382	0.055
	9	0.709	0.033		9	0.592	0.069
G. coccinea	1	1.670	0.092	*D. stylata*	1	1.122	0.054
	2	1.091	0.036		2	0.450	0.019
	3	1.716	0.051		3	1.042	0.024
	4	0.627	0.050		4	0.286	0.012
	5	1.531	0.720		5	0.792	0.036
	6	2.925	0.128		6	1.255	0.048
	7	6.828	0.626		7	2.967	0.324
	8	0.615	0.062		8	0.257	0.018
	9	0.827	0.058		9	0.357	0.020
I. distinguendus	1	1.580	0.025	*R. coronifer*	1	0.926	0.048
	2	0.298	0.013		2	0.444	0.027
	3	1.330	0.019		3	0.928	0.064
	4	0.456	0.034		4	0.328	0.015
	5	0.804	0.058		5	0.904	0.057
	6	1.320	0.068		6	1.432	0.074
	7	3.628	0.276		7	3.126	0.319
	8	0.528	0.033		8	0.202	0.016
	9	0.222	0.029		9	0.346	0.038

Species	Var.	Mean	S.D.
E. ocellaris	1	0.919	0.028
	2	0.464	0.025
	3	0.858	0.027
	4	0.290	0.015
	5	0.847	0.043
	6	1.468	0.102
	7	2.913	0.277
	8	0.243	0.034
	9	0.452	0.025
R. proceps	1	1.552	0.027
	2	0.612	0.028
	3	1.384	0.068
	4	0.480	0.033
	5	1.022	0.100
	6	1.670	0.139
	7	4.106	0.248
	8	0.346	0.050
	9	0.512	0.037
G. ventralis	1	1.538	0.019
	2	0.623	0.034
	3	1.612	0.044
	4	0.532	0.031
	5	1.304	0.040
	6	1.957	0.029
	7	4.653	0.239
	8	0.384	0.043
	9	0.513	0.043
A. mixtus	1	1.574	0.044
	2	0.508	0.027
	3	1.486	0.019
	4	0.598	0.040
	5	1.386	0.093
	6	2.274	0.130
	7	5.286	0.501
	8	0.448	0.061
	9	0.640	0.032
M. grisescens	1	1.538	0.051
	2	0.608	0.033
	3	1.502	0.036
	4	0.502	0.008
	5	1.168	0.064
	6	1.892	0.116
	7	4.112	0.095
	8	0.348	0.027
	9	0.434	0.044
M.parvicauda	1	1.068	0.034
	2	0.558	0.289
	3	0.972	0.035
	4	0.373	0.026
	5	0.992	0.038
	6	1.632	0.053
	7	3.780	0.456
	8	0.277	0.025
	9	0.479	0.029
C.persimilis	1	1.032	0.019
	2	0.452	0.017
	3	0.933	0.016
	4	0.362	0.014
	5	1.036	0.020
	6	1.717	0.017
	7	3.593	0.132
	8	0.282	0.022
	9	0.611	0.033
C.aurantipes	1	1.177	0.024
	2	0.497	0.029
	3	1.082	0.038
	4	0.421	0.011
	5	1.162	0.065
	6	1.952	0.092
	7	4.299	0.175
	8	0.342	0.021
	9	0.732	0.066
E.sulphurella	1	1.058	0.033
	2	0.464	0.005
	3	1.014	0.056
	4	0.354	0.015
	5	1.072	0.062
	6	1.772	0.114
	7	3.660	0.131
	8	0.282	0.025
	9	0.548	0.030

Species	Var.	Mean	S.D.
G. puncti-collis	1	1.242	0.032
	2	0.417	0.022
	3	1.080	0.032
	4	0.385	0.010
	5	0.840	0.058
	6	1.350	0.106
	7	3.982	0.112
	8	0.345	0.033
	9	0.467	0.010
M. sexuotatus	1	0.883	0.032
	2	0.380	0.031
	3	0.779	0.040
	4	0.294	0.026
	5	0.945	0.047
	6	1.463	0.033
	7	3.324	0.313
	8	0.165	0.027
	9	0.256	0.030
B. punctata	1	0.816	0.023
	2	0.240	0.039
	3	0.867	0.020
	4	0.296	0.029
	5	0.662	0.030
	6	1.083	0.042
	7	3.051	0.364
	8	0.217	0.033
	9	0.305	0.024
Z. scutellaris	1	0.612	0.025
	2	0.232	0.007
	3	0.504	0.025
	4	0.213	0.021
	5	0.378	0.035
	6	0.682	0.039
	7	2.145	0.192
	8	0.184	0.021
	9	0.259	0.016
I. lanio	1	2.154	0.103
	2	0.391	0.048
	3	1.992	0.080
	4	0.782	0.032
	5	1.427	0.054
	6	2.231	0.072
	7	6.047	0.527
	8	0.572	0.082
	9	0.810	0.063

APPENDIX IV

Variables with Large Positive and Negative Weights (Greater than the Mean Value) Along the First Five Axes - Principal Component Analyses (42 and 51 Characters)

Table 1 First Axis - Principal Component Analysis (42 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
37. Length of wing pads	0.250	13. Subgenal sulcus	-0.250
39. Apex of hind femora	0.250	16. Antennal depression	-0.250
41. Prominent crown of spines on hind tibiae	0.204	19. Finger-like projection on posterior margin of mesoepisternum	-0.250
20. Posterior portion of mesothoracic furcal sulcus	0.213	21. Raised median line on thorax and abdomen	-0.250
42. Finger-like projections at the tip of hind tarsus	0.185	27. Cleft on the rudiments of the first gonapophyses in female	-0.250
38. Apex of anterior and median femora	0.179	28. Subgenital plate in male	-0.250
33. Bristles with prominent bases	0.174	18. Keels at the sides of pronotum	-0.193

