THE FUNCTIONAL MORPHOLOGY OF THE MOUTHPARTS OF *Acheta domesticus* (L.) (Orthoptera: Gryllidae)

by

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Dedicated

to

my

parents

as

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token

of

respect.

ABSTRACT

The morphology of the head capsule of adult Acheta domesticus (L.) has been described in terms of external features and the internal skeleton or tentorium. The detailed structure of the feeding appendages has been considered. The appendicular mandibles, maxillae and labium are described in addition to the intricate hypopharynx and the sensory clypeo-labrum.

The work attempts to relate the structure of each component to its mode of functioning in the feeding process. Consequently a complete study of the musculature of the head capsule and feeding appendages has been made. The muscles of the cervix have also been included.

The cuticular sensilla have been investigated using a Scanning Electron Microscope in addition to light microscopic techniques. Thirteen different types of sensilla have been identified and described. The precise distribution and abundance of each sensilla type has been considered on all the mouthparts and associated structures. This has been recorded by a series of diagrams, thus sensilla distribution maps for each component. The consistency of the distribution has been assessed by using a number of replicates for adult of both sexes. In order to analyse the mode of development of the pattern of sensilla in the adult, the clypeolabrum has been selected as an example. The

number and distribution of various types of sensilla on the clypeolabrum have been investigated for each nymphal instar.

The nervous supply to the cuticular sensilla and to the muscles of the mouthparts has been analysed using various staining techniques.

Finally, feeding in this species has been carefully described and filmed to facilitate a detailed consideration of the role of each component.

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PART I

GENERAL INTRODUCTION

The insect selected for study, Acheta domesticus (L.), has a wide zoogeographical distribution. In cooler temperate lands the species is confined to buildings, houses, bakeries, restaurants where it is known as House Cricket. It may also be found on rubbish dumps, where the heat generated from the decomposing material is adequate to enable the species to live outdoors (Ragge, 1965). However, nearer the equator the species can survive outdoors and it is known to be serious pest of wheat grain, oil seed, millet and cotton (Ghouri, 1957). Little attention has so far been paid to members of the family Gryllidae and apart from some purely descriptive work at the turn of the century few accounts exist of the behaviour or physiology of these insects (e.g. Voss, 1905). The aim of the present work is to attempt to describe in detail the structure of the head capsule and its appendages and to relate the findings to the feeding mechanism of the species. The project has four main components; a description of the structure of the head capsule and its appendages, the musculature of the head capsule and its appendages, the identification of the cuticular sensilla on the mouthparts and a study of the nervous supply to the sensilla and the muscles involved in feeding.

Although much important work has been carried out describing the anatomy of various arthropod groups, from a functional standpoint, relatively little attention has been paid to the Gryllidae. Hence from an understanding of the above four aspects the feeding mechanism may be described in more detail. The work was centered on the adult female, although males were carefully examined for any obvious sexual dimorphism.

The head of *A. domesticus* may be considered to be a generalized type of Pterygote head displaying the hypognathous condition. Duporte (1957, 1965) studied the comparative morphology of the insect head emphasing features of the facial region. Snodgrass (1928) has described and reviewed the general morphology of the head and his interpretation (Snodgrass, 1935) is used in the present work. Manton (1960, 1964) has investigated the head development and mandibular mechanism in the Arthropoda. This was considered further by Matsuda (1965). In the Orthoptera Gapud (1968) describes the external morphology of the head and mouthparts of some Philippine insects. The excellent work of Yuasa (1920) gives a complete description of the anatomy of the head and mouthparts of Orthoptera.

The head of the closely related species *Gryllus assimilis* Fabr., has been the subject of a study by Duporte (1959). Among the Gryllidae, *Gryllodes sigillatus* (Walker), has been studied in respect of the sclerites of the head capsule and appendages (Narula, 1968). *Grylloblatta campodeiformis* Walker was the subject of a study by Walker (1933) in which he stresses the close resemblance of certain sutures to those found in the Saltatoria.

As regards the internal skeleton or tentorium, Hudson (1945) has presented a detailed account of its structure in some Orthopteroid insects. This was supplemented by Snodgrass (1958). Hudson (1945) considers that the Gryllidae, Tettigoniidae and Acrididae all possess an x-shaped tentorium in which the anterior arms are broadly expanded and heavily sclerotized, whilst the dorsal arms arise as outgrowth from the anterior part of the body of the tentorium. The posterior tentorial pits give rise to posterior tentorial arms from which the strong transverse bars coalesce with the body of the tentorium. The body of the tentorium is not enlarged as in the prognathous Gryllotalpidae. Thus the gryllid tentorium displays no striking modifications.

The functional morphology of the head capsule is incomplete without a thorough understanding of the muscles which are responsible for the movement of the head and mouthparts. Matsuda (1965) studied the evolution of the head musculature in insects in general. Cook (1944) gave an account of the musculature of the labrum and clypeus of insects. The skeleto-muscular mechanism of the head in _Gryllus bimaculatus_ DeGeer has been studied by Thakare (1961). An account of the musculature of _G. assimilis_ has been given by Duporte (1920) although the techniques available at that time somewhat restricted his contribution. Narula (1974) described the muscles of the head capsule and tried to establish the function of each feeding appendage in *G. sigillatus* by mechanical manipulation. There are some similarities of Schizodactylidae, *Schizodactylus monstrosus* Don. with Tettigoniidae but it shows greater resemblance with the family Gryllidae (Khattar, 1964). Crampton (1917) gave an account of the structure of the neck region in insects. The cervicothoracic musculature of the adult cockroach, *Nauphoeta cinerea* (Olivier) was described by Storch (1968). Voss (1905) has described the muscles of the neck, thorax and anterior abdominal segments but did not include the mouthparts of *Gryllus*.

Since a major role in the selection of food is played by the cuticular sensilla, it is necessary to identify and describe all the different types of sensilla and to investigate their distribution on the mouthparts. In this context Thomas (1966) described ten different types of sensilla on the mouthparts of *Schistocerca gregaria* (Forskal) and also suggested their role in the selection of food. Chapman (1966) has described those on the mouthparts of *Xenocheila zarudnyi* (Uvarov) and Marshall (1947) has investigated the sense organs on the labrum of *Melanoplus femur-rubrum* (DeGeer). The contribution of these authors is of great value in enabling comparisons to be made with *A. domesticus*. In this study sensilla on the adult cricket have been described in terms of their external morphology only and no histological work has been carried out. It is, however, possible to classify sensilla according to their length and socket diameter (e.g. Blaney & Chapman, 1969a).

Slifer's (1961) investigation on the structure of the chemoreceptors in insects coupled with Blaney and Chapman (1969b) account of the fine structure of the sensilla on the maxillary palp of S. gregaria assist in elucidating the possible function of sensilla in A. domesticus in relation to feeding. According to Pringle (1938a, b) campaniform sensilla present on certain joints are stress receptors responding to strain in the cuticular skeleton and are therefore mechanoreceptors. The presence of campaniform sensilla and their relation to a mechanical function has already been confirmed (Chapman, 1965; McIver, 1974 and Arnold, 1974). Arnold (1974) investigated these sensilla along with sensilla trichodea and basiconica on the tarsi of cockroaches.

The development of the distribution of sensilla in the adult has been investigated. The number of nymphal instars in A. domesticus is known to vary (Ragge, 1965 and Rummel, 1963). Consequently, this had to be determined for the culture used in the present study. The clypeo-labrum was considered to be a structure which displayed a wide range of types of sensilla. Thus the distribution and number of each type of sensillum was considered in each nymphal instar. Finally a study of the peripheral nervous system associated with the mouthparts was undertaken. This was assisted by a study of the peripheral nervous system of the mouthparts of the final instar nymph of *G. domesticus* carried out by Fudalewicz-Niemczyk and Rosciszewska (1974). These authors traced the main nerves from the suboesophageal ganglion and the tritocerebrum which innervate the sensory organs of the mouthparts. Le Berre and Louveaux (1969) studied the innervation of the mandibles in nymphs of *Locusta migratoria* L. He also considered in detail the pore canals. Louveaux (1972) studied the innervation of the mouthparts of first instar nymphs of *L. migratoria* and also the hypopharynx of *Locusta migratoria migratorioides* R. et F. (Louveaux, 1975). Here the aim is to trace the main nerves and their branches to the muscles of the mouthparts and to the sensilla in the adult female. A list of proprioceptors in *G. domesticus* innervated by a single neuron has been given by Knyazeva, Fudalewicz-Niemczyk and Rosciszewska (1975).

The number of neurons is an important feature in the functional identification of the sensillum.

The mechanism of feeding has been studied by ciné-film and videotape. This detailed observation of the movement of the individual mouthparts enables the author to create a picture of the stages involved in feeding and to make further suggestions on the role and importance of certain types of sensilla. Relatively little work of this nature has been carried out using crickets, emphasis mostly being placed on the Acrididae, although Popham (1961) has considered Periplaneta americana L. which closely resembles Gryllidae in many respects. Gangwere (1960) described the use of the mouthparts of Orthoptera during feeding and classified them as margin feeders and centre feeders, the latter type may also pierce. The author considers that in both margin and centre-feeding the labrum acts as a dorsal lip. In the margin-feeding forms the incisor processes of the mandible cut the food as the mandibles come together. Whilst the laciniae force this cut food into the preoral food cavity where it is masticated by the molar dentes. The galeae merely act as lateral lips. There is usually a distinct pause between the incision and mastication.

In the centre-feeding the laciniae and galeae operate together in opposite directions to the mandibles and assist in handling the food particles loosened by the mandibles. Sometimes a pause occurs during mastication. The mandibles may be used to pierce food material, e.g. in the shield back Katydid the mandibles are repeatedly moved to puncture a piece of meat. It seems that crickets are probably similar to centre feeders which also pierce their food.

The initial selection of food has been the subject of much work. The normal behavioural sequence in Schistocerca in testing the food, prior to ingestion, involves palpation with both the palps and antennae (William, 1954). This importance of the palps has been further stressed by Mordue (1975). In addition to investigating the histology of the hypopharynx (Rietschel, 1953a), he suggests its mode of functioning and the only contribution to the functioning of the mouthparts of _A. domesticus_ has been made by Rietschel (1953b). Despite the generalised structure of the mouthparts of members of the subfamily Gryllinae, the hypopharynx undergoes such extensive differentiation, that in some respects it functions as a dipteran proboscis although of course its origin is different.

PART 2

MATERIALS AND METHODS

2.1 Insects used

Specimens of A. domesticus were received from Imperial College Field Station at Silwood Park and also from a biological supplier (Xenopus Ltd., 151 Frenches Road, Redhill, Surrey). From these insects a culture was maintained.

2.2 Rearing Technique

The method followed for rearing the crickets was similar to that described by Ghouri and McFarlane (1958). Groups of ten to twelve adults or twenty to twenty five nymphs were kept in 4lb glass jars. These were maintained in a constant environment room at a temperature of 28°C and a relative humidity of 40%. Each culture jar was supplied with a round plastic dish six centimeters in diameter and one and half centimeters high. In the base of each dish was a layer of fine, sterilized and moistened sand. Twelve centimeters long glass tubes filled with water were stoppered with a plug of cotton wool and inverted onto the sand. This arrangement provided a readily available supply of water and was replenished every two days. The sand also provided a suitable site for oviposition. The diet used consisted of 75% wheat germ, 20% dried skimmed milk, 5% brewer's yeast (Brown, 1973) and to this was added some finely ground dog biscuits. This diet proved to be very satisfactory. Strips of folded paper were provided to increase the available space for the movement of the crickets. The top of the jars were tightly covered with a piece of muslin to reduce the possibility of mite infestation. The insects were transferred to fresh containers every week.

2.3 Other Techniques

These will be discussed in the appropriate part of the thesis.

PART 3

MORPHOLOGY OF THE HEAD CAPSULE AND ITS APPENDAGES

3.1 Introduction

The object of the present work is to give a detailed account of suitable characters of the head capsule and head appendages of *A. domesticus*. Literature reveals important work dealing generally with the insect head are Hudson (1945), Yuasa (1920), Duporte (1957), Snodgrass (1935, 1960), Matsuda (1965) and Gapud (1968) given in Part 1.

Among Gryllidae the structure of the hypopharynx of *Gryllus* has been fully described by Rietschel (1953a). The terminology for the head capsule is generally based on Snodgrass (1935).

For clarity the term anterior and posterior have been used. Thus in the clypeolabrum the outer surface is considered to be anterior whilst the inner epipharyngeal surface is posterior. For mandibles the surface touching the epipharyngeal surface is considered to be posterior whilst the inner as anterior. The rest of the head appendages on the ventral side of the head are regarded as posterior. The dorsal surface of the hypopharynx is termed anterior whilst the ventral surface facing towards the inner surface of the labrum is considered as posterior.

3.2 Materials and methods

The head of freshly killed adult crickets was severed in front of the prothorax. The head was macerated in warm 10% potassium hydroxide solution for 30 minutes and rinsed thoroughly in distilled water. It was then transferred to 70% alcohol where the mouthparts were carefully dissected from the head capsule as appropriate. The various structures were dehydrated in 90% alcohol for 15 minutes followed by two rinses in absolute alcohol each of 20 minutes. Specimens were either mounted in terpineol in the case of semipermanent preparations or canada balsam or euparal preceded by clearing in xylene for permanent preparations. Alternatively the head capsule was left in cold potassium hydroxide for 24-48 hours and then a similar procedure was adopted.

For examination of the entire head capsule specimens were placed in solid glasses containing terpineol. The position of the tentorium was seen most clearly after the removal of the mouthparts and neck. A Nikon stereoscopic microscope was used to examine the specimens and drawings were made with the aid of camera lucida.

3.3. Structure of the head capsule

(Figs. 1, 3, 4, 5 and 6)

The head of A. domesticus is hypognathous with strongly sclerotized walls. It is attached to the prothorax by the neck membrane in which lie a number of cervical sclerites.

In both sexes the anterior, lateral and posterior walls of the head form a capsule in which the sclerites have largely undergone fusion. The posterior aperture of the

Fig. 1. Anterior view of the head illustrating the position of the mouthparts. The dotted areas indicate membranous zones.

Fig. 2. Mandibles in a closed position from the posterior aspect.

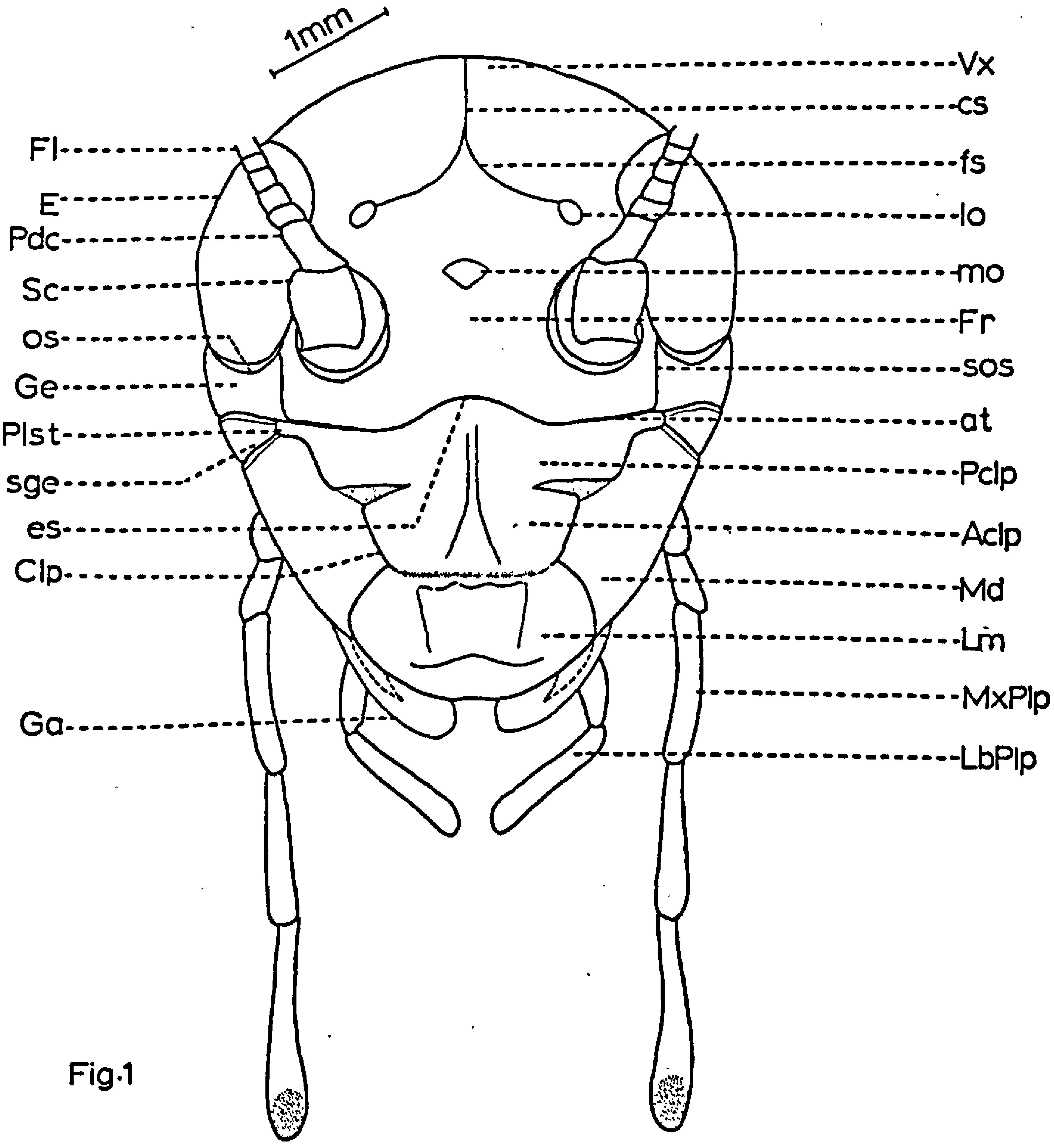
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Fig.1

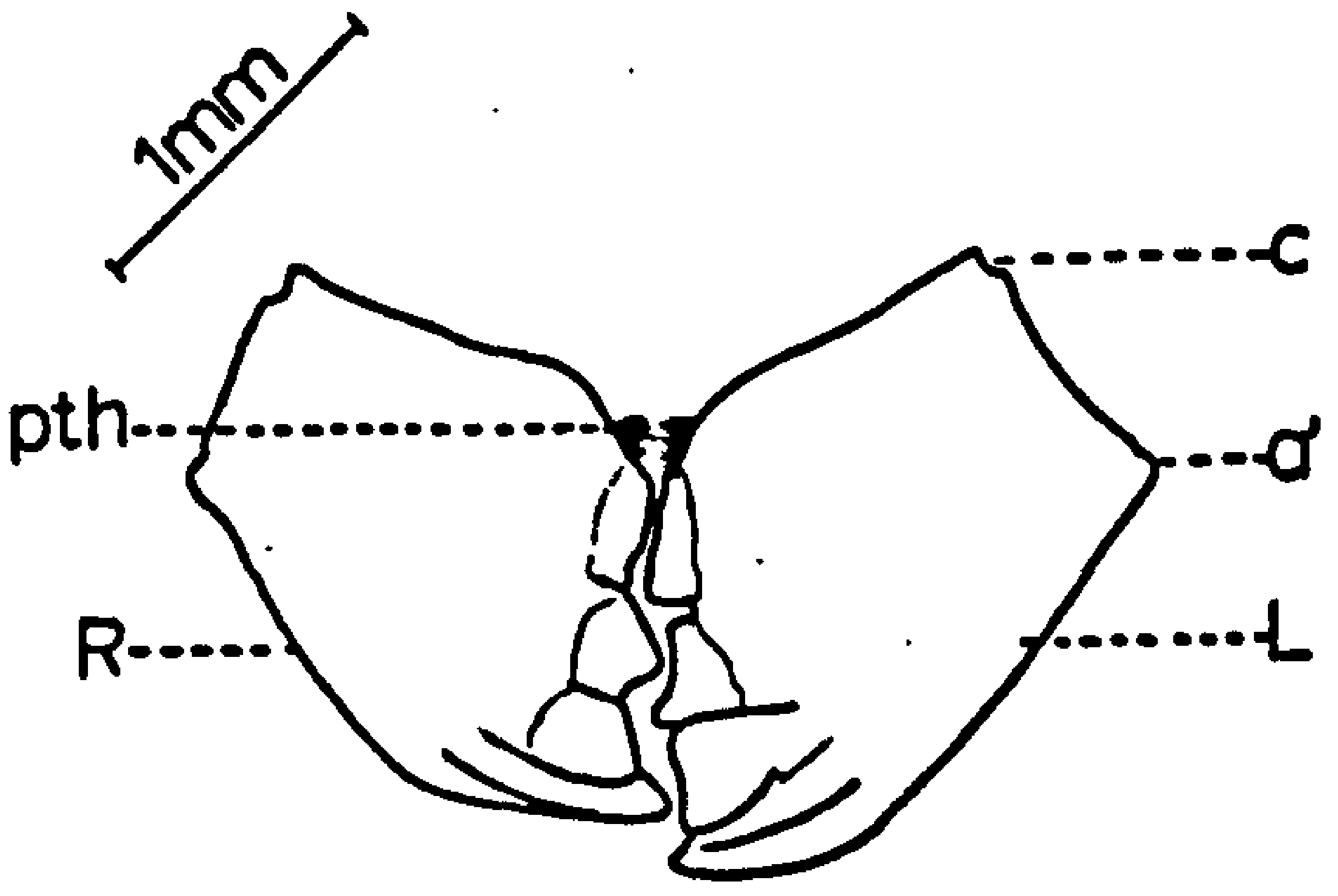
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Fig.2

head, or foramen, is connected by the neck membrane. Internally the head is strengthened by a tentorium (Fig.4).

The components of the head capsule of A. domesticus are the frons, clypeus, labrum, vertex, gena, subgena, occiput and postocciput. The vertex and the gena together make up the parietals referred to by Snodgrass (1935). The ecdysial or cleavage line extends from near the foramen on the midline of the dorsum of the head and bifurcates anteriorly to form an inverted 'Y'. The stem of the 'Y' is known as the coronal suture and the arms the frontal suture (Fig.1).

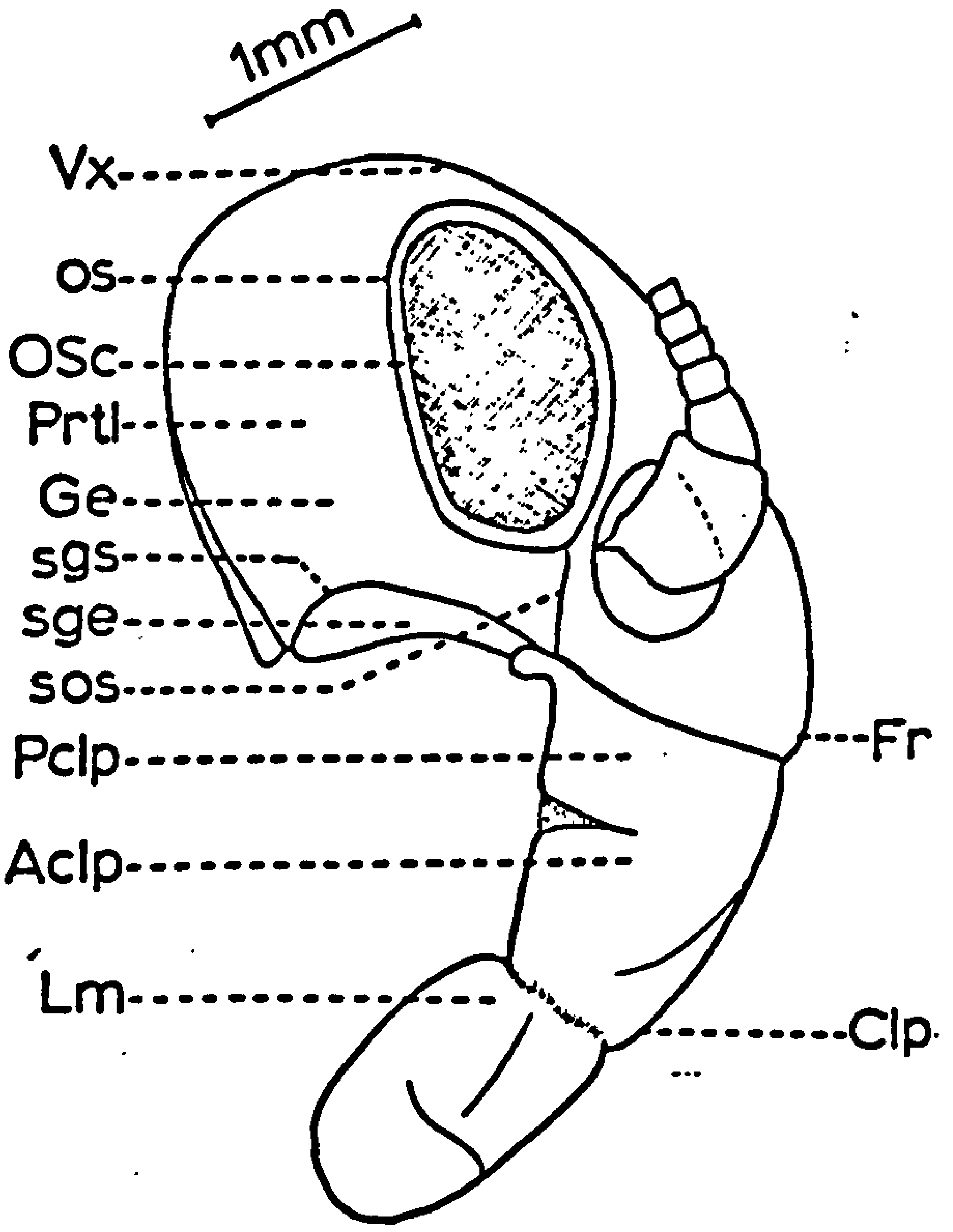
The head consists of an anterior bulging frontoparietal region, and a smaller flat occipital region to which the neck membrane is attached. The frontoparietal region bears a pair of long, articulate antenna, two large compound eyes and three ocelli. The median ocellus is larger than the lateral ocelli (Fig.1).

The facial region is formed by the frons (Figs.1 and 3) which is a sclerite limited proximally by the epistomal sulcus and laterally by the subocular sulcus.

The clypeus and labrum together form the clypeolabral lobe (Figs.1 and 3) which is well sclerotized proximally where it is contiguous with the frons, distally it is a little more membranous. The posterior surface of the clypeolabrum is concave and fits closely over the posterior surface of the mandible. The clypeus is

Fig. 3. Lateral view of the head capsule.

Fig. 4. Posterior view of the head capsule showing the position of the tentorium. Dark areas represent the foramen.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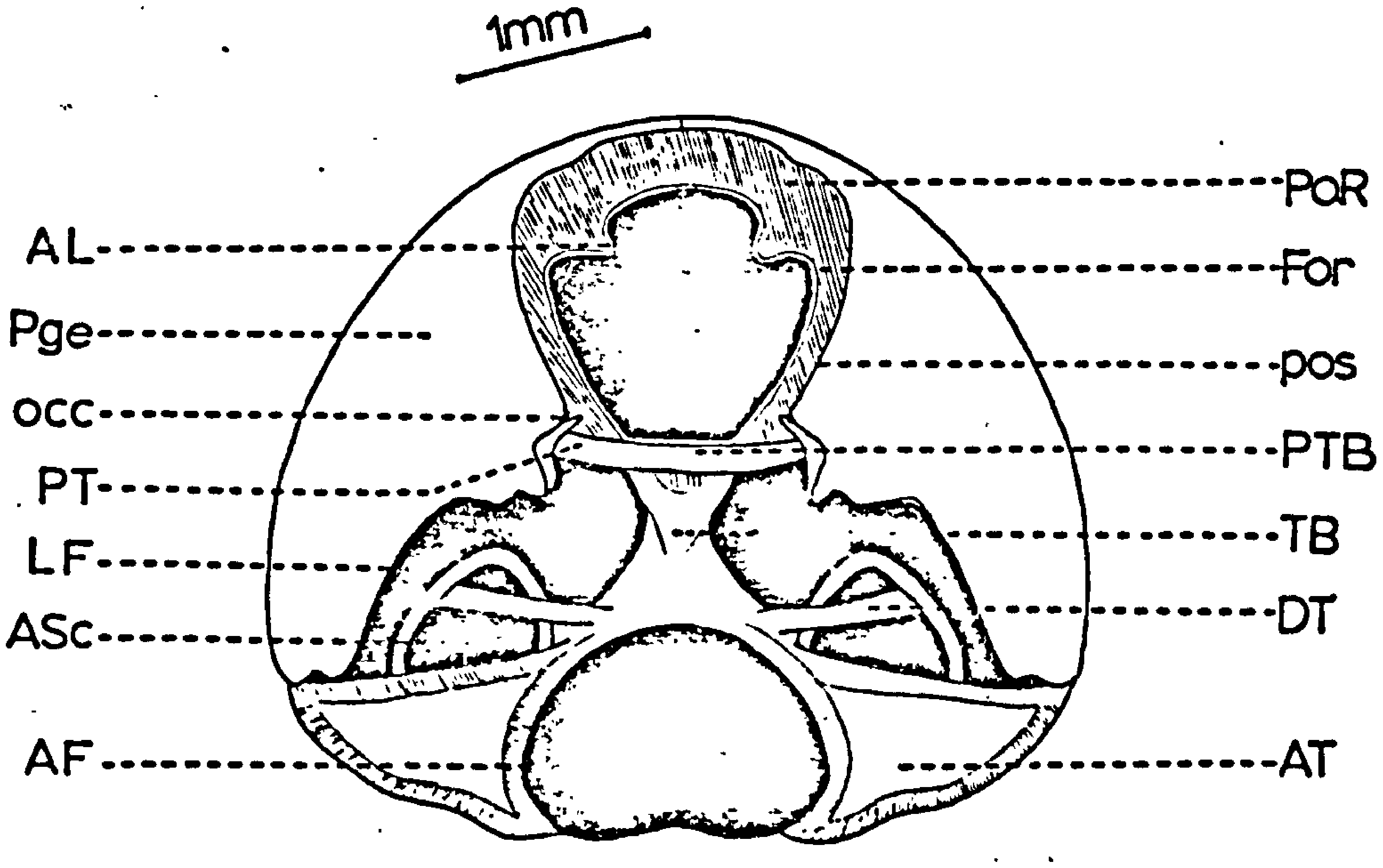
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Fig.4

separated from the frons by the epistomal sulcus (Figs.1 and 3) which form a strong internal ridge (Snodgrass, 1962) and is developed laterally into the anterior tentorial arms. The origins of the arms are visible externally as slits, the anterior tentorial pits, in the epistomal sulcus, medial to the secondary anterior articulation of the mandible. The clypeus is partially divided by two lateral membranous clefts into a proximal postclypeus and a distal anteclypeus (Figs. 1 and 3). This condition of the clypeus is similar to that described in Grylloblatta (Walker, 1933). The extreme lateral margins of the postclypeus are called the pleurostoma (Fig.1), these provide the anterior articulation of the mandible.

The labrum (Figs.1 and 3) which forms an upper lip to the preoral food cavity is a broad almost symmetrical, freely movable plate attached to the distal margin of the clypeus by a flexible transverse membrane. Its distal edge is notched somewhat to the right of the midline. Two less heavily pigmented strips divide the labrum incompletely into median and lateral areas and a transverse sulcus forms the ventral limit of a well defined rectangular area. In the lateral angle of the epipharyngeal wall, between the labrum and the clypeus, there are two small sclerotized areas the tormae (Part 5, Fig. 4) to which the muscles of the labrum are attached. A crescentric ridge known as the intertorma is present on the epipharyngeal side between the tormae

(Part 5, Fig. 4). The relevance of these structures will be seen in a later section, since they serve as the site of insertion of the compressor of the labrum. In the labrum of the sand cricket, Stenopelmatus, Crampton (1930) considers the intertorma serves to distinguish the anterior epipharyngeal region from the posterior epipharyngeal region.

The lateral integument is deflected along its posterior edge to form an inner lining which extends posteriorly through the labral and clypeal region and terminates at the mouth where it becomes continuous with the dorsal wall of the pharynx. The inner wall is the epipharyngeal wall which forms the roof of the preoral cavity. The mouth is at the level of the frontoclypeal sulcus.

Two curved sclerotized bars divide the epipharyngeal surface into a median and two lateral areas (Part 5, Fig.4). The position of these is seen on the outer surface of the labrum as the pigmented strips already described. These sclerotized bars are also found on the epipharyngeal surface of the locust (Marshall, 1947; Chapman, 1966 and Thomas, 1966) and Rietschel (1953a) in his comprehensive study of the labrum in immature G. domesticus refers to them as 'Verstarkungsleiste' which means strengthening rods. Cook (1944) terms the bars fimbriate strips. Their function appears to be a strengthening of the anterior part of the head capsule.

The parietals consist of two areas separated by the coronal suture. Anteriorly each parietal is bounded by the subocular sulcus, the frontal suture and the subgenal sulcus (Figs. 1 and 3) and posteriorly by the occipital sulcus (Fig.5). Each parietal therefore bears an antenna, a lateral ocellus and a compound eye. The subgena is bounded by the subgenal sulcus which lies beneath the gena (Figs. 1 and 3).

The dorsal and lateral walls of the head capsule curve posteriorly to form a horse shoe shaped occiput or occipital arch. This lies between the occipital and post-occipital sulci (Figs. 5 and 6). It is divided dorsally by the posterior end of the coronal suture. The lateral areas of the occiput behind the genae are called the postgenae (Figs.4, 5 and 6). The post occipital sulcus forms a strong internal ridge, the post occipital ridge (Figs.4 and 5). The posterior arms of the tentorium arise from the ventral ends of the ridge and their points of invagination are visible as long open slits, the posterior tentorial pits (Figs. 4 and 6). The maxilla articulates with the lower edge of the postgena below the ventral ends of the tentorial pit (Figs. 5 and 6). The posterior articulation of the mandible is with the ventral edge of the postgena (Fig.6). The post occiput bears an occipital condyle to which the first cervical sclerite is articulated (Figs.4, 5 and 6). The post occipital ridge gives rise to apodemes, the lateral apodemes are better developed and more prominent than the median one. In some specimens the median apodeme is completely reduced (Figs.4, 5 and 6). The muscles of the neck responsible for moving the head are attached to the lateral apodemes. The hypostomal sulcus extends from the mandibular articulation to the posterior tentorial pit and cuts off a narrow marginal sclerite, the hypostoma from the postgena (Fig.6). The hypostoma is a little more than a marginal thickening of the head capsule and the hypostomal sulcus marks the position of an internal hypostomal ridge.

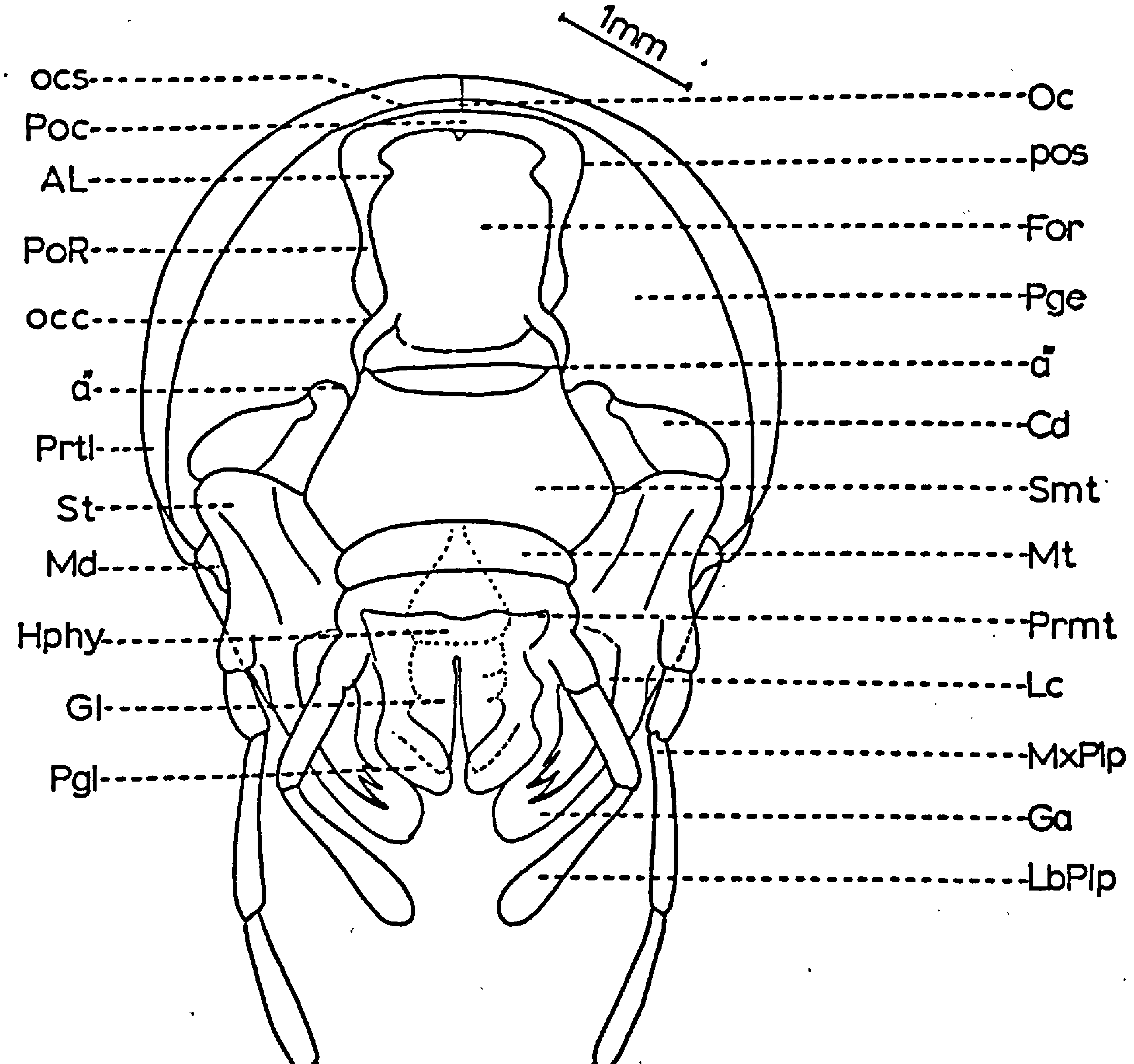
The tentorium of certain Gryllidae, e.g. *Gryllus capensis* Oliv. has been described by Hudson (1945) as an x-shaped structure. The tentorium of *A. domesticus* appears to be similar. In this species it is thick, expanded anteriorly and is heavily sclerotized. The anterior arms are triangular and fan shaped and originate form the anterior tentorial pits. These pits are elongate slits lying on the subgenal and epistomal sulcus above the mandibular articulation (Fig.1). The anterior arms (Fig.4) have heavy marginal sclerotization, they narrow and converge to meet the wide anterior end of the central body of the tentorium (Fig.4). Narula (1968) found the anterior arms in *G. sigillatus* had a similar shape.

The dorsal arms are well developed (Fig.4), they arise as outgrowths of the anterior part of the body of the tentorium immediately below the region which receives the

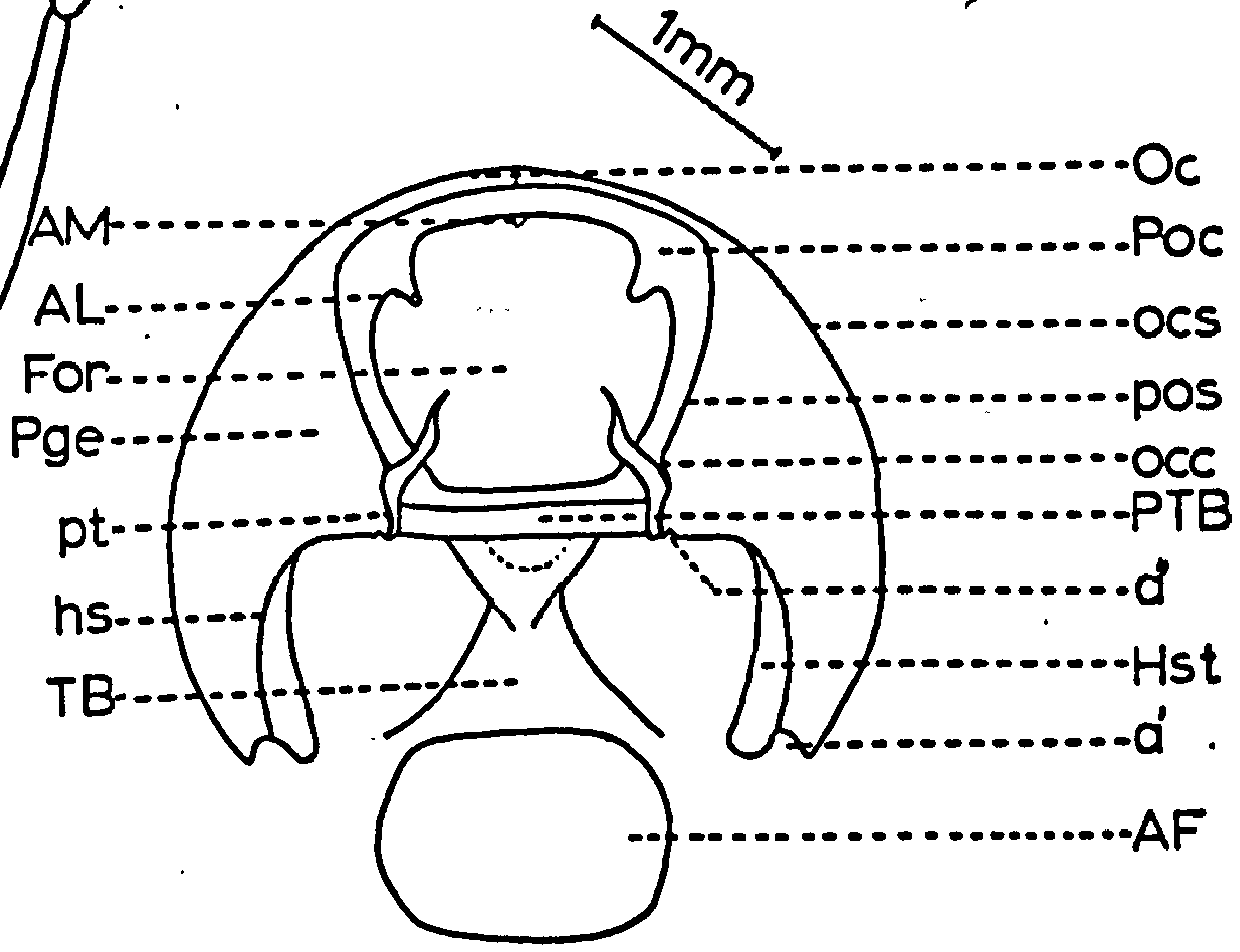
Fig. 5. Posterior view of the head capsule illustrating the mouthparts.

Fig. 6. Posterior view of the head.

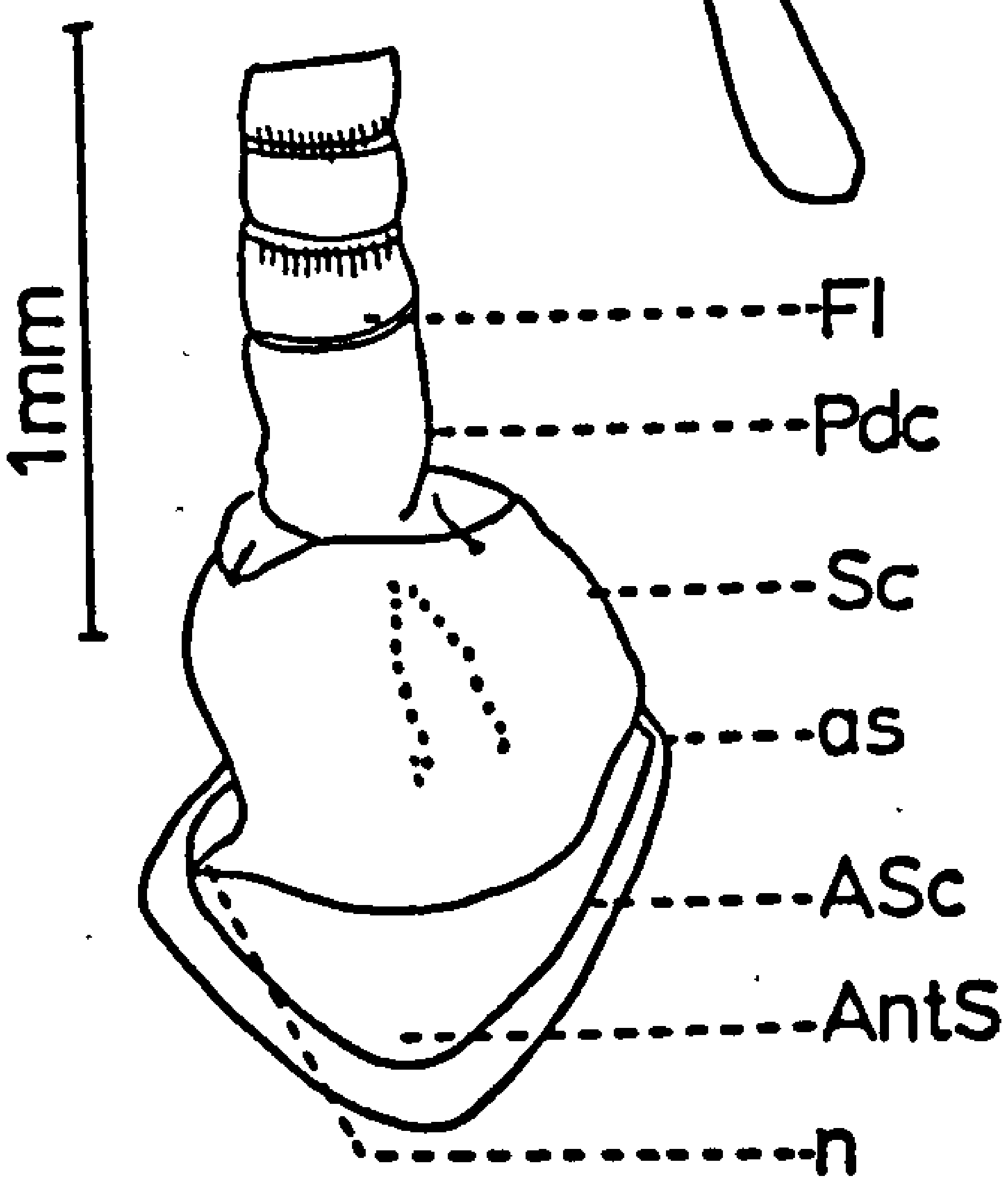
Fig. 7. Anterior view of the antenna.



Fig·5



Fig·6



Fig·7

anterior arms. The dorsal arms of the tentorium are attached to the head capsule at the posterolateral angle of the antenna and they serve for the attachment of the antennal muscles. The body of the tentorium is broad anteriorly but narrows towards the posterior tentorial bridge. The posterior tentorial pits in the lower part of the postoccipital sulcus give rise to the posterior tentorial arms (Fig.4). The arms are joined medially to form the posterior tentorial bridge (Figs.4 and 6) and then coalesce with the body of the tentorium. The posterior tentorial bridge strengthens the ventral ends of occipital foramen and also forms the posterior boundary of the tentorial body (Figs.4 and 6).

The entire tentorium is very stout and well developed, it serves for the attachment of muscles of the antennae, the mouthparts and oesophagus. Its structure gives rise to four foramen; one the foramen magnum (Figs. 4 and 6) serves for the passage of the oesophagus and brain, the anterior foramen leads to epipharyngeal surface and the other two lateral foramens serve for the passage of the mandibular muscles. Due to its rigidity and texture it strengthens the head capsule to bear the strain imposed on the cuticle by the movement of the various mouthparts. Narula (1968) reports the presence of a well developed tentorium in G. sigillatus which appears to closely resemble that found in A. domesticus.

3.4 Structure of the head appendages

3.4.a Mandible (Figs. 1, 2 and 8)

The mandibles are a pair of hollow, conical structures which are suspended ventrally from the pleurostoma by a triangular base. The mandible articulates anteriorly by means of a ginglymus, which is a depression that accommodates a projection formed by the pleurostoma. This articulation is referred to as the secondary anterior articulation of the mandible by Snodgrass (1935). Posteriorly the mandible articulates by a prominent condyle with the facet formed jointly by the lower edge of the postgena and the lower edge of the hypostomal ridge. This is the primary cranial articulation of the mandible.

The mesal margin of the mandible (Fig. 8b) is toothed and is differentiated into a proximal molar lobe and a distal incisor lobe. The molar lobe is a single structure which has raised edges. The incisor lobe is composed of three teeth, the distal tooth is much sharper than the other two. The anterior surface of the mandible is slightly concave (Fig. 8c) whilst the posterior surface tends to be convex (Fig. 8a). The large adductor apodeme arises from the articular membrane at the mesal angle of the mandible, just behind the mouth. This apodeme lies in the cavity formed between the anterior and posterior arms of the tentorium. A small abductor apodeme arises from the articular membrane near the posterior articulation. The two mandibles are not symmetrical, although they interlock

Fig. 8. Mandible a, (i) right, (ii) left, posterior view; b, (i) right, (ii) left, mesal view; c, (i) right, (ii) left anterior view.

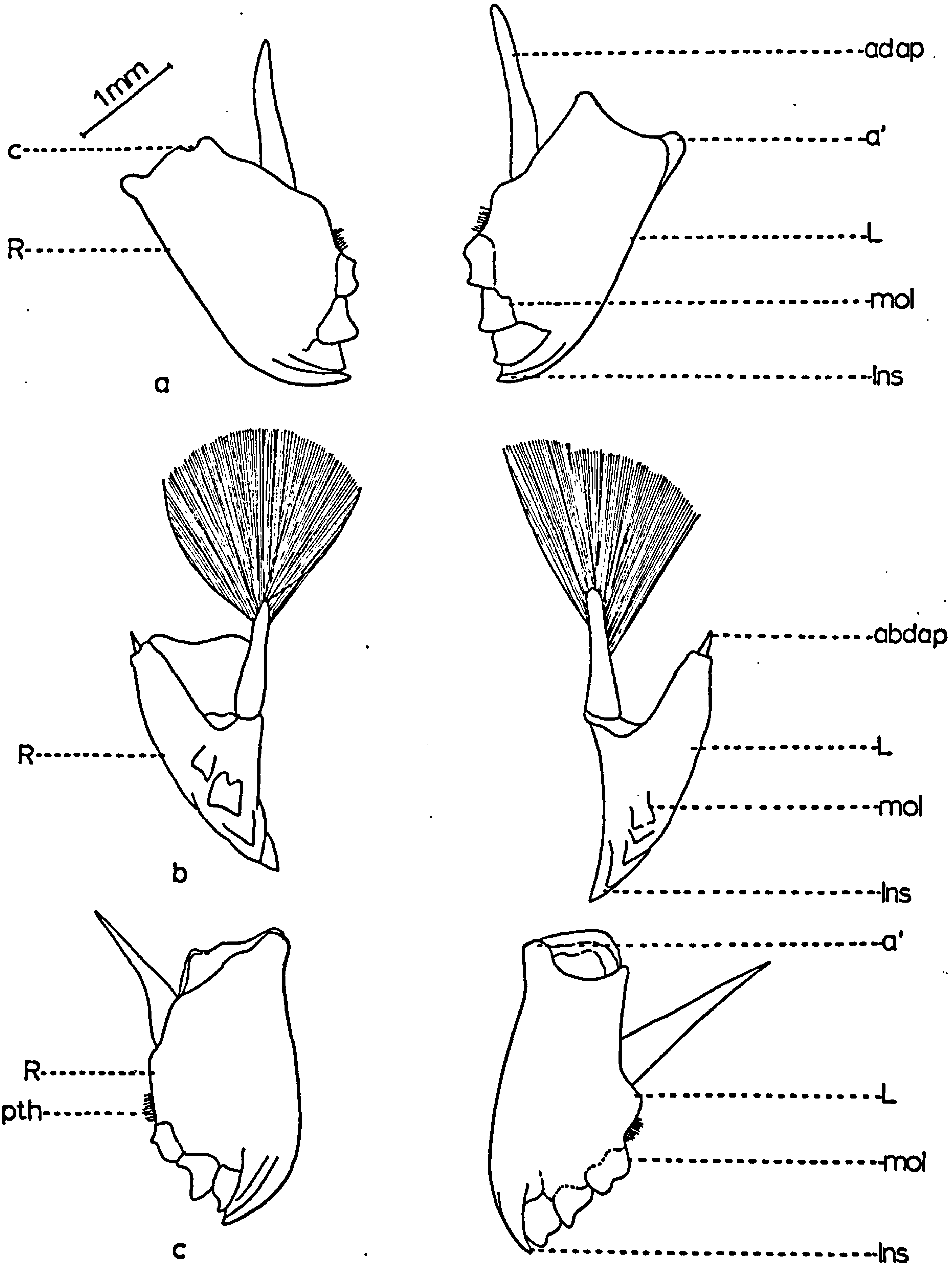


Fig.8

at rest (Fig. 2). The incisor lobe of the right mandible rests upon the space formed by the incisor lobe of the left mandible, whilst the molar lobe of the right mandible rests upon the cavities formed by similar lobes of the left mandible. A brush of fine hairs commonly called the prostheca arise from the anterior base of each mandible behind the molar area and the two brushes unite to form a screen beneath the mouth when the jaws are closed (Fig. 2). Apart from differences in symmetry the mandibles are similar in both sexes.

3.4.b. Maxilla (Figs. 5, 9 and 10)

Each maxilla consists of a cardo, stipes, galea, lacinia, palpifer and maxillary palp (Figs. 5, 9a, b and 11).

The proximal region of the cardo lies transversely and has a single articulation with the head capsule (Fig. 5). It consists of two portions, the subcardo and the alacardo (Figs. 9a, b and 10). The alacardo is much smaller than the subcardo and is attached obliquely to the posterolateral margin of the latter. The sulcus between these regions is distinct on the posterior side (Fig. 10). The surface of the cardo is provided with a number of sensory hairs.

The proximal end of the stipes is attached at right angle to the cardo and has two points of articulation with the cardo; one on the subcardo and the other one on the alacardo. It is large, distinctly sclerotized on the

Fig. 9. Maxilla a, posterior view of left maxilla; b, anterior view of the left maxilla.

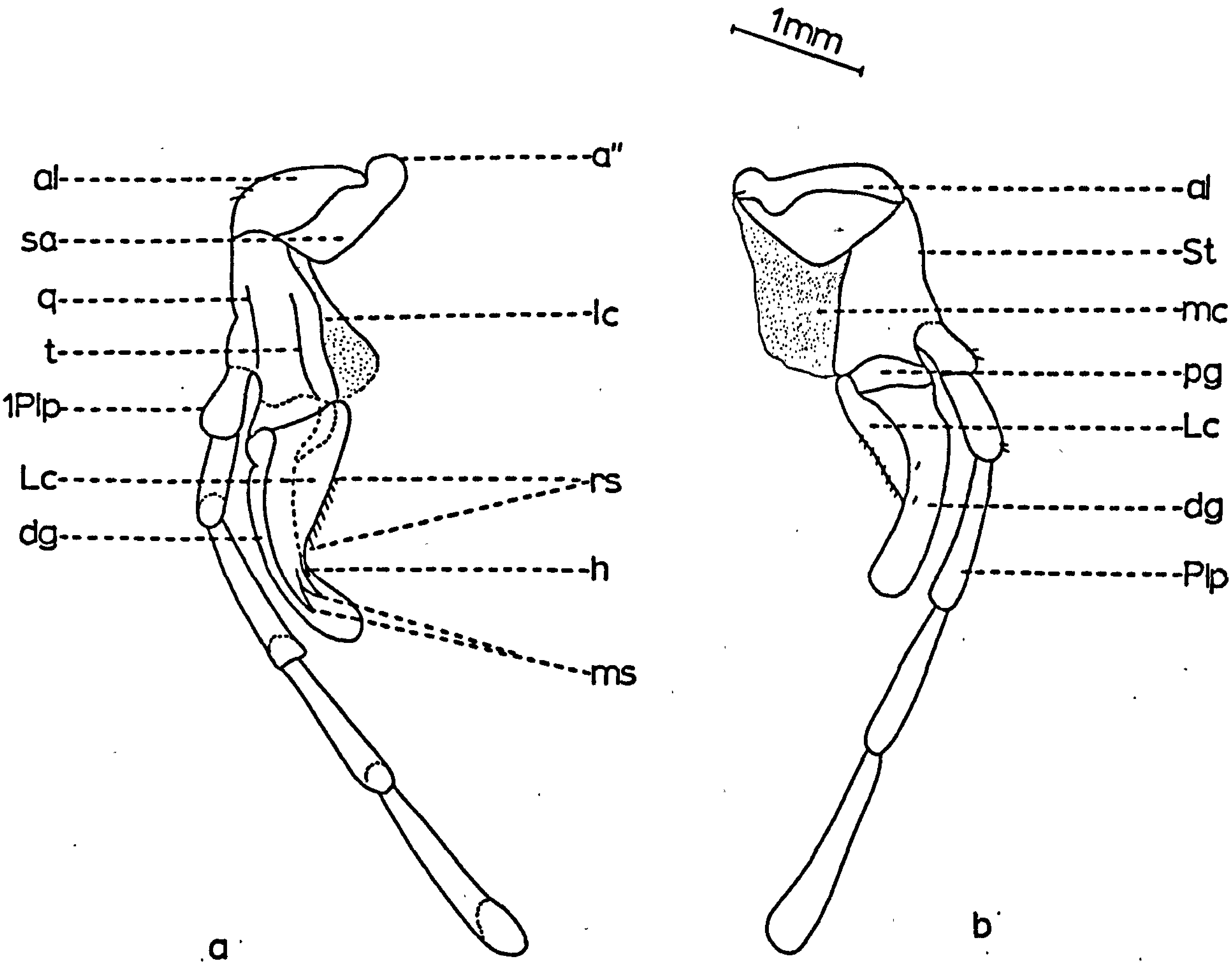


Fig.9

posterior aspect (Figs. 9a and 10), and somewhat less sclerotized and membranous on the anterior side (Fig. 9b). The cardo and stipes are attached posteriorly to the head by a membrane called the labacoria (Figs. 9a and 10) and anteriorly (Fig. 9b) by another membrane called the maxacoria (Yuasa, 1920); their single cavity thus communicates with the cranial cavity.

The stipes, on its posterior side, bears two longitudinal sulci (Figs. 9a and 10) thus dividing its area into three regions. Some of the muscles of the maxilla originate from these sulci. The palpifer, which is a small sclerite near the distolateral part of the stipes, is separated from the stipes by a weakly sclerotized area (Fig. 10).

The maxillary palp is cylindrical in section and consists of five segments, it arises from the palpifer (Figs. 9a, b and 10). The proximal palp segment is small with only its distal portion well sclerotized. The second segment is longer than the first, whilst the third to fifth segments are more or less similar in length, though somewhat longer than the first two. The terminal segment is broader at its distal end. The segments are connected to each other by intersegmental membrane. Both the anterior and posterior surfaces of all segments of the maxillary palp are richly supplied with sense organs. These will be discussed in detail in Part 5.

Fig. 10. Detail of right maxilla from posterior aspect.

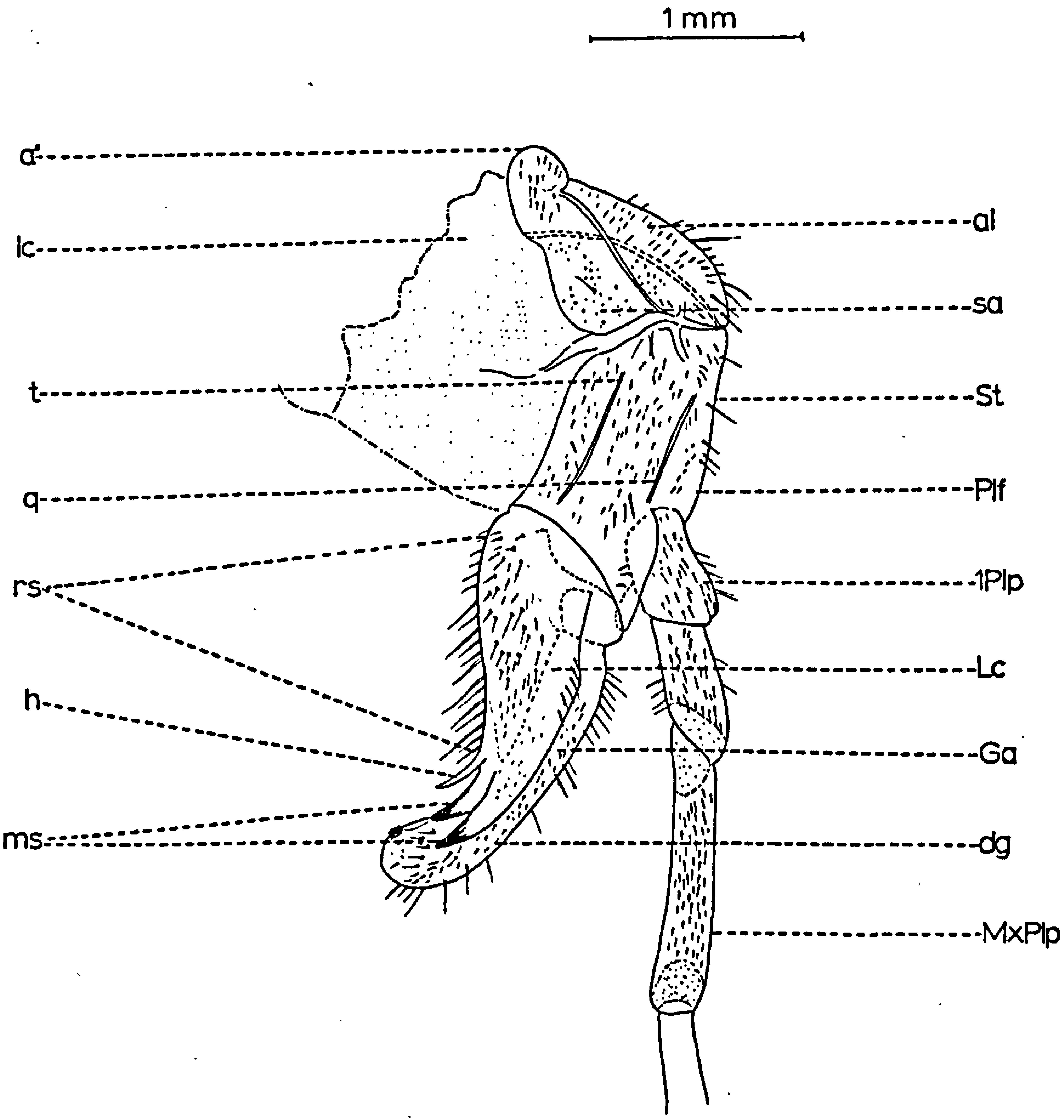


Fig.10

The galea is two segmented. It is attached to the distal margin of the stipes (Fig. 9b). The proximal part of the galea, the proxagalea, is short, transverse and subcylindrical and its distal margin is marked posteriorly by a sclerotized chitinous sulcus and anteriorly by a fold. The distagalea, which is the second segment of the galea, is much longer (Figs. 9b and 10). It is hood shaped and overlaps the distal part of the lacinia. The distal end of the distagalea is slightly membranous and is provided with minute setae. This subdivision of the galea into two segments has also been recorded in G. sigillatus (Narula, 1968).

The lacinia is hook shaped, depressed, chitinized and dentate and articulates with the stipes (Figs. 9a, b and 10). The sulcus between the lacinia and the stipes is obsolete on the anterior aspect (Fig. 9b) but distinct and complete posteriorly (Figs. 9a and 10). The distal end of the lacinia bears sclerotized teeth on its mesal margin. The two maxadentes are sharp, curved and strongly sclerotized (Figs. 9a and 10). The single hamaden is less sclerotized than the maxadentes. It is located proximal to the maxadentes. A number of setae, lacinarastrae are prominently developed on the mesal margin but will be discussed in detail in Part 5.

3.4.c. Labium (Figs. 5, 11 and 12)

The labium or lower lip consists of the submentum, mentum and prementum and the ligula which includes the stipulae, glossae, paraglossae, palpiger and labial palp.

The submentum (Figs. 5, 11 and 12a) is the large basal sclerite of the labium and is subquadrate, being wider than long. It is attached basally to the membranous cuticle at the junction of the neck and the posterior part of the head capsule (Fig. 5). The proximal margin of the submentum is transversally emarginate and is continuous with the membrane, called the microcoria (Fig. 12a) which joins the head capsule (Yuasa, 1920). The lateral margins of the submentum are folded over on to the anterior aspect and form the lateral lobes, the margins of which are continuous with the membrane of the maxilla, the labacoria (Fig. 12a). The submentum is attached proximally to the cranium and its proximal angles (Figs. 11 and 12a) are associated with the postgena adjacent to the posterior tentorial pits.

The mentum is much smaller and narrower than the submentum (Figs. 5, 11 and 12a). The distal portion is lightly sclerotized. The sulcus between the mentum and submentum is distinct. On the sclerotized middle and distal lateral regions of the mentum there are numerous sensilla. The mentum and submentum should be regarded as the subdivisions of a single sclerite, the postmentum

Fig. 11. Posterior view of the labium.

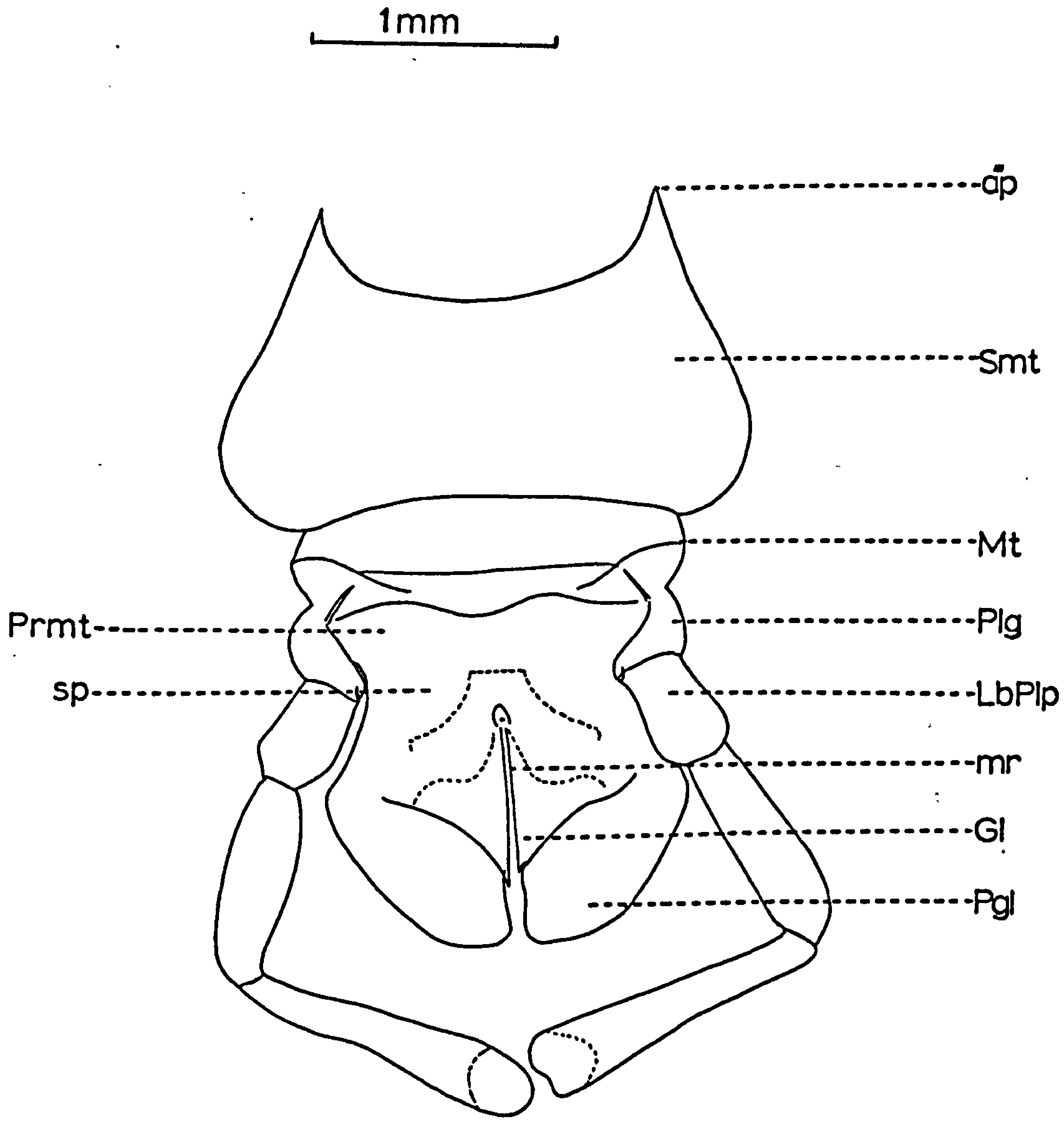


Fig.11

(Chapman, 1975).

The prementum articulates with the mentum (Figs.11 and 12a). At its base two subquadrate transverse stipulae can be seen. Two small sclerites, the palpigers are cut off from the lateral sides of the prementum and each bears a three segmented labial palp (Figs. 11 and 12a). Near to the palpiger the prementum is slightly more sclerotized, this sclerotization forming a hook like structure. The sulcus which separates each stipula from the glossa and paraglossa is incomplete. Distally the prementum bears two pairs of appendicular lobes, the inner one the glossae and the outer one the paraglossae (Figs. 11, 13a and b). Each glossa is a pointed, elongate, triangular appendage, obliquely attached to the mesoposterior margin of the stipula, its mesal surface is called the mesarina (Fig. 11). The distal end of the glossa is covered with hairs (Fig.12a and b). The presence of stipulae and mesarina has previously been mentioned in Gryllidae by Yuasa (1920). The paraglossae (Fig.12b) are much larger than the glossae and are thicker and slightly folded mesally. The anterior part of each paraglossa is less concave than the posterior part and overlaps the glossa to a lesser extent.

The labial palp (Figs. 11 and 12a) is composed of three segments of which the basal segment is the smallest. The distal segment is long, cylindrical and has a hemispherical tip covered with minute sensilla.

Fig. 12. Labium a, posterior view; b, detail of the glossa and paraglossa from the posterior aspect.

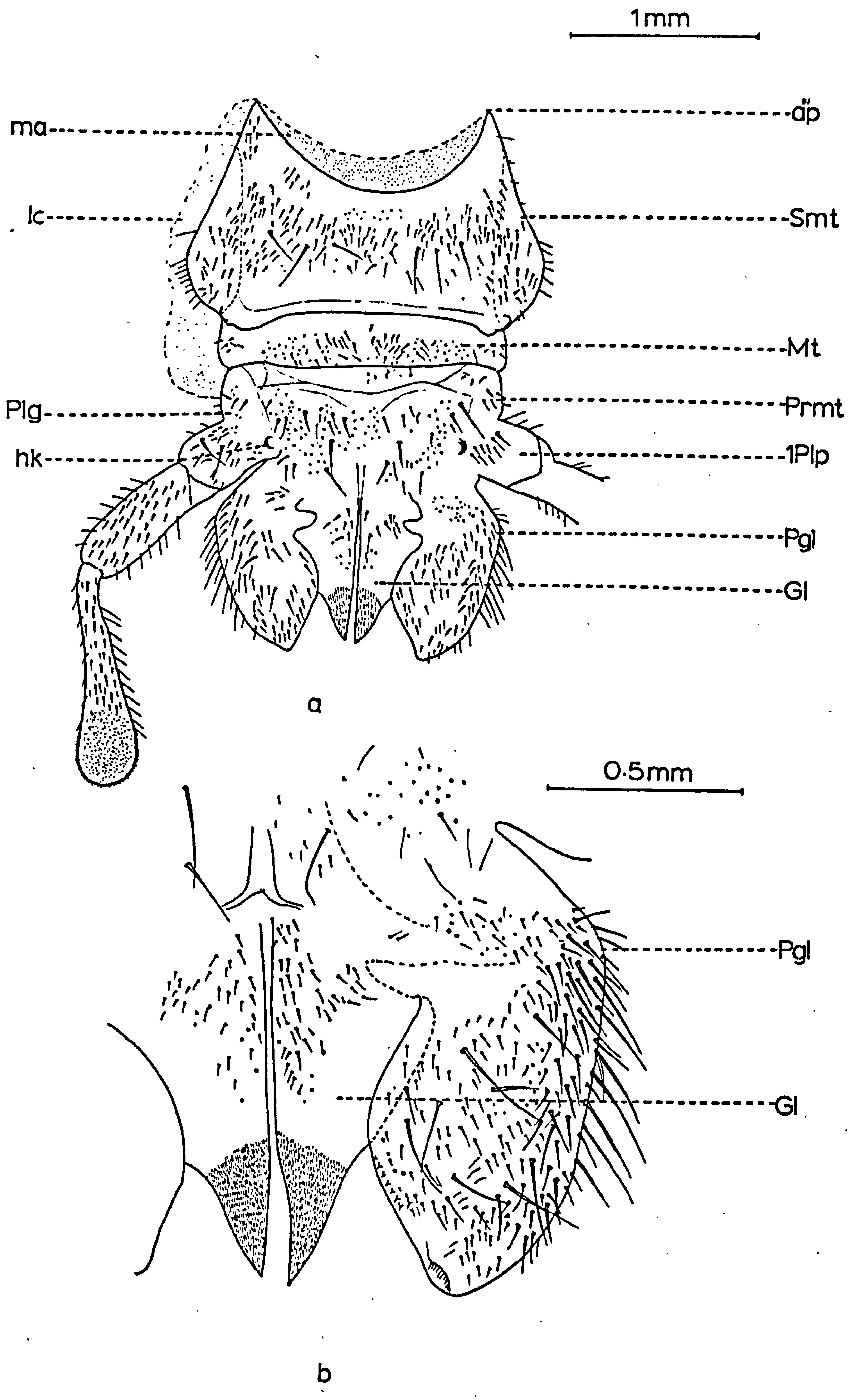


Fig.12

3.4.d. Hypopharynx (Fig. 13)

The hypopharynx is an elongate tongue-like lobe which fills most of the roof of the preoral food cavity and lies between the clypeolabrum and labium. It is a thick structure with a long base and a broadly triangular profile, the posterior surface is much shorter than the oral surface. Viewed from the posterior side (Fig. 13d) it appears broadest near the apex and narrowest at the base, while from the anterior surface (Fig. 13a) it is almost parallel sided. The apical region includes part of the posterior and anterior or oral surface and is membranous and much folded in a retracted state. The folded structure can be expanded by blood pressure to form a biloped rostrum (Fig. 13c). The rostrum is provided anterolaterally with a finely branched system of pseudotracheae which lead into a pair of efferent ducts (Fig. 13c). The efferent ducts open on the anterior side of the hypopharynx (Fig. 13a and c). Rietschel (1953a) has considered the detailed arrangement of the pseudotracheae. The posterior surface of the hypopharynx (Fig. 13d) is partially covered by a pair of thinly sclerotized lobes which are posterior expansions of the lateral bars. The lobes converge towards the base of the hypopharynx at an acute angle meeting the narrow salivary cup which receives the salivary ducts. The anterior surface bears laterally a pair of sclerotized bars (Fig. 13a and b). The most prominent sclerotizations are the suspensorial sclerites on the anterior surface. Each suspensorial

Fig. 13. Hypopharynx a, anterior view; b, lateral view showing the pseudotracheae; c, detail of the pseudotracheae and efferent duct - anterior view; d, posterior view showing salivary duct.

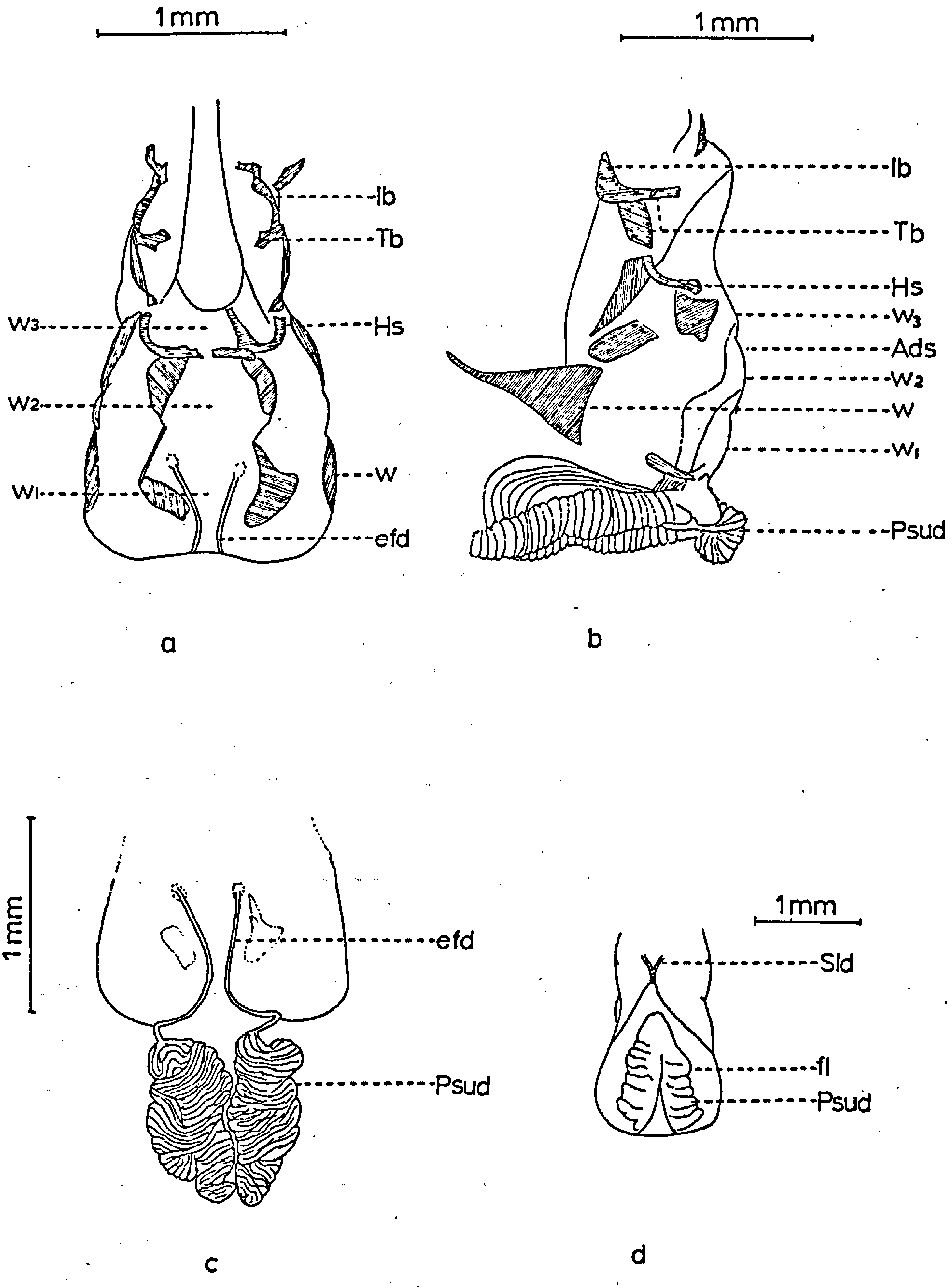

1mm
Ib
Tb
W3
Hs
W2
W
W1
efd
a
1mm
Ib
Tb
Hs
W3
Ads
W2
W
W1
Psud
b
1mm
efd
Psud
c
1mm
Sld
fl
Psud
d

Fig.13

sclerite bifurcates into two arms each side of the longitudinal bar and the transverse bar. These sclerotizations may be referred to as the suspensorium. The hypopharyngeal mandibular muscles are inserted on these bars. The proximal part of the hypopharynx extends upwards and leads into the mouth where it forms the floor of the pharynx as a Y-shaped depression. Rietschel (1953a) divides the anterior surface of the hypopharynx into three areas (w_1, w_2 and w_3). The first portion lies between the efferent ducts. The second or the middle region lies between the suspensorial sclerites and this area is covered with hairs. The third region occupies the space between the proximal suspensorial sclerites.

3.4.e. Antenna (Fig. 7)

The antennae are born on the frons, just mesal to the compound eye. Each antenna consists of two large basal sclerites, the scape and the pedicel and a varying number of tapering annuli forming the flagellum. The scape is articulated to the rim of the antennal socket by an articulatory membrane (Fig. 7). Narula (1968) mentions the presence of this membrane in the antenna of G. sigillatus and terms it the antacorium. The basal segment, the scape, is much larger than the pedicel. It is anteroposteriorly compressed and its lateral edges abut against the rim of the socket so that the horizontal movement is possible. The antennal sulcus has a thickened portion which forms the antennal sclerite. A small pivotal sclerite in the articulatory membrane is united with the lateral edge of the base of the scape. The second segment of the antenna is called the pedicel. The pedicel is smaller in size than the scape and it is subcylindrical. Movement of the pedicel is not restricted and it can move in the vertical as well as in the horizontal plane. Distally the pedicel bears the flagellum, which consists of a large number of short, cylindrical rings, each slightly recessed into the one behind and united with it by a narrow membrane. This arrangement gives complete flexibility to the flagellum. Imms (1940) refers to the flagellar segments as flagellomeres and considers them to be distinct from true antennal segments.

3.5 Structure of the Cervix (Figs. 14 and 15)

The head is drawn back into the neck shield at rest. Dorsally it may be completely withdrawn, whilst ventrally the neck membrane is still visible. The neck membrane is soft and there are three folds (Fig. 14) allowing the head considerable freedom of movement. Dorsally the membrane is restricted to a narrow strip and only becomes wider ventrally to form the throat membrane. Ventrally it is often referred to as the throat plate since it bears numerous chitinous plates or neck sclerites.

The neck sclerites are named according to their

Fig. 14. Ventral view of the neck plates.

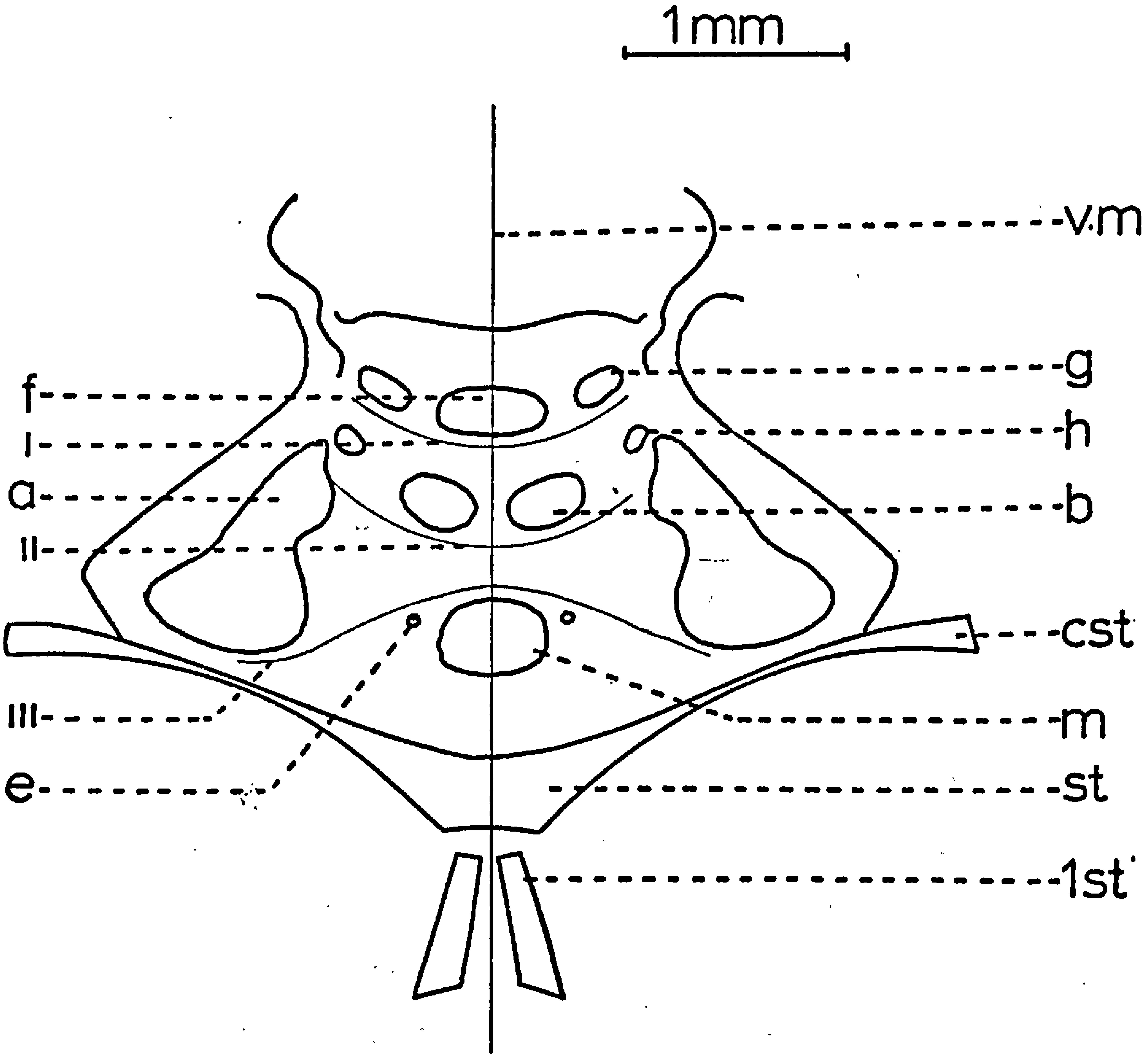


Fig.14

position. Sclerites present on the dorsal membrane are called intertergites, on the ventral side intersternites, whilst laterally they are termed interpleurites. Most of the sclerites are paired structures. The largest pair of sclerites is an interpleurite 'a' (Fig. 14) to which numerous muscles are attached. Interpleurite 'a' is an irregularly shaped curved sclerite which is posteriorly broad. The hind corner of the sclerite is bent inwards and approaches the coxa of the fore leg. The front part 'i' of this interpleurite touches the head sclerites and is the main point of articulation between the head and the neck (Fig. 15). Towards the hind-line there is another much smaller sclerite 'e'. Just anterior to this intersternite the neck membrane is folded. The remainder of the sclerites are rather different from 'a' and 'e', since they are less sclerotized and are mostly without muscle attachments. Near to the anterior edge of interpleurite 'a' there is a median intersternite 'f' which is situated on the ventral median line. To the side of this plate is a small pair of oval intersternites 'g'. Posterior to these sclerites, there is the first fold of the neck membrane. Between the first and second folds lie two pairs of sclerites; the oval intersternites 'b' closely approximated to the mid line and more laterally a pair of small sclerites 'h' terminates near the interpleurite 'i'. The second and third neck folds diverge laterally to accommodate the large interpleurite 'a'. The

Fig. 15. Dorsolateral view of the head and neck plates.

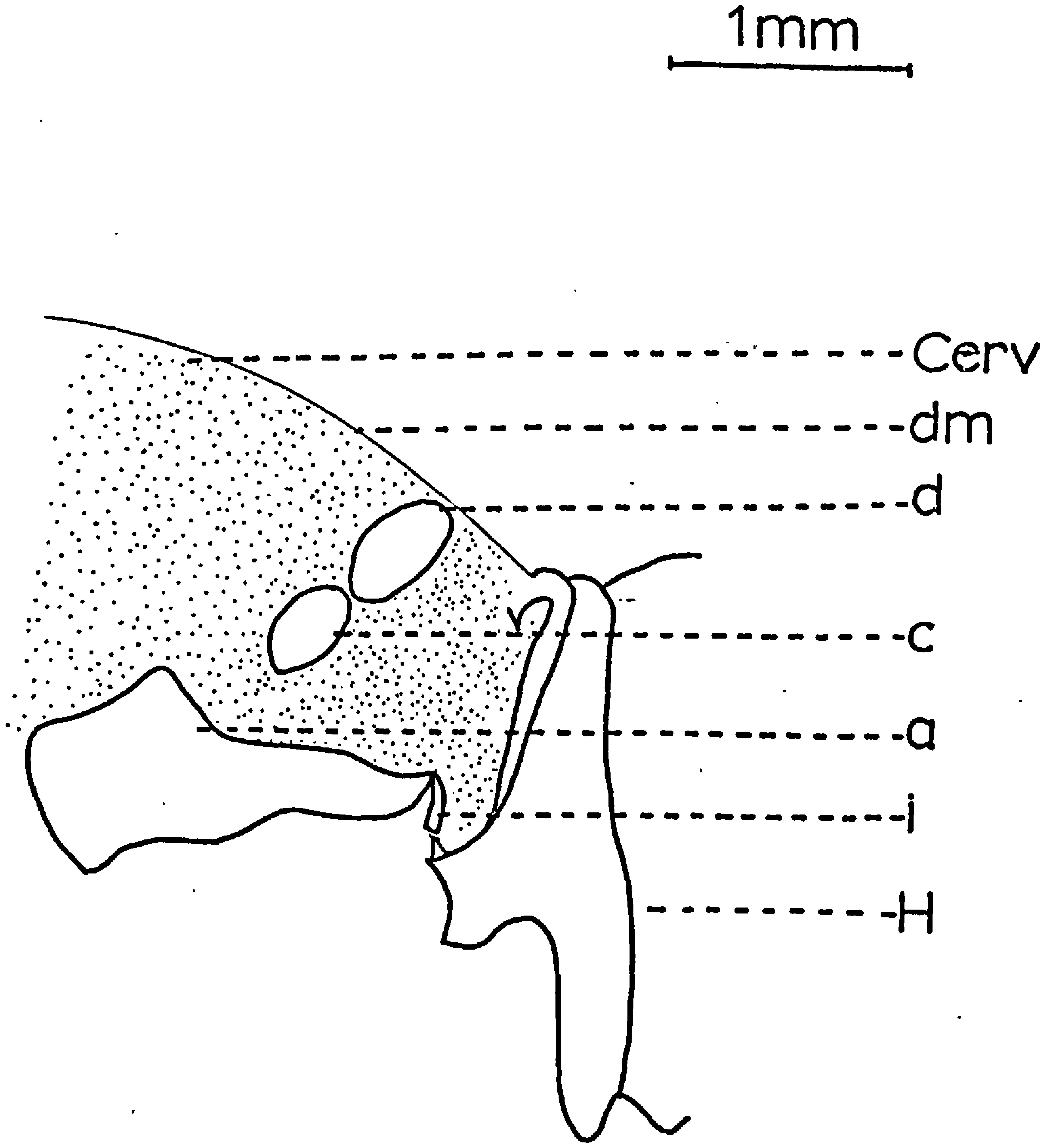


Fig.15

median intersternite 'm' is situated behind the third fold in the mid ventral position (Fig. 14). On the narrow dorsal neck membrane there are two pairs of intertergites 'c' and 'd'. Intertergite 'c' (Fig. 15) lies close to the dorsal part of interpleurite 'a' whilst the second intertergite 'd' is near to the dorsal mid line (Fig. 15).

Abbreviations used in figures of the head capsule and its appendages (all diagrams of adult females)

Aclp = Anteclypeus
AL = Lateral apodeme
AF = Anterior foramen
Ads = Adoral surface of the hypopharynx
AM = Median apodeme
Ant = Antenna
AntS = Antennal socket
ASc = Antennal sclerite
AT = Anterior tentorial arm
a, i = Interpleurites of the neck
ad ap = Adductor apodeme
abd ap = Abductor apodeme
al = Alacardo
as = Antennal sulcus
at = Anterior tentorial pit
a' = Primary cranial articulation of the mandible
a'' = Primary cranial articulation of the maxilla
a''' = Primary cranial articulation of the labium
a'''p = Point of attachment of the submentum with the cranium
b,e,f,g,h = Intersternites of the neck
Cerv = Cervix or neck
Cd = Cardo
Clp = Clypeus

c,d = Intertergites of the neck

c = Secondary anterior articulation of the mandible

cs = Coronal suture

cst = Coxosternite (Part 4) .

DT = Dorsal tentorial arm

dg = Distagalea

dm = Dorsal mid line

E = Compoundeye

es = Epistomal sulcus

efd = Efferent duct of the hypopharynx

Fl = Flagellum

Fr = Frons

For = Foramen magnum

fl = Membranous lobes on the posterior side of the hypopharynx

fs = Frontal suture

Ga = Galea

Ge = Gena

Gl = Glossa

Hphy = Hypopharynx

H = Head

Hs = Suspensorial sclerites of the hypopharynx

Hst = Hypostoma

h = Hamaden

hs = Hypostomal sulcus

hk = Hook shaped sclerite on the prementum

Ins = Incisor

int = Intertorma (Part 5, Fig. 4)

L = Left side

Lb = Labium

LbPlp = Labial palp

Lc = Lacinia

LF = Lateral foramen

Lm = Labrum

lb = Longitudinal bar of the suspensorial sclerite

lc = Labacoria

lo = Lateral ocellus

Md = Mandible

Mt = Mentum

MxPlp = Maxillary palp

ma = Microcoria

mc = Maxacoria

mo = Median ocellus

mol = Molar

mr = Mesarina

ms = Maxadentes

n = Basal articulation of the scape with the antennal socket

O = Ocelli

Oc = Occiput

OSc = Ocular sclerite

occ = Occipital condyle

ocs = Occipital sulcus

os = Ocular sulcus

PT = Posterior tentorial arm

PTB = Posterior tentorial bridge

Pclp = Postclypeus

Pdc = Pedicel

Pge = Postgena

Pgl = Paraglossa

Plg = Palpiger

Plf = Palpifer

Plst = Pleurostoma

Poc = Postocciput

PoR = Post occipital ridge

Prmt = Prementum

Prtl = Parietal

Psud = Pseudotrachae

Plp = Palp

pos = Post occipital sulcus

pg = Proxagalea

pt = Posterior tentorial pit

pth = Prostheca

q = Longitudinal sulcus on the stipes

R = Right side

rs = Lacinarstrae

Sc = Scape

Sld = Salivary duct

St = Stipes

Smt = Submentum

sa = Subcardo

sge = Subgena

sgs = Subgenal sulcus

sos = Subocular sulcus

sp = Stipula

st = Presternum of the prothorax (Part 4, Fig.)

TB = Tentorial body

Tb = Transverse bar of the suspensorial sclerite

Tnt = Tentorium

t = Longitudinal sulcus on the stipes

tor = Torma (Part 5, Fig. 4)

Vx = Vertex

VL = Strengthening ridge or sclerotized bar (Verstärkungsleiste) in Part 5, Fig. 4

vm = Ventral median line

w = Basal sclerite on the hypopharynx

w_1, w_2, w_3 = Areas of swelling on the anterior or adoral surface of the hypopharynx

1,11,111 = Folds of the neck

PART 4

MUSCULATURE OF THE HEAD CAPSULE AND ITS APPENDAGES

4.1 Introduction

The aim of this section is to completely describe the musculature of the head capsule and appendages. Both intrinsic and extrinsic muscles have been investigated. In the Gryllidae there have been only a few studies of musculature e.g. Duporte (1920) described the musculature of G. assimilis and Narula (1974) that of G. sigillatus. The musculature of other representatives of the Orthopteroid orders have been investigated by Snodgrass (1928, 1935), Imms (1937), Misra (1946) and Khattar (1964).

Voss (1905) described the musculature of the thorax of Gryllus but did not include the detail of the muscles of the neck. In the present work the muscles of the neck have been fully discussed since these are responsible for the movements of the whole head capsule.

In naming the muscles of the head, terms descriptive of their function have been employed. In each case the function of the muscle has been assessed by mechanical manipulation. The terminology of Duporte (1920), Snodgrass (1935), Khattar (1964) and Narula (1974) has been used where relevant. In the figures the muscles are given numbers for clarity and a key to these is given on page 138. Important features of difference with other Orthoptera are discussed in the section appropriate to a particular muscle. This approach was adopted for clarity.

In describing the muscles of the stomodaeum the terms dorsal and ventral are used. These refer to the upper and lower surface of the stomodaeum respectively, when the dissection is performed from the dorsal surface of the head. For the tentorium, the term anterior denotes the upper surface of the tentorial body which touches the ventral muscles of the stomodaeum while the posterior surface represents the lower surface of the tentorial body where some extrinsic muscles of the mouthparts originate.

4.2 Materials and methods

Freshly killed adult females were used for study. The head and part of the thorax was severed from the rest of the body and fixed in 70% alcoholic Bouin's fluid for 24-48 hours. Specimens were washed in 70% alcohol and appropriate dissections were performed. All dissections were carried out in cavity blocks containing 5-8mm of paraffin wax. Fine entomological pins mounted on match sticks were found to be invaluable in these delicate dissections.

Each muscle was traced from its origin to point of insertion, and drawn accurately. Specimens, anaesthetised in chloroform, were used in the assessment of the function of individual muscles. Careful manipulation of the muscle using fine forceps proved to be a satisfactory method in most cases.

Fig. 1. Muscles of the clypeolabrum shown from the anterior side.

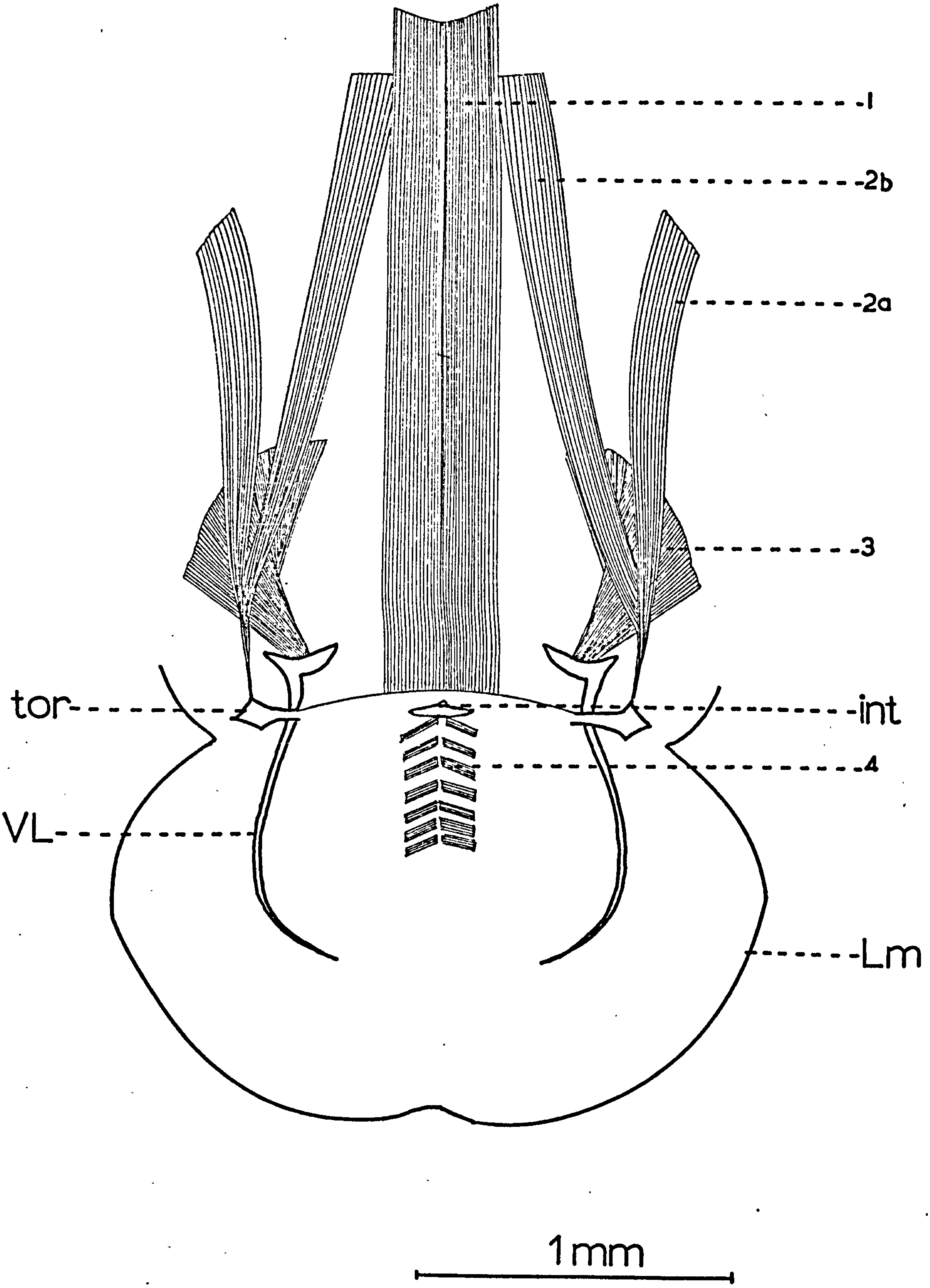


Fig.1

4.3 Muscles of the Clypeolabrum (Figs.1, 2 and 3)

Extrinsic muscles

Abductors of the labrum (Muscle 1)

These are a pair of contiguous muscles which are straight with parallel fibres. They arise from the frons just below the median ocellus and pass ventrally one on either side of the median line. These muscles are inserted in the centre of the base of the labrum (Figs. 1, 2b and 3). They help to lift the labrum and are comparable to the abductors of the labrum described in *G. assimilis* (Duporte, 1920) and *G. sigillatus* (Narula, 1974).

First adductor of the labrum (Muscle 2)

These are a pair of two headed muscles, the heads are widely separated in their place of origin but converge to be inserted on the tormae by small tendons (Figs. 1, 2a, b and 3).

The outer head or first adductor muscle (Muscle 2a) originates from the frons near the proximal inner angle of the base of the antennal socket. It is inserted on the lateral end of the tormae (Fig. 1). The inner head or adductor muscle (Muscle 2b) originates from the frons (Fig. 2a) adjacent to the origin of the abductor muscle of the labrum (Muscle 1) and lies beside it for some distance (Figs. 2b and 3). It is inserted on the lateral end of the tormae (Fig. 1) where it meets the outermost bundle of the adductor

Fig. 2. Longitudinal section, to the side of the midline, through the labrum, clypeus and part of the frons. a, some muscles of the clypeolabrum; b, some muscles of the labrum and hypopharynx.

