

THE FOOD, FEEDING MECHANISM AND ECOLOGY OF
THE CORIXIDAE (HEMIPTERA-HETEROPTERA),
WITH SPECIAL REFERENCE TO LEICESTERSHIRE.

Being a thesis submitted for the degree of Ph.D.
in the Faculty of Science.

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CONTENTS

Plate; <u>Corixa punctata</u>	1
1. Introduction	2
2. Observations and feeding experiments with aquatic Heteroptera.....	3
2.1 Introduction	
2.2 Method for observing corixids in the laboratory.	4
2.21 Distribution of the air bubble.....	4
2.22 Cleaning.....	5
2.23 Reproductive behaviour.....	6
2.24 Feeding in the Corixinae.....	6
2.25 Feeding in <u>Cymatia</u>	9
2.3 Feeding experiments with corixids and other water bugs.....	9
2.31 Feeding of <u>Notonecta maculata</u> (Notonectidae) and <u>Corixa punctata</u> (Corixidae) on adult <u>Drosophila</u> (Diptera)	10
2.32 Behaviour of the rostrum and stylets during feeding.....	11
2.33 Examination of gut contents.....	14
3. External anatomy of the head and forelimb.....	16
3.1 Introduction	
3.2 Material and method.....	16

3.3	A general description of the corixid head and forelimb.....	18
3.4	Description of specific corixid heads and forelimbs.....	20
3.41	<u>Diaprepocoris zealandiae</u>	21
3.42	<u>D. barycephala</u>	23
3.43	<u>Stenocorixa protrusa</u>	24
3.44	<u>Cymatia bonsdorffi</u>	25
3.45	<u>C. coleoptrata</u>	27
3.46	<u>Neocorixa snowi</u>	27
3.47	<u>Corixa punctata</u>	29
3.48	<u>Sigara falleni</u>	31
3.491	<u>S. dorsalis</u>	33
3.492	<u>S. nigrolineata</u>	34
3.493	<u>S. lateralis</u>	35
3.494	<u>Arctocorixa^s germari</u>	35
3.495	<u>Glaenocoris propinqua</u>	36
3.496	<u>Micronecta poweri</u>	37
3.497	<u>Tenagobia selecta</u>	38
3.5	Corixid ny ^m phs.....	39
3.6	<u>Notonecta glauca</u>	39
3.71	Structures associated with the air bubble....	40
3.72	" " " cleaning.....	41
3.73	" " " reproduction.....	43
3.74	" " " feeding.....	46

3.75	Other structures.....	51
3.76	<u>Notonecta</u>	53
Table 3.1.....		54
Figures 3.1-21.....		55
4.	The internal anatomy of the head.....	97
4.1	Introduction	
4.2	Materials and methods.....	97
4.3	Stylets.....	99
4.4	Food pump and other structures of the head.....	103
4.41	<u>Corixa punctata</u> and <u>Sigara falleni</u>	105
4.42	^{ep} <u>Diaprocorys zealandiae</u>	112
4.43	<u>Micronecta poweri</u>	114
4.44	<u>Cymatia bonndorffi</u>	115
4.45	<u>Stenocorixa protrusa</u>	117
4.46	<u>Notonecta glauca</u>	117
4.5	Structure and function.....	118
4.51	Stylets.....	119
4.52	Labium.....	122
4.53	Junction of stylets and food pump.....	123
4.54	Food pump.....	123
4.55	Glands.....	128
4.6	Discussion of the variation in the food pump of the Corixidae.....	129
Tables 4.1.....		132
Figures 4.1-15.....		133

5.	The corixid habitat in Leicestershire.....	163
5.1	Introduction.	
5.2	The fresh water habitat of Leicestershire.....	163
5.3	Changes within ponds.....	165
5.4	Temperature fluctuations within ponds.....	166
	Tables 5.1-4.....	172
	Figures 5.1-7.....	175
6.	The ecology of Leic ^e stershire Corixidae.....	189
6.1	Introduction.	
6.2	Distribution of the Corixidae.....	189
6.3	Life cycle.....	192
6.31	Sex ratio.....	193
6.32	Ovarian development.....	193
6.33	Temperature and embryonic development.....	196
6.34	Flight polymorphism and teneral development.	197
6.35	Migration.....	198
6.4	The effect of Hydracarina on corixids.....	199
	Tables 6.1-10.....	202
7.	Discussion.....	212
8.	Summary.....	223
	Acknowledgements.....	228
	Abbreviations.....	230
	Appendix; the construction and subs ^e quent history of pond at Normanton House Farm, Leicestershire.....	231
	References.....	240



Plate 1 , Corixa punctata: top, female; bottom, male.