Table 2 Second Axis - Principal Component Analysis
(42 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
34. Number of bristles on abdominal segments III to VI	0.289	24. Rudiments of the first gonapophyses in female	-0.237
36. Number of bristles on abdominal segment VIII	0.285	8. Angle between crown and face	-0.209
35. Number of bristles on abdominal segment VII	0.282	12. Transclypeal sulcus	-0.199
4. Ocelli	0.258	3. Sides of anterior margin of vertex	-0.163
22. Length of eighth abdominal tergite	0.237		
23. Size of subgenital plate in male	0.237		
33. Bristles with prominent bases	0.221		
38. Apex of anterior and median femora	0.196		

Table 3 Third Axis - Principal Component Analysis
(42 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
5. Frontogenal sulcus	0.341	7. Extent of clypeoloral and clypeogenal sulci	-0.256
9. Sharp median keel on face	0.321	24. Rudiments of the first gonapophyses in female	-0.255
11. Genae	0.321	32. Dorsal surface of abdominal segments	-0.252
22. Length of eighth abdominal tergite	0.255		
23. Size of subgenital plate in male	0.255		
3. Sides of anterior margin of vertex	0.242		
18. Keels at the sides of pronotum	0.211		

Table 4 Fourth Axis - Principal Component Analysis
(42 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
6. Ante- and postclypeus	0.231	12. Transclypeal sulcus	-0.360
24. Rudiments of the first gonapophyses in female	0.255	2. Anterior margin of vertex	-0.275
9. Sharp median keel on face	0.197	17. Anteclypeus	-0.271
11. Genae	0.197	40. Spines on hind tibia	-0.267
18. Keels at the sides of pronotum	0.196	22. Length of eighth abdominal tergite	-0.255
41. Prominent crown of spines on hind tibia	0.187	23. Size of subgenital plate in male	-0.255
		29. Cleft at the posterior end of the subgenital plate in male	-0.219

Table 5 Fifth Axis - Principal Component Analysis
(42 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
10. Cuticular outgrowths on antennal ledge	0.468	20. Posterior portion of furcal sulcus on mesothorax	-0.286
4. Ocelli	0.263	8. Angle between crown and face	-0.256
30. Posterior end of subgenital plate in male	0.219	38. Apex of anterior and median femora	-0.203
6. Ante- and postclypeus	0.204	41. Prominent crown of spines on hind tibiae	-0.202
40. Spines on hind tibiae	0.204	5. Frontogenal sulcus	-0.190
31. Sides of subgenital plate in male	0.195		
15. Ridge above antennae	0.183		

Table 6 First Axis - Principal Component Analysis
(51 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
37. Length of wing pads	0.242	13. Subgenal sulcus	-0.242
39. Apex of hind femora	0.242	16. Antennal depression	-0.242
20. Posterior portion of furcal sulcus on mesothorax	0.222	19. Finger-like projection on posterior margin of mesoepisternum	-0.242
41. Prominent crown of spines on hind tibiae	0.209	27. Cleft on the rudiments of the first gonapophyses in female	-0.242
42. Finger-like projections at the tip of hind tarsus	0.191	21. Raised median line on thorax and abdomen	-0.242
38. Apex of anterior and median femora	0.179	28. Subgenital plate in male	-0.242

Table 7 Second Axis - Principal Component Analysis
(5 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
43. Head width	0.283	8. Angle between crown and face	-0.160
45. Pronotal width	0.281	19. Anteclypeus	-0.156
46. Pronotal length	0.276		
50. Length of VIII tergite	0.271		
49. Total body length	0.269		
4. Ocelli	0.211		
14. Antennae	0.195		
33. Bristles with prominent bases	0.198		

Table 8 Third Axis - Principal Component Analysis (51 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
22. Length of eighth abdominal tergite	0.327	24. Rudiments of the first gonapophyses in female	-0.327
23. Size of subgenital plate in male	0.327	10. Cuticular outgrowths on antennal ledge	-0.176
5. Frontogenal sulcus	0.246		
42. Finger-like projections at the tip of hind tibiae	0.236		
34. Number of bristles on abdominal segments III to VI	0.196		
1. Shape of vertex	0.194		
36. Number of bristles on abdominal segment VIII	0.192		

Table 9 Fourth Axis - Principal Component Analysis (51 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
9. Sharp median keel on face	0.384	7. Extent of clypeoloral and clypeogenal sulci	-0.255
11. Genae	0.384		
6. Ante- and postclypeus	0.321		
3. Sides of anterior margin of vertex	0.316		
18. Keels at the sides of pronotum	0.225		

Table 10 Fifth Axis - Principal Component Analysis (51 Characters)

Positive Weight		Negative Weight	
Variable	Weight	Variable	Weight
12. Transclypeal sulcus	0.378	41. Prominent crown of spines on hind tibiae	-0.247
40. Spines on hind tibiae	0.328	24. Rudiments of the first gonapophyses in female	-0.239
10. Cuticular outgrowths on antennal ledge	0.251		
22. Length of eighth abdominal tergite	0.239		
23. Size of subgenital plate in male	0.239		
2. Anterior margin of vertex	0.208		
29. Cleft in the center of the posterior end of subgenital plate in male	0.208		