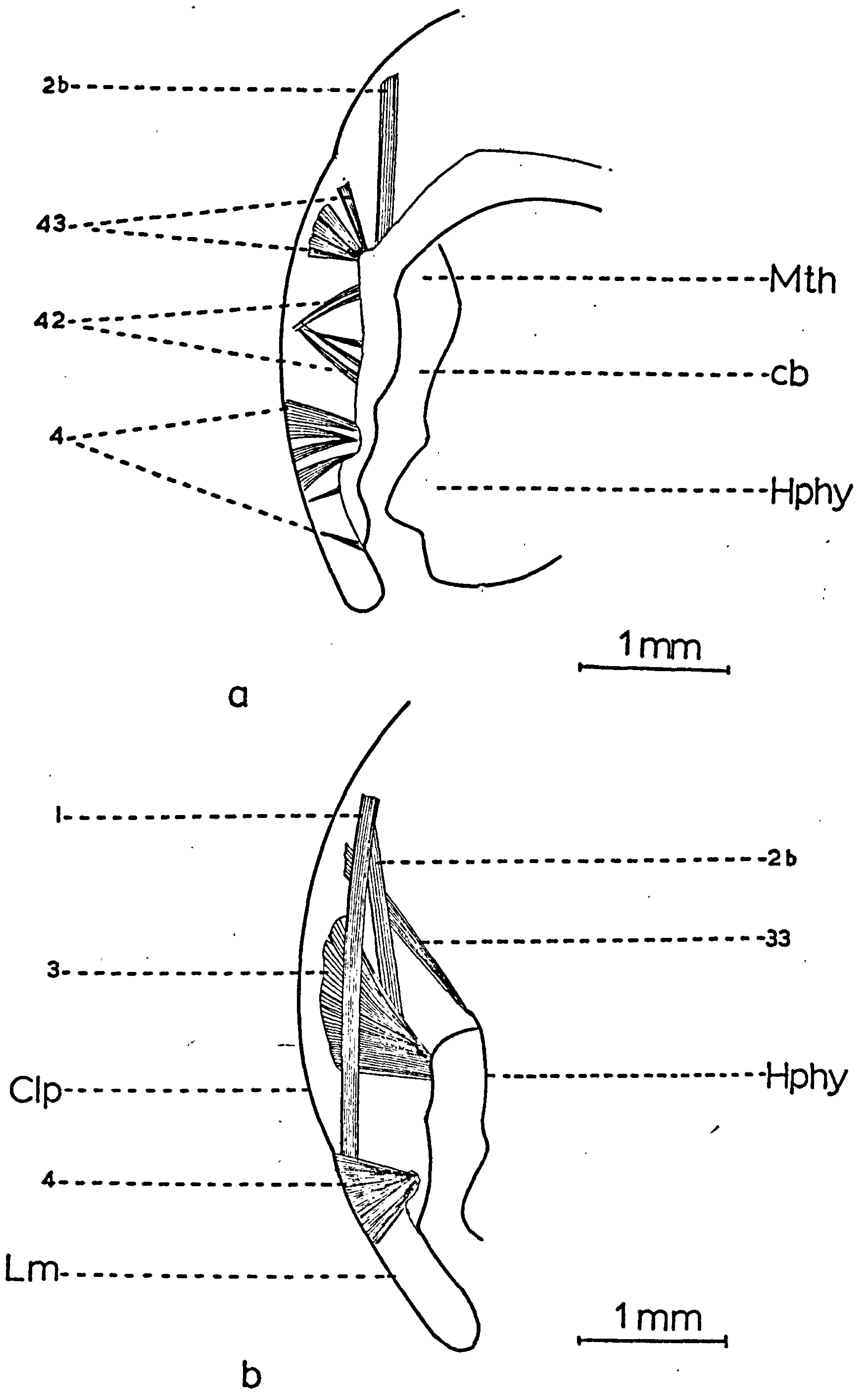


Fig. 2

muscle (Muscle 2a). It is apparent that the first and second adductors (Muscle 2a, 2b) have a common place of insertion on the lateral end of the tormae and are inserted by a small tendon; they separate afterwards to different places of origin. Narula (1974) considers this muscle to be composed of three heads in G. sigillatus.

Second adductor of the labrum (Muscle 3)

This is the bulkiest muscle of the labrum and lies beneath the two heads of the first adductor muscle of the labrum and occupies most of the clypeal area (Figs. 1, 2b and 3). The lateral fibres touch the lateral sides of the clypeus near to its point of separation into ante and post clypeus. The innermost bundles lie below the adductor of the labrum (Muscle 2b) and its edges originate from the lateral side of the groove (inverted Y), where the cibarial muscles (Muscle 43) are inserted.

The uppermost portion of the muscle arises from the epistomal sulcus and spreads out towards the anterior tentorial arm. These muscles are inserted on the proximal portion of the sclerotized bar which lies on the epipharyngeal surface (Fig. 1).

The second adductor of the labrum is comparable to the third adductor described by Berlese (1909) in Acridium lineola. This arises from the epistomal ridge and is inserted on the clypeolabral ridge between the anterior and posterior retractors of the labrum.

Fig. 3. Longitudinal section through the head.

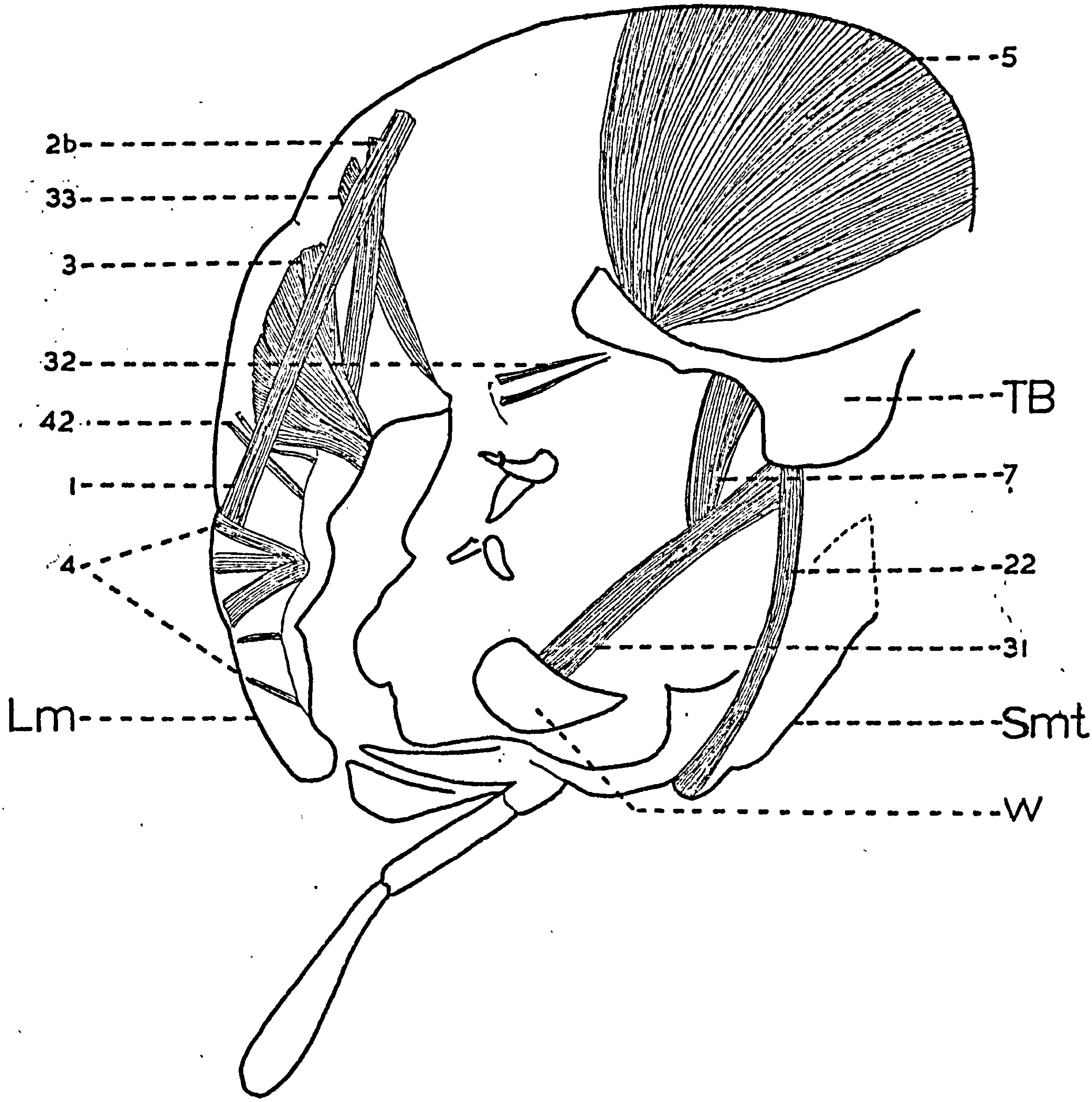


Fig.3

Intrinsic muscles

Median compressor of the labrum (Muscle 4)

The median compressor of the labrum arises in the form of pairs of bundles from the anterior wall of the labrum just below the clypeolabral sulcus. These are directed towards the epipharyngeal surface (Fig. 2b). In some specimens three to four bundles arise from the anterior wall of the labrum. The basal bundle is inserted on the intertorma (Fig.1) and the second and third to the side of the Y-shaped groove. In other specimens a group of two or three pairs of muscles occur between the median portion of the labrum in the rectangular area demarcated by the sclerotized bars (Figs. 2a and 3). The contraction of these muscles brings about a widening of the cibarium in the labral region by the stretching of the epipharyngeal membrane.

There appears to be a considerable similarity with other species previously examined (e.g. Duporte, 1920, Khattar, 1964 and Narula 1974).

The dilator of the cibarium (Muscle 42) and the first anterior dilator of the buccal cavity (Muscle 43), (Figs. 2a and 3) will be discussed in detail in the section describing the muscles of the cibarium.

4.4 Muscles of the appendages of the head capsule

4.4.a. Mandible (Figs. 3, 4, 7, 10 and 14).

The musculature of the mandible is well developed with four extrinsic muscles.

Fig. 4. Muscles of the mandible, part of the posterior side of the left mandible has been removed to show the extrinsic muscles.

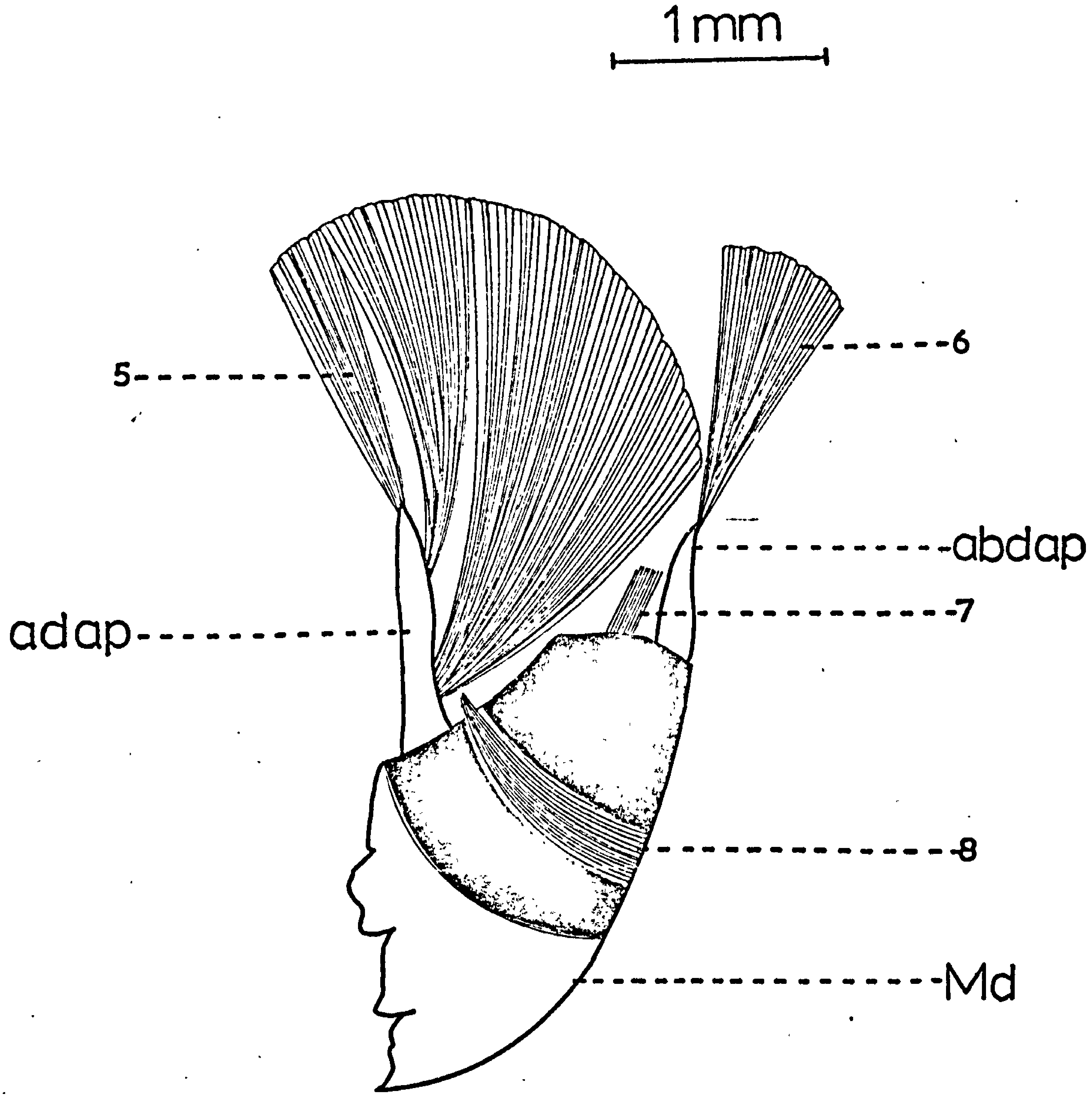


Fig. 4

Extrinsic muscles

Adductor of the mandible (Muscle 5)

This is an extensive complex muscle with many bundles fixed to the mandible by means of an adductor apodeme near to its anterior point of articulation with the head (Fig. 4). The adductor apodeme passes through the foramen formed by the junction of the anterior tentorial arm, dorsal tentorial arm and the tentorial body and enters the vertex as an adductor muscle. The base of this muscle spreads dorsally to the upper inner margin of the eye and touches the upper side of the brain, towards the middle of the head near the vertex (Fig. 14). Posteriorly it lies against the dorsal part of the occipital sulcus. The adductors of the right and left mandible run close together on their mesal side and are positioned on either side of the coronal suture. Their contraction draws the mandibles towards each other so that they meet in the mid-line.

Abductor of the mandible (Muscle 6)

This is a much smaller muscle than the adductor of the mandible (Fig. 4). It is attached to the outer angle of the mandible by a narrow apodeme, the abductor apodeme. It originates on the posterolateral margin of the vertex by a relatively narrow base.

The contraction of this muscle brings about the outward movement of the mandible. This muscle is comparable to the abductor of the mandible of *G. sigillatus*

(Narula, 1974) and *G. assimilis* (Duporte, 1920).

Tentorial adductor of the mandible (Muscle 7)

This is a small, short and simple muscle with only a few fibres (Figs. 3 and 4). It originates from the middle of the lower side of the anterior tentorial arm (Figs. 3 and 10) and is inserted on the posterior wall of the mandible (Fig. 4).

Snodgrass (1935) mentions this muscle but does not suggest its function. In *G. sigillatus* the muscle appears to be rather similar to that just described, whilst in other Orthoptera it assumes a rather different form. For example Khattar (1964) describes the muscle as very short in *Schizodactylus* whilst Berlese (1909), Snodgrass (1928), Misra (1946) and Imms (1951) do not mention the presence of this muscle in the various Orthoptera they studied. Its function seems to be an inward movement of the mandible accompanied by a slight backward movement.

Hypopharyngeal adductor of the mandible (Muscle 8)

This is a stout muscle which is inserted near to the proximal suspensorial sclerite of the longitudinal bar of the hypopharynx (Fig. 7). Its origin is on the outer wall of the mandible (Fig. 4) from where it passes horizontally across the cavity of the mandible through the mesal angle of the mandible to its point of insertion.

The contraction of this muscle draws the mandible towards the midline. This muscle presents one of the most interesting features of the entire head musculature since it is both variable in occurrence and in its site of insertion. Consequently this matter has been reserved for more detailed treatment in the general discussion (Page

4.4.b. Maxilla (Fig. 5)

The musculature of the maxilla is complex with a number of both extrinsic and intrinsic muscles.

Extrinsic muscles

Protractor of the maxilla (Muscle 9)

This is a triangular muscle originating on the gena and postgena near the origin of the abductor of the mandible (Muscle 6). It is inserted by means of a tendon or apodeme, at the upper mesal angle of the disticardo (Fig. 5a), near its junction with the basicardo and lies outside the articulatory angle of the maxilla with the head. The outer edge of this muscle touches the occipital sulcus and its origin spreads transversally over the gena. The contraction of this muscle raises the base of the maxilla at its outer angle and thus moves the maxilla outwards.

The muscle has received a varied terminology from different authors. In *G. sigillatus* it is referred to as the protractor of the cardo, whilst Duporte (1920) prefers the abductor. Snodgrass (1935) considers the muscle to be an anterior rotator of the maxilla and Khattar (1964) names it the promotor of the cardo in *Schizodactylus*.

Fig. 5. Muscles of the maxilla: a, from the anterior side; b, some muscles of the galea and lacinia; c, muscles of the palpifer.


9
12
Cd
10
10
10a
13
11
15
16
17
18
14
19
20
1mm
21
a
15
15
t
16
c
1mm
13
14
Lc
Ga
b
1mm

Fig.5

Adductors of the cardo (Muscle 10,10a)

The adductors of the cardo arise from the middle of the lower side of the tentorial body. The muscles are composed of two bundles which have a common origin although they diverge slightly at their place of insertion. The first adductor of the cardo (Muscle 10) is long, thick and has parallel fibres; it is inserted upon the sulcus between the first and second lobe of the cardo towards the centre (Fig. 5a). The second adductor (Muscle 10a) is similar to the first and is inserted on the cardostipital sulcus almost in the middle or sometimes the outer angle of the second lobe of the cardo (the disticardo and stipial sulcus). This muscle has no tendon and is formed of parallel muscle fibres and is therefore of equal thickness throughout its length (Fig. 5a). The contraction of this muscle pulls the maxilla inward.

In *G. sigillatus*, Narula (1974) reports the presence of similar muscle, although Duporte (1920) considers these as separate muscles in *G. assimilis*.

Adductor of the stipes (Muscle 11)

The adductor of the stipes (Muscle 11) is a strong muscle formed of several muscle bundles with parallel fibres (Fig. 5a). It originates from the posterior side of the middle part of the tentorial body and is inserted on a flat elongated apodemal surface (the parastipial ridge) along the inner edge of the posterior wall of the stipes. This appears behind the flexor of the lacinia (Muscle 13) in Fig. 5a. Duporte (1920) calls this muscle the flexor of the stipes in *G. assimilis* whilst Khattar (1964) and Narula (1974) describe it as the adductor of the maxilla in *S. monstrosus* and *G. sigillatus* respectively.

The adductor of the stipes and the adductor of the cardo when working together are capable of exerting a considerable force so that the maxilla is moved towards the midline.

Cranial flexor of the lacinia (Muscle 12)

This is the longest and slenderest of all the extrinsic muscles of the maxilla. It arises near the base of the protractor of the maxilla (Fig. 5a) but mesal to it for a short distance it stretches along the protractor of the cardo (Muscle 9) and then passes downwards anterior to the adductors of the cardo and stipes. It is inserted on the base of the lacinia towards the mesal side together with the flexor of the lacinia (Muscle 13). A similar muscle has been recorded in *G. sigillatus* (Narula, 1974) and *Schizodactylus* (Khattar, 1964).

Intrinsic muscles

Flexor of the lacinia (Muscle 13)

This is short, stout muscle which arises by a broad base along the proximal outer angle of the stipes and extends inwards over half the width of the stipes (Fig. 5a). The muscle then passes diagonally across the stipes and gradually becomes much narrower towards its insertion, via a short tendon, on the inner region of the base of the lacinia (Fig. 5a and b). The contraction of this muscle bends the lacinia inwards.

Flexor of the galea (Muscle 14)

This is a long muscle with parallel fibres and is of uniform width throughout its length (Fig. 5a and b). It arises from the proximal, mesal edge of the stipes. The muscle passes downwards posterior to the flexor of the lacinia (Muscle 13) which lies diagonally across it (Fig. 5b). It is inserted on the anterior side of the base of the distal segment of the galea. A similar origin and insertion of this muscle has been recorded in G. assimilis and Schizodactylus (Duporte, 1920 and Khattar, 1964 respectively). The contraction of the flexor of the galea apparently bends the galea forwards and inwards.

Levator of the maxillary palp (Muscle 15)

The five segmented maxillary palp has two muscles attached at its base and which lie within the stipes (Fig. 5a and c). These are responsible for the movement of the palpus. One of these, the levator of the maxillary palp (Muscle 15) is a short, thick muscle with two unequal branches (Fig. 5c) which originate from the posterior surface of the stipes along the longitudinal sulcus (Fig. 5c). The two branches cross the palpifer and are inserted at a common point on the posterolateral surface of the base of the first segment of the maxillary palp (Fig. 5a and c). The contraction of this muscle moves the maxillary palp outwards. The levator muscle is homologous to the extensor muscle of the maxillary palp in *G. assimilis* (Duporte, 1920) and *G. sigillatus* (Narula, 1974), but in these species it is recorded as a single muscle whilst in *Schizodactylus* (Khattar, 1964) the muscle is two branched.

Depressor of the maxillary palp (Muscle 16)

This is a small muscle which is slightly thinner and shorter than the levator of the maxillary palp (Muscle 15). It also originates from the stipes in the middle of the longitudinal sulcus 't'. Like the levator muscle (Muscle 15) it also crosses the palpifer and is inserted on the anterolateral surface of the base of the first maxillary palp segment (Fig. 5a and c). The contraction of this depressor muscle bends the palp inwards.

Levator of the first palp segment (Muscle 17)

This is a short muscle which has its origin on the proximal margin of the first palp segment (Fig. 5a). It is inserted on the posterolateral surface of the base of the second palp segment. The contraction of this muscle assists in lifting the maxillary palp.

Depressor of the first palp segment (Muscle 18)

This is also a short, simple muscle like the levator muscle (Muscle 17). It has a similar site of origin on the proximal part of the first palp segment (Fig. 5a). It is inserted on the anterolateral surface of the base of the second palp segment. The contraction of this muscle contributes to the bending inwards of the maxillary palp.

Levator of the second palp segment (Muscle 19)

This is a longer muscle and originates from the mid or distal portion of the first palp segment (Fig. 5a). It crosses the whole length of the second palp segment and is inserted on the posterolateral side of the base of the third palp segment. The contraction of this muscle lifts this segment and contributes to the outward movement of the whole palp.

Levator of the third palp segment (Muscle 20)

This muscle is slightly longer than the muscle of the second palp segment (Muscle 19). It is spindle shaped and tapers to its site of origin on the proximal part of the third palp segment (Fig. 5a) and again to its insertion on the anterolateral surface of the base of the fourth palp segment. The contraction of this muscle has a similar role to the levator of the second palp segment.

Flexor of the fourth palp segment (Muscle 21)

Like the levator muscle of the third palp segment (Muscle 20), the flexor muscle (Muscle 21) also originates from the proximal part of the palp segment but in this case the fourth segment. It is again spindle shaped and is inserted on the anterolateral part of the base of the fifth palp segment (Fig. 5a). The contraction of this muscle bends the fifth palp segment inwards and it also flexes the fourth palp segment.

It has been demonstrated that the movement of the palp as a whole is due to the muscles of the maxillary palp (Muscle 15, 16) in addition to the muscles of the individual segments. Narula (1974) calls the muscles of the palpifer as extensor and flexor in *G. sigillatus*.

4.4.c. Labium (Figs. 6 and 14)

The musculature of the labium is shown in Fig. 6 and consists of both extrinsic and intrinsic muscles arranged in pairs.

Extrinsic muscles

Adductor of the labium (Muscle 22)

This is a very long, slender muscle (Fig. 6) which arises on the lateral, posterior edge of the postoccipital ridge close to the posterior tentorial pit. The origin is close to that of the retractor of the hypopharynx. This muscle passes over the tentorial bridge (Fig. 14), crosses the submentum, mentum, prementum and is inserted on the distal part of the prementum at the base of the outer side of the paraglossa (Fig. 6). In *G. assimilis* (Duporte, 1920) and *G. sigillatus* (Narula, 1974) the origin of this muscle is rather different being from the base of the central plate of the tentorium. *A. domesticus*, however, resembles *Schizodactylus* (Khattar, 1964) in the site of the origin of this muscle. The contraction of this muscle lifts the

Fig. 6. Muscles of the labium from an anterior aspect.

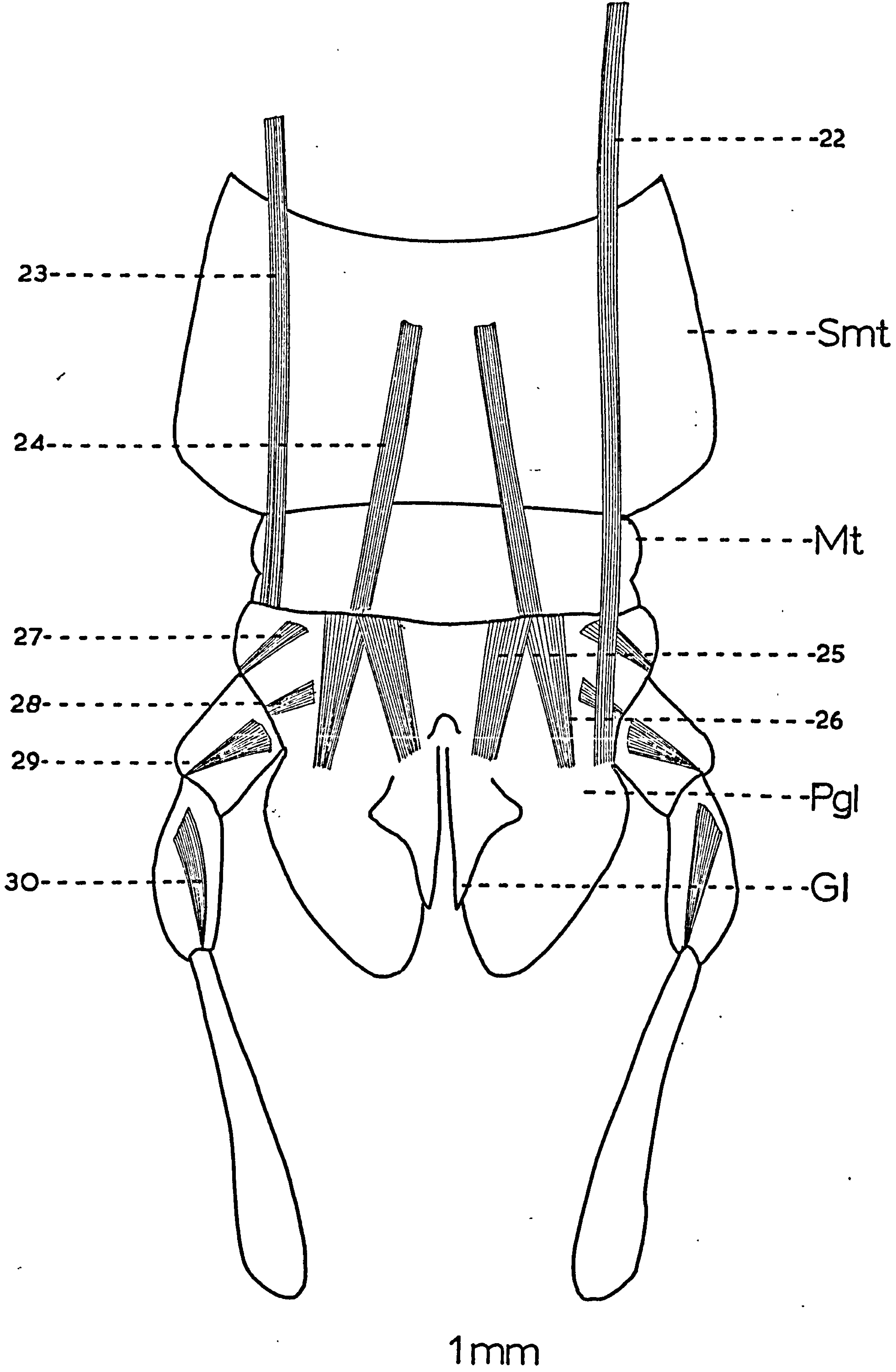


Fig. 6

prementum, in such a way that the whole labium is curved forwards.

Abductor of the labium (Muscle 23)

The abductor of the labium (Muscle 23) is a straight parallel fibred muscle which lies posterior to the adductor of the labium (Muscle 22). It arises from the tubercle which lies on the lower edge of the tentorial bridge. It is inserted directly on the outer angle of the base of the prementum (Fig. 6). It can be demonstrated that this muscle is responsible for lifting the prementum and work in conjunction with adductor of the labium (Muscle 22) to bend the labium inwards and towards the other mouthparts.

Intrinsic muscles

The intrinsic muscles include the median muscles of the prementum, the muscles of the ligula and the labial palp.

Median retractor of the labium (Muscle 24)

These retractors are parallel fibred muscles contiguous at their origin in the mid region of the submentum (Fig. 6). They diverge as they approach the mentum and are inserted on the base of the prementum some distance apart. The median retractor of the labium draws the prementum upwards.

The muscle has been referred to in a variety of ways; as the adductor of the labium in G. assimilis (Duporte, 1920), the flexor of the labium (Snodgrass, 1935) or the anterior retractor of the prementum (Narula, 1974).

Adductor of the glossa (Muscle 25)

This is a pair of short muscles which originate by a broad base on the proximal margin of the prementum (Fig.6). They pass diagonally and are inserted at the base of the glossa just below the insertion of the median retractor of the labium (Muscle 24). The adductor of the glossa (Muscle 25) working in conjunction with the adductor of the paraglossa seem to move these structures backwards and forwards but the glossa does not move independently.

Adductor of the paraglossa (Muscle 26)

This is a pair of muscles which are slightly broader towards their origin (Fig. 6). Each muscle arises from the base of the prementum, lateral to the origin of the adductor of the glossa (Muscle 25), and is inserted in the middle of the proximal part of the paraglossa. This muscle appears to move the paraglossa backward and forward. This muscle is termed the flexor of the paraglossa in *Schizodactylus* (Khattar, 1964).

Levator of the labial palp (Muscle 27)

The musculature of the labial palp is more similar to *G. sigillatus* (Narula, 1974) than to *G. assimilis* (Duporte, 1920). The levator of the labial palp (Muscle 27) is a short muscle originating from the prementum (Fig. 6) towards its proximal boundary. The levator of the labial palp (Muscle 27) crosses the palpiger and is inserted on the outer angle of the base of the first palp segment. The contraction of this muscle produces some lateral movement of the palp and serves to raise the palp.

Depressor of the labial palp (Muscle 28)

This is also a short muscle which originates from the prementum (Fig. 6), like levator of the labial palp (Muscle 27) but somewhat distal to it. It is inserted on middle, posterior portion of the base of the first palp segment. The contraction of this muscle tends to bend the labial palp downwards and inwards.

Extensor of the first palp segment (Muscle 29)

A single muscle arises from the base of the first segment of the labial palp and runs obliquely to its point of insertion, via a short tendon, on the base of the second palp segment (Fig. 6). It assists in straightening and extending the labial palp outwards.

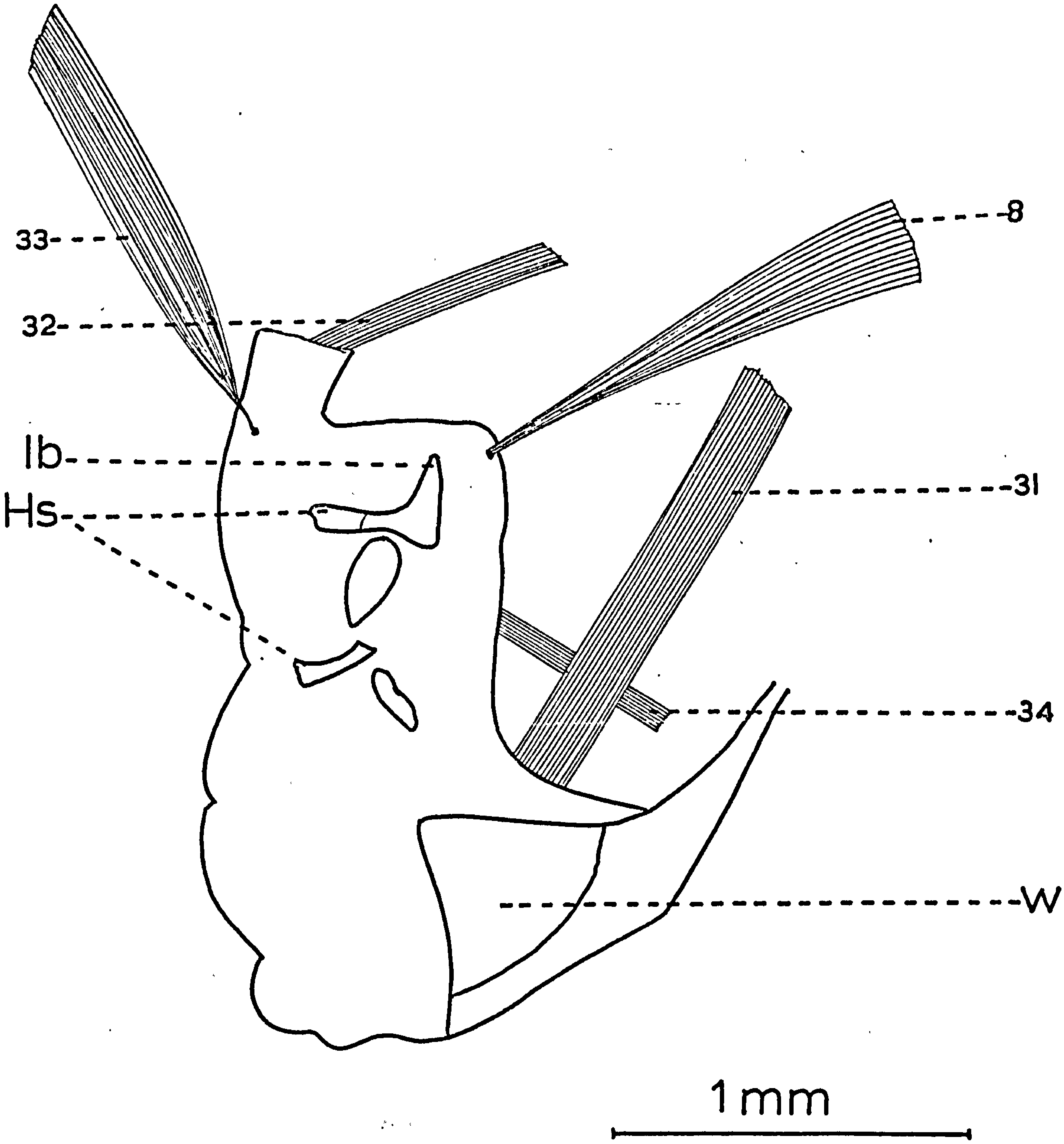
Depressor of the second palp segment (Muscle 30)

This is a long muscle which arises from the base of the second palp segment (Fig. 6). It passes obliquely and is inserted on the median side of the base of the third segment. Its contraction bends the terminal segment inwards.

4.4.d. Hypopharynx (Figs. 2, 3, 7, 8, 9 and 14)

The musculature of the hypopharynx is complex with some muscles associated with the hypopharynx itself and others with the salivarium. These are both extrinsic and intrinsic muscles and with one exception they are paired.

Fig. 7. Lateral view of the hypopharynx.



Fig·7

Extrinsic muscles

Retractor of the hypopharynx (Muscle 31)

The retractor of the hypopharynx is the longest muscle associated with the hypopharynx (Figs. 7 and 8a). It arises on the lower edge of the postoccipital ridge (Fig. 14) close to the origin of the adductor of the labium (Muscle 22). It passes over the tentorial bridge, runs along the adductor of the labium (Muscle 22) for some distance and then diverges forwards. Its insertion is on the lower end of the basal sclerite of the hypopharynx in the angle formed by the union of anterior and posterior side of the hypopharynx. The retractor of the hypopharynx pulls the hypopharynx towards the mouth.

Schizodactylus (Khattar, 1964) resembles *A. domesticus* in the site of origin of this muscle, whilst in *G. sigillatus* and *G. assimilis* the muscles originate on the posterior edge of the tentorial body (Narula, 1974; Duporte, 1920).

Depressor of the hypopharynx (Muscle 32)

The depressor of the hypopharynx forms a contiguous pair of short thin median muscles (Figs. 7 and 8b) which originate from the posterior side of the central plate of the tentorium. They are inserted on the inner integument of the proximal region of the hypopharynx between the proximal suspensorial ligaments, near to the point where the pharynx narrows into oesophagus. The contraction of the depressor of the hypopharynx would assist in the enlargement of the oesophageal region.

Fig. 8. Posterior view of the hypopharynx: a, posterior surface of the hypopharynx showing membranous lobes and the position of the muscles; b, the membranous lobes and the posterior surface of the hypopharynx has been removed to show the muscles.

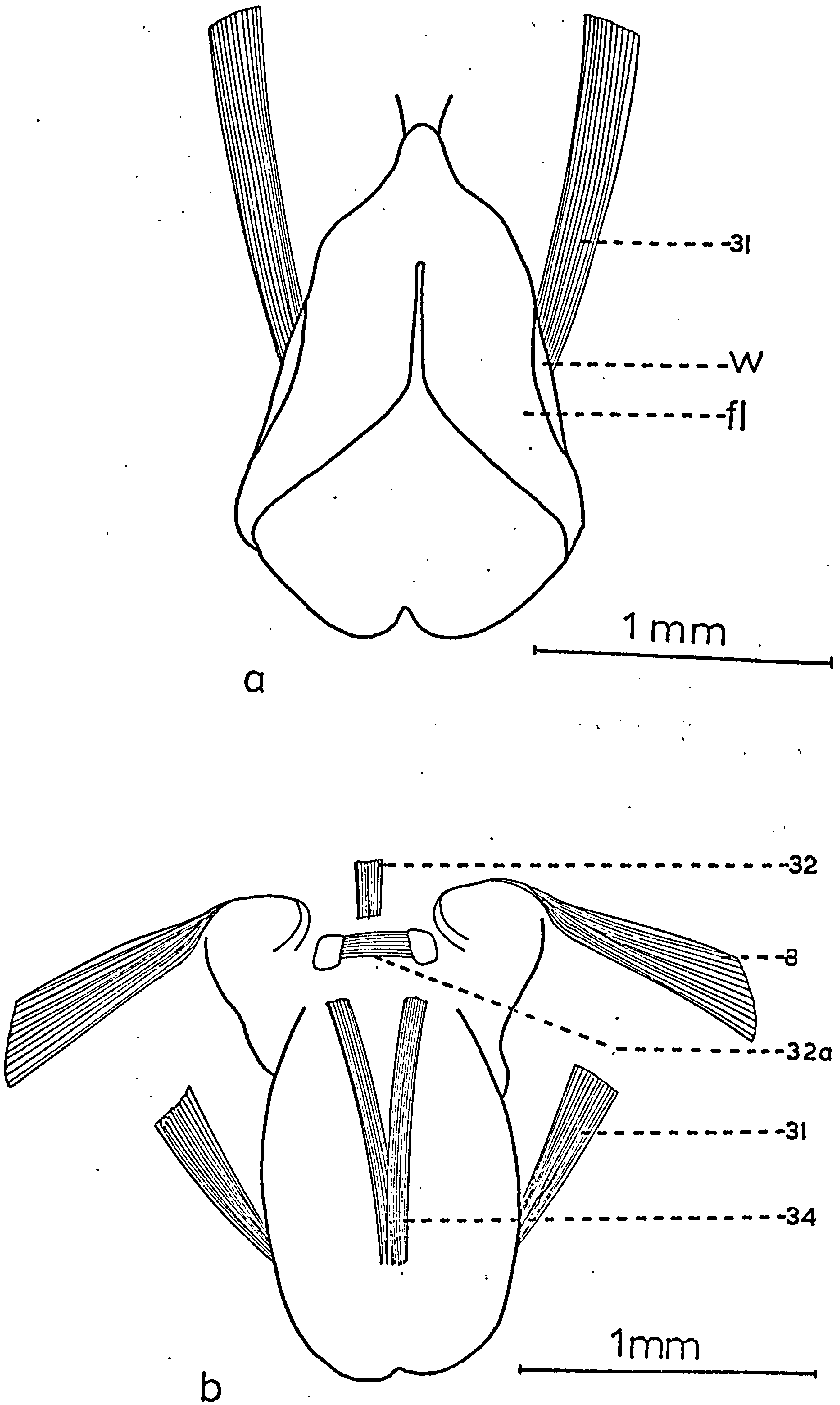


Fig. 8

Elevator of the hypopharynx (Muscle 33)

This is a stout muscle which arises on the frons near the median ocellus (Figs. 2b and 3) and is inserted on the proximal part of the anterior surface of the hypopharynx a little way from the transverse bar of the suspensorium (Fig. 7) and near to the entrance to the stomodaeum. This muscle pulls the base of the hypopharynx against the roof of the pharynx and so closes the entrance to the oesophagus. It is interesting that Snodgrass (1935) refers to the muscle as the retractor of the mouth angle, presumably relating to its function in closing the oesophagus.

Hypopharyngeal adductor of the mandible (Muscle 8)

This muscle has already been discussed in connection with the extrinsic musculature of the mandible (Page It is inserted laterally on the proximal surface of the hypopharynx near the longitudinal bar of the suspensorium (Figs. 4, 7 and 8b). The contraction of this muscle draws the mandible towards the midline and raises the surface of the hypopharynx to close the entrance to the stomodaeum. It is presumably for this latter function that the muscle is referred to as the levator of the hypopharynx in *G. sigillatus* (Narula, 1974).

Intrinsic muscles

Constrictor of the hypopharynx (Muscle 32a)

This is a single transverse muscle which lies on the posterior surface of the hypopharynx (Fig. 8b) immediately

Fig. 9. Muscles of the salivarium: a, shown from the anterior side; b, longitudinal section through the head showing the position of the muscles.

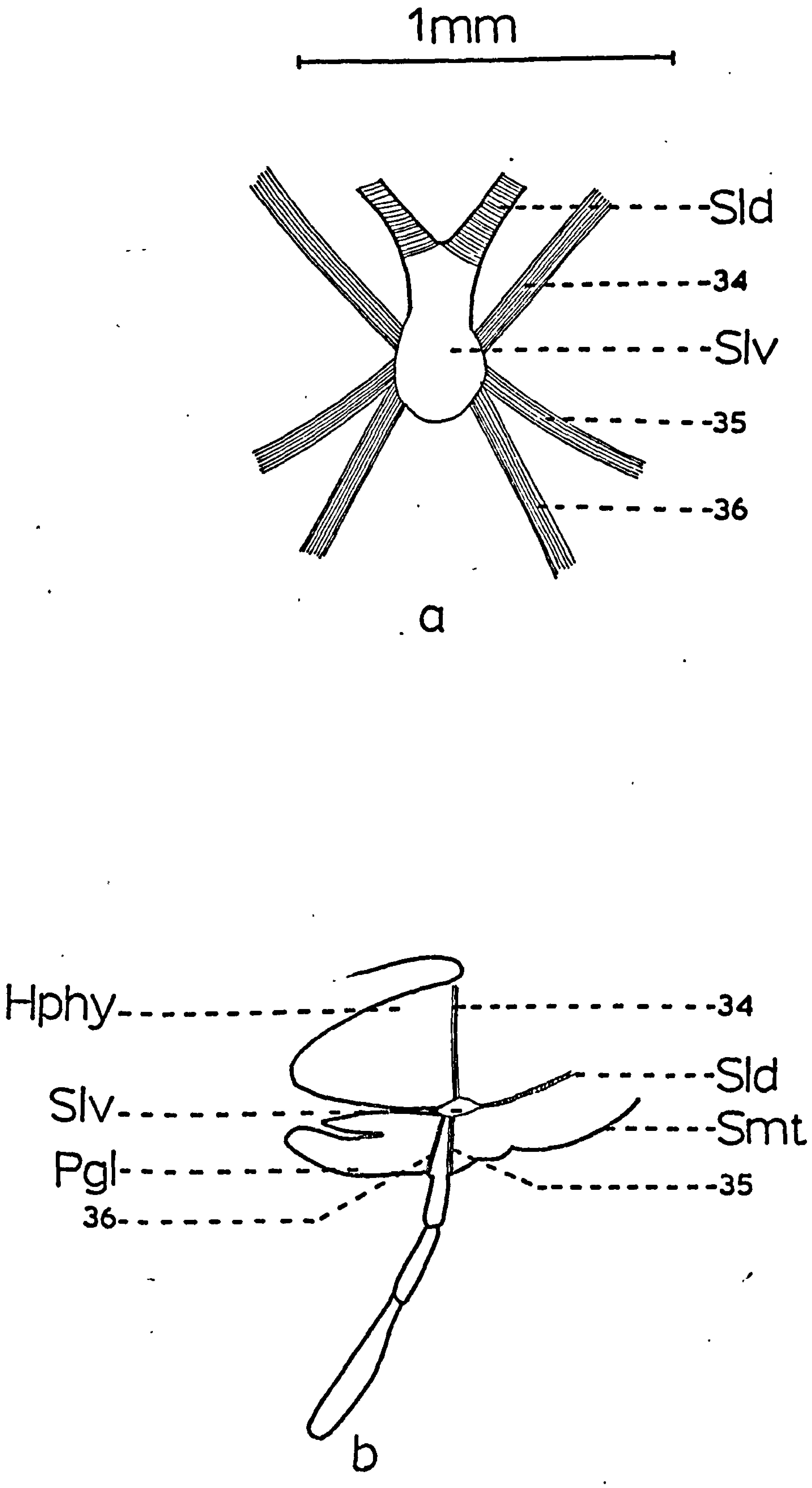


Fig.9

distal to the insertion of the depressor of the hypopharynx (Muscle 32). Its contraction brings about a slight curvature of the base of the hypopharynx and so enlarges the oesophageal region.

Muscles of the Salivarium

The salivarium possesses three pairs of muscles.

First compressor of the salivarium (Muscle 34)

The compressor of the hypopharynx is one of the muscles of the salivarium. Its origin is best displayed by removing the posterior lobes of the hypopharynx. It arises on the interior surface of the hypopharynx (Figs. 7, 8b, 9a and b) near to the position of the inner end of each suspensorial bar. It runs obliquely towards its insertion on the median region of the side of the salivarium (Fig. 9a and b). The pharyngeal opening is enlarged by the contraction of this muscle.

Second compressor of the salivarium (Muscle 35)

The second compressor of the salivarium (Muscle 35) arises from the prementum at the base of the palpiger (Fig. 9b). It is inserted laterally on the salivarium (Fig. 9a and b). The contraction of this muscle pulls the salivarium ventrally against the labium and allows saliva to flow freely during feeding.

Third compressor of the salivarium (Muscle 36)

The third compressor of the salivarium (Muscle 36) originates from the inner angle of the base of the palpiger

(Fig. 9b) and is inserted on the side of the salivarium immediately below the insertion of the second compressor of the salivarium (Fig. 9a and b). The contraction of this muscle supplements the effect of muscle 35.

The three pairs of muscles of the salivarium are homologous to '1 s', '2 s' and '3 s' of Snodgrass (1935).

4.4.e. Antenna (Figs. 10 and 11)

Each antenna possesses three extrinsic muscles which bring about its movement. These muscles all arise from the anterior side of the anterior tentorial arm.

Extrinsic muscles

Levator of the antenna (Muscle 37)

This muscle originates anteriorly from the outer edge of the anterior tentorial arm (Fig.10). The muscle narrows from its origin to its insertion on the anterolateral side of the base of the scape near the inner part of the compound eye. The contraction of this muscle serves to lift the antenna; similar muscles have been found in other species of Gryllidae studied by Duporte (1920) and Narula (1974).

Flexor of the antenna (Muscle 38)

This muscle originates from the inner edge of the anterior tentorial arm (Fig. 10) adjacent to the angle formed by the tentorial body and dorsal tentorial arm. It passes over the dorsal tentorial arm and is inserted on the postero-lateral side of the base of the scape. It is responsible

Fig. 10. Antennal musculature shown from the anterior side.

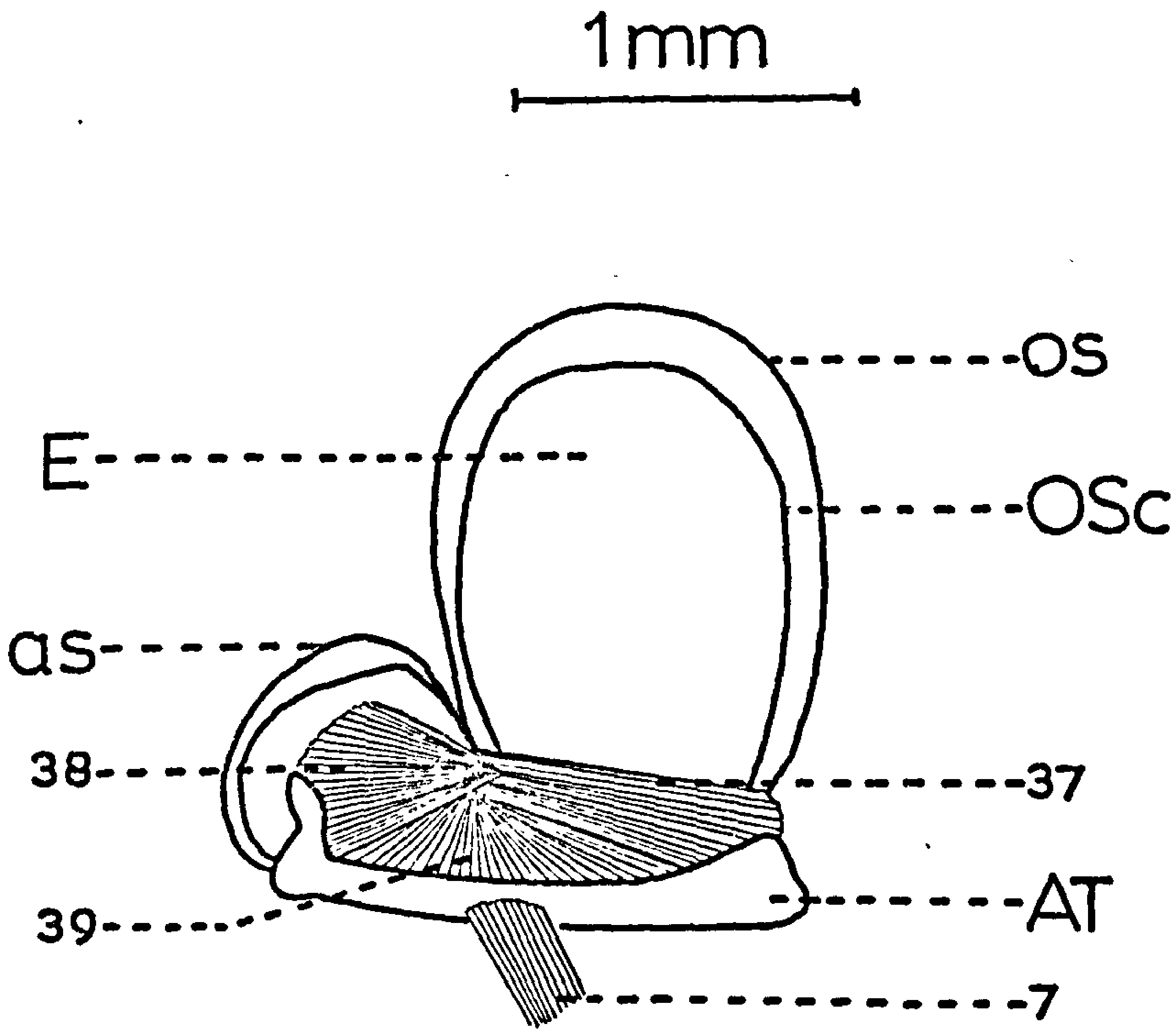


Fig.10

for the lateral movement of the antenna, comparable muscle being found in G. assimilis (Duporte, 1920) and G. sigillatus (Narula, 1974).

Depressor of the antenna (Muscle 39)

This muscle has a very broad base (Figs.10 and 11a - b) which spreads across much of the anterior tentorial arm. Part of this muscle (Muscle 39) lies above and the remainder below the dorsal tentorial arm (Fig. 11a-b). The muscle tapers rapidly and is inserted on to the anterolateral edge of the scape. The contraction of this muscle pulls the antenna downwards. Duporte (1920) and Narula (1974) record a similar muscle in G. assimilis and G. sigillatus respectively.

Intrinsic muscles

The intrinsic musculature of the scape comprises an outer extensor (Muscle 40) and an inner flexor (Muscle 41), both of which arise from the base of the scape (Fig. 11c). These muscles taper towards their insertion on the inner and outer angles of the base of the pedicel. The movement of the flagellum and pedicel is brought about by a combination of the muscles in the scape together with the antennal socket muscles.

The absence of muscles in the pedicel and flagellum is a characteristic feature of most insects with the exception of some primitive Apterygota. Schneider (1964) reports that the majority of insects including Orthoptera have antennae

Fig. 11. Antennal musculature: a, right antenna from anterior side after removal of muscles 37 and 38; b, Depressor muscle (Muscle 39) with part removed; c, muscles of the left scape shown from the anterior side.

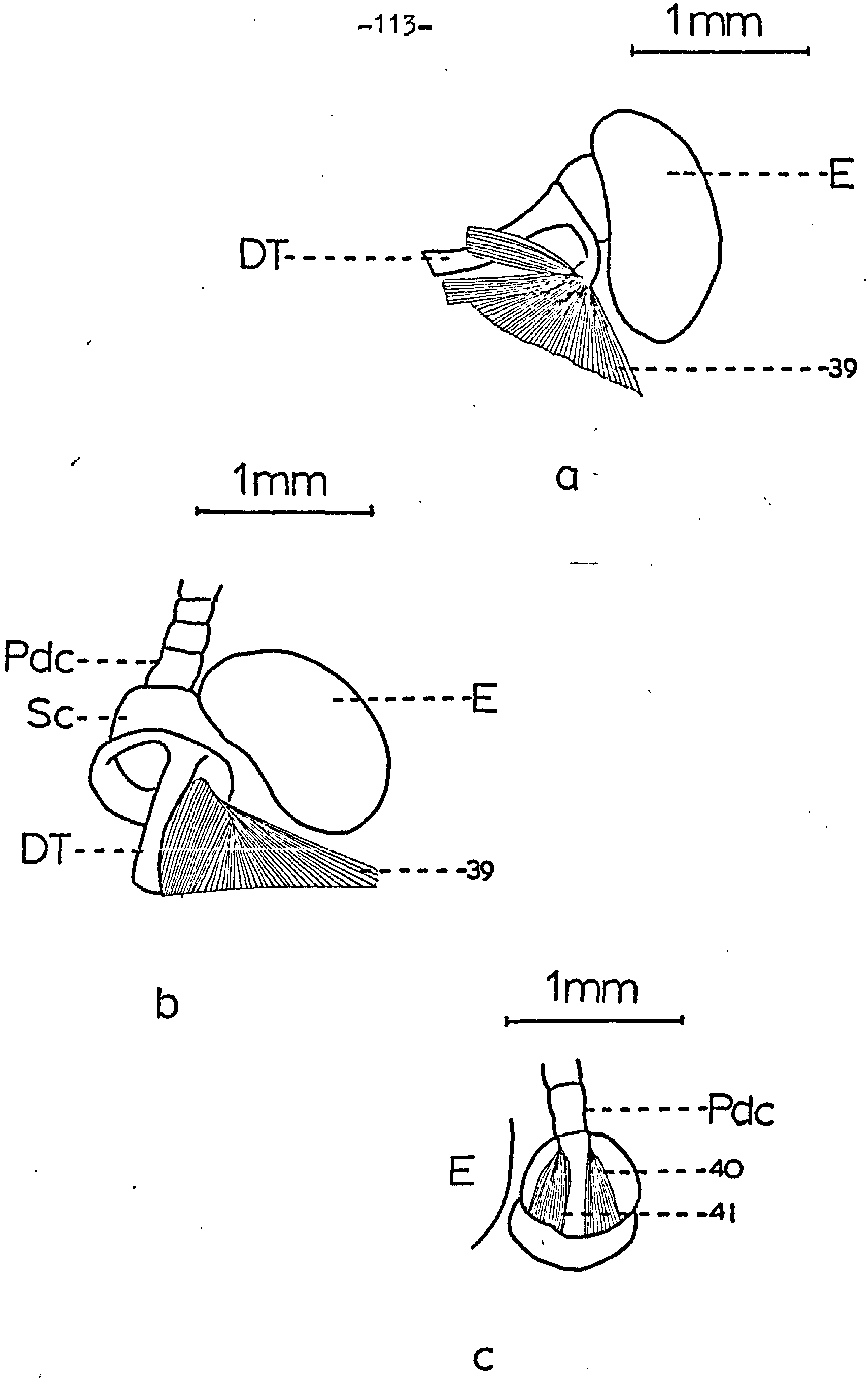


Fig.11

with muscles arising only from the tentorium or scape. It is therefore of great interest that Narula (1974) reports the presence of intrinsic muscles in the scape and a few segments of the flagellum in G. sigillatus. This he considers to be a primitive character. In the early work of Duporte (1920) the presence of a flexor and an extensor muscle in the pedicel and flagellar segments was also suggested, but there is definitely no evidence of this additional antennal musculature in A. domesticus.

4.5. Muscles of the Cibarium and Cephalic Stomodaeum (Figs. 2, 3, 12 and 13)

(i) The Cibarium

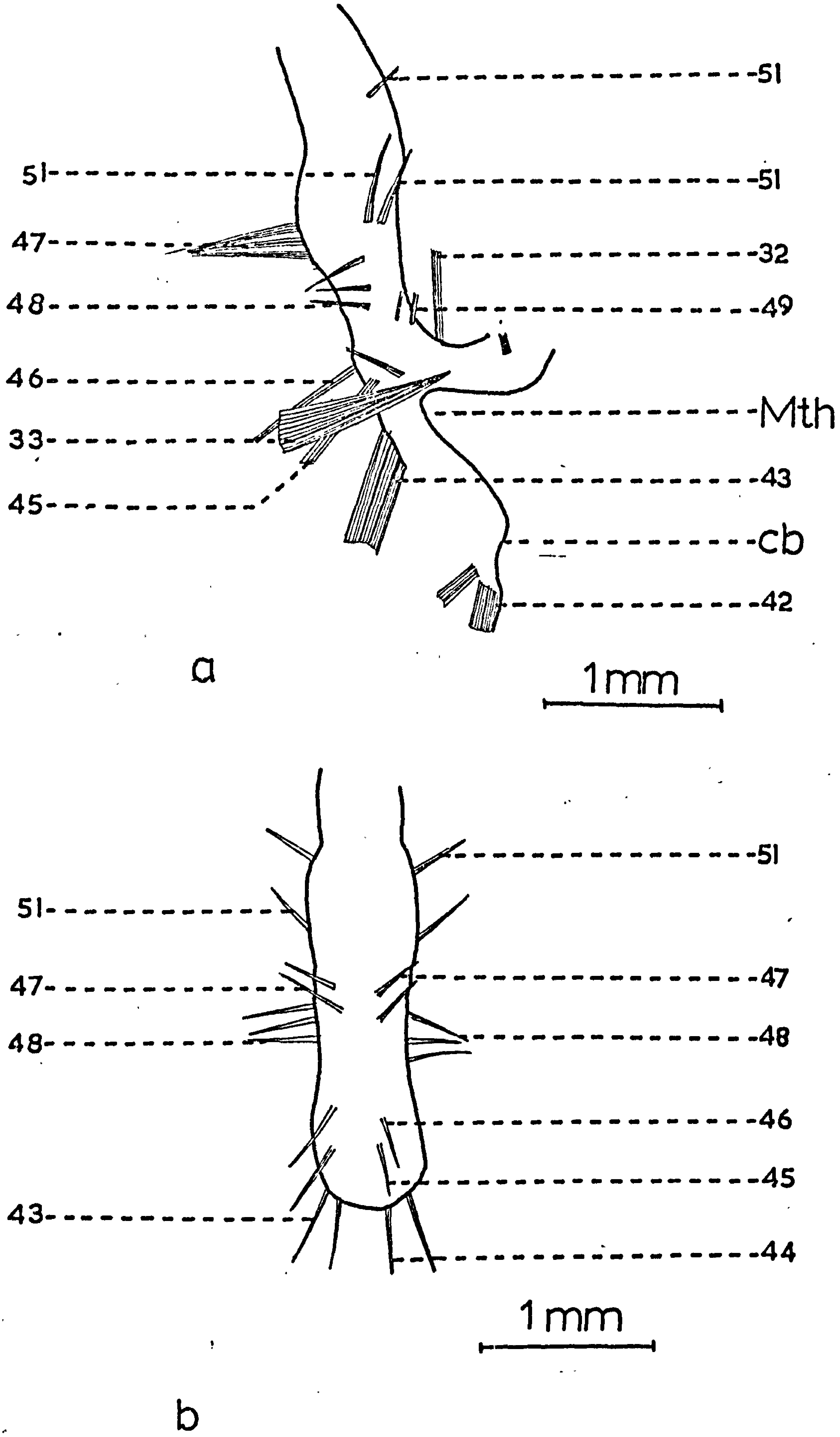
Dilator of the cibarium (Muscle 42)

The dilator of the cibarium (Muscle 42) is composed of five to six muscle bundles and originates from the mid posterior face of the clypeus as separate bundles (Figs. 2a, 3 and 12a). These pass horizontally and obliquely towards the epipharyngeal region and are inserted at the side of the inverted Y-shaped groove on the roof of the epipharyngeal region. The contraction of this muscle causes the dilation of the cibarium as the epipharyngeal wall is pulled toward the clypeus.

(ii) The Cephalic Stomodaeum

In this context it is first necessary to briefly describe the stomodaeum. The first part of the stomodaeum which lies immediately within the mouth is termed the buccal

Fig. 12. Muscles of the stomodaeum: a, lateral view of the stomodaeum showing dorsolateral and ventrolateral muscles; b, dorsal view of the stomodaeum.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Mth
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43
45
cb
42
a
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51
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48
48
46
45
43
44
1mm
b

Fig·12

cavity. This leads into a detailed area, the pharynx, which lies between the frontal ganglion and the cerebral nerve connectives. Posterior to the brain, the stomodaeum assumes the form of a simple oesophageal tube or posterior pharynx. The precereble pharynx is often referred to as the anterior pharynx (e.g. Eidman, 1925).

The musculature of the cephalic stomodaeum consists of both intrinsic and extrinsic muscles. Circular and longitudinal muscles which run on the outer wall of the pharynx and act as compressor muscles are classed as intrinsic muscles. All other muscles which originate from the head are extrinsic and are referred to as dorsal, lateral and ventral dilators according to their place of insertion. These muscles are responsible for the dilation of the stomodaeum.

Dorsal dilators

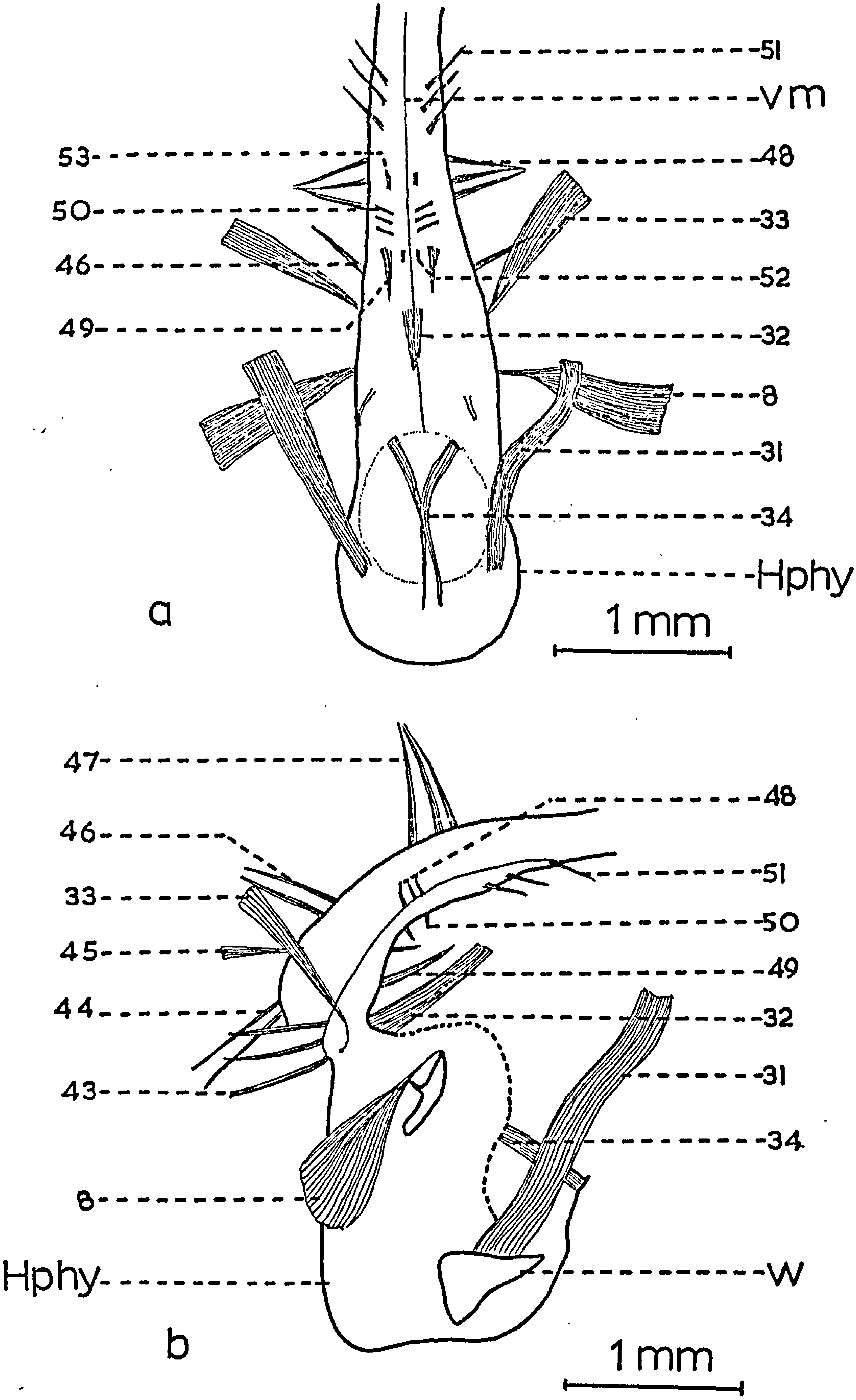
First anterior dilator of the buccal cavity (Muscle 43)

This muscle consists of bundles of fibres which originate from the clypeus and are inserted on the dorso-lateral angle of the stomodaeum just behind the mouth (Figs. 12a and 13b). The contraction of this muscle opens the mouth cavity.

Second anterior dilator of the buccal cavity (Muscle 44)

This muscle comprises two separate slender muscles which originate from the frons above the epistomal sulcus and are inserted dorsally on the roof of the stomodaeum (Figs. 12b and 13b). The function of this muscle appears to

Fig. 13. Muscles of the stomodaeum: a, ventral view of the stomodaeum; b, lateral view of the stomodaeum and hypopharynx.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32
43
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34
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1 mm

Fig·13

be similar to that of muscle 43.

First dilator of the anterior pharynx (Muscle 45)

This is a single muscle which lies below the origin of the elevator of the hypopharynx (Muscle 33). It originates on the frons just below the median ocellus, and is inserted on the roof of the pharynx (Figs. 12a, b and 13b).

Second dilator of the anterior pharynx (Muscle 46)

The second dilator of the anterior pharynx (Muscle 46) lies anterior to the brain and also originates from the frons near the median ocellus. It consists of two discrete bundles which are separate at their sites of insertion on the roof of the pharynx (Figs. 12a, b and 13a, b).

First dilator of the posterior pharynx (Muscle 47)

This muscle normally consists of two or three separate bundles which originate from the epicranium. The edges of these muscles touch the adductor of the mandible (Muscle 5). They are inserted on the dorsal wall of the pharynx near the dorsal median line and just posterior to the brain (Figs. 12a, b and 13b).

Lateral dilators

Dilator of the pharynx (Muscle 48)

The lateral dilator of the pharynx (Muscle 48) consists of two or three short bundles of fibres which originate from the inner edge of the antennal socket and are inserted on the lateral side of the pharynx under the brain (Figs. 12a, b and 13a, b).

Ventral dilators

First dilator of the anterior pharynx (Muscle 49)

The first dilator of the anterior pharynx (Muscle 49) lies ventrally near to the depressor of the hypopharynx (Muscle 32), (Figs. 12a and 13a, b) and arises from the anterior innermost edge of the tentorial body. It is inserted lateral to the ventral median line of the stomodaeum.

Second dilator of the anterior pharynx (Muscle 50)

The second dilator of the anterior pharynx (Muscle 50) is composed of three separate bundles of muscle fibres which originate from the anterior side of the central part of the tentorial body and are inserted on the ventral side or floor of the stomodaeum (Fig. 13a, b).

Third dilator of the anterior pharynx (Muscle 52)

The third dilator of the anterior pharynx (Muscle 52) is very short and barely touches the tentorial body. It is inserted on the ventral part of the pharynx very close to the ventral median line (Fig. 13a).

Fourth dilator of the anterior pharynx (Muscle 53)

This muscle (Muscle 53) is also very short and resembles the third dilator of the anterior pharynx (Muscle 52). It also has its insertion on the ventral part of the pharynx close to the ventral median line (Fig. 13a).

First dilator of the posterior pharynx (Muscle 51)

This muscle is composed of three separate bundles of muscle fibres which originate on the anterior edge of the tentorial body and are inserted on the ventral part of the stomodaeum slightly removed from the median line (Figs. 12a, b and 13a, b).

Fig. 14. Posterior view of the head showing some muscles of the mouthparts and neck.

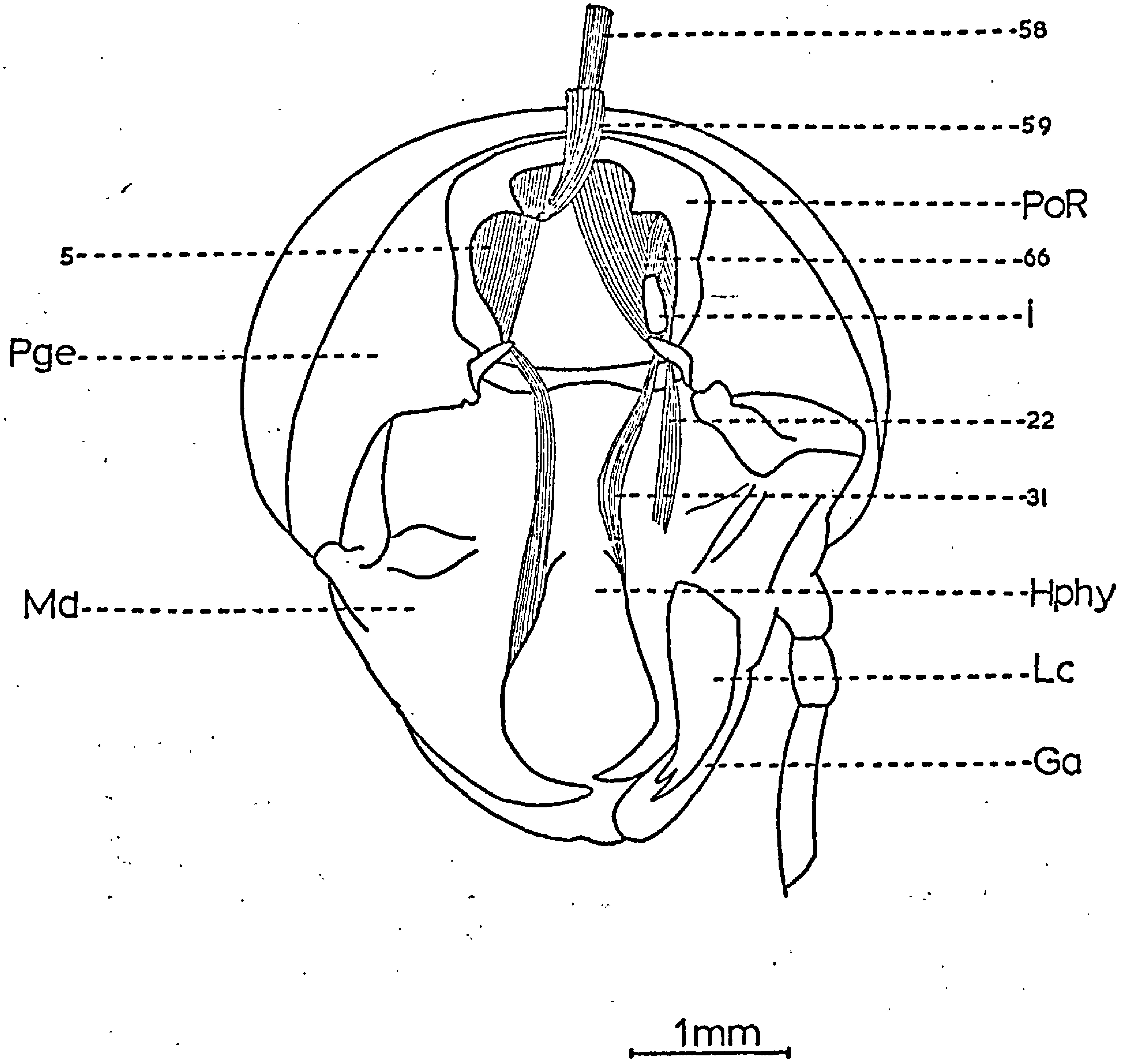


Fig.14

All these muscles, as their names suggest, assist in bringing about the enlargement or dilation of certain areas of the pharynx.

4.6 <u>Cervical Muscles</u> (Figs. 14, 15, 16, 17 and 18)

There are many muscles which control the movement of the head and these can be classified as depressors, elevators, retractors and rotators of the head. These will be discussed according to their position. The function of the muscles is to bring about specific movements of the head relative to the rest of the body. The nature of the movement they cause is indicated by the name of each muscle.

(i) <u>Ventral</u>

<u>Inner depressor of the head</u> (Muscle 54)

This is a fairly strong muscle which originates from the enlarged basal portion of the sternal apophysis. These muscles are inserted on the posterior edge of the central tentorial plate (Figs. 15 and 16b).

<u>Outer depressor of the head</u> (Muscle 55)

This is a strong muscle similar to the depressor of the head (Muscle 54) and originates immediately lateral to it on the sternal apophysis. It is inserted on the anterior face of the tentorial body (Fig. 15).

<u>Short depressor of the head</u> (Muscle 56)

This muscle (Muscle 56) is shorter (Fig. 17) than the outer (Muscle 55) or inner depressor muscle (Muscle 54). It also originates from the sternal apophysis dorsal to the origin of the outer depressor muscle of the head (Muscle 55) and is inserted below the ventral angle of the interpleurite 'a' (Fig.16b).

Fig. 15. Cervical musculature, ventral view.

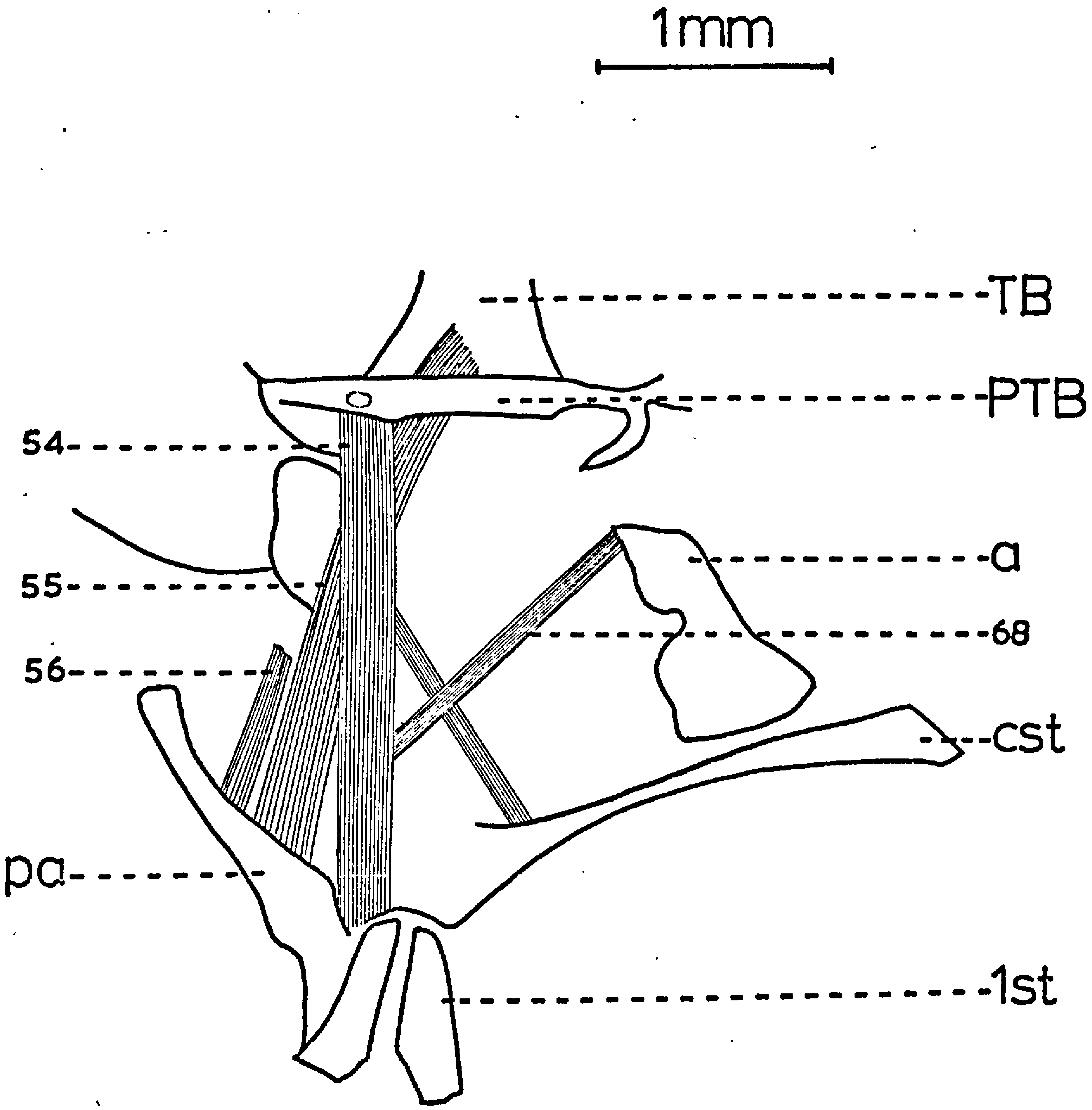


Fig.15

(ii) Dorsal

Elevator of the head (Muscle 57, 58)

This is the strongest intersegmental muscle and is double headed (Figs. 16a, b and 18). One head (Muscle 57) originates from the pronotum whilst the second head (Muscle 58) originates from the junction of the pro and mesothorax, presumably on a phragma. These muscles are inserted on the lateral apodeme of the occipital foramen by a common tendon (Figs. 14 and 18).

(iii) Lateral

Retractor of the head (Muscle 59)

This is a strong muscle which originates from the episternum and is inserted on the postoccipital ridge (Fig. 16a, b).

First rotator of the head (Muscle 60, 61)

This is a double headed, dorsoventral intersegmental muscle which originates from the lateral part of the prosternum near the dorsal side of the interpleurite 'a' (Fig. 16b). One head of the muscle (Muscle 60) passes above and near the anterior edge of the first intertergite 'c', here it meets the second head of the muscle (Muscle 61) which passes below it (Figs.16b and 17a, b). It is inserted on the proximolateral region of the postoccipital ridge near the median apodeme.

Second rotator of the head (Muscle 62)

This is also an intersegmental dorsoventral muscle

Fig. 16. Lateral view of the neck: a, dorsal musculature; b, principally lateral and ventral musculature.

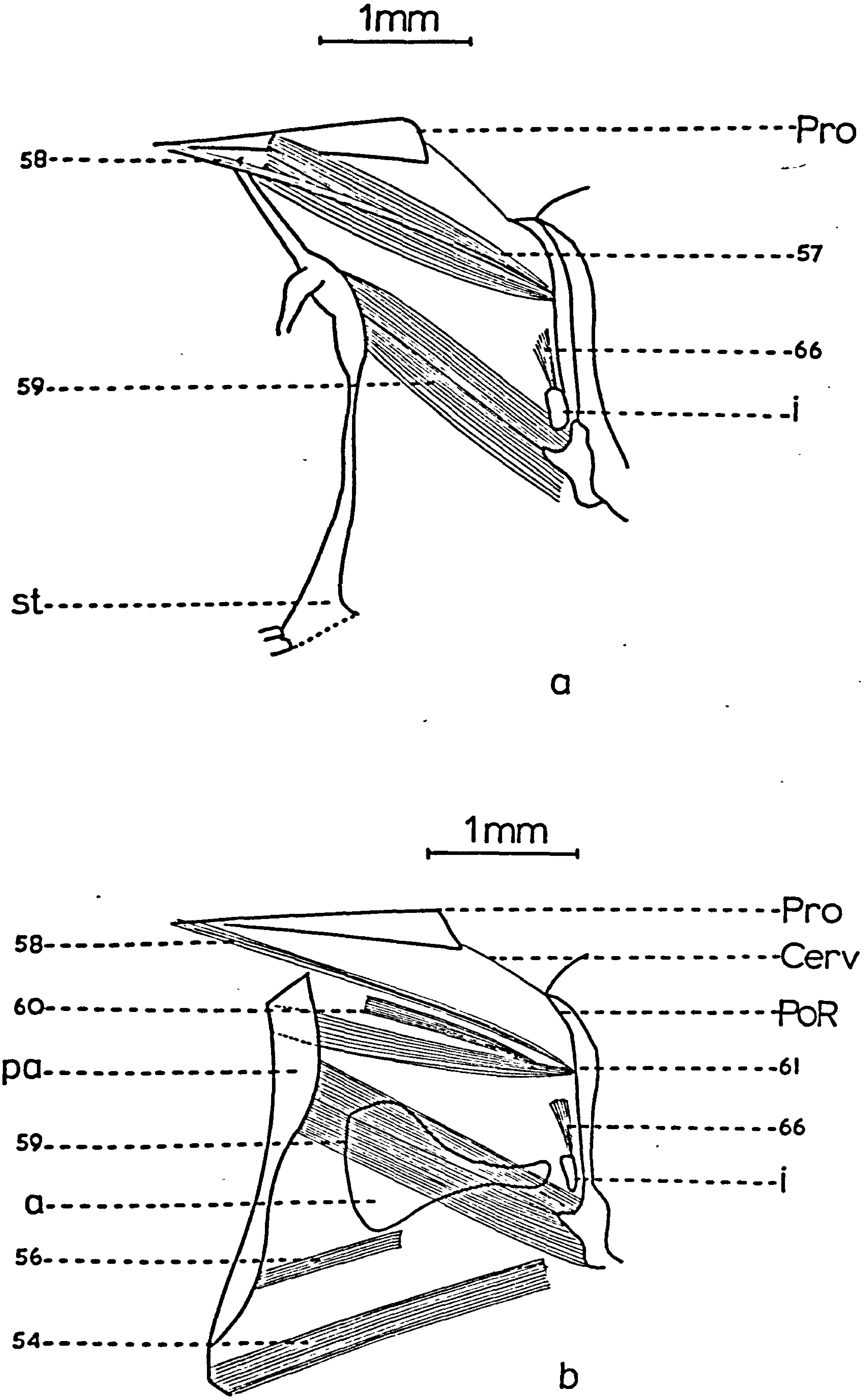
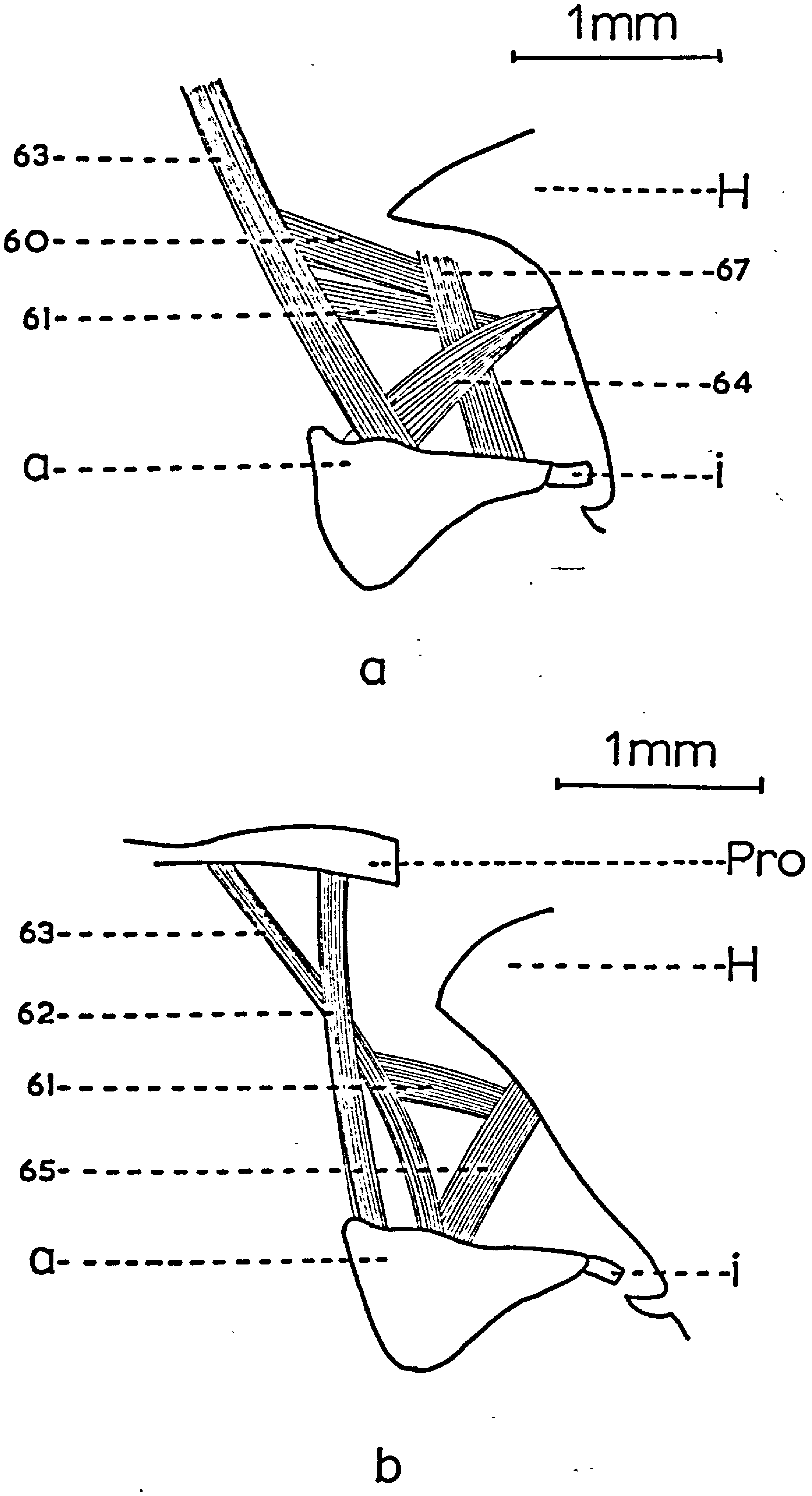

1mm
Pro
58
57
66
59
i
st
a
1mm
Pro
58
Cerv
60
PoR
pa
61
66
59
i
a
56
54
b

Fig.16

Fig. 17. Rotator muscles of the head: a, pronotum and certain muscles have been removed in a lateral position; b, lateral view with pronotum to show muscles.



a

b

Fig.17

(Figs.17b and 18). The muscle is inserted on to the postero-dorsal edge of the interpleurite 'a' and extends dorsally in the prothorax where it passes across the third rotator of the head (Muscle 63). It originates near the midline of the anterior region of the pronotum.

Third rotator of the head (Muscle 63)

This is another intersegmental dorsoventral muscle (Figs. 17a, b and 18). This muscle is fairly broad and arises near the centre of interpleurite 'a'. It passes dorso-posteriorly in front of the second rotator of the head (Muscle 62) and originates obliquely from the pronotum close to the front edge of the half moon shaped spot.

Fourth and Fifth rotators of the head (Muscle 64, 65)

These muscles (Muscle 64, 65) have separate origins on interpleurite 'a'. Muscle 64 is large and circular in section and originates on the broad, flat part of the interpleurite 'a' (Figs. 17a and 18) near to the origin of the second rotator of the head muscle (Muscle 62). It extends dorsoanteriorly and is inserted ventral to the lateral apodeme of the head.

The fifth rotator of the head (Muscle 65) which is a broad flat muscle arises in the middle of interpleurite 'a' (Figs. 17b and 18) beside the third rotator of the head (Muscle 63). It is inserted on the head at the same site as the previous muscle (Muscle 64).

Fig. 18. Lateral semidiagrammatic representation of the muscles of the neck, only interpleurite 'a' has been shown.

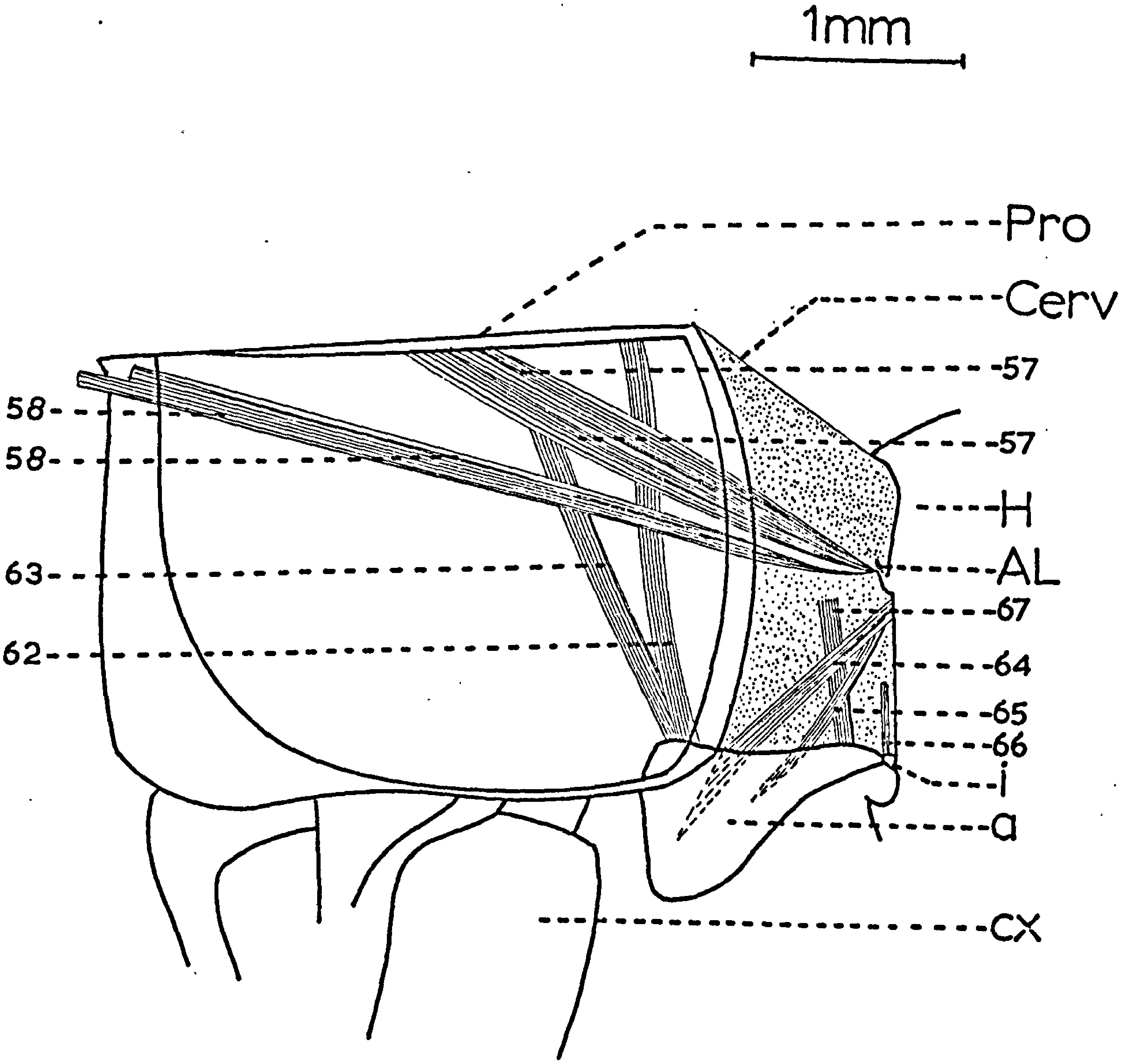


Fig. 18

Sixth rotator of the head (Muscle 66)

This is short rotator muscle which arises on the frontal part 'i' of interpleurite 'a'. It runs upwards to the sides of the occipital foramen where it is inserted below the lateral apodeme (Figs. 14, 16a, b and 18).

Seventh rotator of the head (Muscle 67)

This is a fairly strong, parallel fibred muscle (Figs. 17a and 18). This muscle also originates from interpleurite 'a' but to the anterior part of the sclerite. It travels dorsally as the most central of all the neck muscles. It is inserted on to the neck membrane behind intertergite 'c'. The muscle obviously plays an important role in the regulation of the neck folds during the movement of the head.

Cruciate rotator of the head (Muscle 68)

This muscle originates from the anterior edge of the procoxa (Fig. 15) and is inserted on to the narrow anterior part of the interpleurite 'a' of the opposite side.

Abbreviations used in figures of the musculature associated with the head capsule and its appendages (all diagrams of adult females)

AL = Lateral apodeme

AT = Anterior tentorial arm

a = Interpleurite of the neck

ad ap = Adductor apodeme of the mandible

abd ap = Abductor apodeme of the mandible

as = Antennal sulcus

Cerv = Veracervix or neck

Cd = Cardo

Clp = Clypeus

cst = Coxosternite

cb = Cibarium

cx = Coxa

DT = Dorsal tentorial arm

E = Compound eye

fl = Membranous lobes on the posterior surface of the hypopharynx

Ga = Galea

Gl = Glossa

H = Head

Hphy = Hypopharynx

Hs = Suspensorial sclerite of the hypopharynx

i = Front portion of the interpleurite 'a'

int = Intertorma

Lc = Lacinia

Lm = Labrum

lb = Longitudinal bar of the suspensorial sclerite

Md = Mandible

Mth = Mouth

Mt = Mentum

OSc = Ocular sclerite

os = Ocular sulcus

Pgl = Paraglossa

Pdc = Pedicel

Pge = Postgena

PoR = Post occipital ridge

Pro = Pronotum

PTB = Posterior tentorial bridge

TB = Tentorial body

pa = Sternal apophysis

Sc = Scape

Sld = Salivary duct

Slv = Salivarium

Smt = Submentum

St = Sternum

tor = Torma

t = Longitudinal sulcus on the stipes

VL = Sclerotized bar or strengthening ridge (Verstärkungsleiste)

vm = Ventral mid line

w = Basal bar of the hypopharynx

Key to the numbers applied to the muscles of the head capsule and its appendages

Number of Muscle		Function of Muscle
1	=	Abductor of the labrum
2	=	First adductor of the labrum
3	=	Second adductor of the labrum
4	=	Median compressor of the labrum
5	=	Adductor of the mandible
6	=	Abductor of the mandible
7	=	Tentorial adductor of the mandible
8	=	Hypopharyngeal adductor of the mandible
9	=	Protractor of the maxilla
10, 10a	=	Adductors of the cardo
11	=	Adductor of the stipes
12	=	Cranial flexor of the lacinia
13	=	Flexor of the lacinia
14	=	Flexor of the galea
15	=	Levator of the maxillary palp
16	=	Depressor of the maxillary palp
17	=	Levator of the first maxillary palp segment
18	=	Depressor of the first palp segment
19	=	Levator of the second palp segment
20	=	Levator of the third palp segment
21	=	Flexor of the fourth palp segment
22	=	Adductor of the labium

Number of Muscle		Function of Muscle
23	=	Abductor of the labium
24	=	Median retractor of the labium
25	=	Adductor of the glossa
26	=	Adductor of the paraglossa
27	=	Levator of the labial palp
28	=	Depressor of the labial palp
29	=	Extensor of the first palp segment
30	=	Depressor of the second palp segment
31	=	Retractor of the hypopharynx
32	=	Depressor of the hypopharynx
32a	=	Constrictor of the hypopharynx
33	=	Elevator of the hypopharynx
34	=	First compressor of the salivarium
35	=	Second compressor of the salivarium
36	=	Third compressor of the salivarium
37	=	Levator of the antenna
38	=	Flexor of the antenna
39	=	Depressor of the antenna
40	=	Extensor of the scape
41	=	Flexor of the scape
42	=	Dilator of the cibarium
43	=	First anterior dilator of the buccal cavity
44	=	Second anterior dilator of the buccal cavity
45	=	First dilator of the anterior pharynx

Number of Muscle		Function of Muscle
46	=	Second dilator of the anterior pharynx
47	=	First dilator of the posterior pharynx
48	=	Lateral dilator of the pharynx
49	=	First dilator of the anterior pharynx
50	=	Second dilator of the anterior pharynx
51	=	First dilator of the posterior pharynx
52	=	Third dilator of the anterior pharynx
53	=	Fourth dilator of the anterior pharynx
54	=	Inner depressor of the head
55	=	Outer depressor of the head
56	=	Short depressor of the head
57	=	Elevator of the head
58	=	Elevator of the head
59	=	Retractor of the head
60	=	First rotator of the head
61	=	First rotator of the head
62	=	Second rotator of the head
63	=	Third rotator of the head
64	=	Fourth rotator of the head
65	=	Fifth rotator of the head
66	=	Sixth rotator of the head
67	=	Seventh rotator of the head
68	=	Cruciate rotator of the head

PART 5

DISTRIBUTION OF CUTICULAR SENSILLA AND THEIR DISTRIBUTION ON THE MOUTHPARTS AND ASSOCIATED STRUCTURES

5.1 Introduction

Over the past two decades the functional morphology of the head appendages in relation to their feeding mechanism has been studied in a wide range of arthropod groups. In the Crustacea, for example, Fryer (1964) has studied *Monodella argentarii* Stella whilst in the insects representatives of a number of orders have been considered. Brown (1961) investigated *Chloëon dipterum* L. (Ephemeroptera). Within the Orthoptera most work has been focused on the Acrididae. Marshall (1947) briefly described some of the sensilla on the labrum of *M. femur-rubrum* and Liu and Leo (1960) and Thomas (1966) the sense organs in *Locusta migratoria manilensis* Meyen and *S. gregaria* respectively. Chapman(1966 has thoroughly investigated the sensilla on the mouthparts of *X. zarudnyi*. Blaney and Chapman (1969a) report the presence of hair sensilla and campaniform sensilla on the maxillary palp of *S. gregaria* and Blaney, Chapman and Cook (1971) describe in more detail the structure of the terminal segment of the maxillary palp of *L. migratoria*. Morphological descriptions of the antennal sensilla have been provided by Slifer, Prestage and Beams (1957) who studied the basiconic sensory pegs on the antenna of grasshoppers, *Romalea microptera* (Beauvois), *Melanoplus differentialis* (Thomas) and *Melanoplus mexicanus* (Saussure). More general accounts of insect sensilla include the work of Schneider and Steinbrecht, 1968; Slifer, 1970; Kaissling, 1971; Boo and McIver, 1976 whilst the function of certain mouthpart receptors in relation to feeding has been considered by Haskell and Schoonhoven (1969) in *S. gregaria* and *L. migratoria migratorioides* where electrophysiological techniques have been used to analyse the responses of chemoreceptor and mechanoreceptors on the clypeolabrum.

However, relatively little attention has been paid to the Gryllidae in this context. It is for this reason that a careful consideration of the types of sensilla and their detailed distribution on the feeding appendages has been undertaken. This study has been greatly helped by the use of Stereoscan Electron Microscope. However, it should be made clear that it is not always possible to clearly identify the function of a sensillum in this way. Histological studies of sensilla types and electrophysiological work would be needed for this. These techniques have not been undertaken since it was considered to be outside the scope of the project. However, with the distribution of sensilla types clearly described from the present work, the pathway should now be clear for further work. It is often possible to suggest a function of a sensillum, either from previous work, from ultrastructure or from observations of feeding behaviour and this has been done wherever appropriate.

The distribution of types of sensilla in the adult is complex and the development of this has received very little attention. In a hemimetabolous insect the distribution of types may be followed throughout the nymphal instars. This was carried out in the present study. The large number of instars involved made the task very time consuming and it was for this reason that the development of the adult pattern was only considered for the clypeolabrum. It is suggested that this may be representative of the other feeding appendages.

5.2 Material and methods

Insects were killed in chloroform and the head severed from the rest of the body in the cervical region. Either the entire head capsule was heated in 10% Caustic Potash or sometimes it was found preferable to remove the individual appendages before treating in this way. After dehydration the components were mounted directly in Euparal. The position of the sensilla were plotted with the aid of camera lucida fitted to a Wild M5 stereoscopic microscope. Both sexes of the adult were considered, and the adult female was drawn. Only when there were striking sexual differences was the male drawn as well.