SECTION 1

Introduction

The Corixidae are a world-wide family and one of the most successful groups of aquatic Heteroptera in terms of the numbers of species, the range of habitats and the large populations which are found. All members of the family have a characteristic head and forelimb, which are highly modified (plate 1.). These modifications are believed to be adaptations for detritus feeding (Hungerford 1919, Griffith 1945, Sutton 1951, and Benwitz 1956a), though animal food remains an essential part of their diet (Zwart 1965).

In the British Isles, the Corixidae are represented by thirty-three species with twenty-eight species in the subfamily Corixinae. The Corixinae species are very similar morphologically, particularly those parts connected with feeding (Sutton 1951 and Benwitz 1956a), but each species has a characteristic range of habitats (Macan 1965). These ranges overlap so that a number of species of this subfamily frequently occur together in the same habitat, whilst other species are never found together (Macan 1954). On the 'competitive exclusion principle' (Hardin 1960) which states that if two non-interbreeding populations, A and B, occupy the same ecological niche, the same geographical territory and with population A multiplying faster than population B, then ultimately A will completely displace B. Mayr (1963 page 68) points out, however, that 'two species are rarely as similar as genotypes of a single species' and 'to avoid such fatal competition, the two species must utilize the resources of the environment in a somewhat different way'. Therefore,

the closely related and structurally similar Corixinae species found in the same habitat must avoid direct competition.

This thesis examines in the species of the subfamily Corixinae;

- 1) variation in food, feeding behaviour, and feeding structures;
- 2) spatial distribution of each species within the habitat;
- 3) occurrence and duration of life cycle stages of different species;
- 4) effects of hydrachnid parasites on different species;

in order to discover how direct competition is reduced between these closely related species.

To appreciate fully the variation found in the anatomy of the head and forelimb amongst these species, the investigation was extended to include local representatives of two other subfamilies, the Cymatiinae and Micronectinae, and several foreign species which showed structural peculiarities of the head and forelimb. A comparison was also made with other aquatic Heteroptera.

SECTION 2

Observations and Feeding Experiments with Aquatic Heteroptera.

2.1 Introduction

From laboratory observations, the distribution of the air bubble, the cleaning, feeding, and mating behaviour of corixids are described. Also, more detailed feeding experiments with corixids, Notonecta and Nepa are described.

2.2 The method for observing corixids in the laboratory.

Some useful observations on the behaviour of corixids can be made with the naked eye, but more detailed work on the functioning of the legs requires the aid of a stereoscopic microscope mounted horizontally to see the corixid from the side or front. The microscope can be used this way when corixids are kept in a large aquaria, but where high magnification is required, it is preferable to use a small container which restricts the movements of the insect.

2.21 Distribution of the air bubble. (plate I)

In Corixa punctata, Sigara falleni, and Cymatia bonndorffi, the air bubble covers most of the body except the hemelytra where only the lateral grooves are full of air, the pronotum, the legs where the only parts in contact with the air are those basal areas covered by fine dense bristles, i.e. the coxa, trochanter and the basal end of the femur, and the front of the head including the rostrum where the air bubble is clearly limited by the innermost row of rostral bristles.

The antennae arising from the posterior surface of the head and the long bristles of the dorsal edge of the head, lie on the surface of the

air bubble between the head and pronotum.

2.22 Cleaning

Cleaning behaviour is the same in all species observed, and basically involves the rubbing of one part of the body against another, any organisms or debris are thus removed from both parts. The front and hind pairs of legs are the main appendages involved and have special structures to assist the cleaning process. The front legs rub the front and back of the ventral head and rostrum, and each other. The hind legs rub the top of the head, thorax and abdomen, as well as each other, and the other two pairs of legs.

Plant and animal growths are found on most corixids. Prominent growths of algae are occasionally found on certain of the head bristles and on the elytra.

Two types of Protozoa are seen on various parts of the insect. First, large colonies of peritrich ciliates were found on the rostrum bristles, the lateral edge of the anteclypeus, and on the joint of the fore femur and tibia, with smaller colonies present at the base of strong bristles on most legs examined. Opercularia corisae Faure was the commonest form found on corixids by Iust (1950) and was the only ciliate found on two species^{of} corixid by Green (1953). Second, the suctorian protozoan Acineta which is found less frequently on Leicestershire corixids, is usually against strong bristles on the legs. The species A. notonectae was found on corixids by Iust (1950).

2.23 Reproductive behaviour

Specific sounds are produced by the males of some corixid species prior to copulation (Schaller 1951, and Ieston 1955). The sound produced by Micronecta is from the abdominal region, whereas the sounds made by members of the sub-family Corixinae are produced when rows of strong bristles on the fore femur are rubbed against the side of the head (von Mitis 1935). The sound producing British species include Corixa punctata and Sigara falleni (Southwood and Ieston 1959).

During copulation, the male corixid mounts the female, gripping her with forelimbs which are variously modified for this. The male Corixinae have a special row of pegs on the tarsus between the upper paleal and upper palm bristles, which are used to grip the female on the ridged sides of the hemielytra (Popham 1961). In Cymatia, the male grips the female at the base of the hemielytra with the stout, wide, curved claws.

When the male corixid is mounted, its head is pressed against the female pronotum, and is flattened, or even concave, in the region of the frons.

2.24 Feeding in the Corixinae

Despite the popular theory that corixids are basically herbivorous and detritus feeders, there are many records of corixids showing predatory behaviour.

In the literature, corixids are described feeding upon filamentous algae by extracting cell contents with the stylets (Hungerford 1919) and feeding upon detritus by scooping with the forelimbs, (Hungerford(1919),

Griffith (1945), Sutton (1951), Benwitz (1956a), and others). There are also three cases where corixids have been successfully kept on a diet of detritus or algae. One, Rhamphocorixa, has been successfully reared on a laboratory-made detritus which contained numerous micro-organisms (Hungerford 1919 and Griffith 1945). Two, the females of two Sigara species provided with silt from their natural habitat which was changed daily, were kept for up to two months, during which time each animal laid between 100-300 eggs (Young 1965c). Three, nymphs of Micronecta quadristrigata, but not of Agraptocorixa hyalinipennis, were successfully reared on a diet of the alga Pleurococcus sp. (Fernando and Leong 1964), though it is not clear if the alga was the only food material available.

Corixids have been kept for several weeks on boiled potatoes (Quadri 1951).

Predaceous feeding on small Crustacea, chironomid and mosquito larvae and oligochaetes has been observed by Hale (1922 and 1924b), Walton (1943), Sutton (1951), Benwitz (1956a), and Crisp (1962b), and several species were reared when supplied with mosquito larvae Hale (1922 and 1924b). Corixids have also been observed to feed on their own eggs, Crisp (1962b) and Young (1965c).

In most cases where corixids have been successfully reared, the exact nature of the food material is doubtful, or, as with the boiled potatoes, their nutritional value to the corixids is uncertain, but where the food material is known, it is animal.

Experiments performed by Zwart (1965) support the view that corixids

are predaceous. He kept corixids, adults and nymphs, in cultures supplied with either one of three types of food, or with no food. The three types of food were: one, plant material of several kinds; two, detritus, natural or laboratory made; three, animals of several types. The mortality curves for the cultures supplied with no food, plant material and detritus are similar and significantly different from the corixids in cultures supplied with animal food.

Corixids catch free-swimming animals which vary in size from large Daphnia to a very small copepod. When these animals swim in front of the corixid, the forelimbs are rapidly extended forwards, then back, and moved down to the labial orifice where the prey is held by the two tarsi while the stylets are inserted. The cycle is repeated if the animal is not caught. The animal is caught either directly by this method or it is drawn to the corixid by the powerful water current created by the movements of the forelimbs and trapped between the head and tarsi.

Adults and late nymphs of Corixa punctata, Sigara falleni, and S. lateralis remain stationary while catching free-swimming animals.

Glaenocoris propinqua, on the other hand, catches animals whilst swimming (Walton 1943).

In aquaria, C. punctata swims slowly in wide circles through the water, extending the forelimbs and drawing them into the head, and has been observed to catch a Daphnia during these movements.

Corixids are most frequently seen scraping and digging in the substratum, the palae are extended to the side, and then bring material over the anteclypeus and rostrum to the labial orifice. Here, any organic matter, dead or alive, is held and ingested.

The full length of long objects, such as a strip of dead vegetation or filamentous alga (Hungerford 1919), is passed over the rostrum and then on behind the head between the middle legs. Another version of this searching behaviour is frequently seen in S. falleni where a plant stem is gripped by the front legs and the head pressed against the stem, the front and middle legs now move the animal forwards along the stem and hold the head against it.

If the prey is dropped, the corixid rapidly searches the substratum and the threshold for the leg response is lowered; for example, it is more likely to twirl its forelimbs rapidly if a small object moves nearby. The forelimbs can be stimulated to brush down the front of the head when the bristles in the region of the frons and clypeus are lightly touched. A similar reaction is found in Cymatia.

2.25 Feeding in Cymatia

The two species of this genus were never observed to search for food at any stage of their life history, but they dart out to grab with the forelimbs any moving objects which pass close to them. The prey is often as large as the predator, and is usually larger than the head. Similar observations are recorded and illustrated for Cymatia bonndorffi where the prey so captured is held in the depression on the front of the head (Walton 1943).

2.3 Feeding Experiments on Corixids and other water bugs

Three aspects of feeding were investigated. First: which substances were removed from an insect prey; second; the movements of the stylets during feeding; and third: the gut contents of the animals after they had fed.