The Scanning Electron Microscope (Cambridge Stereoscan Mk 11A) revealed both details of the cuticular sculpturing and of external sensilla structure. Only the adult female was examined in this way.

In preparation for viewing with the Scanning Electron Microscope, the mouthparts from freshly killed specimens were first washed in distilled water that contained a trace of detergent. They were then rinsed several times in distilled water. After that they were passed through the alcoholic grades and finally to acetone or amyl acetate. Then they were transferred to a critical point drying apparatus and liquid carbondioxide gas (CO_2) was passed over them for two hours in order to remove the acetone or amyl acetate by converting the liquid gas into gaseous form. After this procedure the specimen was placed in anhydrous, silica gel with cobalt chloride and mounted on a Cambridge 11 Standard stub using colloidal silver and then coated with gold (Nei and Fujikawa, 1977) with a polaron E 5000 diode sputter coater for two minutes. The stub was tilted at 45^{o} for viewing with the S E M. The photographs were taken on 35mm Ilford film.

The terminology used is the same as that in Part 3 (Page 23). The sensilla on the posterior surface of the labium, anterolateral surface of the hypopharynx, both surfaces of the clypeolabrum, mandible, cardo, stipes, galea, lacinia, maxillary palp, labial palp and antenna have been plotted. Preliminary examination showed the two maxillae to be identical so only the right has been considered. Besides differences in the incisor and molar cusps in the two mandibles, the remainder is the same, so only the anterior view of the right and the posterior view of the left mandibles have been described. Both sexes were considered and ten replicates of each were counted. Some of the results have been tabulated for clarity. Sensilla distribution maps have been produced for the clypeolabrum, galea and lacinia. The presence or absence of each type of sensilla on the various components of the mouthparts of the adult is cited in Table 4. The number of each type in adult females and males is given in Tables 5 and 6 respectively.

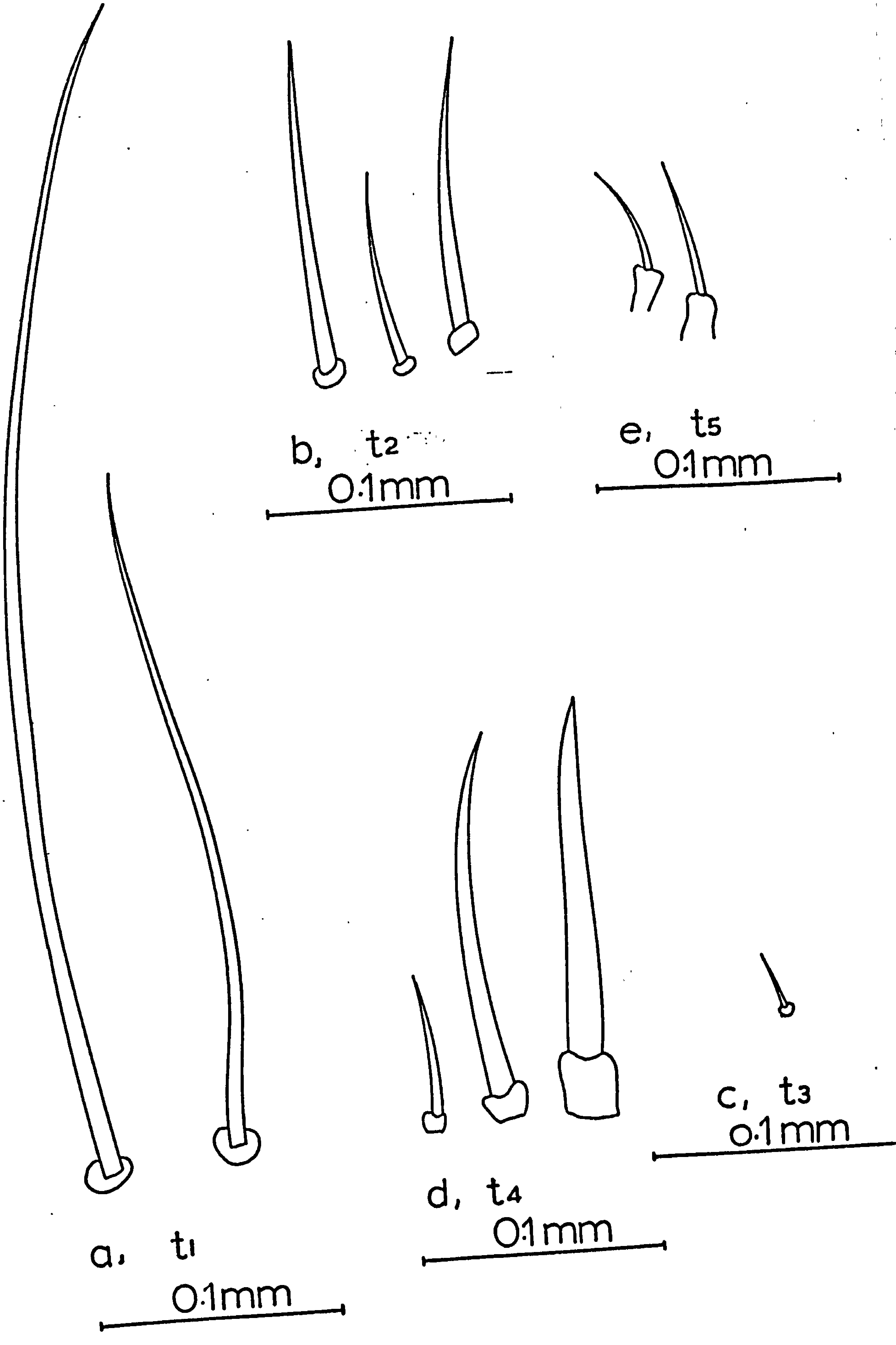
5.3 Types of Sensilla

The subdivision of the sensilla into types is based on their external form as shown by the light microscope and the S E M. The sensilla present on the mouthparts may be classified into thirteen types. Among these Types 1 to 5 have long setae whilst the others have not. Other structures with non-articulated setae have been assumed to be hairs or microtrichia. Besides the hairs cuticular projections have been found. Diagrams showing the general form have been drawn using the light microscope (Figs. 1 - 3) and these supplemented with scanning electron micrographs of certain types (Plates 1, 2, 6 and 9).

Type 1 (t_1 : Fig. 1a)

Sensilla with setae which are more than 145u long and fairly thin relative to their length (Type 1 of Thomas, 1966). Sensilla of this type are generally scattered rather than forming a compact group. The setae vary considerably in length and some are very long. The standard error shows that they mostly lie between 205.69 - 222.59u (Table 1). This type is mostly found on the exposed surfaces of the moutnparts; such as the anterior surface of the labrum, the

Fig. 1. Types of sensilla (Type 1 - 5)
- lateral view.


b, t2
0·1mm
e, t5
0·1mm
a, t1
0·1mm
d, t4
0·1mm
c, t3
0·1mm

maxillary and labial palp, posterior surface of the labium including the submentum, prementum and paraglossa and on the galea of the maxilla. They are present in approximately equal number in both sexes (Table 4). It seems very likely that they are mechanoreceptors. Haskell (1956a, b) showed that some long setae on the abdomen of British grasshoppers respond to vibrations of the subtrate and others probably to air borne vibrations.

<u>Type 2</u> (t_2 : Fig. 1b)

Sensilla with setae which are more than 50u long but less than 145u (Table 1). The standard error shows that they mostly lie between 88.16 - 96.36u. This type is thicker than Type 3. These sensilla are also generally scattered over the mouthparts. The only concentration occurring in the hair plates, where they are smaller and thicker and have larger sockets. These hair plates are found at the joints of the maxillary and labial palp and at the junction of the submentum and prementum. Type 2 sensilla are found associated with Type 3 on almost all exposed surfaces of the mouthparts (Table 4). The sensilla forming a hair plate have been shown to have a proprioceptive function (Pringle, 1938b, Haskell, 1959).

<u>Type 3</u> (t_3 : Fig. 1c)

Sensilla with setae less than 50u (Type 3 of Thomas, 1966 and Type 1 of Blaney and Chapman, 1969a). Type 3 include sensilla with very short, slender setae which may either be level with the surface of the cuticle or extends just above or remain below it. The socket is usually round. The standard error shows that they mostly lie between 22.35 - 27.83u. Sensilla of Type 3 (like Type 2) are scattered over most of the surface of the mouthparts (Table 4). In S. gregaria Thomas (1966) describes Type 2 and 3 sensilla as sensory pegs. Slifer (1954, 1956) and Slifer et al (1957) found these types on almost all parts of the body that came into conduct with the external environment. Slifer (1955) established that the tips of the setae were permeable and concluded that they were probably chemoreceptors.

Type 4 (t_4 : Fig. 1d)

Sensilla with a thick rigid wall. These are extremely variable in size (Table 1). Some of the setae have sockets with protective projections. A group of Type 4 sensilla is present on the posterior side of the labrum (Fig. 4) in both sexes (Table 4). Longer and more rigid ones are situated on the mesal part of the lacinia (Fig.17). The smaller ones are present on the maxillary and labial palps (Table 4). Dethier (1963) considers this type to be mechanoreceptors as they are innervated by a single neuron. The latter being proved by Thomas (1966) in Schistocerca and Fudalewicz-Niemczyk and Rosciszewska (1974) in G. domesticus nymphs.

Fig. 2. Types of sensilla (Type 6 - 11)
- surface view.

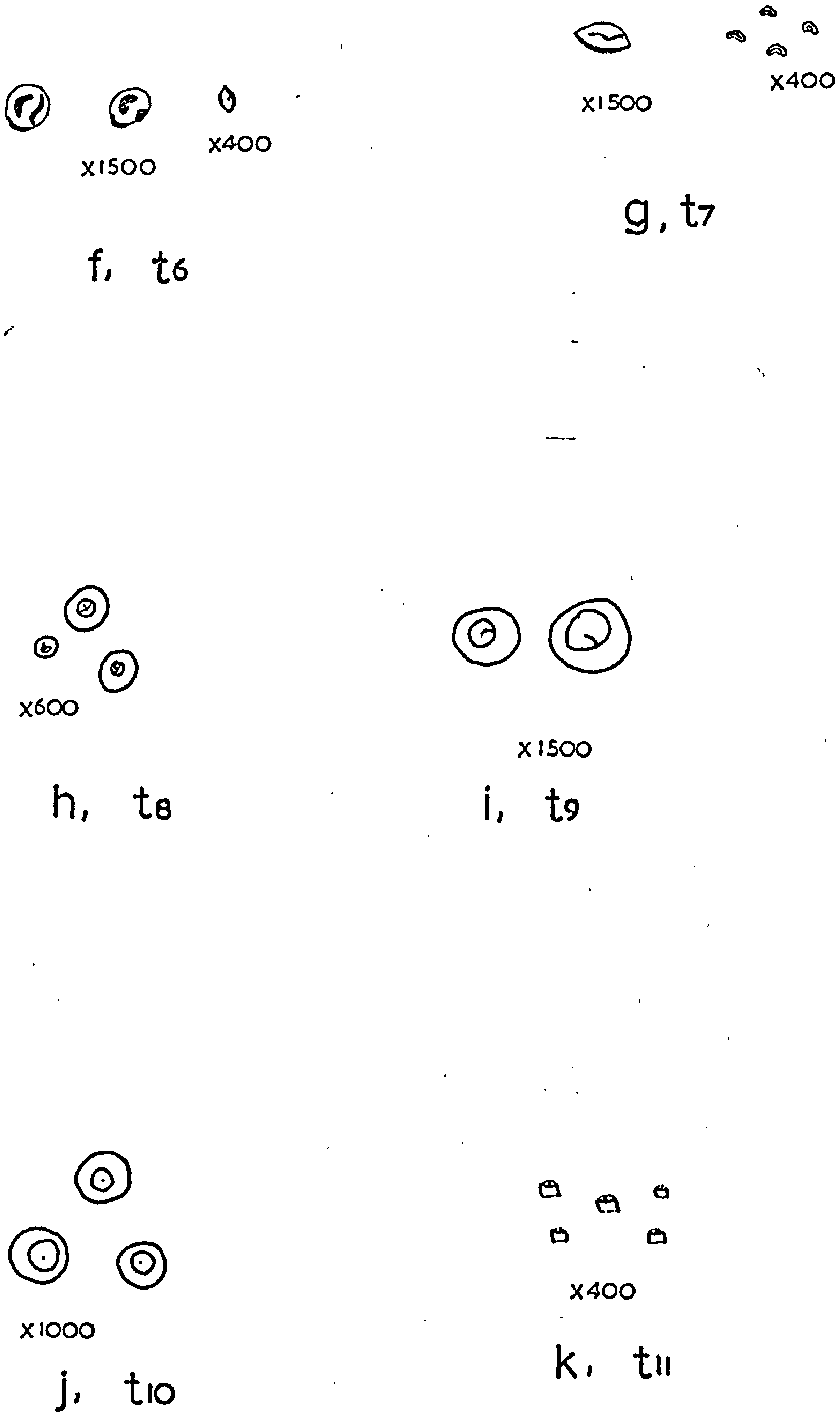

x1500
x400
f, t6
x1500
x400
g, t7
x600
h, t8
x1500
i, t9
x1000
j, t10
x400
k, t11

Fig. 2

Type 5 (t_5 : Fig. 1e)

Sensilla which have slender setae, less than 50u in length (Table 1). The setae are fairly consistent in length and are sunken into socket so that they only project 2 - 3u above the level of the cuticle. Type 5 sensilla are present on the distal portion of the paraglossa, galea and the terminal segment of the maxillary and the labial palps (Table 4 and 5). Their position on the distal part of feeding appendages suggest a role in the initial testing of food material. They are very likely to be contact chemoreceptor.

Type 6 (t_6 : Fig. 2f)

Campaniform sensilla which are mostly spindle shaped. They vary in length (mean 6.9u, range 4 - 14u) and breadth (mean 3.8u, range 2.1 - 7.5u). This type occurs on the clypeolabrum, mandible, stipes, lacinia, galea, maxillary palp, labial palp, hypopharynx and antenna of both sexes (Table 4). Similar mechanoreceptors on the mouthparts and other parts of the body have been found by a number of authors, such as Snodgrass (1935), Pringle (1938b), Dethier (1963), Thomas (1966) in Schistocerca and Chapman (1966) in X. zarudnyi.

Type 7 (t_7 : Fig. 2g)

Type 7 sensilla are referred to as secretory pores (Arnold, 1974) and the plate organ (Slifer, 1970), Lewis and Marshall (1970) have recently used the term sensory plaque for the more complex, though essentially similar, structure found on the antenna of the lantern fly Pyrops candelaria L. Each plate organ, when seen with the light microscope, consists of a shallow oval depression with a small notch on its proximal border. They are always less than 8u in length. They occur commonly on the anterior surface of the labrum, on the cardo, stipes and lacinia (Table 4) in both sexes. They may be regarded as a type of thin walled chemoreceptor (Slifer, 1970); Slifer and Sekhon, 1971).

Type 8 (t_8 : Fig. 2h)

Type 8 sensilla have sunken sockets with stout and peg-shaped setae, and are considered as coeloconic pegs. The thickness of the setae is relatively constant throughout the length of the peg (Plate 1b). They are found mainly on the posterior surface of the clypeolabrum (Table 4) in the A_3 group (Table 2). They vary in socket diameter (range 4.2 - 7.5u) and are larger in size than other coeloconic sensilla found on the posterior surface of the clypeolabrum. The number of Type 8 sensilla varies slightly between the sexes (Table 3). Morphological descriptions of this type of sensilla have been reported for Apis mellifera (Linnaeus) (Slifer and Sekhon, 1961), by the milkweed bug Lygaeus Kalmii Stal (Slifer and Sekhon, 1963) and the beetle Popilius disjunctus (Slifer and Sekhon, 1964).

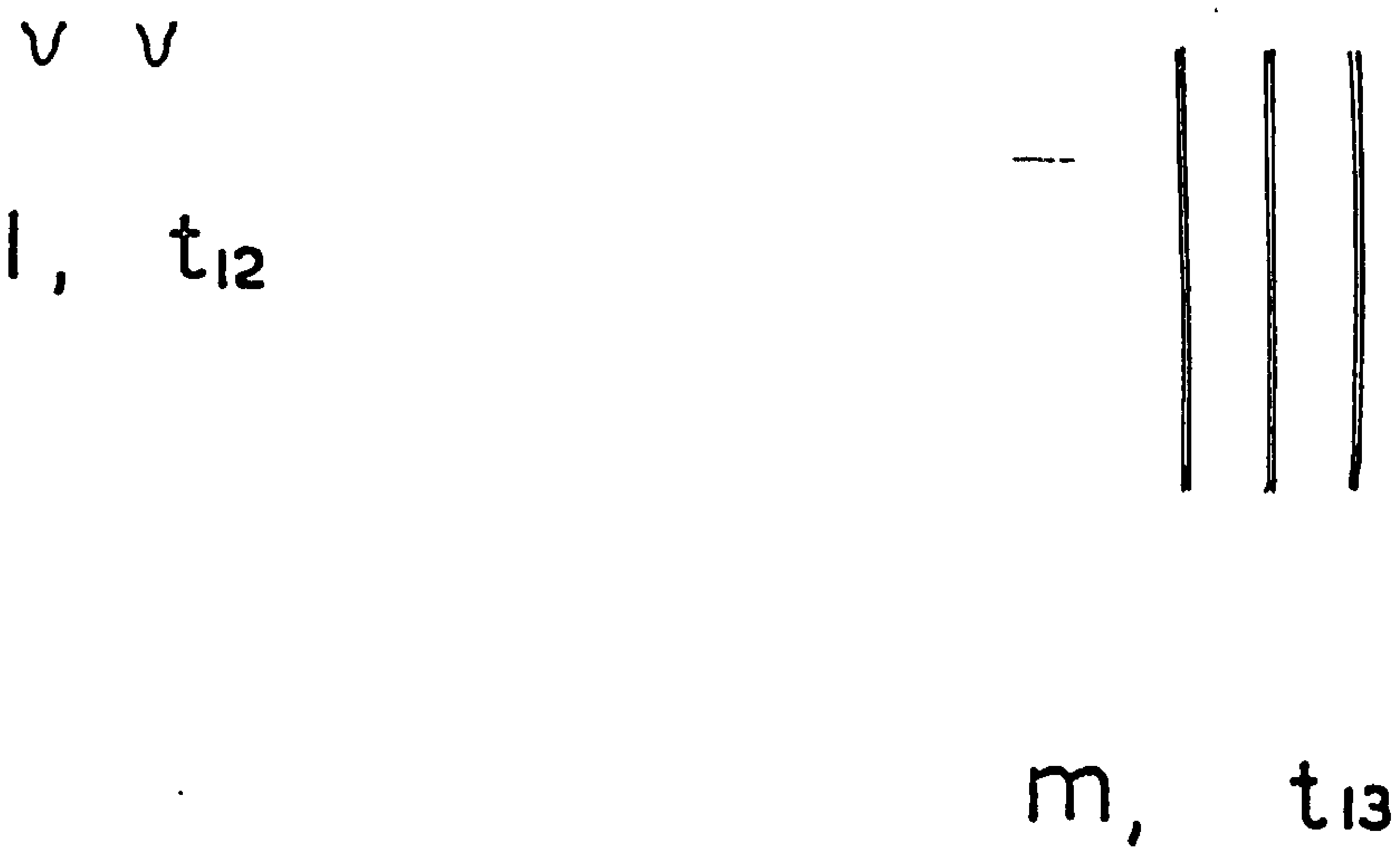
Type 9 (t_9 : Fig. 2i)

Type 9 sensilla are coeloconic pegs displaying a slight variation in the form of the setae. The first form has wavy setae which arise from a sunken socket (Fig. 2i). The second form has stout setae which are broader at their distal end (Plate 1a). Both these forms are found in Group A_2 sensilla near the intertorma on the posterior surface of the clypeolabrum (Fig. 4). The function of Type 9 sensilla is also contact chemoreception.

Type 10 (t_{10} : Fig. 2j)

Type 10 sensilla are round, coeloconic pegs with a depression in the centre which can be seen under the light microscope. The diameter of the socket varies from 3u - 6.2u. The distribution of this type is rather restricted. They are mainly present on the posterior side of the clypeolabrum. They occur in the A_1 group (Plate 2b), the A_9 group just above the tormae (Fig. 4) and in the A_5 group (Plate 5a, b). The only other side where this type is to be found is on the distal posterior side of the galea (Plate 7a), although here their form and size is slightly different. Here they are round and flattened with a depression in the centre. A close study reveals that there is a pore in the centre of the peg. It may be suggested that this type functions as contact chemoreceptors.

Fig. 3. Types of sensilla (Type 12 - 13) - lateral view.



l, t_{12}

m, t_{13}

Fig. 3

Type 11 (t_{11} : Fig. 2k)

Type 11 sensilla have a raised socket with a small projected seta which is cone shaped. They occur on the posterior side of the galea and on the paraglossa (Table 4) in both the sexes. Fudalewicz-Niemczyk and Rosciszewska (1974) call them short basiconic pegs which are considered to be as contact chemoreceptor.

Type 12 (t_{12} : Fig. 3l)

Type 12 sensilla are very different and consist of pore-canals which are long and run in the cusp of the mandible and lacinia. In the mandible they are numerous whilst in the lacinia there are only two in each cusp. They are similar in both the sexes (Table 4). Fudalewicz-Niemczyk and Rosciszewska (1974) report the presence of pore canals in the mandible and lacinial cusps of G. domesticus larvae. Le Berre and Louveaux (1969) also observed these organs in the mandible of the first instar L. migratoria. Their role is undoubtedly that of contact chemoreception.

Type 13 (t_{13} : Fig. 3m)

Type 13 sensilla are flask shaped and often called sensilla ampullacea due to their shape. The length of the cavity varies from 22 - 25u whilst the diameter is about 7.6 - 7.8u. These organs are only found on the distal part of the labrum on its anterior side (Fig. 5) and are present in both sexes. Fudalewicz-Niemczyk and Rosciszewska (1974) reported these on the labrum of G. domesticus larvae.

Fig. 4. Distribution of sensilla on the posterior surface of the clypeolabrum.

Fig. 4

Similar sense organs on the labrum of the larvae of Trichoptera have been reported by Barbier (1961) and on the labrum of adult Dytiscidae by Hamon (1961).

5.4 Distribution of Sensilla on the head capsule

5.4.a. Clypeolabrum (Figs. 4, 5, 6 and 7).

Both surfaces of the clypeolabrum are well supplied with sensilla. The sensilla on the anterior face are scattered more or less randomly whilst on the posterior face they are arranged in discrete groups of different types.

The anterior surface of the clypeolabrum (Fig. 5) is well supplied with sensilla of Types 3 and 7, with a few Types 1 and 2 (Fig. 5). Type 3 sensilla are the most common on the anterior surface and these are widely distributed (Tables 5, 6; Fig. 7a). Type 7 are more widely spaced and mainly occur on the lateral areas of the labrum (Tables 5,6; Fig. 7b). In this respect Type 7 closely resemble Type 2 although only relatively few of these are present, (Tables 5, 6; Fig. 6b). The Type 1 sensilla tend to be arranged in pairs; three pairs are situated in the central part of the labrum whilst the other three pairs occur on the weakly sclerotized distal zone (Tables 5,6; Fig. 5). Unpaired sensilla of this type may occasionally be present as in Fig. 6a. The distal end is notched and is furnished with a double fringe of hairs (Fig. 4) with blunt tips (Plate 6b). The function of this fringe of hairs is unknown but it is

Fig. 5. Distribution of sensilla on the anterior surface of the clypeolabrum.

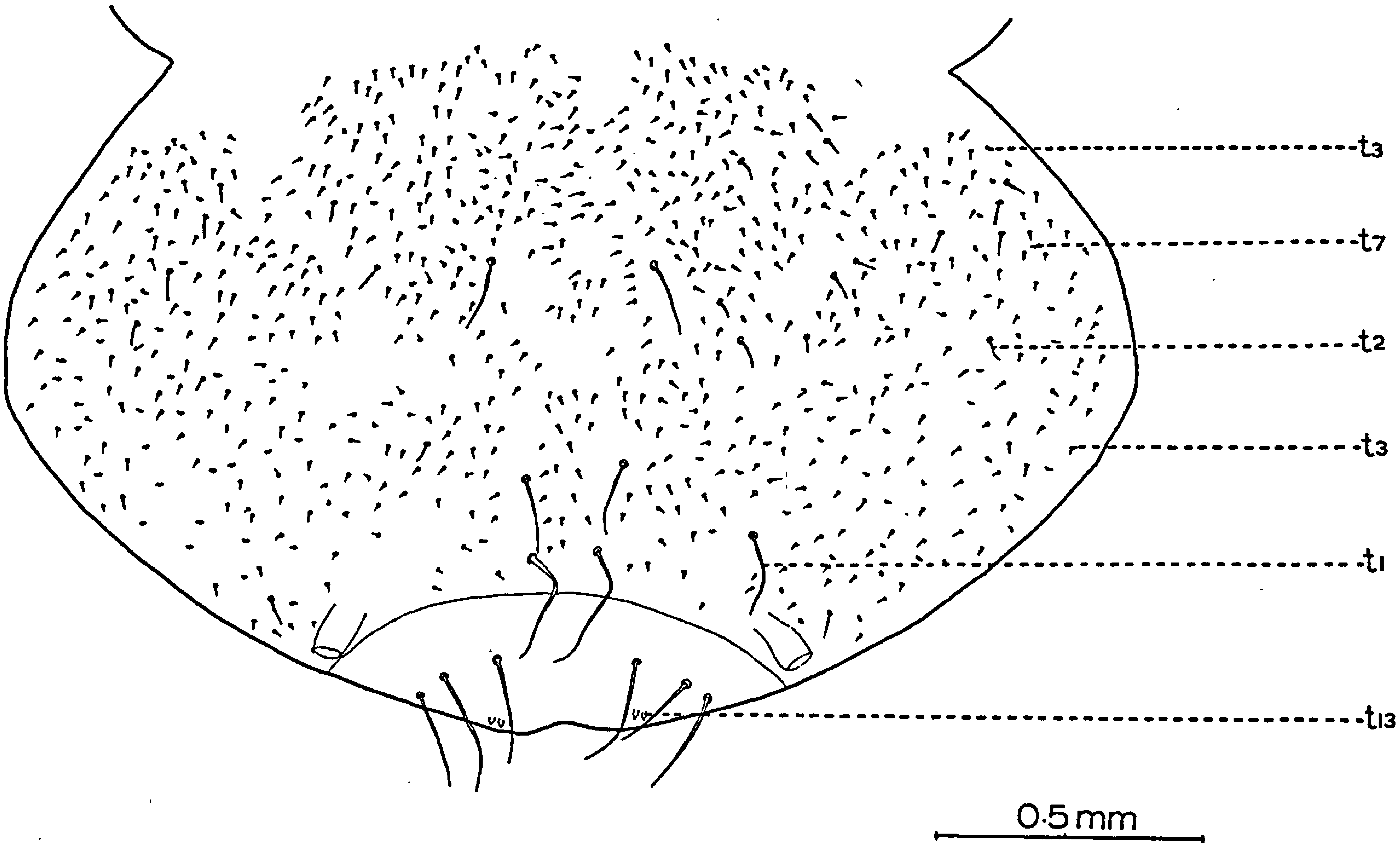


Fig. 5

suggested that it may serve to prevent food particles from falling from the pre-oral cavity. Alternatively these hairs may serve to push the food particles towards the pre-oral cavity. Two pairs of Type 13 sensilla are situated on either side of the notch. Fudalewicz-Niemczyk and Rosciszewska (1974) report the presence of this type of sensilla in the larvae of G. domesticus.

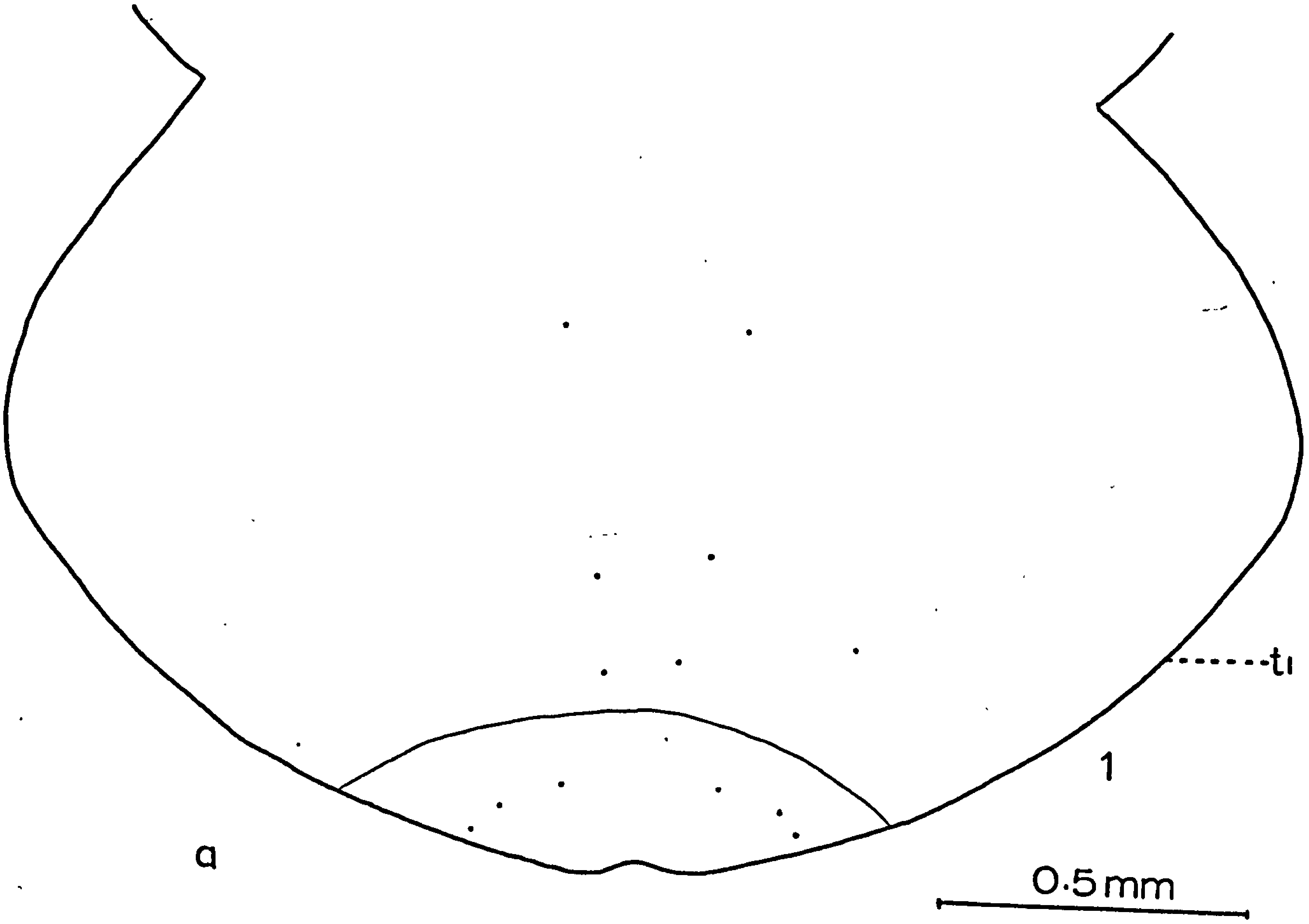
The posterior surface of the clypeolabrum may, for convenience, be subdivided into different regions or fields, these will be discussed in turn. With the exception of minor differences in the number of sensilla, the distribution is similar in the adults of the two sexes.

Field I

This represents the area at the distal end of the clypeus. This field bears two groups, A_1 and A_2, in the median portion (Fig. 4). Another group, A_9, lies above the tormae (Fig. 4). The group A_1 is subdivided into two smaller groups, each with approximately 47 sensilla (Tables 2 and 3). In group A_1 and A_2 the cuticular part of the sensilla consists of a socket with a depression in it, which is slightly smaller in diameter in A_1. These appear to be Type 10 sensilla (Plate 2b) and are probably comparable to the A_1 group of Thomas (1966).

Group A_2 is single, median in position, and lies between the two groups of A_1 (Fig. 4). From the depressed cuticular sockets arise a projection of variable form.

Fig. 6. Distribution of: a, Type 1 sensilla; b, Type 2 sensilla on the anterior surface of the clypeolabrum (each dot represents one sensilla).


t1
1
a
0.5 mm

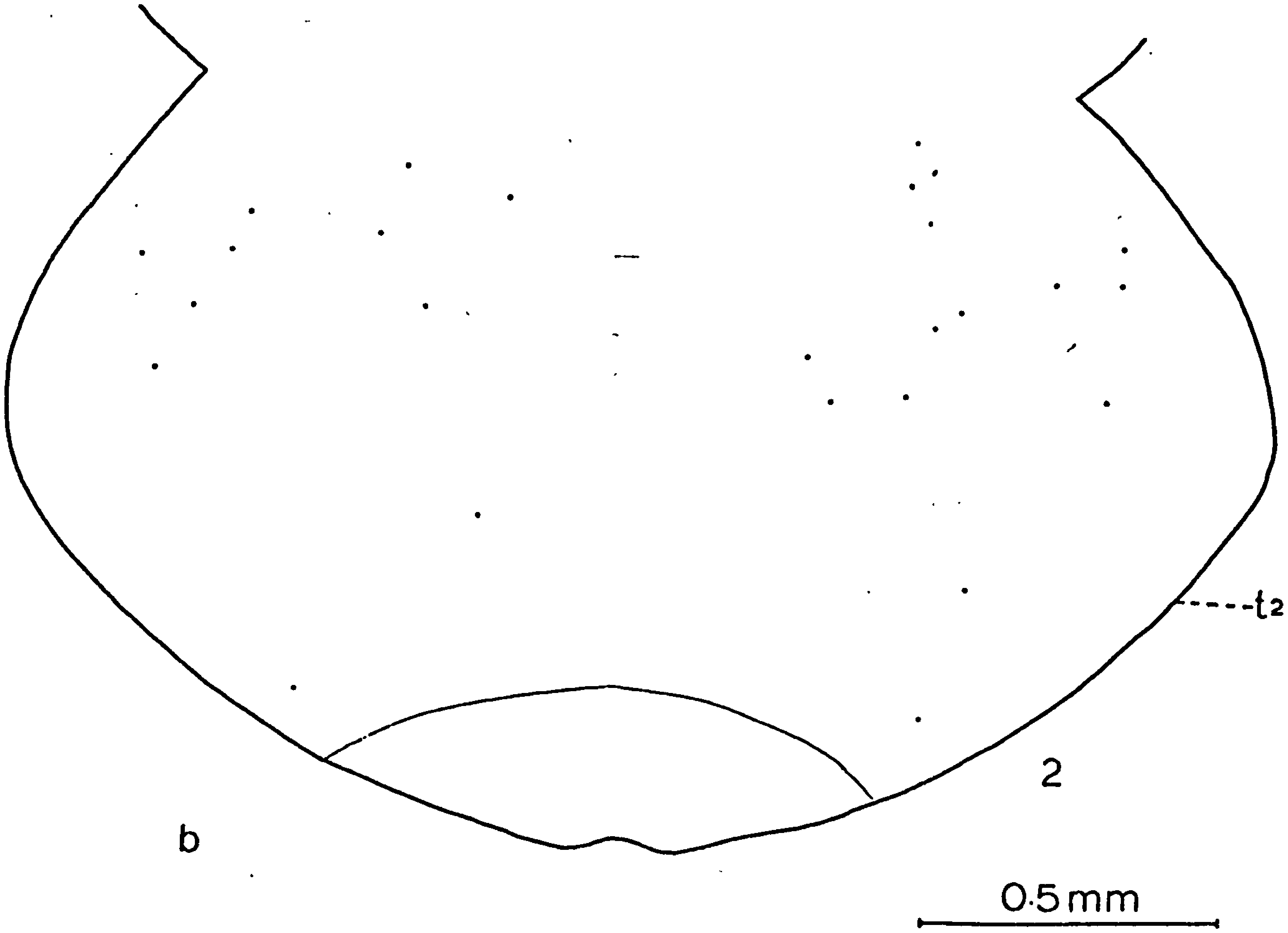
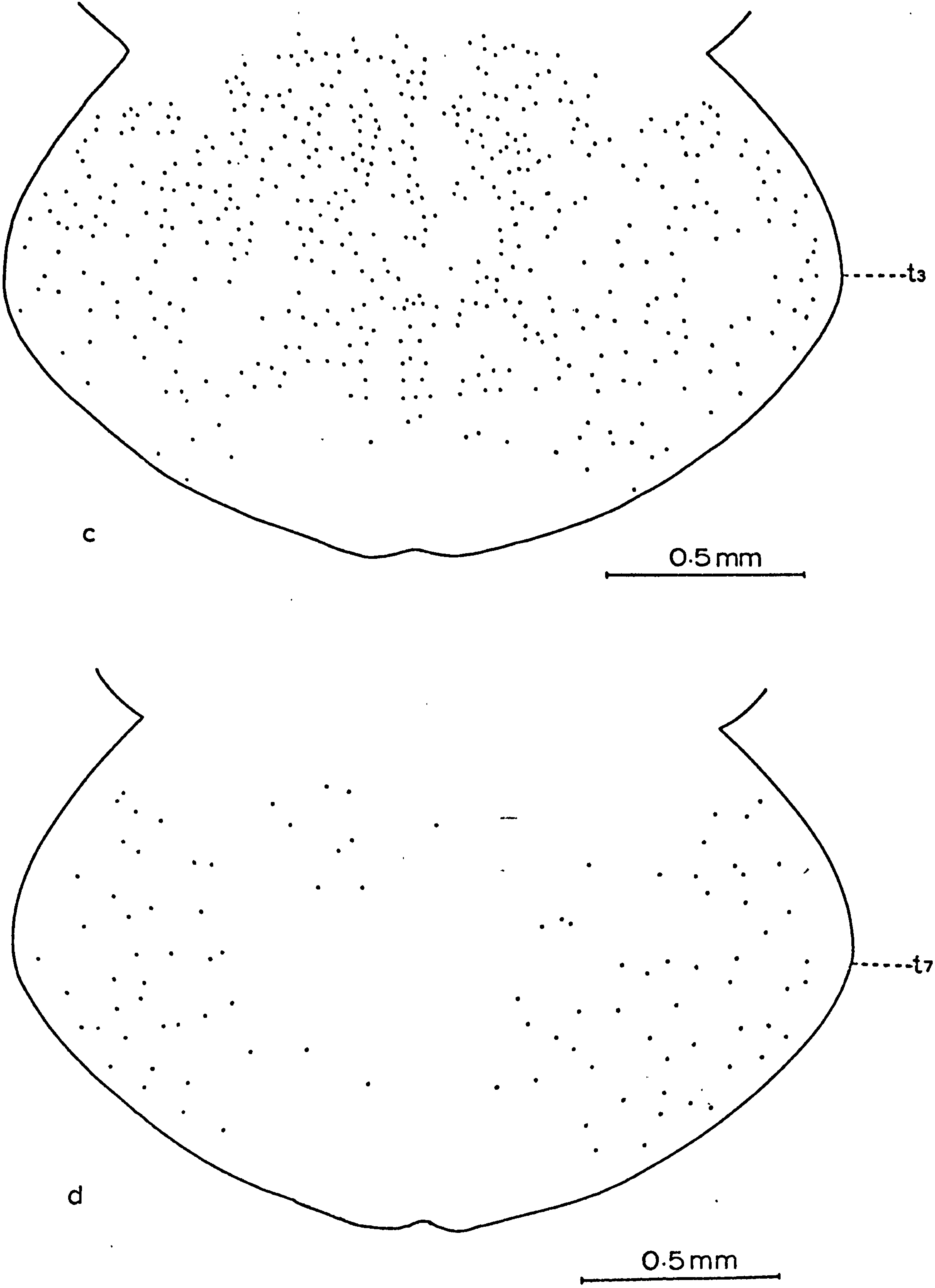

t2
2
b
0.5 mm

Fig. 7. Distribution of: a, Type 3 sensilla; b, Type 7 sensilla on the anterior surface of the clypeolabrum (each dot represents one sensilla).



Fig·7

Sometimes it is blunt (Plate 1a) or it may be weakly sclerotized and slender (Fig. 2i). Group A_1 and A_2 are present even in the first instar, although the number of sensilla in each group is less (Table 8, Fig. 31a). At the side of this field are brushes of fine hairs. The hairs are cuticular processes without sockets and probably have a purely mechanical function. As these hairs are directed towards the median part of the clypeus, where groups A_1 and A_2 are present, they may help to direct the food to this area, prior to swallowing and continuation of feeding. Some hairs in this field are bifurcate at the tip and others trifid (Plate 6a). Chapman (1966) has found similar hairs on the posterior surface of the clypeolabrum in <u>Xenocheila</u> although Thomas (1966) does not record their presence in <u>Schistocerca</u>. Sensilla of group A_9 are present above the tormae (Fig. 4), the number in each group differs slightly in the sexes (Tables 2 and 3). These appear to be Type 10 sensilla (Fig. 4).

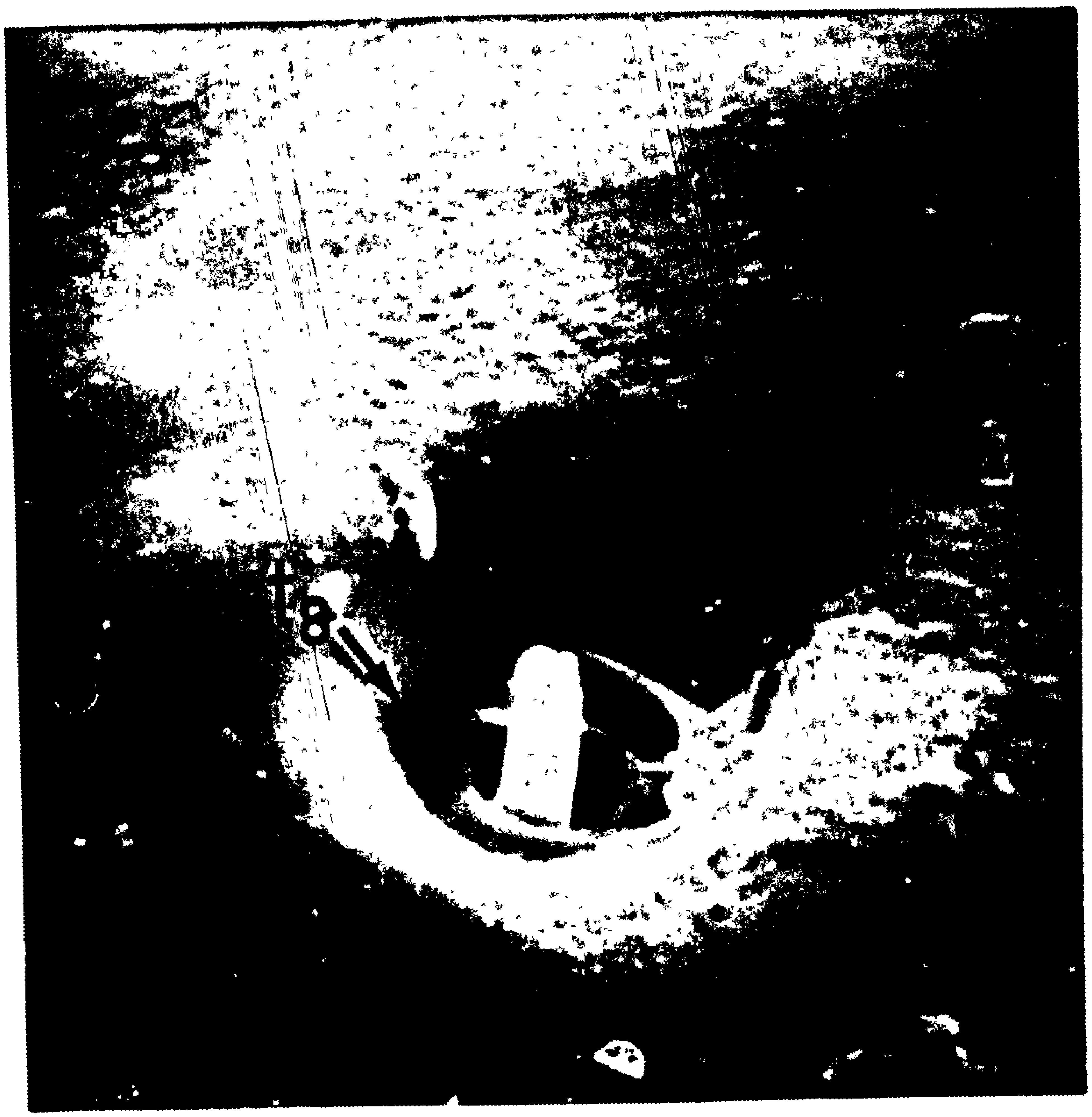
<u>Field II</u>

This field on the labrum starts below the intertorma and is enclosed by the sclerotized bars (Fig. 4). There are two groups of sensilla (A_3 and A_4) in addition to hairs and microtrichia (Plate 3a). Group A_3 consists of Type 8 sensilla (Plate 1b), they are arranged in two rows each of 6 - 7 sensilla on either side of the midline (Tables 2 and 3).

Plate 1a. Scanning electron micrograph of the group A_2 sensilla (Type 9) present on the posterior surface of the clypeolabrum (X 7257).

Plate 1b. Scanning electron micrograph of the group A_3 sensilla (Type 8) present on the posterior surface of the clypeolabrum (X 18142.5).

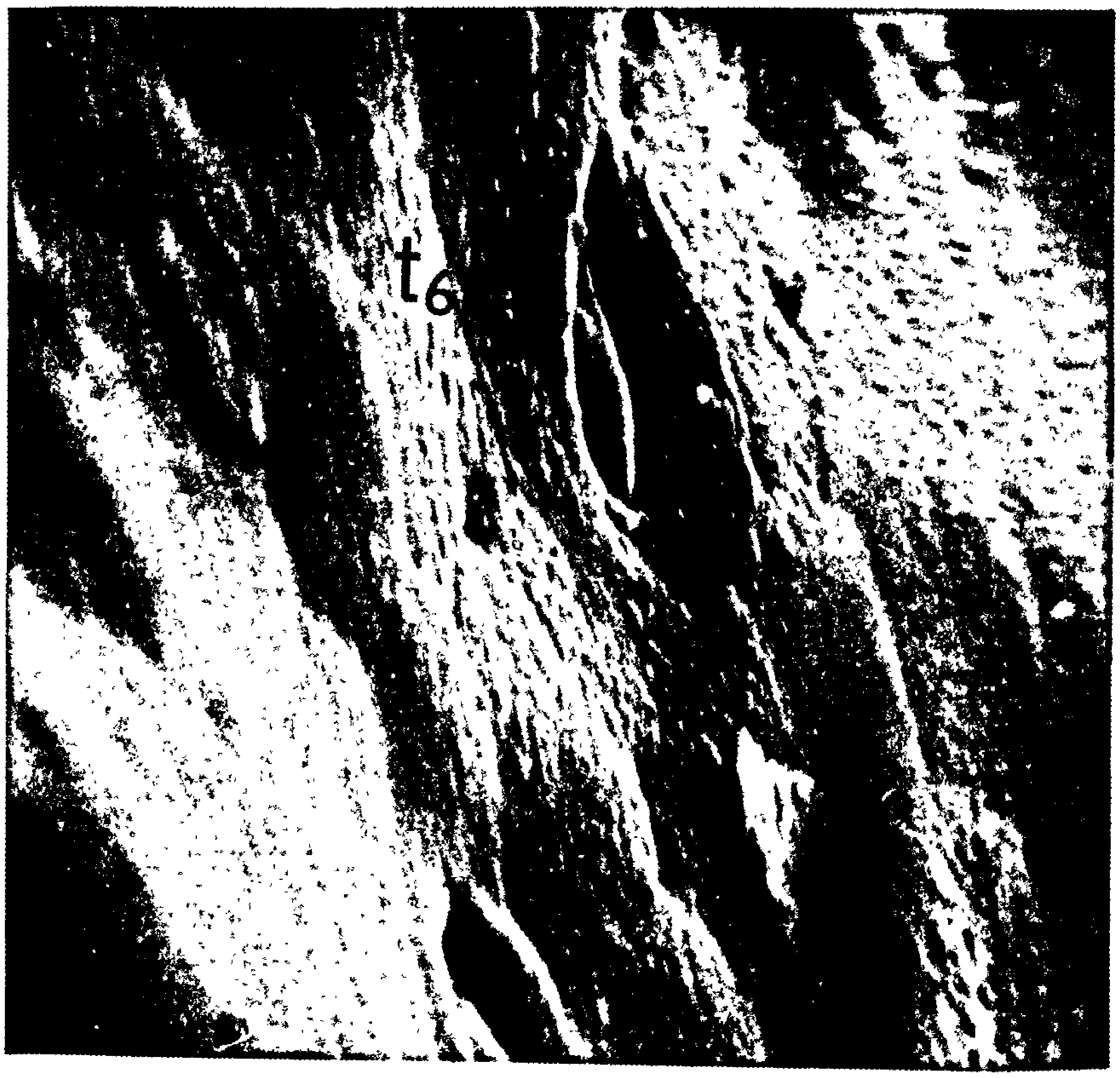
a



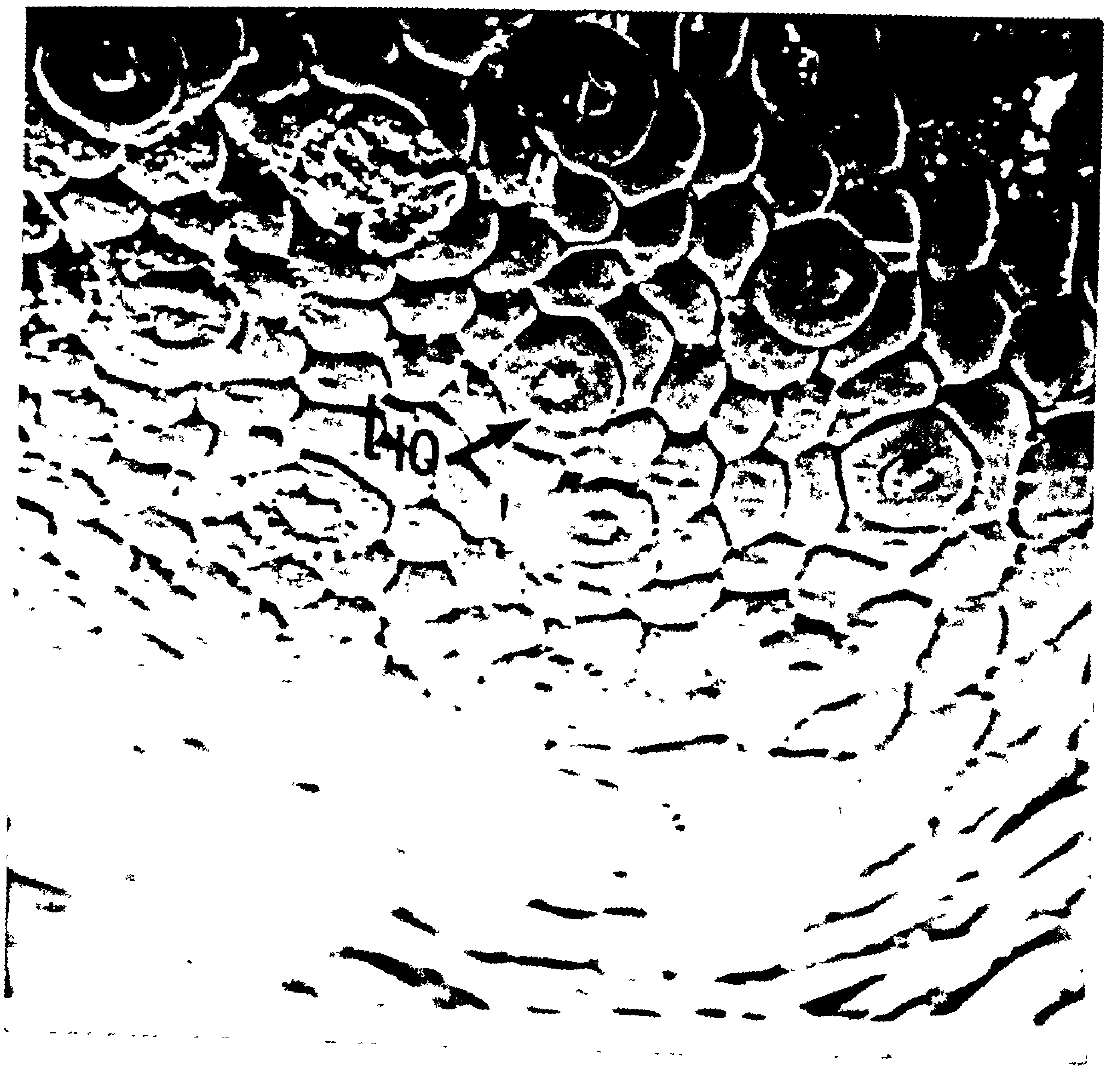
b

Plate 2a. Scanning electron micrograph of the group A_7 sensilla (Type 6) found on the distal portion of the labrum (X 18142.5).

Plate 2b. Scanning electron micrograph of the group A_1 sensilla (Type 10) present on the posterior surface of the clypeolabrum (X 7257).



a



b

The other group A_4 is distal in position to group A_3 (Fig. 4) and consists of a cluster of 9 - 13 sensilla of Type 3 (Tables 2 and 3). The stout setae of Type 4 forms large patches lying lateral to group A_3 and A_4 (Fig. 4) but median to the sclerotized bar. They vary considerably in length (Table 1) and are directed towards the midline. Chapman (1966) found similar brushes in Xenocheila, extending from the tormae (x group of Thomas, 1966), but these were less dense and had smaller setae. The brushes may also have a mechanical function and probably help to direct the food particles towards the pharynx. Hairs are present both outside and between the sclerotized bar (Plate 5a). On the innerside of the sclerotized bar a few very fine cone shaped hairs are present together with finely divided microtrichia (Plate 3b). Chapman (1966) also recorded different forms of microtrichia in the epipharyngeal region in Xenocheila. On the outside of the sclerotized bar, there is an irregular line of sensilla forming group A_8 (Fig. 4). These sensilla are most probably Type 3 since they have very stout setae (Plate 4a). They vary in number in the two sexes (Table 2), the females consistently having fewer sensilla in this group (Table 3). Outside this group there are again very finely divided microtrichia (Plates 3b, 4a and b) which have been examined under the scanning electron microscope up to a magnification of 10,000x.

Plate 3a. Scanning electron micrograph of the posterior surface of the labrum illustrating the sclerotized bar (VL), Type 4 sensilla, hairs on the inner side and group A_8 sensilla on the outer side of the bar (X 725.7).

Plate 3b. Higher power scanning electron micrograph of the posterior surface of the labrum shown in Plate 3a, illustrating Microtrichia (Mtr) and group A_8 sensilla on the outer side of the sclerotized bar (VL), (X 1814.25).

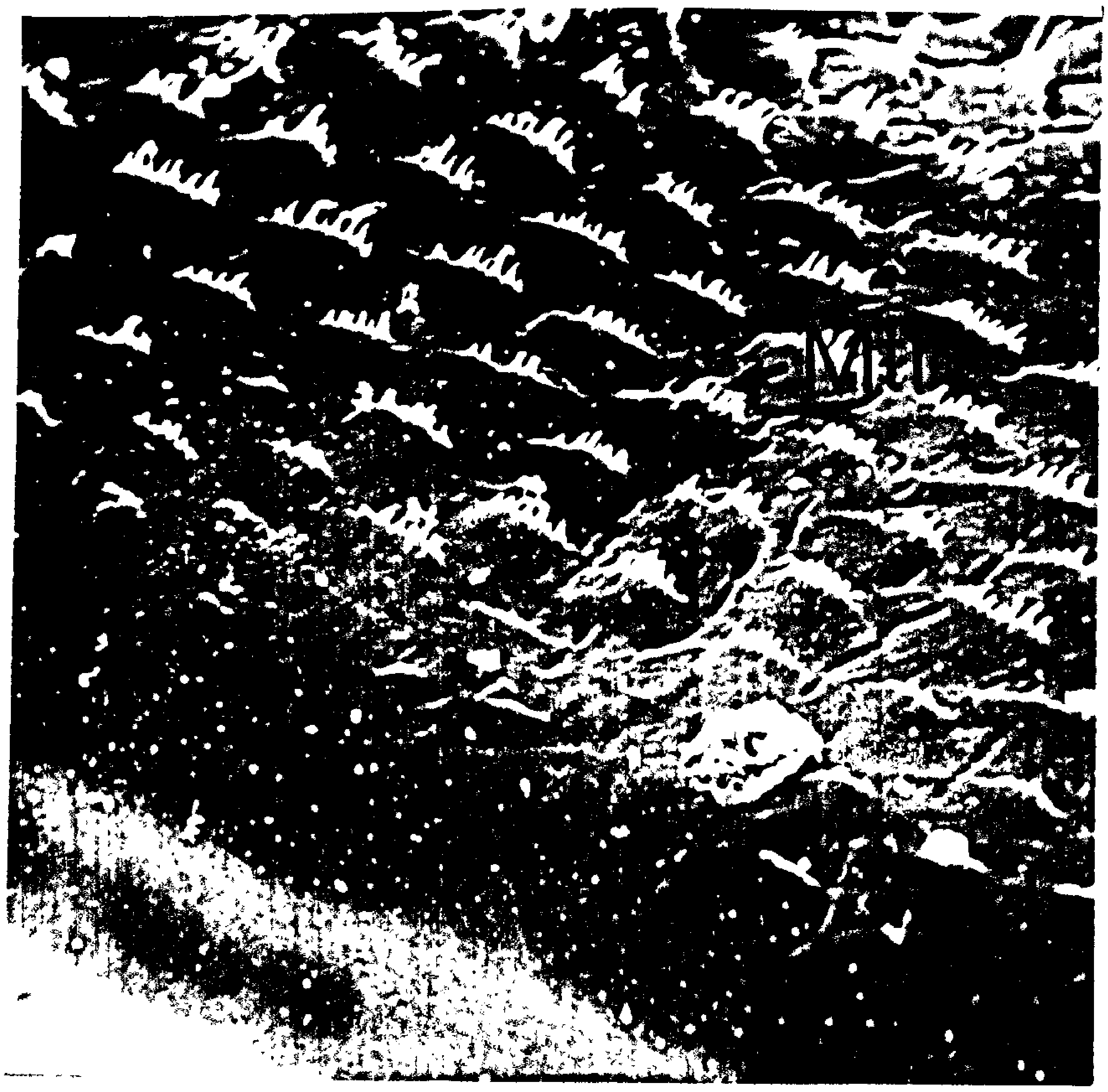
a

b

Plate 4a. Scanning electron micrograph of the group A_8 composed of Type 3 sensilla, and also the microtrichia (Mtr) (X 3628.5).

Plate 4b. Higher power scanning electron micrograph of the microtrichia (Mtr) shown in Plate 4a (X 7257).

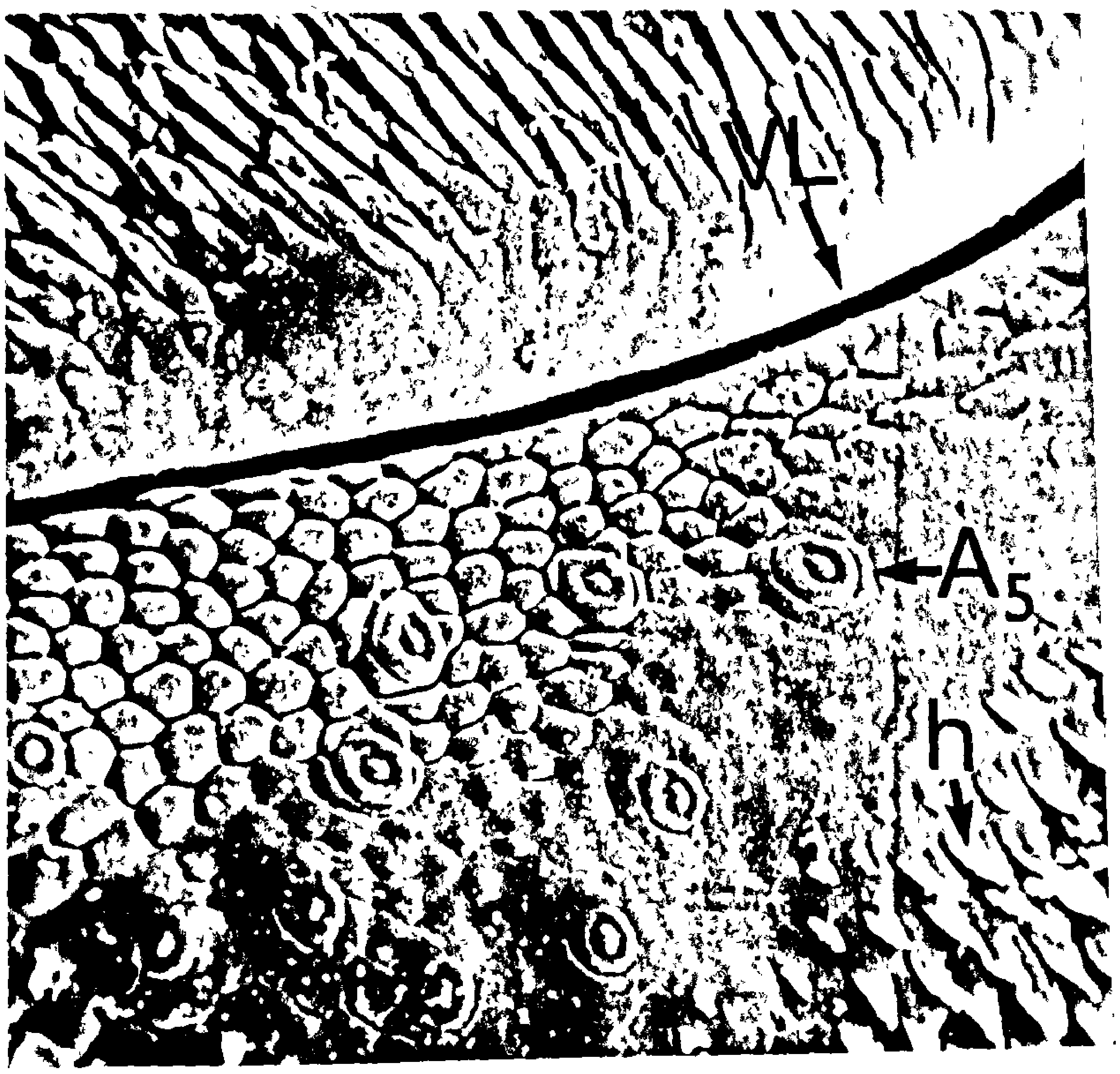
a



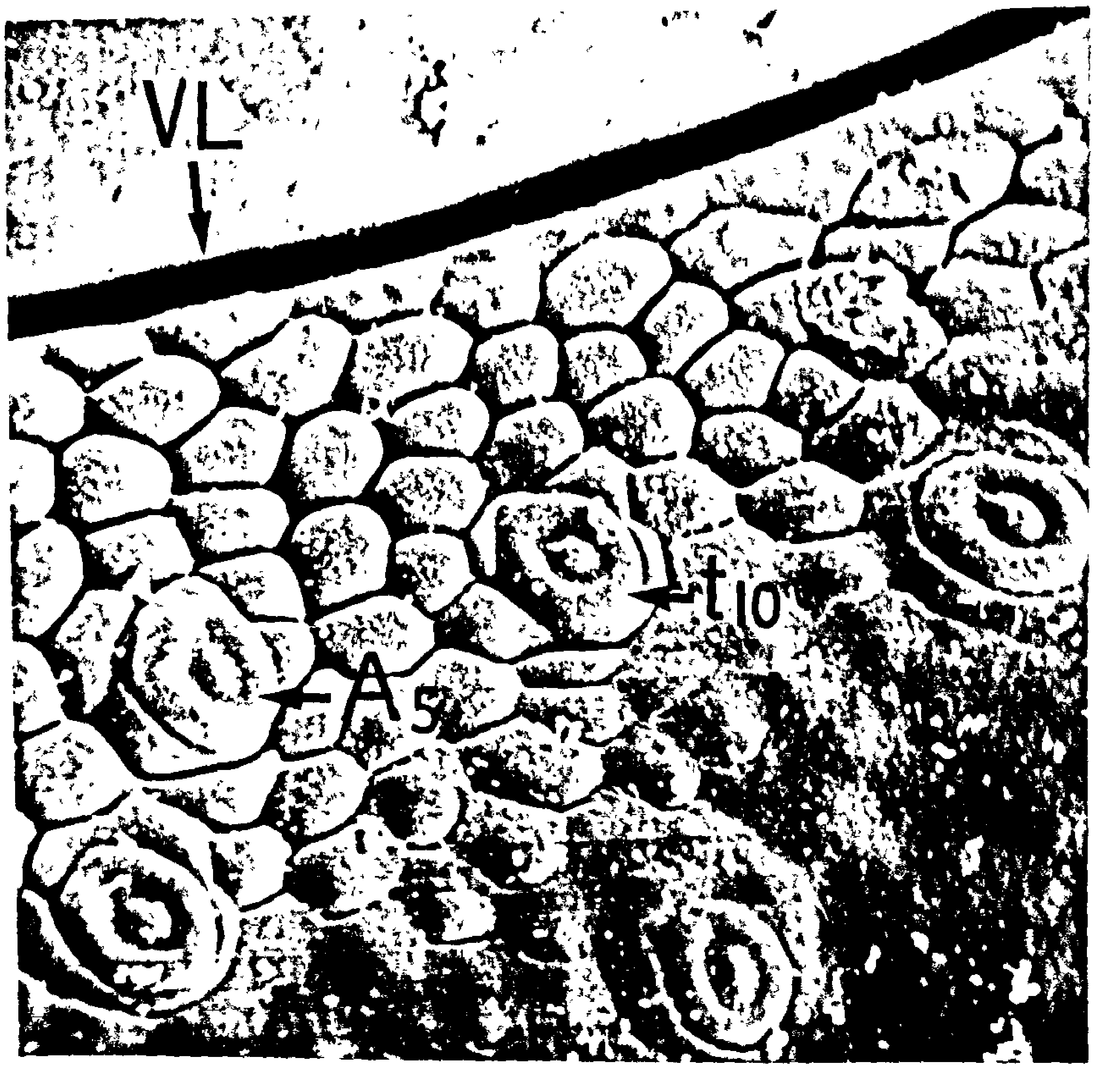
b

Plate 5a. Scanning electron micrograph of a portion of the posterior surface of the labrum illustrating the position of the group A_5 sensilla (Type 10) below the sclerotized bar (VL). Hairs (h) are present on either side of the sensilla (X 3628.5).

Plate 5b. Higher power scanning electron micrograph of the group A_5 sensilla shown in Plate 5a (X 7257).



a



b

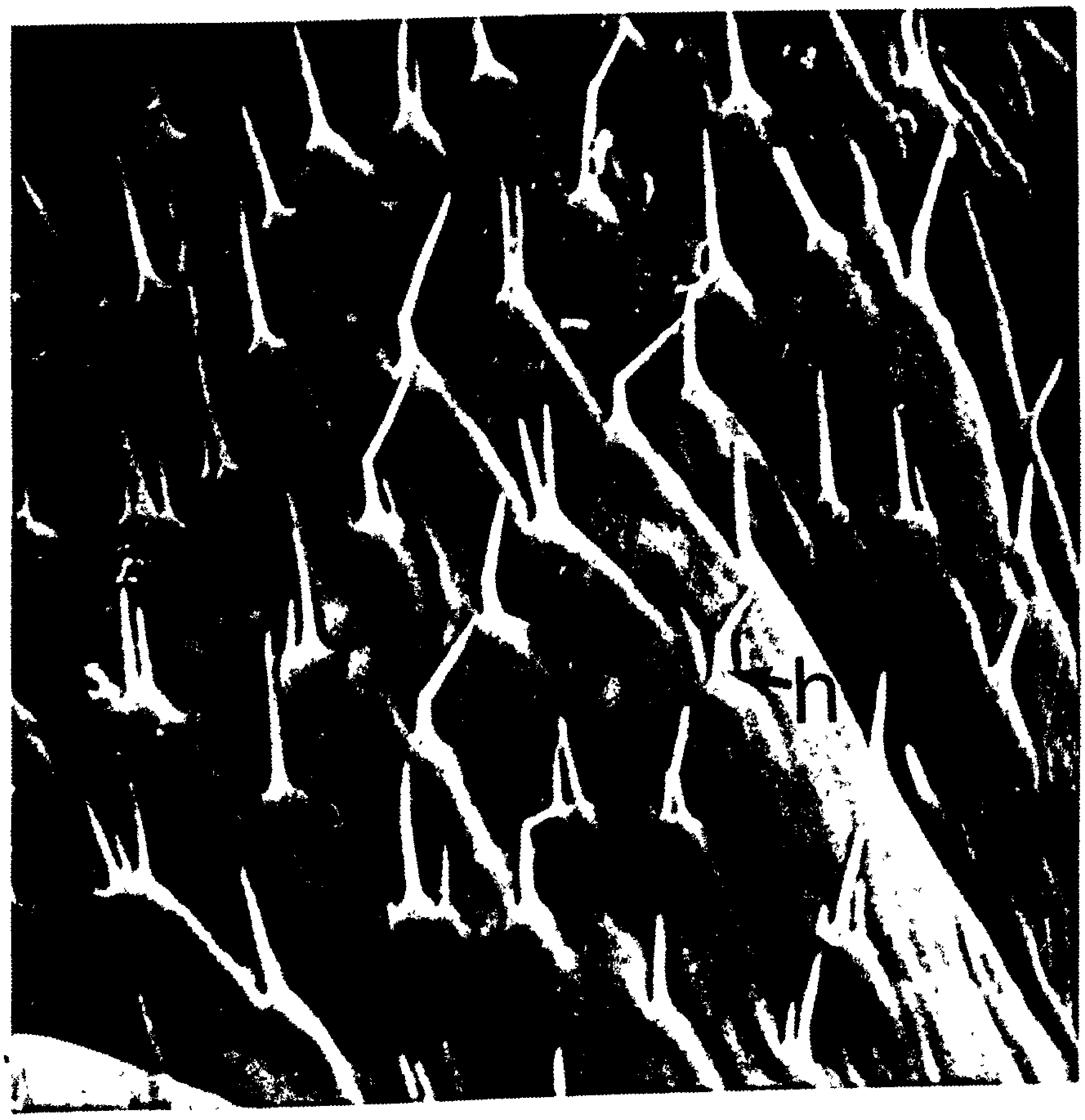
Field III

This field includes the area lateral and distal to the sclerotized bar, and again has several distinct groups of sensilla. Group A_5 consists of a small cluster of sensilla (Fig. 4), distal to the end of the sclerotized bar (Plate 5a, b). Each cluster has an approximately equal number of sensilla and this is similar in both sexes (Table 3). Occasionally only 9 sensilla are present (Table 2) in the female, a number not recorded in the male. The scanning electron micrographs (Plate 5b) show the sensilla to have sockets with a very small central protuberance hardly projecting above the surface of the cuticle. The socket is round and varies in diameter from 5 - 6u. These are considered to be Type 10 sensilla. Below the group A_5 is a brush of very fine hairs (Plate 5a). Similar hairs are also present above the sclerotized bar (Plate 5a). These may be referred to as macrotrichia. Comparable hairs are present in the Trichoptera (Chapman, 1975).

Distal and slightly median to the group A_5 is another group, A_6 (Fig. 4). This group is situated on the lateral side of the inverted Y depression (Fig. 4). There are more sensilla in this group than in group A_5 and the number in the right and left group varies considerably. The female has more sensilla in this group than the male (Table 3). They are probably Type 3 sensilla since the sockets are round with a very small slender seta. Most of

Plate 6a. Scanning electron micrograph of bifid and trifid hairs on the posterior surface of the clypeolabrum in field 1 (X 3628.5).

Plate 6b. Scanning electron micrograph of the fringe of hairs on the notch at the distal end of the labrum (X 3628.5).



a

b

Table 1 Length of setae from Type 1 - 5 sensilla (taken from a range of mouthparts)

Type of sensilla	Number measured (n)	Mean ($\bar{x}$)	Standard Error (S.E.)	Range
1	50	214.14u	± 8.45	145 - 470u
2	50	92.26"	± 4.10	50 - 145"
3	52	25.09"	± 2.74	3 - 47"
4	54	131.22"	± 9.65	47 - 326"
5	55	19.14"	± .85	10 - 31"

Table 2 Number of sensilla in groups on the posterior surface of the clypeolabrum of the adult (*right; ** left side)

Groups of sensilla

Number of Replicates	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
	* **								
1	48,45	13,14	7,6	10,11	11,12	37,26	10,11	79,78	16,16
2	48,52	13,12	6,7	10,10	10,10	28,36	8, 7	86,75	16,16
3	49,47	13,12	6,7	9, 9	9,11	37,31	10, 8	74,80	17,19
4	44,42	12,11	6,6	10,10	10,10	28,35	8, 7	76,71	14,13
Female 5	50,48	16,12	6,6	12,12	11,10	31,38	11,12	78,79	14,17
6	55,48	12,13	6,7	9, 9	10,11	34,30	12,12	80,78	19,19
7	45,42	11,12	6,7	9, 9	10, 9	33,30	12,12	78,79	18,18
8	46,53	18,14	7,7	11,11	12,11	36,32	12,12	82,79	18,18
9	45,53	12,13	7,7	10,11	12,11	35,31	12,12	80,80	18,18
1	52,46	15,14	6,6	10,12	10,11	30,26	14,15	84,87	15,15
2	53,53	18,12	6,6	10,11	10,10	26,28	15,14	98,100	18,19
Male 3	48,42	12,13	5,6	9,11	10,10	22,25	9, 9	76,78	16,16
4	44,47	16,12	6,7	11,13	11,11	23,26	16,16	98,100	17,16
5	51,50	10,15	5,7	11,10	11,10	31,23	17,15	84,96	18,17

Table 3 Number of sensilla in groups on the posterior surface of the clypeolabrum of adults. (Upper value = right side; lower value = left side)

		A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
Female (9 specimen)	Mean ($\bar{x}$)	47.8 47.8	12.8 12.5	6.3 6.7	10 10	10.5 10.5	32.2 31.5	10.5 10.3	79.2 77.7	16.7 17.1
	Standard Error (S.E.)	± 1.13 ± 1.43	± 0.46 ± 0.34	±0.17 ±0.17	±0.33 ±0.37	± 0.34 ± 0.29	± 1.17 ± 0.99	± 0.55 ± 0.76	± 1.15 ± 0.97	± 0.61 ± 0.63
Male (5 specimen)	Mean ($\bar{x}$)	49.6 47.6	14.2 13.2	5.6 6.4	10.2 11.4	10.4 10.4	26.4 25.6	14.2 13.8	88 92.2	16.8 18.6
	Standard Error (S.E.)	± 1.63 ± 1.87	± 1.42 ± 0.58	±0.24 ±0.24	±0.14 ±0.51	± 0.32 ± 0.32	± 1.80 ± 0.81	± 1.39 ± 1.24	± 4.33 ± 4.26	± 0.58 ± 0.68

the seta of this type are 3 - 8u in length, with a basal diameter 1.5 - 2.2u and socket diameter 4 - 6.2u.

At the distal end of the labrum, on either side of notch, are positioned groups A_7 (Fig. 4). These may be similar to the A_3 groups of Thomas (1966). There are usually eleven sensilla in each group, although a range of 7 - 17 has been recorded (Table 2). These are Type 6 campaniform sensilla (Plate 2a) and they are present even in the early instars. These may serve as chemoreceptors involved in the initial selection of food. Spreading around the distal margin of the labrum from the notch is a dense marginal group of Type 4 sensilla (Fig. 4), again serving a mechanical function. The outermost setae are directed outwards whilst the slightly smaller inner setae are directed towards the mid-line. Finally the notch itself is bordered by a fringe of hairs. Under the scanning electron microscope this fringe appears to be composed of two rows of hairs (Plate 6b).

5.5 Distribution of Sensilla on the head appendages

5.5.a. Mandible (Figs. 8 and 9)

Both surfaces of the mandible bear sensilla of various types. The posterior surface has more sensilla with Types 3, 4, 6 and 7 being present (Fig. 8). Type 7 sensilla are the most common and are generally scattered over this surface, although they tend to be more concentrated

Fig. 8. Distribution of sensilla on the posterior surface of the mandible.

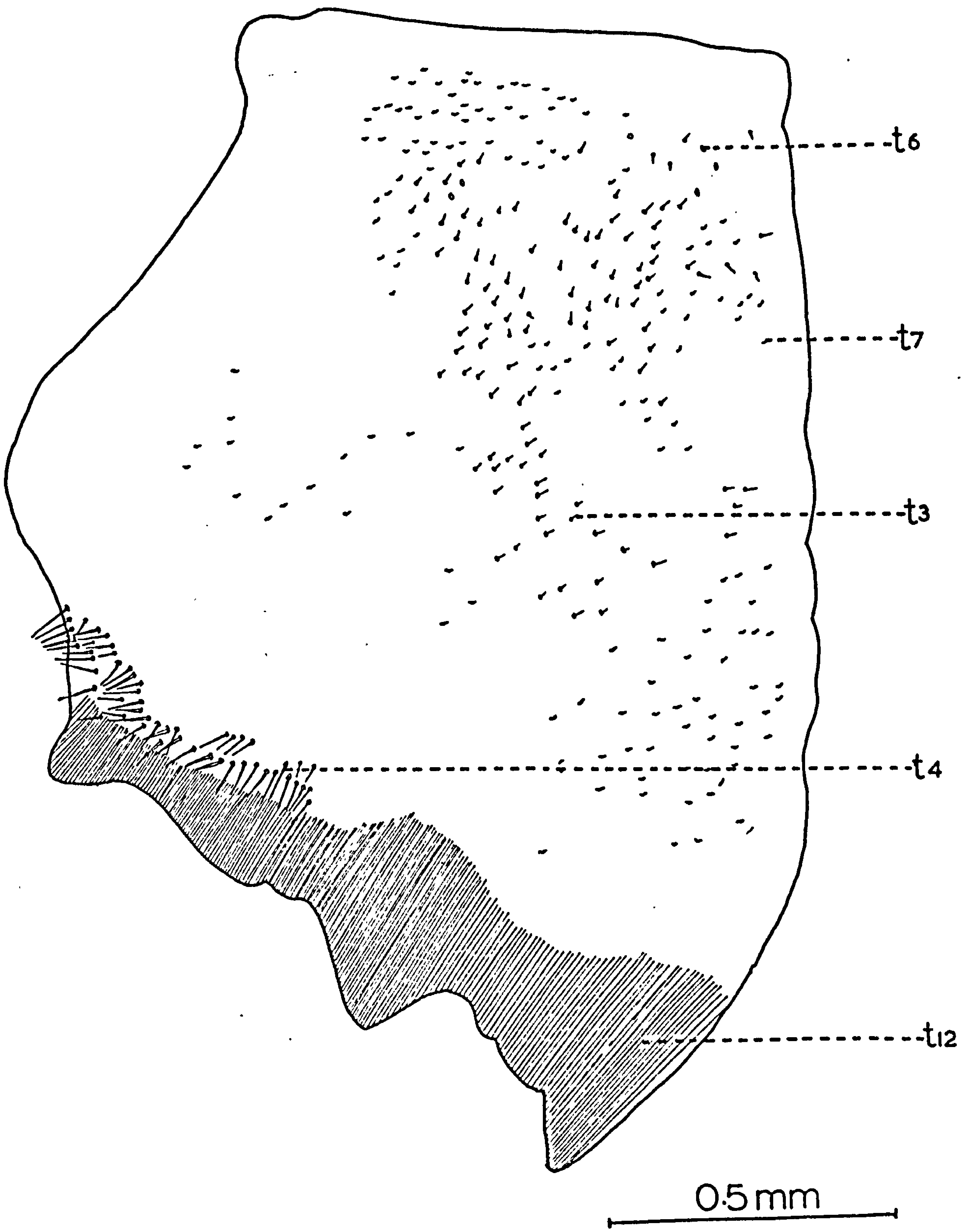


Fig. 8

in the proximal and outer areas. Type 3 has a similar distribution, whilst Type 6 occurs only as a small group in the proximal and outer corner of the mandible. Type 4 sensilla are restricted to the region just above the molar area (Fig. 8). The molar and incisor cusps are penetrated by pore canals; these have been referred to as Type 12 sensilla.

On the anterior surface of the mandible sensilla of Type 3, 6 and 7 are present (Fig.9) although here Type 3 is the most common. They are concentrated in the distal and outer region of the mandible. Type 6 sensilla are found in three discrete groups. Two of them occur towards the inner lateral region whilst the third group is present more or less in the centre of the mandible. Type 7 sensilla are far less numerous than on the posterior surface. They are concentrated on the proximal outer corner of the mandible as well as a cluster just above the incisor cusps. Their shape strongly suggests a secretory function. Similar secretory pores are present on the tarsi of cockroach, Blaberus discoidalis Serville (Arnold, 1974). In addition to sensilla some cuticular sculpturing in the form of ridges is present on the outer lateral surface of the mandible. It is interesting that similar sculpturing has been found at the base of the arolium of Parcoblatta pennsylvanica (De Geer), (Arnold, 1974).

Fig. 9. Distribution of sensilla on the anterior surface of the mandible.

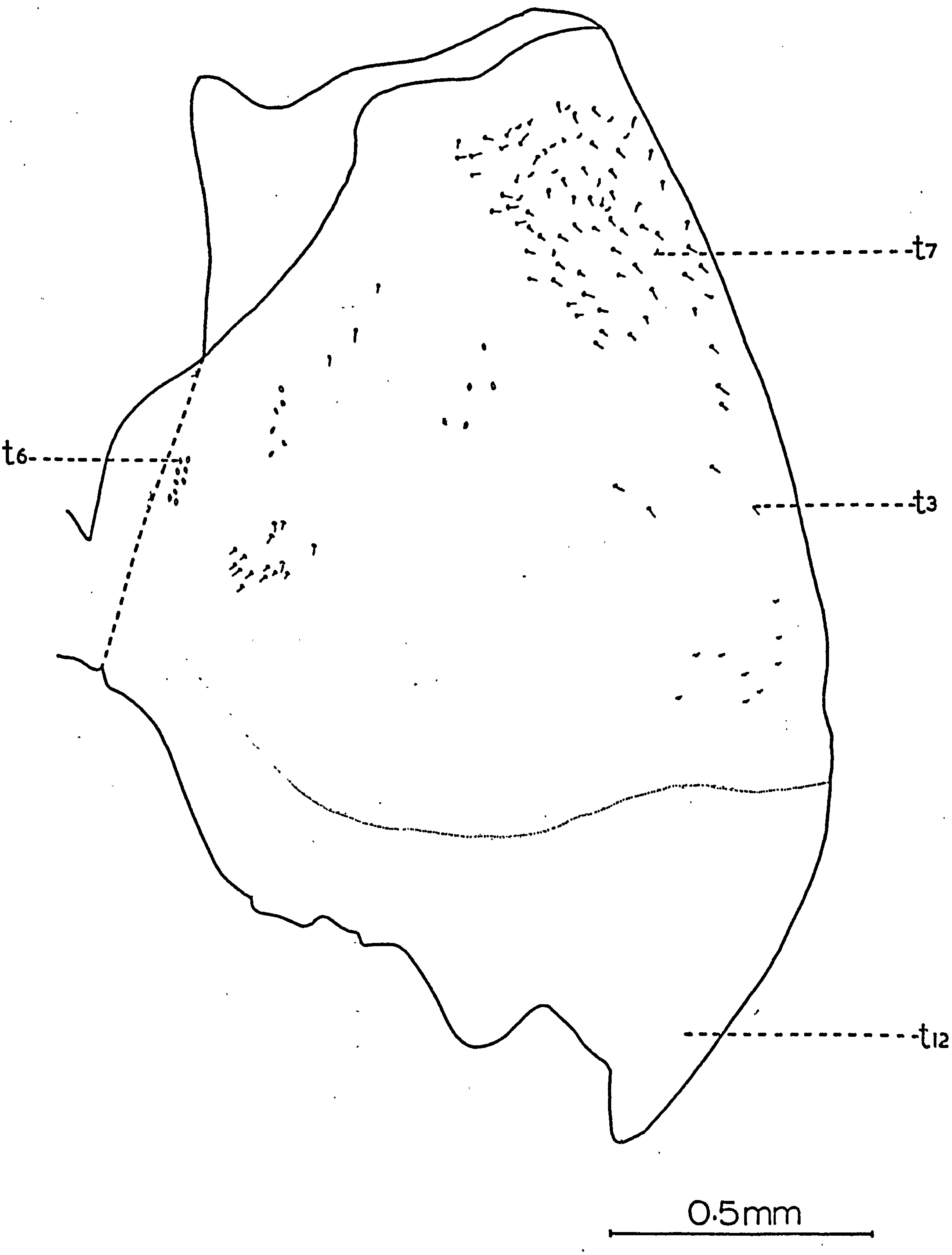


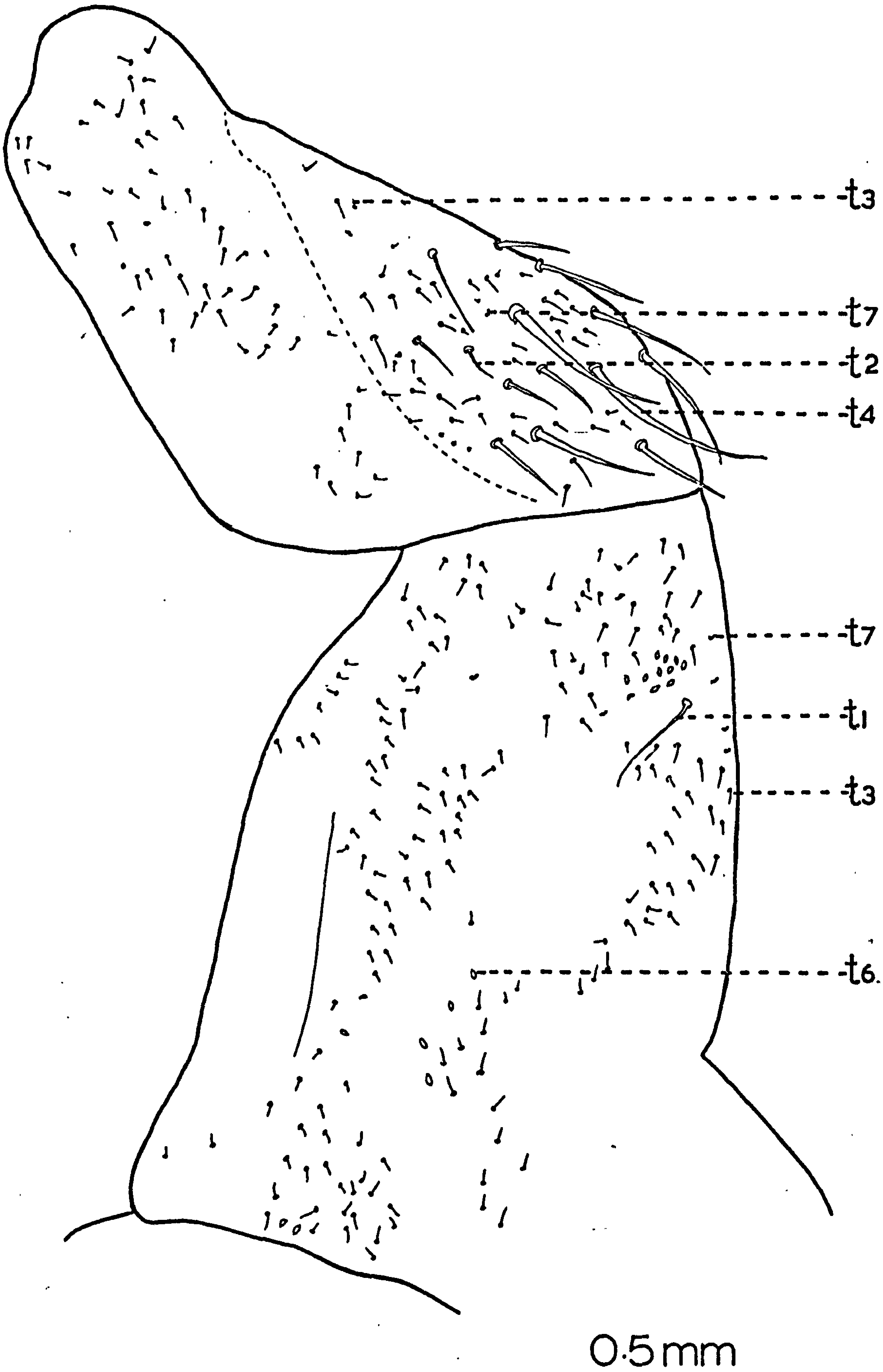
Fig. 9

5.5.b. Maxilla (Figs. 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20 and 21)

The relatively complex structure of the maxilla made the description of the distribution of sensilla very difficult. For this reason the various components have been treated separately. Thus the anterior and posterior surfaces of the cardo, stipes, galea, lacinia and maxillary palp have been described. This treatment means that certain sensilla occurring on the lateral margin of these structures may have been omitted.

On the posterior surface of the cardo sensilla of Types 2, 3, 4 and 7 are present (Fig. 10). Type 3 are generally distributed over the whole surface of the cardo. Types 2 and 4 are more restricted in distribution and are confined to the proximal outer corner of the cardo, where it articulates with the stipes. The longest setae are of Type 4 and measure 315 - 325u in length with a basal diameter of 13.7 - 15.7u and a socket diameter of 25 - 28u. Type 7 sensilla have a similar distribution to the Type 4 sensilla. These appears to be an interesting difference in the number of sensilla between the sexes. All types are more common in the male, although there is a striking difference in the number of Types 3 and 7, as can be seen in Tables 5 and 6, Figs. 10 and 12. Types 2 and 4 extend further towards the proximal end of the cardo in the male.

Fig. 10. Distribution of sensilla on the posterior surface of the cardo and stipes.



Fig·10

Fig. 11. Distribution of sensilla on the anterior surface of the cardo and stipes.

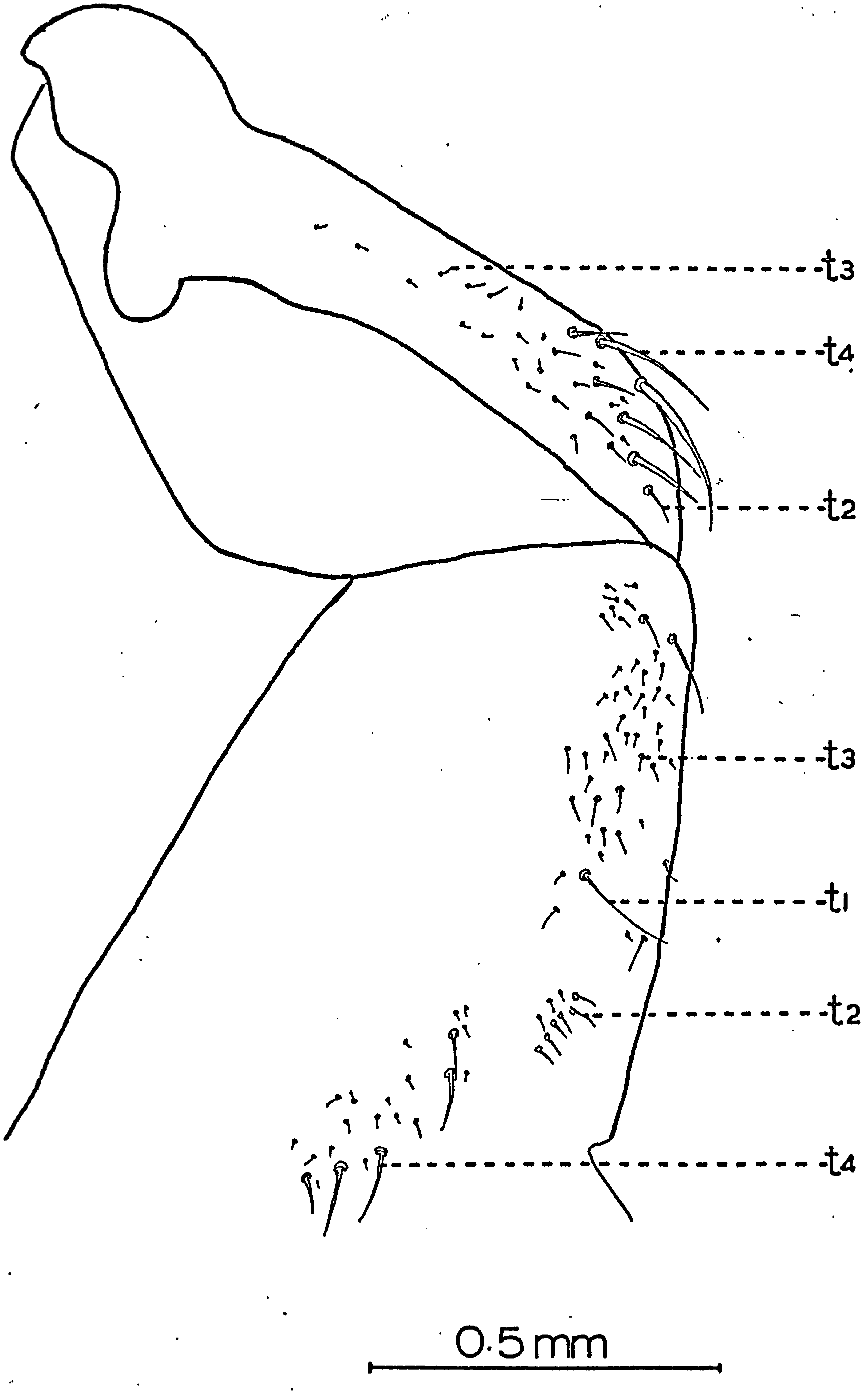


Fig.11

Fig. 12. Distribution of sensilla on the posterior surface of the cardo in the adult male to show sexual differences.

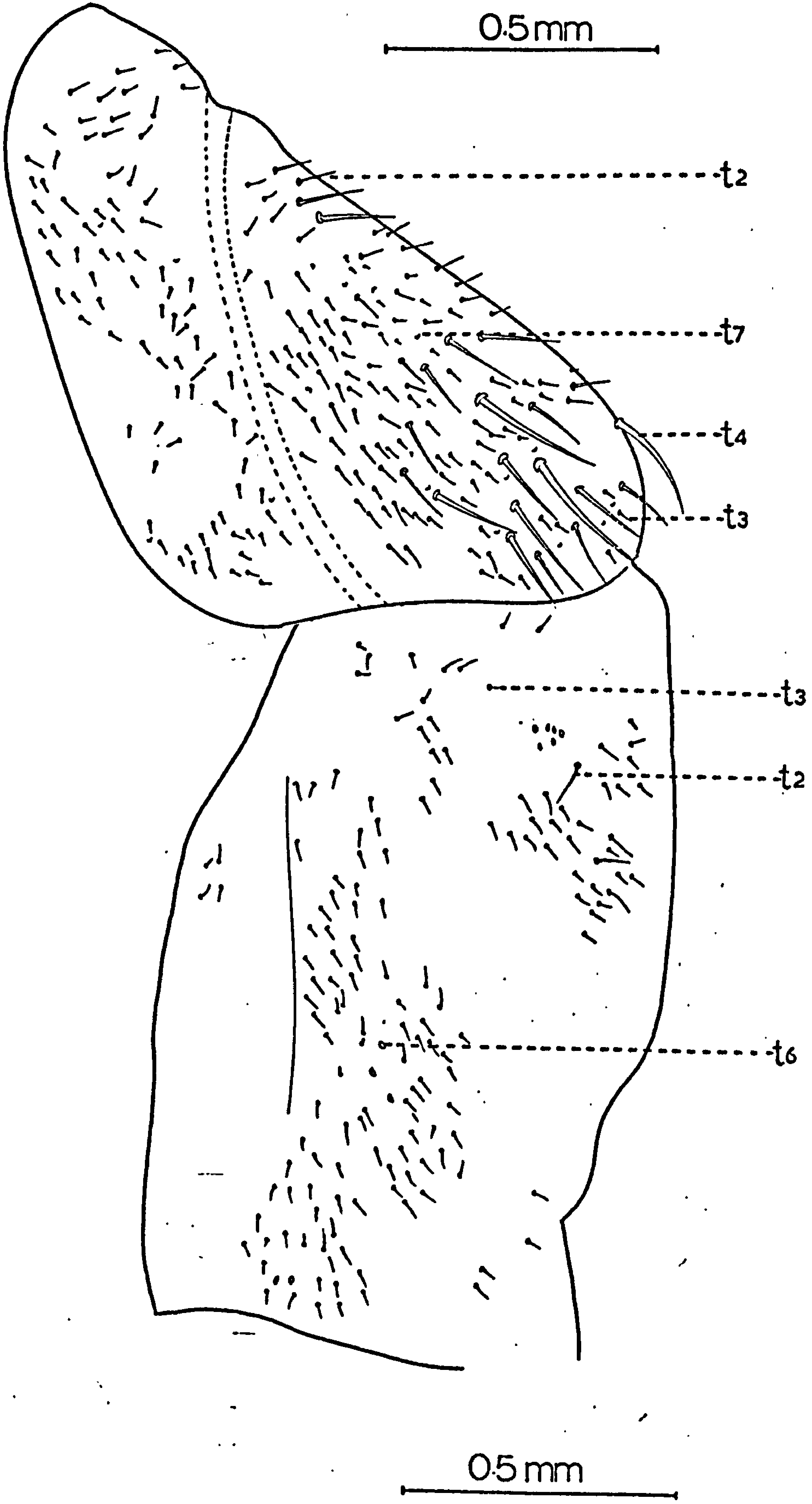


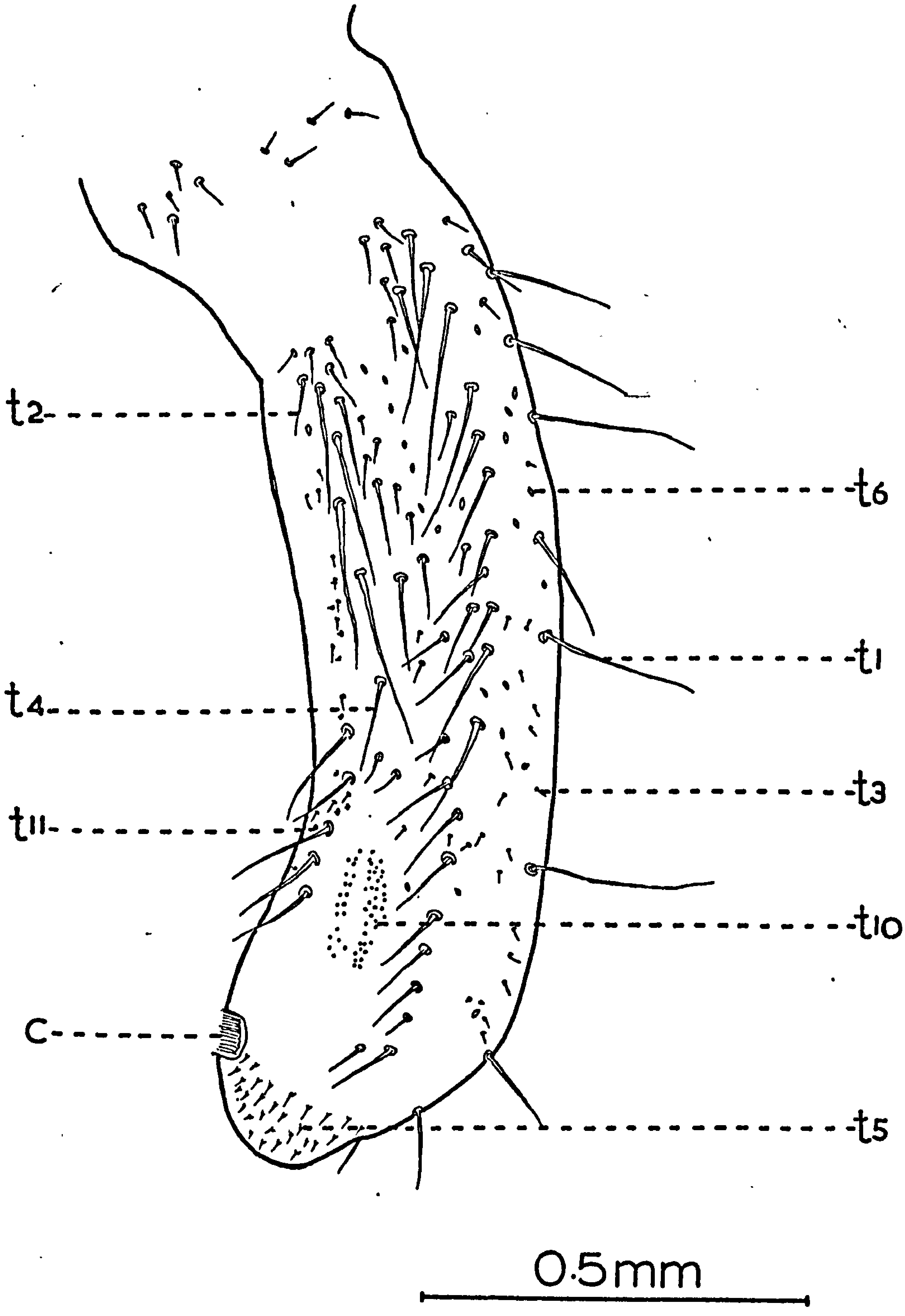
Fig.12

On the anterior surface of the cardo Types 2, 3 and 4 occur (Fig. 11), although they are only found on the distal and outer corner of the cardo. On this surface the number of sensilla present in sexes is similar (Tables 5, 6).

The stipes of the female bears, on its posterior surface sensilla of Types 1, 3, 6 and 7 (Fig. 10). Again Type 3 is generally distributed whilst Type 6 occurs in three small groups. Some of these campaniform sensilla have a length diameter of 9 - 10u whilst a few are of 14u, the breadth diameter is constant at 3u. Type 7 is present in very small numbers and there is a single Type 1 sensilla, with a setae of length 196u, a basal diameter of 3u and a socket diameter of 6.2u. It is of considerable interest that Type 7 sensilla are completely lacking in the male and the single Type 1 sensilla is replaced by two of the slightly smaller Type 2 sensilla (Table 4).