2.31 Feeding of Notonecta maculata (Notonectidae) and Corixa punctata (Corixidae) on adult Drosophila (Diptera).

Adult Drosophila were fed to Notonecta and Corixa, and the remains were fixed and sectioned, first: to see what was left inside, second: to compare the effects of feeding on an animal by these water bugs, using the technique described by Cheng (1967) for Limnogonus fossarum (Gerridae: Heteroptera).

Starved Notonecta were isolated in plastic bowls ^{filled} with pond water and left at 18 degrees centigrade for 2-3 hours before each experiment. Females of Corixa were similarly treated, but kept singly in glass tubes with a wide meshed woven plastic material on the bottom.

Notonecta readily feeds under these conditions when living flies are dropped singly on to the water surface, but Corixa had to be induced to feed. Here the flies were lightly anaesthetized with ether, and then attached by the wings to thin wire with quick drying dope, so that the fly could be presented to the corixid and recovered afterwards. Before presenting the fly to the corixid, it was dipped in 50% alcohol to make it hydrophilic, then washed in distilled water. Once feeding had started, the fly was held tightly to the rostrum. Feeding behaviour lasted about 10-15 minutes.

The remains of these insects and other undamaged Drosophila, for comparison, were fixed in alcoholic Bouins', then embedded in polyester wax, sectioned longitudinally and stained with Mallory's triple stain. The results are similar to those obtained by Cheng (1967) for Limnogonus.

The large thoracic muscles, as well as much other internal tissue,

of the Drosophila, are removed and the remains show signs of lysis. There are no obvious differences between flies fed upon by either Notonecta or Corixa, and histological preparations suggest that both species inject a protease enzyme into the prey. The obvious source of this enzyme is the salivary glands in Notonecta where a protease and a lipase have been discovered (Baptist 1941). However, only carbohydrases are seen in the salivary glands of Corixa punctata (Baptist 1941).

2.32 Behaviour of the rostrum and stylets during feeding

Observations were made on the role of the rostrum and stylets played in feeding in Corixa punctata, Cymatia bonndorffi, Notonecta maculata, N. glauca, and Nepa cinerea.

While Corixa is feeding on Drosophila, the stylets, mandibles and maxillae, protrude a little way through the labial orifice. The maxillae are rapidly moved in and out of the orifice, which is actively opened and closed, giving the impression of nibbling. The maxillae also move rapidly relative to each other. Similar observations were made on Cymatia. Here, however, the maxillae are stuck out further.

Both species of Notonecta treat the prey in the same way. It is held at the base of the forelimbs by the first and second pairs of legs, or by the first pair of legs only. The rostrum is moved about until its tip comes into contact with the prey; the terminal segment of the rostrum is particularly mobile. The tip of the rostrum is then moved over the prey, and the stylets penetrate ^{it} ~~the prey~~ through an area of non-hardened cuticle. The mandibles do not protrude far into the prey, their main function being to hold it. The maxillae continually move about within

the prey, and when Notonecta is fed on Drosophila, the maxillae can reach the head and tip of the abdomen from one central point of insertion. In larger prey, the length of maxillae extended is greater. While inside the prey, these two stylets are continually moving in and out relative to each other, with the tip of the right maxillae always extended further. After feeding, the stylets are withdrawn and the fly turned round. The rostrum then finds a second point for insertion of the stylets, and feeding again commences. Before the fly is rejected, this behaviour is repeated several times. The fly is turned alternately in a clockwise and anti-clockwise direction, and the periods of feeding become progressively shorter. After the fly is rejected, an orange-red viscous substance is regurgitated from the stylets, which continue to move in and out of the rostrum for a short time after feeding. The colour of the fluid ejected by Notonecta after feeding on Drosophila is the same as the flies' eye coloration. The eye pigment of zygopteran nymphs is also ejected, but immediately after it has been sucked up.

These observations show that material can move both up and down the food channel in the maxillae. The eye pigment of the zygopteran nymphs is rejected immediately, which suggests that the material was distasteful, or that a filter mechanism was blocked. In the much smaller Drosophila, however, the eye-pigmented material was retained until after feeding had ceased, suggesting that it is not distasteful but the filter mechanism in the food pump (Parsons 1966a) was cleaned after feeding had ceased. With the large zygopteran nymphs, the eye pigment material probably completely blocked up the filter ^{which} had to be immediately cleaned.

Nepa cinerea was observed feeding on zygopteran nymphs. This predator is particularly suitable for observing feeding behaviour because it does not readily react to outside disturbances. Nepa exhibits the same mobility of the rostrum, particularly of the last segment, and the same searching behaviour of the rostrum tip over the surface of the prey as seen in Notonecta. The stylets are usually inserted through an area of non-hardened cuticle, which is often a joint between a segment of the body or a leg, and only rarely are they inserted through a region of hardened cuticle. It seems that the discontinuity of the surface at a joint enables the stylets to be pushed in without slipping off the cuticular surface. The maxillae can be extended a long way into the prey. The maximum length they were extended out of the rostrum was 1.5mm, which compares with the total length of the maxilla of 4.5mm, the length of the rostrum 1.4mm, and the rostrum and head 3.8mm. The mandibles are 3.3mm long. The maxilla^{ry} tube is always straight in the prey, and no movement of the two maxillae relative to each other was observed. Like Notonecta, the stylets were inserted in several places in the prey, and the prey was alternately moved to the left and right.

The maxillae of both Notonecta and Nepa, once inside the prey, were never seen to penetrate the cuticle at any point which would cause them to come out of the prey, even though they would probe legs and other appendages. Both predators are able to judge the quality of the fluid ingested. After the material in a particular region of the prey has been removed, the stylets are withdrawn, and if they are re-inserted into this region, they are rapidly removed.

2.33 Examination of gut contents

The gut contents of Corixa punctata and Notonecta maculata were examined after they had fed upon Drosophila. The predator was lightly anaesthetized with ether and dissected in an insect saline (Pantin 1948). The first part of the corixid mid-gut contains an amorphous mass of partially digested material, many lipid droplets and a few pieces of transparent membrane of entomophagous origin and the remains of fine bristles. Numerous bacteria of several types and flagellates were found in the rest of the mid-gut. No recognizable ingested structures were found in the Notonecta mid-gut. The contents of ^{the} hind-gut of both Corixa and Notonecta were bright red.

It is a common observation that corixids from their natural habitat or after feeding on detritus, have mid-guts containing an amorphous green or brown mass with some broken algal cells and parts of animals (Hungerford 1919 and others).

Similar observations were made in this present work. Parts of small Crustacea and dipterous larvae are found in the mid-gut and numerous chaetae of fresh-water oligochaetes are found in the winter and spring. Most of the algae found in the mid-gut, including diatoms and fragments of filamentous algae, are broken. In Sigara lateralis fed on a mud with a surface layer of a long, thin diatom^s, the mid-gut is packed with these cells, all of which had been broken into equal lengths.

Three species of algae with spherical cells, were used to determine the maximum size of particle different species of corixid could ingest. The diameter of these cells is Chlorella, 5 μ , Chlamydomonas 10 μ , and

Haematococcus 25 μ . Before the corixids were introduced, the algae were allowed to settle in the container which had a rough surface for the corixids to hold onto. All the algal cells found in the mid-gut were broken and could only be used to give an approximate measure of the maximum size of particle ingested. However, the maximum size of particle which each corixid species could ingest as determined by this method, is in agreement with the approximate diameter of the food channel of the maxilla of that species.

SECTION 3

The External Anatomy of the Head and Forelimbs.

3.1 Introduction

A wide range of species ~~is~~ examined, covering all but one of the six sub-families of Corixidae, as defined by Hungerford (1948). This work reveals details not previously described, and brings together scattered observations from the literature which has concentrated on naming the parts of these structures. The^{past} descriptions lack detail and are in some respects misleading.

Accurate detail and close observations are necessary if the feeding mechanism is to be understood.

This thesis makes no attempt to review critically the literature, but the relevant papers are referred to in the text; the most important of these are Griffith (1945), Benwitz (1956a), and Parsons (1966).

3.2 Materials and method

The country of origin of corixids not available locally is given, together with the number of specimens examined. The foreign had all been mounted on card points or pinned, except Diaprepocoris zealandiae, which had been stored in alcohol. Nymphs, as well as the imago, of English corixids were examined.

List of species

Corixidae

Diaprepocorinae: Diaprepocoris zealandiae Hale, (New Zealand), 20[♂] 30[♀]

D. barycephala Kirkaldy, (South Australia), 20[♀]

Stenocorixinae: Stenocorixa protrusa Horvath, (Sudan) 10[♂] 20[♀]

Cymatiinae: Cymatia bonsdorffi (Sahlb.)

C. coleoptrata (Fab.)

Micronectinae: Micronecta poweri (Douglas and Scott)

Tenagobia selecta (White), (South America) 10♂ 20♀

Corixinae:

Tribe Glaenocorisini: Glaenocorisa propinqua (Fieb.)

Tribe Graptocorixini: Neocorixa snowi (Hungerford),
(Central America), 30♂ 30♀

Tribe Corixini: Corixa punctata (Illig.)

Sigara falleni (Fieb.)