The anterior surface of the stipes is supplied with sensilla of Types 1, 2, 3, 4 (Fig.11). Most of the inner portion of the stipes is without sensilla. Type 3 is again distributed throughout the lateral part of the stipes, with only a relatively few Types 2 and 4. In the female there is a single Type 1 sensillum which is lacking in the male (Table 4).

Fig. 13. Distribution of sensilla on the posterior surface of the galea.



Fig·13

Most of the posterior surface of the galea is well furnished with sensilla of Types 1, 2, 3, 4, 5, 6, 10 and 11 (Fig. 13) in both sexes (Table 4). The distribution of these sensilla is clearly shown by the maps for the individual types (Fig. 16). Sensilla of Type 4 are widely distributed on the posterior surface of the galea, those in the central region have setae less than 180u whilst the remainder have setae in excess of this length. The number of this type of sensillum tend to be higher in the male (Table 6). Towards the distal end there is a tight oval group of round sensilla (Fig. 16) with a variable socket diameter of 2.9 - 6.2u. These are probably Type 10 sensilla (Plate 7a). It has been noticed that the number of Type 10 sensilla in this group is greater in the male (Table 6) than in the female (Table 5). Their presence at the distal end of the galea suggests that they may be chemoreceptors and play a role in testing the food. Type 5 sensilla are completely restricted to the distal end of the galea (Fig. 16) and the number is more or less constant in both sexes (Tables 5, 6). Type 2 sensilla are randomly distributed on the posterior surface and are slightly more numerous in the female than in the male (Tables 5, 6). Type 1 sensilla are more lateral in position and are again more common in the female. Type 3 sensilla occur mainly on the inner side and in this type more are present in the male. Unlike the cardo and stipes Type 6 sensilla are not restricted to groups

Fig. 14. Distribution of sensilla on the anterior surface of the galea.

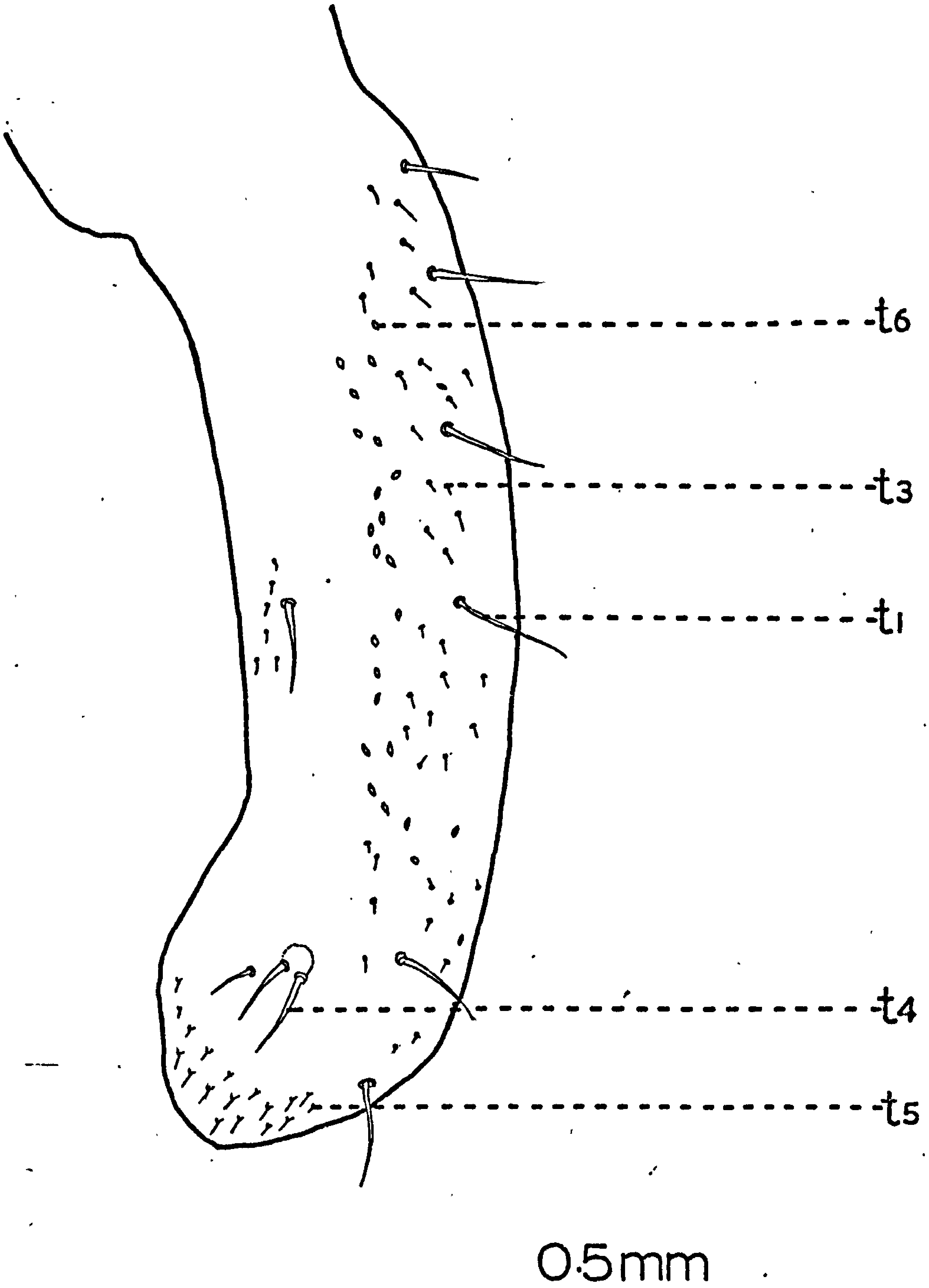


Fig.14

Fig. 15. Distribution of sensilla on the anterior surface of the galea in the adult male to show sexual differences.

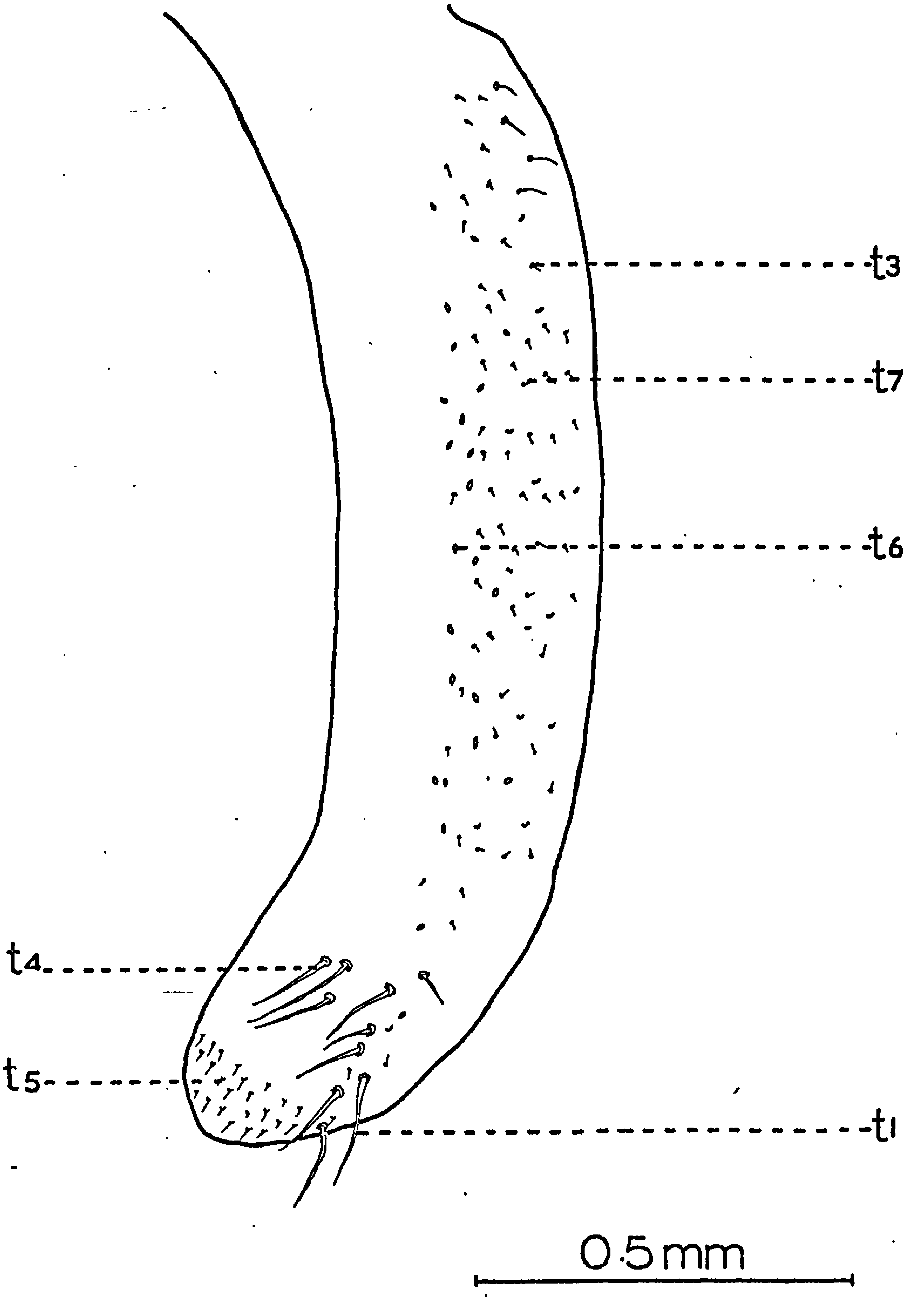
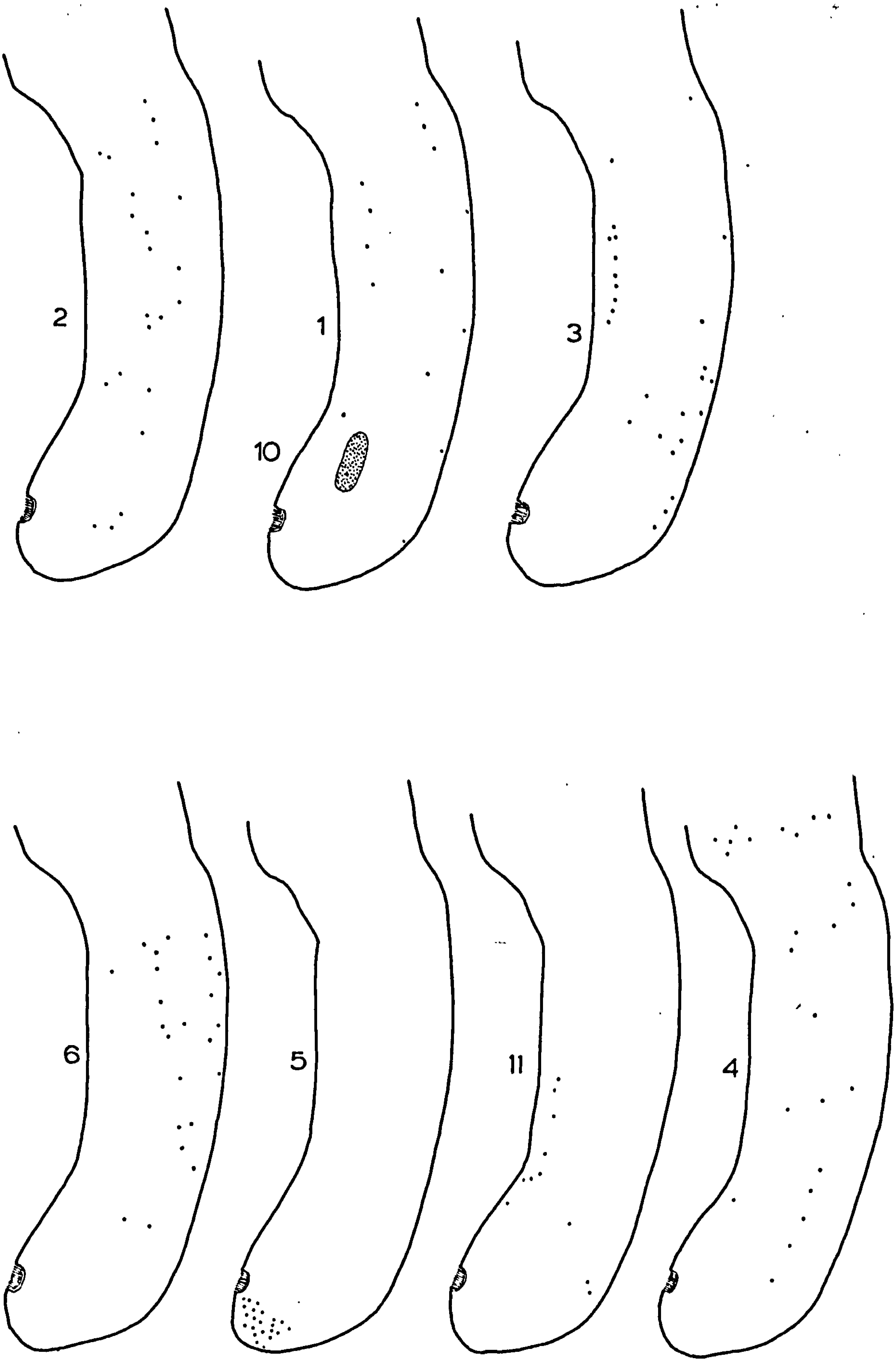


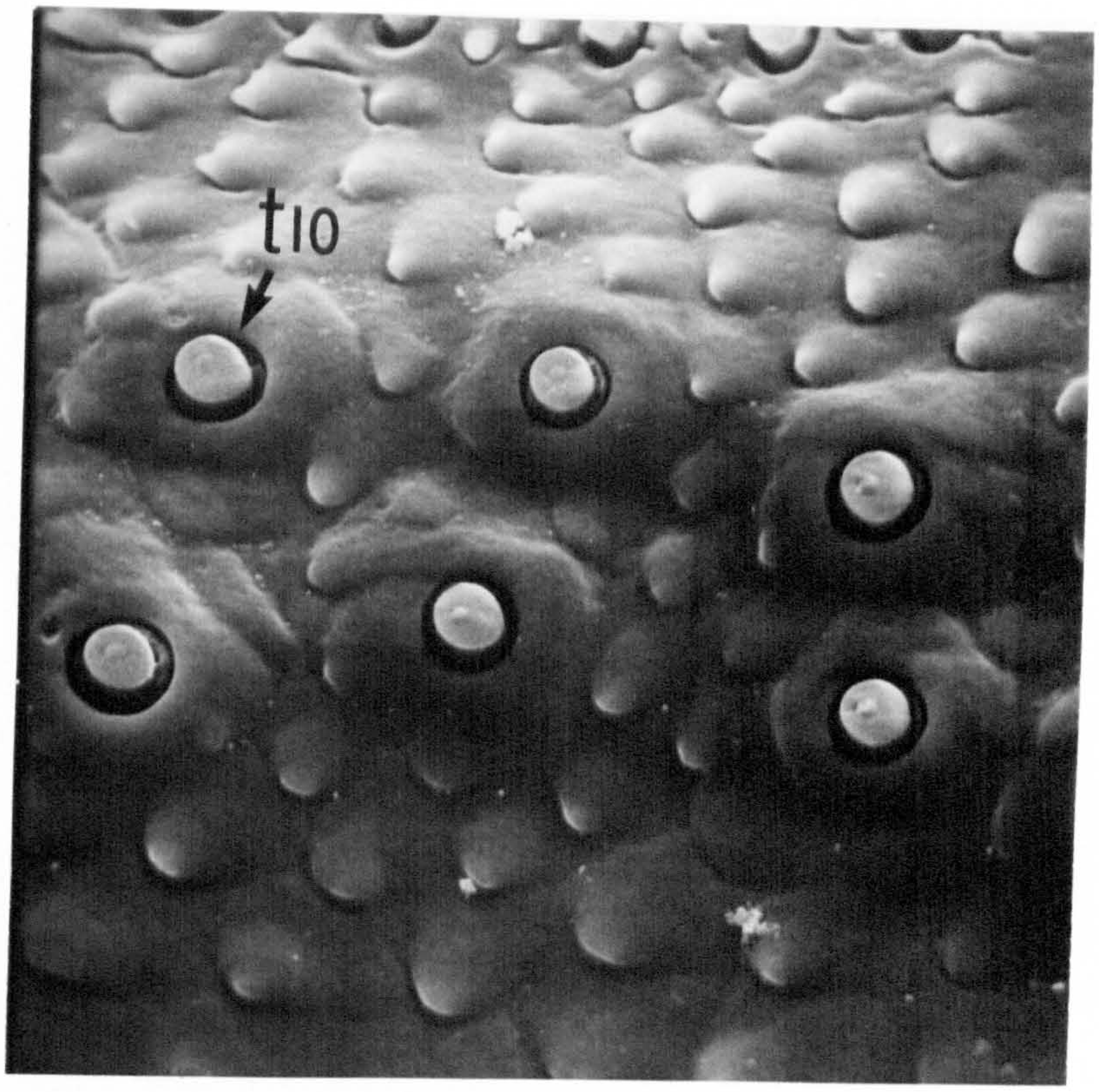
Fig.15

Fig. 16. Distribution of sensilla of Types 1, 2, 3, 4, 5, 6, 7, 10 and 11 on the posterior surface of the galea.



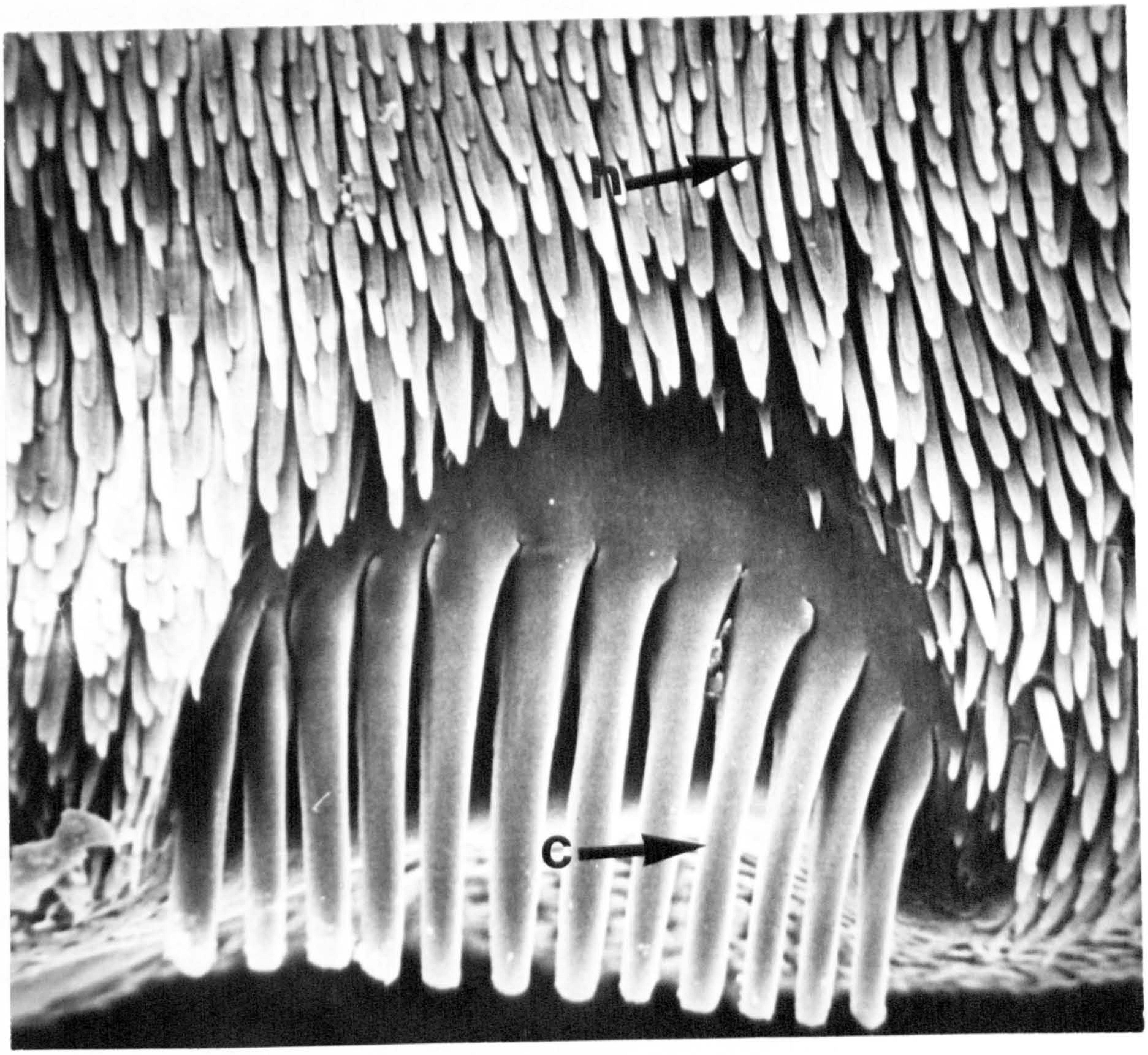
Fig·16

Plate 7a. Scanning electron micrograph of Type 10 sensilla present on the posterior side of the galea (X 7257).



a

Plate 7b. Scanning electron micrograph of the comb (c) together with hairs (h) present on the distal portion of the galea (X 4354.2).

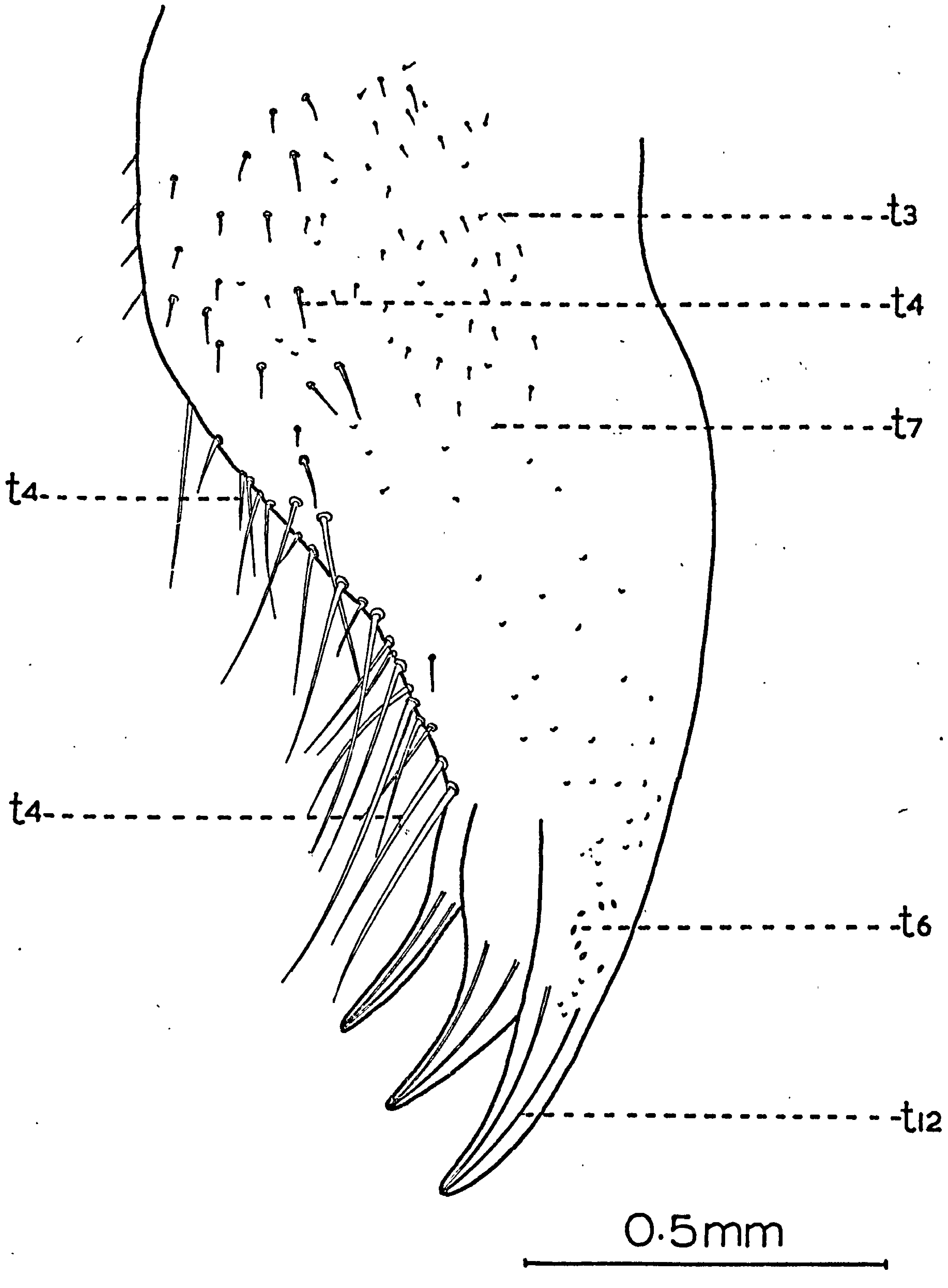


b

but are more generally dispersed. Finally Type 11 sensilla are mostly found on the inner margin of the galea and are more numerous in the female (Table 5). One outstanding and interesting feature of the galea is the presence of a comb, usually with twelve teeth (Plate 7b), situated on the inner distal part of the posterior surface (Fig. 13). The comb is present in both sexes and may be used for cleaning the food particles, for holding them or for sweeping them towards the preoral food cavity. The area surrounding the comb is well supplied with hairs (Plate 7b). There has been no previous record of a comb on the mouthparts of Orthoptera, although similar structures have been found in other insects but are not always associated with the head appendages. Thus, in the Hymenoptera at the distal end of the fore tibia a comb or scraper is present and is used to clean the antenna. In mosquito larvae, certain hairs on the upper surface of the maxillae form a comb. In the Lepidopteran family in Lycaenidae a comb is present on the serrate distal margin of the rostellum (Nabokov, 1945).

The anterior surface of the galea is furnished with sensilla of Types 1, 3, 4, 5 and 6 (Fig. 14) in the female (Table 5) and also Type 7 in the male (Table 4, Fig. 15). In the female there is a row of Type 1 sensilla situated on the anterolateral side of the galea (Fig. 14), whilst in the male only two sensilla of this type are present at the distal end of the galea (Fig. 15). Two closely spaced stout setae

Fig. 17. Distribution of sensilla on the posterior surface of the lacinia.



Fig·17

Fig. 18. Distribution of sensilla on the anterior surface of the lacinia.

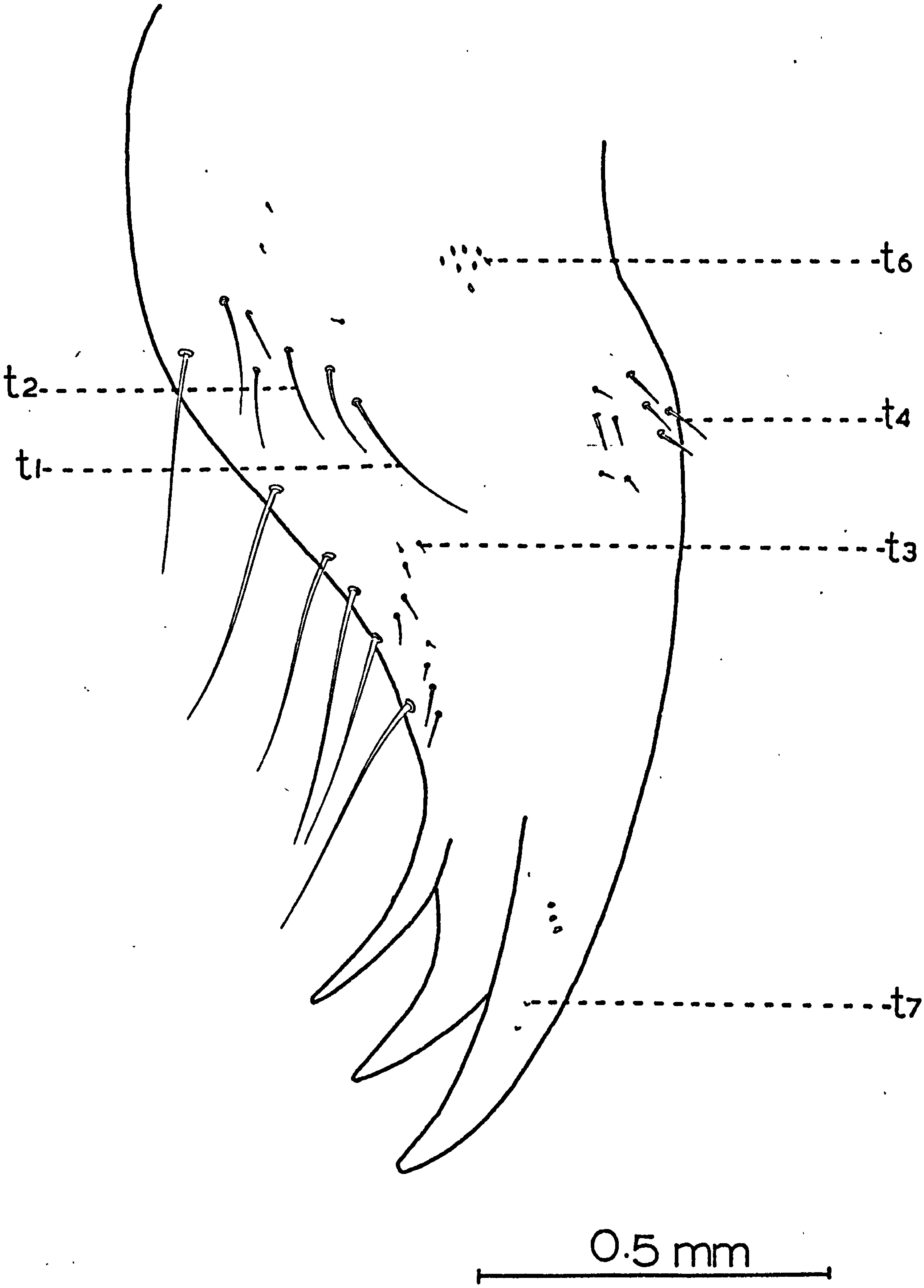


Fig.18

Fig. 19. Distribution of: a, Types 3, 4, 6 and 7 sensilla on the posterior surface of the lacinia; b, Type 1, 3 and 6 sensilla on the anterior surface of the lacinia.

Fig.19

of Type 4 are found centrally positioned at the distal end in the female (Fig. 14). Type 5 sensilla are restricted to the extreme tip of the galea (Fig. 14) as on the posterior surface. The number of Types 3, 4 and 5 sensilla is greater in the male, whilst Type 6 is represented by the same number in both sexes (Tables 5 and 6).

The posterior surface of the lacinia is well supplied with sensilla of Types 3, 4, 6 and 7 (Fig. 17). The distribution of maps of the individual sensilla types are given in Fig. 19a. Type 4 sensilla form a fringe of long setae on the inner side of the lacinia. Other Type 4 sensilla on the lacinia are shorter and stouter and these are more proximal in position. The long setae vary in length from 262 - 326u with a basal diameter of 12 - 24u and a socket diameter of 28 - 31u. The Type 3 sensilla are restricted to the proximal and central part of the lacinia (Fig. 19a). The number of Type 4 and 7 sensilla is greater in the female (Table 5) than in the male (Table 6) whilst the reverse situation occurs in Type 3 (Table 6). There are two pore canals in each of the three cusps. These have been referred to as Type 12 sensilla.

The anterior surface of the lacinia (Fig. 18) is supplied with sensilla of Types 1, 2, 3, 4, 6, 7 and 12 (Fig. 19a and b) in both sexes (Table 4), although as can be seen from Tables 5 and 6 the overall number of sensilla

Fig. 20. Distribution of sensilla on the posterior surface of the segments of the maxillary palp.

Fig·20

is greater in the male. There is a tendency for most of the sensilla to be positioned on the mesal side of the lacinia. Type 3 sensilla are the most widely distributed type and are more numerous in the male than in the female. Type 4 again provide a fringe on the mesal border with a shorter stouter group more central in position. Type 6 and 7 occur as small clusters with more Type 7 in the male (Table 6).

The five segments of the maxillary palp have numerous sense organs on both surfaces, these are mainly of Types 1, 2, 3, 4, 5, 6 and 7 (Table 5).

On the posterior surface of the first segment sensilla of Types 2, 3 and 4 are present (Fig. 20). Type 3 is the most common in both the sexes (Tables 5 and 6) and with the exception of the distal margin of the segment is generally distributed. On the anterior side of this segment (Fig. 21) Type 1 is present in addition to Types 2, 3 and 4. There is also a hair plate in the proximal lateral region of the segment, which is formed of Type 2 sensilla. Sensilla of Type 3 are again the most numerous in both sexes.

On the posterior surface of the second segment, sensilla of Types 2, 3, 4 and 7 are present together with a proximally positioned hair plate. The Type 4 sensilla are restricted to the distal half of this segment (Fig. 20).

Fig. 21. Distribution of sensilla on the anterior surface of the segments of the maxillary palp.

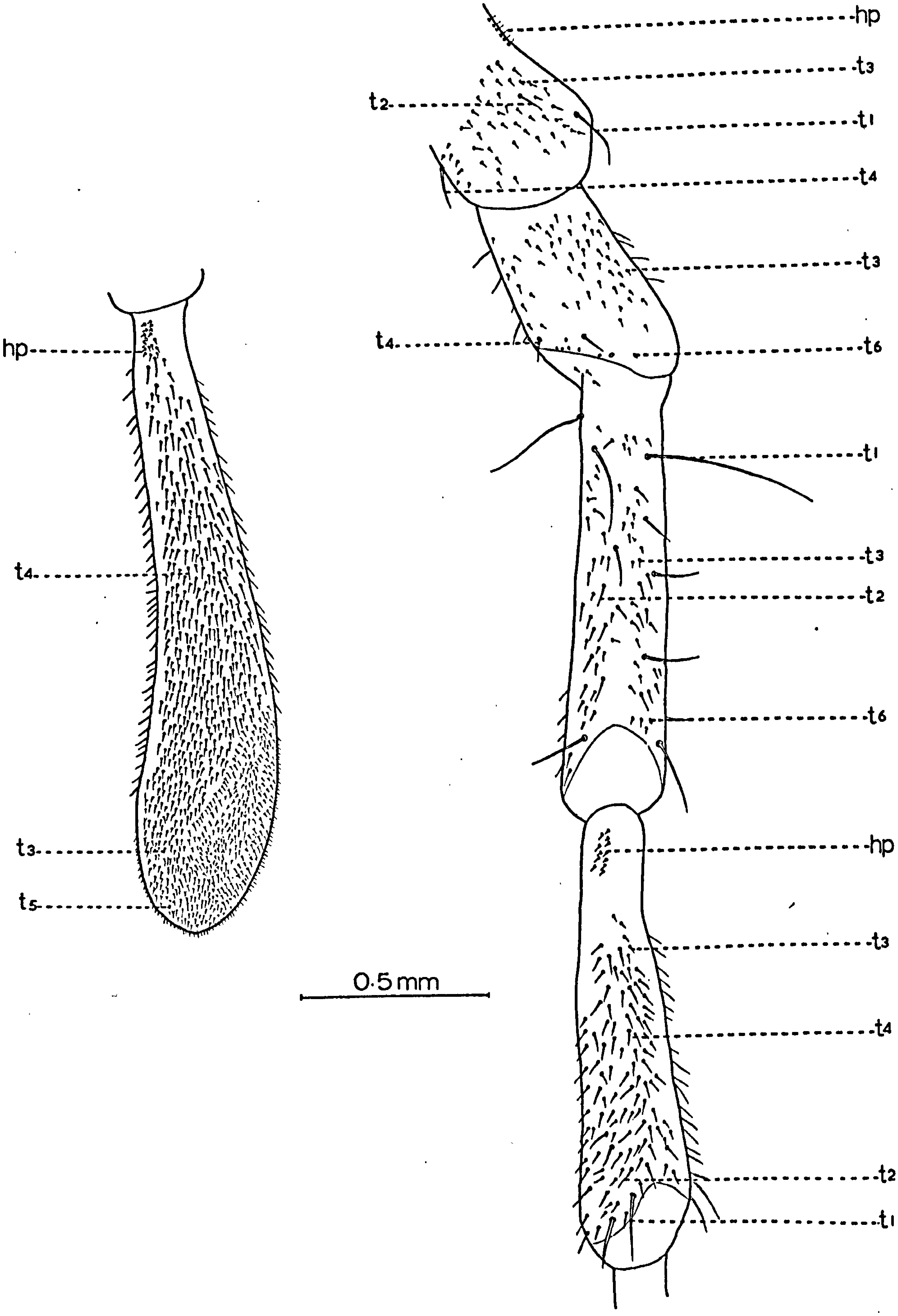


Fig. 21

Anteriorly, sensilla of types 3, 4 and 6 are present on the second segment (Fig. 21). Type 3 is again generally distributed, whilst Type 4 and 6 are represented by only a few sensilla confined to the distal boundary of the segment. One major sexual difference is in the occurrence of Type 2 sensilla which are present in the male but not in the female (Tables 5 and 6).

The posterior surface of the third segment has sensilla of Types 2, 3 and 4 distributed over the whole surface (Fig. 20). A hair plate occupies a central position on the proximal boundary of the segment, whilst at the distal end there are a few Type 6 sensilla. Anteriorly Types 3 and 6 sensilla are also present (Fig. 21). Type 1 only occurs on this segment and Type 2, present on the posterior surface is absent. The number of various types is similar in both sexes (Tables 5 and 6).

The posterior surface of the fourth palp segment is supplied with sensilla of Types 2, 3 and 4 which are scattered generally over its surface, whilst Type 6 is restricted to the distal portion of this segment (Fig. 20). Sensilla of Type 3 are the most abundant (Table 5) and the only type which extends throughout the segment. Anteriorly, there is a hair plate in the proximal part of the segment, together with sensilla of Types 1, 2, 3 and 4 (Fig. 21). Unlike the previous segment Type 1 sensilla are restricted to the distal extremity of the segment.

Fig. 22. Distribution of sensilla on the posterior surface of the submentum of the labium.

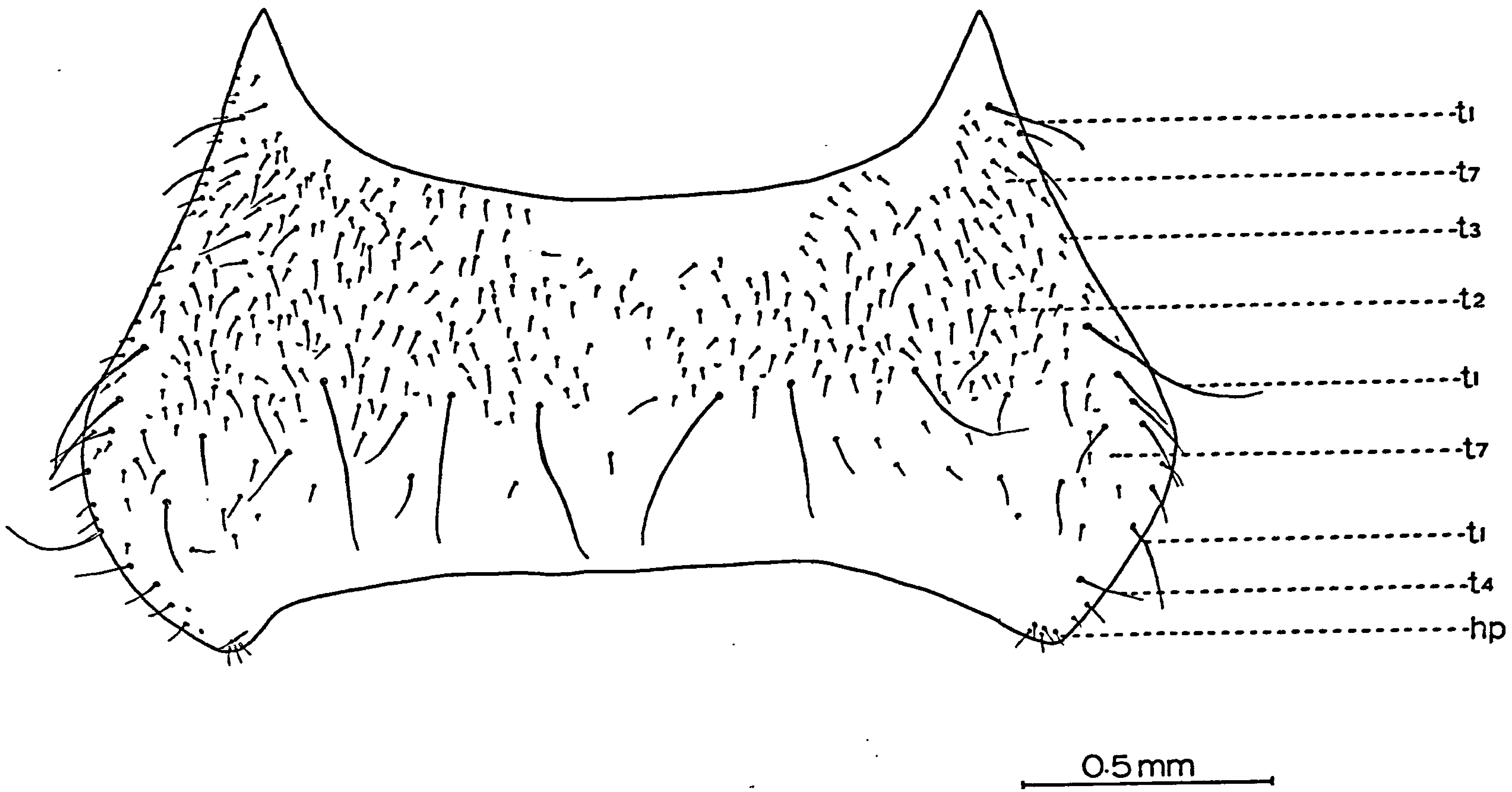


Fig.22

The fifth segment has numerous sensilla and is the most densely covered of all segments. Types 2, 3 and 4 are scattered over the whole surface of the segment, whilst Type 5 is restricted to the tip of the palp (Fig. 20). Anteriorly there is hair plate similar in position to that of the previous segment. Types 3 and 4 are found over the whole surface of the segment except for the tip where Type 5 is again dominant (Fig. 21).

5.5.c. Labium (Figs. 22, 23, 24, 25, 26 and 27)

The labium like the maxilla, is very well supplied with sensilla of various types. For this reason the individual components of the labium: submentum, mentum, prementum, paraglossa, glossa and labial palp will be discussed in turn.

Sensilla of Types 1, 2, 3, 4 and 7 are present on the posterior surface of the submentum in both sexes (Table 4). A horizontal row of Type 1 sensilla is situated in a median position on this surface (Fig. 22). Some of these sensilla have setae more than 200u in length with a basal diameter of 6u and a socket diameter of 14u. Sensilla of Types 2 and 3 are more generally scattered over the submentum, although they are lacking from the distal border. Sensilla of Type 2 have setae with lengths from 55 - 70u, a basal diameter of 5 - 4u and socket diameter of 7 - 8u, whilst Type 3 have much shorter setae ranging from 13 - 33u in length with a basal diameter of 2.9 - 4u and a socket

Fig. 23. Distribution of sensilla on the posterior surface of a, mentum; b, prementum.

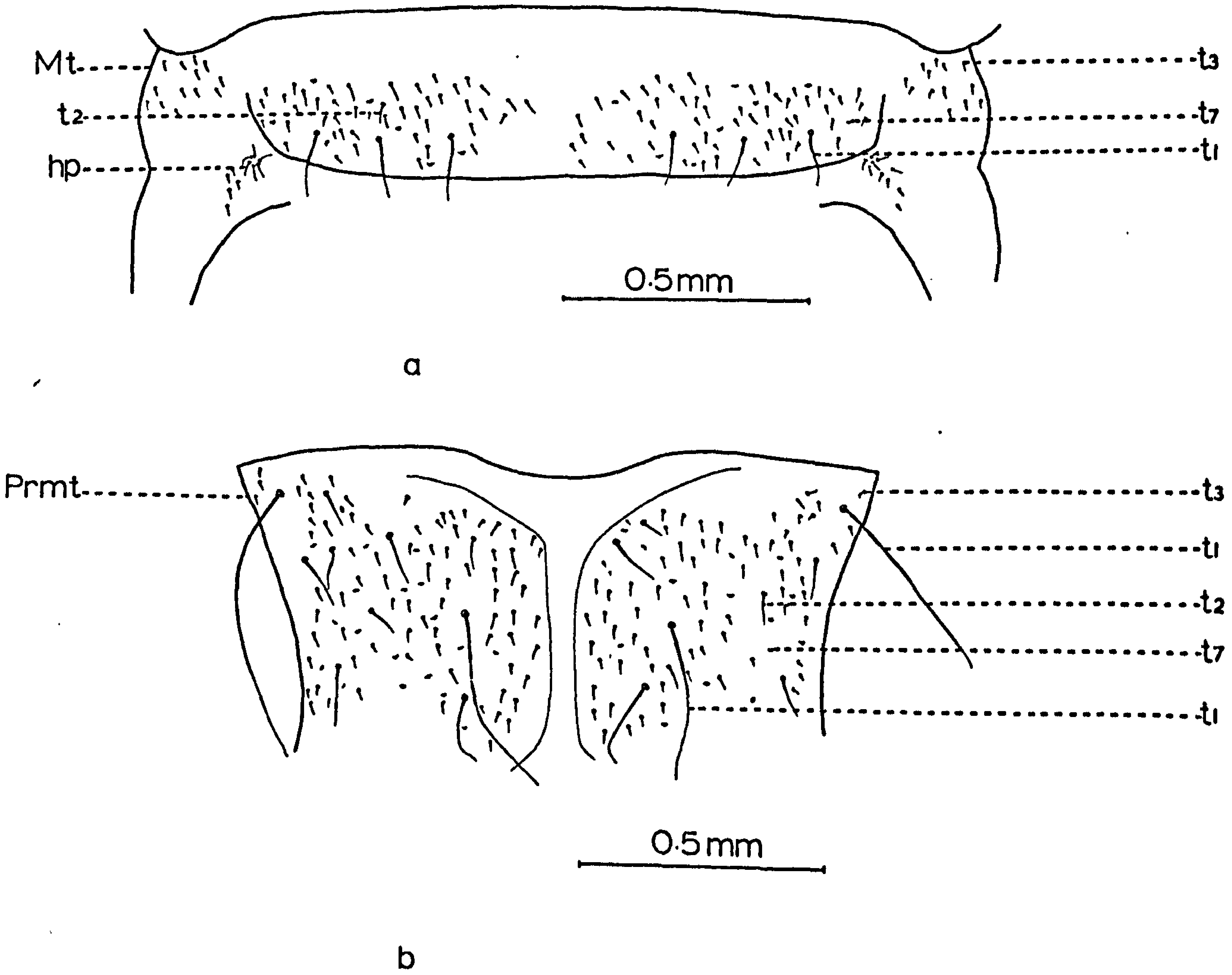


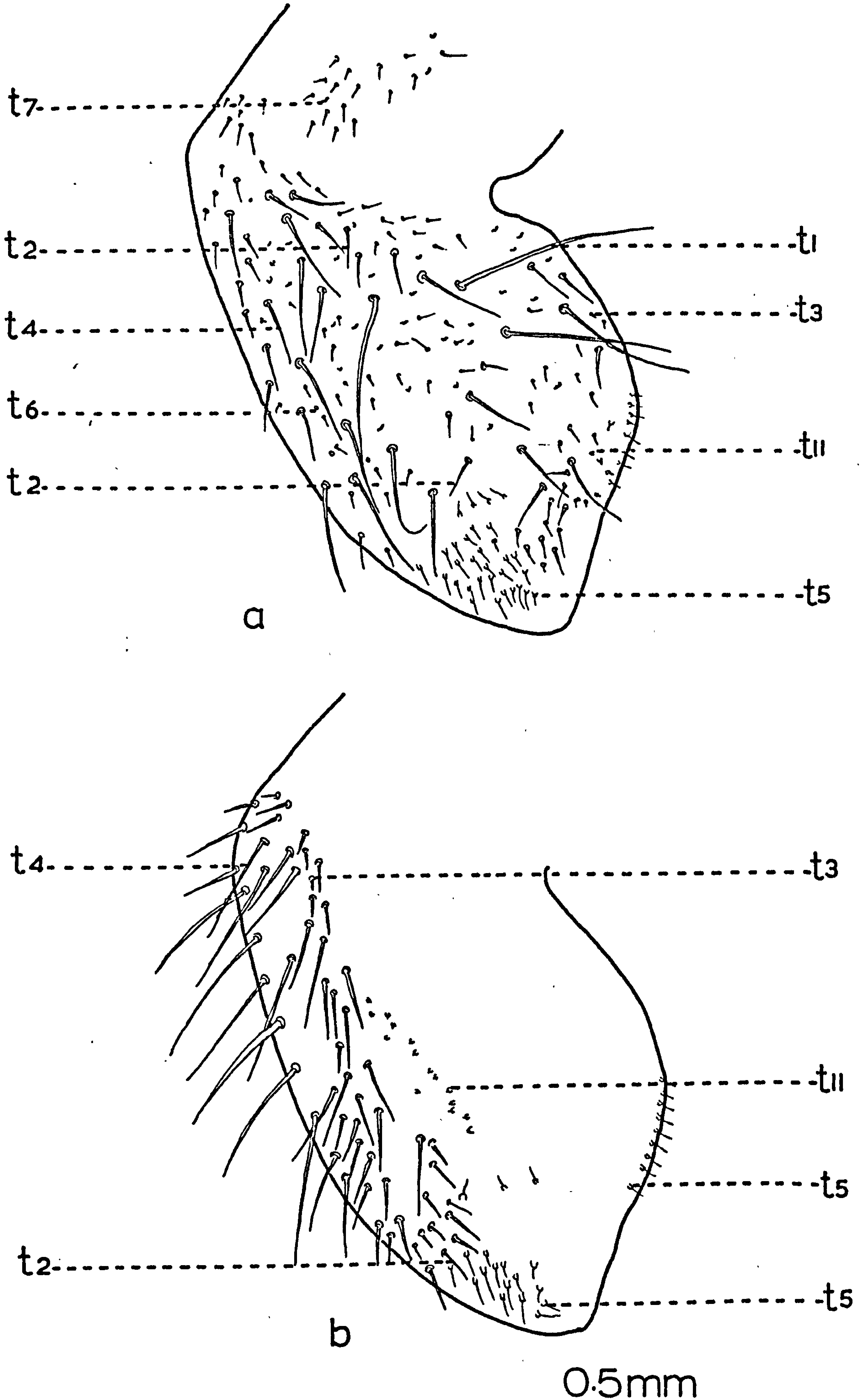
Fig- 23

diameter of 6 - 8u. Type 7 are distributed in a wide band across the submentum but are absent from the distal margin. The number of Type 3 and 7 sensilla is greater in the male than in the female (Tables 5 and 6). Eight Type 4 sensilla are present and are restricted to the lateral region of the posterior surface of the submentum (Fig. 22). A pair of hair plates composed of Types 2 and 3 sensilla, is present one on each distal lateral angle of the posterior surface (Fig. 22).

The anterior surface of the submentum is mostly membranous and only a few sensilla occur on the sclerotized lateral lobes. These, however, have not been recorded.

Types 1, 2, 3 and 7 sensilla are found on the posterior surface of the mentum in both the sexes (Table 4). The anterior surface is without sensilla with the exception of the proximal border of the submentum, sensilla of Type 3 are generally dispersed. Type 7 sensilla share a similar distribution but are also absent from the central part of the mentum. Type 7 sensilla are considerably more common in the female than the male (Tables 5 and 6). The six sensilla of Type 1 are symmetrically arranged near to the distal margin of the mentum (Fig. 23a). In the male there is just a single pair of this type of sensillum (Table 6). Type 2 sensilla are few in number (Table 5) and are found towards the lateral part of the mentum above the origin of

Fig. 24. Distribution of sensilla on the paraglossa; a, posterior surface; b, anterior surface.



Fig·24

Plate 8a. Scanning electron micrograph of the Type 1 sensilla present on the posterior surface of the paraglossa (X 362.85).

Plate 8b. Scanning electron micrograph of the Type 6 sensilla present on the distal margin of the second labial palp segment (X 7257).

a

b

the Type 1 sensilla. A pair of hair plates is found on the membranous proximal portion of the prementum (Fig. 23a).

A similar range of sensilla types is found on the posterior surface of the prementum (Fig. 23b). The anterior surface is devoid of sensilla. In both sexes six very long sensilla of Type 1 are to be found symmetrically arranged. These have setae of more than 300u in length, a basal diameter of 6 - 8u and a socket diameter of 15 - 19u. Type 3 sensilla are dispersed over the whole surface and are slightly more numerous in the male (Tables 5 and 6). The relatively few Type 2 sensilla appear to be randomly dispersed between those of Type 3. Like Type 2, Type 7 sensilla are also distributed over the whole surface and are more numerous in the female than the male (Tables 5 and 6).

The posterior surface of the paraglossa has a wide range of sensilla types. Types 1, 2, 3, 4, 5, 6, 7 and 11 are present in both sexes (Table 4). Type 5 sensilla only occur towards the distal extremity of the paraglossa (Fig. 24a), they appear to be more numerous in the female (Tables 5 and 6). Some of the setae of the Type 1 sensilla (Plate 8a) are more than 400u in length. They are generally spread over this surface (Fig. 24a) and the number is similar in both sexes (Tables 5 and 6). Types 2, 3, 4 and 7 sensilla are also generally distributed; the number of Types 3 and 7

Fig. 25. Distribution of sensilla on the posterior surface of the glossa.

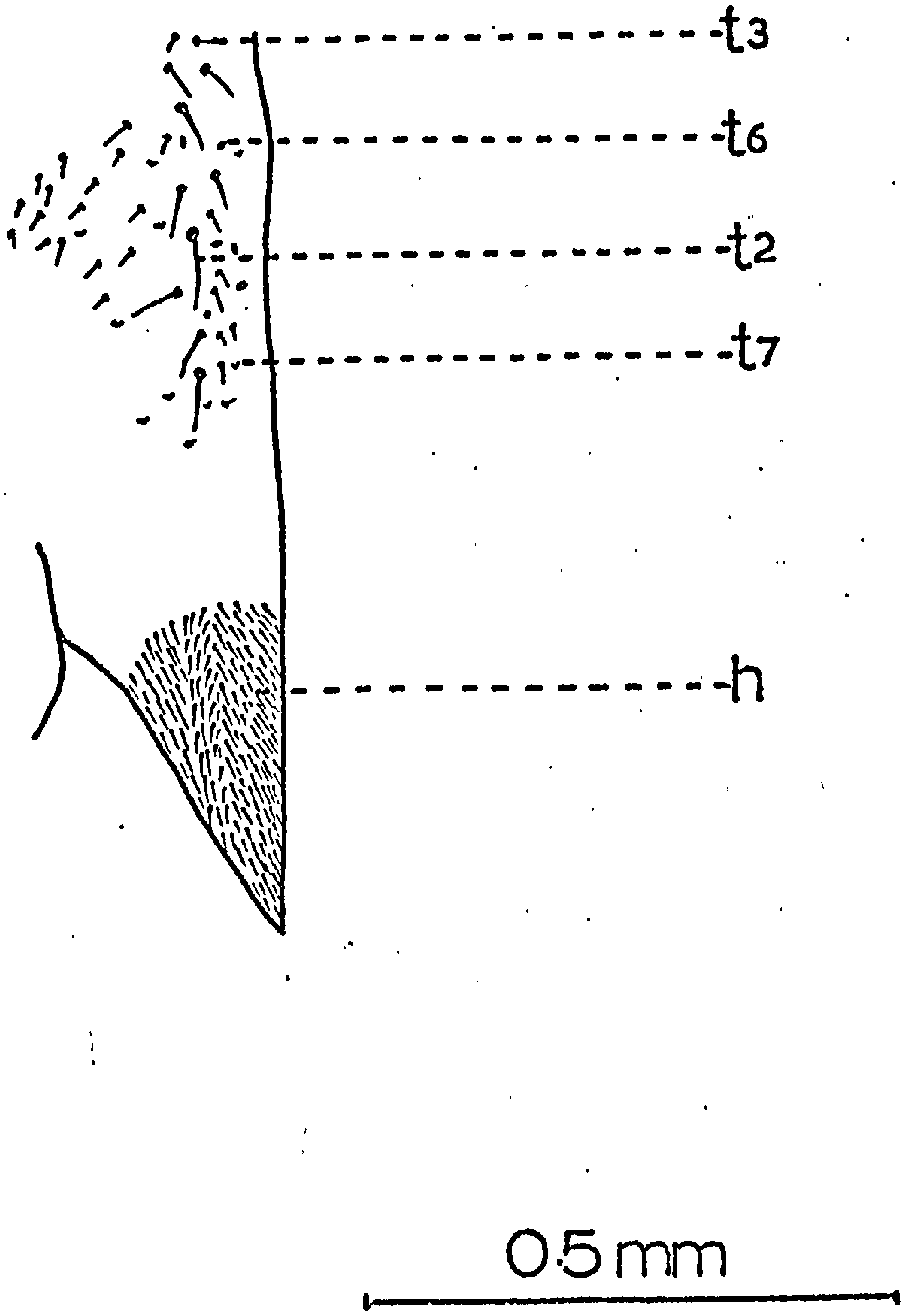


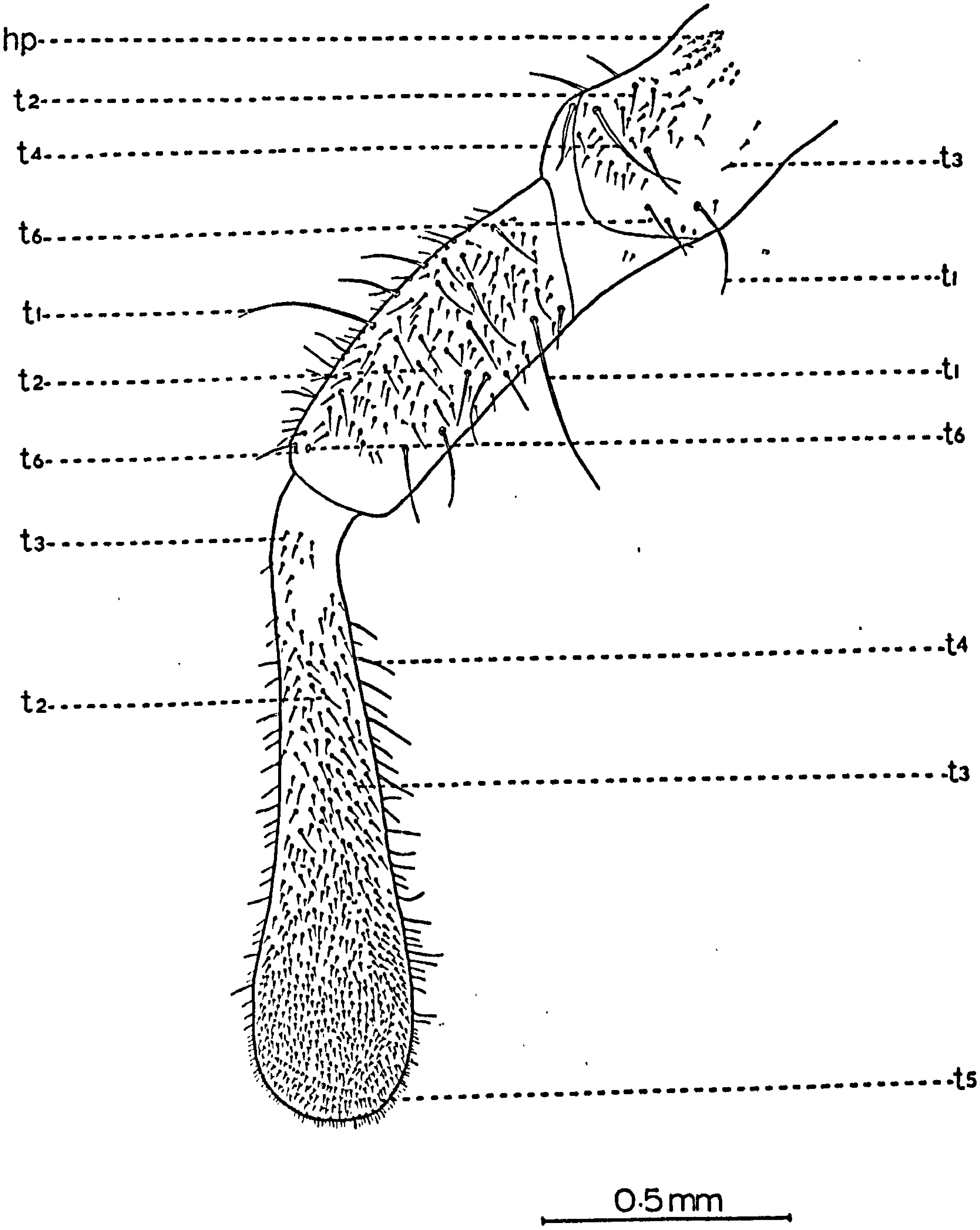
Fig.25

is slightly greater in the female, whereas Type 2 is more numerous in the male (Tables 5 and 6). Type 6 sensilla occur on the outer posterolateral border of the paraglossa and the same number is present in both sexes. Two or three Type 11 sensilla are present, towards the inner margin of the paraglossa in the male and female respectively (Tables 5 and 6).

On the anterior surface of the paraglossa of both sexes are sensilla of Types 2, 3, 4, 5 and 11 (Table 4). With few exceptions, the sensilla occur on the outer lateral part of the paraglossa. The stout setae of Types 2 and 4 produce a definite lateral, setaceous border to the paraglossa (Fig. 24b). Type 5 are again restricted to the tip of the paraglossa and together with Type 4 appear to be more numerous in the female than the male (Tables 5 and 6). However, the number of Type 11 sensilla is greater in the male. The lateral median surface of the paraglossa is also supplied with hairs.

The posterior surface of the glossa bears sensilla of Types 2, 3, 6 and 7 in both sexes (Table 4). All the sensilla are found in a cluster at the base of the paraglossa. The setae of Type 2 sensilla are somewhat longer in the male than the female, although only two instead of four are present in the male (Tables 5 and 6). Types 3 and 7 are also more numerous in the female (Tables 5 and 6)

Fig. 26. Distribution of sensilla on the posterior surface of the segments of the labial palp.



Fig·26

whilst Type 6 is marginally more common in the male (Tables 5 and 6). The distal portion of the glossa is densely covered with hairs (Fig. 25). The anterior surface of the glossa is membranous and bears no sensilla (Table 5).

The three segments of the labial palp are described in turn. The labial palp displays sensilla of Types 1, 2, 3, 4, 5 and 6 in both sexes (Table 4). On the posterior surface of the first palp segment is a proximal hair plate (Fig. 26). Of the sensilla types found on the labial palp only Type 5 is missing. Near the hair plate is a small group of Type 6 sensilla with another group positioned distally. Type 3 sensilla are the most widespread. The distribution and number of sensilla is remarkably consistent between the sexes.

The anterior surface of the first segment has the same sensilla types as the posterior surface. In the female there is a single Type 6 sensillum positioned in the middle of the segment (Fig. 27), whilst in the male there are two, both distally positioned. The other types have a similar distribution to that on the posterior surface (Fig. 26), although there is no hair plate anteriorly.

The posterior surface of the second segment of the palp bears sensilla of Types 1, 2, 3, 4 and 6 (Fig. 26). The Type 6 sensilla are distal in position and their typical campaniform structure can be seen in Plate 8b.

Fig. 27. Distribution of sensilla on the anterior surface of the segments of the labial palp.

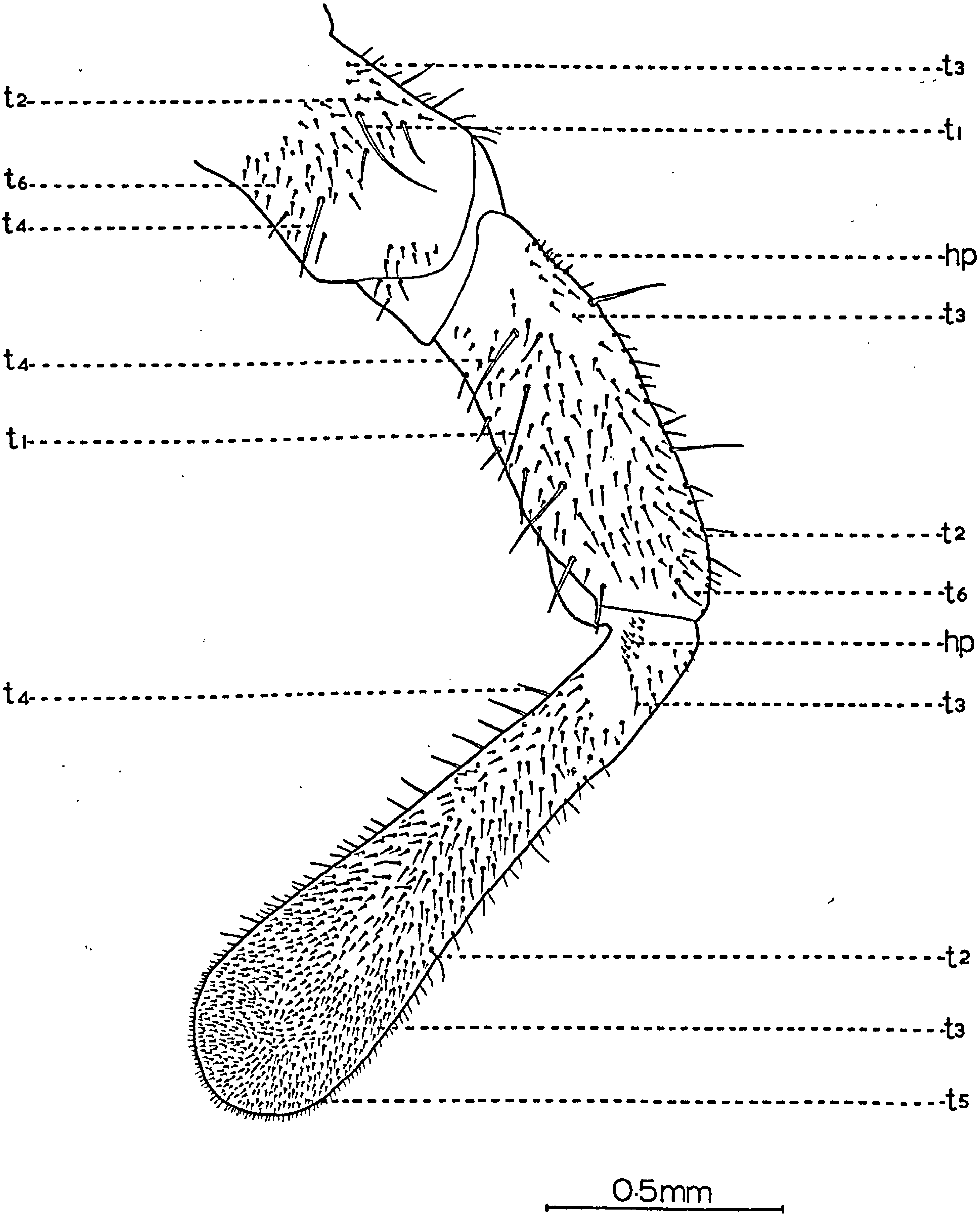


Fig. 27

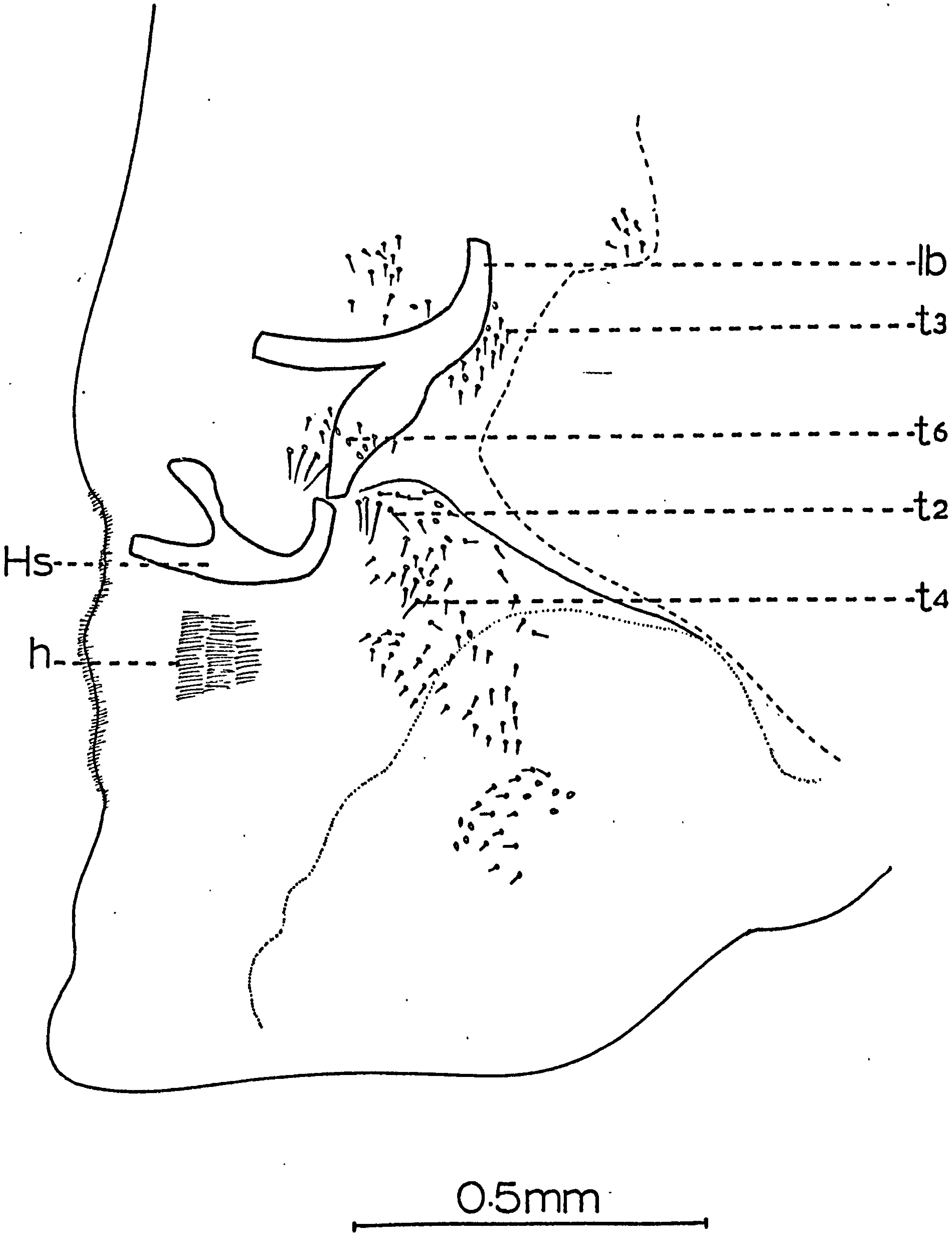
More Type 3 sensilla are found in the male than in the female, whilst the remaining types are similar in number in both sexes (Tables 5 and 6).

The anterior surface of the second segment is supplied with the same sensilla types as the posterior surface (Tables 5 and 6). Sensilla of Type 6 are again distal in position, whilst Types 2, 3 and 4 are widely scattered over the surface. There is a proximal hair plate on the outer side of the segment (Fig. 27).

The posterior surface of the third segment of the palp bears sensilla of Types 2, 3, 4 and 5 (Fig. 26). Types 1 and 6 are absent. Type 5 is restricted to the distal part of the segment. Type 4 sensilla are found only on the inner side of the segment, whilst Types 2 and 3 are scattered generally over its surface (Fig. 26).

The anterior surface of the terminal segment has a proximal hair plate formed of Type 3 sensilla (Fig. 27). Type 5 sensilla, although restricted in position to the distal end of this segment, are far more numerous in the female (Tables 5 and 6). A similar sexual difference is seen in the number of Type 2 sensilla (Tables 5 and 6). Thick, stout sensilla of Type 4 are situated laterally (Fig. 27). With the exception of Type 5 sensilla, there is a general similarity, both in the distribution and number of the sensilla, on both surfaces of this segment.

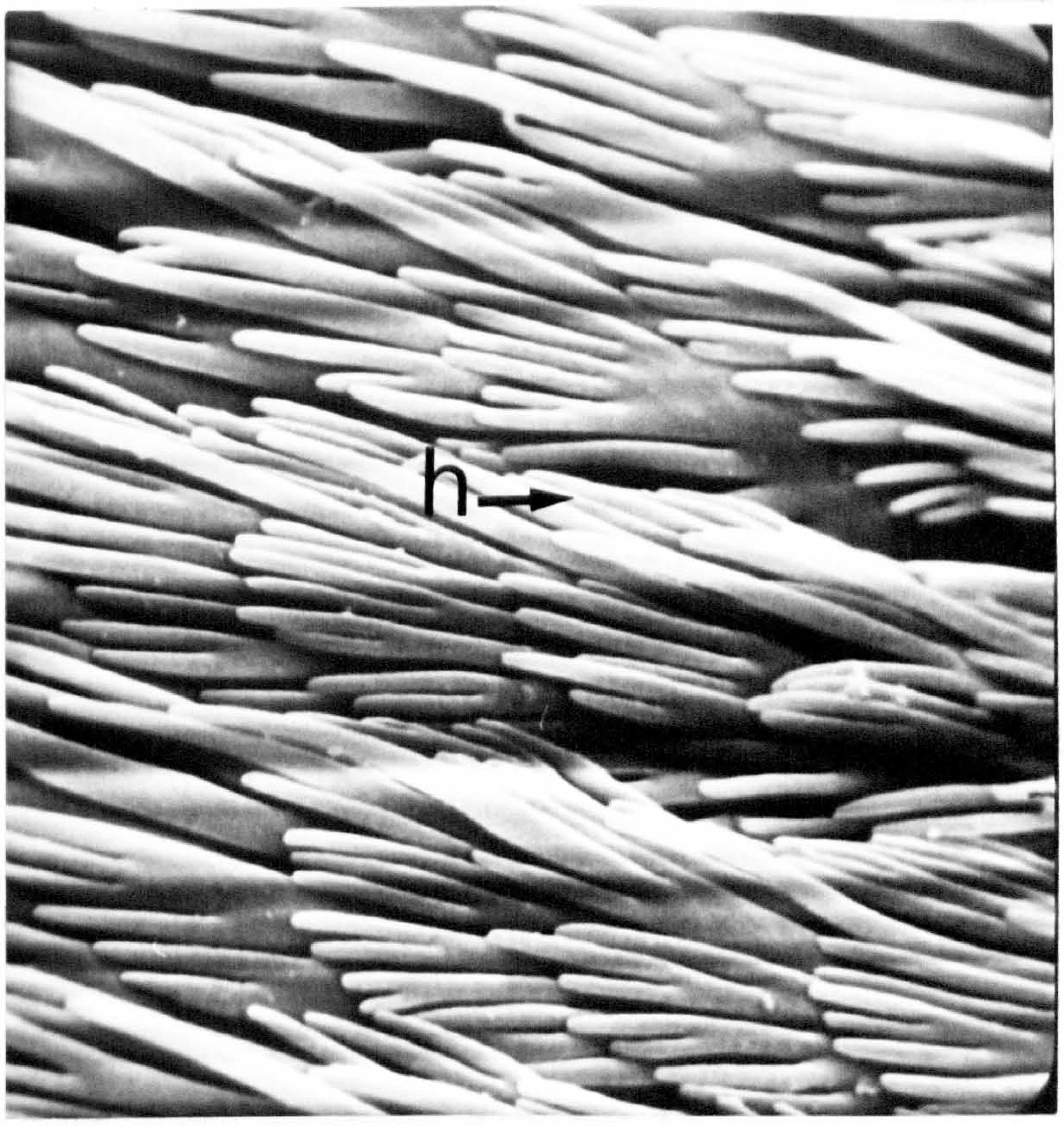
Fig. 28. Distribution of sensilla on the anterolateral surface of the hypopharynx.



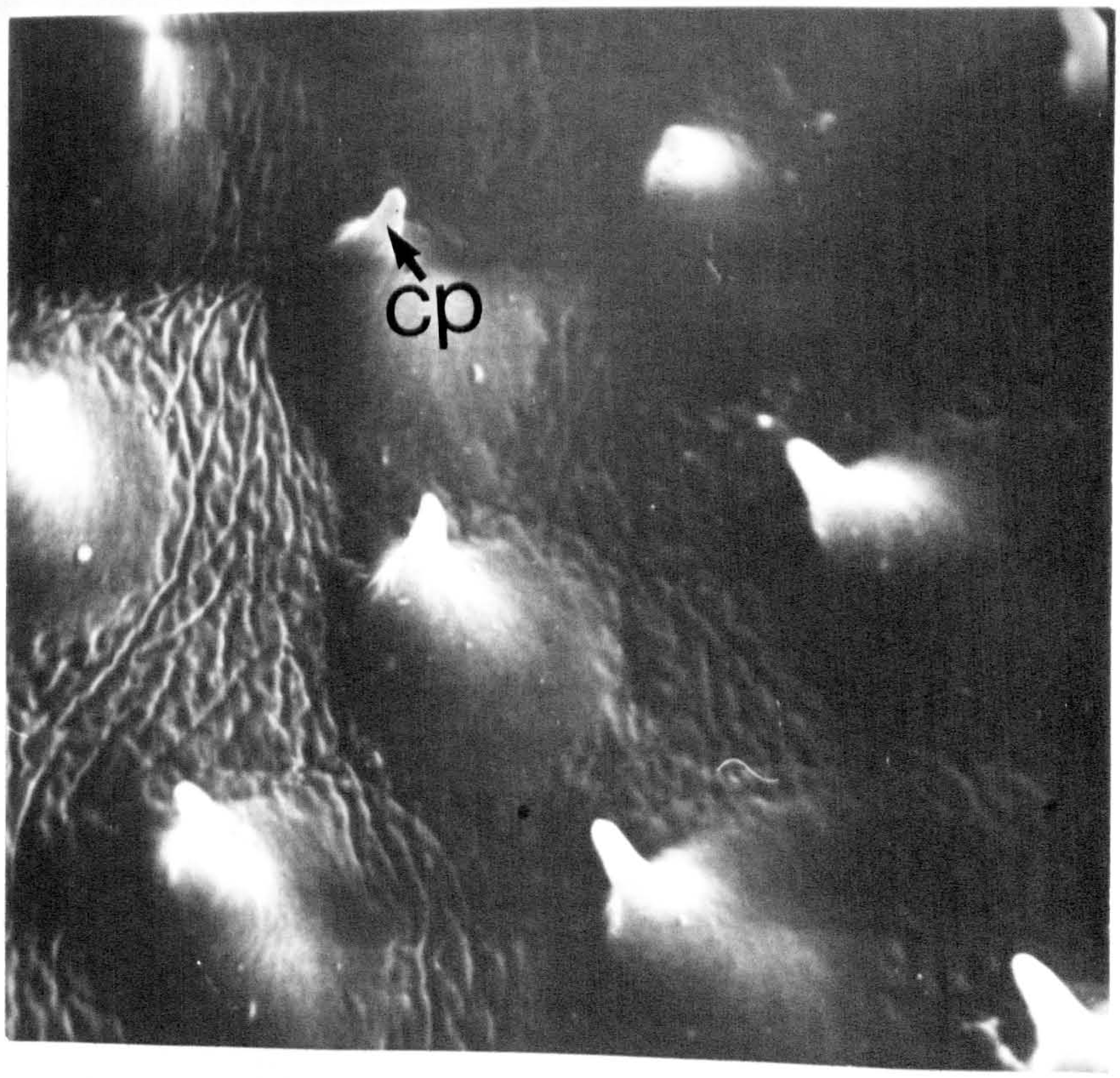
Fig·28

Plate 9a. Scanning electron micrograph of the finger-like hairs (h) present on the anterior surface of the hypopharynx (X 18142.5).

Plate 9b. Scanning electron micrograph of the cuticular projections (cp) found on the anterior surface of the hypopharynx at its distal end (X 18142.5).



a



b

5.5.d. Hypopharynx (Fig. 28)

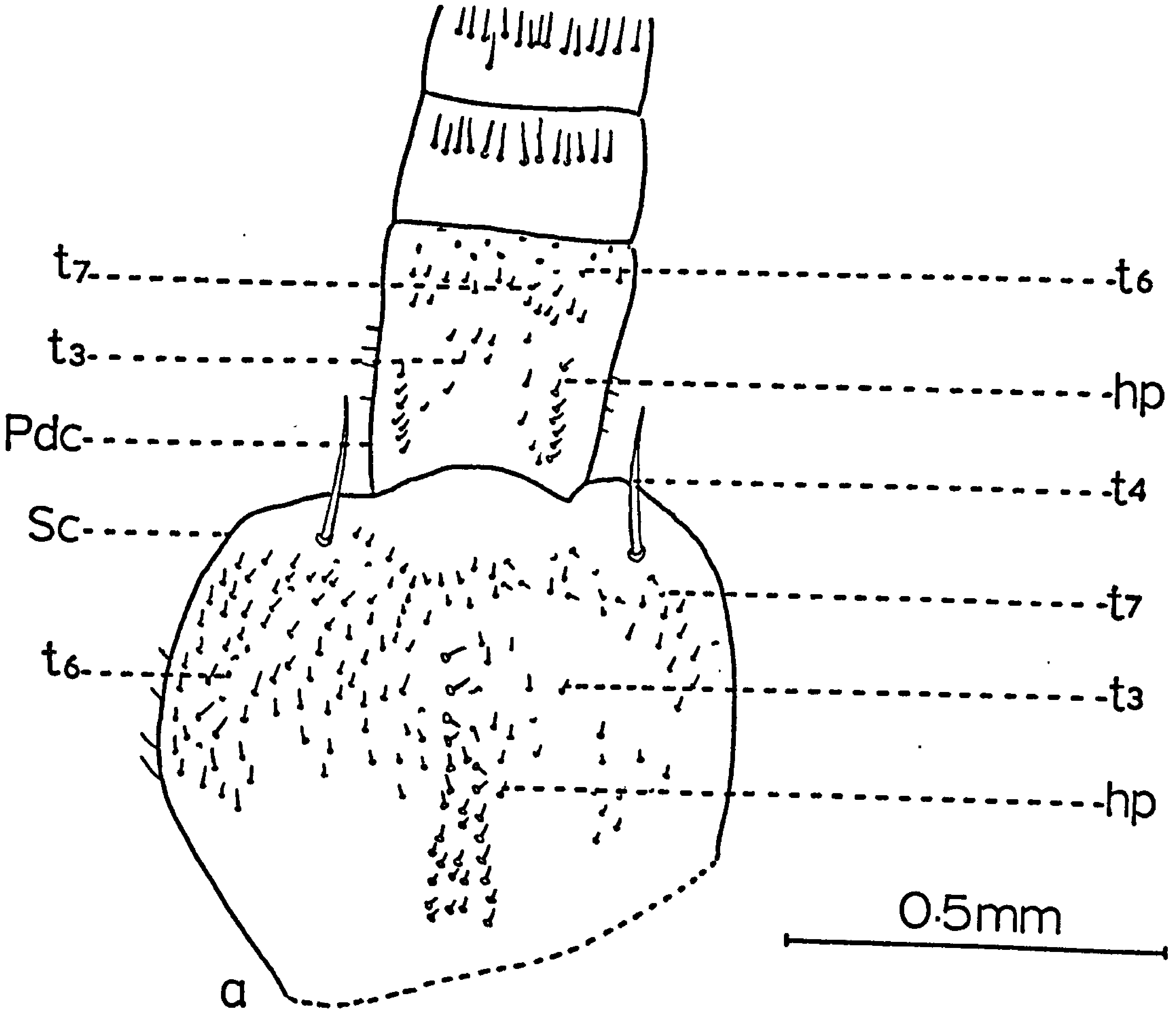
The hypopharynx is a bulbous tongue-like structure. The distribution of its sensilla is best described from an anterolateral aspect. Sensilla of Types 2, 3, 4 and 6 are present and are similar in distribution and number in both sexes (Tables 5 and 6). The sensilla are restricted to a lateral area (Fig. 28) around the suspensorial sclerite. In the most distal region, sensilla of Types 3 and 6 are situated laterally (Fig. 28). Type 6 occurs in small groups, whereas sensilla of Type 3 are distributed throughout this area and are the most common sensilla.

Approaching the suspensorial sclerite is a small cluster of Type 4 sensilla. A small number of Type 2 sensilla occurs below and between the suspensorial sclerite. In the proximal region of the hypopharynx sensilla of Types 3 and 6 are found in small groups around the suspensorial sclerite (Fig. 28). The scanning electron micrograph (Plate 9a) illustrates the presence of branched finger-like hairs on the anterior surface of the hypopharynx. These hairs may be mechanical in function and help in sweeping the food particles towards the mouth. In addition to the hairs there are also cuticular projections on the anterior surface of the hypopharynx (Plate 9b).

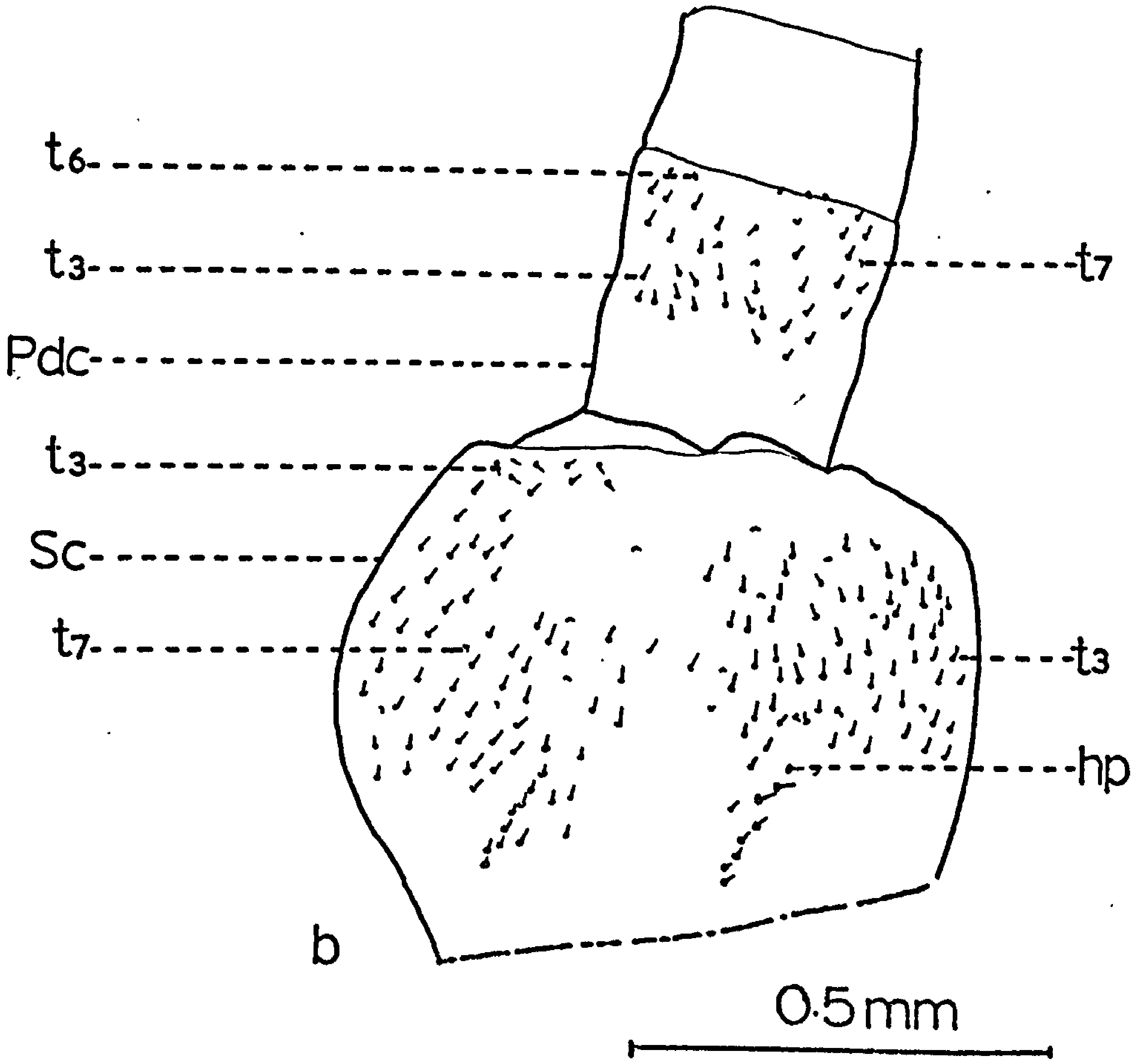
5.5.e. Antenna (Fig. 29)

Anteriorly the scape has a median row of setae with large sockets, these are of Type 2 sensilla and together form

Fig. 29. Distribution of sensilla on the scape and pedicel of the antenna; a, anterior surface; b, posterior surface.


t7
t3
Pdc
Sc
t6
t6
hp
t4
t7
t3
hp
0.5mm

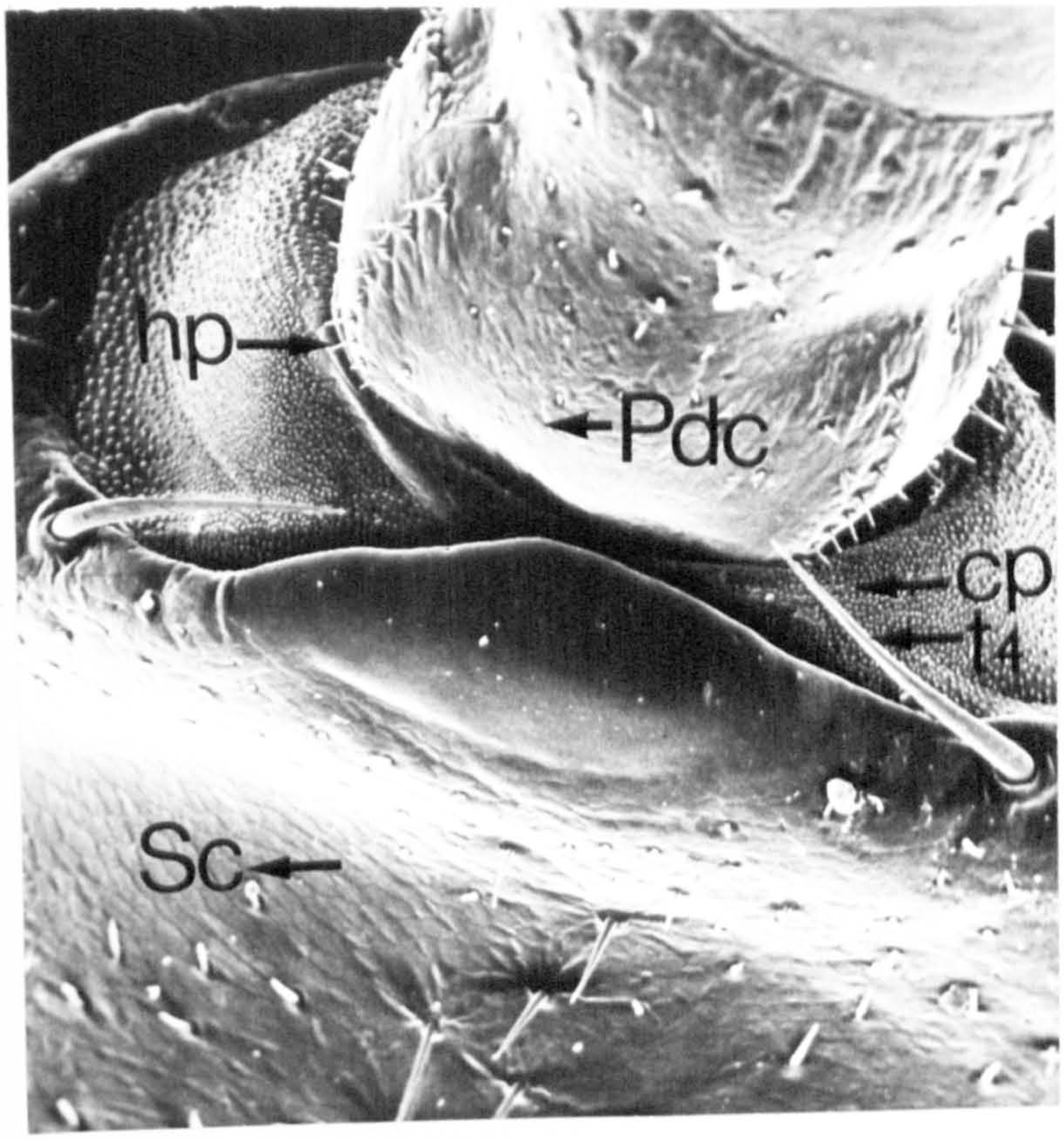
a


t6
t3
Pdc
t3
Sc
t7
t7
t3
hp
0.5mm

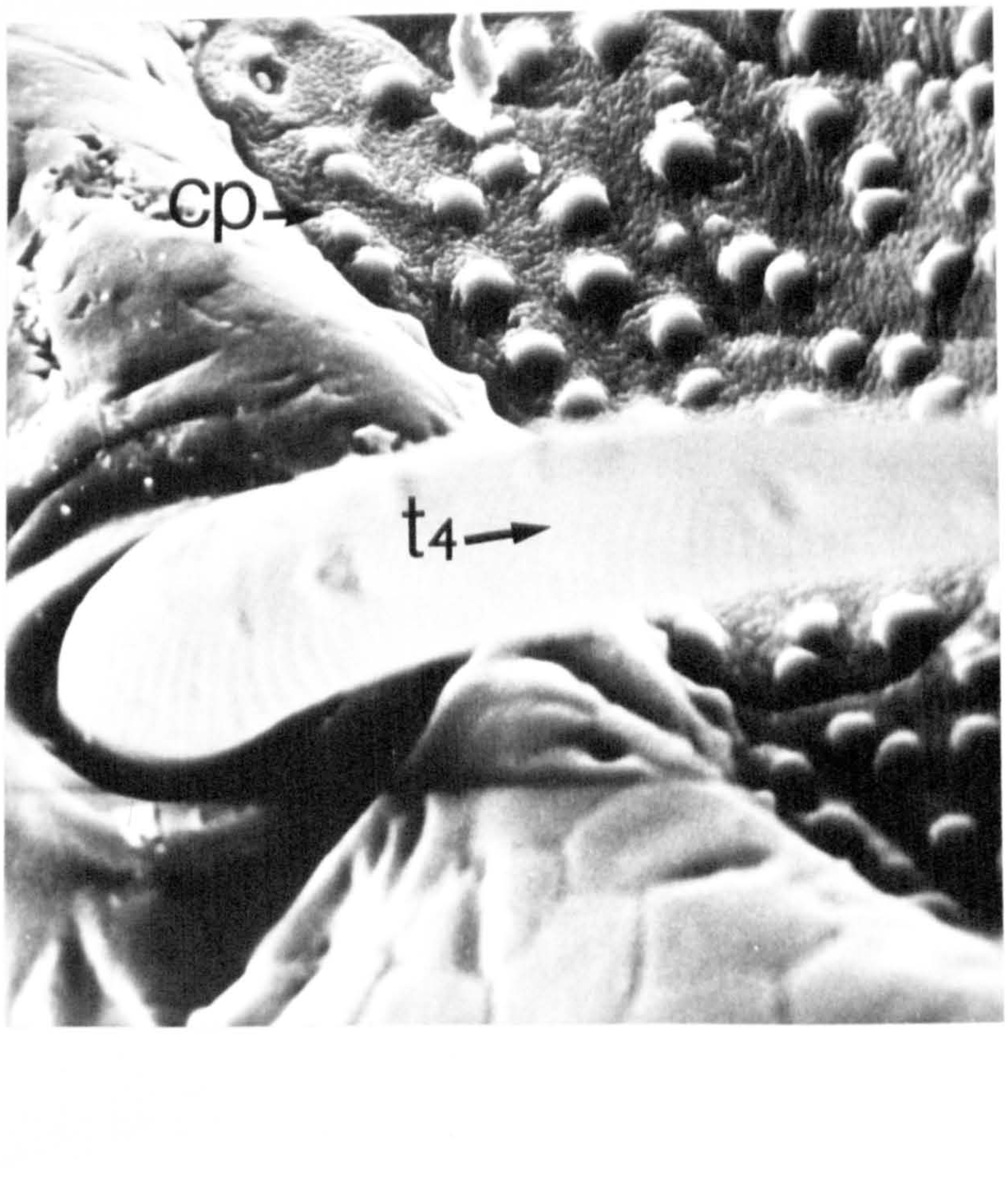
b

Plate 10a. Scanning electron micrograph of the Type 4 sensilla on the distal margin of the scape (Sc). The cuticular projections (cp) are present on the membrane between the scape (Sc) and pedicel (Pdc). Sensilla forming hair plates (hp) are also present on the pedicel (X 725.7).

Plate 10b. Higher power scanning electron micrograph of the Type 4 sensilla, together with the cuticular projections (cp) (X 7257).



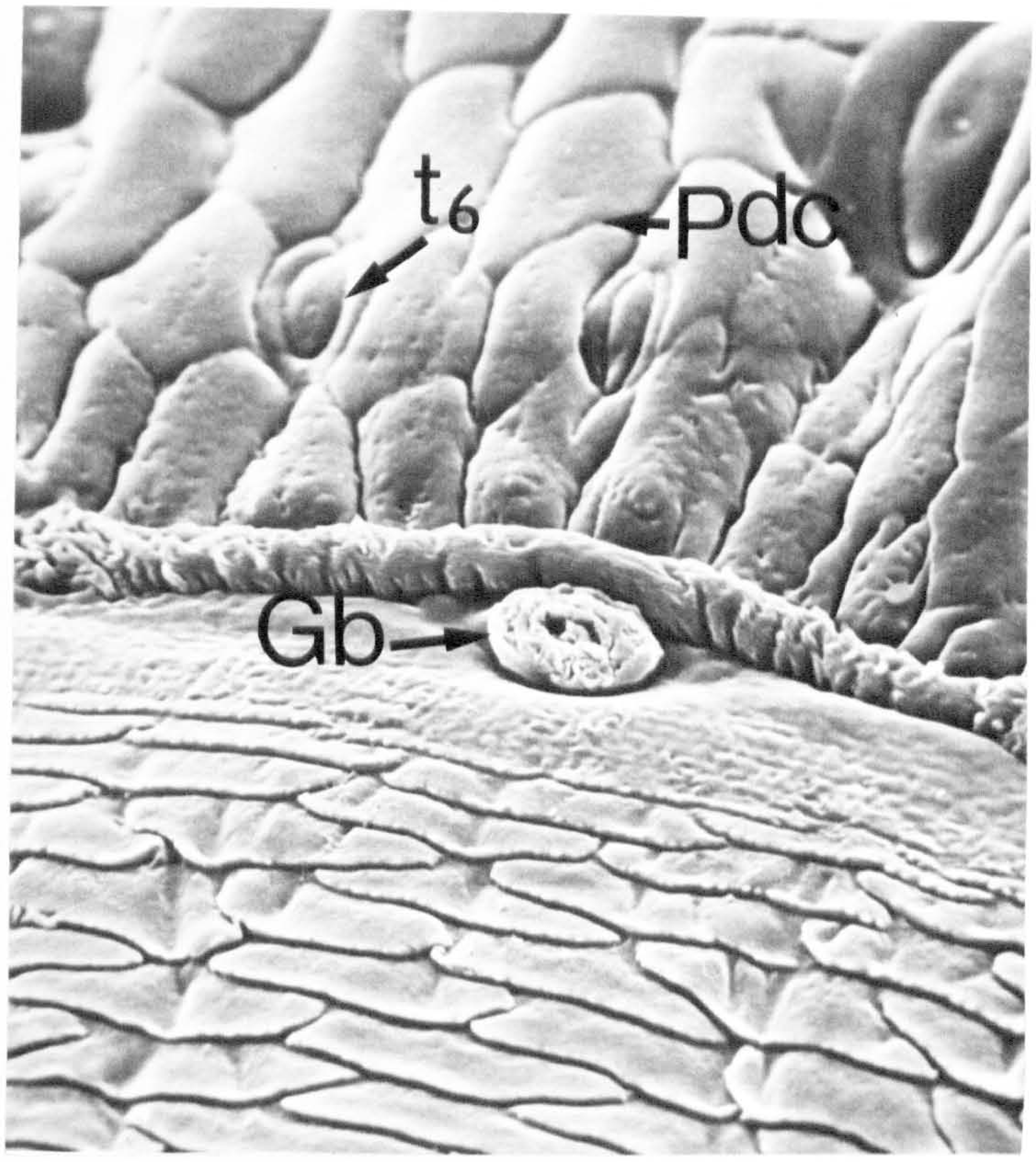
a



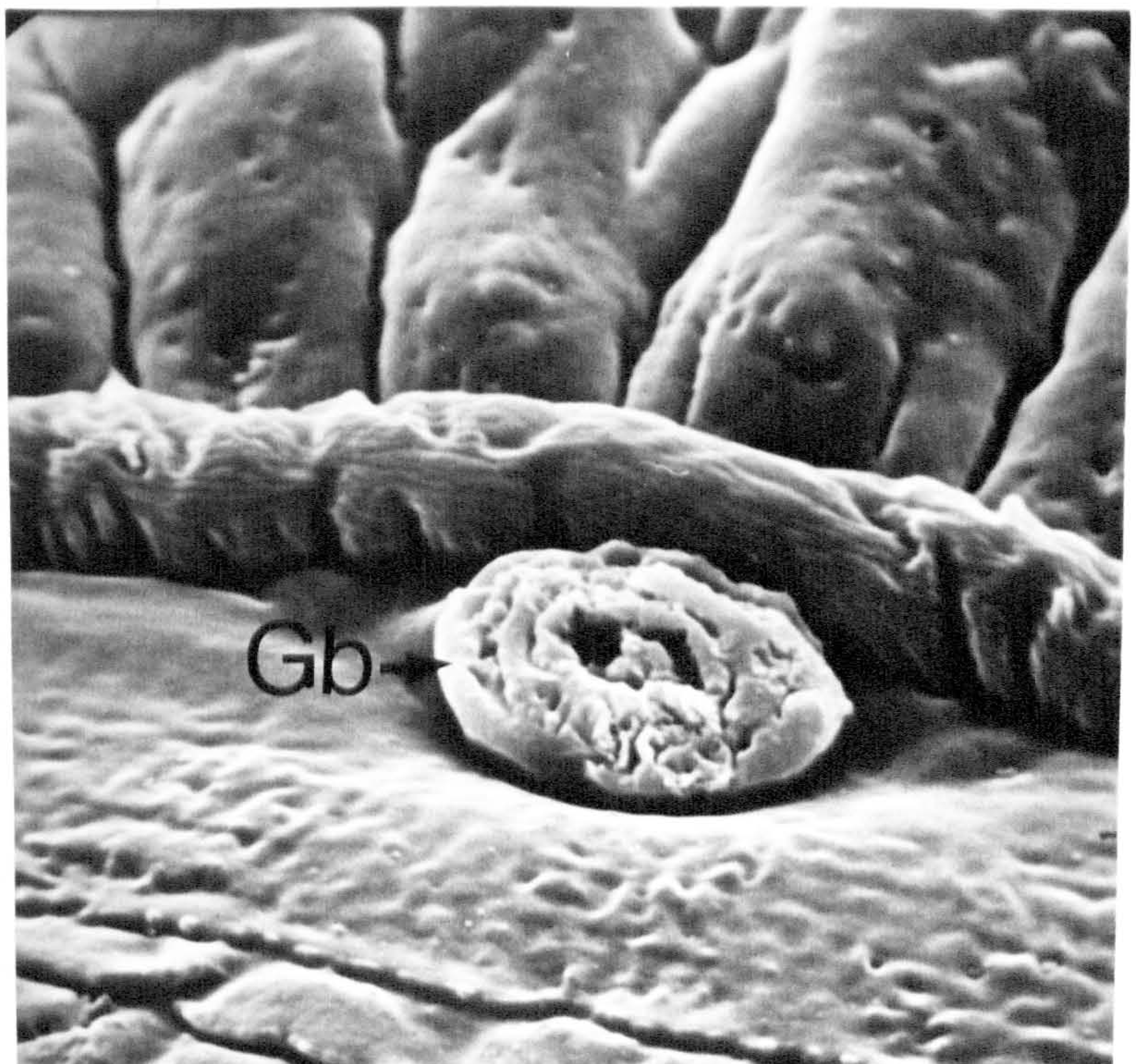
b

Plate 11a. Scanning electron micrograph of the Type 6 sensilla found on the distal portion of the pedicel (Pdc) and the globular sensilla (Gb) on the first segment of the flagellum (X 7257).