S. dorsalis (Leach)

S. nigrolineata (Fieb.)

S. lateralis (Leach)

Arctocorisa germari (Fieb.)

Notonecta glauca (Notonectidae) is described as an example of a more typical water bug.

The heads and legs were examined wherever possible on living animals, and in 70% alcohol. Some heads were cleared in glycerol or methylbenzoate; the latter is particularly useful for showing up the relationships between internal and external structures. All specimens for drawing were mounted in cells of polyvinyl lactophenol, which had one side left open, making it possible to add to the mountant when it contracted, and to orientate the specimen. Alternatively the specimens were mounted in Canada balsam.

The drawings are based upon the projection of an image from the slide on to Bristol board, a camera lucida being used for some of the more

detailed work. Where practical, all the bristles on a structure are drawn, and an impression of their relative thickness given. Where there is a very dense group of bristles, for example on the labium, only a limited number of these is shown. Ridges on the labium are represented by a line, and the numerous sense organs associated with these ridges by a row of dots.

The terminology is that of Griffith (1945) and Benwitz (1956a), incorporating the slight modifications used by Parsons (1966).

3.3 A general description of the corixid head and forelimb, (figs. 3.1 to 3.4).

The head is roughly triangular with a ventral blunt point. It is convex anteriorly and a posterior concave surface closely fits the pronotum. Two large compound eyes (E) are situated dorsolaterally, separated by the vertex (V), which extends from the area between the eyes to the posterior side of the head and down to the occipital foramen (FO). Ventral to each eye are the gena (G) and the loreal plate (LP) (Mandibular plate of Benwitz 1956a), which is separated by the clypeolorel cleft (CLC) from the anteclypeus (AC). Dorsal to the anteclypeus are the postclypeus (PC) and the frons (F).

The visible part of the rostrum is formed by the third and fourth labial segments (L3 and L4) (Griffith 1945). The median line of fusion of the labial groove is interrupted by ^{the} labial orifice (LO) through which the stylets protrude.

On the third labial segment, numerous sense organs are arranged along cuticular ridges, but on the fourth labial segment, the sense organs are arranged in groups around the labial orifice.

There is a distinct group of long bristles along the lateral edge of the anteclypeus, and another group of long bristles on the central anteclypeus, postclypeus, frons, loreal plates, and gena^e.

The four-segmented antennae (A), situated on the back of the head, have bristles on each segment. These bristles are not illustrated. The occipital foramen has two pairs of lateral processes (PR), and a dorsal ridge (R). It is surrounded laterally by the occiput (O), and ventrally is the subocciput (SO) to which the first and second labial segments are fused (Griffith 1945). The cephalic gland orifice (CGO) in the maxillary plates (MXPL) is adjacent to the lateral extension of the anteclypeus.

There is a group of central long bristles and short bristles along the line separating the anterior and posterior surfaces of the head. These bristles have ~~only~~^{only} been illustrated in figs. 3.7 and 3.13. Similar short bristles are found on the lateral occiput, the subocciput, and the third labial segment.

The complex arrangement of bristles on the back of the rostrum is illustrated in fig. 3.17. On the third labial segment are three distinct groups of long bristles. There is a dense lateral group of bristles, behind which runs the middle row of bristles. This row of bristles also extends along the ventral edge of the segment. Near the mid line, some of these bristles are very long, curving downwards and forwards. Laterally, the middle-row bristles stick out at right angles to the labium. The inner row of bristles is very variable. On the fourth labial segment, there is only one dense lateral group of long bristles on each side.

The corixid forelimb has a characteristic tarsus (TA), the pala. There are two rows of long bristles, the upper and lower paleal bristles (UP and LP), between which lies the concave palm. The upper edge of the palm is bounded by a row of short strong bristles, the upper palm bristles (UPM), and in the concavity are the inner palm bristles (IPM). On the outer side of the tarsus are long thin bristles which are not shown in the drawings. The terminal claw (C) has a single short bristle (BC) at its base.

The tibia (TI) is sometimes fused to the tarsus, and has a variable arrangement of bristles, while the femur (F) has short fine basal bristles (B), and short, strong bristles are concentrated along a diagonal row (D). The coxa and trochanter are also covered by short fine bristles.

Microsculpturing is found on the head and forelimb. It may have a polygonal surface pattern, or the appearance of pointed or round ending fish scales. The pointed or rounded end may have one or more micro-setae. This scale-like pattern, when found on the head, is orientated away from the centre. On the leg, such a pattern is orientated distally.

Prominent pores of dermal glands, typically with a radial surface pattern, are found on the head and forelimbs.

3.4 Description of specific corixid heads and forelimbs.

The head and forelimbs of each species are described, though, where the differences between male and female are slight, only female structures are illustrated. Species, very similar to those already illustrated, are described less fully. For the purposes of comparison between species,

the maximum width of the head is used as a measure of size.