Plate 11b. Higher power scanning electron micrograph of the globular sensilla (Gb) on the first segment of the flagellum (X 18142.5).



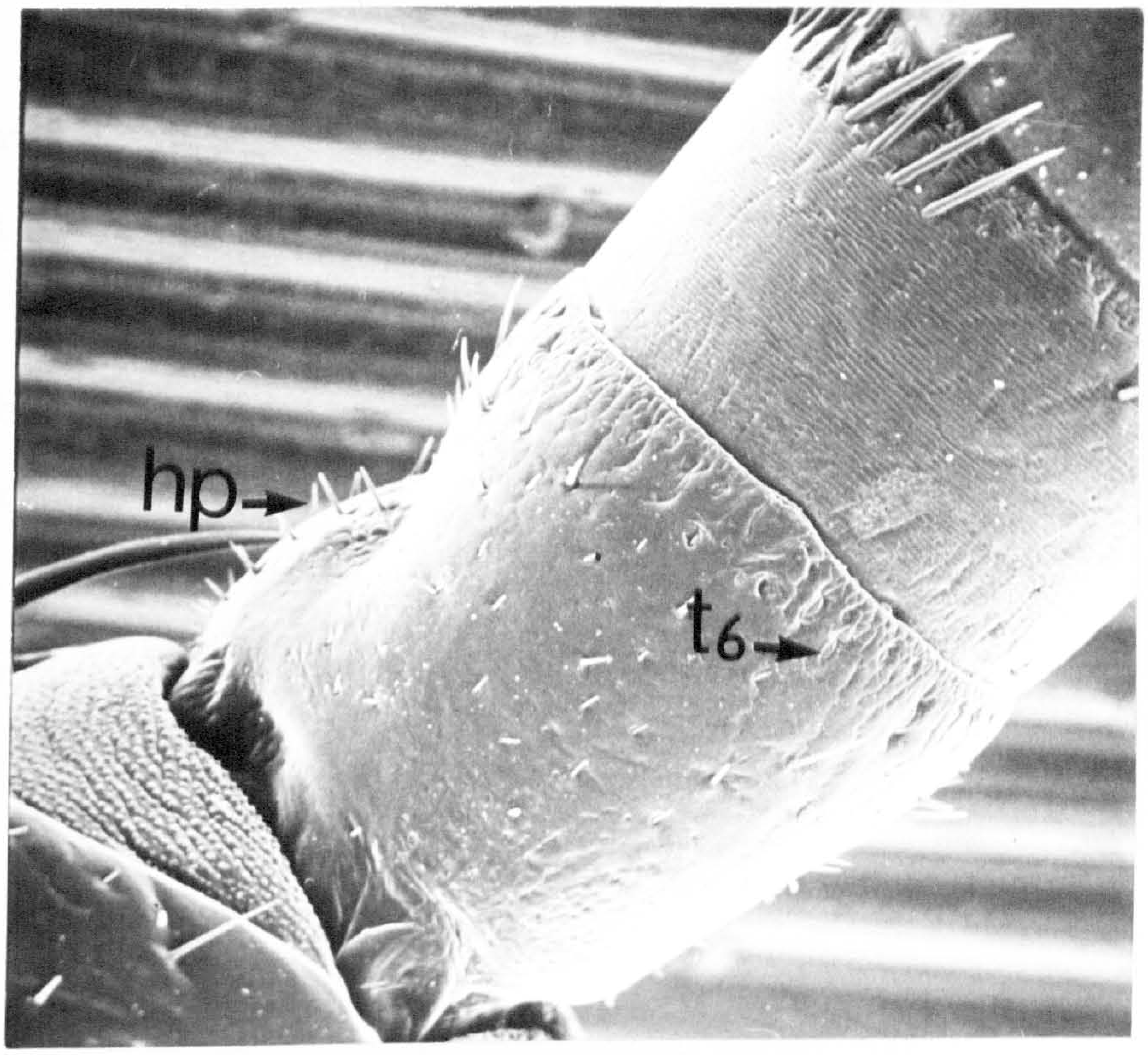
a

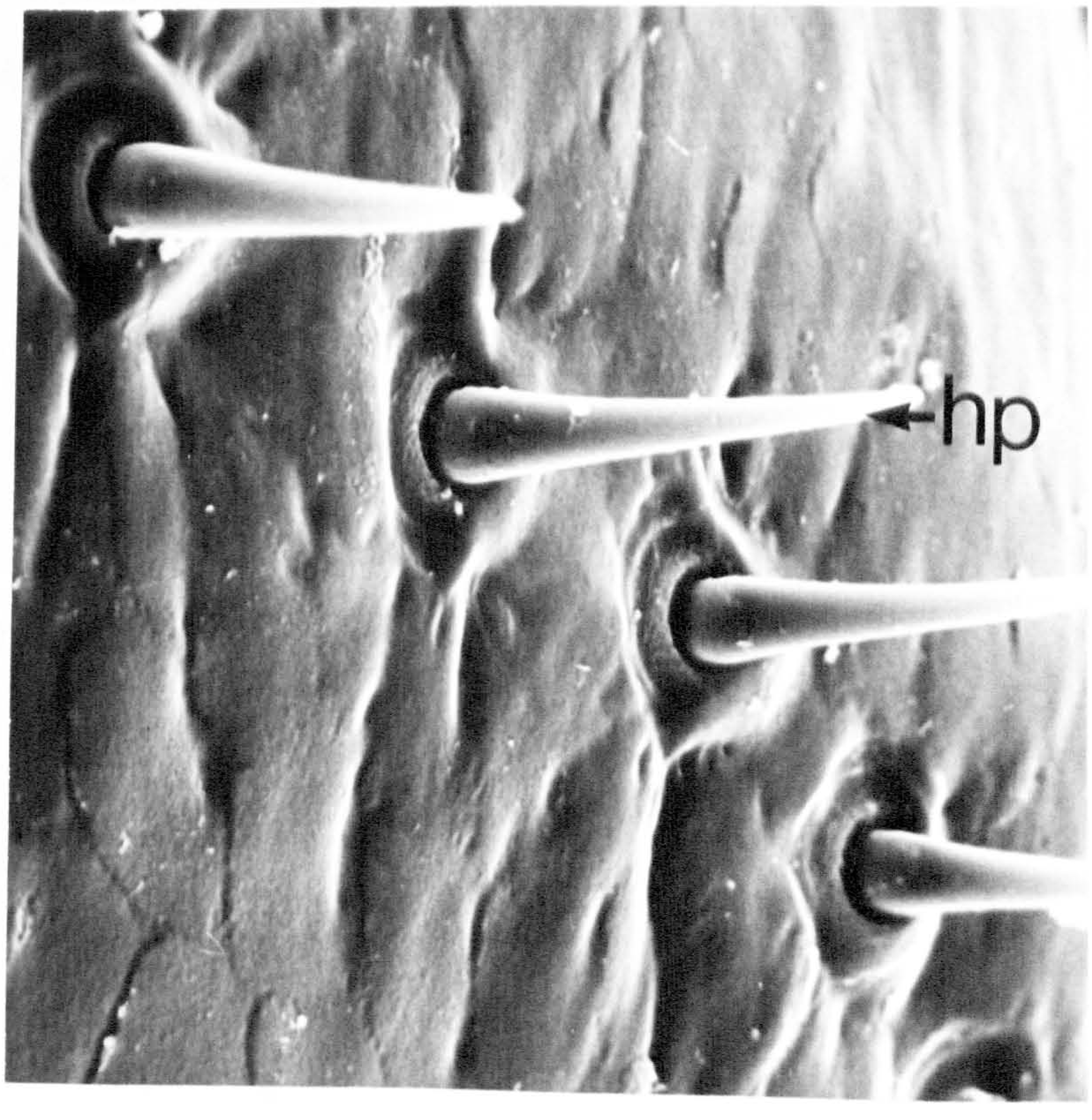


b

Plate 12a. Scanning electron micrograph of the pedicel of the antenna illustrating the lateral hair plate (hp) and the Type 6 sensilla present on the distal margin (X 362.85).

Plate 12b. Scanning electron micrograph of the hair plate sensilla (hp) present on the pedicel (X 7257).


hp
t6
a


hp
b

a hair plate (Plate 10a). The remainder of this surface is covered with sensilla of Types 3, 4 and 6 (Fig. 29a). Type 3 is the most numerous, although sensilla of this type do not extend to the base of the segment. On the distal margin there are two prominent stout setae of Type 4 sensilla (Fig. 29a). These lie on each side of the scape, their separation being slightly greater than the basal diameter of the pedicel (Plate 10a). These setae are fairly consistent in length (203 - 208u) and have a basal diameter of 12.5 - 13u and a socket diameter of 23.5 - 24u. Scanning electron micrographs demonstrate that the wall of these sensilla has a spiral sculpturing (Plate 10b).

On the posterior surface of the scape there are two rows of sensilla of Type 2 forming hair plates (Fig. 29b). Types 3 and 7 sensilla are generally scattered over the surface and Type 3 is again the dominant type (Table 5).

The membranous portion between the scape and the pedicel bears cuticular projections on its surface (Plates 10a, b and 12a).

On the anterior side of the pedicel there are two hair plates running parallel to the sides of the segment (Plates 10a and 12a, b). The other sensilla of Types 3 and 7 are mostly found in the distal half of the segment and these spread around to the anterior side also. Type 6 campaniform sensilla are present in a ring around the distal margin of the pedicel (Plate 11a). The number of sensilla

Table 4 Types of sensilla on the mouthparts and related structures of adults of both sexes. (+ = presence; – = absence of sensilla. Sign in parenthesis indicate situation in male only)

Structure				Types of sensilla												
			t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
Clypeolabrum		ant. surface	+	+	+	–	–	–	+	–	–	–	–	–	+
		post. "	–	–	+	+	–	+	–	+	+	+	–	–	–
Mandible		ant. "	–	–	+	–	–	+	+	–	–	–	–	+	–
		post. "	–	–	+	+	–	+	+	–	–	–	–	+	–
Maxilla	Cardo	post. "	–	+	+	+	–	–	+	–	–	–	–	–	–
	"	ant. "	–	+	+	+	–	–	–	–	–	–	–	–	–
	Stipes	post. "	(–) +	(+) –	+	–	–	+	(–) +	–	–	–	–	–	–
	"	ant. "	(–) +	+	+	+	–	–	–	–	–	–	–	–	–
	Galea	post. "	+	+	+	+	+	+	–	–	–	+	+	–	–
	"	ant. "	+	–	+	+	+	+	(+) –	–	–	–	–	–	–
	Lacinia	post. "	–	–	+	+	–	+	+	–	–	–	–	+	–
	"	ant. "	+	+	+	+	–	+	+	–	–	–	–	–	–

Table 4 (Continued)

Types of sensilla

Structure	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
Palp post.surface	–	+	+	+	+	+	(–)	–	–	–	–	–	–
" ant. "	+	+	+	+	+	+	±	–	–	–	–	–	–
<u>Labium</u> Submentum post. "	+	+	+	+	–	–	+	–	–	–	–	–	–
Mentum " "	+	+	+	–	–	–	+	–	–	–	–	–	–
Prementum " "	+	+	+	–	–	–	+	–	–	–	–	–	–
Paraglossa " "	+	+	+	+	+	+	+	–	–	–	+	–	–
" ant. "	–	+	+	+	+	–	–	–	–	–	+	–	–
Glossa post. "	–	+	+	–	–	+	+	–	–	–	–	–	–
" ant. "	–	–	–	–	–	–	–	–	–	–	–	–	–
Palp post. "	+	+	+	+	+	+	–	–	–	–	–	–	–
" ant. "	–	+	+	+	–	+	–	–	–	–	–	–	–
<u>Hypopharynx</u> anterolateral "	–	+	+	+	–	+	–	–	–	–	–	–	–
<u>Antenna</u> Scape ant. "	–	+	+	+	–	+	+	–	–	–	–	–	–
" post. "	–	+	+	–	–	–	+	–	–	–	–	–	–
Pedicel ant. "	–	+	+	–	–	+	+	–	–	–	–	–	–
" post. "	–	–	+	–	–	+	+	–	–	–	–	–	–

Table 5 Types and number of sensilla on the mouthparts and related structures of adult female A. domesticus

Types of sensilla

Structure		t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
Clypeolabrum	ant. surface	13	26	577	-	-	-	98	-	-	-	-	-	4
	post. "	-	-	240	194	-	21	-	13	24	150	-	-	-
Mandible	ant. "	-	-	80	-	-	20	24	-	-	-	-	+	-
	post. "	-	-	110	55	-	6	146	-	-	-	-	+	-
Maxilla Cardo	post. "	-	12	91	8	-	-	3	-	-	-	-	-	-
"	ant. "	-	4	22	4	-	-	-	-	-	-	-	-	-
Stipes	post. "	1	-	153	-	-	17	9	-	-	-	-	-	-
"	ant. "	1	10	54	5	-	-	-	-	-	-	-	-	-
Galea	post. "	14	19	27	12	27	21	-	-	-	152	10	-	-
"	ant. "	6	-	43	4	18	24	-	-	-	-	-	-	-
Lacinia	post. "	-	-	38	36	-	7	50	-	-	-	-	6	-
"	ant. "	5	7	12	12	-	11	2	-	-	-	-	-	-
1st plp.seg.post.	"	-	7	31	12	-	-	-	-	-	-	-	-	-
2nd " " "	"	-	13	35	10	-	-	4	-	-	-	-	-	-
3rd " " "	"	-	22	71	39	-	2	-	-	-	-	-	-	-
4th " " "	"	-	10	38	32	-	4	-	-	-	-	-	-	-
5th " " "	"	-	37	167	103	130	-	-	-	-	-	-	-	-

Table 5 (Continued)

Structure	Types of sensilla												
	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
1st plp.seg.ant.surface	1	3	46	1	–	–	–	–	–	–	–	–	–
2nd " " " "	–	–	52	2	–	7	–	–	–	–	–	–	–
3rd " " " "	6	7	53	–	–	2	–	–	–	–	–	–	–
4th " " " "	1	5	32	19	–	–	–	–	–	–	–	–	–
5th " " " "	–	–	170	125	186	–	–	–	–	–	–	–	–
<u>Labium</u> Submentum post. "	12	37	260	8	–	–	35	–	–	–	–	–	–
Mentum " "	6	2	123	–	–	–	16	–	–	–	–	–	–
Prementum " "	6	13	130	–	–	–	30	–	–	–	–	–	–
Paraglossa " "	7	20	68	10	35	4	25	–	–	–	3	–	–
" ant. "	–	2	4	52	27	–	–	–	–	–	14	–	–
Glossa post. "	–	4	25	–	–	6	10	–	–	–	–	–	–
" ant. "	–	–	–	–	–	–	–	–	–	–	–	–	–
1st plp.seg. post. "	1	5	46	3	–	8	–	–	–	–	–	–	–
2nd " " " "	3	12	38	4	–	2	–	–	–	–	–	–	–
3rd " " " "	–	19	460	18	122	–	–	–	–	–	–	–	–
1st " " ant. "	1	4	44	3	–	1	–	–	–	–	–	–	–
2nd " " " "	2	7	68	10	–	3	–	–	–	–	–	–	–
3rd " " " "	–	21	452	15	262	–	–	–	–	–	–	–	–

Table 5 (Continued)

Structure	Types of sensilla												
	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
<u>Hypopharynx</u> anterolateral surface	-	8	106	6	-	24	-	-	-	-	-	-	-
<u>Antenna</u> Scape ant. "	-	29	112	2	-	2	14	-	-	-	-	-	-
" post. "	-	17	109	-	-	-	13	-	-	-	-	-	-
Pedicel ant. "	-	15	21	-	-	13	5	-	-	-	-	-	-
" post. "	-	-	38	-	-	22	3	-	-	-	-	-	-

Table 6 Types and number of sensilla on the mouthparts and related structures of adult male *A. domesticus*

Types of sensilla

Structure		t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
Clypeolabrum	ant. surface	12	24	581	-	-	-	91	-	-	-	-	-	4
	post. "	-	-	252	196	-	22	-	11	27	150	-	-	-
Mandible	ant. "	-	-	76	-	-	21	29	-	-	-	-	+	-
	post. "	-	-	115	51	-	5	145	-	-	-	-	+	-
Maxilla Cardo	post. "	-	10	122	12	-	-	15	-	-	-	-	-	-
"	ant. "	-	7	24	6	-	-	-	-	-	-	-	-	-
Stipes	post. "	-	2	142	-	-	11	-	-	-	-	-	-	-
"	ant. "	-	11	51	6	-	-	-	-	-	-	-	-	-
Galea	post. "	12	16	31	22	28	21	-	-	-	128	8	-	-
"	ant. "	2	-	61	8	23	24	14	-	-	-	-	-	-
Lacinia	post. "	-	-	46	21	-	8	31	-	-	-	-	6	-
"	ant. "	5	8	26	13	-	12	5	-	-	-	-	-	-
1st plp.seg.post.	"	-	4	35	17	-	-	-	-	-	-	-	-	-
2nd " " "	"	-	12	32	9	-	-	-	-	-	-	-	-	-
3rd " " "	"	-	18	75	33	-	2	-	-	-	-	-	-	-
4th " " "	"	-	11	40	25	-	3	-	-	-	-	-	-	-
5th " " "	"	-	35	310	92	102	11	-	-	-	-	-	-	-
1st plp.seg.ant.	"	1	2	46	1	-	-	-	-	-	-	-	-	-
2nd " " "	"	-	4	48	2	-	7	-	-	-	-	-	-	-

Table 6 (Continued)

Types of sensilla

Structure	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
3rd plp.seg.ant.surface	6	8	56	–	–	2	–	–	–	–	–	–	–
4th " " " "	1	5	39	12	–	–	–	–	–	–	–	–	–
5th " " " "	–	–	178	131	190	–	–	–	–	–	–	–	–
Labium Submentum post. "	12	39	419	8	–	–	62	–	–	–	–	–	–
Mentum " "	2	4	113	–	–	–	4	–	–	–	–	–	–
Prementum " "	6	10	165	–	–	–	8	–	–	–	–	–	–
Paraglossa " "	7	22	65	8	26	4	22	–	–	–	2	–	–
" ant. "	–	5	10	35	6	–	–	–	–	–	22	–	–
Glossa post. "	–	2	16	–	–	10	4	–	–	–	–	–	–
" ant. "	–	–	–	–	–	–	–	–	–	–	–	–	–
1st plp.seg.post. "	1	4	48	2	–	8	–	–	–	–	–	–	–
2nd " " " "	3	5	51	7	–	2	–	–	–	–	–	–	–
3rd " " " "	–	12	469	16	143	–	–	–	–	–	–	–	–
1st plp.seg.ant. "	2	5	31	2	–	1	–	–	–	–	–	–	–
2nd " " " "	1	5	63	6	–	3	–	–	–	–	–	–	–
3rd " " " "	–	9	454	15	116	–	–	–	–	–	–	–	–
Hypopharynx anterolateral "	–	8	109	6	–	28	–	–	–	–	–	–	–
Antenna Scape ant. "	–	27	119	2	–	1	11	–	–	–	–	–	–
" post. "	–	16	114	–	–	–	12	–	–	–	–	–	–
Pedicel ant. "	–	14	22	–	–	13	4	–	–	–	–	–	–
" post. "	–	–	36	–	–	21	3	–	–	–	–	–	–

are similar in both sexes (Tables 5 and 6).

Although the sensilla of the flagellum have not been given detailed treatment, it is worth mentioning that on the first flagellar segment, near to the junction of the pedicel, are globular sensilla (Plate 11a and b). These were only investigated in the female. To the author's knowledge they have not been recorded in any other insect species.

5.6 Distribution of Sensilla on the Clypeolabrum of nymphal instars

In order to fully appreciate the adult complement of sensilla and possibly to throw light on the function of certain types of sensilla, the distribution of sensilla in the immature stages was investigated. This was not intended to be a major section of the work; consequently, only the development of the sensilla of the clypeolabrum was investigated. This structure was particularly appropriate to a study of development since a large number of different types of sensilla are present and they are often arranged in discrete groups. This makes their identification simpler and more accurate.

The number of nymphal instars is known to vary from eleven to thirteen (Ragge, 1965; Rummel, 1963). For this reason a small number of measurements were taken on freshly moulted instars to determine accurately the number of instars in the culture being used in this work. The structures

Table 7 Measurement of parts of the body to determine the number of instars (mean value in mm)

Instar	Mean ($\bar{x}$)	Length of body	Breadth of head	Length of Promotum	Length of Forewing	Length of hind femur	Length of Ovipositor
1	$\bar{x}$	2.16	0.43	0.33	-	0.93	-
2	$\bar{x}$	3.6	0.85	0.85	-	1.7	-
3	$\bar{x}$	4.15	1	1	-	2	-
4	$\bar{x}$	5.1	1	1	-	2.25	-
5	$\bar{x}$	6.5	1.07	1.02	-	3.15	rudiment
6	$\bar{x}$	8.1	1.75	1.3	-	4.2	rudiment
7	$\bar{x}$	9	1.85	1.45	-	4.35	.4
8	$\bar{x}$	12.33	2.5	1.96	-	5.96	1
9	$\bar{x}$	14.1	2.7	2.3	-	6.6	1.6
10	$\bar{x}$	14.55	3	2.5	2.05	7.5	2
11	$\bar{x}$	17.35	3.58	2.78	3.84	8.77	4.52
Adult	$\bar{x}$	18.87	4.15	2.92	11.77	9.15	10.77

measured were the length of the body, the breadth of the head, the length of the pronotum, the length of the forewing, the length of the hindwing and the length of the ovipositor. The results are summarized in Table 7, and the full data given in Appendix I. From these results, it became apparent that there were twelve instars including the adult. This number agrees with that suggested by Ragge (1965).

Table 8 gives a summary of the number of sensilla in the various A groups discussed on Page 279.
The full data is given in Appendix II. Table 9 gives the total number of each sensilla type found on the anterior and posterior face of the clypeolabrum. Diagrams of the first, fifth, seventh and eleventh instars are included as examples (Figs. 30, 31 and 32).

On the anterior surface of the clypeolabrum of the first instar (Fig. 30a) sensilla of Types 1, 2 and 13 occur. There are 10 sensilla of Type 1, 6 of which are arranged in two rows in the middle of the labrum, thereby closely resembling the condition found in the adult. By the third instar this type has reached the full number found in the adult.

The rudiments of the four Type 13 sensilla present in the adult are apparent in the first instar (Fig. 30a), but are only fully developed in the fifth instar (Fig. 30b). Eight Type 2 sensilla are present in the first and second instars and are widely scattered in the area lateral to the

Fig. 30. Distribution of sensilla on the anterior surface of the clypeolabrum: a, first instar; b, fifth instar; c, seventh instar.

Fig. 30

Type 1 sensilla. These increase in number in the third instar and continue to do so until the adult complement of 24 is reached in the eighth instar (Table 9). As the number increases this type of sensilla spreads to lateral margins of the labrum.

It is interesting to note that the most widespread type (Type 3) is absent from the anterior surface of the first instar but after the second instar generally increases at each ecdysis by ten or more. However, a far more striking increase occurs at the moult into the fifth instar (Fig. 30b), where the number increases from 16 to 70, and also at the moult into the seventh (Fig. 30c) when the number reaches 182 (Table 9). In the adult (Fig. 5) the labrum is densely covered with this type of sensilla. A very similar picture is seen in the Type 7 sensilla but here the increase in is more gradual (Table 9).

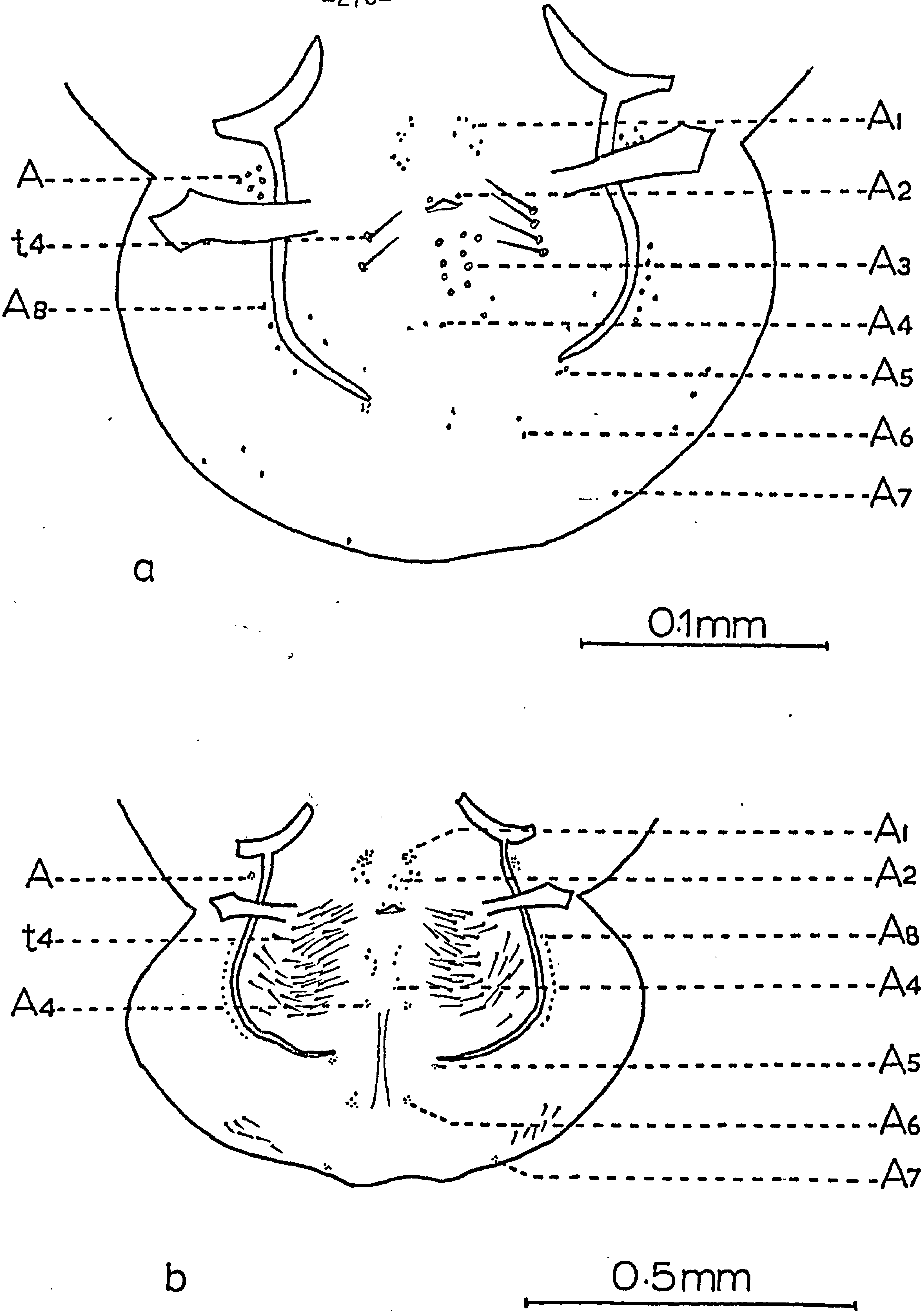
Thus it may be said that there is a gradual increase in the number of Types 2 and 7 sensilla whereas more abrupt changes occur in the development of Type 3 sensilla. In the sensilla of Type 1 there is no further increase in number after the third instar. Type 13 is present at least as rudiments in its full adult complement throughout development.

On the posterior surface of the clypeolabrum are many different groups of sensilla. Even in the first instar 9 groups (A_1 - A_9) occur. Table 8 gives a summary of the number of sensilla in each group for each instar. In most groups, there is a gradual increase in number throughout development.

Although groups are present throughout development in most cases the number of sensilla in a group increases. Group A_3 is centrally positioned, and distal to the intertorma, and is the only group where the number of sensilla remains constant. Groups A_4, A_5 and A_7 have only a relatively small number of sensilla in the adult and this is reached by a steady increase in each instar. Although a more marked increase in the number of group A_7 sensilla occurs at the moult into the second and eighth instars. An even more dramatic increase at the moult to the eighth instar occurs in Group A_8 and to a lesser extent group A_1. Group A_6 is composed of a fairly consistent number of sensilla up to the ninth instar when an increase occurs. Group A_2 is represented by a single sensillum in the first instar and it is not until the fourth instar that any marked increase occurs.

The posterior surface of the clypeolabrum is devoid of sensilla of Types 1, 2, 5, 11, 12 and 13 (Table 9). The number of Type 8 sensilla may remain constant throughout development, but sometimes an additional sensillum is added in the ninth instar (Table 9). Type 3 sensilla increase in number gradually from the first to the last instar. Type 4 sensilla increase in number more erratically, the greatest increases occurring in fourth, sixth and eighth instars.

Fig. 31. Distribution of sensilla on the posterior surface of the clypeolabrum: a, first instar; b, fifth instar.



Fig·31

Fig. 32. Distribution of sensilla on the posterior surface of the clypeolabrum: a, seventh instar; b, eleventh instar.

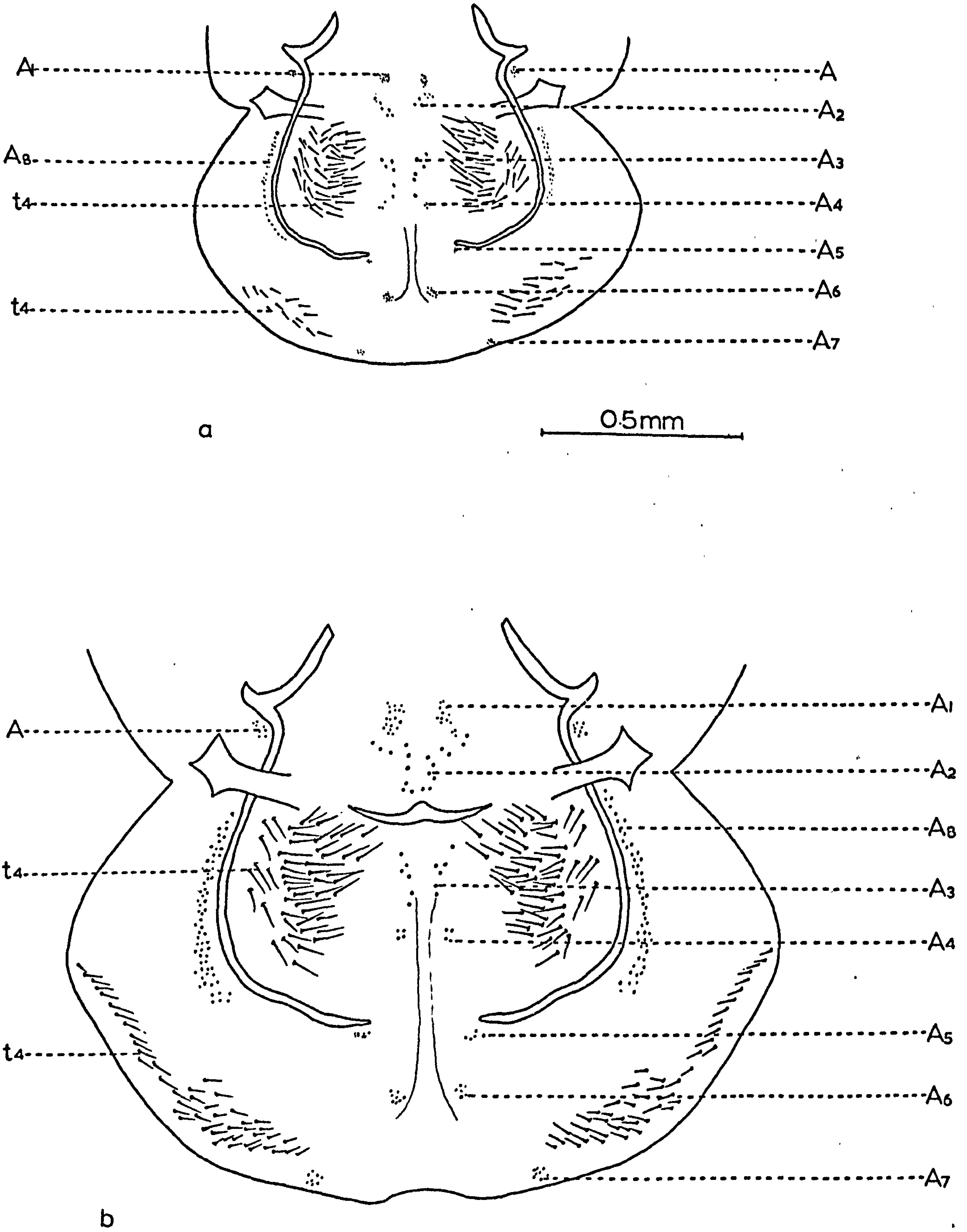

A
A
A2
A8
A3
t4
A4
A5
A6
t4
A7
a
0.5mm
A1
A
A2
A8
t4
A3
A4
A5
t4
A6
A7
b
0.5mm

Fig. 32

Table 8 Sensilla on the posterior surface of the Clypeolabrum of all instars

Groups of sensilla

No. of Instars counted	Instars	Mean ($\bar{x}$)	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
5	1	$\bar{x}$	17.6 17.6	1 1	6 5.8	3 3	4.8 4.4	14.2 14	1 1.4	5.8 6.4	6.6 6
2	2	$\bar{x}$	18 18	2 2.5	6 6	3 3	4 4.5	14.5 15	3.5 3.5	8.5 7.5	8 7.5
2	3	$\bar{x}$	17.5 18.5	1.5 2.5	6 6	3 4	4 4.5	14.5 15	3.5 3.5	10 10.5	10 10
2	4	$\bar{x}$	18.5 18.5	6 6.5	6 6	4 3.5	5 4.5	14.5 14.5	3.5 3.5	20 18.5	12 12.5
7	5 ♀	$\bar{x}$	18.7 19.2	9 8.8	6 6.4	4.2 4.1	6.1 5.7	13.5 13.2	3.8 3.7	18.8 19.1	11.2 11.2
3	6	$\bar{x}$	21 19	9.3 8.6	6 5.6	4.3 4.3	6.3 7.3	13.6 13	5.6 5.6	27 27.3	13 13.3
4	7	$\bar{x}$	22.2 23	8.5 8.75	6.25 6	4.7 4.7	8 8	13.5 13.5	6.2 6.5	26.2 27.5	13.5 13.5
2	8	$\bar{x}$	32 35.5	11 12	6.5 6.5	6.5 7.5	8 8	14 15	10 10	58 63	16 16
2	9	$\bar{x}$	32.5 35	13 13.5	6.5 6.5	6.5 7	8.5 7.5	19.5 17.5	8.5 8	59.5 59.5	16.5 17
3	10	$\bar{x}$	39 38.3	14 13	6 6.3	6.6 6.6	9.3 9	26 25.6	9.3 9.6	72.3 78.3	16.3 17
2	11	$\bar{x}$	46 47	12.5 13	6.5 7	7.5 7.5	10 8.5	29.5 28.5	9.5 9	65.5 65	16.5 16.5

(Upper value = right side; lower value = left side)

Table 9 Total number of sensilla types on the two surfaces of the clypeolabrum of all instars (Values represent means of 2 - 5 insects)

Instar	Surface	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
1	Ant.	10	8	-	-	-	-	-	-	-	-	-	-	4
"	Post.	-	-	46	14	-	2	-	12	2	58	-	-	-
2	Ant.	11	8	16	-	-	-	8	-	-	-	-	-	4
"	Post.	-	-	48	18	-	6	-	12	3	58	-	-	-
3	Ant.	12	12	18	-	-	-	12	-	-	-	-	-	4
"	Post.	-	-	58	29	-	8	-	12	5	66	-	-	-
4	Ant.	12	14	24	-	-	-	22	-	-	-	-	-	4
"	Post.	-	-	62	60	-	8	-	12	13	70	-	-	-
5	Ant.	12	21	70	-	-	-	27	-	-	-	-	-	4
"	Post.	-	-	63	73	-	8	-	12	17	74	-	-	-
6	Ant.	12	21	86	-	-	-	38	-	-	-	-	-	4
"	Post.	-	-	66	129	-	12	-	12	17	78	-	-	-
7	Ant.	12	23	182	-	-	-	45	-	-	-	-	-	4
"	Post.	-	-	66	132	-	13	-	12	18	88	-	-	-
8	Ant.	12	24	185	-	-	-	48	-	-	-	-	-	4
"	Post.	-	-	72	178	-	17	-	12	24	112	-	-	-
9	Ant.	12	24	281	-	-	-	63	-	-	-	-	-	4
"	Post.	-	-	80	181	-	17	-	13	24	118	-	-	-
10	Ant.	12	24	314	-	-	-	78	-	-	-	-	-	4
"	Post.	-	-	94	194	-	18	-	13	24	132	-	-	-
11	Ant.	12	24	447	-	-	-	85	-	-	-	-	-	4
"	Post.	-	-	106	194	-	19	-	13	24	142	-	-	-
Adult	Ant.	13	26	577	-	-	-	98	-	-	-	-	-	4
"	Post.	-	-	240	194	-	21	-	13	24	150	-	-	-

Type 6 sensilla are present in group A_7 only and their development has already been described. Type 10 sensilla display a steady increase in number throughout postembryonic development. The number of Type 9 sensilla slowly increases from the first to the ninth instar from which no further increase occurs.

It is interesting to note that the different types of sensilla display a range of developmental pattern, some not increasing in number at all (e.g. Type 13) others increase steadily (Types 2, 6, 7, 9 and 10) and others with more abrupt changes in the number of sensilla (Types 3 and 4).

5.7 Discussion

From a detailed study of the distribution of the sensilla many interesting facts have come to light. On the mouthparts of A. domesticus there is a wide range of types of sensilla and many types are abundant. There appears to be relatively little difference in the distribution or number of sensilla in individuals of the same developmental stage and sex. However, it was interesting to note the occasional occurrence of sexual dimorphism in terms of number and even types of sensilla. The brief study of the development of the adult pattern of sensilla also demonstrated considerable differences between the types of sensilla in this context, a subject not previously considered.

An analysis of the overall distribution of some of the sensilla types may be used to suggest their function. Sensilla of Type 1 only occur on parts that are in contact with the external environment, such as the anterior surface of the clypeolabrum (Fig. 5), the posterior surface of the labium and the maxillary and labial palps (Table 5). Sensilla of Type 7 occur mainly on the posterior surface of the labium (Table 5), the anterior surface of the clypeolabrum (Fig. 7b) and both surfaces of the mandible (Figs. 8 and 9). Type 13 sensilla have a very restricted distribution and are only found on the anterior surface of the labrum near the membranous notch. On the other hand Type 3 sensilla are the most common type and are generally distributed over most of the mouthparts. Type 5 sensilla occur only on the distal extremities of the mouthparts where they are often abundant. The tips of the paraglossa (Fig. 24), galea (Figs. 13 and 14), labial palp (Figs. 26 and 27) and maxillary palp (Figs. 20 and 21) are covered with Type 5 sensilla. Type 8 and 9 sensilla are only found on the posterior surface of the clypeolabrum (Fig. 4) in groups A_3 and A_2 respectively. Type 12 sensilla, often called pore canals, are present on the well sclerotized incisor and molar areas of the mandible (Figs. 8 and 9) and in the distal cusps of the lacinia (Fig. 17). Fudalewicz-Niemczyk and Rosciszewska (1974) also report the pore canals in the lacinia and mandible in the larvae of _G. domesticus_. The presence of the pore canals in these distal positions strongly suggests that they are chemosensory. The posterior surface of the labrum is devoid of sensilla of Type 2. However, these are present on the anterior surface of the clypeolabrum, the posterior and anterior surfaces of the cardo, anterior surface of the stipes, posterior surface of the galea, anterior surface of the lacinia and anterior and posterior surfaces of the maxillary palp. Besides these positions Type 2 also occurs on the posterior surfaces of the labium, labial palp, hypopharynx and antenna (Table 5). The hair plates are formed of Type 2 sensilla. They occur on the joints of the labial palp (Figs. 26 and 27) and maxillary palp (Figs. 20 and 21), in the labium at the junction of the submentum with the mentum (Fig. 22) and mentum with the prementum (Fig. 23a). It is interesting to note that no hair plate is present at the junction of the clypeus with the labrum. According to Dethier (1963) applies the term touch receptors to the hair plates.

Regarding Type 4 sensilla, they are present on the posterior surface of the clypeolabrum, the mandible, on both surfaces of the maxilla and on the labium including the submentum, both surfaces of the paraglossa and the labial palp. In the hypopharynx Type 4 sensilla are found on the anterolateral surface (Table 5). The presence of Type 4 sensilla on the antenna proved to be of particular interest, since scanning electron micrographs have shown the walls to be spirally grooved (Plate 10b). These sensilla may have some special function in the detection of the food.

Type 6 sensilla have an interesting distribution on the anterior surface of the clypeolabrum they are absent whilst on the posterior surface they occur in group A_7. Due to the position of these campaniform sensilla of Type 6 near the joints of the maxillary (Figs. 20 and 21) and labial palp (Figs. 26 and 27), they have been considered to be proprioceptors (Pringle, 1938a). Their function on the hypopharynx is not very clear. The anterior and posterior surface of the clypeolabrum is devoid of sensilla of Type 11. It has been noticed that these occur only on the posterior surface of the galea and on both surfaces of the paraglossa. Again it is difficult to be conclusive about their function, but it may be suggested that they may act as chemoreceptors (Table 5).

The clypeolabrum is richly supplied with sensilla of various different types and some are only found on this structure. This is almost certainly indicative of the important role of the clypeolabrum in feeding. This suggestion is further enhanced by the fact that all sensilla types are present, although often in small numbers, even in the early instars.

The intention of this section is to describe the distribution of different types of sensilla on all the feeding appendages and associated structures. It has not always been possible to deduce accurately the function of the types of sensilla, since this would require further experimental work. However, it is hoped that this work may provide the necessary background to extend the subject along physiological lines.

List of abbreviations for the sensilla and associated structures of the head capsule and mouthparts

t_1 = Type 1 sensilla
t_2 = Type 2 "
t_3 = Type 3 "
t_4 = Type 4 "
t_5 = Type 5 "
t_6 = Type 6 "
t_7 = Type 7 "
t_8 = Type 8 "
t_9 = Type 9 "
t_{10} = Type 10 "
t_{11} = Type 11 "
t_{12} = Type 12 "
t_{13} = Type 13 "
Hs = Suspensorial sclerite
tor = Torma
int = Intertorma
VL = Sclerotized bar
h = Hair
c = Comb
lb = Longitudinal bar
Sc = Scape
Pdc = Pedicel
hp = Hair plate

Mtr = Microtrichia
cp = Cuticular projection
Gb = Globular sensilla

Appendix I Measurements of parts of the body to determine the number of instars (in mms)

Instar	Length of the body	Breadth of the head	Length of the Pronotum	Length of the Forewing	Length of the hind femur	Length of the Ovi-positor
1	2.5 2 2	.5 .4 .4	.3 .3 .3	- - -	1 .9 .9	- - -
2	3.5 3.7	.9 .8	.9 .8	- -	1.6 1.8	- -
3	4.2 4.1	1 1	1 1	- -	2 2	- -
4	4.5 5.7	1 1	1 1	- -	2 2.5	- -
5	6 6 7 7	1 1 1 1.3	.9 1 1.1 1.1	- - - -	2.8 3 3 3.8	rudiments " " "
6	7.5 8.7	1.4 2.1	1.1 1.5	- -	3.9 4.5	rudiments "
7	9 9	1.8 1.9	1.4 1.5	- -	4.5 4.2	.4 .4
8	13 11 13	2.5 2.4 2.6	1.9 2 2	- - -	5.9 6 6	1 1 1
9	14.1	2.7	2.3	-	6.6	1.6
10	14.5 14.6	3 3	2.5 2.5	2 2.1	7.5 7.5	2 2
11	15.9 18 17.9 16.2 18.6 18.7 16.2	3.2 4 3.9 3.4 3.8 3.5 3.3	2 2.5 3 3 3 3 3	3.8 3.5 3.8 4 4 3.8 4	8 9 9 9 8.5 8.9 9	4 4 4.7 5 5 4.5 4.5
Adult	18.1 19 19.2 19.2	4.1 4.1 4.2 4.2	2.8 2.8 3.1 3	12 11.5 11.6 12	9.2 9 9 9.4	10.5 10.6 10.8 11.2

Appendix II Sensilla on the posterior surface of the Clypeolabrum of all the instars (* = right; ** = left group)

Groups of sensilla

Instar	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
	* **	* **	* **	* **	* **	* **	* **	* **	* **
1	17,16	1,1	6,6	3,3	4,4	14,13	1,1	5,7	7,6
	17,17	1,1	6,6	3,3	5,4	13,13	1,1	5,8	7,6
	18,19	1,1	6,6	3,3	5,5	16,15	1,1	7,5	6,5
	18,18	1,1	6,5	3,3	5,5	16,16	1,1	5,6	7,7
	18,18	1,1	6,6	3,3	5,4	13,13	1,3	7,6	6,6
2	17,18	1,2	6,6	3,3	4,5	13,14	3,3	7,8	7,7
	19,18	3,3	6,6	3,3	4,4	16,16	4,4	10,7	9,8
3	17,18	1,2	6,6	3,4	4,5	13,14	3,3	10,12	10,10
	18,19	2,3	6,6	3,4	4,4	16,16	4,4	10,9	10,10
4	18,17	6,7	6,6	4,3	5,4	13,14	3,3	20,18	12,13
	19,20	6,6	6,6	4,4	5,5	16,15	4,4	20,19	12,12
5	20,17	10,10	6,6	4,4	4,4	14,12	4,4	18,20	10,10
	18,20	10,9	6,6	4,4	5,5	14,13	4,4	20,22	10,10
	19,18	8,9	6,6	4,4	5,4	13,14	4,4	18,20	13,13
	18,21	9,8	6,7	5,4	8,8	14,13	4,3	19,18	11,11
	19,18	8,9	6,6	4,4	5,4	13,14	4,4	18,20	13,13
	18,21	9,8	6,7	5,4	8,8	14,13	4,3	19,18	11,11
	19,20	9,9	6,7	4,5	8,7	13,14	3,4	20,18	11,11
6	21,18	10,10	6,6	4,4	7,8	14,12	6,5	32,28	14,14
	22,21	9,8	6,6	5,4	5,6	14,14	6,6	25,27	13,13
	20,18	9,8	6,5	4,5	7,8	13,13	5,6	24,27	12,13
7	23,24	9,9	6,6	5,5	8,8	14,13	6,7	26,28	14,14
	25,23	9,9	6,6	5,5	8,9	14,13	7,8	30,27	14,14
	21,22	8,9	7,6	4,5	8,7	13,14	6,6	25,28	13,13
	20,23	8,8	6,6	5,4	8,8	13,14	6,5	24,27	13,13
8	32,35	10,11	6,6	6,7	7,8	14,15	10,10	60,64	16,16
	32,36	12,13	7,7	7,8	9,8	14,15	10,10	56,62	16,16
9	31,33	13,14	6,7	7,7	8,8	19,18	8,8	58,60	17,17
	34,37	13,13	7,6	6,7	9,7	20,17	7,8	61,59	16,17
10	40,38	15,13	6,7	7,9	10,11	28,31	8,9	76,86	17,18
	43,45	14,14	6,7	8,7	9,7	27,25	12,12	76,82	17,18
	34,32	13,12	6,5	5,4	9,9	23,21	8,8	65,67	15,15
11	45,44	13,13	7,7	9,8	11,8	31,30	10,8	66,68	16,16
	47,50	12,13	6,7	6,7	9,9	28,27	9,10	65,62	17,17

PART 6

PERIPHERAL NERVOUS SYSTEM OF THE MOUTHPARTS

6.1 Introduction

Relatively few studies have concentrated on the peripheral nervous system of insects and the Gryllidae are no exception. The only major works in this field include those of Fudalewicz-Niemczyk and Rosciszewska (1973, 1974) who have studied the peripheral nervous system of the antenna and mouthparts of the last instar of *G. domesticus* and Rummel (1963) who concentrated on the morphometrics of the instars of *G. domesticus* during metamorphosis. Knyazeva *et al* (1975) later investigated the distribution of the proprioceptors on the body of *G. domesticus*. In the Acrididae Louveaux (1972) described the nervous supply of the mouthparts of first instar larvae of *L. migratoria*, and a later study described the detailed innervation of the hypopharynx of *L. migratoria migratorioides*. The innervation of the mandible of the first instar larva of this species was described by Le Berre and Louveaux in 1969. Other more general studies involving Orthoptera include those of Albert *et al* (1976) who studied the nervous innervation of the sensilla in the wing of the grasshopper, *Melanoplus sanguinipes* and McFarlane (1953) who elucidated the morphology of chordotonal organ of the head appendages of the migratory grasshopper *Melanoplus mexicanus mexicanus* (Saussure).

The chief purpose of this part of the work is to provide a description of the peripheral nervous system of the mouthparts of adult female A. domesticus. To achieve this, efforts have been made to trace the pathway of the nerves both to the muscles and the sensilla. In some cases the nature of the sensilla can be suggested by the number of neurons innervating it. To complete the study the origin of the nerves from the suboesophageal ganglion, the tritocerebrum or the frontal ganglion have been traced, a feature often omitted from earlier studies. The results have been expressed in the form of diagrams and the main features have also been tabulated for clarity. The detailed innervation of certain muscles of the mouthparts has been investigated and drawn and in this case the position of the prominent tracheal branches has been included.

6.2 Materials and methods

The specimens used for studying the nervous innervation of muscles and sensilla were newly moulted adult female crickets. The low pigmentation of the integument and the thinner, softer cuticle at this stage facilitated microscopic examination.

The literature describes several techniques for staining the nerves of arthropods and annelids (e.g. Allen, 1894; Alexandrowiez, 1932; Bliss and Welsh, 1952; Harridge, 1959 and Barber, 1960). In this case the study of the distribution of nerves was based primarily on whole mounts stained intravitally with Methylene Blue. Preliminary work involved testing the techniques of Pantin (1946), Zacharuk (1962), Larimer and Ashby (1964), Stark et al (1969), Fudalewicz-Niemczyk and Rosciszewska (1974), Thomas (1971), Louveaux (1975) and Moulin (1971). Finally the method due to Moulin (1971) was adopted.

A 0.4% stock solution of Methylene Blue (Gurr's Methylene Blue, Vital and Fluorchrome supplied by George T. Gurr Ltd., London) was prepared in the physiological solution developed by Moulin (1971) (9gm Nacl; 0.2gm KCl; 0.2gm $CaCl_2$; 4gm dextrose dissolved in 1 litre of distilled water). The pH was adjusted to pH_5 - pH_7. Using a micro-syringe 0.1ml of the staining solution was injected through the neck membrane and after an interval of 15 minutes another injection was given. Sometimes a third injection, after 10 minutes, was necessary. The specimens were left for 30 minutes and then killed. The head was severed from the rest of the body and fixed in 8% cold ammonium molybdate for 24 - 48 hours. Specimens were dissected in distilled water in a wax based dissecting dish. Temporary mounts were generally used since the stain faded during the process of preparing a permanent mount.

Although several staining methods were tested and subsequently the following method proved to be helpful initially. 0.2ml injection of 5% stock solution as well as Leuco Methylene Blue solutions were used on newly moulted specimens. The stock solution was prepared by dissolving 0.5gms of Methylene Blue in 100ml of water, the solution was heated, stirred, filtered and cooled.

There are two types of Leuco Methylene Blue solutions. The first, Unna's solution is made by adding 6 drops of concentrated HCl to 30ml of Methylene Blue stock solution. This was reduced with 6ml of 12% (W/v) sodium formaldehyde sulfoxalate (commonly known as rongalit). Alternatively, modified Unna's solution was prepared in the same way but not acidified. The reduction of the Leuco Methylene Blue solution causes it to change from green to colourless. If the solution is not used immediately it oxidises but can readily be reduced by addition of small amounts of sodium dithionite. Attempts were also made to stain the nerves directly in dissected specimens by pouring 1% Methylene Blue and Rongalit onto the relevant tissue but few satisfactory results were obtained.

The investigation of the nervous innervation of the sensilla proved to be both difficult and time consuming. Particular difficulty was experienced in the maxillary and labial palps where it was found to be virtually impossible to achieve complete penetration of the stain into the terminal segments. In the case of the maxillary palp segments the intersegmental membrane between segments was also used as a site of injection of Methylene Blue and the terminal segment itself was punctured and then immersed in Methylene Blue. Alternatively some palp segments were injected with 0.4% Methylene Blue solution and after 10 minutes were given another injection of 0.5% Methylene Blue prepared in physiological solution (Moulin, 1971). Better results were attained if the fixation time was reduced to 12 hours.

Finally, results were obtained which enabled a complete study of the peripheral nervous system. Some of these were photographed under the light microscope.

General comments

When the stock solution of Methylene Blue was injected into the living specimen and allowed to act for a sufficient time, there was nearly always some staining of the nerve cell bodies and axons. The quality of the staining produced depended on the stock solution used, the volume injected and the time interval between injection and dissection. If too little stain is injected or the interval is too short, the stain does not penetrate into the nervous tissue satisfactorily. Alternatively, too much stain or too long an interval causes unselective staining of the nerves and even surrounding tissue. The optimum volume of staining solution was that which would distend the abdomen slightly. In most cases approximately a total of 0.2ml staining solution was given. pH also affects the quality of Methylene Blue staining (Harris and Peter, 1953); a slight change in pH can cause a considerable difference to the quality of staining. The optimum pH of the staining solution was found to be pH_5.

Fig. 1. Diagrammatic representation of the peripheral nervous system.

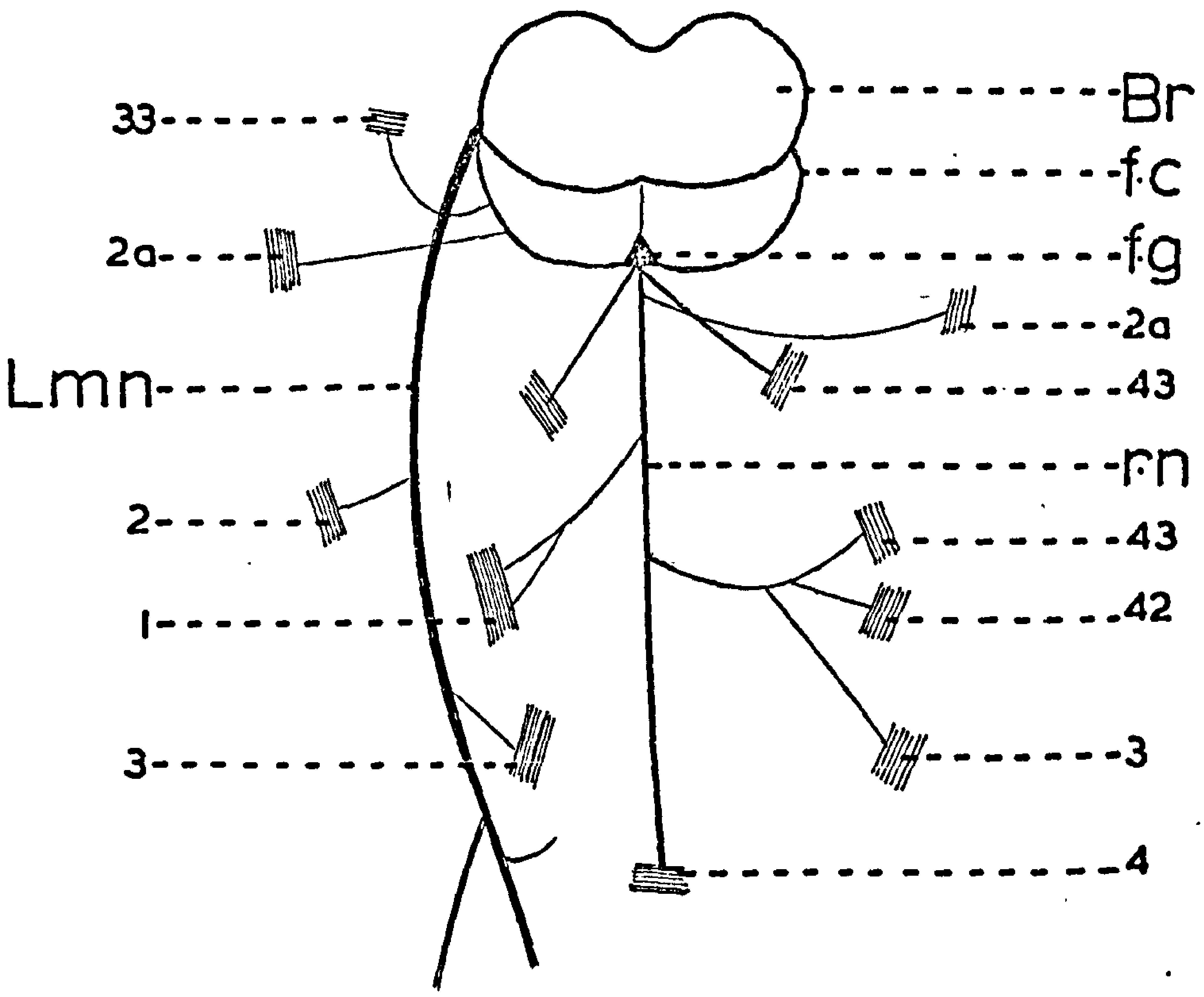


Fig.1

6.3 Origin and innervation of the nerves

6.3.a. Labral nerve and associated nerves

The labral nerve 'Lmn', which is motor and sensory, originates from the tritocerebrum of the brain (Fig. 1). As it passes to the labrum it gives off a branch of nerve fibres to the first adductor of the clypeolabrum (Muscle 2) (Fig. 1) and another branch to the second adductor of the clypeolabrum (Muscle 3), (Table 1; Fig. 1). The labral nerve then bifurcates into 2 branches 'A' and 'B' which innervate the sensilla (Figs. 2 and 3). Besides the labral nerve, some muscles of the clypeolabrum are innervated by the frontal connective and frontal ganglion (Table 1; Fig. 1). As in most insects, the frontal ganglion gives off a nerve, the recurrent nerve 'rn'. From the base of the recurrent nerve a nerve is given off to the dilator of the buccal cavity (Muscle 43) (Table 1; Fig. 1) and distal to this another nerve to the first adductor of the clypeolabrum (Muscle 2a), (Table 1; Fig. 1). The first abductor of the clypeolabrum (Muscle 1) is innervated by another branch of the recurrent nerve (Table 1; Fig. 1). A more distal branch of the recurrent nerve sends nerves to the second adductor of the clypeolabrum (Muscle 3), the dilator of the buccal cavity (Muscle 43) and dilator of the cibarium (Muscle 42), (Table 1; Fig. 1). The recurrent nerve terminates by innervating the median compressor of the labrum (Muscle 4), (Table 1; Fig. 1). The frontal

Fig. 2. Innervation of the anterior surface of the clypeolabrum.

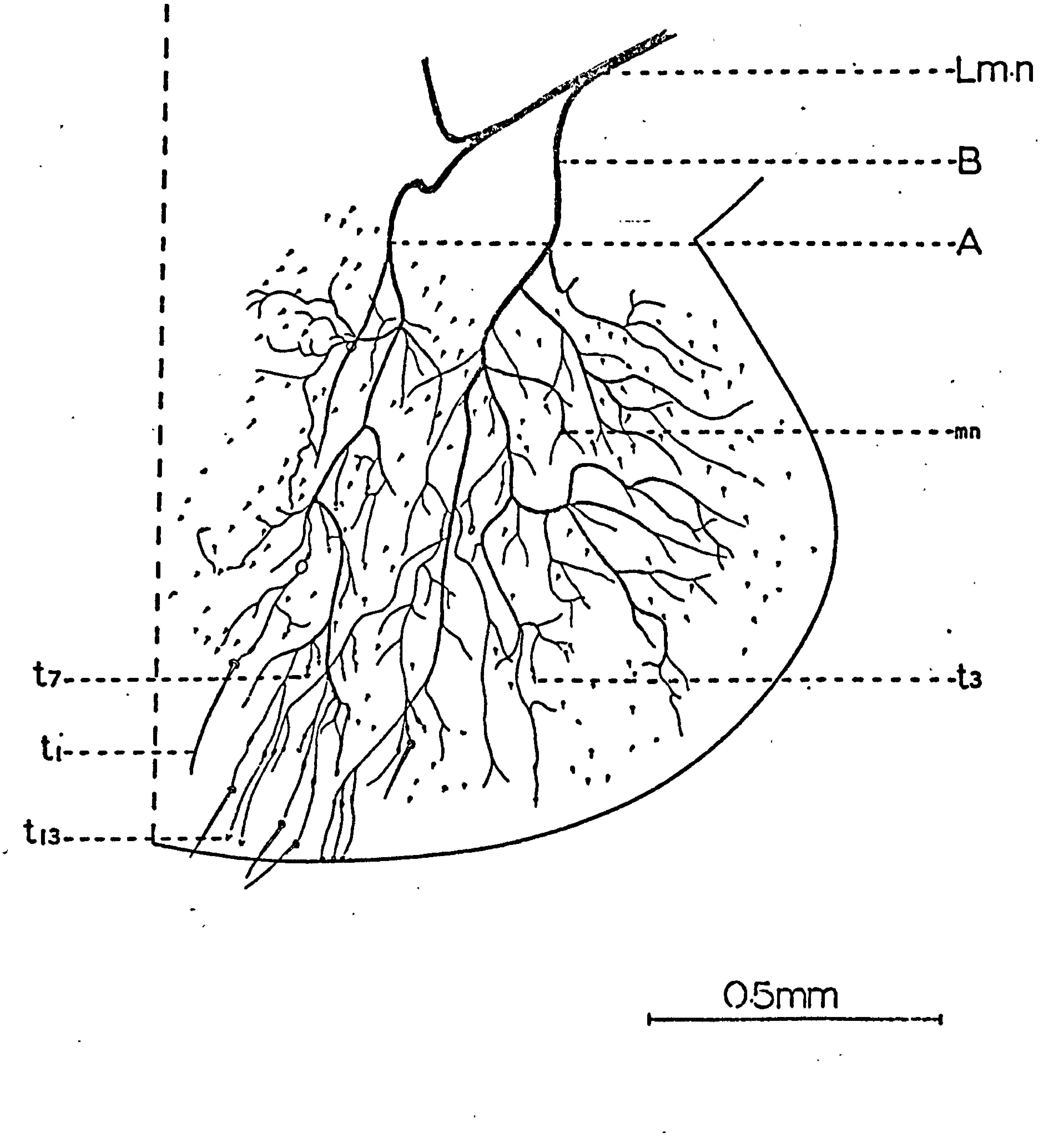


Fig. 2

connective 'fc' has two branches along its length, one innervating the elevator of the hypopharynx (Muscle 33) and the other, the first head of the first adductor muscle (Muscle 2a), (Table 1; Fig. 1).

Innervation of the Clypeolabrum (Figs. 2, 3 and 4)

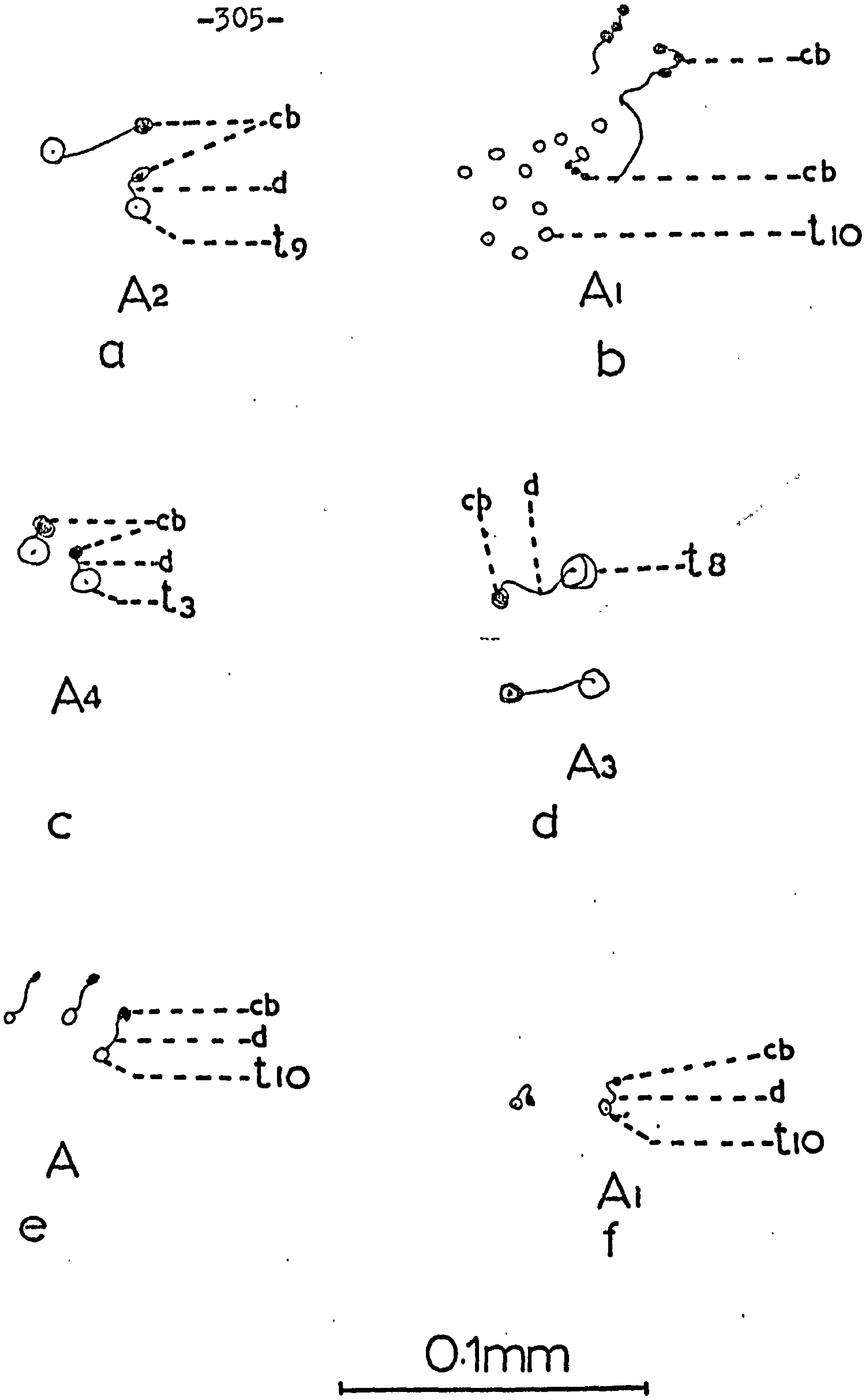
The labral nerve 'lmn' bifurcates into two branches 'A' and 'B' (Figs. 2 and 3) which innervate the sensilla on both surfaces of the clypeolabrum (Figs. 2 and 3). On the anterior surface the inner branch 'A' innervates sensilla of Types 1, 3, 7 and 13 towards the centre of the clypeolabrum (Fig. 2). These sensilla are all innervated by a single neuron. There is a slight variation in the course of the nerve 'A' in different individuals. Sensilla of Type 7 (Fig. 2) have a neuron with an oblong cell body and a long dendrite (Fig. 4i). The outer branch of the labral nerve 'B' has branches to Types 1, 2 and 3 sensilla present on the lateral areas of the labrum (Fig. 2). Some of the branches of this nerve innervate sensilla of Type 1 present on the anterior surface by a single neuron and also gives off branch to a multiterminal neuron having a triangular cell body with 3 dendrites (Fig. 2). These multiterminal neuron are referred to as Type II by Zawarzin (1912).

The posterior surface of the clypeolabrum is also innervated by nerves 'A' and 'B'. The inner branch 'A' gives off a nerve (Figs. 2 and 3) which innervates the sensilla of groups A_1 and A_2 (Fig. 3c). Group A_1 is

Fig. 3. Innervation of the posterior surface of the clypeolabrum: a, pathways of the two subbranches of the labral nerve; b, detail of the branching of sub-branch B; c, some of the sensilla innervated by sub-branch B.

Fig·3

Fig. 4. Detail of the innervation of different types of sensilla on the posterior surface of the labrum: a, Type 9 sensilla in group A_2; b, Type 10 sensilla in group A_1; c, Type 3 sensilla in group A_4; d, Type 8 sensilla in group A_3; e, Type 10 sensilla in group A_9; f, Type 10 sensilla in group A_1; g, Type 4 (together with stretch receptors); h, Type 3 in group A_8 and i, Type 7 (on anterior surface).


cb
cb
d
t9
A2
a
cb
cb
t10
A1
b
cb
d
t3
A4
c
cp
d
t8
A3
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cb
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t10
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e
cb
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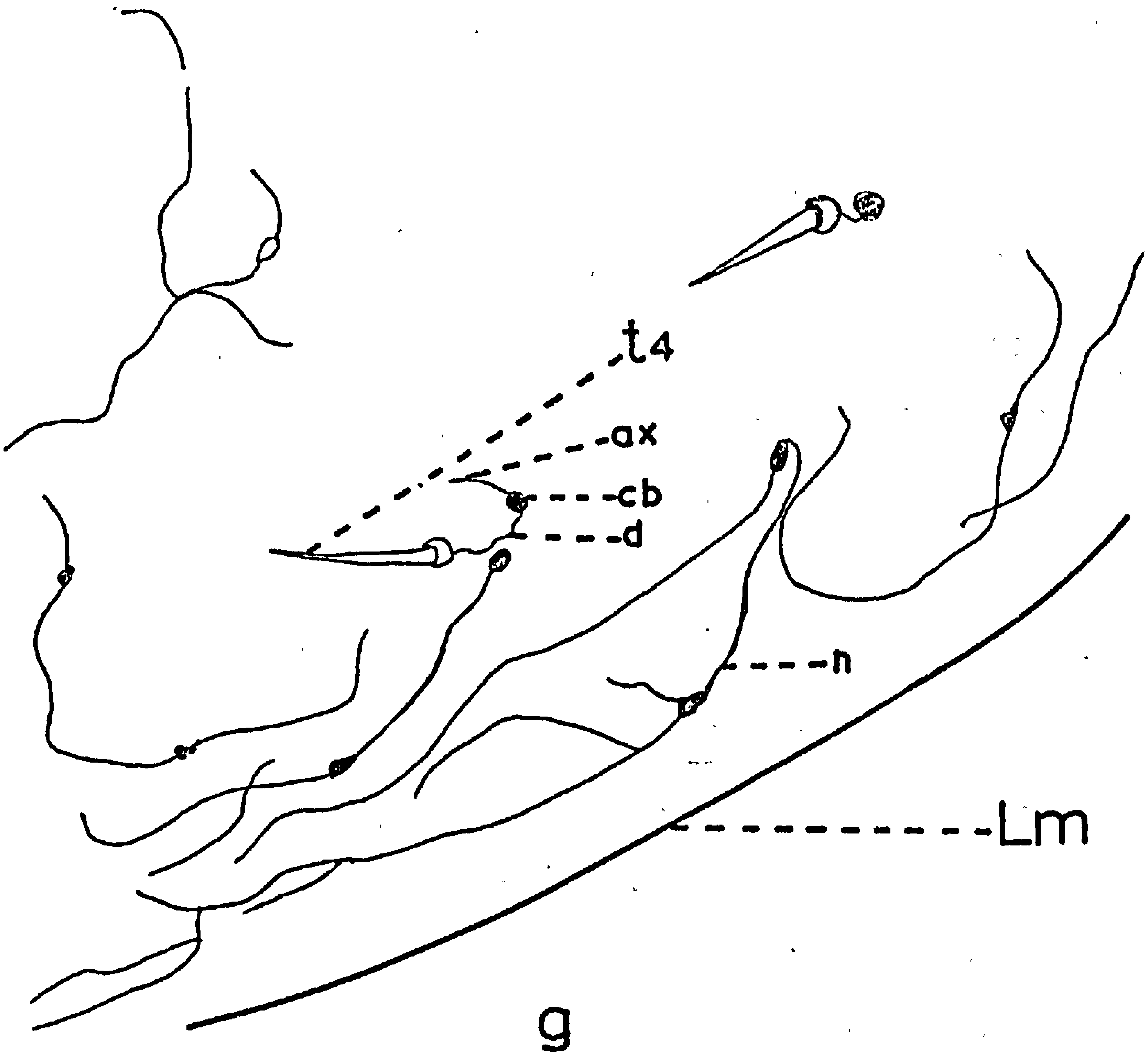
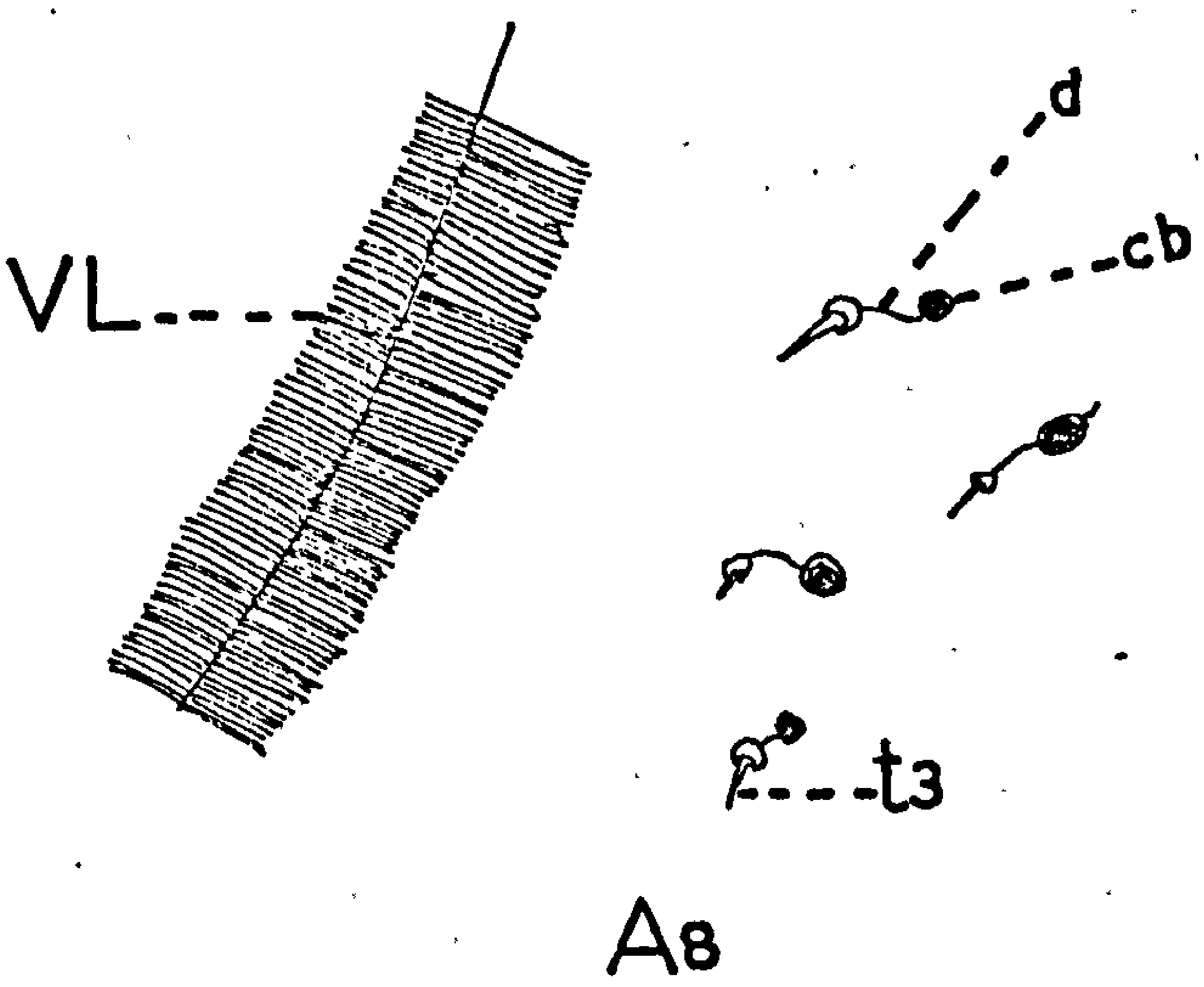
A1
f
0·1mm

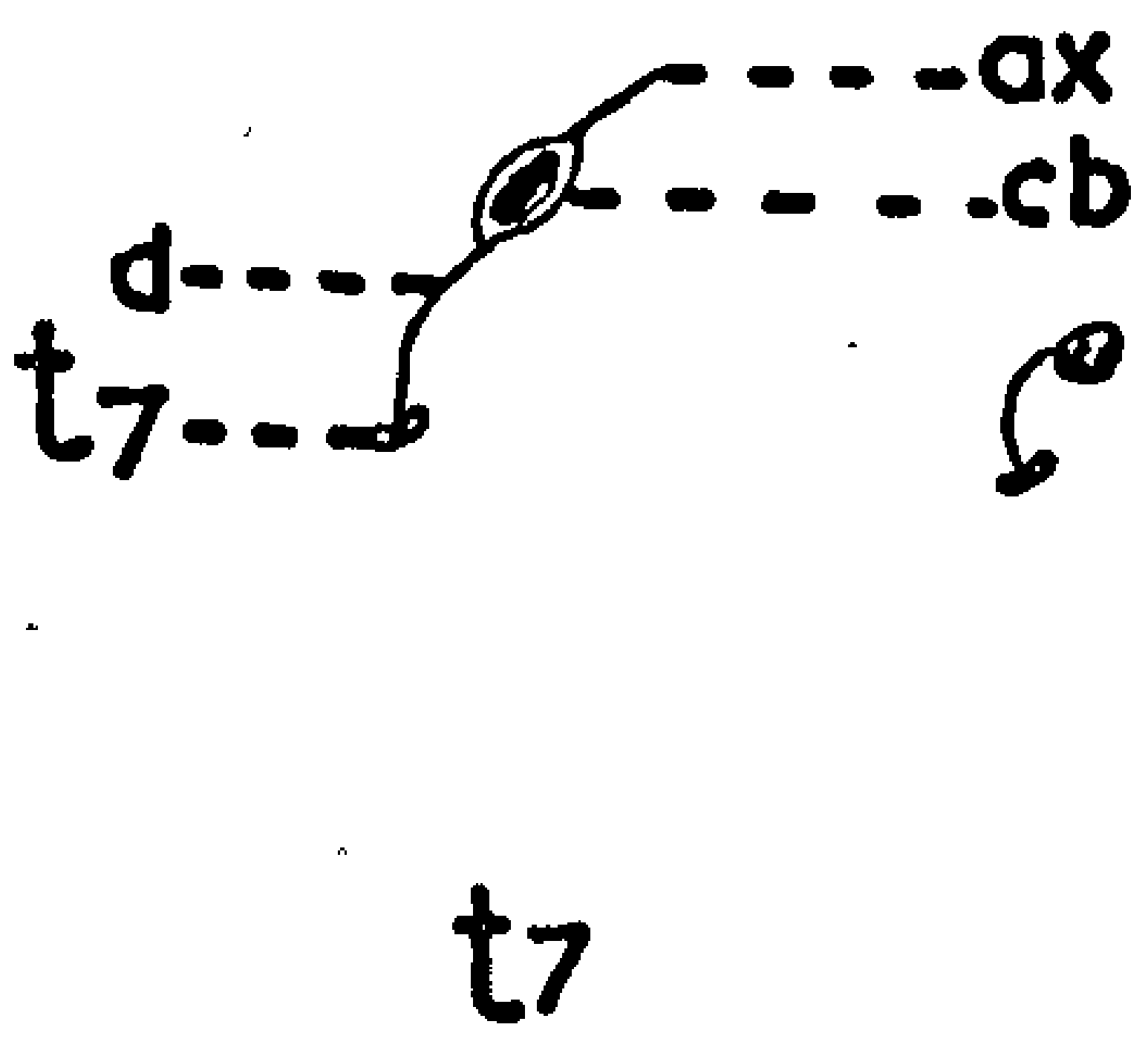
Fig. 4



g



h



i

0·1mm

composed of sensilla of Type 10, these are generally innervated by three neurons with round cell bodies (Fig. 4b) and although some have only a single neuron, a round cell body and a slightly curved dendrite (Fig. 4f). The outer branch 'B' ramifies to the periphery of the labrum (Fig. 3a). Sensilla of Type 4 are innervated by a single neuron with a curved dendrite (Fig. 4g). A number of stretch receptors are present towards the edge of the posterior surface of the labrum (Fig. 4g). These appear to penetrate the soft transparent cuticle and may provide an independent source of information on gradual movement. Finlayson and Lowenstein (1958) found similar cells in muscular and connective tissue strands in the abdomen of various insect species. Guthrie (1967) also mentioned the occurrence of stretch receptors in the leg joints of cockroaches. These provide an independent source of information and are involved in slow contraction. The sensilla in group A_3 are innervated by one of the branches of nerve 'B' (Fig. 3c). These are Type 8 sensilla and have a single neuron with an almost circular cell body and a long dendrite (Fig. 4d). The Type 10 sensilla in group A_9 (Fig. 3c) are also innervated by nerve 'B' (Fig. 3c). These neurons have either round or oblong cell bodies and a curved or wavy dendrite (Fig. 4e). Sensilla in group A_4 have a round cell body and a short dendrite (Fig. 4c). These are Type 3 sensilla. Group A_8 sensilla, which are present outside the sclerotized bar have

Table 1 Innervation of muscles and sensilla by the labral nerve, the frontal connective and the recurrent nerve

Nerve	Site and Structure of Innervation
Labral nerve	(i) First adductor of the labrum (Muscle 2a, 2b) (ii) Second adductor of the labrum (Muscle 3) (iii) Sensilla of the clypeolabrum
Frontal connective	(i) Elevator of the hypopharynx (Muscle 33) (ii) First adductor of the labrum (Muscle 2a)
Recurrent nerve	(i) First adductor of the labrum (Muscle 2a) (ii) Dilator of the buccal cavity (Muscle 43) (iii) Abductor of the labrum (Muscle 1) (iv) Dilator of the cibarium (Muscle 42) (v) Second adductor of the labrum (Muscle 3) (vi) Depressor of the labrum (Muscle 4)

a round cell body with a small dendrite (Fig. 4h). Finally, group A_7 sensilla are of Type 6 (Fig. 3a) and have a single neuron and like group A_8 are innervated by nerve 'B' (Fig. 3a).

6.3.b. Mandibular nerve

The mandibular nerve 'Mdn' originates from the suboesophageal ganglion (Fig. 5). It is composed of motor as well as sensory nerve fibres. The mandibular nerve 'Mdn' divides into three. One branch of this nerve innervates the adductor of the mandible (Muscle 5) (Figs. 5, 6a and b), whilst a sub-branch of this nerve supplies the tentorial adductor of the mandible (Muscle 7), (Figs. 5 and 7a). Another branch of the mandibular nerve innervates the abductor of the mandible (Muscle 6), (Fig. 5) whilst the final branch innervates the sensilla on the anterior and posterior side of the mandible (Figs. 8 and 9) and one of its smaller branches also innervate the hypopharyngeal mandibular muscle (Muscle 8), (Fig. 7b).

The branch of the mandibular nerve which innervates the sensilla on the posterior side of the mandible (Fig. 8) enters the mandible near its base and splits into two branches. One of the branches passes diagonally towards the outer proximal part of the mandible and gives off branches which innervate the Type 3 sensilla, in the central part of the mandible, and Type 7 nearer to the incisor teeth. Some of the nerves terminate in multiterminal neurons (Fig. 8).

Fig. 5. Diagrammatic representation of the mandibular nerve 'Mdn'.

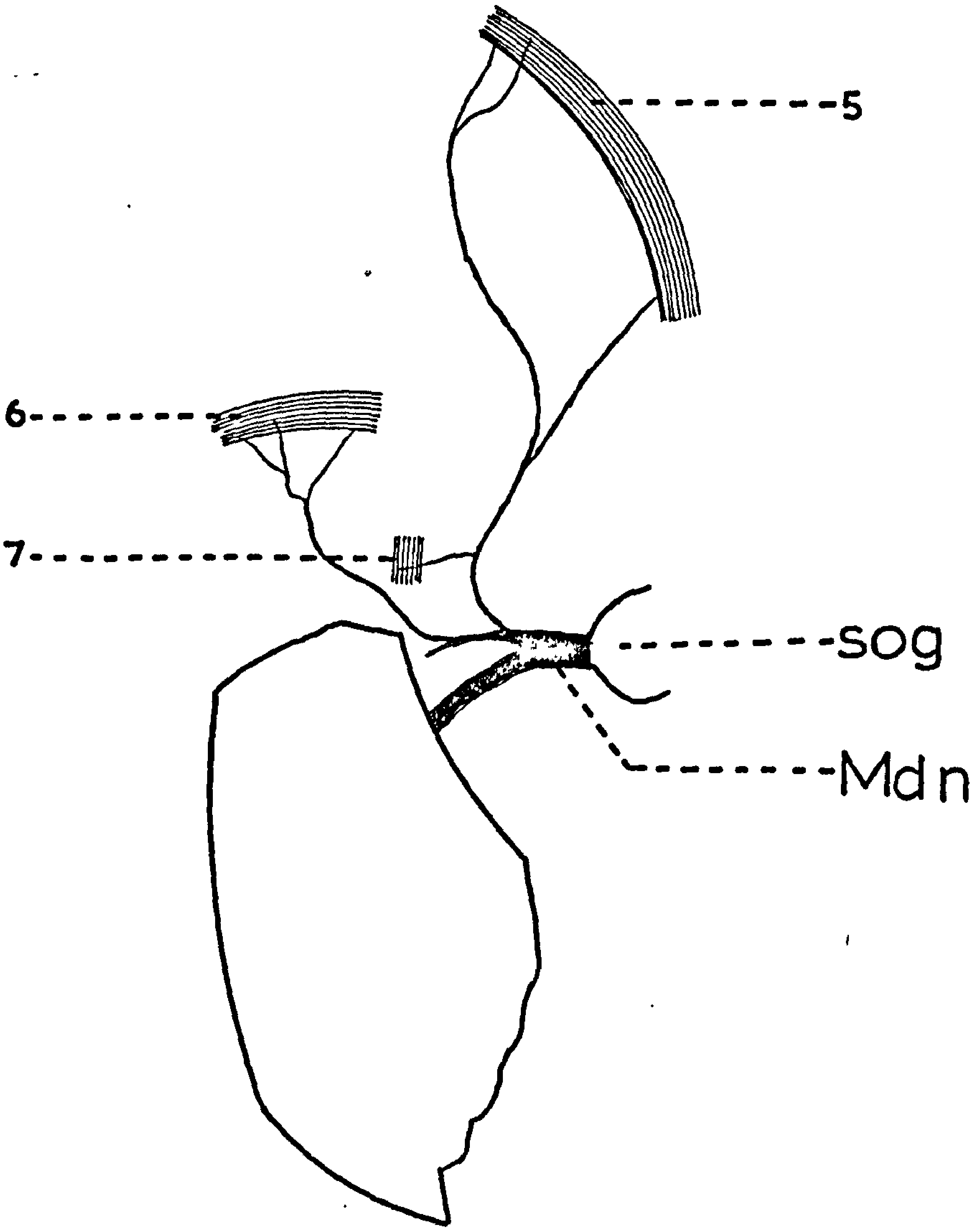
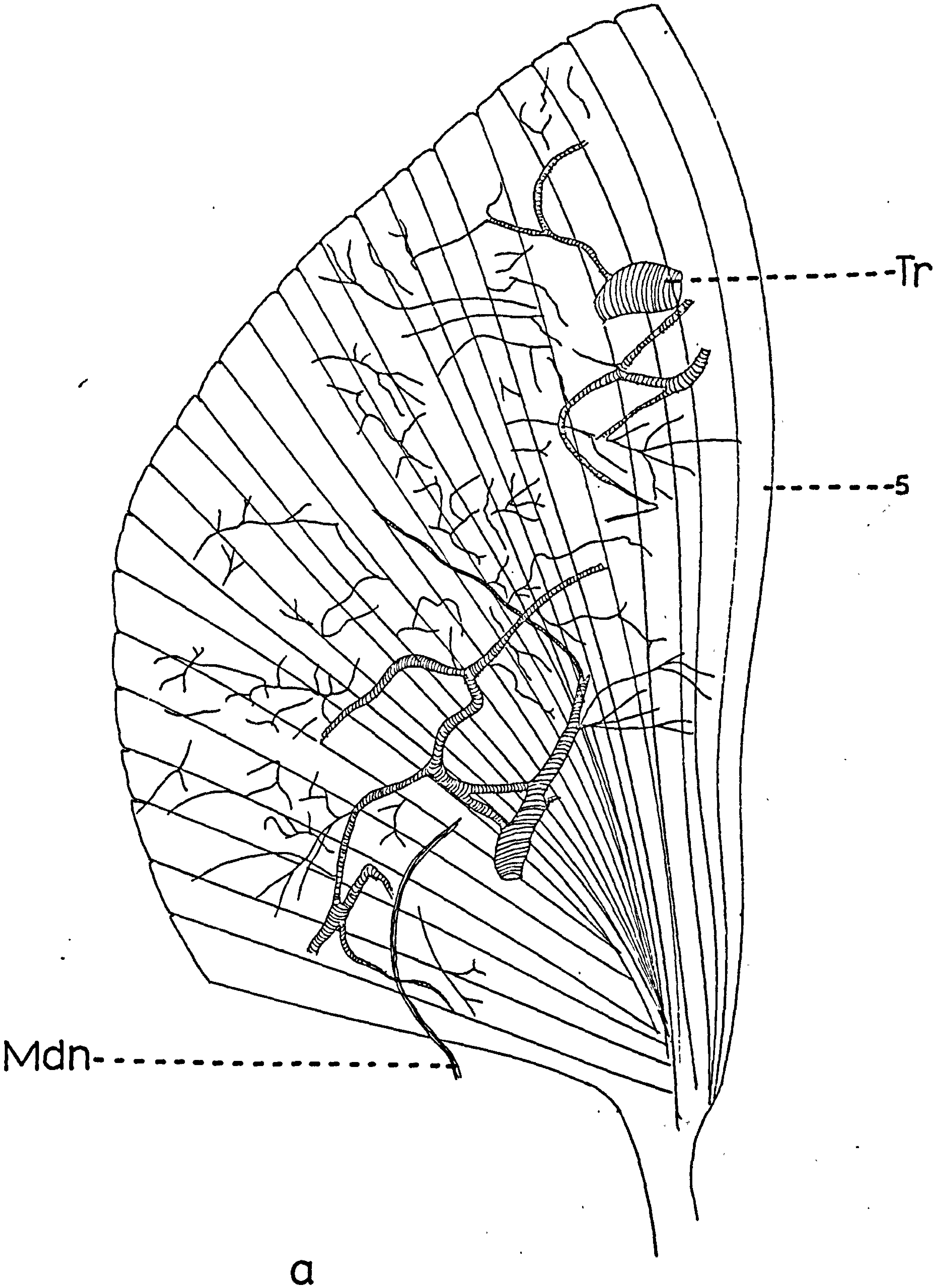


Fig.5

Fig. 6. Mandibular nerve innervating the adductor of the mandible (Muscle 5): a, periphery of muscle; b, part of the muscle removed.



a

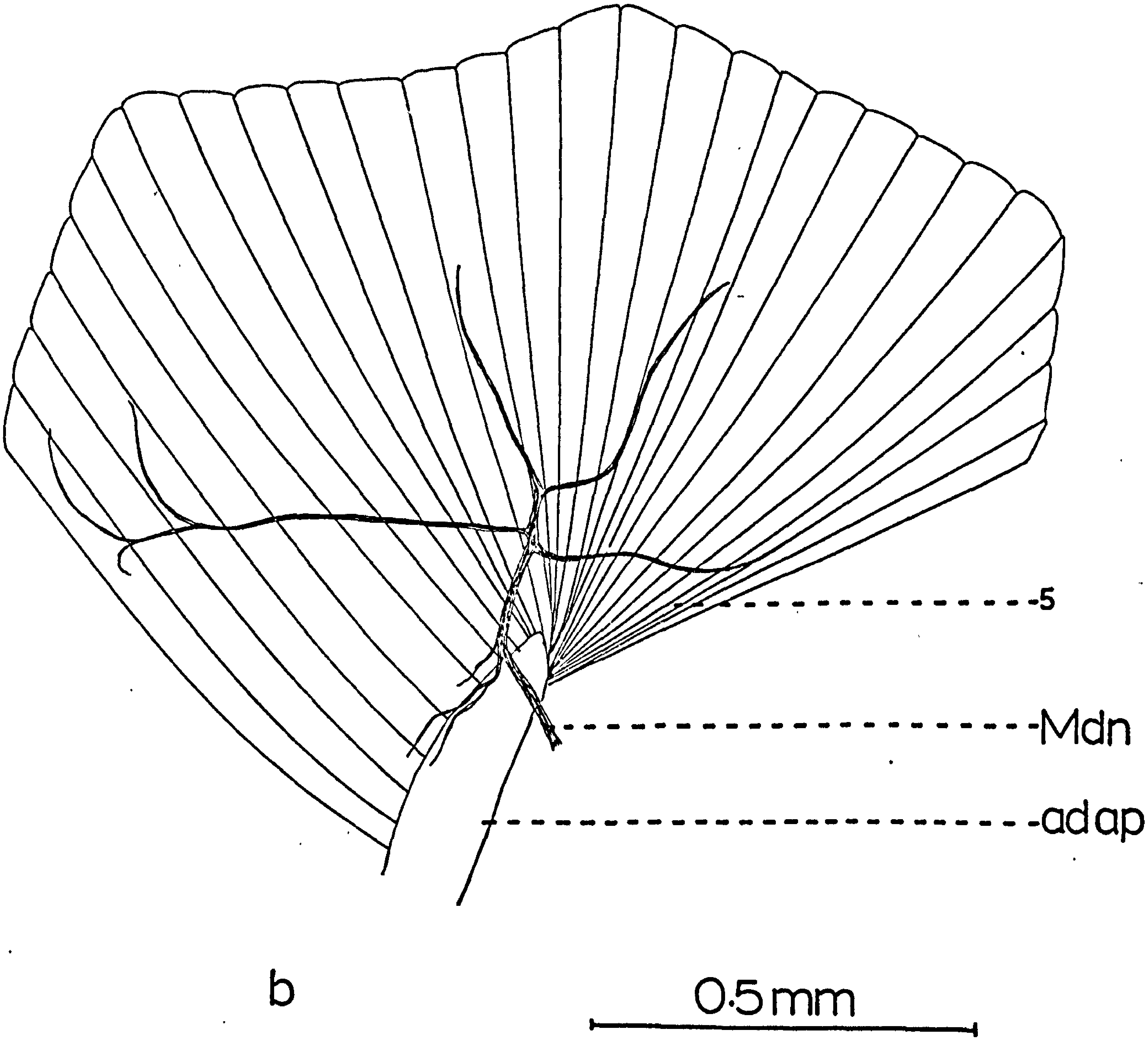


Fig. 6

Fig. 7. Mandibular nerve innervating: a, tentorial adductor of the mandible (Muscle 7); b, hypopharyngeal adductor of the mandible (Muscle 8).

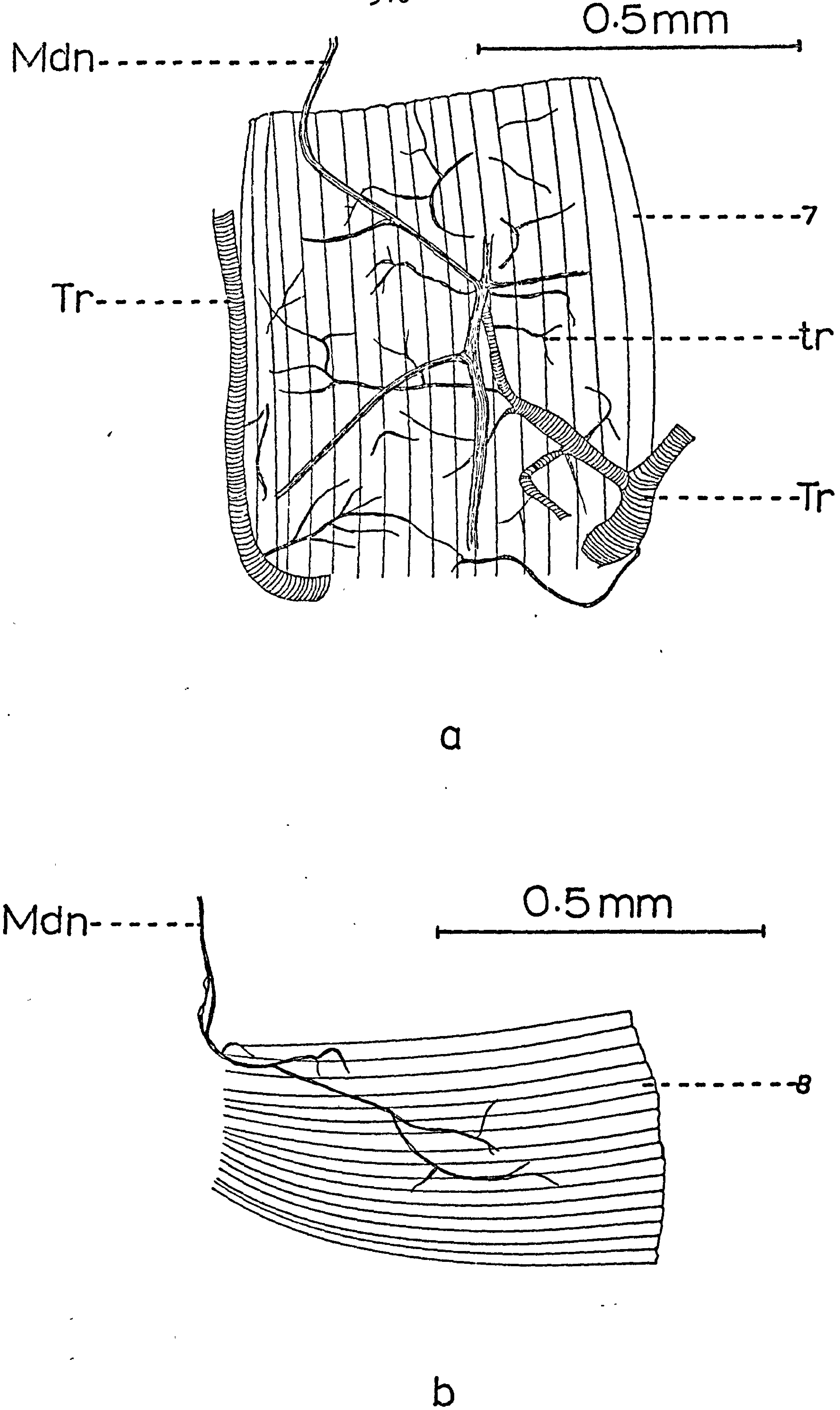


Fig. 7

Fig. 8. Posterior surface of the mandible illustrating the innervation of different types of sensilla by the mandibular nerve 'Mdn'.