3.41 Diaprepocoris zealandiae Hale

The three species of this genus are described by Hale (1924a). A fuller description of D.zealandiae is given by Young (1962).

The head, figs. 3.6 and 3.7

The head, 2.0 to 2.3 mm. wide, has two ocelli situated on the top near the compound eyes. The clypeoloral clefts are almost straight and bear the mandibular articulation about half way along. There are several groups of ^{peculiar} bristles on the anteclypeus. Beneath the clypeoloral cleft is a row of long bristles. On the lateral edge of the anteclypeus is a group of 6 to 7 short, strong bristles; 4 to 5 bristles of the ventro-lateral group of long bristles have several points. Along the ventral edge of the anteclypeus is a row of rectangular flat bristles (fig. 4.2). The other bristles on the front of the head capsule have an approximately symmetrical arrangement.

The sense organs on the third labial segment are arranged along four ridges, while the sense organs on the fourth labial segment are not grouped in any obvious way.

On the third labial segment, the outer group of bristles are short and curved, 10 - 12 pairs ^{being} found on each side, with the front bristles of each pair curving inwards most strongly. The bristles of the middle row are long and straight, those near the mid line crossing over each other. The bristles of ^{the} inner row are long and thin, forming a continuous row which is densest at the extremities. The rest of the segment is covered with short fine bristles.

On each side of the fourth labial segment are 16 - 20 bristles, those in front curving inwards strongly.

Short fine bristles cover the maxillary plates, most of the sub-occiput, the lateral edge of the occiput, and the dorsal edge of the head capsule.

On the front of the head, between the eyes, the microsculpture is hexagonal, but taking on the appearance of curved scales towards the lateral edges of the head. Similar curved markings are found on the anteclypeus at the back of the head, and they radiate from the bulges ventrolateral to the occipital foramina to the antennal sockets.

The pores of the dermal glands are densely distributed on the vertex, gena, and frons, but not all the pores have the radial pattern.

The male vertex, when viewed from above, is more pointed between the eyes than in the female (Young 1962).

Forelimb, figs. 3.8 and 3.9

The fusion of the tibia and tarsus and a strong, wide claw, ~~are~~ common to the forelimb of both sexes, which, in most respects, are remarkably similar.

The fine basal bristles are longest on the outer edge of the femur. Most of the short, strong bristles form a simple diagonal row, but the arrangement of the bristles is not characteristic.

There is no sign of a line of fusion between the tibia and tarsus. The tibial region has scattered bristles, while the tarsal region shows the typical corixid arrangement. The 12 to 14 upper paleal bristles are thin and curved, and the 24 lower paleal bristles, particularly the

shorter distal bristles, are thicker. The 16 widely spaced, short, thick upper palm bristles also become stronger distally, the thinner upper palm bristles merging with a group of fine bristles, which mark the proximal end of the palm. The inner palm bristles are short, strong, curved pegs. The curved claw is short, thick, and wide, with a thin basal bristle almost as long as the claw.

Pores are found towards the outer side of the distal end of the femur, and only on the upper surface. Microsculpture, with a pattern of round ended scales covers most of the femur and tibia-tarsus. The markings vary in the length and width of the 'scales', being very pointed on the femur in the region between the fine basal bristles and the diagonal row of strong bristles.

3.42 Diaprepocoris barycephala Kirkaldy

The head, 2.6 to 2.8 mm. wide, is very similar to that of D.zealandiae, but in each ventro-lateral group of long anteclypeal bristles, only one bristle has two points. The tibia-tarsus of the forelimb is very different, having fewer and shorter paleal bristles. There are 7 to 8 thin curved upper paleal bristles and 12 lower paleal bristles which are short, strong, and wide, and about as long as the claw. The 12 upper palm bristles are widely spaced. The inner palm bristles, the distribution of the glands, and microsculpturing, are all similar to D.zealandiae.

The female forelimbs examined are similar to the male forelimb described by Hale (1922 and 1924a). Hale, however, shows a line dividing the tibia and tarsus in the male of both D.barycephala and D.zealandiae. This feature in D.zealandiae is not reported by Jaczewski

(1939) or by Young (1962), or seen in this present work.

The palae of a third species, D.personata, ^{that of} are similar to D.zealandiae, (Hale 1924a).

3.43 Stenocorixa protrusa Horvath

This species is described by Horvath (1926), Jaczewski (1927), and Poisson and Jaczewski (1928).

The Head

The head, 2.0 - 2.4 mm. wide, is relatively long, especially the ^{the} region below eyes (Jaczewski (1927)). The vertex between the eyes bulges outwards in both sexes. The curved shape of the clypeoloral cleft and the distribution of the bristles on the head capsule ^{of the corixid} are similar to Sigara falleni (see fig. 3.1), but the bristles on the postclypeus are shorter than similar bristles on S.falleni.