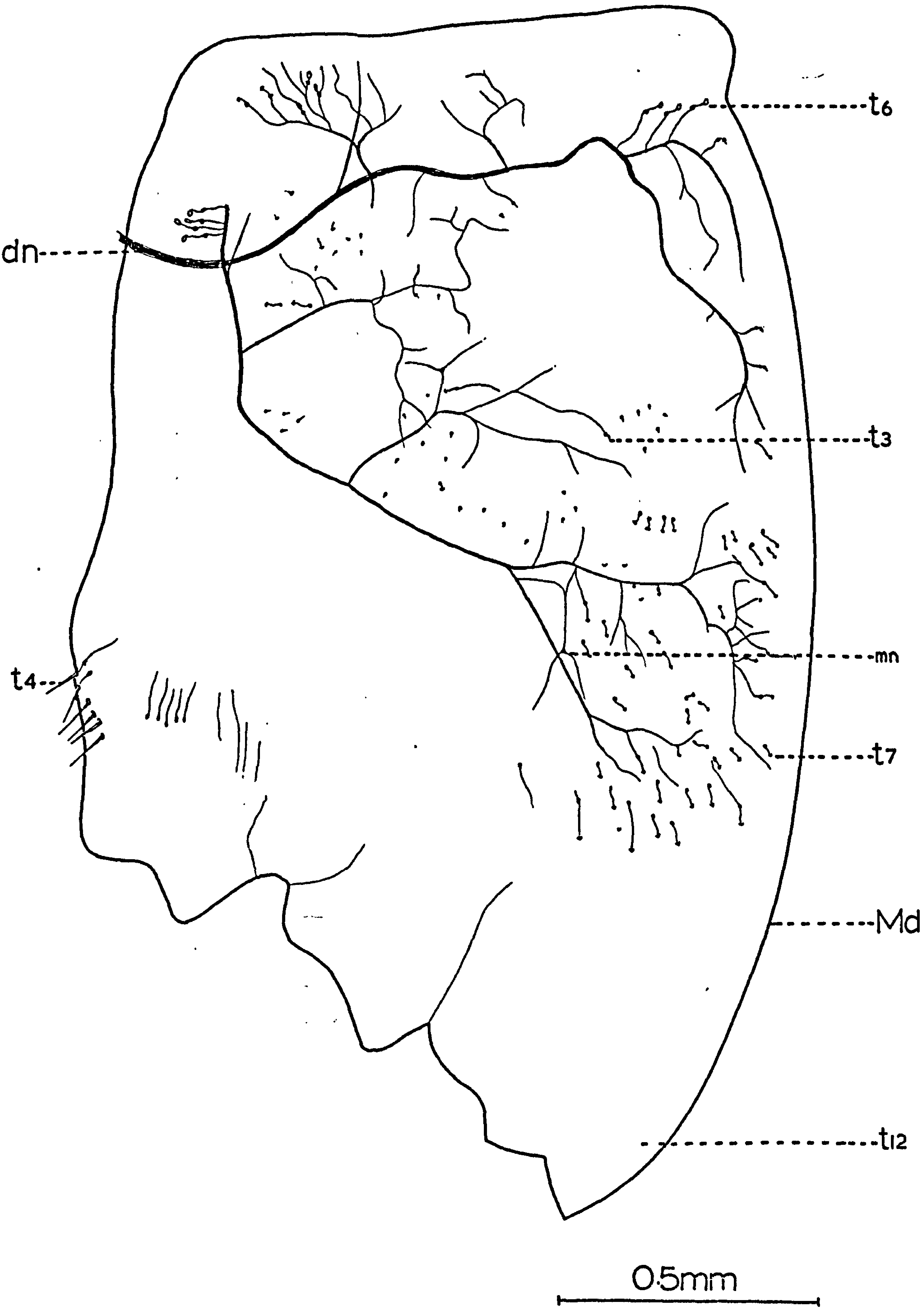


Fig.8

Fig. 9. Anterior surface of the mandible illustrating the innervation of different types of sensilla by the mandibular nerve 'Mdn'.

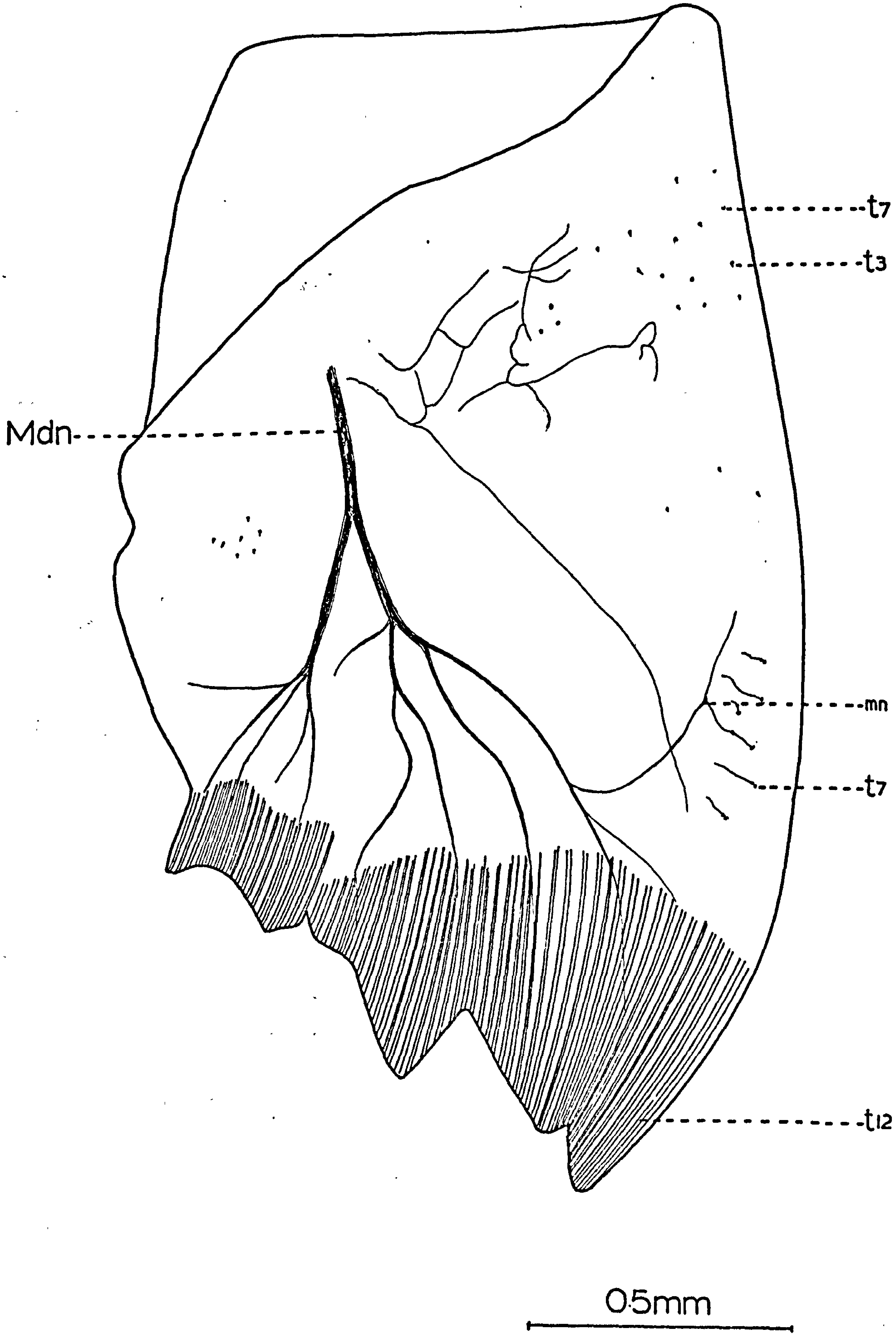


Fig.9

The other branch passes horizontally across the mandible parallel to its base and gives off further branches which then innervate the Type 6 sensilla. Sensilla of Types 3, 6 and 7 are innervated by a single neuron (Fig. 8). Sensilla of Type 4, which are present above molar lobe on the posterior surface, are innervated by the nerve fibres of the mandibular nerve which mainly innervate sensilla on the anterior side of the mandible.

The branch of the mandibular nerve which supplies the anterior surface of the mandible splits fan wise so that nerve fibres radiate to the incisor and molar lobes of the mandible where they innervate the pore canal sensilla (Fig. 9). One of its branches innervates sensilla of Type 7 and also the multiterminal neuron in the distal part of the mandible. Type 7 sensilla are innervated by a single neuron. In the basal region Type 3 and 7 sensilla appear to be innervated by a very fine branch of the mandibular nerve (Fig. 9).

6.3.c. Maxillary nerve

The suboesophageal ganglion gives off two pairs of main maxillary nerves 'IMx' and 'IIMx'. These nerves provide innervation to all the muscles and sensilla of the maxilla (Table 2).

First main maxillary nerve

The first main maxillary nerve 'IMx' is thinner than the second main maxillary nerve 'IIMx' and arises from the suboesophageal ganglion above the second nerve (Fig. 10). A short distance after its origin it splits into two branches 'a' and 'b' (Fig. 10); the upper slender branch 'a' is mainly motor and passes through the adductor of the stipes (Muscle 11). After leaving this muscle it bifurcates into two sub-branches (Table 2) which innervate each of the adductors of the cardo (Muscle 10, 10a), (Fig. 10). The lower branch 'b' is made up of motor and sensory nerve fibres and lies below the adductor of the stipes (Muscle 11). It bifurcates into two sub-branches 'b_1' and 'b_2'. The branch 'b_1' is purely sensory and enters the proximal part of the stipes (Fig. 10) where it subdivides further into '$1b_1$' and '$2b_1$' (Fig. 15); the former branch of nerve fibres innervates all the sensilla of the cardo (Fig. 16) while the latter innervates a large number of sensilla of the stipes (Fig. 17).

The sub-branch 'b_2' (Table 2) is made up of both motor and sensory bundles of nerve fibres and again splits into branches '$1b_2$' and '$2b_2$'; the former branch, '$1b_2$', is motor and innervates the flexor of the galea (Muscle 14), (Figs. 10 and 15) where it bifurcates again; one sub-branch goes to the distal portion of the flexor of the galea (Muscle 14) and the other passes deep into this muscle (Fig. 15). The other sub-branch '$2b_2$' (Table 2) innervates the levator of the palp (Muscle 15), (Fig. 15).

Fig. 10. Major subdivision of the first and second main maxillary nerves 'IMx', 'IIMx'.

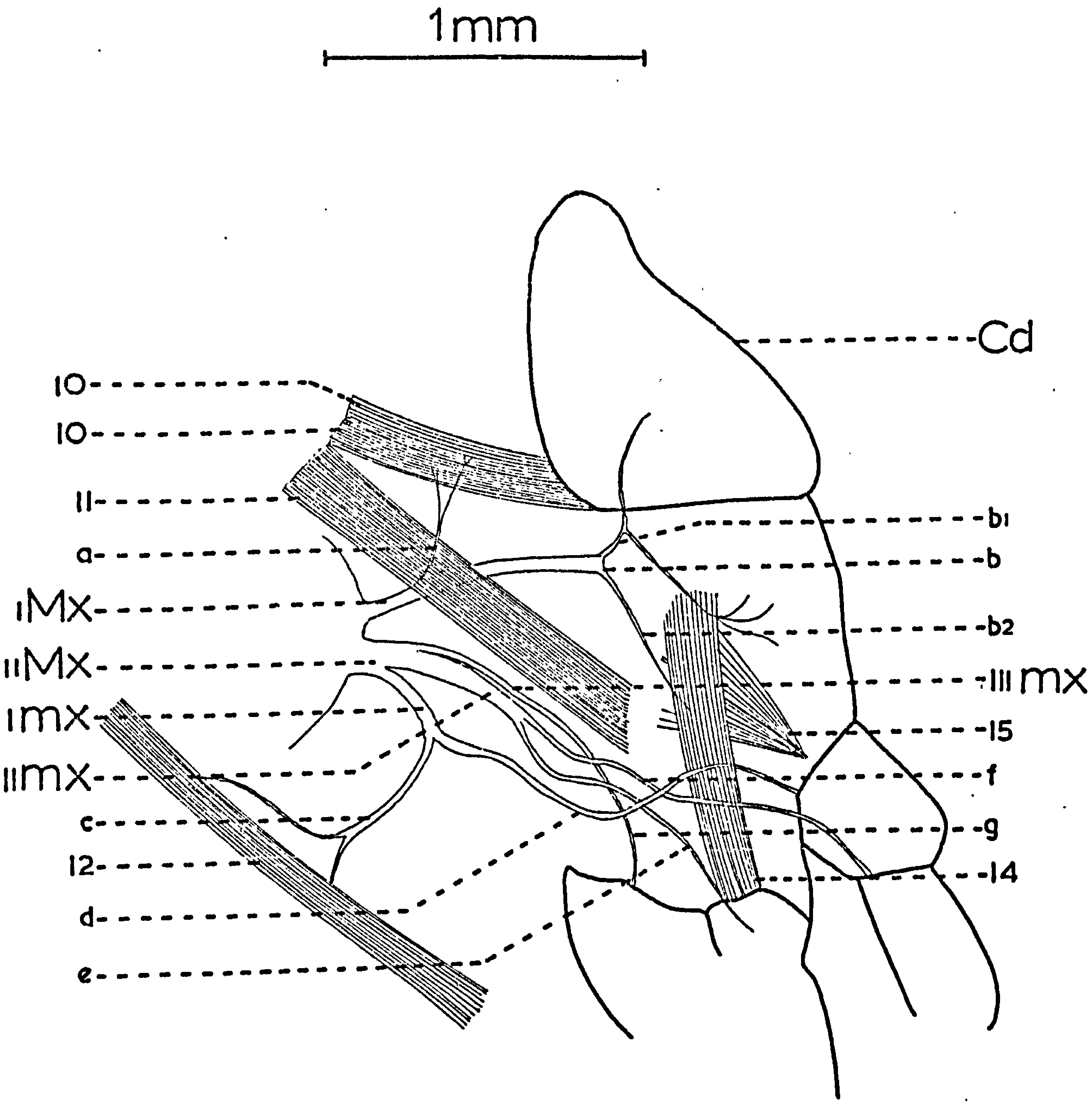


Fig.10

Fig. 11. Division of the second main maxillary nerve: a, innervation of the muscles of the stipes (Muscle 11) and levator of the palpifer (Muscle 15);
b, innervation of other muscles of the maxilla.


1 mm
11
sog
Imx
IImx
IIImx
15
a
9
12
10
10a
11
c
sog
13
IIMx
15
Imx
16
IImx
17
d
Lc
Ga
b

Fig.11

Fig. 12. Second main maxillary nerve 'IIMx': a, fine branch to adductor of the stipes (Muscle 11); b - c, adductor of the stipes (Muscle 11) dissected to illustrate detailed innervation.

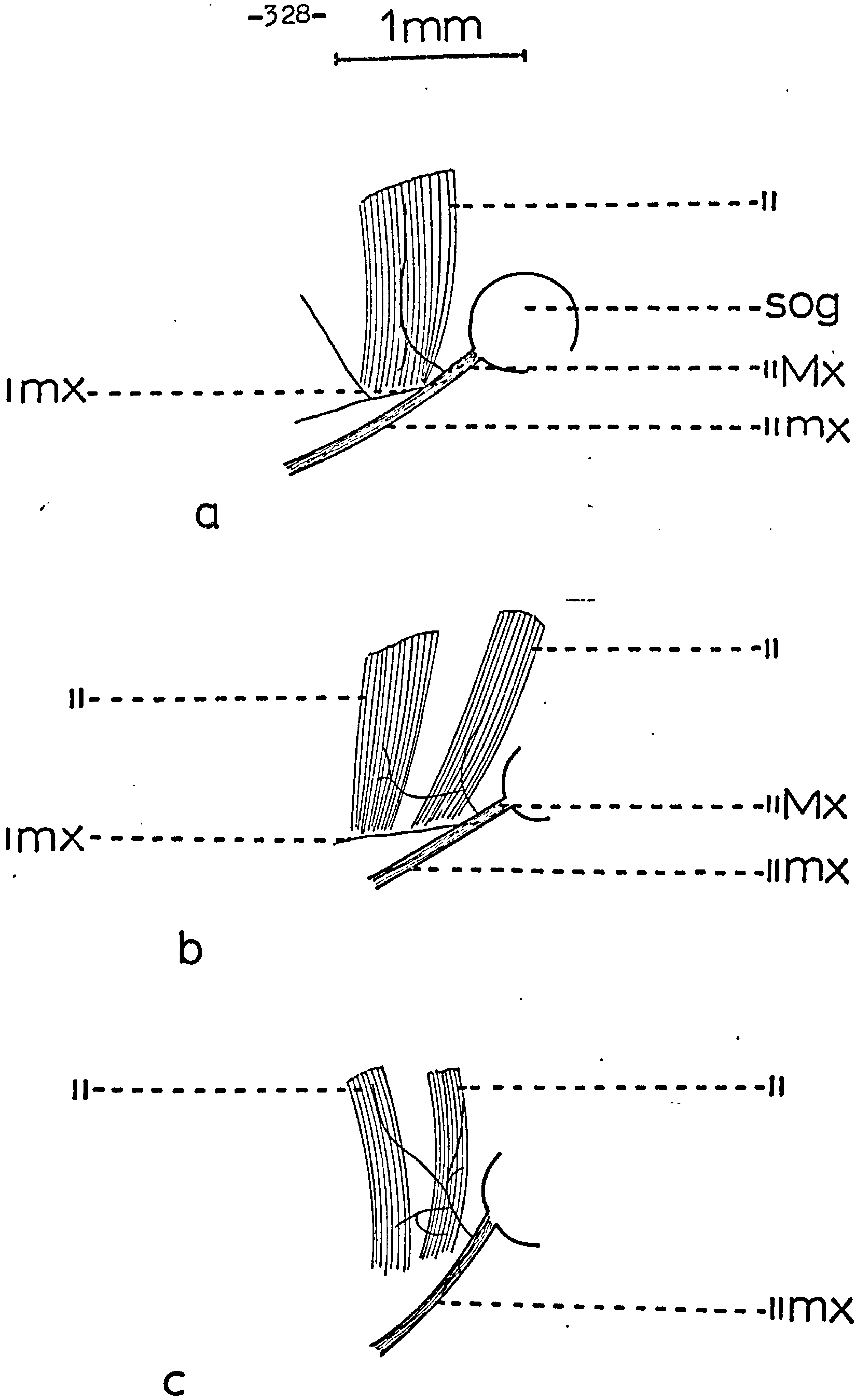


Fig.12

Fig. 13. Innervation of cranial flexor of the lacinia (Muscle 12) and protractor of the cardo (Muscle 9) by branch 'c' of the first maxillary nerve 'Imx'.

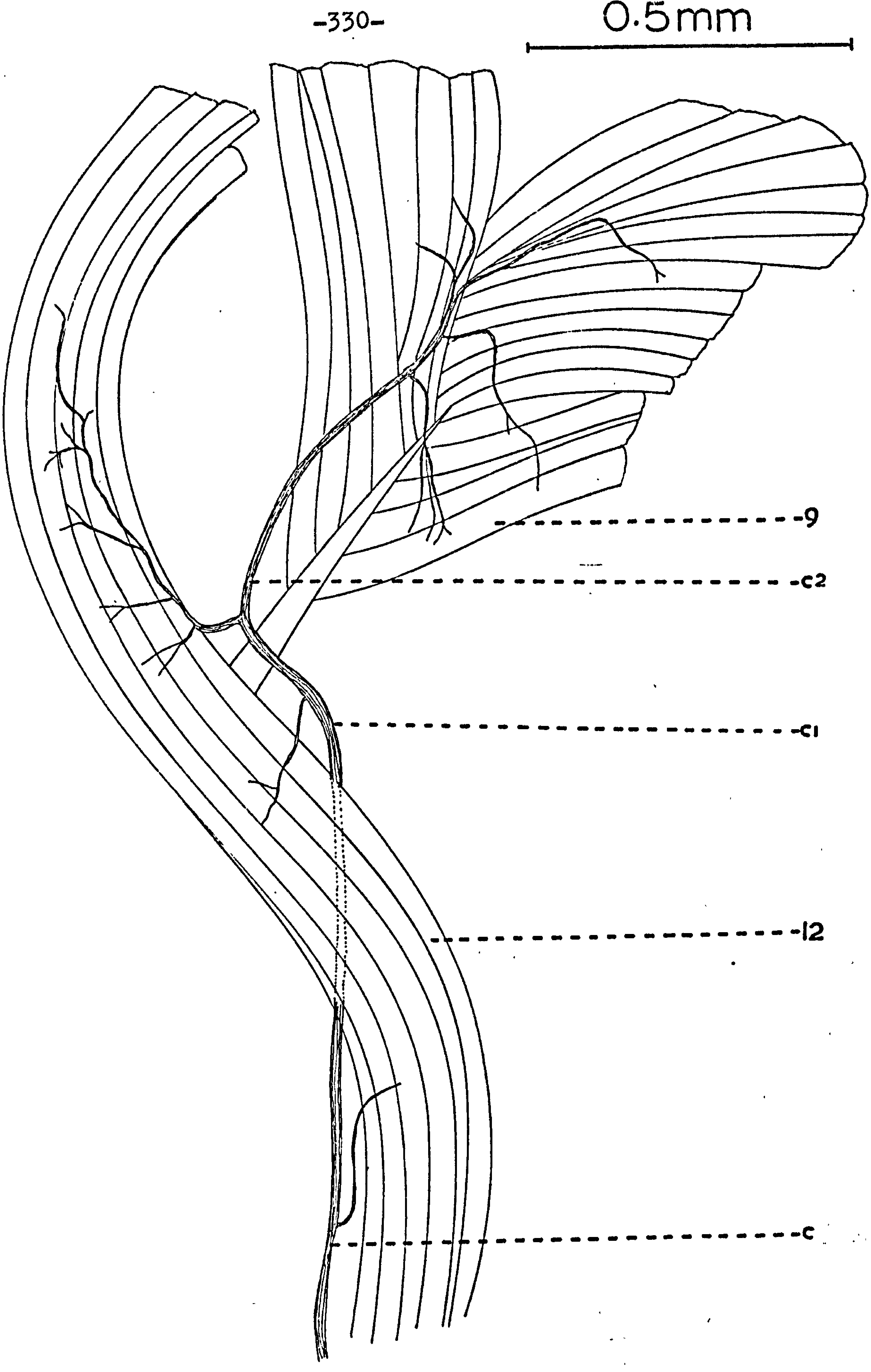


Fig.13

Fig. 14. Innervation supplied by branch 'd' of the second main maxillary nerve: a, cranial flexor of the lacinia (Muscle 12), flexor of the lacinia (Muscle 13); b, flexor of the lacinia (Muscle 13).

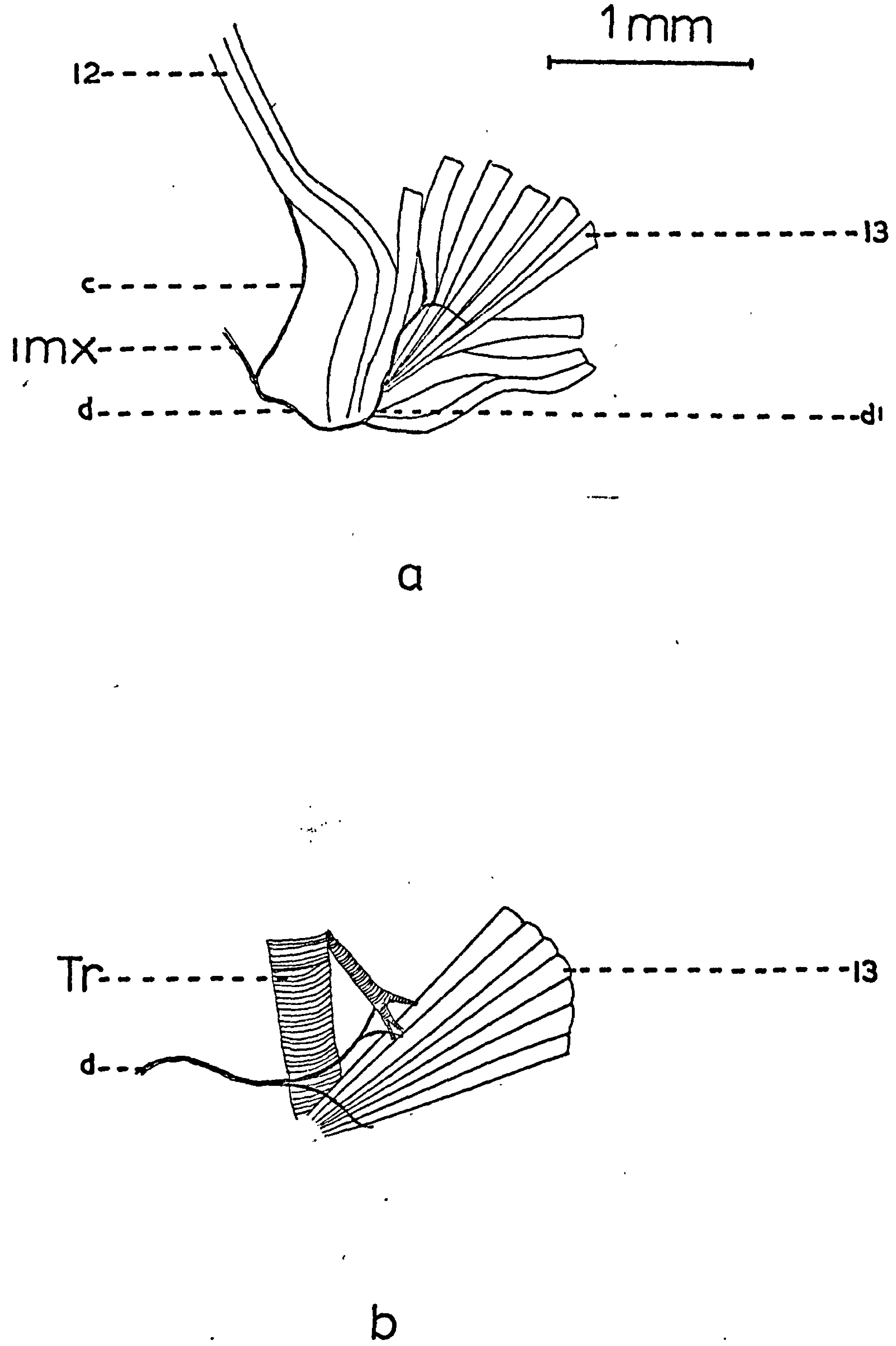


Fig.14

Fig. 15. Innervation of the flexor of the galea (Muscle 14) and levator of the palp (Muscle 15) by branch 'b_2' of the first main maxillary nerve 'IMx'.

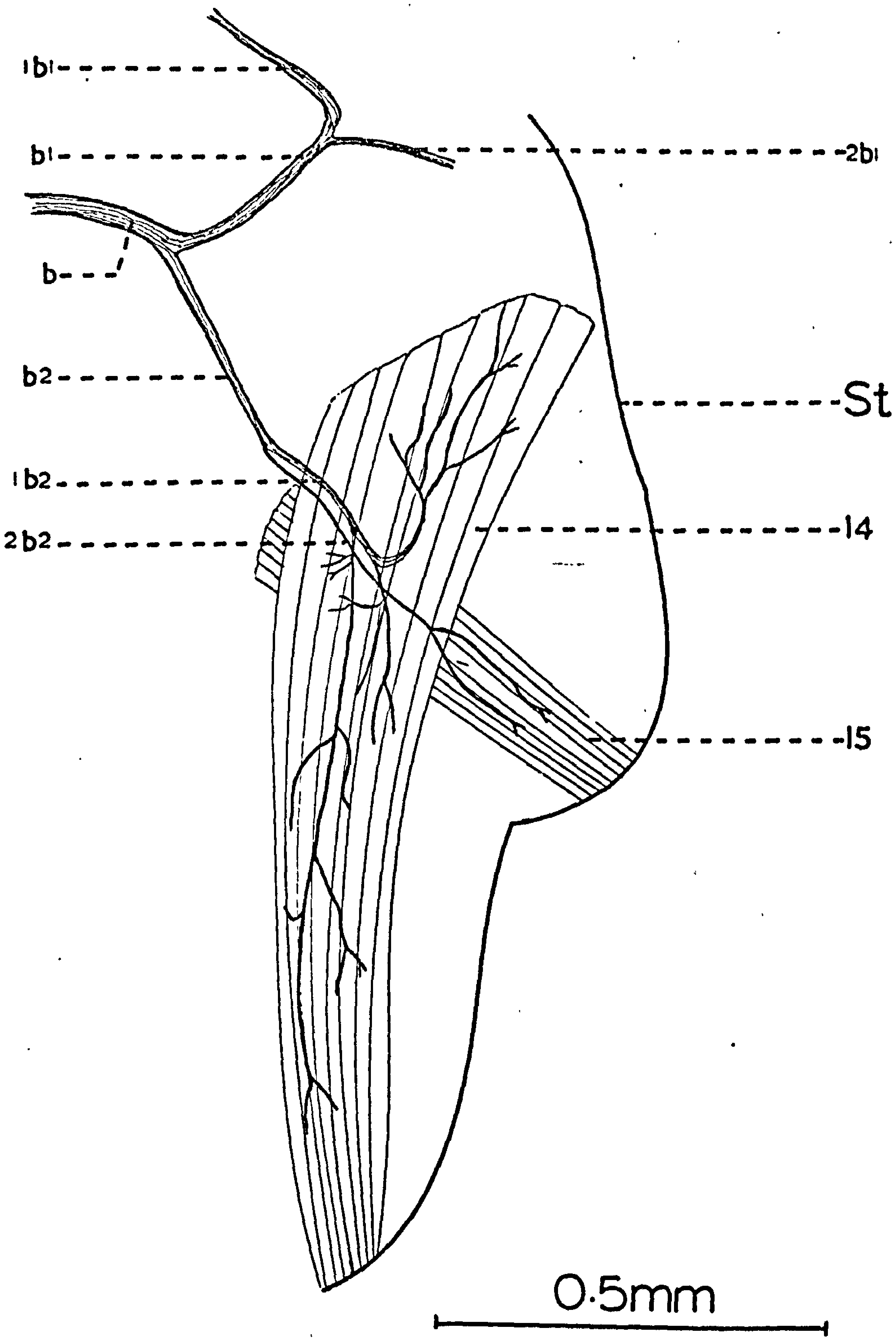


Fig.15

Innervation of the Cardo (Fig. 16)

The nerve fibres which innervate the sensilla of the cardo have been carefully traced. The sensory branch '$1b_1$' enters the cardo and splits into two sub-branches. One branch mainly ramifies in the posterior surface of the cardo and forms a network of nerve fibres. The Type 4 sensilla are innervated by a single neuron which in most cases is spindle shaped but occasionally may be round. Some of the Type 3 and 7 sensilla are also supplied by a single neuron which is mainly round. The dendrites in both types are not very long. Some of the nerves apparently end blindly, this may be explained by the fact that they merely terminate in the cuticle or due to the vagaries of staining their connection with the cuticular sensilla may have been masked. A number of neurons have been seen to end just short of the base of the sensilla, in this case it was assumed that the stain had not penetrated into the base of the sensilla. In certain parts of the cardo there are some apparent cross connections between the nerves. There is a certain degree of variability in the path taken by nerve '$1b_1$'.

Innervation of the Stipes (Fig. 17)

The sensory nerve '$2b_1$' (Table 2) enters the stipes where it splits into two branches. The first branch travels towards the proximal region of the stipes (Fig. 17a). Along its route gives off branches which innervate some of Type 3 sensilla on the proximal region of the posterior surface of the stipes above and outside the sulci of the stipes 'q' and 't'.

The second branch travels distally towards the outer border of the stipes and innervates the Type 3 sensilla by a single neuron. Type 1 and 7 sensilla situated here are also innervated by a single neuron. The sensilla within the longitudinal sulci of the stipes 'q' and 't' may be supplied by one of the nerve bundles of the 'b_2' branch which is both motor and sensory (Fig. 17b). Some of the Type 3 sensilla in this portion are innervated by a single neuron. The distal part of the stipes is innervated by a sub-branch 'h' of the second main maxillary nerve 'IIMx' (Table 2). One of the bundles of fibre 'h' from the nerve 'g' reaches the distal portion of the stipes (Fig. 17b) and seems to innervate some of Type 3 sensilla. Some of the Type 6 sensilla are also innervated by a single neuron. The same branch seems to be sensory but the precise nervous connection with the sensilla is not completely clear, this is probably a result of inadequate staining.

It has been noticed that there is some variability in the nervous innervation of the stipes between individuals of the same sex. The nerve fibre which arises from nerve 'b_2' is in the form of a multiterminal neuron, giving rise to three to four dendrites (Fig. 17b).

Fig. 16. Posterior view of the cardo showing the innervation of the sensilla by a sub-branch of the first main maxillary nerve 'IMx'.

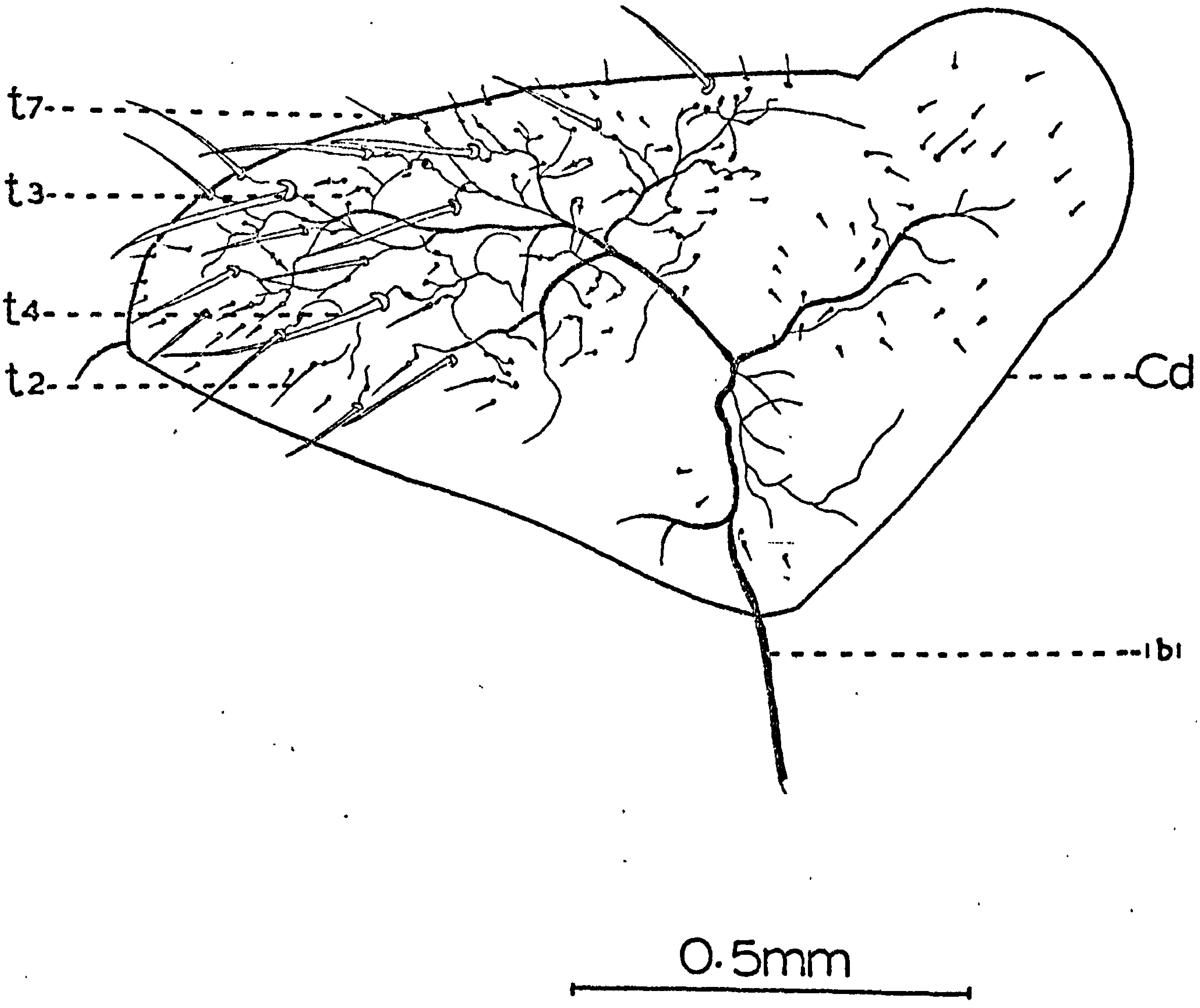


Fig.16

Fig. 17. Posterior view of the stipes:
a, showing innervation of the sensilla by a sub-branch of the first main maxillary nerve 'IMx'; b, a sub-branch 'h' of the second main maxillary nerve 'IIMx'.

Fig.17

Second main maxillary nerve

The second main maxillary nerve 'IIMx' (Figs. 10 and 11a) is very thick compared with the first main maxillary nerve 'IMx' and arises from the suboesophageal ganglion. Immediately after its origin from the suboesophageal ganglion, the nerve branches into three, the first, second and third maxillary nerves, 'Imx', 'IImx', 'IIImx' (Table 2) as seen in Fig. 11a. From first maxillary nerve 'Imx' a fine nerve innervates the adductor of the stipes (Muscle 11), (Fig. 12a).

First maxillary nerve

The first branch of the second main maxillary nerve 'IIMx' immediately gives rise to a fine nerve which innervates the adductor of the stipes (Muscle 11), (Fig. 11a). After a short distance, the first maxillary nerve 'Imx' bifurcates into two branches 'c' and 'd' (Table 2). The first branch 'c' is motor and gives off a branch 'c_1' (Fig. 10) which travels dorsally to innervate the cranial flexor of the lacinia (Muscle 12) (Figs. 10, 13 and 14a). A further branch of this nerve 'c_2' innervates the protractor of the cardo (Muscle 9), (Figs. 11b and 13). The second branch 'd' (Table 2), which is also motor, enters the stipes where it splits into two nerves 'd_1' and 'd_2' (Table 2). The former nerve, 'd_1' innervates the flexor of the lacinia (Muscle 13), (Figs. 11b, 14a and b). The other branch 'd_2' passes into the palp where it supplies nerves to the levator and depressor of the palp (Muscle 15 and 16), (Figs. 10 and 15) and then passes into the first maxillary palp segment where it provides nervous innervation to the levator of the first palp segment (Muscle 17), (Fig. 11b).

Second maxillary nerve

The second maxillary nerve 'IImx' (Table 2) is the thickest of the three branches of the second main maxillary nerve 'IIMx'. It enters the distal part of the stipes (Figs. 10, 11a and b) and runs for more than half of its length before it divides into two sensory branches 'e' and 'f' (Table 2). The first branch 'e' runs into the galea (Fig. 10) whilst the other branch 'f' enters the palp and innervates all segments of the palp giving off small branchlets to each segment.

Innervation of the Galea (Figs. 18 and 19)

The sensory branch 'e' of the second maxillary nerve fork as it enters the galea into two nerves 'e_1' and 'e_2' (Plate 1a and b) which innervate the posterior and anterior surfaces of the galea respectively (Table 2). Each nerve, as it passes towards the tip of the galea (Fig. 18), gives off a lateral branch about a quarter of the way along its length. This nerve passes towards the base of the galea and its branches provide innervation to the Type 3 sensilla along the length of the outer side of the galea. Most of these sensilla have two neurons whilst the Type 4 sensilla innervated by this nerve have only a single neuron. At the

Fig. 18. Posterior surface of the galea illustrating innervation of sensilla.

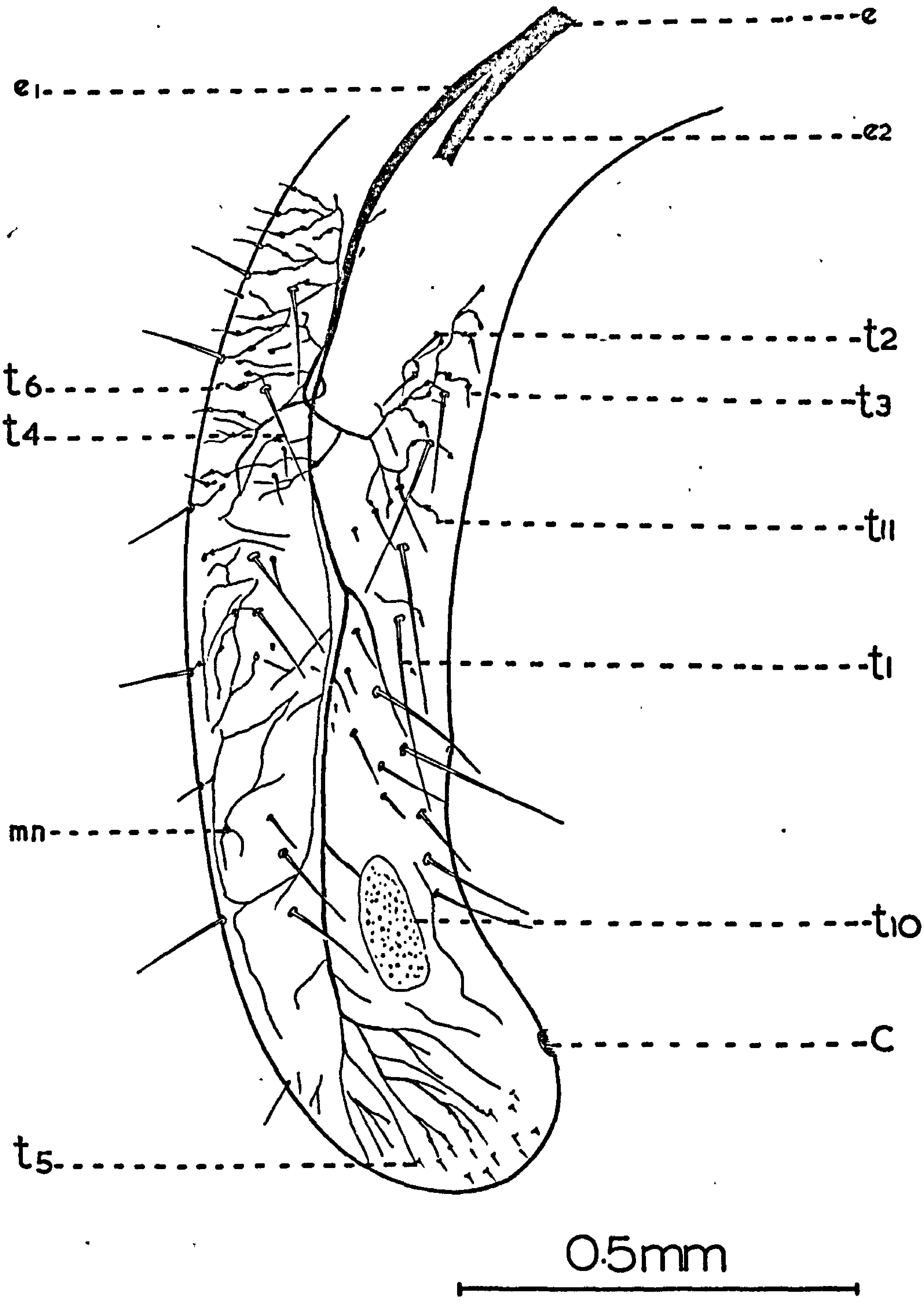
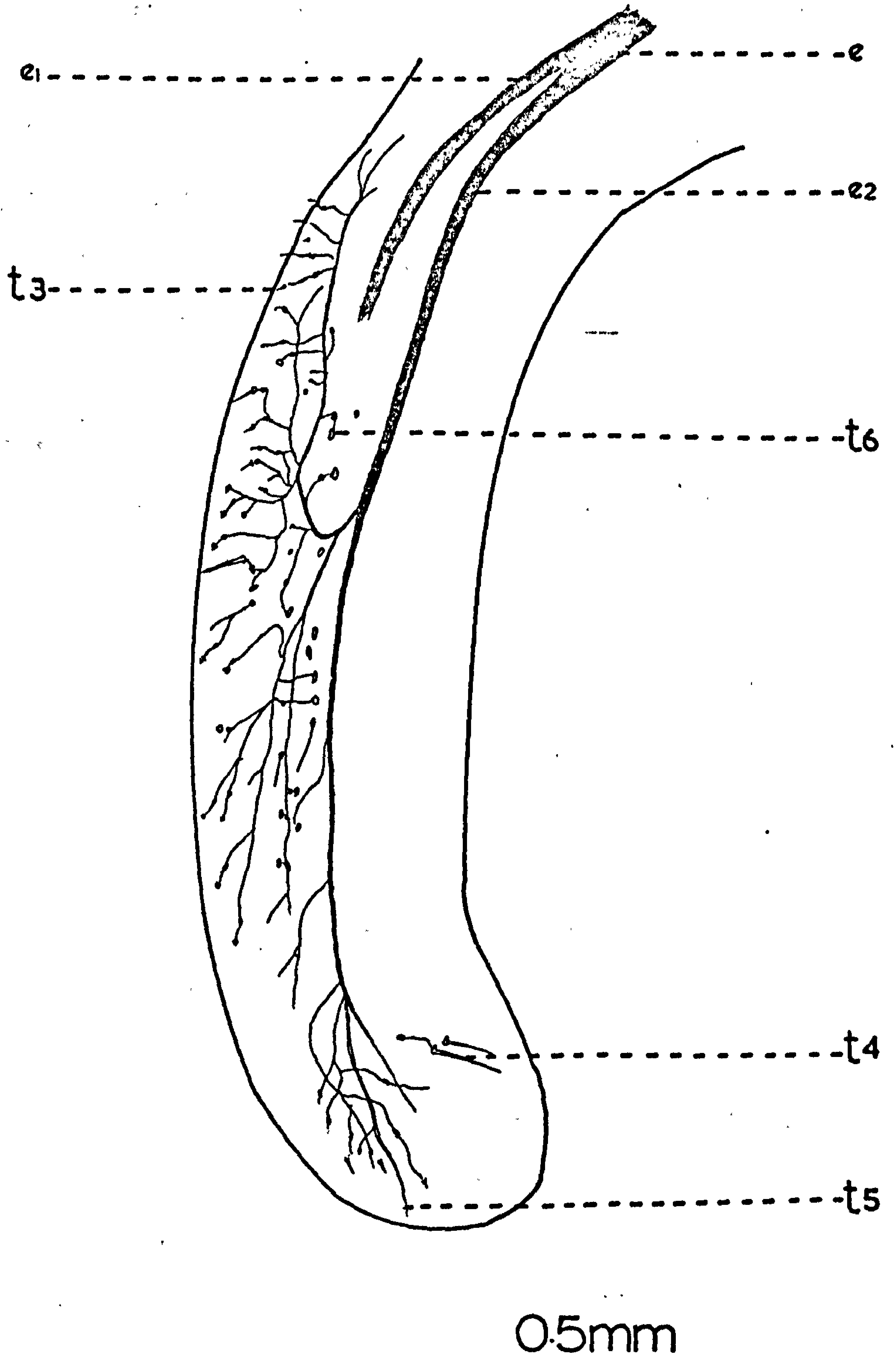


Fig.18

Fig. 19. Anterior surface of the galea illustrating innervation of sensilla.



Fig·19

site of origin of this lateral branch of 'e_1' arise two more branches, one of which assumes the form of a loop (Fig. 18). The first one curves, crosses over the main branch of 'e_1' and then undergoes further subdivision. One branchlet gives off numerous fibres which supply innervation to the many sensilla situated on the inner margin of the proximal region of the galea (Fig. 18). The Type 3 sensilla present in this area are mostly innervated by four neurons, whilst the large Type 1 sensilla and also Type 11 are innervated by a single neuron. A smaller bundle of nerve fibres arises from this loop-shaped branchlet; they run towards the outer part of the galea and appear to innervate sensilla of Type 3 and 4. As the main branch of 'e_1' passes towards the tip of the galea, it gives off another smaller branchlet. Immediately after its origin this branchlet curves towards the outside of the galea and so crosses over the loop-shaped branchlet, and innervates the sensilla in this area. Just distal to this, 'e_1' gives off a very fine nerve which runs parallel to 'e_1' for some distance before it becomes further subdivided and bends proximally to supply the sensilla situated in the mid outer regions of the galea (Fig. 18). However, the detail of this branch was hard to elucidate. The main nerve 'e_1' then bifurcates about half way along its length. One branch is thick and travels distally in the midline of the galea, giving off some side branches. When it reaches the end of the galea, it subdivides many times to thoroughly

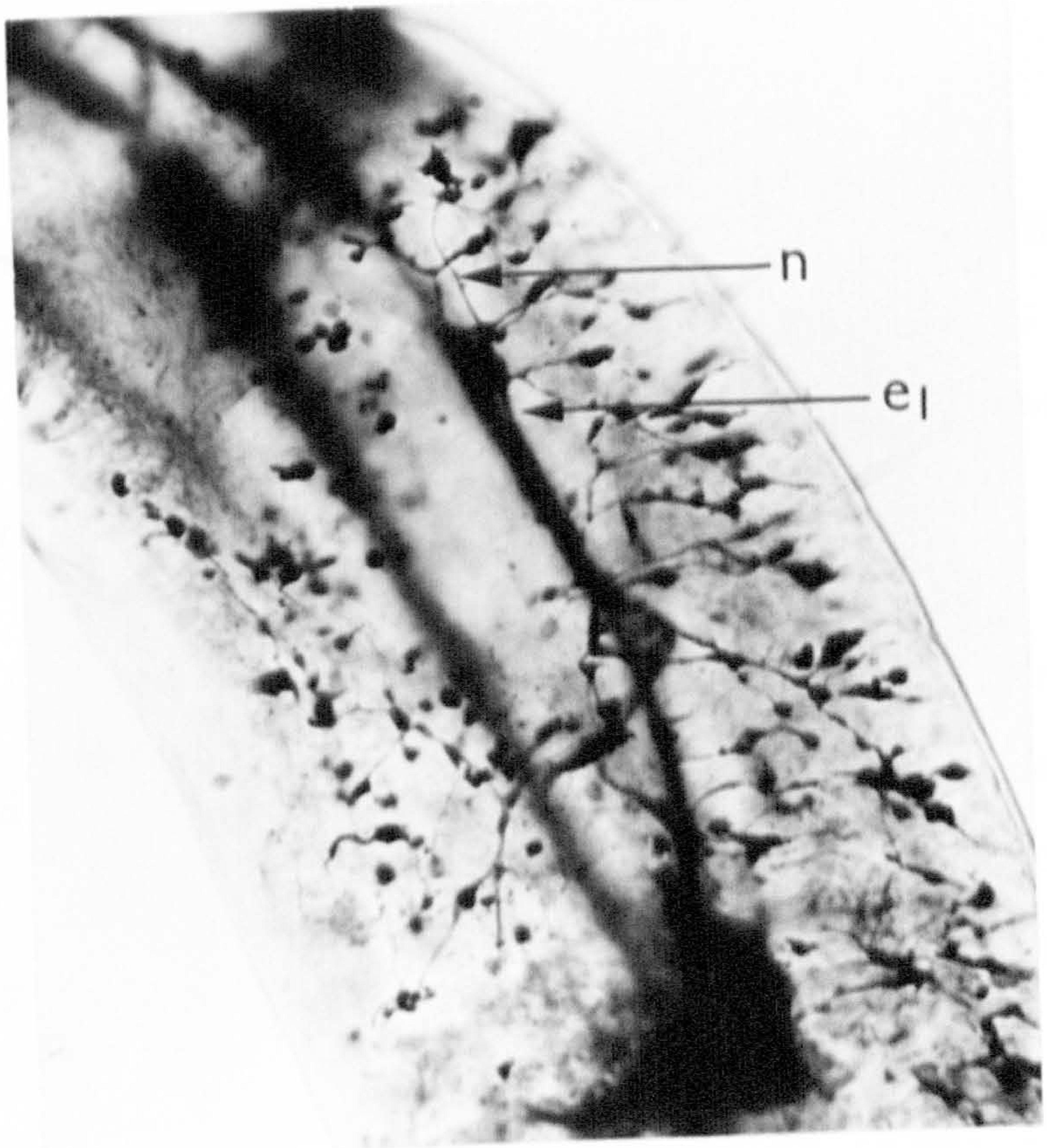
Explanation of the Plates

All the photographs in this section have been taken under a light microscope.

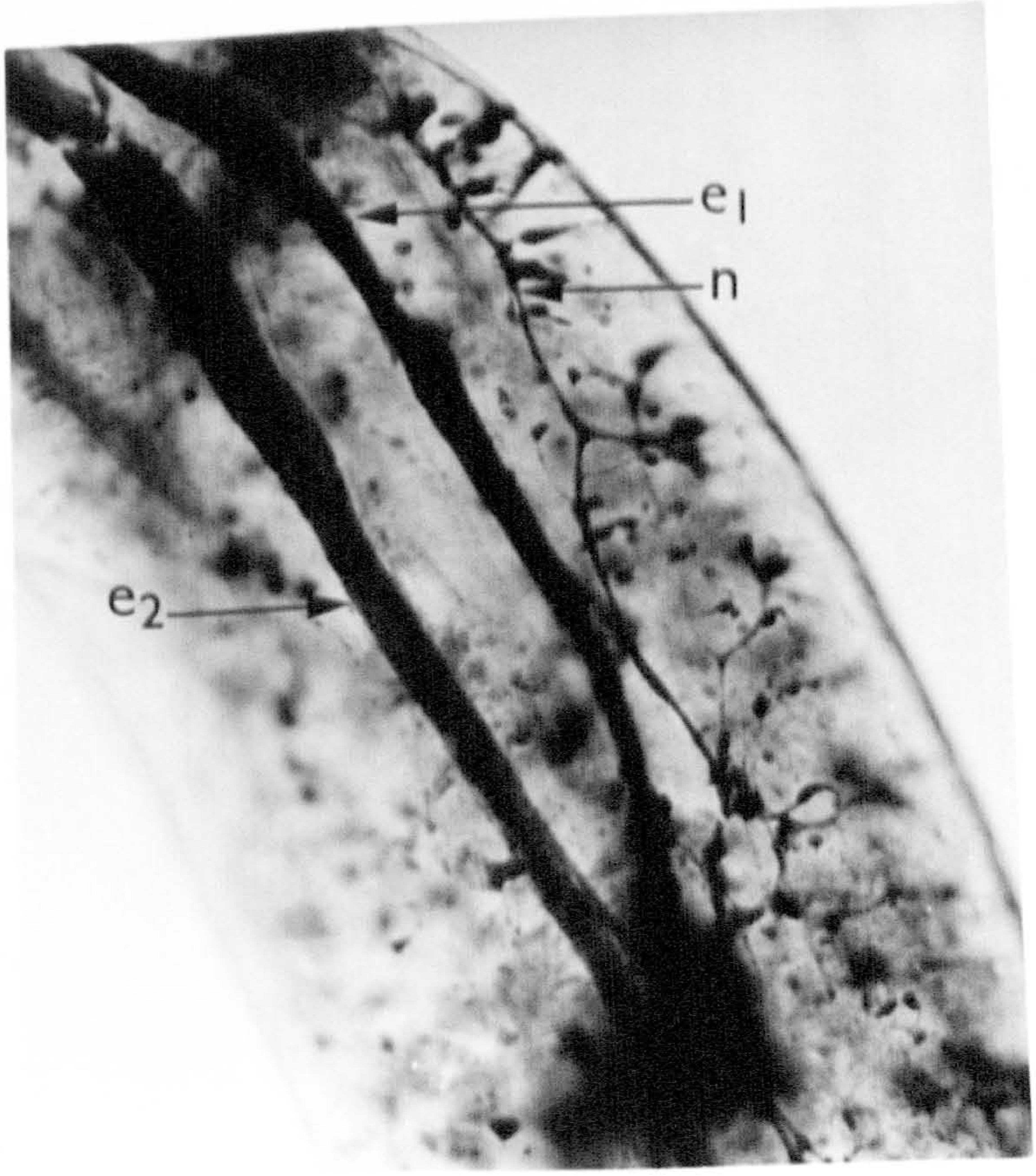
Plate 1. Light micrograph of the galea:

a. posterior view;

b. anterior view (X320).



a



b

ramify the area. The Type 5 sensilla which are densely packed in this region are innervated by this nerve. The group of Type 10 sensilla also receive a branch from this nerve although the individual neurons could not be traced (Fig. 18).

The second branch passes towards the inner side of the galea and innervates the sensilla found in this region. On the outer side of the galea, approaching the apex, multi-terminal neurons have been found, these each have three dendrites.

The anterior surface of the galea (Fig. 19) is mainly innervated by the branch 'e_2' (Plate 1b) of the second maxillary nerve 'IImx'. This passes in the midline to the apex of the galea and gives off many branchlets throughout its course. The most significant branch emerges half way along its length. This branch bifurcates soon after its origin from 'e_2'. One of the branchlets passes proximally to innervate the Types 3, 6 and 7 sensilla, each having a single neuron. The other branchlet runs distally almost parallel to 'e_2' and gives off finer nerves which innervate Types 6 and 7 sensilla each having a single neuron. The branch 'e_2' (Fig. 19) then continues towards the apex of the galea giving off a couple of small nerves along its route. Finally it splits into many branchlets which supply the sensilla in this region. The sensilla are mostly of Type 5 and again have a single neuron.

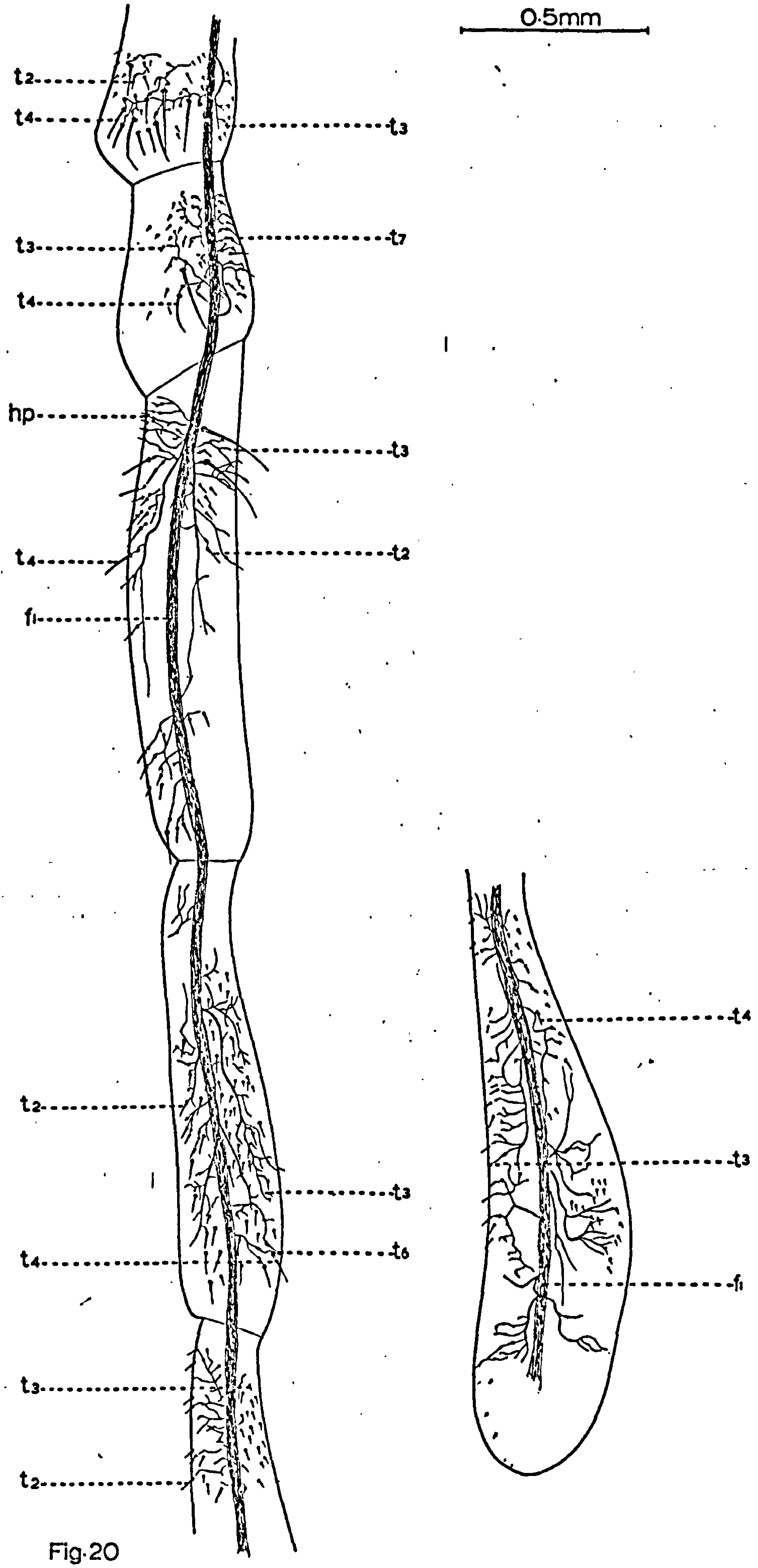
Innervation of the Maxillary Palp (Figs. 20 and 21)

The sensilla of the maxillary palp are innervated by nerve 'f' of the second maxillary nerve 'IImx'. Branch 'f_1' supplies the posterior surface and 'f_2' the anterior surface.

On the posterior surface 'f_1' passes throughout the length of the palp and gives off nerves to each segment (Fig. 20). Towards the base of the palp 'f_1' lies towards the outer side and gives off a branch which passes distally for a short distance and then passes horizontally across the segment. Finer branches of these nerves supply the sensilla in the segment. Most of the Types 3 and 4 sensilla have a single prominent neuron (Plate 2a). In the second segment 'f_1' gives off a branch towards the distal end of the segment (Fig. 20). The branch passes proximally for some distance before it subdivides into a network of nerves to innervate the sensilla of this segment, these are mainly Type 3 which again have a single neuron (Plate 3a).

The remaining segments of the palp are longer and therefore appear to have a more substantial nervous supply. A branch from 'f_1' (Fig. 20) arises at the junction of the second and third segments (Plate 4a). After a short distance it bifurcates into two nerves which diverge slightly and in turn divide to innervate the sensilla of the segment. The outer branch innervates the hair plate sensilla and other sensilla in the proximal outer corner of the segment. The

Fig. 20. Posterior surface of the maxillary palp illustrating innervation of sensilla.



Fig·20

Fig. 21. Anterior surface of the maxillary palp illustrating innervation of sensilla.

Fig.21

exact pathway followed by these nerves can be seen in Plate 5a and b. The inner branch innervates the sensilla at the base of the segment including the Types 2, 3 and 4 sensilla. This branch also supplies the sensilla in the distal part of this segment mostly of Types 4 and 6.

The proximal part of the fourth palp segment has only a few nerves. However, about one third of the way down the segment 'f_1' gives off two substantial branches. These subdivide many times in a rather dichotomous fashion and supply most of the sensilla in the segment. Types 2, 3, 4 and 6 sensilla are all innervated by a single neuron.

In the fifth segment the nervous supply to the sensilla is very complex. To some extent this may be an artefact due to difficulty in staining this segment. Near the base of this segment there are numerous small branches from 'f_1', some of which seem to stop short of the sensilla. The pattern of innervation in the middle of the fifth segment (Fig. 20) illustrates that Type 3 sensilla are mostly innervated by three neurons. One fine branch arises from 'f_1' near the proximal region of the segment and it travels more than half of the length of the segment. It innervates some of the sensilla on the inner side of the segment. Other small nerves arise from nerve 'f_1' and all tend to pass towards the distal end of the palp. Towards the tip a more prominent branch arises which splits into three. Some of the Type 3 sensilla in this region are provided with four neurons (Plate 6a). The extreme tip of the segment could not be examined in detail because of the problems experienced with staining.

Nerve 'f_2' supplies the anterior surface of the maxillary palp (Fig. 21). At the base of the palp this nerve is situated towards the outer side of the segment but it assumes a more median position in the third and terminal segments. The hair plate sensilla and some of the Type 3 sensilla on the first palp segment are innervated by a separate branch of nerve 'f' which arises before the nerve enters the maxillary palp. A prominent branch of 'f' arises at the base of the first segment and runs parallel to 'f' through the first segment and into the proximal half of the second segment. In the first segment this branch gives off a few lateral branches which innervate the Type 3 sensilla. A very fine nerve also arises from 'f' and follows a course parallel to the branch just described. Midway along its length there is a multiterminal neuron (Plate 2b).

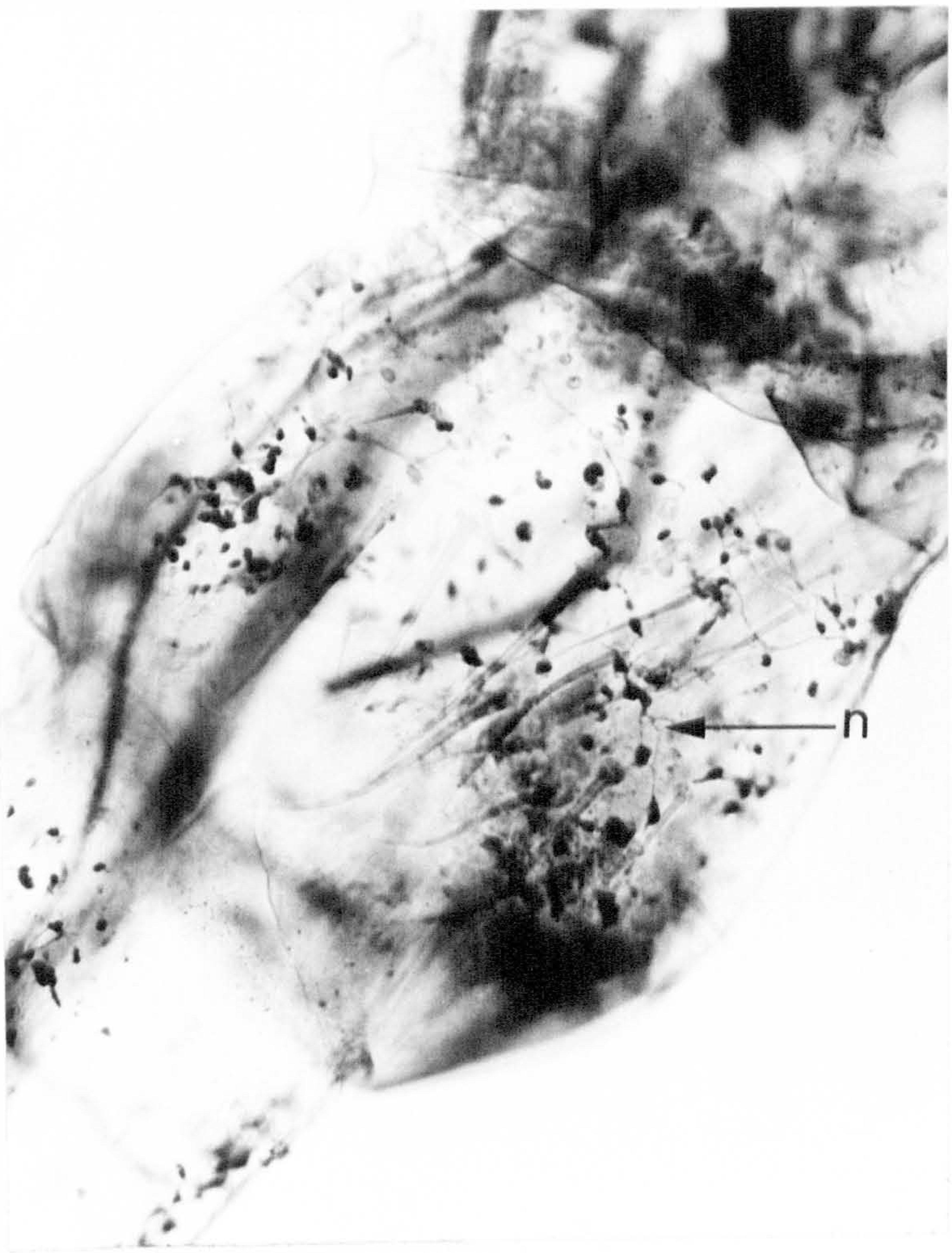
The second palp segment is also completely innervated by the branch of 'f' which originated in the first segment (Plate 2b). Lateral branchlets are given off at various intervals along the length of the nerve (Plate 3b) and supply sensilla of Types 3, 4 and 6. Types 3 and 4 sensilla both have a single neuron (Fig. 21).

Two main branches emerge from 'f_2' towards the base of the third palp segment (Plate 4b). At the origin of

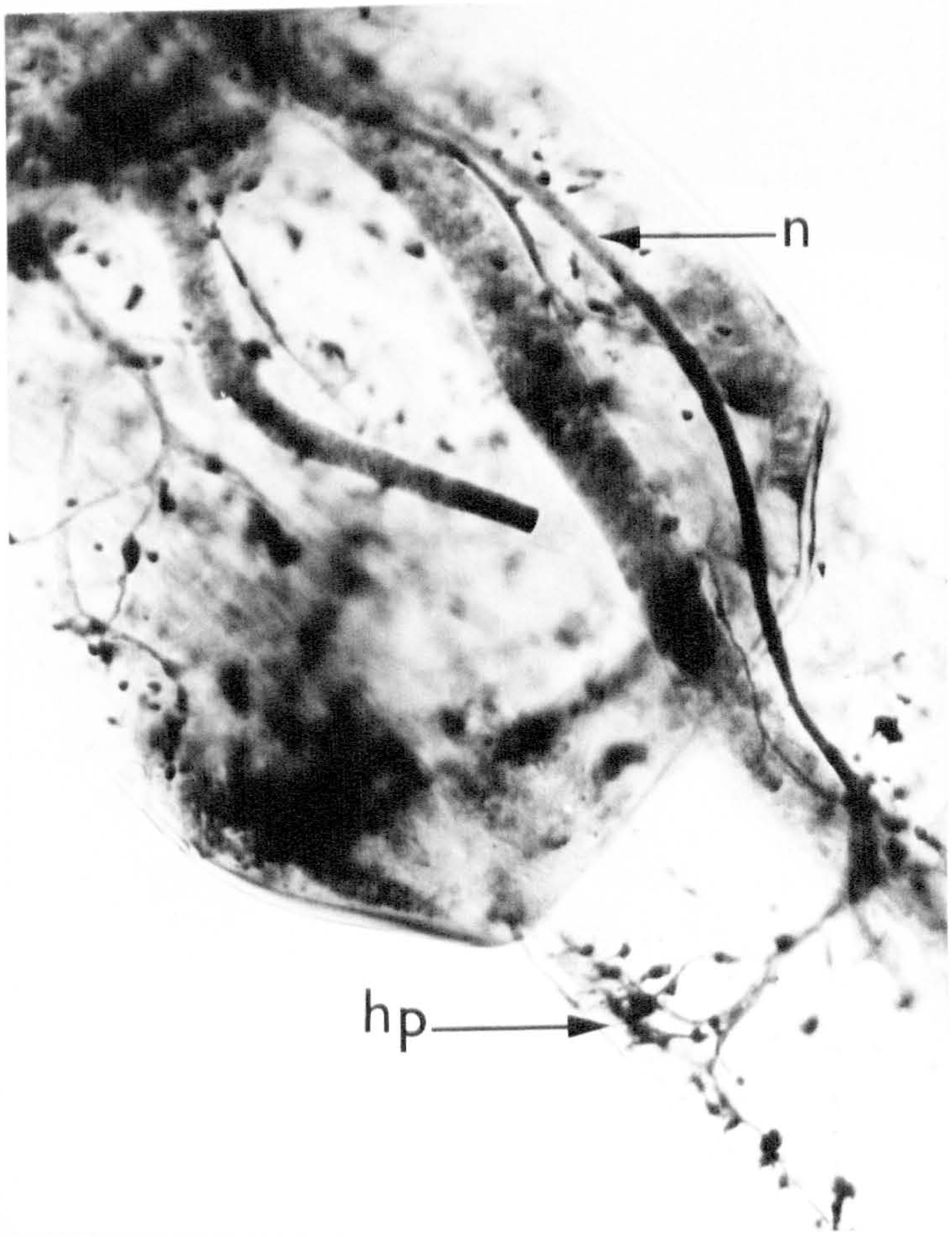
Plate 2. Light microscope of the first maxillary palp segment:

a. posterior view,

b. anterior view (X320).



a

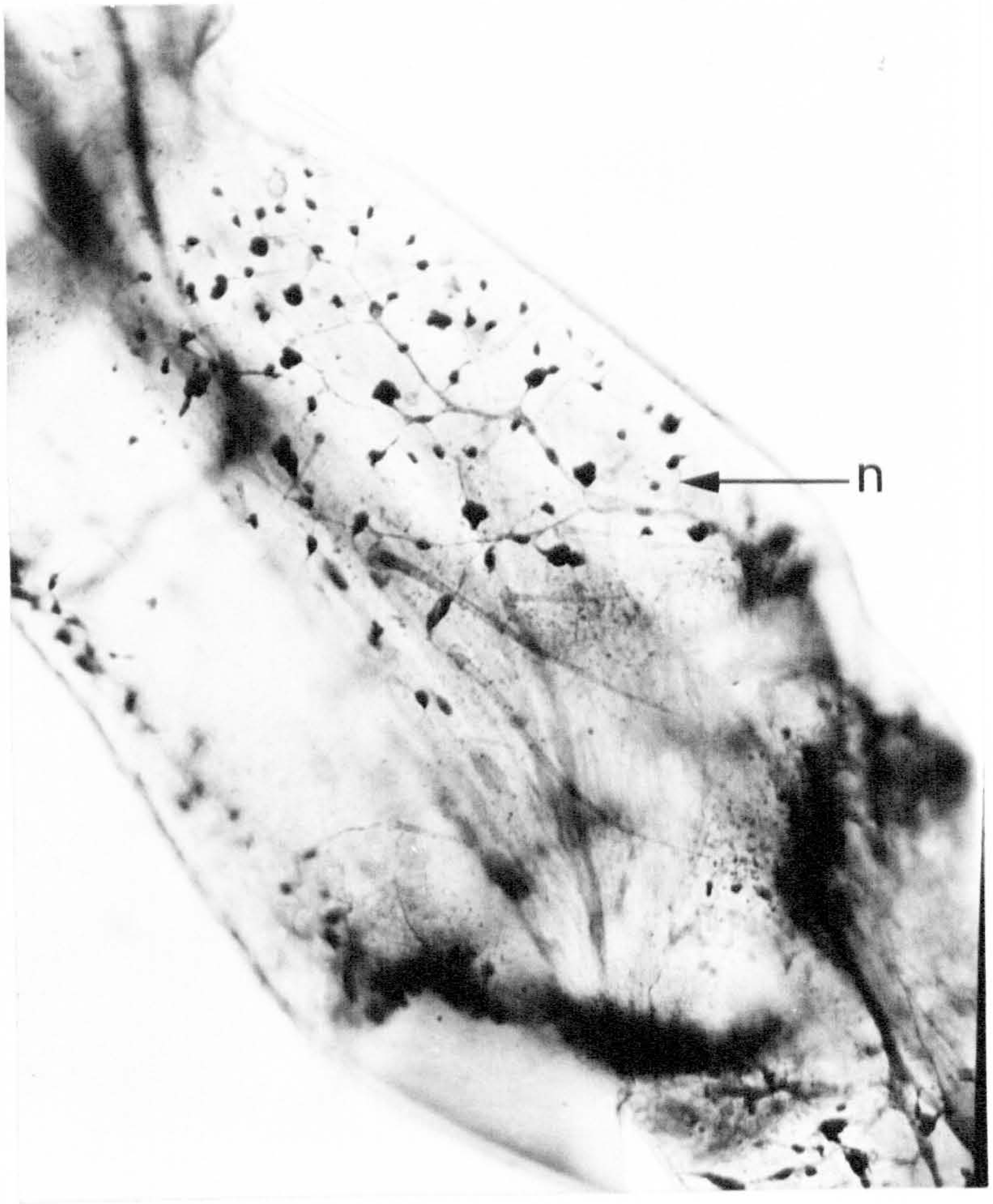


b

Plate 3. Light micrograph of the second maxillary palp segment:

a. posterior view,

b. anterior view (X 320).



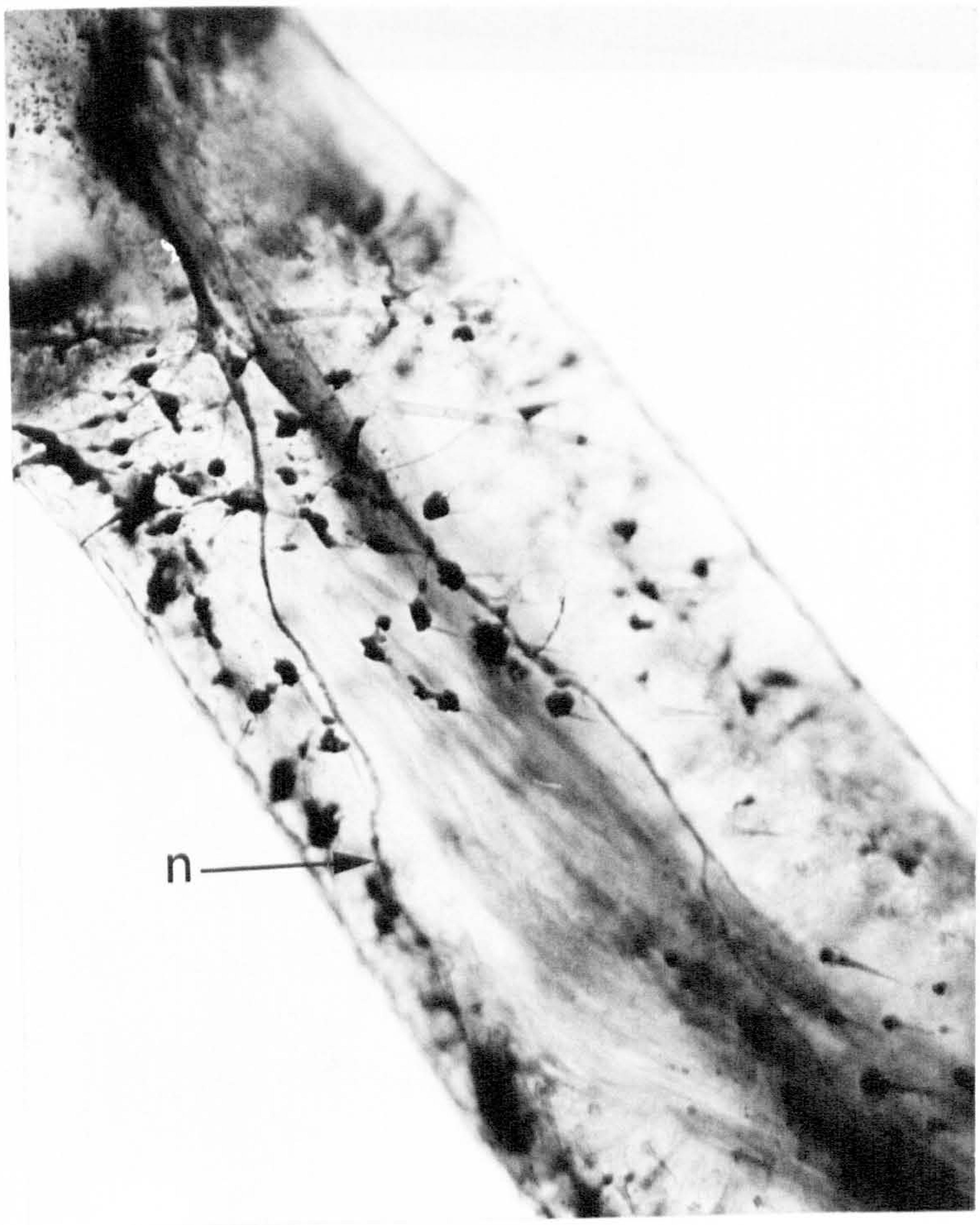
a

b

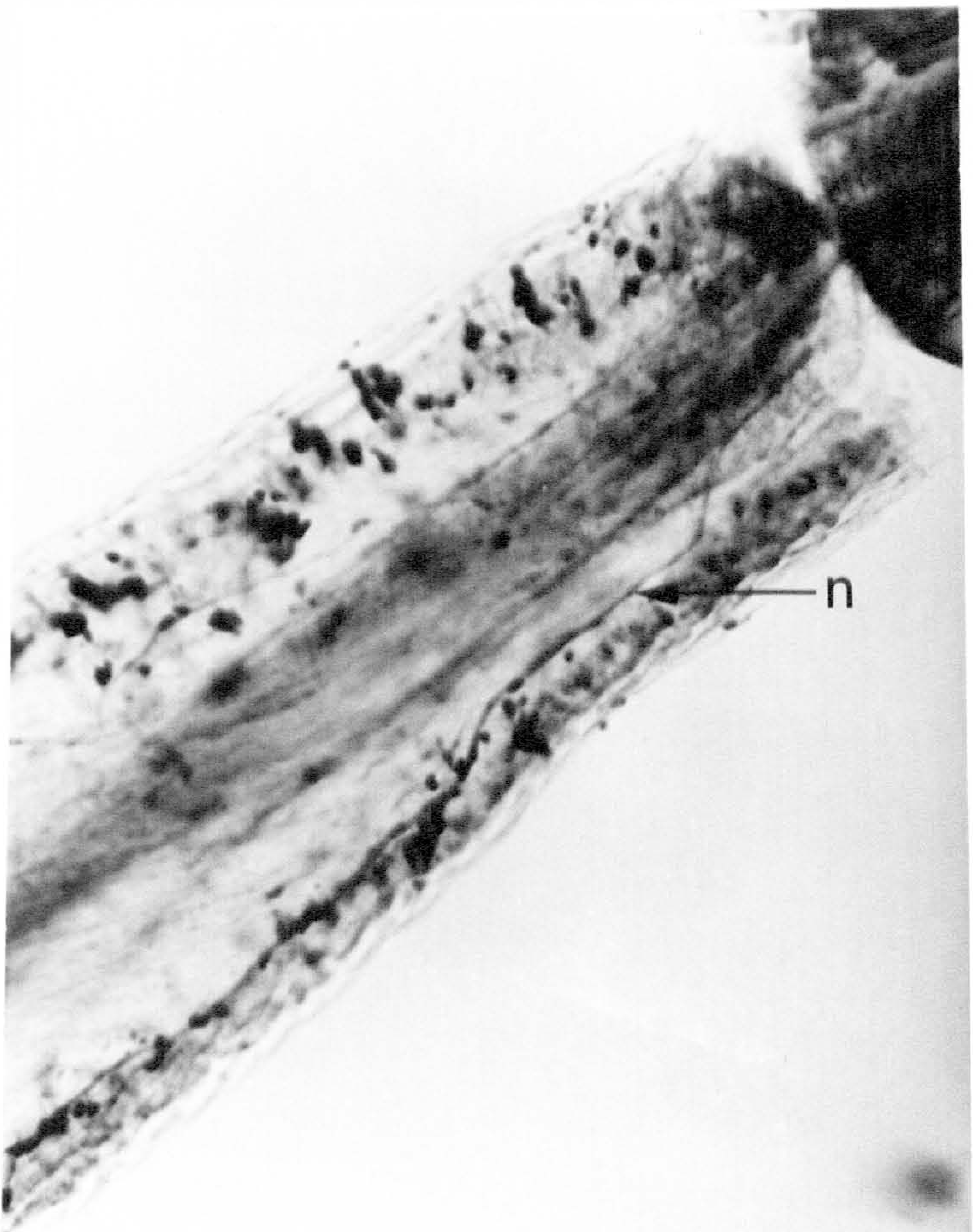
Plate 4. Light micrograph of the third maxillary palp segment:

a. posterior view;

b. anterior view (X 320).



a



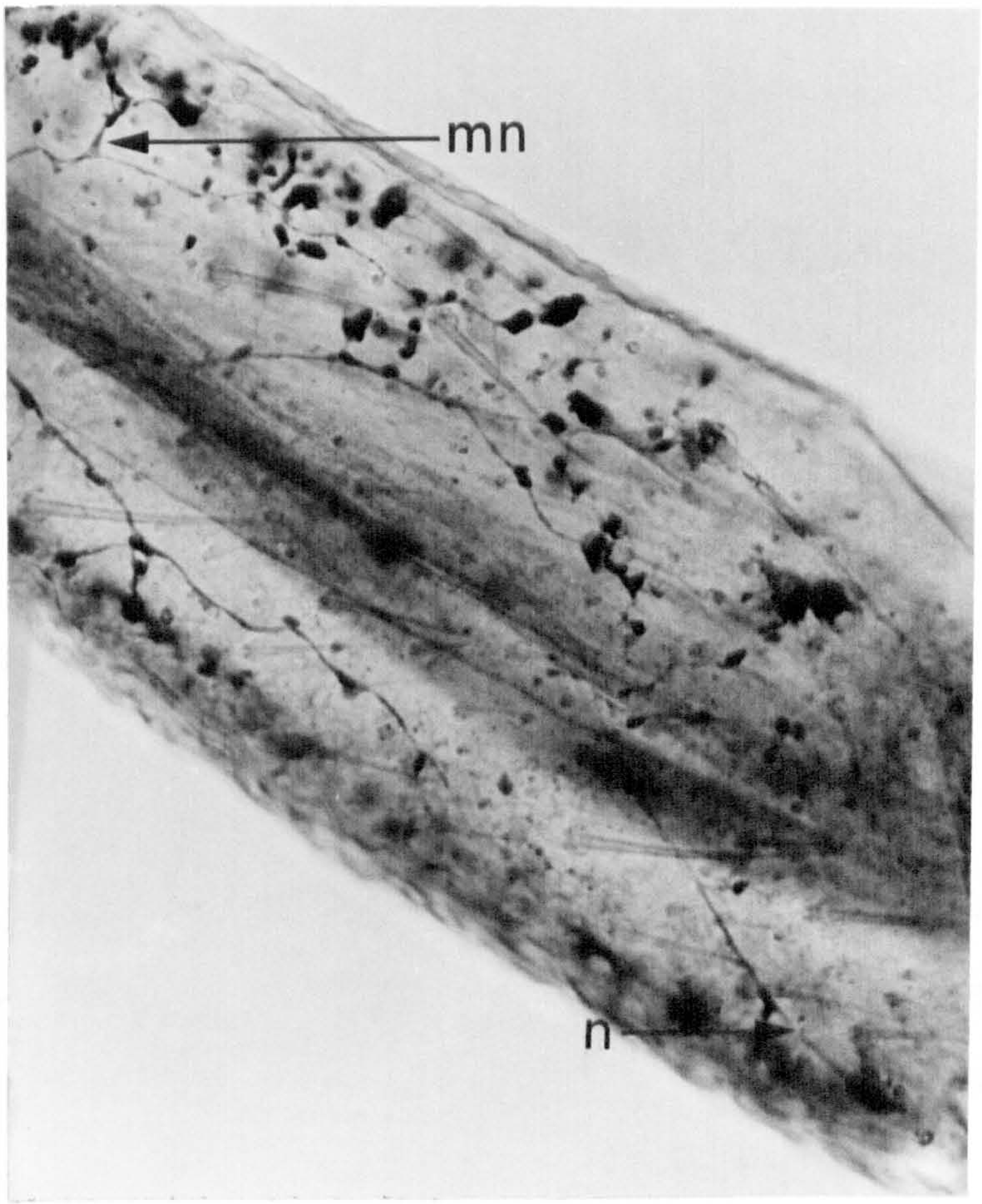
b

Plate 5. Light micrograph of the third maxillary palp segment:

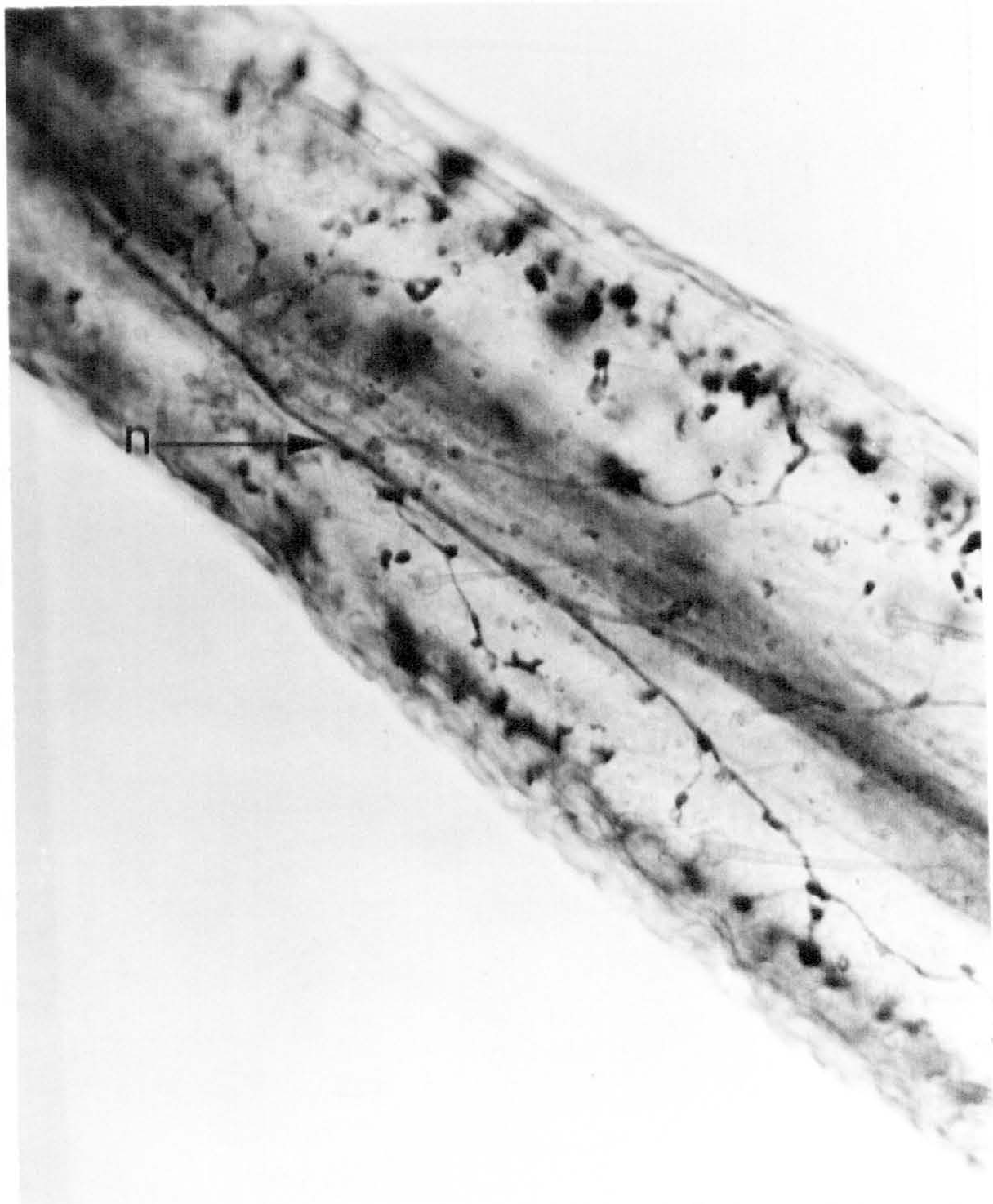
a. posterior view distal part;

b. posterior view proximal part

(X 320).



a



b

these branches a number of small nerve fibres are given off which supply the sensilla at the base of the segment. The two main branches of 'f_2' pass distally one on either side of the mid-line. These send branches to innervate, presumably, all the sensilla on the anterior surface of the segment. However, the nervous connection of all sensilla could not be clearly seen. Both Types 1 and 3 sensilla have a single neuron.

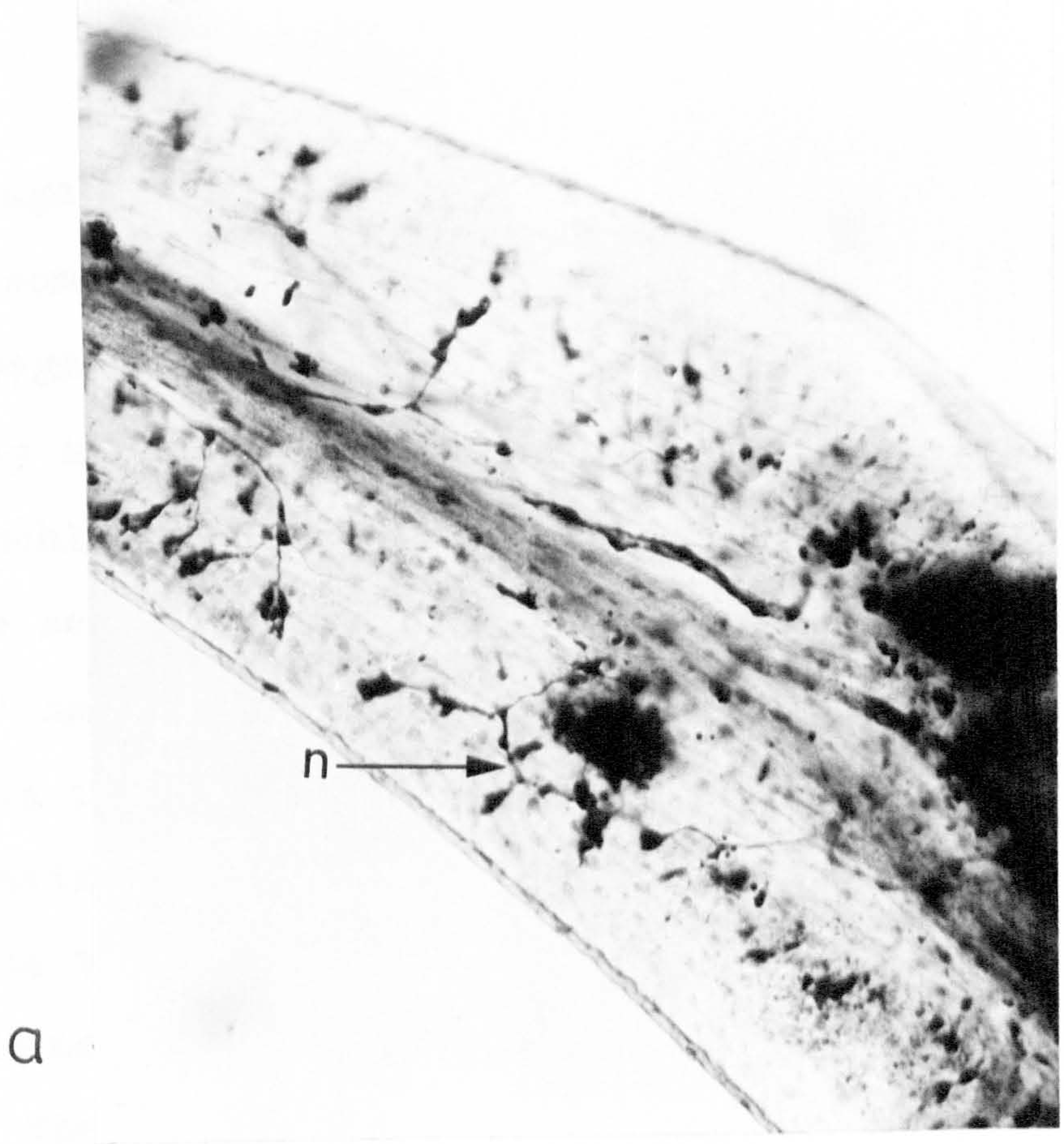
A nerve from the apex of the third segment passes into the fourth segment but the subject of its innervation is not clear. The hair plate sensilla are innervated directly by short nerves arising from the proximal part of the fourth palp segment. Almost half way through this segment nerve 'f_2' gives off a branch which itself soon bifurcates and by further branching ramifies the entire distal half of the segment and innervates the sensilla in this area (Fig. 21).

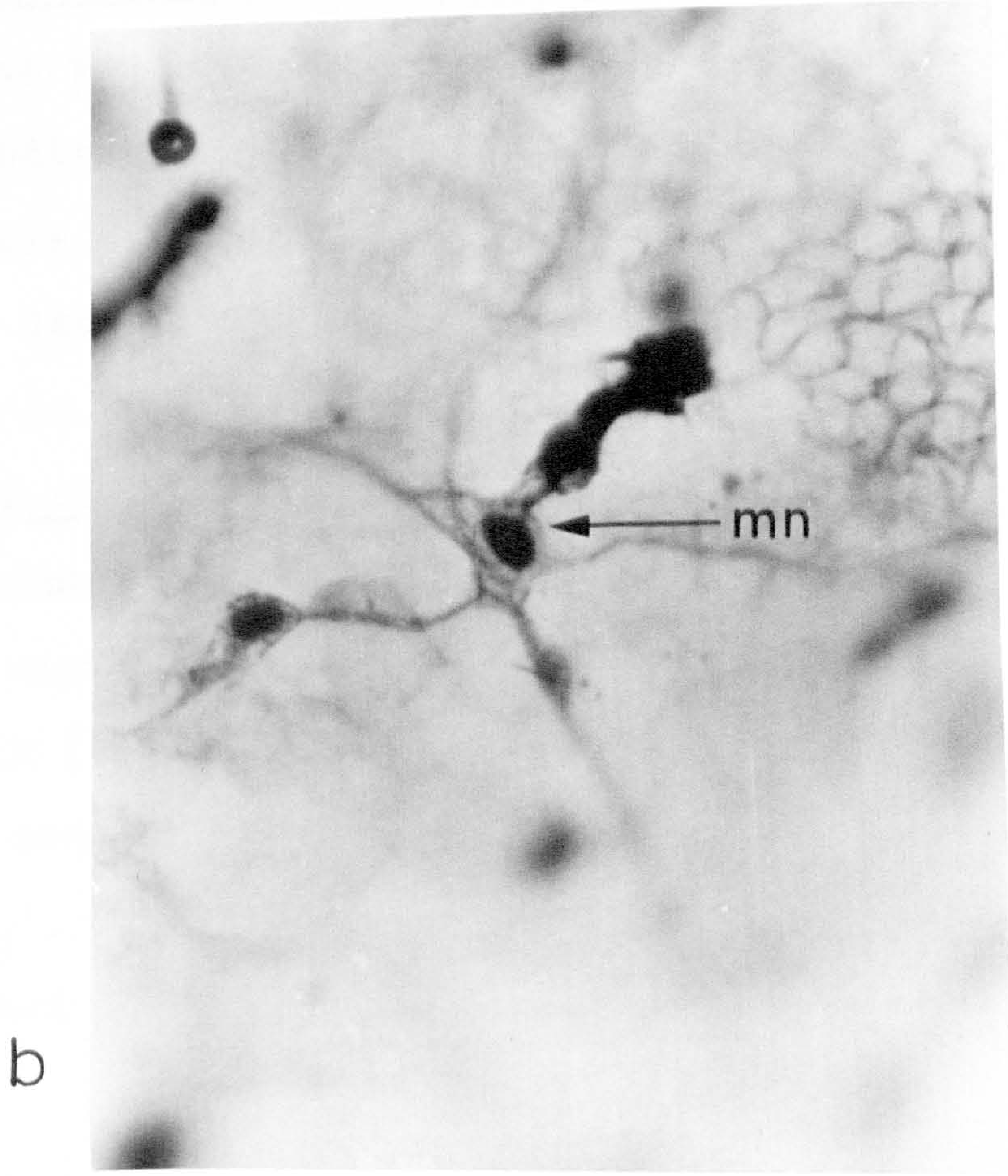
The nervous innervation of the sensilla on the fifth palp segment is quite complex. A few fine nerves leave 'f_2' at the base of the segment to supply innervation to the hair plate sensilla. Approximately in the middle of the terminal palp segment two branches are given off from 'f_2'. One of these on the outer side of the segment curves around and passes to the base of the segment supplying the sensilla in this area. The other branch bifurcates immediately after its origin from 'f_2' (Fig. 21). One

Plate 6. Light micrograph of:

a. posterior view of the fifth maxillary palp segment (X 320);

b. multiterminal neuron on the prementum (X 1280).


n
a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b

branchlet again splits into two and travels distally to innervate some of the sensilla on the inner side of the terminal segment. The remaining sensilla in this area are supplied by another small branch from 'f_2' (Fig. 21). The other branchlet passes in the opposite direction towards the tip of the segment. Two other branches arise directly from nerve 'f_2' and are probably also involved in the innervation of sensilla in this area although unfortunately this could not be confirmed, again due to difficulty in staining. Towards the tip of the segment nerve 'f_2' splits into a fan of smaller nerves which supply the numerous sensilla in this region. These sensilla are mostly of Types 3 and 5 and have a single neuron.

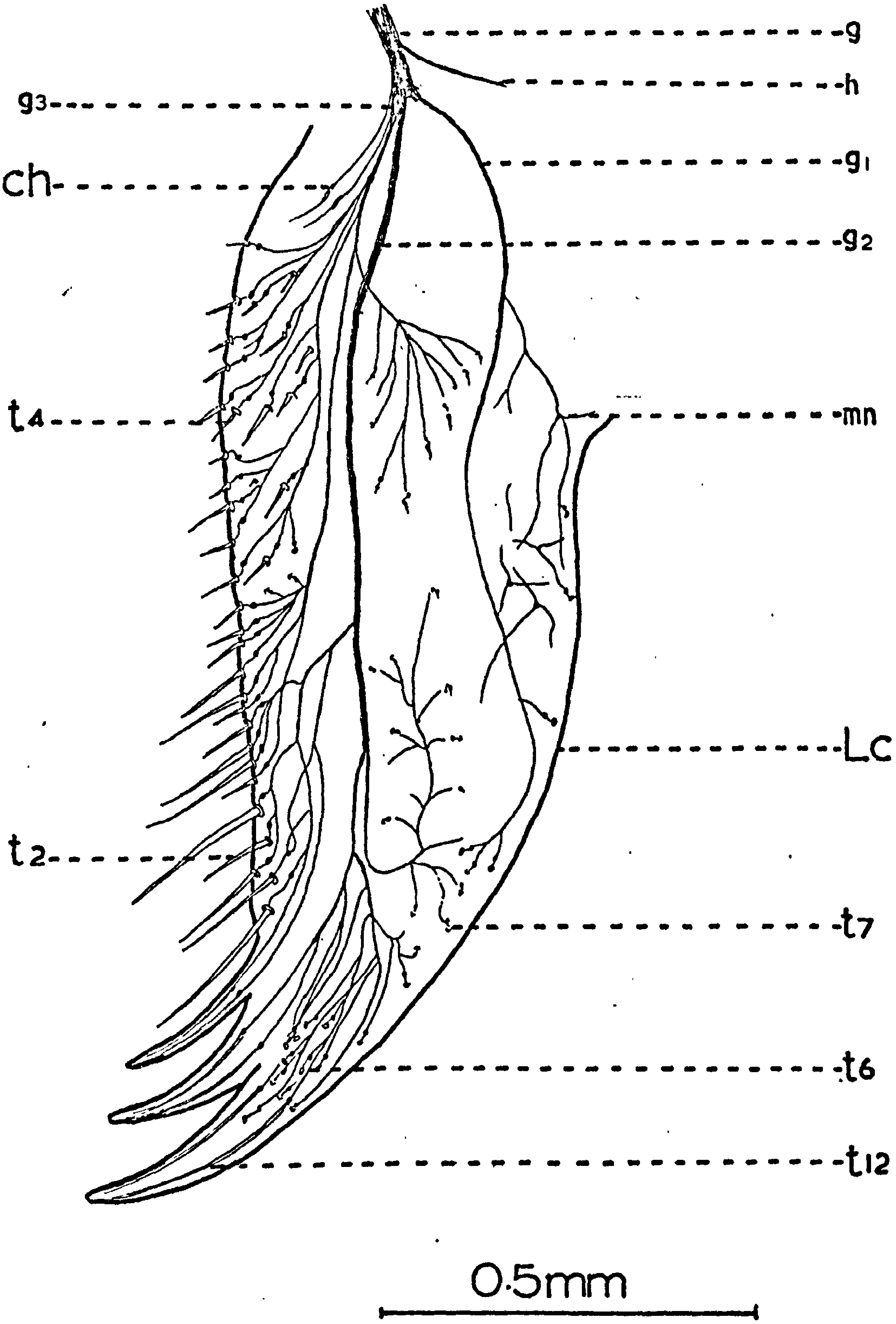
Third maxillary nerve

The third maxillary nerve 'IIImx' (Table 2) is a slender subdivision of the second main maxillary nerve 'IIMx' (Table 2). It passes into the lacinia as nerve 'g' (Figs. 13, 14a and 22) whilst a very small branch 'h' terminates in the distal part of the stipes.

Innervation of the Lacinia (Figs. 22 and 23)

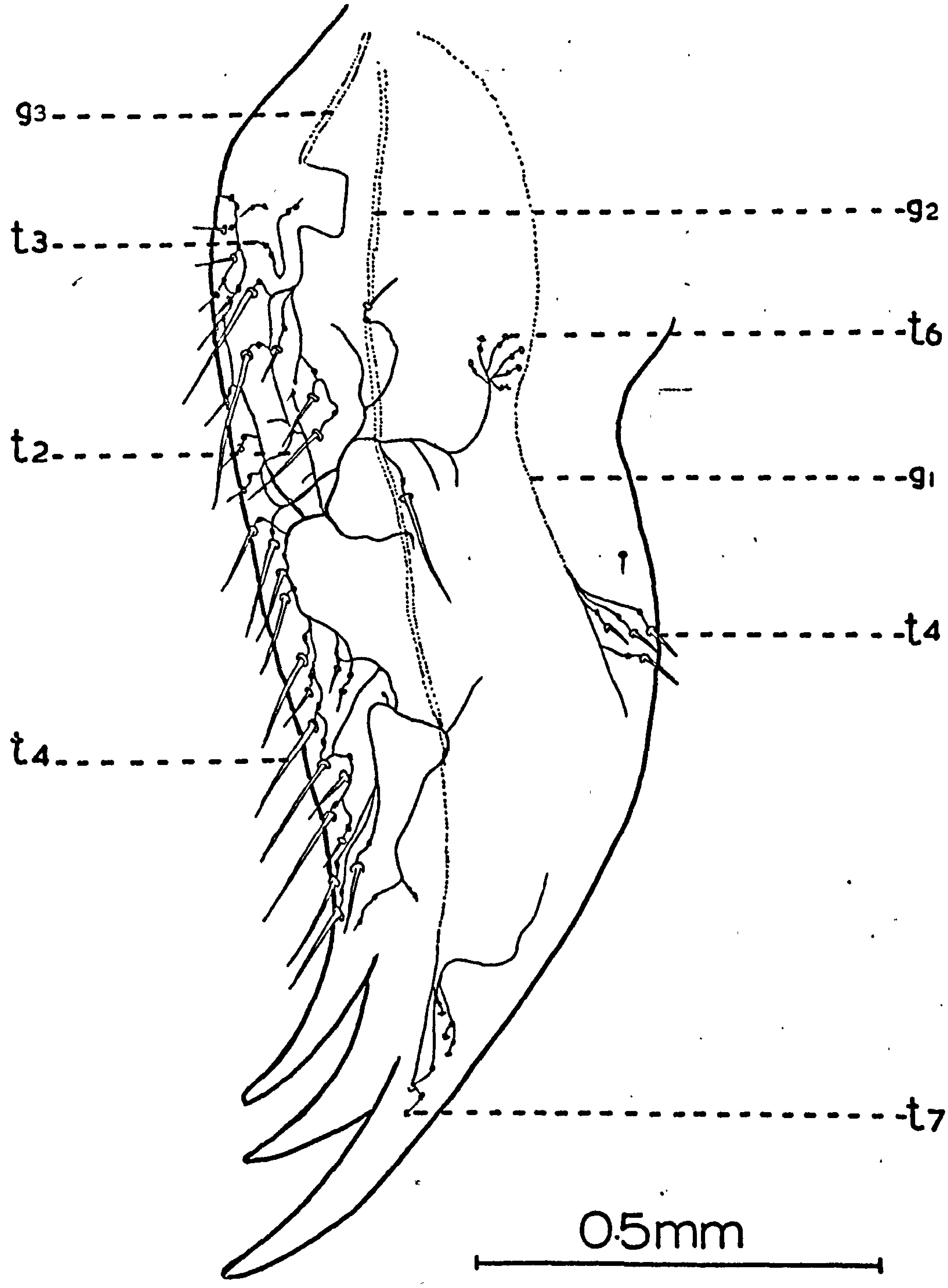
Branch 'g' of the third maxillary nerve 'IIImx' (Fig. 10) divides into three branches, immediately it enters the lacinia (Fig. 22). These branches are referred to as the outer branch 'g_1', the middle branch 'g_2' and the inner branch 'g_3'. Prior to this subdivision it gives off a very small branch 'h' (Fig. 22) which innervates the sensilla on

Fig. 22. Posterior surface of the lacinia illustrating innervation of sensilla.



Fig·22

Fig. 23. Anterior surface of the lacinia illustrating innervation of sensilla.



Fig·23

the distal portion of the stipes (Fig. 17b). Branch 'g_3' is relatively fine and gives off a number of branches to the mesal surface of the lacinia which supply the Type 4 sensilla (Fig. 22). A few sensilla of Types 2, 3, 6 and 7 are also innervated by 'g_3' and these together with Type 4 all have a single neuron. One branch of 'g_3' passes to the outer side of the lacinia to innervate the basal part of the structure.

The two chordotonal organs of the lacinia (Fig. 22), which consist of two scoloparia, are innervated by two fine branches arising from the extreme base of 'g_3'. The first one is more median in position and has three or occasionally four scolopidia, whilst the second one possesses only one to two scolopidia. Slifer (1936), McFarlane (1953) and Fudalewicz-Niemczyk and Rosciszewska (1974) have recorded similar organs in _M_. _mexicanus_, _M_. _differentialis_ and larval _G_. _domesticus_ respectively.

The middle branch 'g_2' is the thickest branch of 'g' and lies in the centre of the lacinia. This innervates sensilla on the posterior surface. It is undivided for about half of the length of the lacinia, but then gives off a branch, which after further subdivision, innervates Types 2 and 4 sensilla on the mesal surface of the galea and distal to those innervated by 'g_3'. This branch also innervates the two pore canals (Type 12 sensilla) in the smallest and most proximal tooth. A more distal branch of 'g_2' forms a

Table 2 Innervation of muscles and sensilla by the maxillary nerve

Main nerve	Subdivision of nerve			Site and structure of innervation
IMx	a	a_1		Adductor of the cardo (Muscle 10)
		a_2		Adductor of the cardo (Muscle 10a)
	b	b_1	$1b_1$	Sensilla of the cardo
			$2b_1$	Sensilla of the stipes
		b_2	$1b_2$	Flexor of the galea (Muscle 14)
			$2b_2$	Levator of the palp (Muscle 15)
IIMx	Imx	c	c_1	Cranial flexor of the lacinia Muscle 12)
			c_2	Protractor of the cardo (Muscle 9)
		d	d_1	Flexor of the lacinia (Muscle 13)
			d_2	Levator and depressor of the palp (Muscle 15,16) and levator of the first palp segment (Muscle 17)
	IImx	e	e_1	Sensilla on the posterior surface of the galea
			e_2	Sensilla on the anterior surface of the galea
		f	f_1	Sensilla on the posterior surface of the maxillary palp
			f_2	Sensilla on the anterior surface of the maxillary palp
	IIImx	g		Sensilla of the lacinia
		h		Sensilla of the stipes

loop which then passes proximally to innervate the Type 7 sensilla. Finally 'g_2' divides fanwise to supply innervation to the tip of the lacinia. The two pore canals in the most distal cusps are innervated by 'g_2'. A number of Types 6 and 7 sensilla are also innervated by this branch. This particular cluster of nerve fibres innervate the sensilla on both anterior and posterior surfaces of the tip of the lacinia.

The outer branch 'g_1' passes down the outer margin of the lacinia but does not extend to the tip of the lacinia. This branch supplies innervation to a group of Type 4 sensilla (Fig. 23) and a few of Types 6 and 7 present on the anterior surface (Fig. 23). There are three to four multiterminal neurons present on the posterior surface of the lacinia (Fig. 22). It is interesting that only a single neuron of this type has been recorded by larval G. domesticus by Fudalewicz-Niemczyk and Rosciszewska (1974).

6.3.d. Labial nerve

The labium is innervated by two pairs of labial nerves, the first pair being thicker than the second.

First main labial nerve

The first main labial nerve 'ILb' (Table 3) is mainly sensory. After leaving the suboesophageal ganglion, the first labial nerve gives off a very small nerve 'i' (Table 3) to the adductor of the labium (Muscle 23), (Fig. 24). In the region of the submentum, the first main labial

Fig. 24. Muscular innervation supplied by the first and second main labial nerve, 'ILb', 'IILb'.

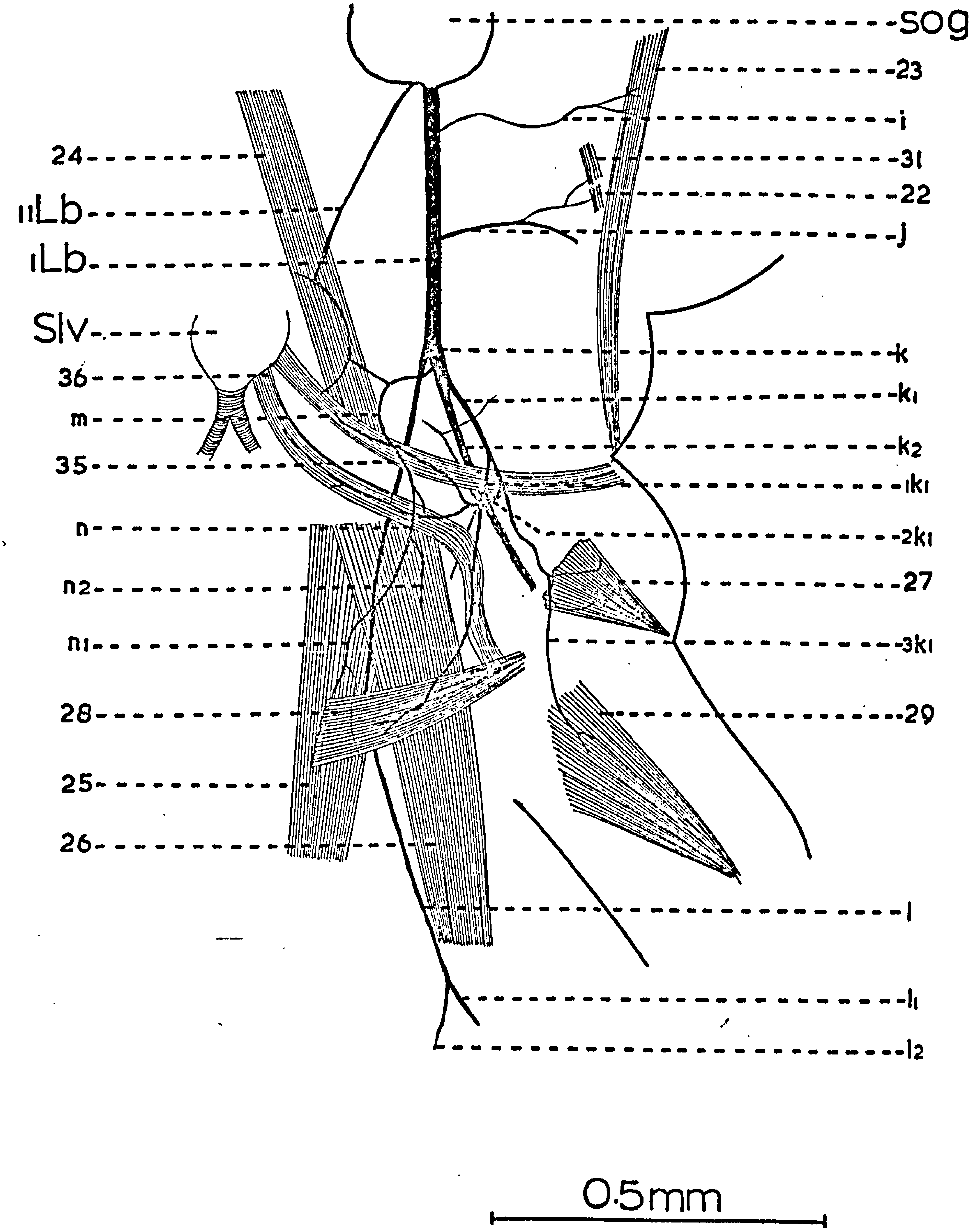

sog
23
i
31
22
j
24
IILb
ILb
Slv
k
36
k1
m
k2
35
1k1
n
2k1
27
n2
n1
3k1
28
29
25
26
l
l1
l2
0.5mm

Fig. 24

Fig. 25. Posterior view of the submentum: a, diagrammatic representation of the nervous innervation; b, initial branching of 'j'; c, innervation of sensilla.

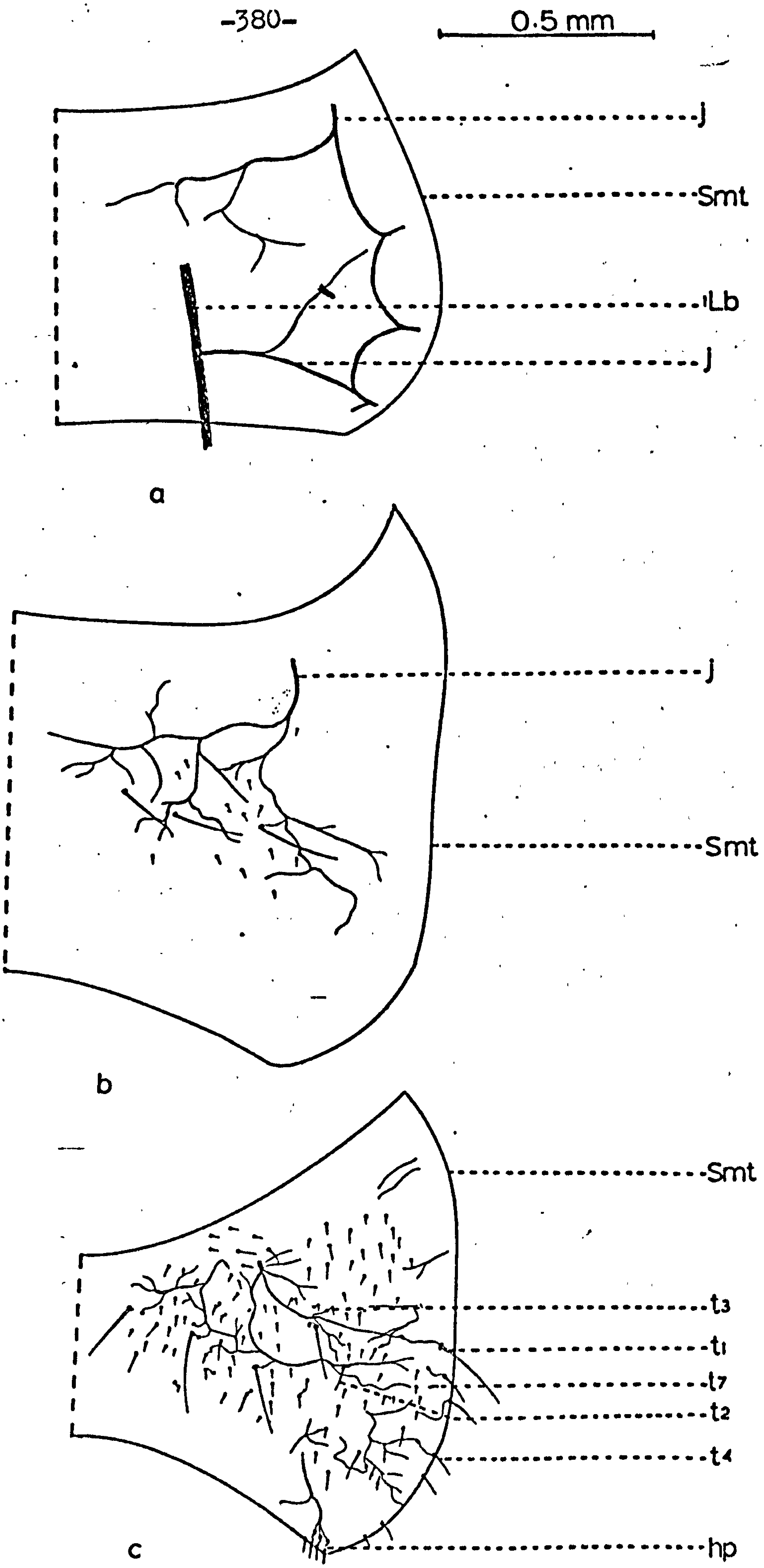


Fig.25

nerve gives off a branch 'j' which is mainly motor (Table 3). The retractor of the hypopharynx (Muscle 31) is innervated by one of the branchlet from nerve 'j' (Table 3). Nerve 'j' also innervates the retractor of the labium (Muscle 22), (Fig. 24). After innervating these muscles the nerve becomes purely sensory and supplies nervous innervation to the sensilla of the submentum (Figs. 24 and 25a).

Innervation of the Submentum, Mentum and Prementum

The branch 'j' of the first labial nerve passes horizontally to the lateral border. This then forms three loops and so terminates in the proximal corner of the submentum. These loops provide innervation to sensilla present on the lateral border of the submentum (Fig. 25a). From here the nerve bifurcates and then becomes further subdivided to ramify the central area of the submentum (Fig. 25b). Sensilla of Types 1, 2, 3, 4, 7 and the hair plates are innervated by this branch and each have a single neuron (Fig. 25c). The detailed connections to all the sensilla could not be traced.

As the first labial nerve leaves the submentum, it bifurcates into nerve 'k' and 'l' (Table 3). The first labial nerve 'k' (Fig. 24) is both motor and sensory. This branch innervates the muscles of the salivarium and labial palp and the sensilla of the mentum, prementum and labial palp (Table 3).

Fig. 26. Nervous innervation of the sensilla on the posterior surface of: a, half of the mentum; b, the prementum.

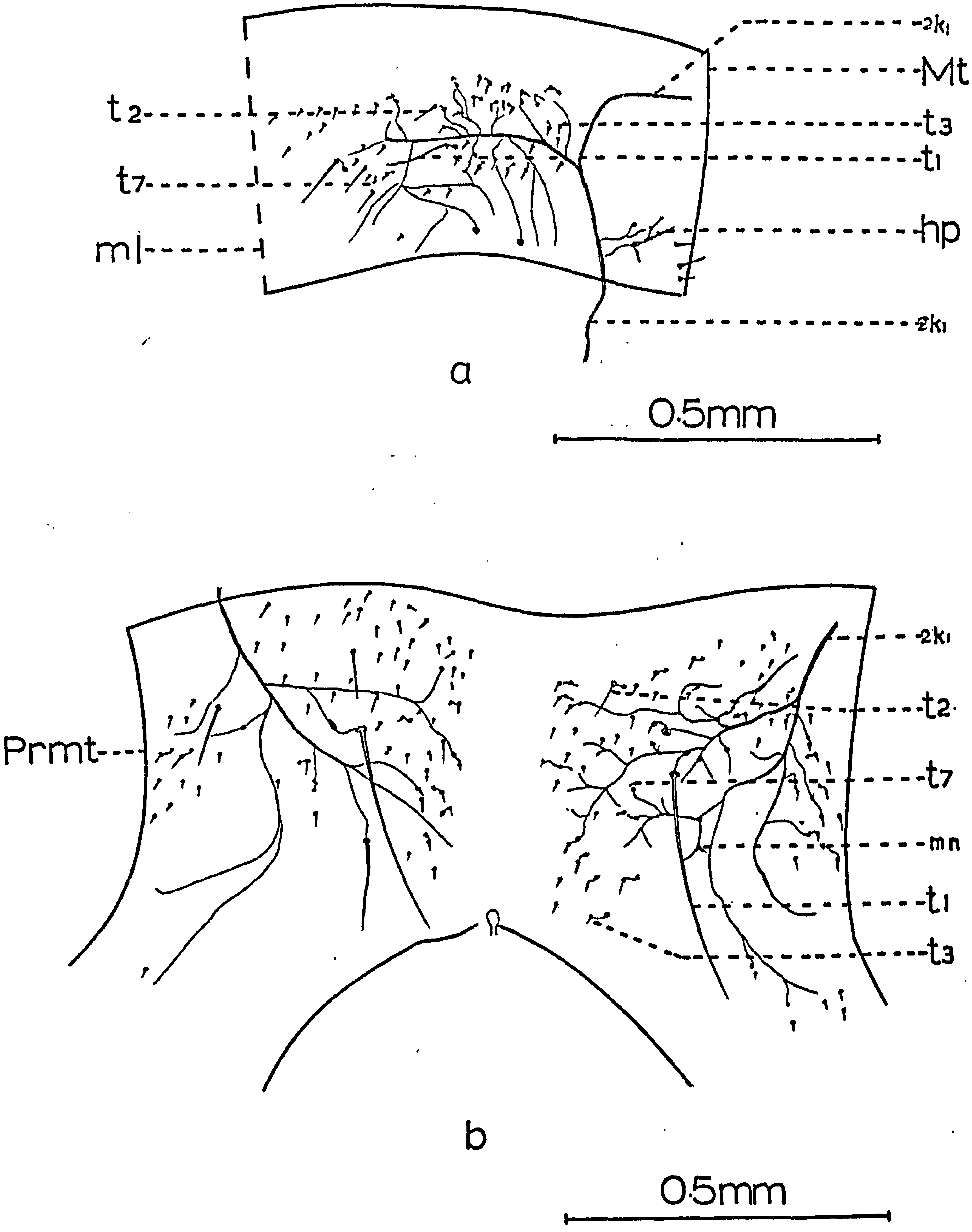


Fig.26

Fig. 27. Multiterminal neuron on the posterior surface of the prementum: a (X 100); b (X 400).

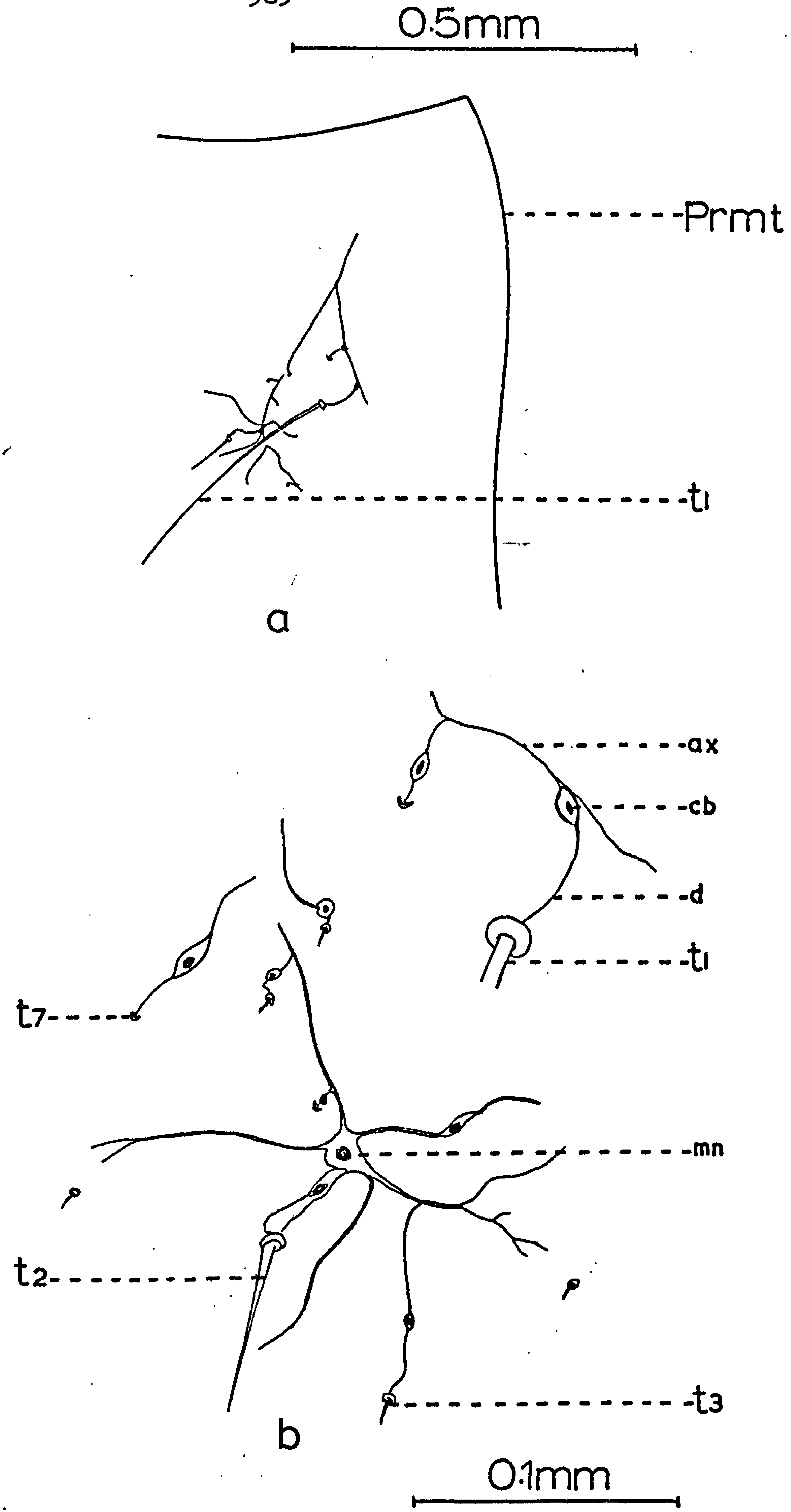


Fig.27

The nerve 'k' divides into two sub-branches 'k_1' and 'k_2' (Table 3). The branch 'k_1' is both sensory and motor and gives rise to three smaller nerves referred to as '$1k_1$', '$2k_1$' and '$3k_1$' (Table 3). The first branch '$1k_1$' penetrate the depressor of the palpiger (Muscle 28), (Fig. 24). The second or middle branch '$2k_1$' (Table 3) innervates the second and third pairs of compressors of the salivarium (Muscle 35 and 36), (Fig. 24). The third nerve '$3k_1$' is contiguous with '$2k_1$' for a short distance but then passes into the prementum giving off two short branches which innervate the levator of the palpiger (Muscle 27), (Fig. 24). The nerve ends finally by innervating the extensor of the first palp segment (Muscle 29), (Fig. 24).

The nerve responsible for the innervation of the mentum and prementum is '$2k_1$' (Table 3) which is a branch of the nerve 'k_1'. This nerve is positioned towards the side of the mentum, and at about half way along its length gives off a horizontal branch which crosses the mentum to approach the midline (Fig. 26a). From the horizontal branch, nerves are given off to the Types 1, 2, 3 and 7 sensilla, and these form a complex network of nerve fibres. Near to the distal boundary of the mentum a couple of fine nerves emerge and innervate the hair plate sensilla which have a single neuron (Fig. 26a).

Nerve '$2k_1$' also innervates the prementum by a branch from the nerve which innervates the mentum. From its lateral position '$2k_1$' passes diagonally towards the centre of the prementum. Initially it bifurcates and each branch undergoes further subdivision to reach all the sensilla. Types 1 and 7 and some Type 3 are innervated by a single neuron (Figs. 26b; 27a and b) whilst other Type 3 sensilla are supplied by four neurons. Multiterminal neurons in the central and lateral part of the prementum are present (Fig. 27b; Plate 6b). In some cases there appears to be a gap between the sensilla and the axon, this may be a reflection of the staining method or that the dendrite actually penetrate between the cells of the epidermis as suggested by Osborne (1964).

The other branch of 'k' nerve 'k_2' (Table 3) serves two functions, firstly to innervate the muscle of the second palp segment and secondly to innervate the sensilla of the labial palp. The latter function necessitating the subdivision of 'k_2' into '$1k_2$' and '$2k_2$' (Table 3) which pass through the whole length of the palp. Nerve '$1k_2$' supplies the sensilla on the posterior side and '$2k_2$' those on the anterior side.

Innervation of the Labial Palp (Figs. 28 and 29)

The nerve '$1k_2$' innervates the sensilla on the posterior surface of the labial palp (Fig. 28). The nerve passes through the centre of the labial palp. At the base of the first segment a small branch from '$1k_2$' divides and innervates the hair plate sensilla on the proximal border of the first palp segment (Plate 8a). This branch, after innervating the hair plate sensilla, passes distally and innervates some of the Types 3 and 4 sensilla situated on the postero-lateral surface of the first segment. Another branch which appears to originate from '$1k_2$' again passes distally where it splits into many nerves which spread in all directions to innervate particularly the Types 4 and 6 sensilla situated at the distal end of the segment. There are some multiterminal neurons found in the central region of this segment. Some of the dendrites have been seen to end blindly in the intersegmental membrane. It is conceivable that they do in fact innervate the intersegmental membrane. Knyazeva _et al_ (1975) found dendrites innervating the intersegmental membrane in the abdomen of _G. domesticus_.

In the second segment, the sensilla on the posterior surface are innervated by a branch from '$1k_2$' which passes towards the distal end of the segment nearly parallel to '$1k_2$' (Plate 9a). Along its route lateral branches are given off to innervate the Types 1, 2, 3 and 6 sensilla of the segment, most of these have a single neuron.

The pattern of innervation on the posterior side of the third segment is shown in Fig. 28. Near to the proximal end of the segment a very fine nerve arises from '$1k_2$' and this innervates some of the Type 3 sensilla in this area. Almost midway along the length of this segment

Fig. 28. Posterior surface of the labial palp illustrating innervation of sensilla.

Fig. 28

0.5mm

Fig. 29. Anterior surface of the labial palp illustrating innervation of sensilla.

Fig. 29

a very thin nerve arises from one side of the nerve '$1k_2$'. This immediately splits into two branches, one of which travels distally and the other proximally to innervate the Type 4 sensilla present at the inner edge of the palp (Fig. 28). Another more prominent nerve arises from nerve '$1k_2$' in this area and passes towards the tip of the palp. Initially it gives off branches to the outer side of the palp and then splits fanwise to ramify the whole end of the palp (Plate 9b). The detailed innervation of the Type 5 sensilla could not be clearly seen, although it was obvious in some preparations that a number of Type 3 sensilla were supplied by three neurons in this region (Plate 9b).

The anterior surface of the labial palp is innervated by a branch of nerve 'k_2' referred to as '$2k_2$'. This branch passes throughout the length of the palp. In the distal region of the first palp segment (Fig. 29) the nerve '$2k_2$' gives off a branch from its innerside which forms a hair pin-shaped loop and crosses over '$2k_2$' to form branches which spread throughout the segment. These branches innervate the Types 1, 2 and 3 sensilla which all have a single neuron.

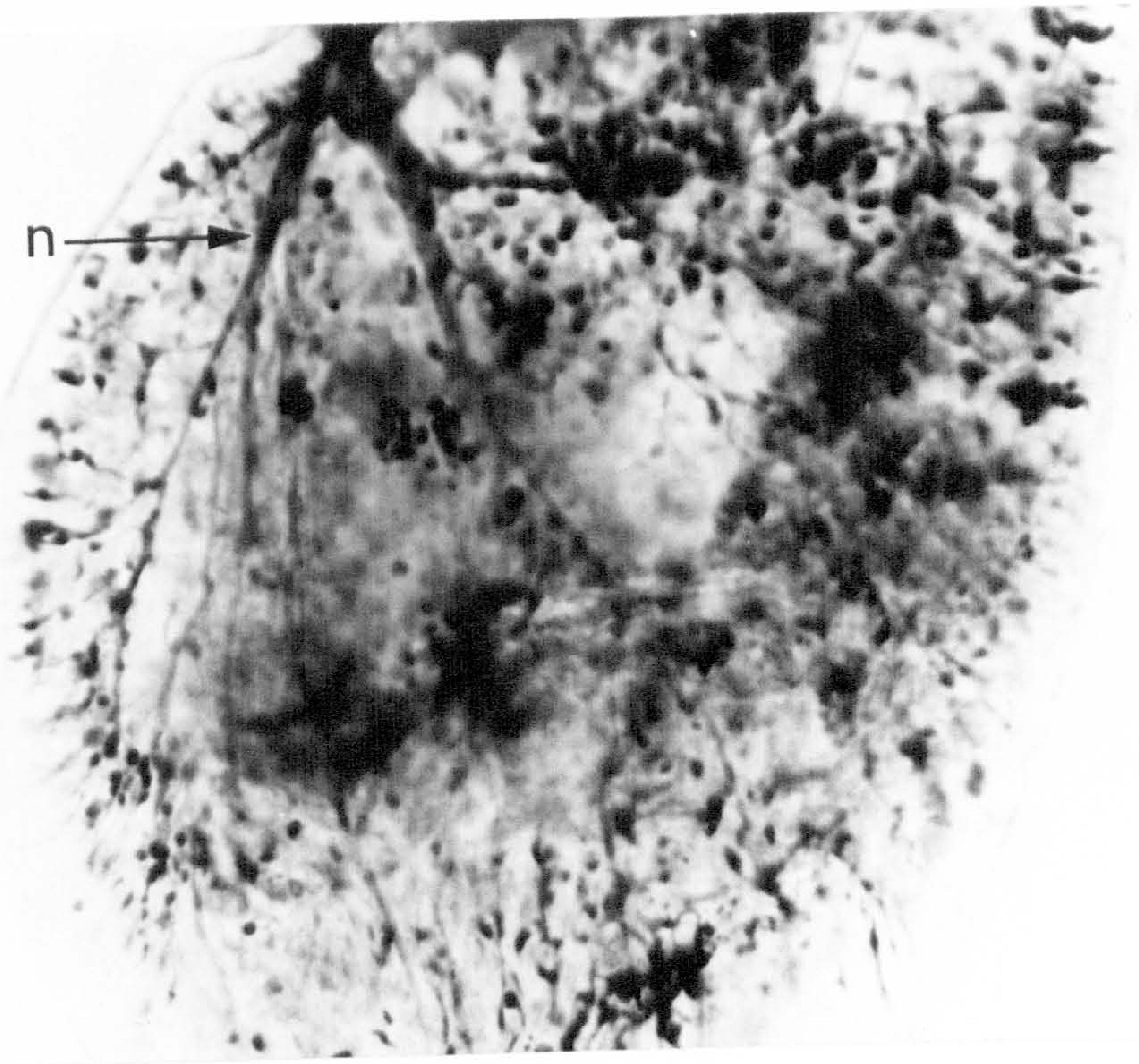
Within the second palp segment a branch, which actually arises from the distal portion of the first palp segment, bifurcates and one branchlet supplies the hair plate sensilla (Plate 8b). From the hair plate a fine nerve passes distally to supply the Types 3 and 4 sensilla (Fig.

Plate 7. Light micrograph of:

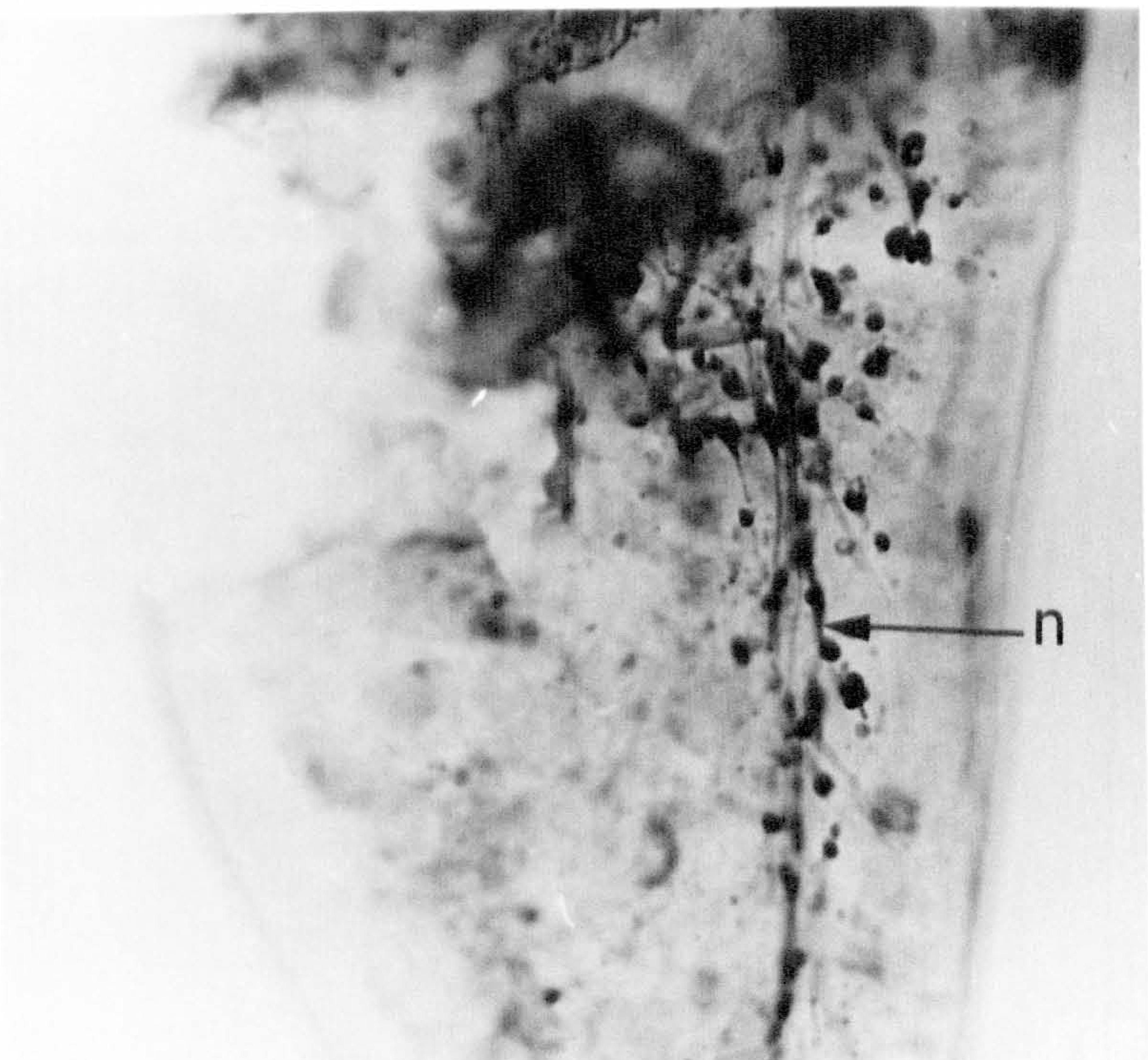
a. posterior view of the paraglossa;

b. posterior view of the glossa

(X320).



a

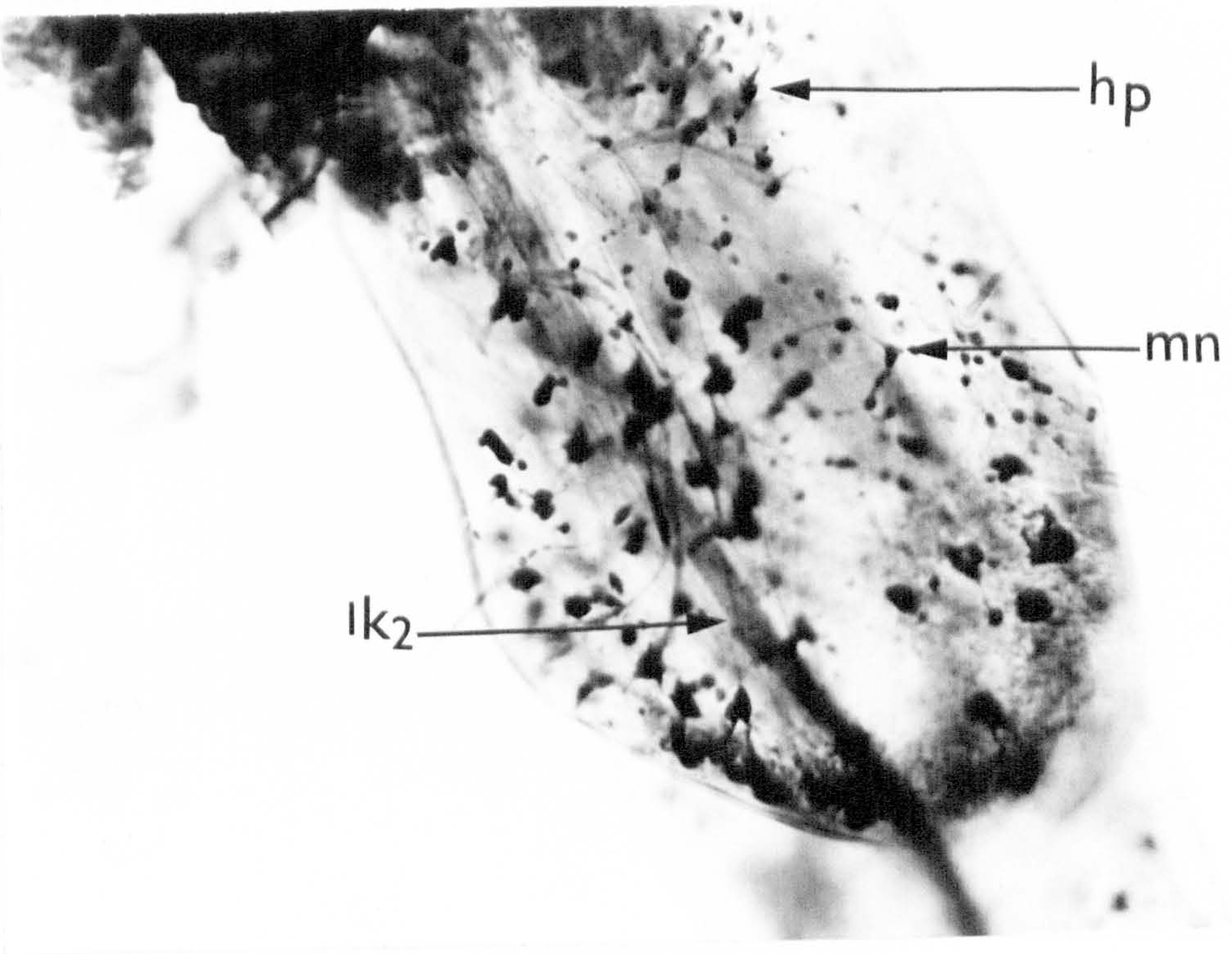


b

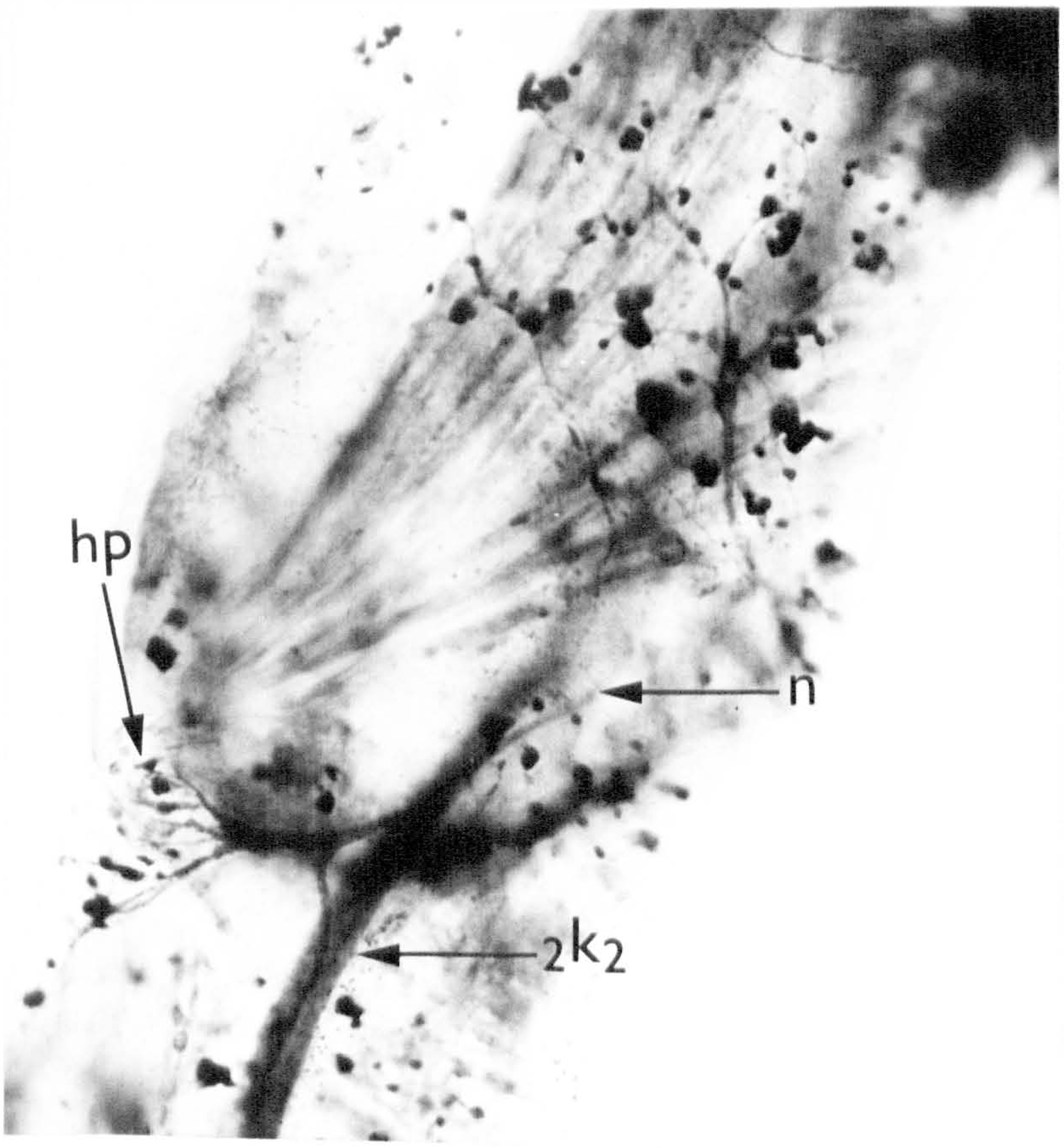
Plate 8. Light micrograph of the first labial palp segment;

a. posterior view;

b. anterior view (X320).



a

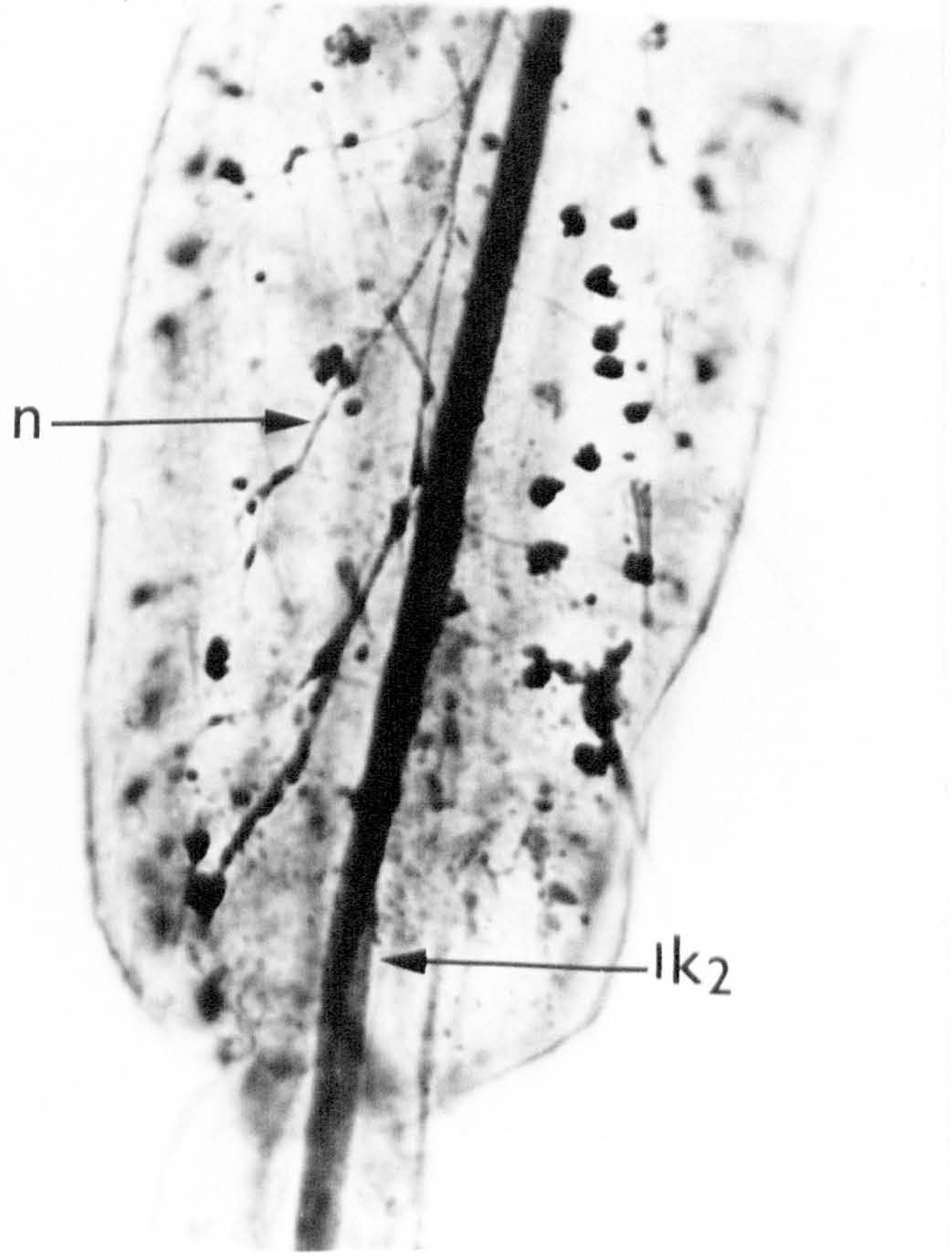


b

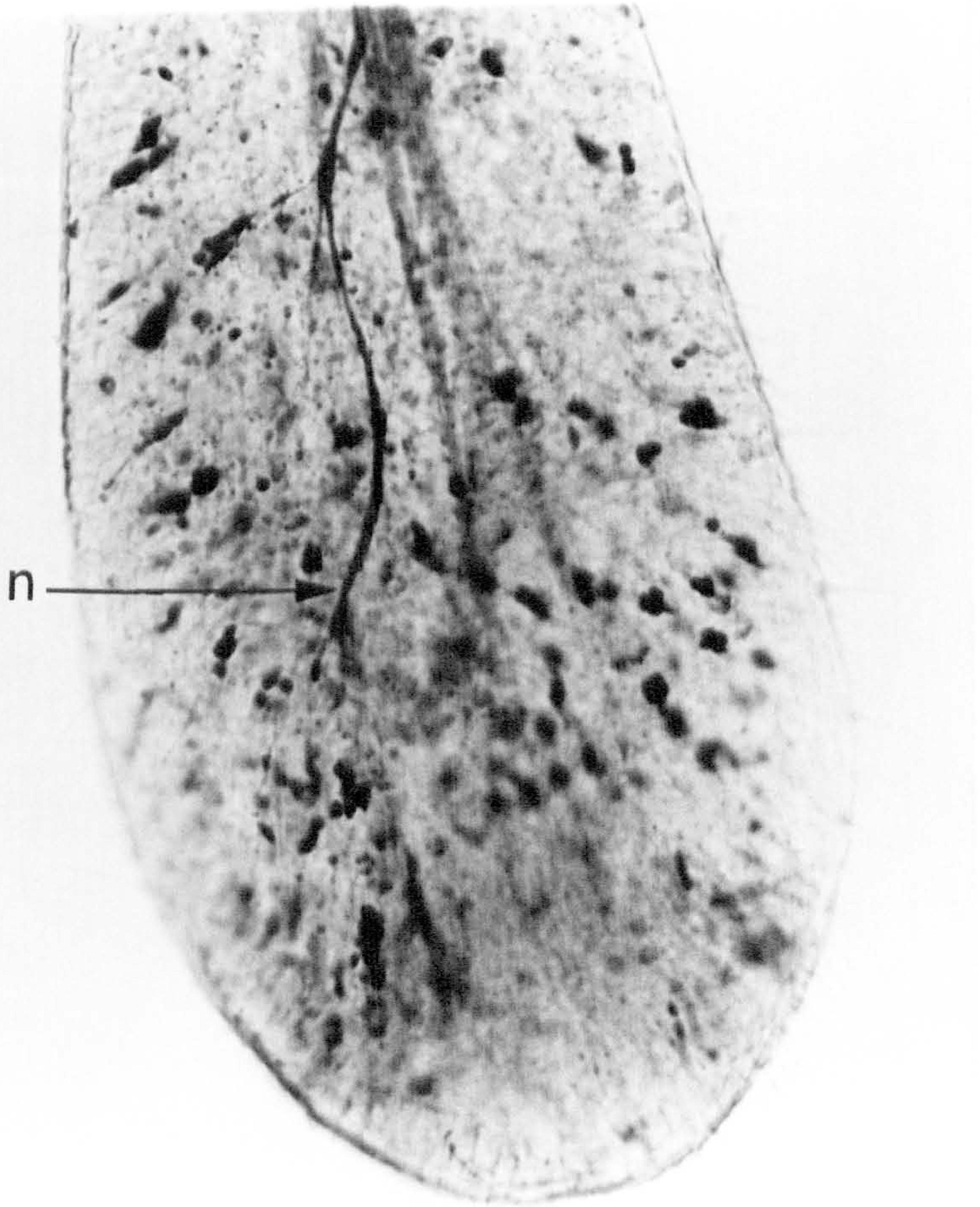
Plate 9. Light micrograph of:

a. posterior view of the second labial palp segment;

b. posterior view of the third labial palp segment (X 320).



a



b

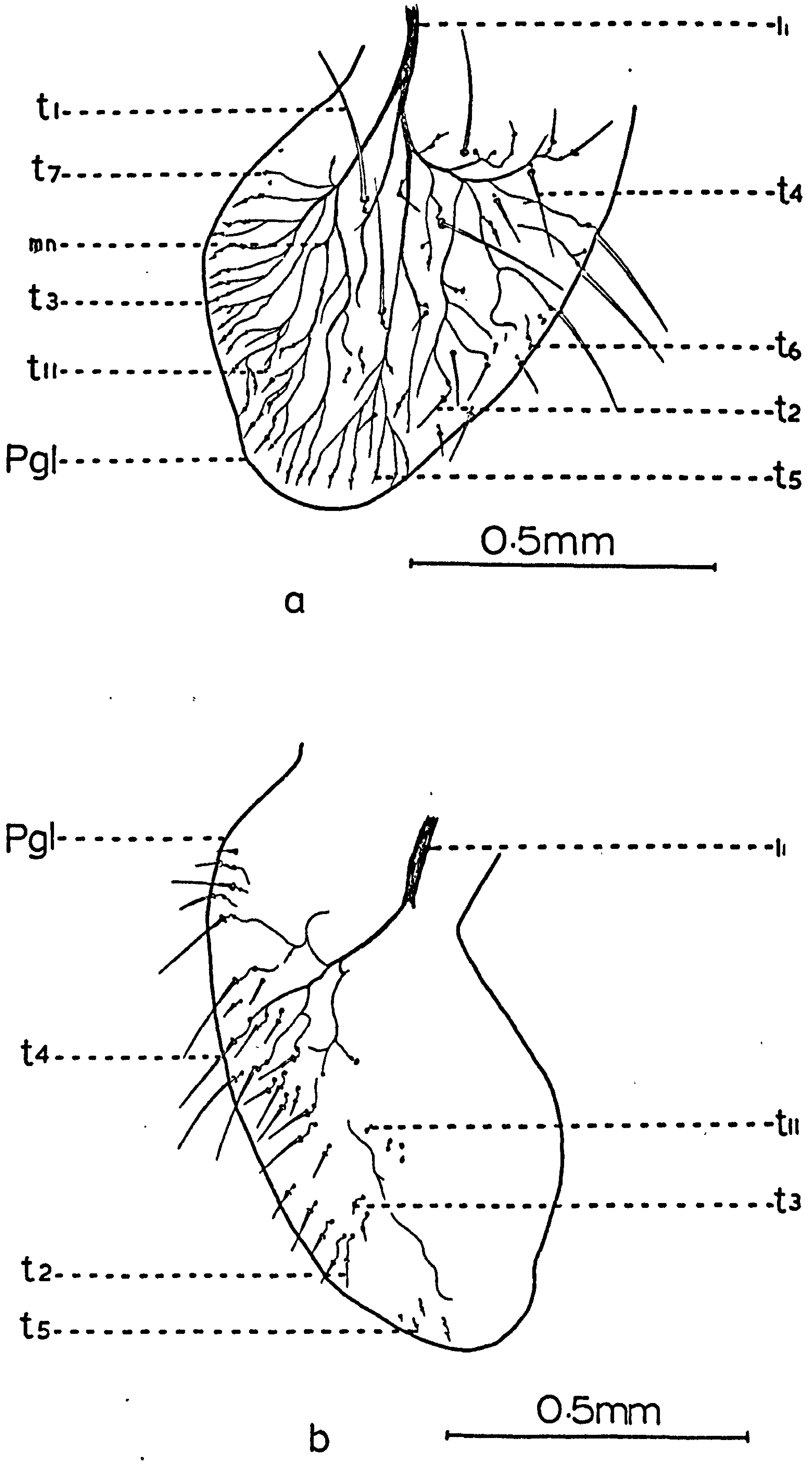
29). Before innervating the hair plate sensilla on the outer surface of this segment a branch is given off which passes diagonally through the segment to its distal end and innervates many of the sensilla in the segment. The innervation of the Type 1 sensilla, with a single neuron, is particularly clear. The Type 6 sensilla present in the extreme distal part of this segment are innervated by fine nerves arising directly from '$2k_2$'. These sensilla again have a single neuron.

The hair plate sensilla present at the base of the third palp segment are innervated by a branch '$2k_2$' (Fig. 29). From about one third of the length of the segment a branch of '$2k_2$' emerges which after further subdivision innervates the sensilla in the centre of this side of the palp segment. Sensilla on the outer side of this region are innervated by short nerve fibres arising directly from '$2k_2$'. Towards the tip of the segment two branches are given off which diverge from the midline to supply nervous innervation to the sensilla on either side. Unfortunately, the nervous supply to sensilla at the extreme tip of the palp could not be ascertained.

Innervation of the Paraglossa (Fig. 30)

The second branch 'l' of the first labial nerve '1Lb' (Table 3) divides into two nerves 'l_1' and 'l_2' (Fig. 24). The nerve which innervates the paraglossa is referred to as 'l_1' (Fig. 30a). On the posterior surface

Fig. 30. Nervous innervation of sensilla of the paraglossa: a, posterior surface; b, anterior surface.

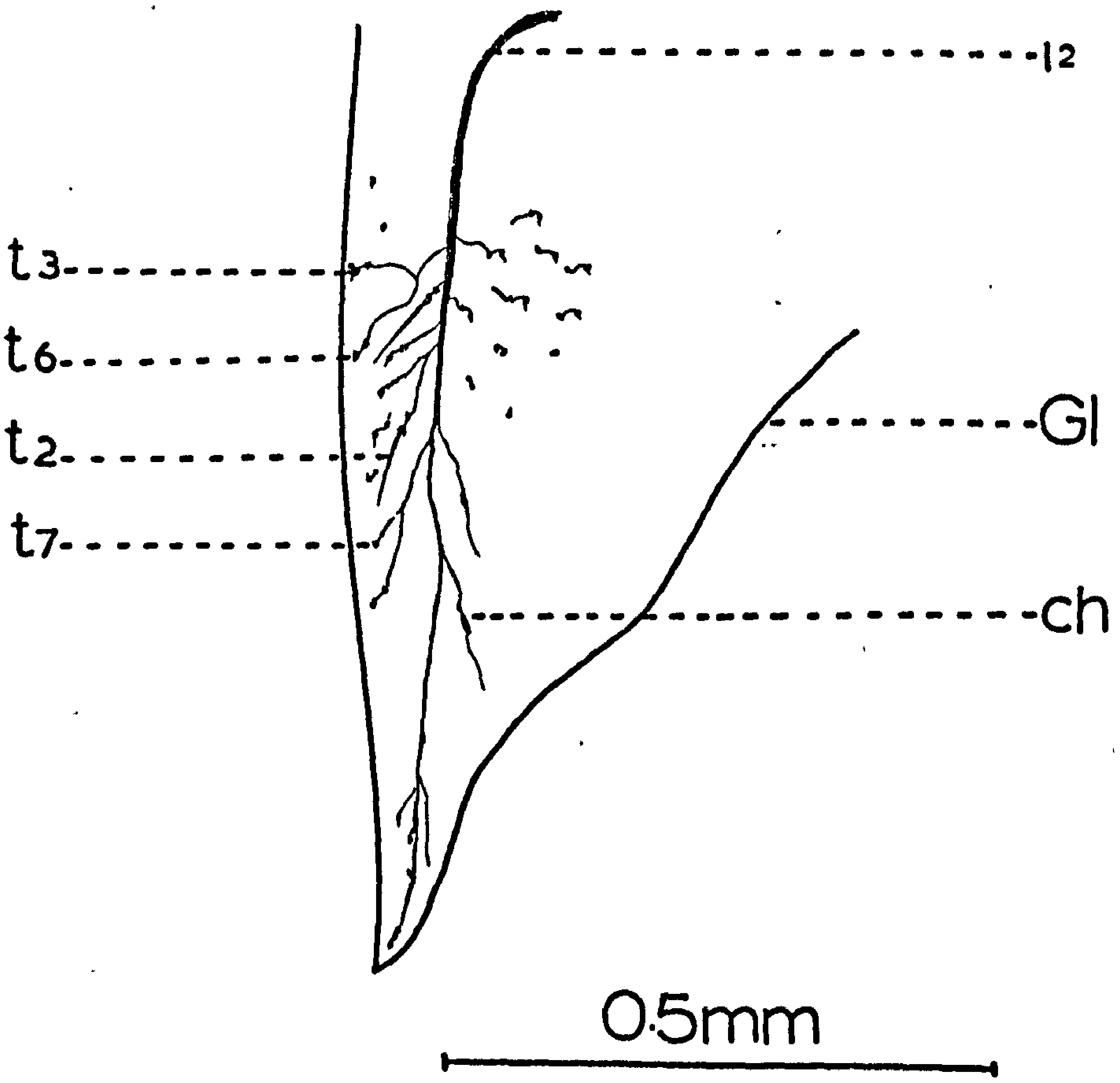


a

b

Fig.30

Fig. 31. Posterior surface of the glossa illustrating innervation of sensilla.



Fig·31

of the paraglossa, near its base 'l_1' divides fanwise (Fig. 30a) into an array of nerves which reach all areas of the paraglossa and supply innervation to the sensilla (Plate 7a). Types 1, 2, 3, 4, 6, 7 and 11 sensilla are all innervated by a single neuron whilst Type 5 have more than one neuron. Multiterminal neurons have been recorded on the lateral border of the paraglossa (Fig. 30a).

The anterior surface of the paraglossa (Fig. 30b) is also innervated by sub-branches of 'l_1'. These are particularly prominent on the outer side of the structure. As on the posterior surface Type 5 sensilla are the only type with more than one neuron.

Innervation of the Glossa (Fig. 31)

The nerve 'l_2' enters the glossa (Fig. 31) and passes to its distal extremity. As it passes through the structure it gives off laterally a number of fine bundles of fibres which innervate Types 2, 3, 6 and 7 sensilla all having a single neuron. However, some of the Type 3 sensilla are innervated by three or four neurons (Plate 7b). A similar bundle of nerve fibres innervates the two scolopidia of the chordotonal organ in the distal region of the glossa.

Second main labial nerve

The second main labial nerve 'IILb' (Table 3) is very thin compared with the first main labial nerve 'ILb'. It originates from the suboesophageal ganglion just median to the origin of 'ILb' (Fig. 24). The nerve 'IILb' may be

Table 3 Innervation of muscles and sensilla by the labial nerve

Main nerve	Subdivision of nerve			Site and structure of innervation
ILb	i			Abductor of the labium (Muscle 23)
	j			Retractor of the hypopharynx (Muscle 31) Adductor of the labium (Muscle 22) Sensilla of the submentum
	k	k_1	$1k_1$	Depressor of the palpiger (Muscle 28)
			$2k_1$	Second and third pairs of compressor of the salivarium (Muscle 35, 36) Sensilla of the mentum and prementum
				Levator of the palpiger (Muscle 27) Extensor of the first labial palp (Muscle 29)
		k_2	$1k_2$	Sensilla on the posterior surface of the labial palp
			$2k_2$	Sensilla on the anterior surface of the labial palp
	l	l_1		Sensilla of the paraglossa
		l_2		Sensilla of the glossa
IILb	m	Connected with k		Median retractor of the labium (Muscle 24) Second pair of compressor of the salivarium (Muscle 35) Third pair of compressor of the salivarium (Muscle 36)
	n	n_1		Adductor of the glossa (Muscle 25)
		n_2		Adductor of the paraglossa (Muscle 26)

considered as two branches 'm' and 'n' (Table 3). Branch 'm' innervates the median retractor of the labium (Muscle 24), (Table 3). Branch 'm' is also connected (Table 3) to the branch 'k' of the first main labial nerve (Fig. 24). Thomas (1971) has reported similar cross connections between nerves whilst considering the abdominal sensilla of locusts. The nerve 'm' (Fig. 24) also innervates the second and third compressors of the salivarium (Muscles 35 and 36), (Fig. 24). These muscles receive supplementary innervation from branches of the first labial nerve (Fig. 24). After innervating these muscles branch 'm' is referred to as 'n' which subsequently bifurcates into two branches 'n_1' and 'n_2'. These nerves innervate the adductors of the glossa and paraglossa (Muscles 25 and 26) respectively.

6.3.e. Hypopharyngeal nerve (Fig. 32)

The hypopharyngeal nerve originates from the suboesophageal ganglion. It is thinner than the mandibular nerve. The hypopharyngeal nerve 'Hphyn' enters the hypopharynx and level with the suspensorial sclerite gives off a number of branches of nerve fibres which pass towards the sensilla (Fig. 32a). Detail of the nervous supply of some of these sensilla could not be attained. After giving innervation to sensilla of the hypopharynx, the nerve then passes to the distal part of the hypopharynx where branches are seen to penetrate the pseudotracheae (Fig. 32b). A more intensive study of this structure alone would be of considerable interest.

Fig. 32. Lateral view of the hypopharynx:

a, innervation of some sensilla;

b, relationship of the hypopharyngeal nerve and the pseudotracheae.

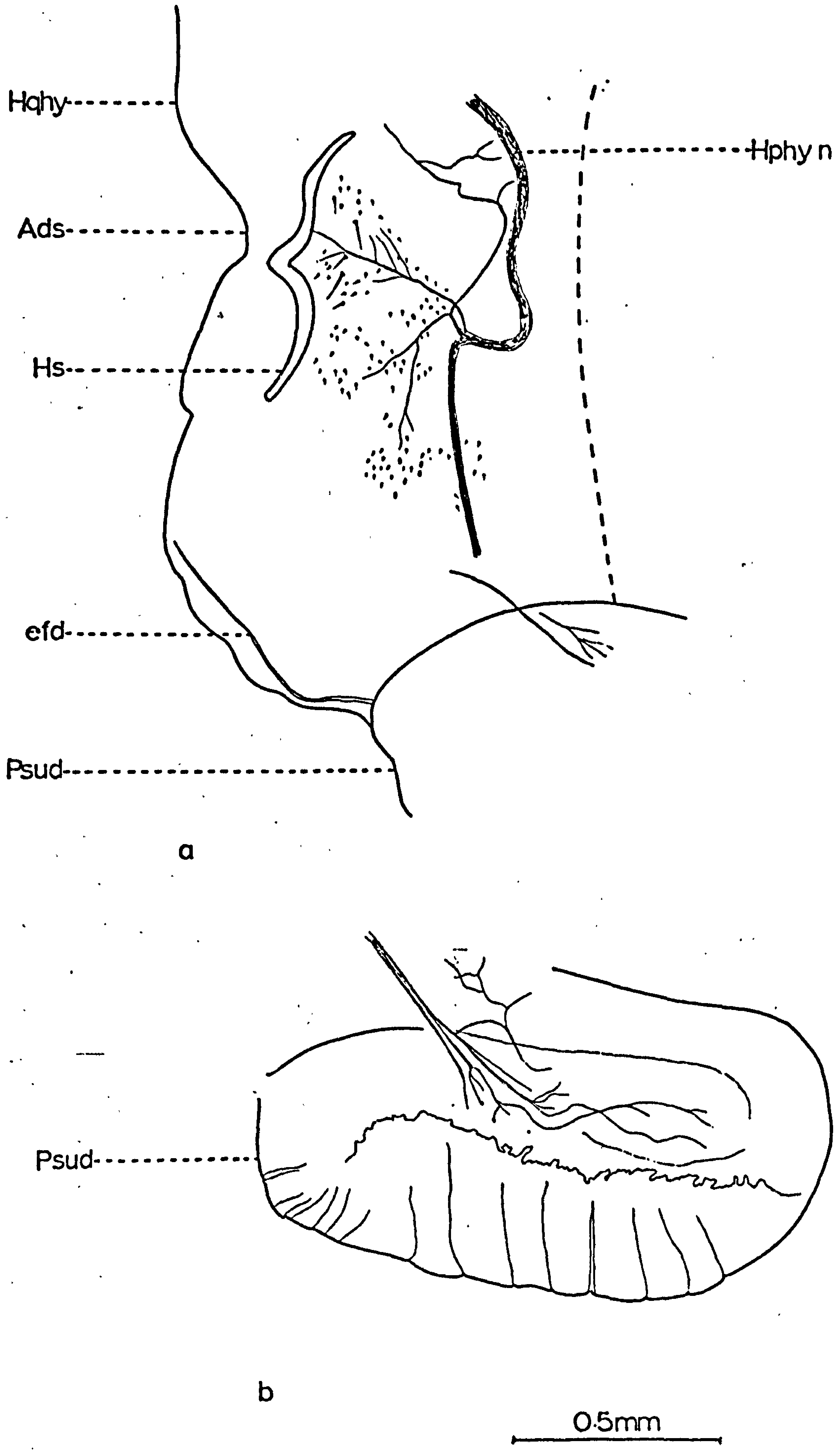


Fig.32

Abbreviations applied to the innervation of the muscles and sensilla associated with the head appendages

A,B = Sub-branches of the labral nerve

Ads = Adoral surface

ad ap = Adductor apodeme

Br = Brain

Cd = Cardo

c = Comb

cb = Cell body

ch = Chordotonal organ

d = Dendrite

efd = Efferent duct

fc = Frontal connective

fg = Frontal ganglion

Ga = Galea

Gl = Glossa

Hs = Suspensorial sclerite

Hphy = Hypopharynx

Hphyn = Hypopharyngeal nerve

hp = Hair plate

Lc = Lacinia

Lm = Labrum

Lmn = Labral nerve

ILb = First main labial nerve

IILb = Second main labial nerve

Md = Mandible

Mdn = Mandibular nerve

Mt = Mentum

IMx = First main maxillary nerve

IIMx = Second main maxillary nerve

mn = Multiterminal neuron

ml = Midline

n = Nerve

Pgl = Paraglossa

Prmt = Prementum

Psud = Pseudotracheae

rn = Recurrent nerve

St = Stipes

Slv = Salivarium

Smt = Submentum

sog = Suboesophageal ganglion

Tr = Trachea

tr = Tracheole

tor = Torma

t, q = Longitudinal sulcus of the stipes

t_1 = Type 1 sensilla

t_2 = Type 2 "

t_3 = Type 3 "

t_4 = Type 4 "

t_5 = Type 5 "

t_6 = Type 6 "

t_7 = Type 7 "

t_8 = Type 8 sensilla
t_9 = Type 9 "
t_{10} = Type 10 "
t_{11} = Type 11 "
t_{12} = Type 12 "
t_{13} = Type 13 "
VL = Sclerotized bar on labrum

PART 7

THE ROLE OF THE MOUTHPARTS AND ASSOCIATED STRUCTURES IN FEEDING

7.1 Introduction

In spite of many advances that have been made in understanding the functional morphology of the mouthparts and the associated feeding behaviour of insects over the last two decades, there are still many gaps in our knowledge of the subject. The work that has so far been documented in the Orthoptera has been confined mainly to the Acrididae. The closely related family, Gryllidae, has received very little attention.

The act of feeding involves a combined and highly synchronized action of the oral appendages. In the preceding chapters (Parts 3, 4 and 5) the scene has been set, in so far as the structure and musculatures of the head capsule and its appendages, the distribution of sensilla and the nervous innervation of both muscles and sensilla have been fully described. Literature relating to the functional morphology of the mouthparts of insects from a range of taxonomic groups has been reviewed by a number of workers (e.g. Rietschel, 1953b; William, 1954; Crichton, 1957; Brown, 1961; Gangwere, 1960; Evans, 1964; Popham, 1961; Blaney and Chapman, 1970).

According to Gangwere (1960) insects may be regarded as either margin feeders or centre feeders, the latter type may be subjected to a further modification that of piercing. Feeding may be broken down into a series of stages often with different stimuli and structures involved.

According to Dethier (1966) the feeding behaviour of an insect consists of the following: locomotion bringing the insect to its food, cessation of locomotion on arrival near the food, biting, continued feeding and termination of feeding.

Many workers have restricted their studies to an appraisal and analysis of the mode of functioning of a single component of the feeding apparatus. It is these investigations which are invaluable in an attempt to describe the overall feeding process. Without exception, these studies in the Orthoptera have been carried out using representatives of the Acrididae as experimental tools. This must be clearly understood when relating these findings to the Gryllidae, many of which feed on rather different food substances.

Blaney and Chapman (1970) investigated the functioning of the maxillary palps in the Acrididae and suggested that palpation is essentially related to feeding behaviour. The palps play an important role in food selection, but if insects are starved for more than 24 hours the palps become less important. However, Sinoir (1969), working on Locusta, considered that the stimuli perceived by the palps and which result in the lowering of the head are tactile and not chemical. Furthermore it is the mechanical stimulation of the labrum which leads to biting. The pattern of feeding and regulation of feeding in larvae of L. migratoria has been described by Blaney, Chapman and Wilson (1973). Mordue (1975) studied the role of the mouthparts and antennal receptors in S. gregaria and suggested that the palps are important both in food selection and in the maintenance of continued feeding. She further explained that in the absence of the palps the antennae could assume a more important role in the exploration of the food before and during a meal.

The role of individual receptor cells in feeding is a relatively new field of study. Electrophysiological techniques have now been employed by a number of workers. In L. migratoria Haskell and Schoonhoven (1969) described the function of certain mouthpart receptors in relation to feeding and the electrophysiological work of Haskell and Mordue (1969) demonstrated that some of the palp receptors tested responded to both chemical and mechanical stimulation. More recently Blaney (1974, 1975) reported that on the tip of the maxillary palp in L. migratoria larvae there are three morphologically and functionally different types of sensilla all of which respond to chemical stimuli. Furthermore it was demonstrated that within each sensillum the same neuron may respond to different chemicals.

In this study it was proposed to investigate the detailed feeding mechanism of A. domesticus. This was undertaken by close observation under a dissecting binocular microscope, by ciné photography and by the use of a videorecorder. From this it was hoped to analyse the sequence of events in the feeding process, the mode of action of the various components and their synchronisation with other components and finally to assess, where feasible, the role of each component in the overall process. The initial searching for food often involves locomotory activity (Mordue, 1975) and this was also noted.

It is appreciated that the present work is only an introduction to a relatively unstudied group of insects. However, this may form the basis for further research involving techniques such as amputation and electrophysiology.

7.2 Methods

In order to study the feeding mechanism in A. domesticus the insects were maintained and cultured as described earlier (Part 2). Previous studies on the feeding behaviour of locust hoppers have shown that environmental factors play an important role (Uvarov, 1977). Furthermore it was noted by Blaney and Chapman (1970) that excessive starvation produced a non-typical feeding response, particularly in respect of the role of the maxillary palps. Under normal conditions the maxillary palps play an integral part in feeding, though after starvation they become non functional.

It was therefore of utmost importance to examine the feeding process under conditions which would closely simulate normal field conditions, and yet enable one to see as much of the process as possible. Insects were selected at random from the breeding jars. Only adult female insects were used. In the past it has been common practice to deprive the insects of food for a certain period of time in order to facilitate observations on feeding (Pfadt, 1949 and Sinoir, 1969). Although it is obviously undesirable to starve the insects for a prolonged period before observation, 12 - 24 hours deprivation was found to have no marked effect on the feeding behaviour and yet did enable more regular and predictable investigations.

Several different techniques have been employed to study the feeding mechanism of *A. domesticus* each one providing additional information.

a. *Ciné photography*

Ciné photography was used initially to analyse the overall feeding process. The camera used for this purpose was a Beaulieu, 4008 ZM2. 10 - 15 female insects were placed in a rectangular glass aquarium, both water and food were provided. The aquarium was illuminated, but the lights were fitted with heat filters to prevent the insects becoming overheated. The insects moved about at random in the aquarium but started feeding when they came in contact with the food. When a suitably positioned insect was settled and feeding the insect was filmed. This technique proved partially successful; the rapid movement of the head and its appendages in feeding were observed and also the imbibing of water. The movement of the individual mouthparts, however, was not detectable by this technique.

b. Observations using a Microscope

Female insects were mounted on a glass microscope slide in such a way that the dorsal side of the insect was facing towards the slide and the ventral side of the insect faced upwards towards the observer. The insect was secured with a small strip of cellotape across the thorax. The food was offered in a pair of fine forceps. First observations of this type were made under the low power of a binocular dissecting microscope (Wild M5). In this way the movement of the glossae, paraglossae, galeae and laciniae could be clearly seen in addition to the more obvious movements of the palps.

To get more detailed observations the mounted insect was observed under higher magnifications. Photographs were then taken using a camera (Nikkormmat) fitted to the Wild M5, and with an electronic flashgun held 25cms from the objective stage. A series of such photographs records the position of the various mouthparts during feeding and the relationship between components. The relative position of the mandibles maxillary palps, galeae, laciniae, clypeolabrum and labium became clear in this way.

Plate 1a. The use of a Videorecorder to demonstrate the feeding behaviour of _A_. _domesticus_.

a

The above method obviously has some limitations in that only isolated incidents in the feeding process can be recorded. In order to record the complete sequence a videorecorder was used.

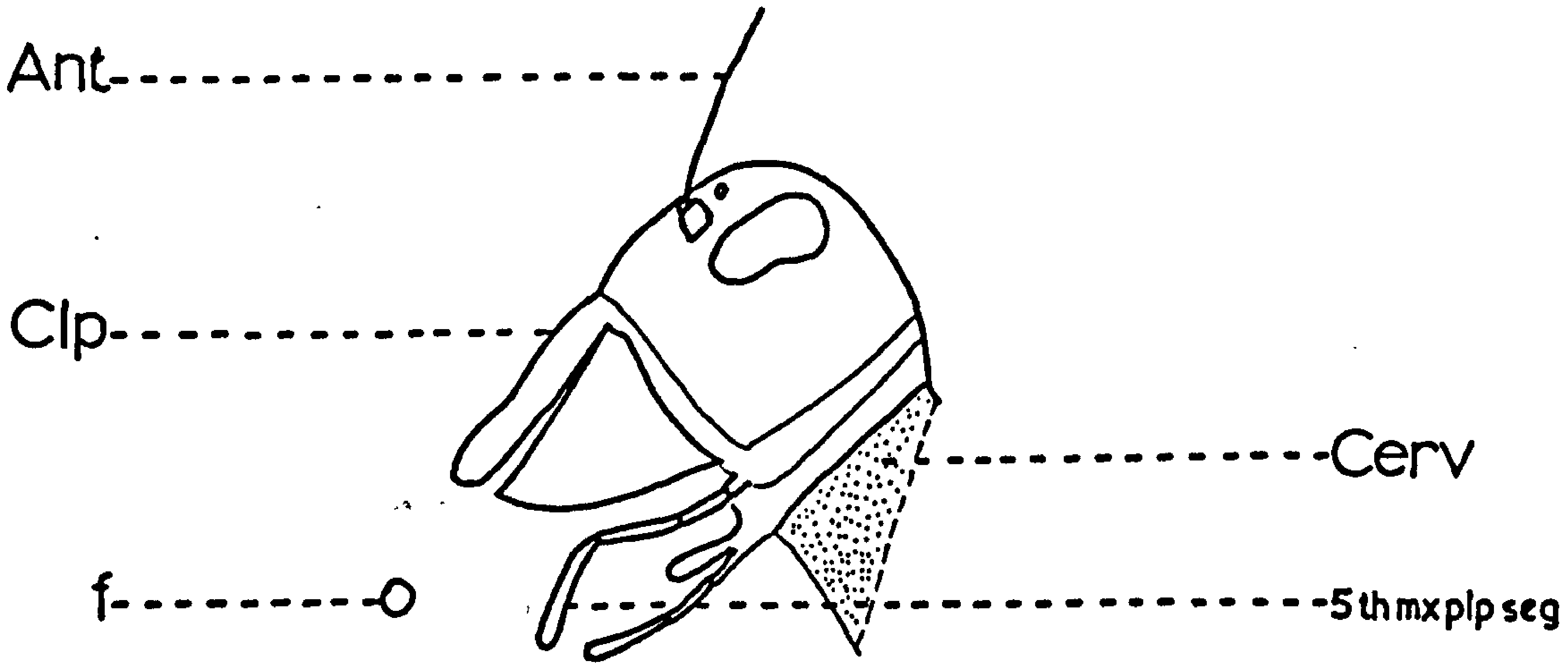
c. Videorecording

An attempt was made to record the entire feeding process including the initial orientation to the food, its sampling and then continued feeding.

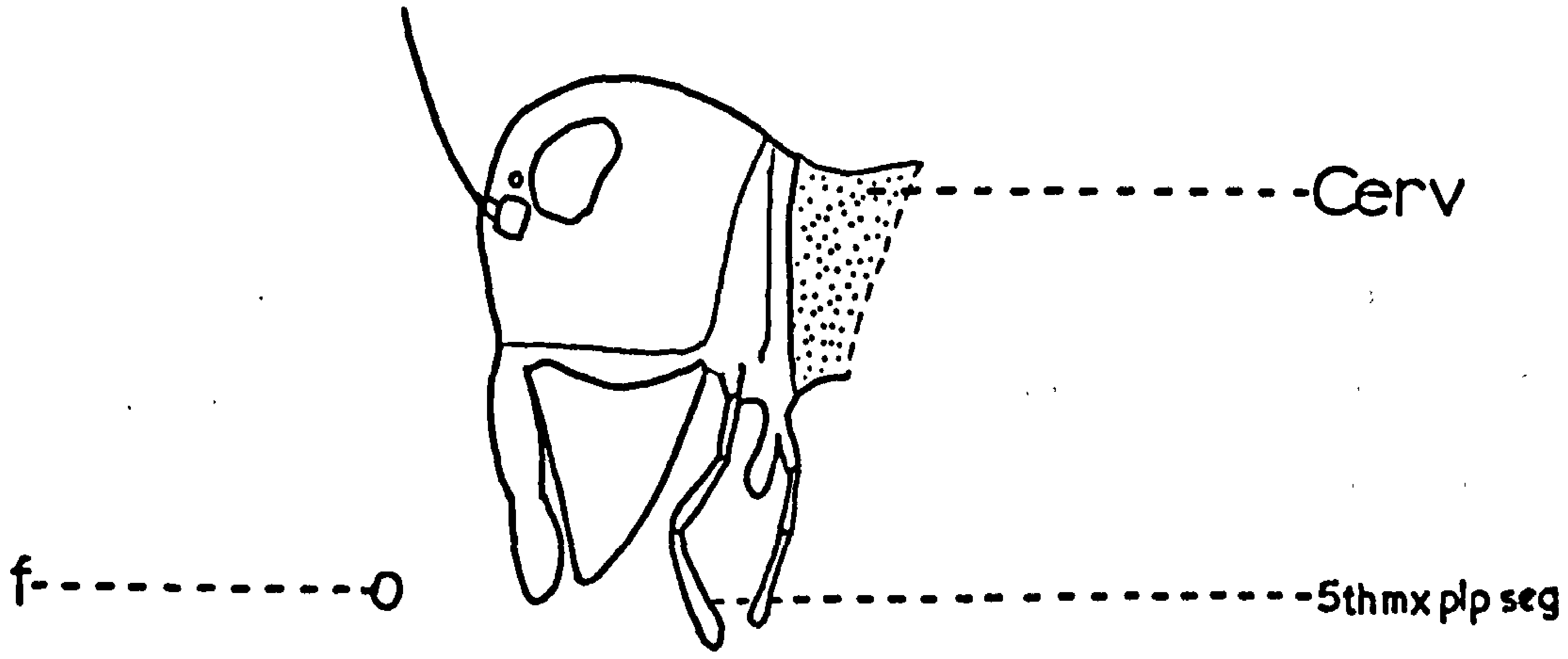
A single female insect was placed in an empty falcon culture flask (Falcon plastic, U.S.A.). This container offered only a limited space to the insect and was chosen to facilitate filming and to ensure that the insect did not take too long searching for the food. The insect was allowed about ten minutes to settle down before food was introduced into the container. A pre-arranged T V camera (Takumar) and close circuit television filmed the insect from the time of introduction of the food. The videorecording was then subjected to careful observation which was facilitated by slow motion playback. This technique proved invaluable in understanding the feeding process. The movement of the individual mouthparts and their role in touching, tasting and the acceptance or rejection of food was noted. In addition to this the actual processes of biting, mastication and ingestion of the food was recorded.

To assist in the description of feeding certain stages have been expressed diagrammatically and relevant

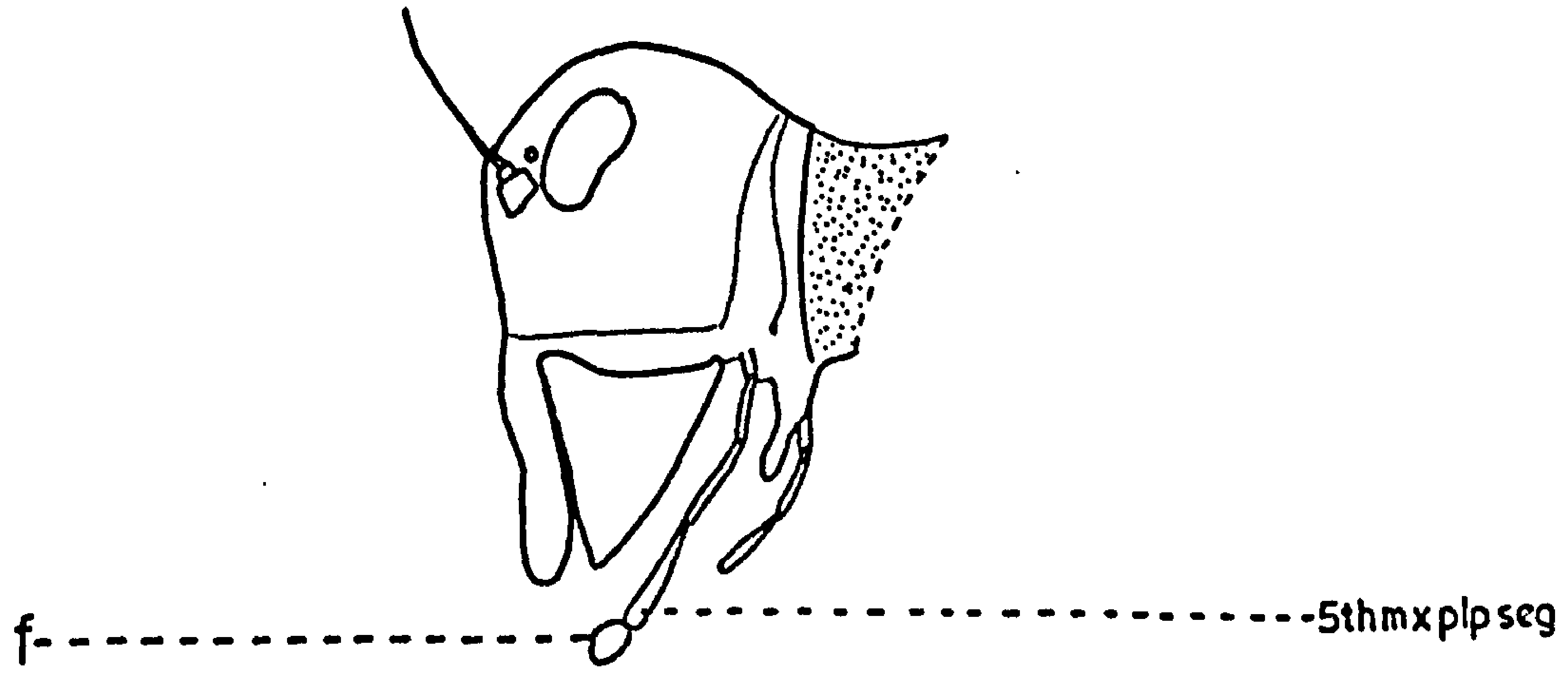
Fig. 1a - c. Orientation of the head during feeding.


Ant
Clp
Cerv
f
5thmxplpseg

a


Cerv
f
5thmxplpseg

b


f
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c

photographs included. The films taken during the course of the work have been submitted to the film collection, accommodated in the Department of Zoology, Imperial College.

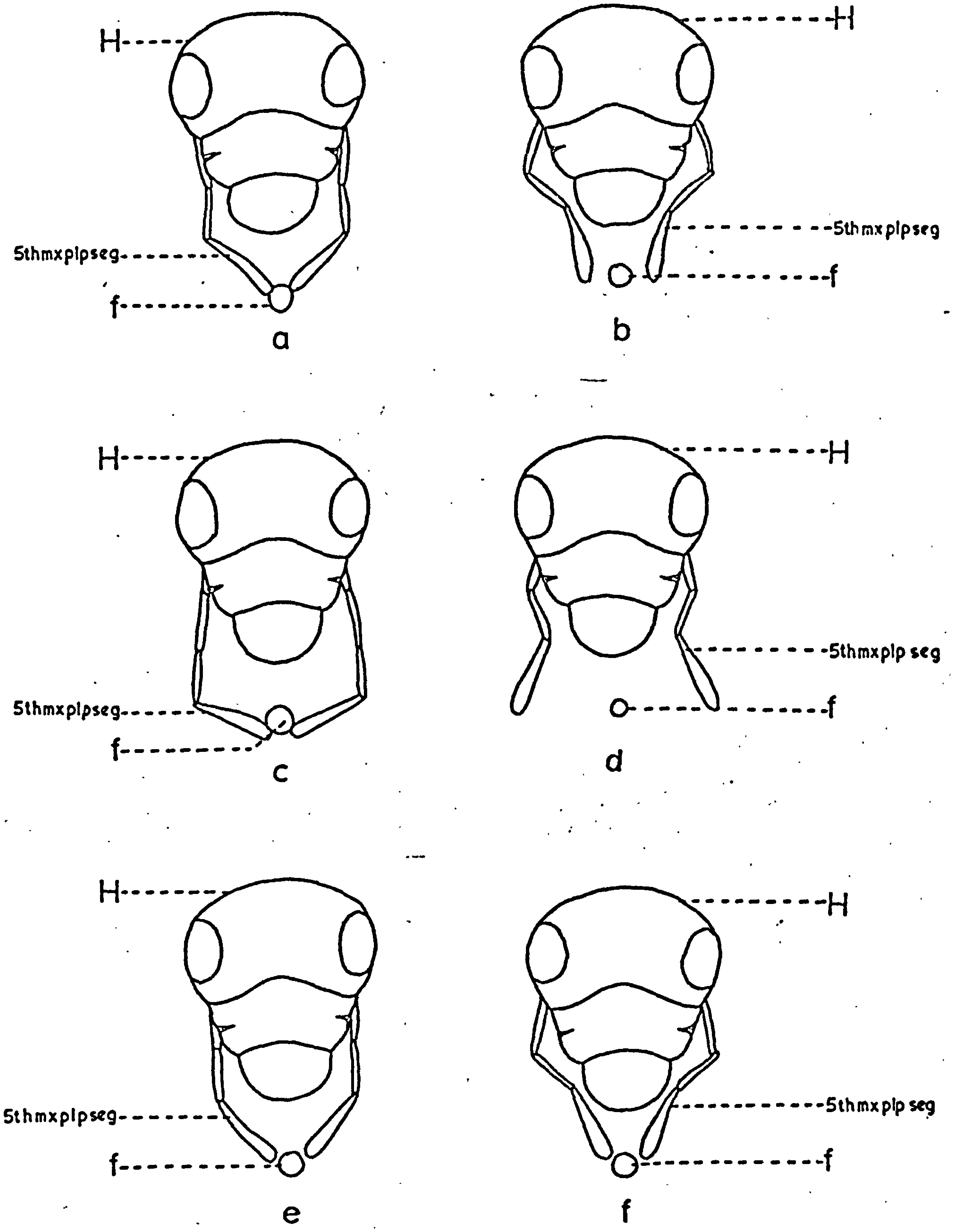
7.3 Results and conclusion

Feeding in A. domesticus is a very complex process involving the highly synchronised and integrated movement of the head capsule and its appendages.

After the insect has been allowed to equilibrate, food is introduced and orientation to the food commences. The insect generally walks towards the food. As it does so, the antennae move in all directions and then the maxillary palps start moving as well. These initial actions which occur before the insect comes into contact with the food, lead one to speculate that the initial searching behaviour is controlled by odour attraction. As the insect approaches the food, it clearly orientates itself towards the food. The head is moved rapidly and is lifted by expanding the neck membrane ventrally (Fig. 1a). When the insect is close to the food particle the head is flexed dorsally and so assumes the typical hypognathous condition (Fig. 1b). These movements of the head are brought about by the cervical muscles. The cervix, or neck, is provided with depressor, elevator and rotator muscles which bring about the rapid multidirectional movement of the head. The antenna continue to move without touching the substratum or the food. It may be suggested that after initial orientation to the food the

Fig. 2. Diagrammatic representation of the movement of the maxillary palp in feeding.

(f = food particle).


H
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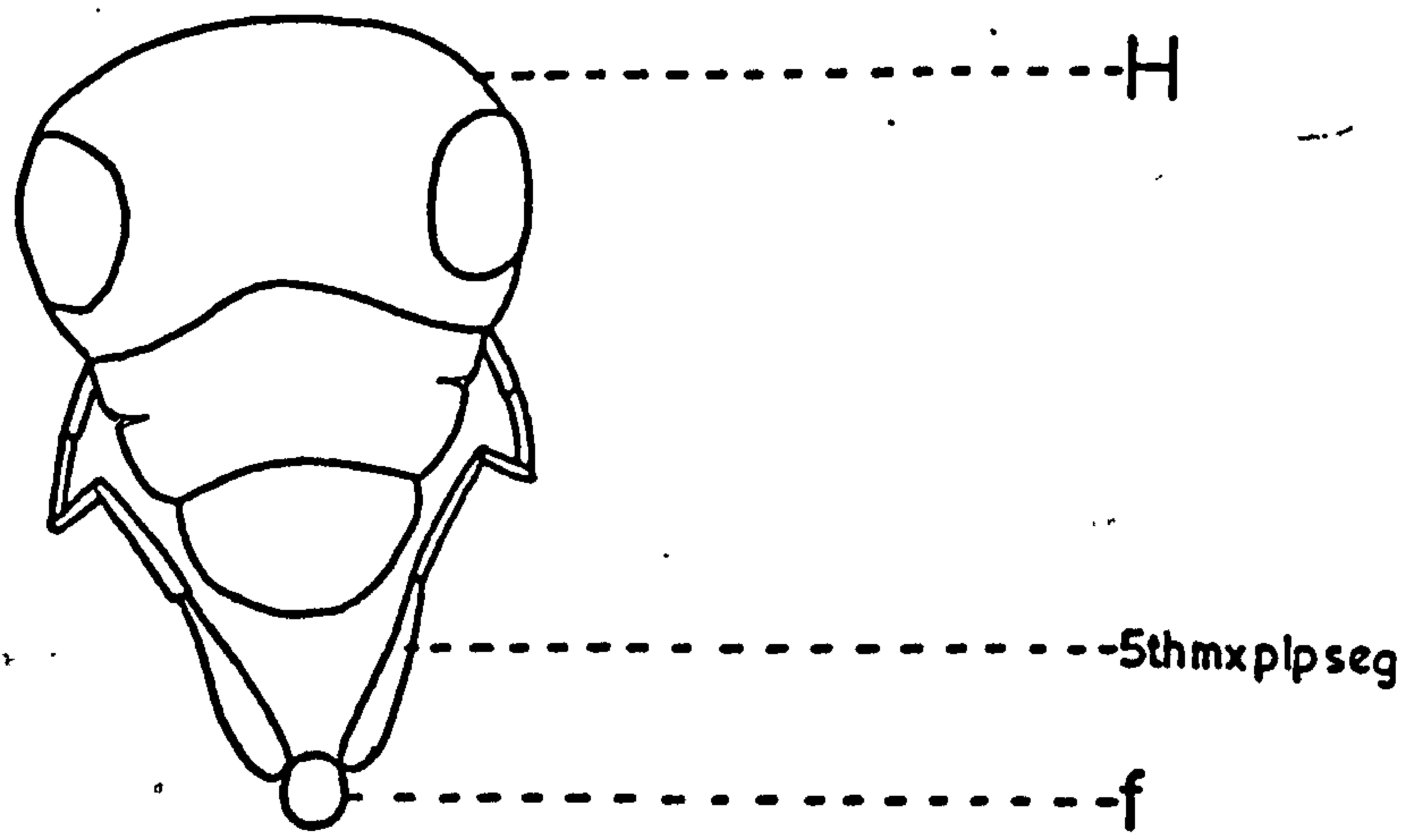
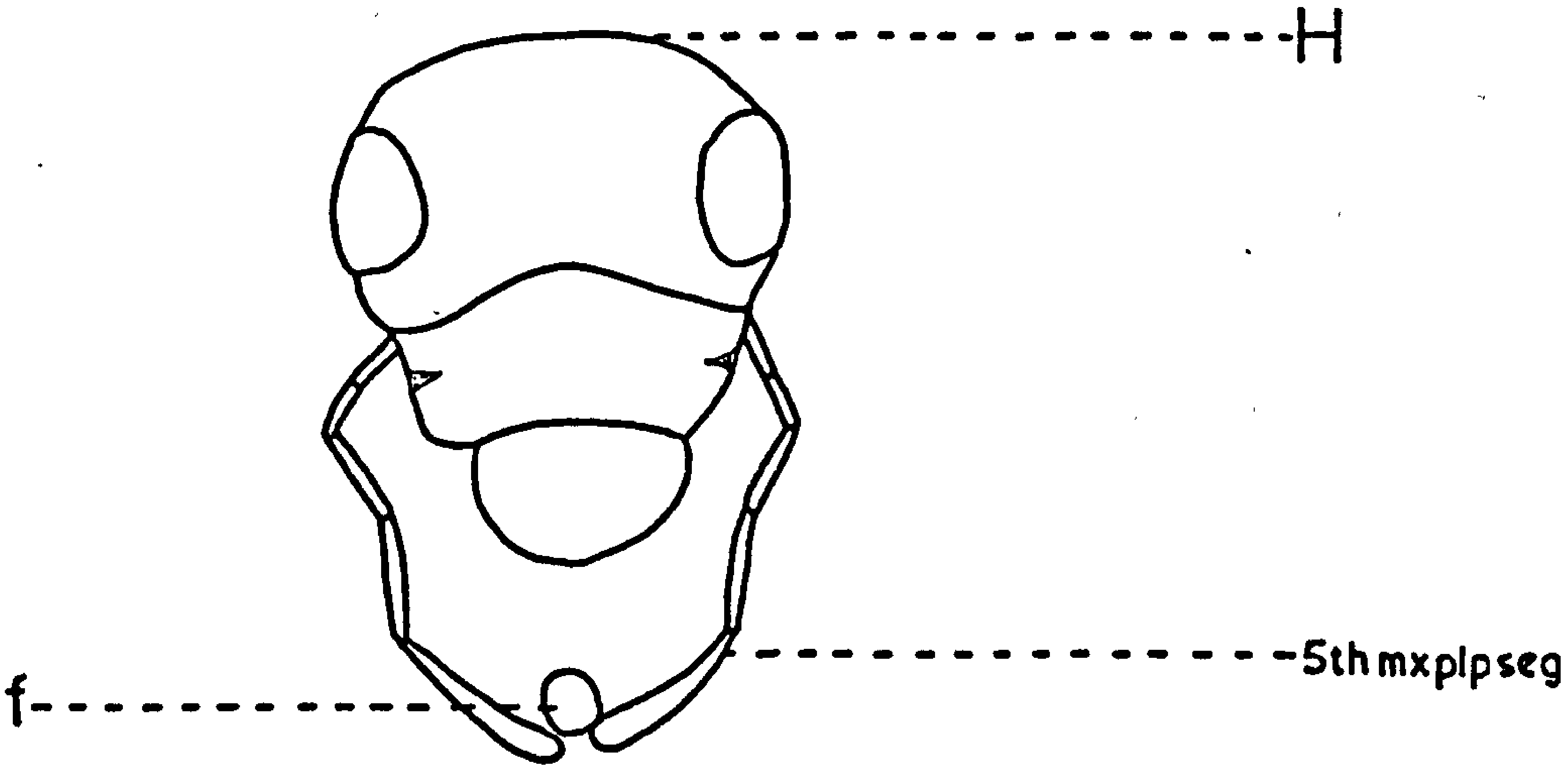
Fig·2



g



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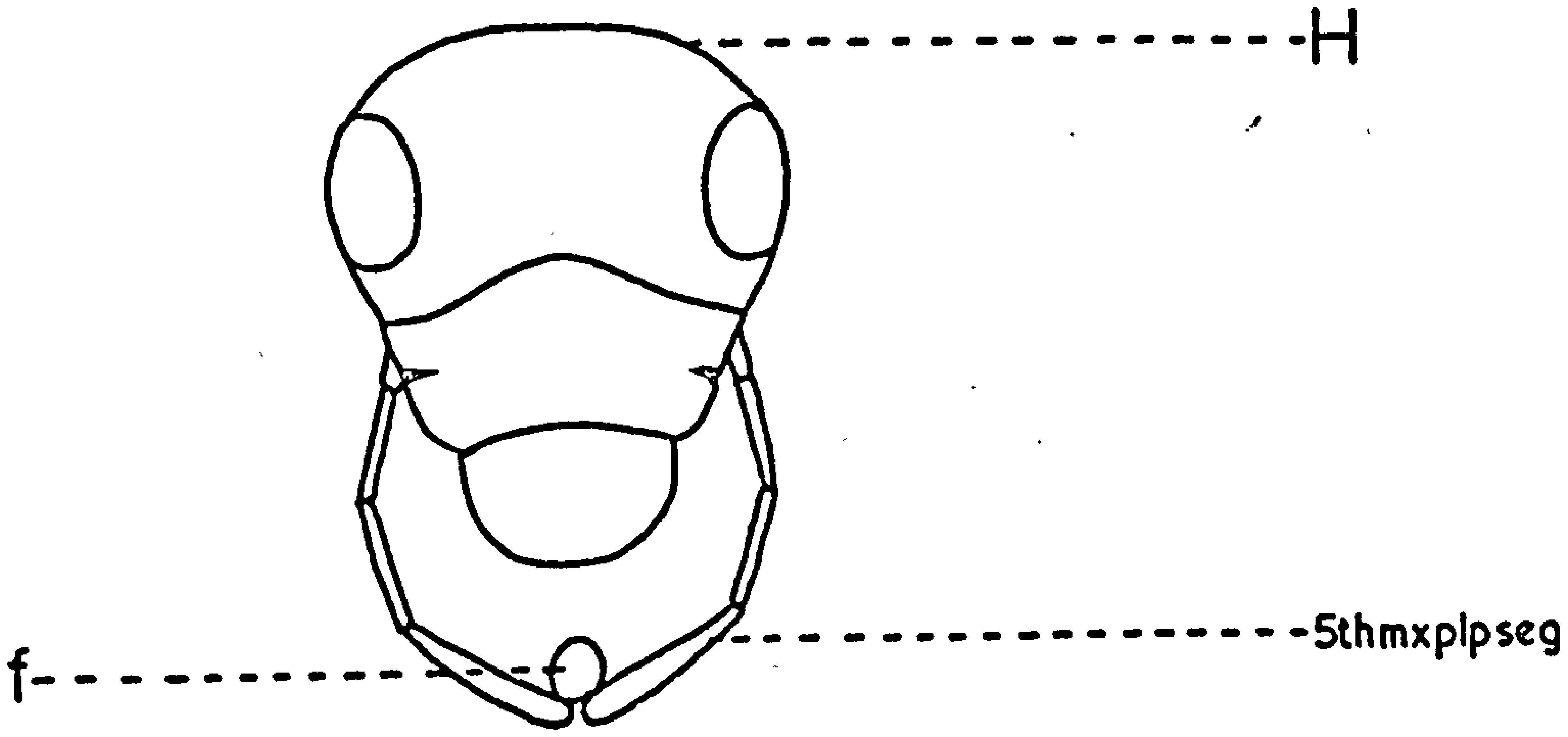
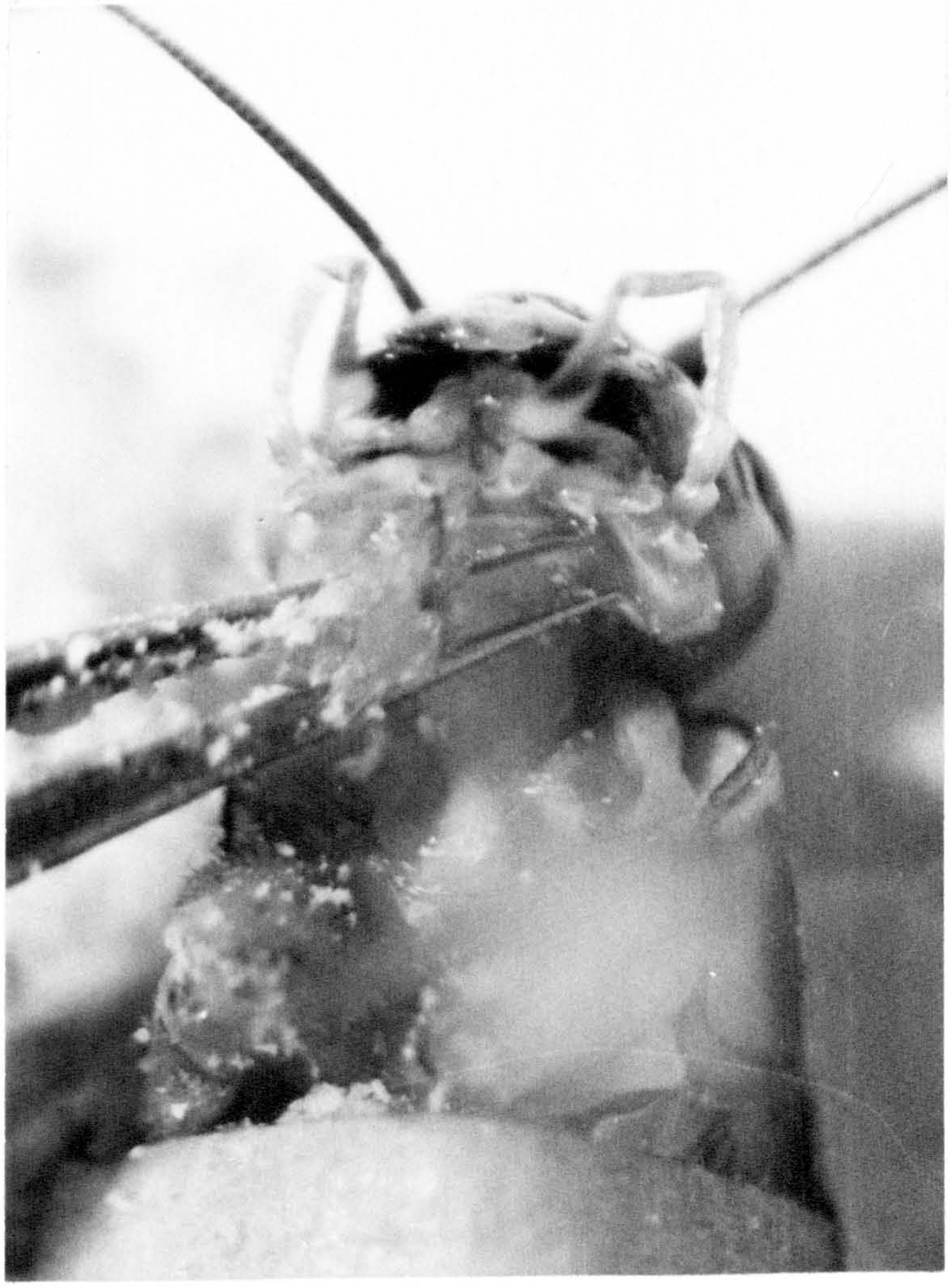


i

antennae play no further part in food selection. The maxillary palps then come into contact with food and make small, irregular, flicking movements. The flicking movements of the maxillary palps are then converted into more rapid and extensive vibrations. This process appears comparable to the palpation recorded in the Acrididae (Blaney and Chapman, 1970). The food is touched with the tip of the fifth maxillary palp segment (Fig. 1c). This segment obviously plays a vital role in the initial testing of the food. The sensilla which have been found to be concentrated on the tip of the maxillary palp are likely to be contact chemoreceptors. The complete action of the maxillary palps can be seen in Figs. 2 and 3. Fig. 2a - c shows the initial touching of the food particle, firstly on top and subsequently at the side. The palp then moves away from the particle (Fig. 2d) and then returns to the particle (Fig.2e, f). Later the two palps move synchronously to surround the particle and draw it towards the pre-oral food cavity. In Fig. 2g - i appeared to be the basic behaviour of the maxillary palp and was observed in several specimens. However, the occasional individual digressed from this pattern. For example the antennae may touch the substratum whilst the maxillary palps are testing the food. Alternatively, an insect may test one particle and then reach for another food particle and test that for a minute or so before returning to the original particle and moving that towards the pre-oral

Plate 2a. Initial testing of food.

of the fifth maxillary palp segment.
Some food particles are at the tip of
the palp.



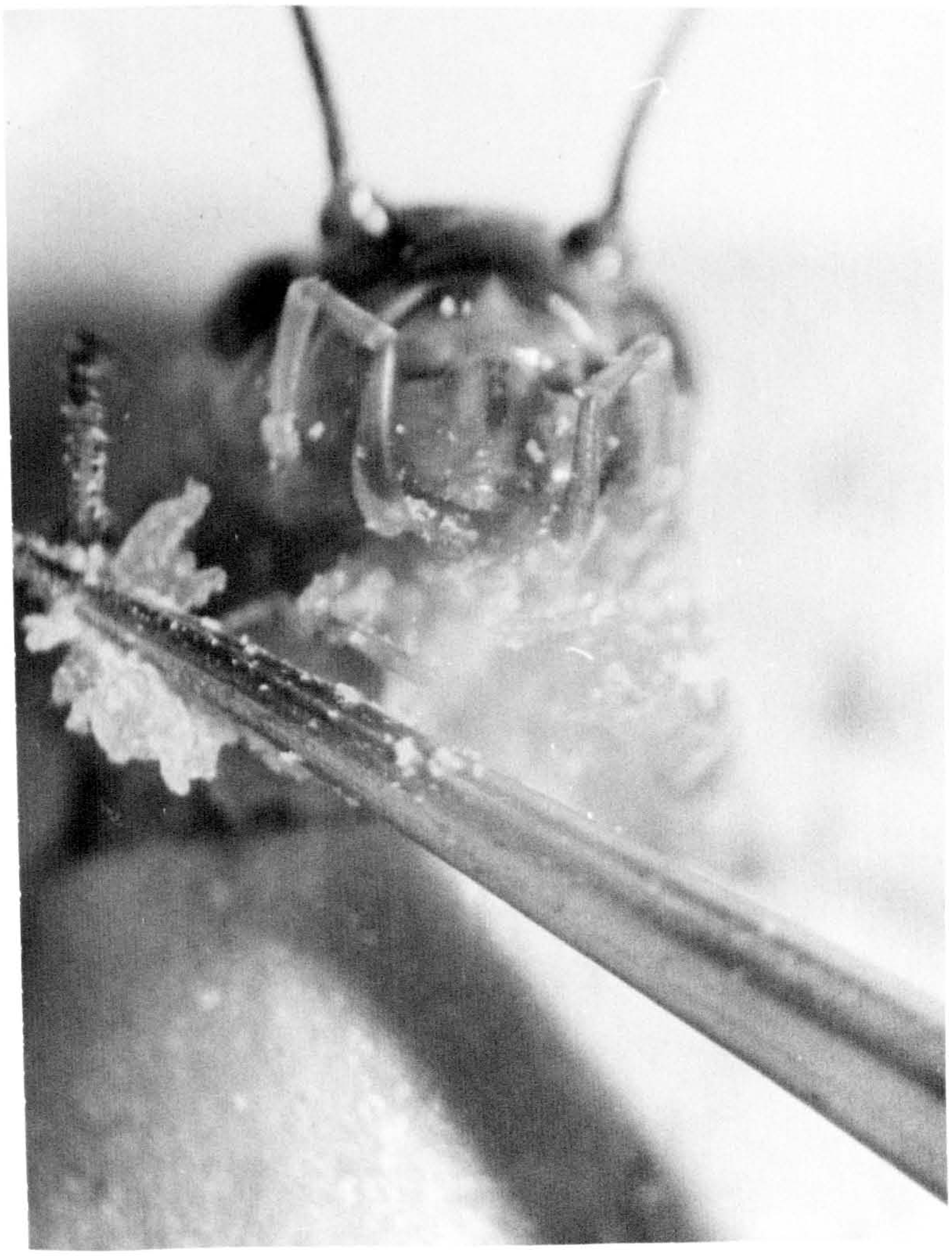
a

b

Plate 3a. Food particle between the labrum and hypopharynx.

Plate 3b. Food held in pre-oral cavity by the labrum, labial palp and labium.

a

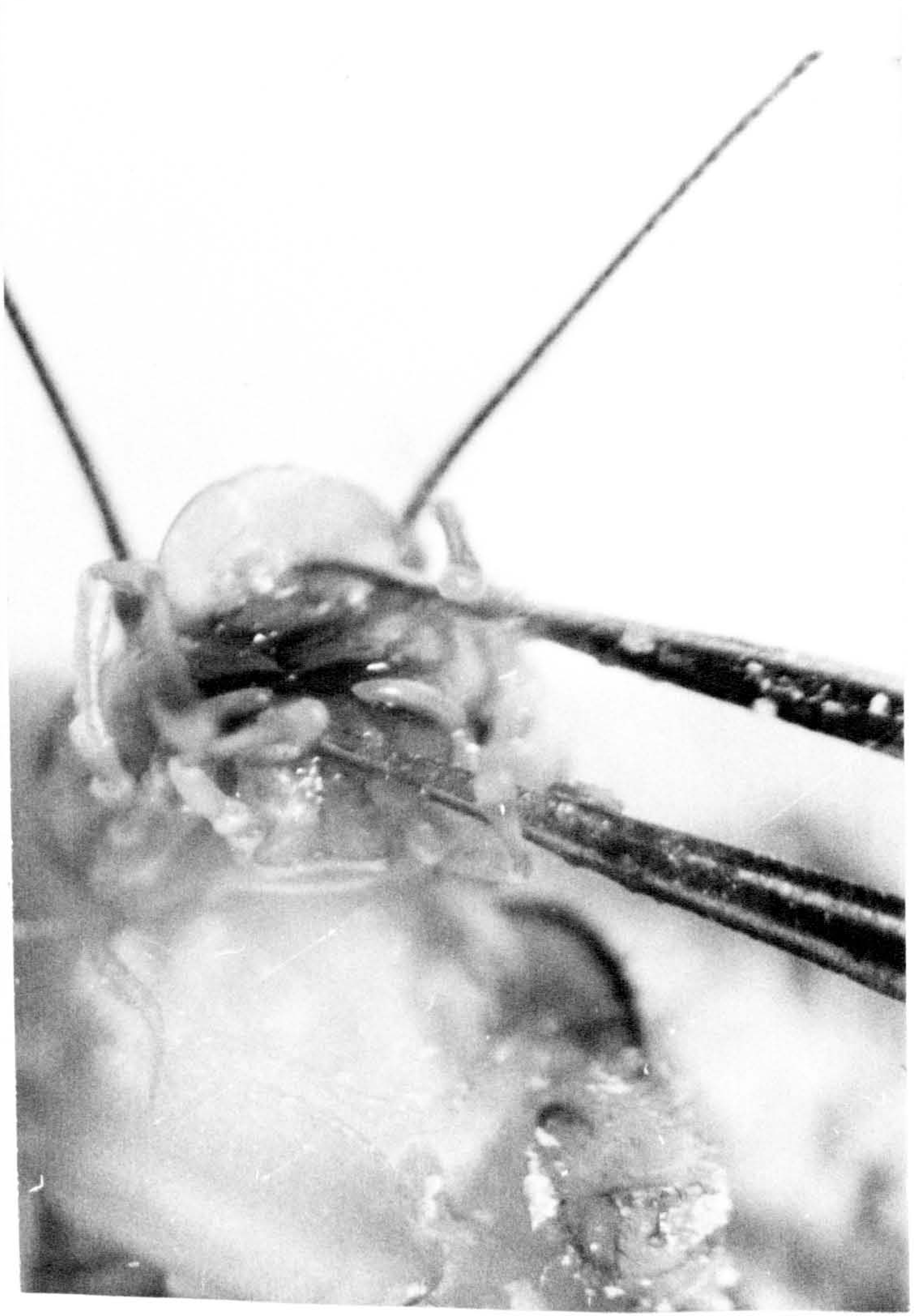


b

Plate 4a. Galeae in closed position, mandibles slightly apart.

Plate 4b. Epipharyngeal region of labium exposed to show the position of the mouthparts.

a



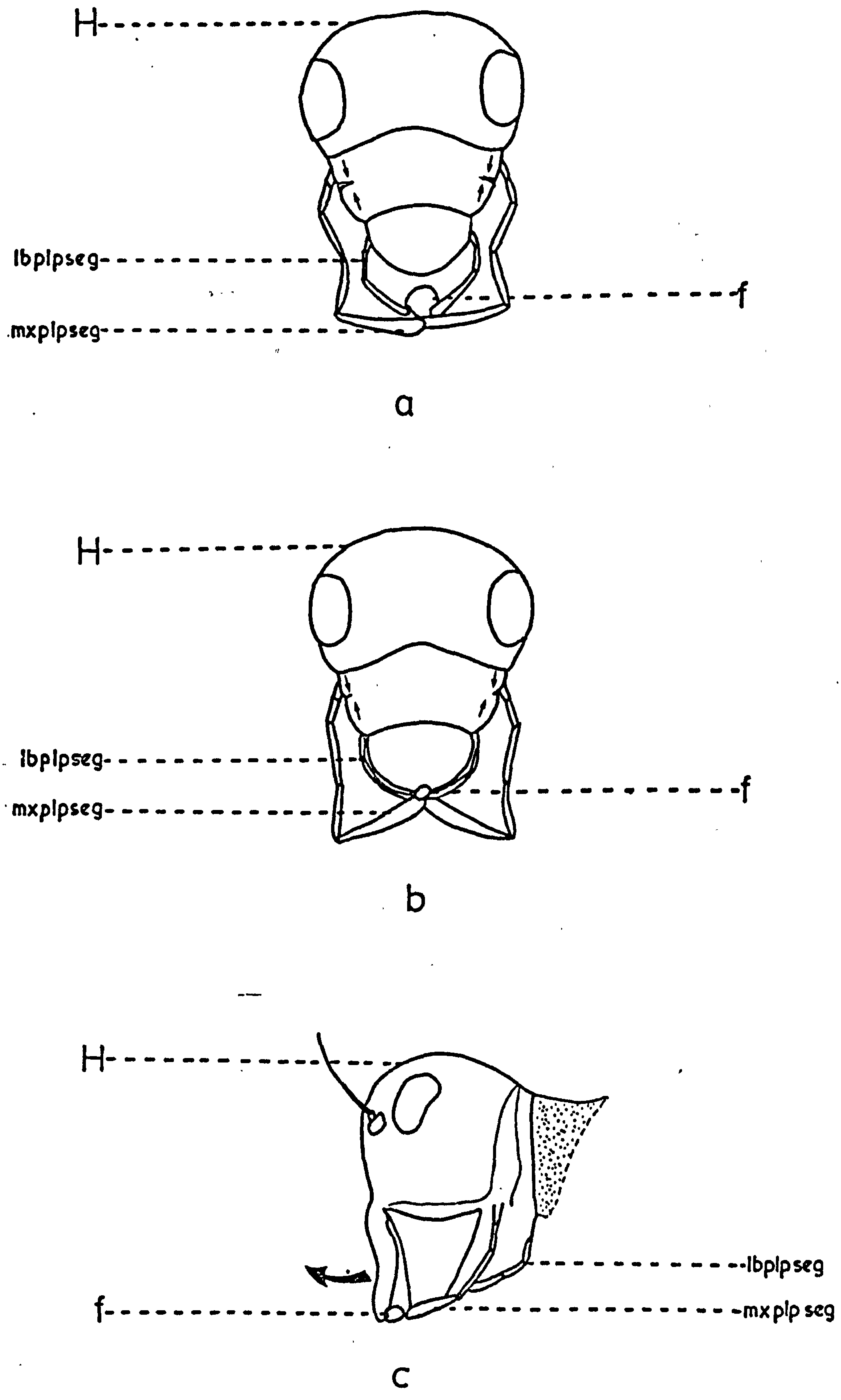
b

food cavity (Fig. 3a, b). The movement of the particle towards the mouth was assisted by the labial palp (Fig. 3a, b) in some specimens.

The agile manipulation performed by the maxillary palp is brought about by the movement of the individual palp segments relative to each other. There is little flexibility between the basal three segments (Plates 2 - 4). In particular very little movement occurs between the first and second segments although these were obscured during part of the videorecording. Slight flexibility exists between the second and third segments. However, the third and fourth segments form a type of elbow and movement through 90° or more is a common feature displayed by the junction between the third and fourth segments (Plates 1a and 2 - 4). There is also considerable flexibility between the fourth and fifth segments. During various stages the angles between the third and fourth, and fourth and fifth segments vary greatly.

These intricate movements of the palp are brought about by its complex musculature. The levator muscle of the palp lies within the stipes and is a short thick muscle with two unequal branches, its contraction brings about the outward movement of the palp. The smaller depressor muscle also lies in the stipes and its contraction results in the inward bending of the palp. The rigidity of the first three segments makes these move as a unit, the process being

Fig. 3. Diagrammatic representation of the movement of the maxillary and the labial palp in feeding.
(f = food particle).


H
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Fig·3

brought about by the flexor and depressor muscles of the palp. The muscles of the individual palp segments also play a part in the movement of the palp in feeding. The muscles of the first, second and third segments would presumably contribute to the movement of the whole of the base of the palp and assist in the maintenance of rigidity. The slightly longer levator muscle of the third segment would enable greater flexibility between this and the fourth segment and similarly the flexor muscle of the fourth segment would facilitate the characteristic inward bending of the fifth segment.

The process of palpation leads to head lowering and to the biting of the food particle once it has been collected by the maxillary and labial palp. As the food particle is taken into the pre-oral food cavity (Plate 3a) the labrum is lifted up towards its base or proximal end by the action of its abductor muscles. The flexibility of the clypeus at its point of separation into ante and post clypeus also facilitates in lifting the labrum (Fig. 3c). The movable part of the clypeolabrum namely the labrum, fulfils the role of a dorsal lip and both covers the pre-oral food cavity and keeps the food within it. Once within the pre-oral food cavity, food comes into contact with the hypopharynx and the distal part of the labrum. Some of the food particles have been seen to be rejected at this stage once they come into contact with the labrum. This serves to confirm the presence of some taste receptors on the labrum. Such receptors have been reported in insects such as S. gregaria and L. migratoria migratorioides (Haskell and Schoonhoven, 1969).

The lifting of the labrum coincides with the outward movement of the mandible. When the food particles are taken in, the epipharyngeal membrane of the labrum stretches resulting in a widening of the cibarium. The contraction of the median depressor muscles of the labrum performs this function. Once the food particle is within the pre-oral cavity the labrum moves backwards and presses against the mandibles. This backward movement of the labrum is brought about by the first and second adductors of the labrum.

The hypopharynx pushes the food further into the pre-oral cavity where it comes into contact with the mandibles. Biting and mastication are carried out simultaneously and presumably during this process saliva is added to the food, although the timing of this is difficult to determine. The incisor processes cut the food whilst the molar process grind the food particles. Each mandible articulates with the head capsule at two points which restrict the structure to a lateral movement. Since the mandibles are asymmetrical more effective grinding is possible. The overall movement of the mandible is controlled by its four extrinsic muscles. The closing or adduction of the mandibles is due to the adductor muscle which originates from the top

Fig. 4. A diagrammatic representation of the position of the mandibles, galeae and laciniae during feeding.

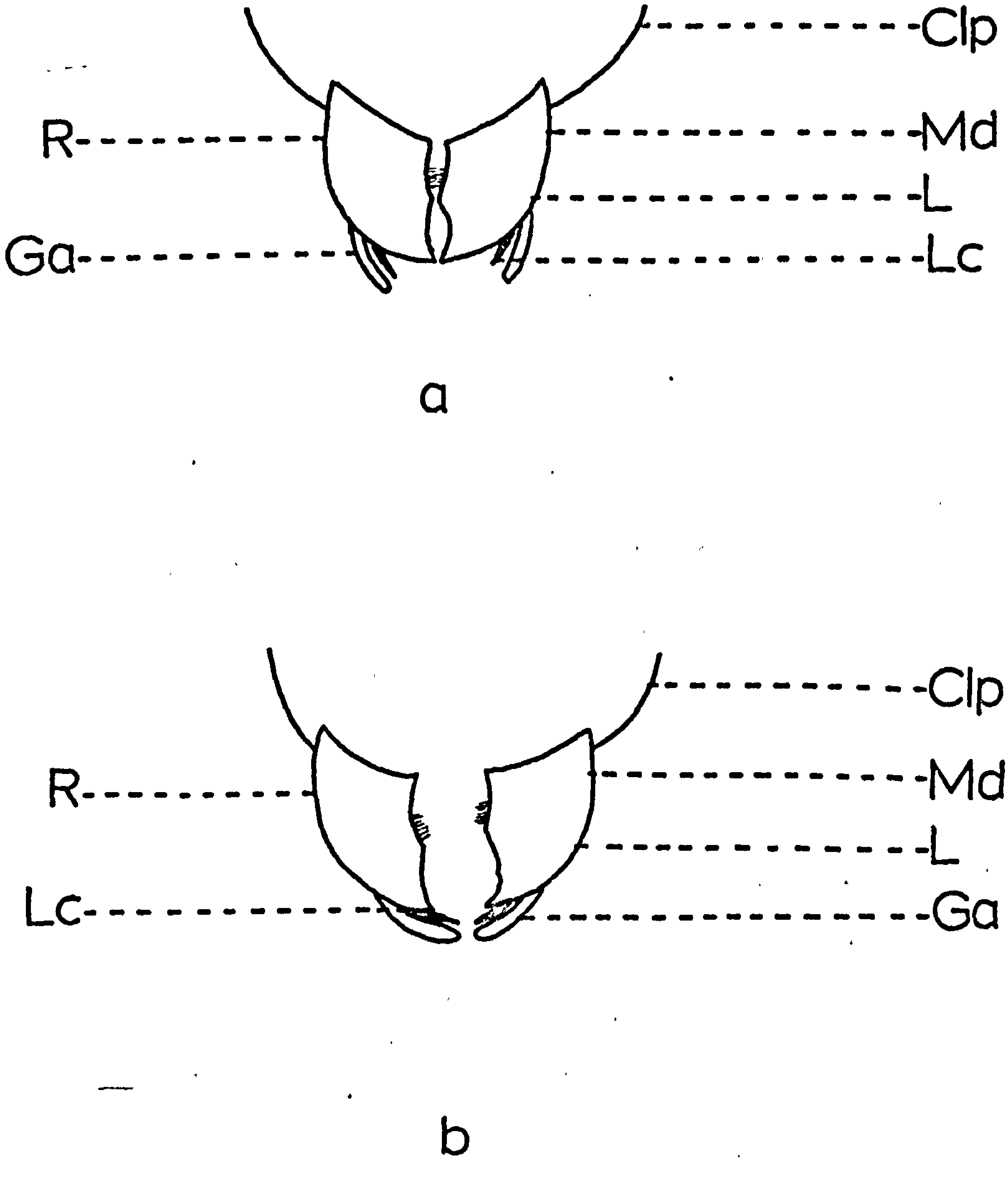

Fig. 4

of the head capsule. This movement is probably assisted by the hypopharyngeal mandibular adductor muscle. The outward movement of the mandible or abduction is due to the abductor muscle. Whilst the inward and slightly backward movement of the mandible during mastication is accomplished by the tentorial adductor muscle. The actual movement of the hypopharynx is difficult to see although its elevation pushes the food between the closing mandibles and probably assists in the distribution of saliva.

The mandibles are opened by the contraction of the abductor muscles and the ground food particles escape from the mandibles to be pushed towards the mouth by the laciniae and galeae. When the mandibles are closed the galeae and laciniae of the two sides are widely separate (Fig. 4a), but when the mandibles are opened the galeae and laciniae are closely approximated to the midline (Fig. 4b). Thus the mandibles and maxillae act in time but in anti-phase. The presence of a comb on the distal portion of each galea probably serves to push the smaller pieces of food towards the mandibles for further mastication. The galea thus acts as a lateral lip. Its movement may be easily explained by reference to its musculature. The laciniae are stout at their distal part and provided with teeth like structures. The laciniae help in the collection of the fragments of food which get loosened by the mandibles during biting and appear to push them inwards towards the pre-oral food cavity. The movement of the galeae and laciniae is brought about by their flexor muscles which allow them to move sideways. The contraction of the adductor of the stipes, adductor of the cardo, protractor of the cardo and cranial flexor muscles also facilitates in the bending of the maxilla towards the other mouthparts whilst the cranial flexor of the lacinia also helps in bending the lacinia inwards.

The glossae and paraglossae of the labium help in the manipulation of the food, but their main function is the provision of a lower lip for the oral cavity. The glossae and paraglossae move backwards and forwards in unison. The glossae appear incapable of independent movement and always move in conjunction with the paraglossae. The movement of the glossae and paraglossae is brought about by their adductor muscles.

The labial palp, like the maxillary palp, is supplied with two muscles at the base of the first palp segment, referred to as the levator and depressor of the labial palp. The depressor has its insertion on the middle posterior portion of the base of the first palp segment. The lateral movement of the labial palp results in either the raising or the bending of the palp downwards and inwards and is due to the levator and depressor muscles of the palp. The extensor muscle of the first segment and depressor of the second segment cause the labial palp to extend outwards whilst the depressor muscle of the second segment results in the terminal itself devoid of muscles, being bent inwards.

When the food is thoroughly chewed it is ready to be swallowed. This is done by the contraction of the compressor muscles of the salivarium which press the hypopharynx against the labium. These compressor muscles also prevent the escape of excess saliva. The food mixed with saliva is passed through the cibarium to the pharynx. Its passage is assisted by tracts of orally directed sensilla and hairs on the epipharyngeal surface of the clypeolabrum. During swallowing the dilation of the cibarium and stomodaeum is brought about by the contraction of the dilator muscles of the cibarium and relevant muscles of the stomodaeum. The food material is sucked into the crop by the contraction of the stomodael constrictor muscle which moves the food backwards and pushes it into the crop.

One interesting process which may be considered in relation to feeding is the imbibing of water. This was observed particularly well by ciné photography. During this process the lobes of the hypopharynx swell. The swelling of the proboscis is considered to be partly due to an increase in blood pressure (Rietschel, 1953b) and also to the presence of water in the pseudo-tracheae. The pseudotracheae are small, open canals which facilitate the uptake of water and its passage towards the mouth.

7.3.a. Summary of the role of each structure

Clypeolabrum

When the food particles are taken in, the labrum is displaced towards its base. Flexibility of the clypeolabral complex is provided by the partial division of the clypeus into ante and post clypeus. The labrum serves as a mobile covering to the mouthparts. The epipharyngeal surface of the clypeolabrum possesses intertorma besides tormae on which some of the compressor muscles of the labrum are inserted. The labrum acts as a dorsal lip which keeps the food within the pre-oral cavity. It also plays an important role in food selection, many of the sensilla on the epipharyngeal surface having a gustatory function.

Mandibles

The mandibles bear incisor and molar lobes; the former being used for cutting the food and the latter for masticating or grinding the particles. Cutting and mastication are done simultaneously. The mandibles move laterally and are slightly asymmetrical on their medial surface.

Maxillae

The galeae play an important role in holding the food during feeding and help to push it towards the food cavity. They therefore act as lateral lips. They do not move independently but are moved backwards and forwards by the displacement of the mandibles. Usually the galeae and laciniae move together a movement assisted by the flexor muscles of these structures.

The laciniae are heavily sclerotized and are armed with teeth, they play an important part in holding the small particles of food cut from the mandibles. The mandibles push the food towards the mouth between the molar lobes which masticate it until it is swallowed.

The maxillary palps are densely covered with sensilla. These sense organs are used for the orientation to the food and its initial testing. The palps begin to palpate when the insect approaches the food and this is continued during sampling. The palps are also responsible for lifting the food towards the pre-oral cavity.

Labium

The labium acts as a ventral lip, whilst the labial palps may help to introduce the food into the pre-oral cavity. The glossae and paraglossae rock back and forth with the movement of the mandibles and probably prevent the saliva falling from the inner side of the prementum during feeding.

Hypopharynx

The hypopharynx serves as the floor of the cibarium and during mastication its surface is raised by the hypopharyngeal adductor muscles of the mandible. This elevation of the hypopharynx pulls the base of the hypopharynx against the roof of the pharynx and so closes the entrance to the oesophagus. The food, after mastication, is swallowed by the widening of the pharyngeal opening which is brought about by the contraction of the depressor muscles of the hypopharynx.

Antennae

During feeding the antennae apparently play no special role in food selection, although they are obviously important in the initial orientation to the food. The movement of the antenna in all directions is assisted by the levator, flexor and depressor muscles in addition to the extensor and flexor muscles of the scape.

7.4 Discussion

This analysis of the feeding mechanism of A. domesticus has resulted from direct observations, ciné photography and videorecording. The functional significance of many structural features have been suggested. Four distinct phases in the feeding of A. domesticus may be recognised. The first phase is orientation to the food. The second phase involves the testing of the food by the maxillary palps and the subsequent introduction of the food to the pre-oral cavity. The third phase is initiated when the hypopharynx pushes the food material upwards between the mandibles for mastication and the fourth and final stage when food material is sucked into the crop by the action of the cibarial and oesophageal dilator muscles.

The mouthparts of A. domesticus are essentially of the generalized Orthopteroid type. This relatively unspecialised type of mouthpart may be adapted to feed on any type of food substance and within the order Orthoptera examples may be cited of herbivores and carnivores in addition to omnivores. It seems as if A. domesticus is an omnivore, but it must be emphasised that materials on which it feeds in the laboratory are not necessarily its natural food. The species has been recorded to feed on skimmed milk, fish meal, yeast, molasses, salts and vitamin mixture (Ghouri, 1957). Besides these it damages vegetables and crops particularly vegetables in the seedling stage in addition to household articles such as foodstuffs and fresh fruit. It is referred to as by Latif et al (1957) omnivorous since it can feed upon any type of organic matter.

One unusual feature of the mouthparts is the hypopharynx which is very different from that found in the Acrididae. In many respects the hypopharynx resembles the proboscis of clyclorraphan Diptera. The presence of pseudotracheae enables the species to imbibe fluid diets. Among other crickets this type of structure has been recorded in the black field cricket Liogryllus campestris L. (Rietschel, 1953b).

The role of the antenna in the discrimination of the food is controversial. William (1954) holds the opinion that the antennae have nothing to do with the acceptance of food, whereas Goodhue (1962) reported that insects such as Schistocerca make use of their antennae. In some aeromatic plants stimulation of the antenna alone may lead to rejection. The role of the antennae of the acridid, *Poekilocrus hieroglyphicus* (Klug) in the perception of the food from a distance is discussed by Abushama (1968), whilst Chen-Ning-Sheng (1964) has described the importance of the antenna of *L. migratoria manilensis* in recognizing food at close quarters.

During orientation the importance of the maxillary palp has been noticed in *A. domesticus*. Their role in this context has already been reported in some other insects. The rapid flicking movement of the maxillary palps are described as palpation (Blaney and Chapman, 1970). The palpation serves to maintain a continuous flow of information to the central nervous system (Blaney and Chapman, 1970). Mordue (1975) suggests the palps in *Schistocerca* are important both in food selection and in the maintenance of continued feeding. It is mentioned that in the absence of the palps the antennae could assume a more important role in the exploration of the food both before and during a meal. However, Goodhue (1963) considers that testing the food prior to ingestion in *Schistocerca* involves palpation with both the palps and the antennae. In *A. domesticus* palpation leads to ingestion which supports Mordue's (1975) view.

Studies on the structure and distribution of the sensilla on certain of the mouthparts have been made by Blaney and Chapman (1969a), Le Berre and Louveaux (1969) and

Sinoir, Boulay and Le Berre (1968). Behavioural studies on food selection in insects in relation to the sensilla present have been undertaken by William (1954) and Abushama (1968). According to them removal of the palps enhanced the amount of feeding on distasteful plants. Blaney and Chapman (1970), Haskell and Mordue (1969) and Sinoir (1969) have described the functions and role of the sensilla on the mouthparts in feeding behaviour. Some electrophysiological studies have been carried out by Haskell and Schoonhoven (1969), Blaney (1974, 1975) and Blaney and Duckett (1975).

The sensory basis for food selection depends on testing the food surface with exteroreceptors, sampling and the feeding. William (1954) has shown that selectivity is reduced by amputation of the palps and it has been confirmed that chemoreceptor sensilla are concentrated on the tips of the maxillary palps of the Acrididae (Frings and Frings, 1949; Haskell and Mordue, 1969). The act of palpation in _A. domesticus_ suggests that Types 3 and 5 sensilla at the tip of the maxillary palp act as contact chemoreceptors which are involved in the initial selection of an appropriate food. The rejection of the food once in the pre-oral cavity illustrates that there are some taste receptors present on the posterior surface of the epipharyngeal region and possibly on the anterior surface of the hypopharynx. Some of the sunken receptors on the inner surface of the clypeolabrum of _S. gregaria_ and _L. migratoria migratorioides_ act as chemoreceptors (Haskell and Schoonhoven, 1969). In *A. domesticus* it seems that the Types 6 and 13 sensilla on the clypeolabrum may fulfil the same role whilst receptors on the other mouthparts permit continued feeding.

Although the present work does not aim at confirming the function of the receptors, based on electrophysiological evidence, it may suggest the function of certain of the dominant groups of sensilla.

PART 8

GENERAL DISCUSSION

The present study was undertaken in order to investigate the structure and mode of functioning of the head capsule and appendages, in relation to feeding, in A. domesticus. The detailed external anatomy of the head capsule was complemented by an investigation of the musculature of the head capsule and mouthparts. This enabled a more precise understanding of the movement of each appendage. The nervous innervation of the musculature was also investigated. The cuticular sensilla play a vital role in the detection of suitable food, its sampling and continued feeding. Consequently the detailed distribution of the various sensilla types on the mouthparts and their nervous innervation completed the study.

Two types of head capsule are recognised by Hudson (1945), depending on the orientation of the longitudinal axis of the head. In the prognathous type, the longitudinal axis of the head is horizontal and the mouthparts are anteriorly directed, whilst in the hypognathous type, the longitudinal axis of the head is vertical, and the mouthparts are directed ventrally. According to Walker (1932) prognathism is common among carnivorous insects that chase and capture their prey with their mandibles, whilst hypognathism is found in carnivorous species which await their prey, e.g. mantids and nymphs of dragonfly. This type is also present in phytophagous insects with perching habits such as the Tettigoniidae and Acrididae.

In discussing the occurrence ofprognathism Hudson (1945) uses certain examples from the Orthopteroid insects. In some groups such as the Phasmida, Tettigoniidae and Gryllotalpidae a change in shape of the head capsule is reflected by a corresponding change in its internal skeleton or tentorium. In the Phasmida, the elongation of the ventral region of the head capsule in *Diapheromea femorata* Say. causes the occipital region to change its plane from perpendicular to oblique resulting in very simple tentorial body (Hudson, 1945). Whilst in the Gryllotalpidae, where the fossorial habit has favoured prognathism, the elongation of post-ocular region of the head in e.g. *Gryllotalpa africana* Pal. has resulted in the occipital foramen becoming oval and lying at an inclined plane to the body axis. In this case the tentorial body is very elongated. In the Tettigoniidae, the elongation of the head capsule of *Oecanthus capensis* Saus. has taken place in the anterior region because the mouthparts have become forwardly directed. This change has effected the dorso-anterior elongation of the head capsule and has caused an elongation of the body of the tentorium which thus shows a great similarity to that of the Gryllotalpidae.

The greatly elongated body of the tentorium suggests a phenomena of secondary evolution of prognathism, since in primitive prognathous insects the elongated body of the tentorium is not encountered. This agrees with Walker (1932) and Hudson's (1945) view that secondary evolution of prognathism in G. africana and O. capensis has occurred as a result of change of habits or habitat. Hudson (1945) considers that the Phasmida fall into a separate group which retain a primitive prognathous type of head and possess a very small posteriorly placed tentorial body without a median aperture. The absence of a median aperture separates them from another cursorial group, the Dictyoptera, in which a median aperture is present and the posterior tentorial arms are well developed.

In the saltatorial Orthoptera the head is hypognathous and the tentorium is essentially X-shaped. The three main groups, Tettigoniidae, Acrididae and Gryllidae, however, differ. In the Tettigoniidae and Acrididae a dorsoventral elongation of the head capsule results in shortening of the body of the tentorium. In the Gryllidae, however, the body of the tentorium is widest anteriorly whereas, in the Tettigoniidae and Acrididae the reverse condition is found. The dorsal arms in the Tettigoniidae and Acrididae are very delicate unlike the Gryllidae where they are very strong.

According to Snodgrass (1960) "in the Orthopteroid and other lower insects with strong biting and chewing mandibles, the tentorium may be strengthened by the development of a central plate, the 'carpotentorium' in which the four arms are united". In A. domesticus the carpotentorium is well developed. In Popham's (1961) interpretation of the function of the tentorium, he compared the mouthparts of a cockroach with those of the Hemiptera. In the Hemiptera, the mandibles and maxillae are reduced to stylets and the tentorium is consequently absent. In these forms the mouthparts play no major role in the actual collection of food by lifting it into the cibarial cavity. In this case the movement of the fluid food material is brought about by a cibarial sucking pump. In P. americana the tentorium is perforated by a foramen in the tentorial body through which pass the circumoesophageal commissures. Popham (1961) gives a functional explanation for the form of the tentorium in Periplaneta and in Locusta. In both forms the maxillae are used to pass food to the mouth. In Locusta, the maxillae are moved forwards and pass food towards the mandibles, whilst in Periplaneta the movement of the maxilla is in transverse plane. In Periplaneta the maxillary muscles extend towards the midline, this results in an extension of the anterior arms of the tentorium towards the midline to accommodate the origins of the maxillary adductor muscles. The anterior arms of the tentorium then become extended inwards around the circumoesophageal commissure and causes a special foramen to develop in the tentorial body. In A. domesticus the maxillae also move in a transverse plane, but here the tentorial body serves as a site of attachment for the muscles and thus no extension of the anterior arms is necessary.

The tentorium of _A_. _domesticus_ is X-shaped and displays the generalised structure displayed by the Orthoptera and has anterior, posterior and dorsal arms. Hudson (1945) suggests that an X-shaped tentorium confers rigidity to the head capsule and provides a base for the attachment of the cephalic muscles. In addition it strengthens the points of insertion of certain muscles of the mouthparts (Imms, 1951). Bigelow (1954) also emphasizes the importance of the tentorium as a brace for the head in addition to providing a rigid base from which movement can be transmitted. He believes that stresses applied to the tentorial arms by the muscles attached to them are transmitted to the facial integument between the anterior tentorial pits and that this accounts for the origin of the frontoclypeal inflection which reinforces this region. The tentorium is particularly important in insects with strong mandibles since the muscles operating these structures need particularly strong sites of attachment. However, according to Duporte's (1957) interpretation it is the secondary mandibular articulation which causes stresses on the frontoclypeal sulcus and it is in response to these that an inflection or ridge develops to reinforce the cranial wall. In _A_. _domesticus_ the presence of this inflection may be due to the secondary mandibular articulation in addition to the increased strength of the tentorium itself.

Essentially the head capsule is a rigid, box-like structure. The junction between the clypeus and frons in *L. migratoria* is rigid and does not allow movement of the clypeus against the frons (Cook, 1976). According to the same author the clypeolabral junction, on the other hand, is flexible and allows movement of the labrum in an anterior and forwards direction relative to the clypeus. It has been seen in *A. domesticus* that although the junction between the clypeus and frons is again rigid, some flexibility of the clypeolabral complex is provided by the partial division of the clypeus into ante and post-clypeus. Thus the clypeolabrum serves as a mobile covering to the mouthparts. Narula (1968) records a similar condition in *G. sigillatus*, where the clypeus is divided into two portions by the transclypeal sulcus, whilst Cook (1944) calls this partition the intraclypeal suture in *G. assimilis*. The clypeolabral suture in *A. domesticus* is incomplete and membranous unlike *G. sigillatus* where it is complete and well developed (Narula, 1968).

The cuticular thickenings between the clypeus and labrum are called the tormae. The structure of the tormae has been investigated by Anderson and Weis-Fogh (1964) who consider them to be composed of resilin. Resilin is known to be modified cuticle which possesses elastic properties, thus the tormae would act by their inherent elasticity to return the labrum to its resting position against the mandibles. The epipharyngeal surface of the labrum possesses an intertorma in addition to the tormae on which some of the compressor muscles of the labrum are inserted. Crampton (1930) records similar structures in the sand cricket, Stenopelmatus (Stenopelmatidae). These demarcate the anterior epipharyngeal region from the posterior epipharyngeal region. The presence of the sclerotized bar on the epipharyngeal surface (Verstärkungsleiste of Rietschel, 1953a) gives support to the membranous region. This is necessary because the second pair of adductor muscles of the labrum are inserted on its proximal side.

The role of the labrum of L. migratoria in feeding has been examined by Sinoir (1969), who showed that stimulation of the terminal sensilla on the maxillary palps leads to a 'head lowering' response which brings the distal region of the anterior surface of the labrum into contact with the substratum or food.

The importance of the elasticity of the cuticle in relation to the functioning of the mouthparts has been discussed by Brown (1961) in the mayflies C. dipterum and Baetis rhodani Pictet. The same author also shows how the tips of the mouthparts are used to collect food in Centroptilum by virtue of their flexible cuticle. In A. domesticus, as in many other insects, the tips of the maxillary palps are important in collecting the food and drawing it towards the pre-oral food cavity and other mouthparts assist in this.

However, it is difficult to separate the importance of the sensory role of these structures from their purely mechanical role.

The structure of the head has an important bearing on the feeding mechanism (William, 1954). Isely (1944) showed that in grasshoppers, the mandibles are specially adapted to the type of vegetation which is normally consumed, whilst William (1954) explains that they may be adapted to a range of food substances. The presence of both the incisor and molar teeth suggest that the mandibles of A. domesticus are of the cutting, chewing and grinding type. These are referred to in the Acrididae as the graminivorous type (William, 1954).

Perhaps one of the most interesting features of the structure of the feeding appendages is the similarity in the hypopharynx of A. domesticus and the proboscis of some cyclorrhaphan Diptera. In both cases the structure is modified for sucking. A sucking proboscis is seen in several groups of insects although the structures involved are not always the same. In the Diptera the labium is highly modified and the palps are transformed into labella lobes. In certain Hymenoptera e.g. the honey bee, Apis, the labium is again specialized and together with the maxillae is elongated to form the maxillolabial complex. However, in the Lepidoptera the galeae of the maxillae are modified to form a long coilable proboscis. In the above mentioned orders, the hypopharynx is reduced, this deficiency being overcome by other mouthparts which perform a suctorial role. An interesting parallel can be drawn between the Trichoptera and A. domesticus. Crichton (1957) has reported the presence of a hypopharynx in adult Trichoptera which is adapted for taking up fluids. This modification occurs in conjunction with the presence of biting and chewing mouthparts. In forms where the mandibles were reduced the hypopharynx is particularly enlarged and specialized.

The detailed structure of the hypopharynx of A. domesticus reveals the presence of pseudotracheae which lead to efferent ducts which in turn open on the anterior surface of the hypopharynx. Thus the hypopharynx forms a well developed proboscis (Rietschel, 1953a) similar to that seen in some Diptera where the labium is the structure involved. In A. domesticus the labium displays the typical Orthopteroid structure. As Rietschel (1953b) concludes the proboscis of A. domesticus and certain Diptera have different origins but are identical in function; they are therefore analogous but not homologous to each other (Rietschel, 1953b). In the Acrididae so far described the hypopharynx shows no special modification to sucking. Even within the Gryllidae differences occur in the hypopharynx. The hypopharynx of L. campestris resembles that of A. domesticus although no specialisation occurs in the wood cricket, Nemobius sylvestris Fabr. or G. sigillatus (Narula, 1968) and G. assimilis

(Duporte, 1920).

The surprising similarity of the cricket proboscis to that of some flies suggests that the mode of life and in particular their feeding habits may be similar (Rietschel, 1953b). It suggests that both insects live on juices. Flies live on openly exposed juices produced, in most cases, by chemical breakdown of either animal or plant substances (Rietschel, 1953b), whilst crickets probably feed on juices exposed by the mechanical breakdown of plants and animals brought about by mastication by the well developed mandibles. In Diptera the biting jaws are absent and mechanical breakdown would be impossible. Crickets, on the other hand, in addition to their proboscis, possess the same Orthopteroid mouthparts as cockroaches and grasshoppers. They can, therefore, deal with solid food in addition to liquid food. It is possible that crickets with a highly modified proboscis use it mainly for drinking. In captivity they are often seen "drinking" from a cotton wool pad soaked in water.

There are several features of the muscular system associated with the head and its appendages which warrant special attention and discussion. Generally the most interesting features are comparative, either between closely related species or between different insect groups.

The mandible is characterised by having an adductor and an abductor muscle in most insects, but in addition other subsidiary muscles may be present. In _A_. _domesticus_, a tentorial adductor of the mandible (Muscle 7) and a hypopharyngeal adductor of the mandible (Muscle 8) are present. In the case of the tentorial adductor muscle, Snodgrass (1935) has reported the presence of this muscle in lower Pterygote insects whilst Khattar (1964) has recorded its presence in Schizodactylus (Schizodactylidae) where it closely resembles the Gryllidae (Khattar, 1959). However, these authors do not report its function. In A. domesticus the function of the tentorial adductor (Muscle 7) appears principally to be that of adduction. It draws the mandibles towards each other in the midline, a process which is accompanied by a limited backward movement of the mandibles. In many respects this mode of action resembles that reported by Narula (1974) in G. sigillatus. It is of interest that this muscle has not been discussed by a number of authors in the various Orthoptera they studied e.g. (Berlese (1909), Duporte (1920), Snodgrass (1928), Misra (1946) and Imms (1951).

In the case of the hypopharyngeal adductor of the mandible, Snodgrass (1935) has mentioned its presence in the lower Pterygota and in the Lepismatidae of the Thysanura. He refers to the muscle as the ventral adductor of the mandible. According to him, the muscle is present in the larvae of Ephemeroptera and Odonata, where it arises from the anterior arms of the tentorium, and also in adult Isoptera and most Orthoptera, except the Acrididae where it is absent. Chapman (1975) confirms these views and regards the origin of the muscle to be the hypopharyngeal apophysis. The muscle is however absent in the higher insects. Narula (1974) reports the presence of this muscle in G. sigillatus where, contrary to its name, it has no connection with the hypopharynx. He considers the muscle to be homologous with the ventral adductor of more primitive insects, which has lost its connection with the anterior tentorial arm and due to the increase in size of the mandibles lies completely within the cavity of the mandible. In addition to this muscle Vishoni (1962) has mentioned the presence of a second adductor in the termite Odontotermes. A comparable muscle has not been found in A. domesticus.

From a review of the literature on the musculature of the mandible it is apparent that there are considerable differences even within the Orthopteroid insects. This opinion was also voiced by Narula (1974). A comparative study of the mandibular musculature in a selection of species would be an invaluable contribution to comparative and functional morphology.

From the careful work of Khattar (1964), it can be seen that although Schizodactylus shows certain features of its head musculature common to the families Tettigoniidae and Acrididae, it more closely resembles members of the family Gryllidae. Within the Gryllidae, its musculature appears more similar to A. domesticus than G. sigillatus (Narula, 1974) or G. assimilis (Duporte, 1920). To take one example, the origin of certain labial and hypopharyngeal muscles vary in relatively closely related species of Orthopteroid insects. In A. domesticus the adductor of the labium (Muscle 22) and the retractor of the hypopharynx (Muscle 31) originate on the posterior edge of postoccipital ridge close to the posterior tentorial pit and in this respect are similar to those in Schizodactylus (Khattar, 1964). However, in the Gryllids, G. assimilis and G. sigillatus the origin of these muscles is on the tentorial body (Duporte, 1920 and Narula, 1974 respectively). The difference in the reported origin of these muscles is of interest and needs to be considered from a functional standpoint.

The structure of the antennae of insects is reviewed generally by several authors, e.g. Chapman (1969), Imms (1930) and Richards and Davies (1977). The flagellum is generally considered to be secondarily annulated. The annuli are joined by membranes which give considerable mobility and flexibility to the structure. In the Pterygota and Thysanura of the Apterygota, there are no muscles in the flagellum, and the nerve which passes through the flagellum is purely sensory. Flagellar muscles are only found in the Collembola, Diplura among the insecta and also in the Myriapoda (Schneider, 1964). It has been demonstrated conclusively in the present work that muscles are absent from the pedicel and flagellum. In this way A. domesticus is characteristic of the Pterygota. However, in G. assimilis

(Duporte, 1920) and G. sigillatus (Narula, 1974) intrinsic muscles have been reported to be present in the flagellum. Since this feature is found only in certain Apterygotes, its presence in certain representatives of the Gryllidae would perhaps indicate a primitive character. In addition to these two species, antennal musculature has been recorded in Blatta, Gryllus and certain Thysanura (Imms, 1939), and in Termes by Basch (1865). However, Imms (1939) cast doubt on these reports and considers the muscles to be two prominent branches of the antennal nerve. This he confirms by using stained whole mounts examined under polarized light and also by serial sections and dissections. The absence of intrinsic muscles in the flagellum of A. domesticus confirms it to be of the annulated type, typical of Pterygote insects. One may conclude initially that the recorded presence of intrinsic muscles in the closely related species, G. assimilis (Duporte, 1920), may be due to confusion in interpretation and that the muscles may in fact be the two sub-branches of the antennal nerve. This explanation was in fact confirmed by Imms (1939) during his reinvestigation of the antenna of G. assimilis. However, further confusion occurred when intrinsic muscles in the pedicel and a few segments of the flagellum were recorded recently in G. sigillatus by Narula (1974). Narula (1974) considers that the presence of the muscles in G. sigillatus suggests an intermediate condition between the Collembola and Pterygota. This would indicate the primitive nature and possibly early ancestry of the Gryllidae. It is apparent that a detailed study of the antennal musculature throughout the group, in the type of detail displayed in the present study, needs to be undertaken before any conclusive statement can be made. To date, A. domesticus is the only representative of the family Gryllidae, studied in detail, that has been shown to demonstrate the Pterygote condition in respect of this character.

The mouthpart and associated appendages of A. domesticus are well supplied with sensilla of various types and functions. Thirteen different types of sensilla have been recognised by description and measurement of their external characteristics. By careful examination of their nervous innervation, it is often possible to suggest a function of a particular sensilla type, a subject which would need confirmation by physiological methods.

According to Slifer (1970) the classification of sensilla may be based on the thickness of the sensillar cuticle. However, in this work a scheme based on the shape of the sensillum is used. A similar scheme was adopted by Thomas (1965, 1966).

Here the mechanoreceptors on the mouthparts will be dealt with first. McIver (1975) explains the term mechanoreceptor in a broad sense, by defining mechanoreception as "the perception of mechanical distortion of the body caused by the external stimuli of touch, air or water-borne vibrations or due to the internal forces generated by activities of the muscles". The articulated sensory hairs, known as trichoid sensilla, are excited by the mechanical deformation of some part of the receptor (e.g. Dethier, 1963; McIver, 1975). Their role as proprioceptors occurs by their response to mechanical stresses set up in the cuticle. This subject has been fully discussed by Finlayson (1968). It can be concluded that of the trichoid sensilla (Types 1 - 5), Types 1, 2 and 4 sensilla in A. domesticus are mechanoreceptors and these are provided with a single neuron. Types 3 and 5 most probably play a part in mechanoreception since the number of neurons varies from 1 - 3 depending on their position. Often trichoid sensilla are grouped to form hair plates. In A. domesticus trichoid sensilla of Type 2 are sometimes grouped together into hair plates. These probably act as proprioceptors. The hair plates in P. americana have been studied by Pringle (1938c), Haskell (1959) and others. According to Pringle (1938c) the hairs of the hair plates are mechanical sense organs with a slow rate of adaptation, and in life the hairs are excited by the deformation of a fold of intersegmental membrane. The level of excitation varies with the position of the joint. The hair plate sensilla in S. gregaria are innervated by a single neuron and monitor the movement of one segment relative to the next (Blaney and Chapman, 1969a). The 'hair plates' on the vertex of Locusta and Schistocerca form cephalic airflow receptors which help in flight regulation (Guthrie, 1966; Gewecke, 1972). It has been demonstrated in A. domesticus that the hair plate sensilla are innervated by a single neuron.

Sensilla of Type 1 appear to have one neuron and certainly seem to be the same as the Type III of Blaney and Chapman (1969a). According to Haskell (1956a, b) the long setae present on the abdomen of British grasshoppers respond to vibrations of the substrate whilst others probably receive airborne vibrations. It is possible that in A. domesticus some of the long setae of Type 1 present on the mouthparts may respond to vibrations of the air.

In A. domesticus, as in other insects studied, it is evident that hairs with pores or openings in the setae are innervated by a single neuron. These may bear cuticular sculpturings such as grooves or spicules, whilst the sockets sometimes bear inward projecting ribs or diaphragms. It has been noticed that the height and the diameter of the socket, together with any projection of the socket, restrict the movement of the hairs and probably assist in its mechanoreceptive function. Bernays et al (1976) also report the presence of longitudinally grooved trichoid sensilla on the first instar nymph of S. gregaria. Here they are involved in the prenymphal ecdysis.

It has been reported that a number of sensilla with a presumed mechanoreceptive function have two dendrites.

Thomas (1971) reported that trichoid sensilla of Type 'a_1' were provided with two neurons instead of a single neuron found in sensilla from other location on the body. Bernays et al (1976) suggest that the double innervation may be a general property of mechanoreceptors although its significance is unknown. Sensilla of Types 3 and 5 in A. domesticus most probably act as chemoreceptors, although it is not precluded that they may also play some part in mechanoreception. The number of neurons varies from 1 - 4.

Campaniform sensilla which act as proprioceptors respond to strains in the cuticle (Pringle, 1938a, b). Albert et al (1976) suggest that campaniform sensilla monitor the degree of cuticular stress with changes in air pressure at various locations on the wing of Melanoplus sanguinipes, whilst Arnold (1974) found similar sensilla on the tarsi of cockroaches.

The campaniform sensilla are referred to as Type 6 in A. domesticus. They are innervated by a single neuron. The shape of such sensilla has been described by a number of authors as semispherical or semiellipsoidal (Ismail, 1962; McIndoo, 1929; Schneider and Kassling, 1956). This type of sensilla has been recorded on a variety of head structures in A. domesticus. On the pedicel of the antenna, where they are arranged in a definite row and at the joints of the labial and maxillary palp where they are found in small groups. Both their position and earlier work suggests their function is proprioception (Schneider, 1964; Pringle, 1938a, b and McIver, 1975).

It is interesting to note that Berlese (1909) first used the term campaniform to describe the whole class of sensilla previously known as dome, bell and cupola shaped structures. These have subsequently been described by a number of authors (McIndoo, 1920; Lees, 1942; Snodgrass, 1935; Dethier, 1963; Schmidt, 1973 and McIver, 1975). It has been noticed that the presence of a single neuron is typical of campaniform sensilla. Similar campaniform sensilla have been described from various regions of the exoskeleton of insects where compression occurs (Thurm, 1964, 1965; Stuart and Satir, 1968; Chevalier, 1969; Smith, 1969; Moran, Chapman and Ellis, 1971 and Quennedey, 1975). According to McIver and Siemicki (1975) the morphologically different campaniform sensilla on the palp of _A. stephensi_ are functionally distinct. Pringle (1961) suggests that oval sensilla are selectively sensitive to strains in a particular direction, whilst according to Gettrup (1973) the type of reaction to a given stimulus is determined by the degree of elevation of the cap.

Of the chemoreceptors, Type 7 are probably olfactory in function.

The Type 7 sensilla seem to be typical sensilla placodea. They appear to be thin, oval or elliptical plates of cuticle and are present mostly on the outer surfaces of the mouthparts. All of the Type 7 sensilla recorded in A. domesticus are innervated by a bipolar neuron with a very long dendrite. Only a single triangular shaped pore could be seen in the centre of the sensillum, although presumably pores are scattered over the entire surface but could not be seen at the resolution used. The presence of sensilla placodea has been demonstrated by a number of authors in a range of insects, e.g. Slifer and Sekhon (1961) have recorded numerous sensilla of this type on the antenna of Apis. Those on the antennae of Aphidoidea have been shown to consist of an outer perforated cuticular plate, separated from an inner plate by a space containing many fine dendritic branches (Slifer and Sekhon, 1963). Slifer (1970) and Lewis and Marshall (1970) have recently used the term sensory plaque for sensilla placodea when referring to similar structures on the antenna of the lanternfly, Pyrops. The sensilla placodea of A. domesticus have a small notch on the border of the depression are therefore comparable to those sensilla found on the flagellum, maxillary and labial palp of the caddisfly F. missa (Slifer and Sekhon, 1971). Lacher and Schneider (1963), Slifer and Sekhon (1961, 1964), all report their function to be olfactory.

Other chemoreceptors in A. domesticus are concerned with gustation. The sensilla are generally abundant on the mouthparts of insects but less so on the antennae. They may also be found on the tarsi (Richards and Davies, 1977).

There are a variety of types of contact chemoreceptor, e.g. sensilla trichoidea, basiconica and coeloconica. Typically insect contact receptor possess four or five neurons, whilst six have been recorded by Blaney and Chapman (1969a), although Dethier (1955) recorded only three in many Diptera. Both the mouthparts and the surface of the pre-oral food cavity is richly supplied with this type of chemoreceptor (Thomas, 1966; Chapman, 1966).

Trichoid sensilla of Type 3 present in _A. domesticus_ are likely to serve, at least in part, as gustatory sensilla. These are comparable to the Type 3 of Thomas (1966) and Type 2 of Blaney and Chapman (1969a). The Types 3 and 5 sensilla are present in an aggregated form at the tip of each palp. Their role in gustation is suggested by the 'palpation' which can be seen once in contact with the food. Similar sensilla have been recorded on the maxillary palps of Acrididae (Blaney and Chapman, 1969a) and also on the labella of Diptera (Adams and Forgash, 1966) where they mediate taste. Blaney and Chapman (1970) and Blaney, Chapman and Wilson (1973) showed that the terminal sensilla on the maxillary palps of _L. migratoria_ are important in food selection in the unstarved insect. However, it has also been reported in many insects that sensilla of Type 3 may have an olfactory function (Jefferson _et al_, 1970 and Myers and Brower, 1969). Le Berre _et al_ (1967) recognised two types in this situation, one with a blunt end and an opening and the other with a pointed end and no pore. The latter type presumably serve as mechanoreceptors. Blaney and Chapman (1969b) showed that the terminal sensilla on the maxillary palps of *Schistocerca* were chemoreceptors and similar sensilla were present in *Locusta* (Blaney *et al*, 1971). Haskell and Schoonhoven (1969) confirmed the chemoreceptive function of these terminal sensilla on the maxillary palp of *L. migratoria* by using electrophysiological techniques and showed that the sensilla respond to a wide range of chemicals from different chemical classes. Haskell and Mordue (1969) found that receptors on the palps in *Schistocerca* stimulated feeding whilst deterrents were picked up by receptors on the labrum. The importance of the palps in food selection is debatable. Dadd (1963) and Mulkern (1967) have shown that selection is only performed when the insect bites the plant. These observations were contradicted by William (1954) who suggested that selectivity is reduced by amputation of the palp. Recently many features of the structure and function of insect contact chemoreceptors has been clarified using electron microscopy (Slifer, 1970) and electrophysiology (Hodgson, 1968).

In *A. domesticus* the sensilla basiconica are represented by Types 8 and 9 sensilla present on the posterior surface of the clypeolabrum. These are comparable to the sensilla basiconica of Dethier (1955). They are thick peg like structures and respond to various chemical stimuli.

Dethier (1955) has shown that the intensity of the response varies according to the nature of the chemical stimulant. The importance of these sensilla in feeding has been demonstrated in Lepidopterous larvae by Schoonhoven (1969).

Less conspicuous sensilla are the Type 12 sensilla. These are pore canals in the mandibles and laciniae of *A. domesticus*. They appear open and are therefore probably contact chemoreceptors. They are innervated by a bipolar neuron. Similar pore canals have also been reported by Le Berre and Louveaux (1969) in the mandibles of the first instar larvae of *L. migratoria* and in other insects such as the wireworm, *Ctenicera destructor* (Brown), (Zacharuk, 1962). According to Le Berre *et al* (1969) the dendrites which infiltrate the tips of the mandibular teeth in the first instar of grasshopper, *L. migratoria* are also mechanoreceptors.

The Type II sensilla of *A. domesticus* found on the galea and paraglossa are comparable to the H type sensilla of Thomas (1965) in *Schistocerca*. They are conical in shape and have projections forming guards of variable length at the base of the socket. Thomas (1965) considers the function of these guards to be the restriction of movement of the seta to one plane. These sensilla were referred to as basiconic pegs in *G. domesticus* by Fudalewicz-Niemczyk and Rosciszewska (1974). It may be suggested that these function as chemoreceptors.

Type 13 sensilla of *A. domesticus* are comparable to the sensilla ampullacea or sensory flasks reported by a number of authors (Barbier, 1961; Fudalewicz-Niemczyk and Rosciszewska, 1974; Schenk, 1903; Richards, 1952; Kuwabara and Takenda, 1956; Slifer and Sekhon, 1961). These are innervated by a single neuron, as in *A. domesticus* where it may be suggested that they function as mechanoreceptors. McIver (1974) found sensilla ampullacea on the antenna of *A. stephensi* and *Aedes aegypti* (L.), these have an elliptical-shaped orifice opening into a flask-shaped chamber. However, these are innervated by three neurons and are thought to play a role of thermoreception.

This study of *A. domesticus* has also revealed the presence of multipolar stretch receptors on the various mouthparts. These are a specialised type of mechanoreceptor and form part of the proprioceptor sensory system. Similar multipolar cells with triangular cell bodies and a distinct nucleus have been studied by Wilczek (1967) in the blowfly *Phormia regina* Meigen. Peter (1961) considers them to play an important role in integrating information from the sense organs. Guthrie (1967) considers the multipolar stretch receptors to provide an independent source of information concerning gradual movement at a joint. The presence of stretch receptors has been given by a number of authors (Finlayson and Lowenstein, 1958; Guthrie, 1962).

The main contribution of the present work is to describe fully the types of sensilla and their distribution on the head appendages of *A. domesticus*. From this one is able to indicate their role in feeding. The next logical step should be to confirm some of these tentative suggestions by electrophysiological work.

SUMMARY

(1) The gross structure of the head capsule of A. domesticus has been described, together with the neck region or cervix.

(2) The internal skeleton of the head or tentorium is X- shaped with well developed anterior, posterior and dorsal arms.

(3) The structure of the head capsule and mouthparts has revealed several interesting features:

(i) On the epipharyngeal surface of the labrum there is a well developed intertorma in addition to the tormae. A well developed sclerotized bar strengthens and gives support to the anterior part of the head capsule.

(ii) The galea of the maxilla is two segmented and at its distal end is furnished with a well developed comb.

(iii) The lacinia of the maxilla at its distal end is provided with three cusps, two of which are well sclerotized.

(iv) The hypopharynx has a complex structure and bears pseudotracheae. In many respects its structure resembles the modified labium seen in Cyclorrhaphan Diptera.

(4) The muscles associated with the mouthparts and those responsible for the movement of the head have been carefully described. A total of

sixty eight muscles have been investigated and particular emphasis placed on the sites of origin and insertion of these muscles. The mode of action and probable function of the muscles has been described wherever possible.

(5) Particular features of interest in respect of the head musculature include:

(i) In the mandibles two extra extrinsic muscles, the hypopharyngeal adductor of the mandible (Muscle 8) and the tentorial adductor of the mandible (Muscle 7), are present in addition to the normal adductor and abductor of the mandibles (Muscles 5 and 6 respectively).

(ii) The origin of the retractor of the hypopharynx (Muscle 31) and the adductor of the labium (Muscle 22) on the occipital ridge differs from other Gryllidae.

(6) Thirteen different types of cuticular sensilla have been identified on the feeding appendages. The accurate distribution of these sensilla types in adult female crickets has been recorded and compared with that of the adult male.

(7) The density of sensilla on the different feeding appendages varies, the clypeolabrum, maxillary and labial palps have numerous sensilla whereas

the glossae are provided with a relatively small number of sense organs.

(8) A close similarity is evident between the maxillary palp and the labial palp in the types and distribution of sensilla.

(9) The development of the adult sensilla pattern was studied by examining the number and distribution of sensilla in the eleven nymphal instars. Since such a wide range of sensilla types are seen on the clypeolabrum, the developmental study concentrated on this structure. Although most types are present from an early instar their rate of increase varies considerably.

(10) Cuticular sculpturing is present on certain of the feeding appendages and microtrichia are present on the epipharyngeal surface of the labrum.

(11) A thorough study of the nervous innervation to the sensilla and muscles was undertaken. All the main nerves originating from the brain, suboesophageal ganglion and frontal connective have been traced.

(12) Each main nerve divides into many sub branches and the course of these to their site of innervation has also been traced.

(13) An attempt was made to relate the structural investigation to the feeding mechanism of the

insect. To record feeding in living insects various techniques including light microscope observation, ciné photography and videorecording were employed. The role of the various components could be suggested by collating the information obtained from each method.

(14) In the field it seems that A. domesticus is omnivorous, feeding on both hard food stuffs and fluids which it can imbibe by means of its specialised proboscis.

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REFERENCES

ABUSHAMA, F.T. 1968. Food-plant selection by *Poecilocerus hieroglyphicus* (Klug) (Acrididae: Pyrgomorphidae) and some of the receptors involved. *Proc. R. ent. Soc. Lond. (A)* *43*: 96-104.

ADAMS, J.R. & FORGASH, A.J. 1966. The location of the contact chemoreceptors of the stable fly, *Stomoxys calcitrans* (Diptera: Muscidae). *Ann. ent. Soc. Am.* *59*: 133-141.

ALBERT, P.J., ZACHARUK, R.Y. & WONG, L. 1976. Structure, innervation and distribution of sensilla on the wings of a grasshopper. *Can. J. Zool.* *54*: 1542-1553.

ALEXANDROWICZ, J.S. 1932. The innervation of the heart of the Crustacea. 1. Decapoda. *Q. Jl. microsc. Sci.* *75*: 181-249.

ALLEN, E.J. 1894. Studies on the nervous system of Crustacea. *Q. Jl. microsc. Sci.* *36*: 461-482.

ANDERSON, S.O. & WEIS-FOGH, T. 1964. Resilin. A rubber-like protein in arthropod cuticle. *Adv. Insect Physiol.* *2*: 1-66.

ARNOLD, J.W. 1974. Adaptive features on the tarsi of Cockroaches (Insecta: Dictyoptera). *Int. J. Insect. Morphol. & Embryol.* *3*: 317-334.

BARBER, S.B. 1960. Structure and properties of Limulus articular proprioceptors. *J. exp. Zool.* *143*: 283-321.

BARBIER, R.P. 1961. Contribution à l'étude de l'anatomie sensorinerveuse des insectes Trichopteres. *Ann. Sc. Natur. Zool.* *3*: 173-183.

BASCH, S. 1865. Untersuchungen uber das Skelett und die Muskeln des Kopfes von *Termes flavipes* Kollar. *Z. wiss. Zool.* *15*: 56-75.

BERLESE, A. 1909. *Gli Insetti*. Vol. 1, 1004 pp. Milan Soc. Editrice Libraria.

BERNAYS, E.A., COOK, A.G. & PADGHAM, D.E. 1976. A club-shaped hair found on the first instar nymphs of *Schistocerca gregaria*. *Physiol. Ent.* *1*: 3-13.

BIGELOW, R.S. 1954. Morphology of the face in the Hymenoptera.
Can. J. Zool. *32*: 378-392.

BLANEY, W.M. 1974. Electrophysiological responses of the terminal sensilla on the maxillary palps of *Locusta migratoria* (L.) to some electrolytes and non-electrolytes.
J. exp. Biol. *60*: 275-293.

BLANEY, W.M. 1975. Behavioural and electrophysiological studies of taste discrimination by the maxillary palps of larvae of *Locusta migratoria* (L.).
J. exp. Biol. *62* (3): 555-569.

BLANEY, W.M. & CHAPMAN, R.F. 1969a. The anatomy and histology of the maxillary palp of *Schistocerca gregaria* (Orthoptera: Acrididae).
J. Zool. Lond. *157*: 509-535.

BLANEY, W.M. & CHAPMAN, R.F. 1969b. The fine structure of the terminal sensilla on the maxillary palps of *Schistocerca gregaria* (Forskal) (Orthoptera: Acrididae).
Z. Zellforsch. mikrosk. Anat. *99*: 74-97.

BLANEY, W.M. & CHAPMAN, R.F. 1970. The functions of the maxillary palps of Acrididae (Orthoptera).
Entomologia exp. appl. *13*: 363-376.

BLANEY, W.M., CHAPMAN, R.F. & COOK, A.G. 1971. The Structure of the terminal sensilla on the Maxillary Palps of *Locusta migratoria* (L.), and changes associated with moulting.
Z. Zellforsch. *121*: 46-48.

BLANEY, W.M., CHAPMAN, R.F. & WILSON, A. 1973. The pattern of feeding of *Locusta migratoria* (L.) (Orthoptera: Acrididae).
Acrida. *2*: 119-137.

BLANEY, W.M. & DUCKETT, A.M. 1975. The significance of palpation by the maxillary palps of *Locusta migratoria* (L.). An electrophysiological and behavioural study.
J. exp. Biol. *63*: 701-712.

BLISS, D.E. & WELSH, J.H. 1952. The neurosecretory system of brachyuran crustacea.
Biol. Bull. *103*: 157-169.

BOO, K.S. & McIVER, S.B. 1976. Fine structure of surface and sunken grooved pegs on the antenna of female *Anopheles stephensi* (Diptera: Culicidae. *Can. J. Zool*. *54*: 235-244.

BROWN, D.S. 1961. The morphology and functioning of the mouthparts *Chloeon dipterum* L. and *Baetis rhodani* Pictet (Insecta: Ephemeroptera). *Proc. Zool. Soc. Lond*. *136*: 147-176.

BROWN, V.K. 1973. Collection and culture of field-dwelling Cockroaches for experimental purposes. *The Entomologist* *106*: 114-117.

CHAPMAN, K.M. 1965. Campaniform sensilla on the tactile spines of the legs of the cockroach. *J. exp. Biol*. *42*: 191-203.

CHAPMAN, R.F. 1966. The mouthparts of *Xenocheila zarudnyi* (Orthoptera: Acrididae). *J. Zool. Lond*. *148*: 277-288.

CHAPMAN, R.F. 1969. *The insects: Structure and Function*. English Univ. Press, London. 818pp.

CHAPMAN, R.F. 1975. *The insects: Structure and Function*. The English Univ. Press, Ltd. 819pp.

CHEN NING-SHENG, 1964. The olfactory response of *Locusta migratoria manilensis* Meyer and the function of its antennae. *Acta Biol. exp. Sin*. *9*: 27-37.

CHEVALIER, R.L. 1969. The fine structure of campaniform sensilla on the halteres of *Drosophila melanogaster*. *J. Morph*. *128*: 443-464.

COOK, A.G. 1976. Structure and function of the clypeo-labrum of *Locusta migratoria* with particular reference to the sensilla. *Ph. D. Thesis, University of London*.

COOK, E.F. 1944. The morphology and musculature of labrum and clypeus of Insects. *Microent*. *9*: 1-35.

CRAMPTON, G.C. 1917. The nature of the veracervix or Neck Region in Insects. *Ann. ent. Soc. Am*. *10*: 187-197.

CRAMPTON, G.C. 1930. The head structures of the Orthopteron *Stenopelmatus* - a contribution to the study of the external anatomy of *Stenopelmatus*. *Pan-Pacif. Ent.* *6*: 97-110.

CRICHTON, M.I. 1957. The structure and function of the mouthparts of adult caddis flies (Trichoptera). *Phil. Trans. R. Soc. Ser. B.* *241*: 45-91.

DADD, R.H. 1963. Feeding behaviour and nutrition in grasshoppers and locusts. *Adv. Insect Physiol.* *1*: 47-109.

DETHIER, V.G. 1955. The Physiology and histology of the Contact chemoreceptors of the Blowfly. *Q. Rev. Biol.* *30*: 348-371.

DETHIER, V.G. 1963. *The Physiology of Insect Senses.* Methuen and Co., Ltd., London. 266pp.

DETHIER, V.G. 1966. Feeding behaviour. *In*: Insect Behaviour. Ed. Haskell, P.T. *Symp. R. ent. Soc. Lond.* *3*: 46-58

DUPORTE, E.M. 1920. The muscular system of *Gryllus assimilis* Fabr. (= *Pennsylvanicus* *Burm.*) *Ann. ent. Soc. Am.* *13*: 16-52.

DUPORTE, E.M. 1957. The comparative morphology of the insect head. *A. Rev. Ent.* *2*: 55-70.

DUPORTE, E.M. 1959. *Manual of Insect Morphology.* Reinhold Pub. Corp. N.Y. 224pp.

DUPORTE, E.M. 1965. Notes on the morphology of the facial region in insects with special reference to that of larval Lepidoptera. *Proc. R. ent. Soc. Lond. (A)* *40*: 73-76.

EIDMANN, H. 1925. Vergleichend-anatomische Studien über die Pharynx muskulatur der Insekten. *Zool. Anz.* *62*: 49-64.

EVANS, M.E.G. 1964. A comparative account of the feeding methods of the beetles *Nebria* *brevicollis* (F) (Carabidae) and *Philonthus* *decorus* (Grav.) (Staphylinidae). *Trans. R. Soc. Edinb.* LXVI: 91-109.

FINLAYSON, L.H. 1968. Proprioceptors in the invertebrates. *Symp. zool. Soc. Lond.* *23*: 217-249.

FINLAYSON, L.H. & LOWENSTEIN, O. 1958. The structure and function of abdominal stretch receptors in insects. *Proc. R. Soc. (B)*. *148*: 433-449.

FRINGS, H. & FRINGS, M. 1949. The loci of contact chemoreceptors in insects. *Am. Midl. Nat.* *41*: 602-658.

FRYER, G. 1964. Studies on the functional morphology and feeding mechanism of *Monodella argentarii* Stella (Crustacea: Thermobaenacea). *Trans. R. Soc. Edinb.* *66*(4): 51-90.

FUDALEWICZ-NIEMCZYK, W. & ROSCISZEWSKA, M. 1973. The peripheric nervous system of the larva of *Gryllus domesticus* (Orthoptera) Part I. Antenna. *Acta Biol. Cracov. Ser. Zool.* *16*: 209-217.

FUDALEWICZ-NIEMCZYK, W. & ROSCISZEWSKA, M. 1974. The peripheral nervous system of the larva of *Gryllus domesticus* L. (Orthoptera). Part II Mouthparts. *Acta. Biol. Cracov. Ser. Zool.* *17*: 19-39.

GANGWERE, S.K. 1960. The use of the Mouthparts of Orthoptera during feeding. *Ent. News* *71*: 193-206.

GAPUD, V.P. 1968. The external morphology of the head and mouthparts of some Philippine Orthoptera. *Philipp. Entomol.* *1*: 11-32.

GETTRUP, E. 1973. Stimulus transmission in cuticular mechanoreceptors. *Naturwissenschaften* *60*: 52-53.

GEWECKE, M. 1972. Antennen und Stirnscheitelhaare von *Locusta migratoria* L. als Luftstromüngs-Sinnesorgane bei der Flugstencrung. *J. comp. Physiol.* *80*: 57-94.

GHOURI, A.S.K. 1957. The effect of natural grains on the development of the house cricket, *Acheta domesticus* (L.) (Gryllidae: Orthoptera). *Proc. Pakist. Sc. Conf. IX Lahore* p.52.

GHOURI, A.S.K. & McFARLANE, J.E. 1958. Observation on the development of crickets.
Can. Ent. 90: 158-165.

GOODHUE, D. 1963. Feeding stimulants required by a polyphagous insect, Schistocerca gregaria.
Nature, Lond. 197: ~~405-406~~

GOODHUE, R.D. 1962. The effects of stomach poisons on the desert locust.
Ph. D. Thesis, University of London.

GUTHRIE, D.M. 1962. Control of the ventral diaphragm in an insect.
Nature, Lond. 196: 1010-1012.

GUTHRIE, D.M. 1966. The function and fine structure of the cephalic airflow receptor in Schistocerca gregaria.
J. Cell. Sci. 1: 463-470.

GUTHRIE, D.M. 1967. Multipolar stretch receptors and the insect leg reflex.
J. Insect Physiol. 13: 1637-1644.

HAMON, P.M. 1961. Contribution à l'étude de la morphogenese sensori-nerveuse des Dytiscidae (Insectes: Coleopteres).
Ann. Sc. Natur. Zool. 3: 153-171.

HARRIS, J.E. & PETERS, A. 1953. Experiments on vital staining with Methylene Blue.
Q. Jl. micrsc. Sci. 94: 113-124.

HASKELL, P.T. 1956a. Hearing in certain Orthoptera. I Physiology of sound receptors.
J. exp. Biol. 33: 756-766.

HASKELL, P.T. 1956b. Hearing in certain Orthoptera. II The nature of the response of certain receptors to natural and imitation stridulation.
J. exp. Biol. 33: 767-776.

HASKELL, P.T. 1959. Function of certain prothoracic hair receptors in the desert locust.
Nature, Lond. 183: 1107.

HASKELL, P.T. & MORDUE, A.J. 1969. The role of mouthpart receptors in the feeding behaviour of Schistocerca gregaria.
Entomologia exp. appl. 12: 591-610.

HASKELL, P.T. & SCHOONHOVEN, L.M. 1969. The function of certain mouthpart receptors in relation to feeding in Schistocerca gregaria and Locusta migratoria migratorioides.
Entomologia exp. appl. 12: 423-440.

HODGSON, E.S. 1968. Taste receptors of arthropods. In: Invertebrate Receptors. eds.,J.D. CARATHY AND G.E. NEWELL.
Symp. zool. Soc. Lond. 23: 269-277.

HORRIDG, G.A. 1959. Analysis of the rapid responses of Nereis and Harmothoe (Annelida).
Proc. R. Soc. (B) 150: 245-262.

HUDSON, G.B. 1945. A study of the tentorium in some orthopteroid Hexapoda.
J. ent. Soc. sth. Afr. 8: 71-90.

IMMS, A.D. 1930. A general textbook of entomology.
2nd ed. Methuen & Co. Ltd. London. 703pp.

IMMS, A.D. 1937. Recent advances in Entomology.
2nd ed. J. & A. Churchill Ltd. London. 431pp.

IMMS, A.D. 1939. On the antennal musculature in Insects and other Arthropods.
Q. Jl. micros. Sci. 81: 273-320.

IMMS, A.D. 1940. On growth processes in the antennae of Insects.
Q. Jl. micros. Sci. 81: 585-593.

IMMS, A.D. 1951. A general textbook of entomology.
8th ed. Methuen & Co.Ltd. London. 727pp.

ISELY, F.B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers.
Ann. ent. Soc. Am. 37: 47-67.

ISMAIL, I.A.H. 1962. Sense organs in the antennae of Anopheles maculipennis atroparvus (V. Thiel) and their possible function in relation to the attraction of female mosquito to man.
Acta. Trop. 19: 1-58.

JEFFERSON, R.N., RUBIN, R.E., McFARLAND, S.U. & SHOREY, H.H. 1970. Sex pheromones of noctuid moths. XXII. The external morphology of the antennae of Trichoplusia ni, Heliothis zea, Prodenia ornithogalli and Spodoptera exigua.
Ann. ent. Soc. Am. 63: 1227-1238.

KAISSLING, K.E. 1971. Insect Olfaction. In: *Handbook of sensory Physiology. Volume IV. Chemical Senses. Part I Olfaction.* ed. Beidler, L.M. p.351-431. Springer-verlag. N.Y.

KHATTAR, N. 1959. Inter-Relationship of *Schizodactylus monstrosus* Don. (Orthoptera). *Sci. Cult.* *25*: 275-276.

KHATTAR, N. 1964. Cephalic Musculature of *Schizodactylus monstrosus* Don. (Orthoptera). *J. Morph.* *115*: 121-134.

KNYAZEVA, N.I., FUDALEWICZ-NIEMCZYK, W. & ROSCISZEWSKA, M. 1975. Proprioreceptors of the house-cricket (*Gryllus domesticus* L.) (Orthoptera). *Acta Biol. Cracov. Ser. Zool.* *28*: 33-44.

KUWABARA, W. & TAKEDA, K. 1956. On the hygroreceptor of the honeybee *Apis mellifica*. *Physiol. Ecol. Kyushu Univ.* *7*: 1-6.

LACHER, V. & SCHNEIDER, D. 1963. Electrophysiologischer Nachweis der Riechfunktion von porenplatten (Sensilla placodea) auf den Antennen der Drohne under der Arbeitsbiene (*Apis mellifica* L.). *Z. Vergl. Physiol.* *47*: 274-278.

LARIMER, J.L. & ASHBY, E.A. 1964. Reduced Methylene Blue as a stain for crustacean nerves. *Stain Technol.* *39*: 369-371.

LATIF, A., HAQ, K.A. & ASGHAR, M.A. 1957. Bionomics of *Acheta domesticus* (L.). *Proc. Pakist. Sci. Conf. IX Lahore*. pp.30-31.

LE BERRE, J.R. & LOUVEAUX, A. 1969. Equipment sensoriel des mandibules de la larve du premier stade de *Locusta migratoria* L. *C.R. Acad. Sci. (Paris)*. *268*: 2907-2910.

LE BERRE, J.R., SINOIR, Y. & BOULAY, C. 1967. Etude de l'equipement sensoriel de l'article distal des palpes chez la larve de *Locusta migratoria migratorioides* (R. et F.). *C.R. Acad. Sci. (Paris)*. *265*: 1717-1720.

LEES, A.D. 1942. Homology of the campaniform organ on the wing of *Drosophila melanogaster*. *Nature, Lond.* *150*: 375.

LEWIS, C.T. & MARSHALL, A.T. 1970. The ultrastructure of the sensory plaque organs of the antennae of the Chinese lantern fly, Pyrops candelaria L., (Hem., Hom., Fulgoridae). Tissue & Cell. 2: 375-385.

LIU, Y.S. & LEO, P.L. 1960. Histological studies on the sense organs and the appendages of the oriental migratory locust, Locusta migratoria manilensis Meyen. Acta ent. sin. 10: 243-272.

LOUVEAUX, Par.A. 1972. Equipement sensoriel et systeme nerveux peripherique des pieces buccales de Locusta migratoria L. Insectes Soc. 19: 359-368.

LOUVEAUX, Par.A. 1975. Etude de l'innervation sensorielle de l'hypopharynx de larves de Locusta migratoria migratorioides R. et F. (Orthoptere, Acrididae). Insectes Soc. 22: 3-12.

MANTON, S.M. 1960. Concerning Head Development in the arthropods. Biol. Rev. 35: 265-282.

MANTON, S.M. 1964. Mandibular mechanism and the Evolution of Arthropods. Phil. Trans. R. Soc. Ser. B. 247: 1-183.

MARSHALL, W.S. 1947. The labral sense organs of the red-legged grasshopper, Melanoplus femur-rubrum (De Geer). Trans. Wis. Acad. Sci. Arts. Lett. 37: 137-148.

MATSUDA, R. 1965. Evolution of the head musculature in Insects. Proc. 12th Int. Congr. Ent. London. pp.141.

McFARLANE, J.E. 1953. The morphology of the chordotonal organs of the antenna, mouthparts and legs of the lesser migratory grasshopper, Melanoplus mexicanus mexicanus (Saussure). Can. Ent. 85: 81-103.

McINDOO, N.E. 1920. The olfactory sense of Orthoptera. J. Comp. Neurol. 31: 405-427.

McINDOO, N.E. 1929. Tropism and sense organs of Lepidoptera.
Smithson. misc. Collns. *81*(10): 1-59.

McIVER, S.B. 1974. Fine structure of antennal grooved pegs of the mosquito, *Aedes aegypti*.
Cell Tissue Res. *153*: 327-337.

McIVER, S.B. 1975. Structure of cuticular mechanoreceptors of arthropods.
A. Rev. Ent. *20*: 381-397.

McIVER, S. & SIEMICKI, R. 1975. Campaniform sensilla on the palps of *Anopheles stephensi* Liston (Diptera: Culicidae).
Int. J. Insect. Morphol. & Embryol. *4*: 127-130.

MISRA, S.D. 1946. Studies on the somatic musculature of the desert locust, *Schistocerca gregaria* (Forskal). Part I. The head.
Indian J. Ent. *7*: 103-138.

MORAN, D.T., CHAPMAN, K.M. & ELLIS, R.A. 1971. The fine structure of cockroach campaniform sensilla.
J. Cell Biol. *48*: 155-173.

MORDUE, A.J. 1975. Studies on the role of mouthpart and antennal receptor of *Schistocerca gregaria* (Forskal).
Ph. D. Thesis, University of London.

MOULINS, P.M. 1971. La cavite preorale de *Blabera craniifer* Burm. (Insecte; Dictyoptere) et son innervation: Etude anatomo-histologique de l'epipharynx et l'hypopharynx.
Zool. Jb. (Anat.) Bd. *88*: 527-586.

MULKERN, G.B. 1967. Food selection by grasshoppers.
A. Rev. Ent. *12*: 59-78.

MYERS, J. & BROWER, L.P. 1969. A behavioural analysis of the courtship pheromone receptors of the queen butterfly, *Danaus gilippus berenice*.
J. Insect Physiol. *15*: 2117-2130.

NABOKOV, V. 1945. Notes on Neotropical Plebejnae (Lycaenidae, Lepidoptera).
Psyche Camb. Mass. *52*: 1-61.

NARULA, J.S. 1968. Studies on the skeleton of the Indian House cricket *Gryllodes sigillatus* (Walker) (Gryllidae: Orthoptera) I. The sclerites of the head capsule and head appendages. *Bull. ent. Soc. India*. *9*: 134-146.

NARULA, J.S. 1974. The musculature of the Indian house cricket *Gryllodes sigillatus* (Walker) (Orth., Gryllidae). I. The Head. *Entomologist's mon. Mag*. *110*: 133-142.

NEI, T. & FUJIKAWA, S. 1977. Freeze-drying process of biological specimens observed with a scanning electron microscope. *J. Microsc*. *3*: 137-142.

OSBORNE, M.P. 1964. Sensory nerve terminations in the epidermis of the blowfly larva. *Nature, Lond*. *201*: 526.

PANTIN, C.F.A. 1946. *Notes on microscopical technique for zoologists*. Cambridge Univ. Press, Cambridge. 75pp.

PETERS. W. 1961. Die sogenannten Fuss-stummel-sinnesorgane der Larven von *Calliphora erythrocephala* Mg. (Diptera). *Zool. Jb. (Anat*.). *79*: 339-346.

PFADT, R.E. 1949. Food plants as factors in the ecology of the lesser migratory grasshopper *Melanoplus mexicanus* (Sauss.). *Bull. Wyo. agric. Exp. Sta*. no 290: 51pp.

POPHAM, E.J. 1961. The functional morphology of the mouthparts of the cockroach *Periplaneta americana* L. *The Entomologist* *94*: 185-192.

PRINGLE, J.W.S. 1938a. Proprioception in Insects. I. A new type of mechanical receptor from the palps of the cockroach. *J. exp. Biol*. *15*: 101-113.

PRINGLE, J.W.S. 1938b. Proprioception in Insects. II. The action of the campaniform sensilla on the legs. *J. exp. Biol*. *15*: 114-131.

PRINGLE, J.W.S. 1938c. Proprioception in Insects. III. The function of the hair sensilla at the joints. J. exp. Biol. 15: 467-473.

PRINGLE, J.W.S. 1961. Proprioception in arthropods. In: The Cell and the Organism. eds. RAMSAY, J.A. and WIGGLESWORTH, V.B. 256-282. Cambridge Univ. Press, Cambridge, England.

QUENNEDEY, A. 1975. The labrum of Schedorhinotermes minor soldier (Isoptera: Rhinotermitidae). Morphology, Innervation and Fine-Structure. Cell Tiss. Res. 160: 81-98.

RAGGE, D.R. 1965. Grasshopper, Crickets and Cockroaches of the British Isles. Frederick Warne & Co.Ltd., London. 299pp.

RICHARDS, A.G. 1952. Studies on arthropod cuticle. VIII. The antennal cuticle of Honeybees with particular reference to the sense plates. Biol. Bull. 103: 201-225.

RICHARDS, O.W. & DAVIES, R.G. 1977. Imm's general textbook of entomology. Volume I. Chapman & Hall, London. 418pp.

RIETSCHEL, P. 1953a. Der Hypopharynx von Gryllus und anderen Gryllinae, ein dem Fliegenrüssel analoges Organ. Z. Morph. Ökol. Tiere. 41: 386-410

RIETSCHEL, P. 1953b. Unsere Grillen haben einen Tupfrüssel. Umschau Wissenchaft Technik. 23: 720-721.

RUMMEL, H. 1963. Einige biometrische Untersuchungen zum Metamorphosegeschehen bei Acheta domesticus L. (Orthoptera: Saltatoria). Dt. ent. Z. 10: 261-314.

SCHENK, O. 1903. Die antennalen Hautsinnesorgane einiger Lepidopteren und Hymenopteren mit besonderer Berücksichtigung der sexuellen Unterschiede. Zool. Jb. Abt. Anat. Ontog. Tiere 17: 573-616.

SCHMIDT, K. 1973. Vergleichende morphologische Untersuchungen an Mechanorezeptoren der Insekten. Verh. dt. Zool. Ges. 66: 15-25.

SCHNEIDER, D. 1964. Insect Antennae. *A. Rev. Ent.* 9: 103-122.

SCHNEIDER, D. & KAISSLING, K.E. 1956. Der Bau der Antenne des Seidenspinners *Bombyx mori* L. j. Architektur und Bewegungsapparat der Antenne sowie Struktur der Cuticula. *Zool. Jb. Abt. Anat. Ontog. Tiere* 75: 287-310.

SCHNEIDER, D. & STEINBRECHT, R.A. 1968. Checklist of insect olfactory sensilla. *Symp. zool. Soc. Lond.* 23: 279-297.

SCHOONHOVEN, L.M. 1969. Gustation and foodplant-selection in some Lepidopterous larvae. *Entomologia exp. appl.* 12: 555-564.

SINOIR, Y. 1969. Le role des palpes et du labre dans le comportement de prise de nourriture chez la larve du criquet migrateur. *Annls. Nutr. Aliment.* 23: 167-194.

SINOIR, Y., BOULAY, C. & LE BERRE, J.R. 1968. Etude de l'equipement sensoriel du labre chez la larve de *Locusta migratoria migratorioides* (F. et R.). *C.R. Acad. Sci. (Paris)* 266: 1505-1507.

SLIFER, E. 1936. The scoloparia of *Melanoplus differentialis* (Orthoptera: Acrididae). *Ent. News* 47: 174-180.

SLIFER, E.H. 1954. The permeability of the sensory pegs on the antennae of the grasshopper (Orthoptera: Acrididae). *Biol. Bull.* 106: 122-128.

SLIFER, E.H. 1955. The distribution of permeable sensory pegs on the body of the grasshopper (Orthoptera: Acrididae). *Ent. News* 66: 1-5.

SLIFER, E.H. 1956. Permeable spots on the cuticle of the thin walled pegs on the antenna of the grasshopper. *Science, N.Y.* 124: 1203.

SLIFER, E.H. 1961. The fine structure of insect sense organs. *Int. Rev. Cytol.* 11: 125-159.

SLIFER, E.H. 1970. The structure of arthropod chemoreceptors. *A. Rev. Ent.* *15*: 121-142.

SLIFER, E.H., PRESTAGE, J.J. & BEAMS, H.W. 1957. The fine structure of the long basiconic sensory pegs of the grasshopper (Orthoptera: Acrididae) with special reference to those on the antenna. *J. Morph.* *101*: 357-397.

SLIFER, E.H. & SEKHON, S.S. 1961. Fine structures of the sense organs on the antennal flagellum of the honey bee, *Apis mellifera* (Linnaeus). *J. Morph.* *109*: 351-381.

SLIFER, E.H. & SEKHON, S.S. 1963. Sense organs on the antennal flagellum of the small milkweed bug, *Lygaeus Kalmii* Stal (Hemiptera: Lygaeidae). *J. Morph.* *112*: 165-191.

SLIFER, E.H. & SEKHON, S.S. 1964. Fine structure of the thin walled sensory pegs on the antenna of a beetle, *Popilius disjunctus* (Coleoptera: Passalidae). *Ann. ent. Soc. Am.* *57*: 541-548.

SLIFER, E.H. & SEKHON, S.S. 1971. Structures on the antennal flagellum of a caddisfly, *Frenesia missa* (Trichoptera: Limnephilidae). *J. Morph.* *135*: 373-388.

SMITH, D.S. 1969. The fine structure of haltere sensilla in the blowfly, *Calliphora erythrocephala* (Meig.), with scanning electron-microscopic observations on the haltere surface. *Tissue & Cell* *1*: 443-484.

SNODGRASS, R.E. 1928. Morphology and evolution of the insect head and its appendages. *Smithson. misc. Collns.* *81*(3): 1-158.

SNODGRASS, R.E. 1935. *Principles of Insect Morphology*. McGraw Hill, New York. 667pp.

SNODGRASS, R.E. 1958. The Insect tentorium and its antecedent. *Proc. 10th Int. Cong. Ent. Montreal* *1*: 487.

SNODGRASS, R.E. 1960. Facts and Theories concerning the insect head. *Smithson. Misc. Collns.* **142**(1): 1-61.

SNODGRASS, R.E. 1962. Suture or Sulcus? *Proc. ent. Soc. Wash.* **64**: 222-223.

STARK, M.J., SMALLEY, K.N. & ROWE, E.C. 1969. Methylene Blue staining of Axons in the ventral nerve cord of insects. *Stain. Technol.* **44**: 97-102.

STORCH, R.H. 1968. The adult cervicothoracic musculature of the cockroach *Nauphoeta cinera* (Olivier). *J. Morph.* **126**: 107-122.

STUART, A.M. & SATIR, P. 1968. Morphological and functional aspects of an insect epidermal gland. *J. Cell Biol.* **36**: 527-549.

THAKARE, V.K. 1961. Skeleto-muscular mechanism of the head in *G. bimaculatus*. *Bull. Zool. Soc. Coll. Nagpur.* **4**: 1-25.

THOMAS, J.G. 1965. The abdomen of the female locust (*Schistocerca gregaria* Forskal) with special reference to the sense organs. *Anti-Locust Bull.* No. **42**: 1-20.

THOMAS, J.G. 1966. The sense organs on the mouthparts of the desert locust (*Schistocerca gregaria*). *J. Zool. (Lond.)* **148**: 420-448.

THOMAS, J.G. 1971. The integument and sensilla of the pregenital abdomen of the Desert locust (*Schistocerca gregaria*) (Orthoptera: Acrididae). J. Zool. (Lond.) **164**: 335-351.

THURM, U. 1964. Mechanoreceptors in the cuticle of the honey bee. Fine structure and stimulus mechanism. *Science* **145**: 1063-1065.

THURM, U. 1965. An insect mechanoreceptor. Part I. Fine structure and adequate stimulus. *Cold Spring Harb. Symp. quant.Biol.* **30**: 75-82.

UVAROV, B. 1977. *Grasshoppers and Locusts.* Centre for overseas pest Research Publication (London). Vol. 2. 613pp.

VISHNOI, H.S. 1962. Musculature of a common Indian termite, Odontotermes obesus (Rambur) (Isoptera, Termitida). I. Cephalic musculature. Bull. Ent. Loyola Coll. Madras 3: 13-30.

VOSS, F. 1905. Ueber den Thorax von Gryllus domesticus. II, Die Muskulatur. Z. wiss. Zool. 78: 355-521.

WALKER, E.M. 1932. Prognathism and hypognathism in insects. Can. Ent. 64: 223-229.

WALKER, E.M. 1933. On the anatomy of Grylloblatta campodeiformis Walker. II. Comparisons of the head with those of other orthopteroid insects. Ann. ent. Soc. Am. 26: 309-344.

WILCZEK, M. 1967. The distribution and neuro-anatomy of the labellar sense organs of the blowfly, Phormia regina Meigen. J. Morph. 122: 175-201.

WILLIAMS, L.H. 1954. The feeding habits and food preference of Acrididae and factors which determine them. Trans. R. ent. Soc. Lond. 105: 423-454.

YUASA, H. 1920. The anatomy of the head and mouth-parts of orthoptera and Euplexoptera. J. Morph. 33: 251-307.

ZACHARUK, R.Y. 1962. Sense organs of the head of larvae of some Elateridae (Coleoptera): their distribution, structure and innervation. J. Morph. 111: 1-33.

ZAWARZIN, A. 1912. Histologische Studien über Insekten. II. Das sensible Nervensystem der Aeschna Larve. Z. wiss. Zool. 100: 245-286.