The arrangement of the labial sense organs and the bristles of the fourth labial segment and the outer row on the third segment, is also similar to the arrangement in S.falleni. The numerous bristles of the middle and inner rows on the third labial segment are long and thin.

Most of the pores of the large number of dermal glands which are only on the lorae plates, have a radial surface pattern, the other pores are plain.

Microsculpturing is only found on the anterior vertex and has polygonal shapes.

Forelimb, figs. 3.10 and 3.11.

The femur is long and thin, with the fine basal bristles longest on the outer edge, and most of the short strong bristles forming a short,

diagonal row.

The tibia is also long and thin. It has a few scattered bristles and a distal comb of 6 strong bristles.

On the tarsus, 6 - 7 long thin, curved bristles form the upper paleal row and the 17 - 18 lower paleal bristles have small projections near their base (fig. 3.11D). The 17 upper palm bristles are short, strong, and curved, whilst the numerous inner palm bristles are short, strong, but mainly straight. The claw of the female is slender with a serrated edge at its base, and the straight thin basal claw is about half the length of the claw.

A forward extension of the outer side of the tibia and a large stout claw distinguishes the male forelimb from that of the female. Near the base of the male claw are a few small rounded bristles. Figs. 3.11A and B show how the size of the male claw affects the shape of the tarsus.

Pores of dermal glands are found at the distal end of the femur and on the under side of the tibia, in both sexes. All segments of the forelimb have varied microsculpture.

3.44 Cymatia bonsdorffi (Sahlb.)

The head, figs. 3.12 and 3.13

The head, 2.0 mm. wide, has large protuberant eyes. There is a depression in the frons and clypeus, which is deeper in the male than the female. The numerous bristles on the front of the head capsule are varied in size. Those which are long have a symmetrical arrangement. A central group are separated from the others by a bare area which corresponds to the internal insertion of the food pump dilator muscles.

The bristles on the lateral edge of the anteclypeus are few and small.

There are relatively few bristles on the rostrum. On the third labial segment, the outer row is represented by 7 long bristles on each side, while the middle row has only four ~~long bristles~~. The inner row of rostral bristles is absent. In the mid line, there are many short strong bristles, and there are fine bristles on the rest of the segment. On the fourth labial segment there are only four small bristles on each side.

On the back of the head capsule, fine bristles are only found on the lateral subocciput. The bristles round the top of the head are relatively numerous and long.

Pores of dermal glands are not present on the head, and microsculpturing is found only on the front of the rostrum and in the region ventrolateral to the occipital foramen. The scale-like markings of the rostrum are found on the ventral half of the third labial segment.

Forelimb, figs. 3.14 and 3.15

At the distal end of the fine basal bristles of the femur is a row of long fine bristles. Strong bristles form the inner group on the femur, some of which are almost as long as the single bristle found on the posterior side of the femur. The arrangement of the group of strong bristles is varied, but 2 strong basal bristles are very constant in their position.

The tibia is short with few strong bristles and bears a long bristle which is a continuation of the upper paleal row of bristles.

The tarsus is long and sub-cylindrical with 7 long, curved bristles

in both the upper and lower paleal rows. Between these, several rows of short, strong bristles are found in the place of the usual palm structure. Between these short strong bristles and the upper paleal bristles is a row of short fine bristles. The claw of the female is long and slender, that of the male is shorter, strong, and wide. There is no basal bristle in either sex.

There are no pores of dermal glands, but scale-like microsculpture is present on each segment.

3.45 Cymatia coleoptrata (Fab.)

This species, smaller than C.bonsdorffi, has a head width of 1.3 - 1.5 mm. The structure of the head and forelimb is basically the same as the corresponding structures in C.bonsdorffi, but has fewer bristles on the rostrum and palae. Only 4 - 5 bristles are found on each side of the third labial segment; the upper and lower paleal rows of the fore tarsus each have only 6 bristles.

3.46 Neocorixa snowi Hungerford

The head

This species, described by Hungerford (1948), has a head 2.5 - 2.8 mm. wide, which has a similar shape to the head of Cymatia, but shows no frontal depression. Numerous medium-length bristles are present on the loreal plate, frons, and clypeus, though they are absent from the ventro-lateral region of the anteclypeus. The bristles of the lateral edge of the anteclypeus are of medium length, and similar to the outer row of bristles on the rostrum. On the rostrum these medium-length curved bristles are dense on both labial segments. On the third labial segment, the middle row is confined to the ventral region with about 12 long, strong

bristles curving downwards, and a few shorter thinner bristles. Short, strong bristles about the mid line extend to an inner row of bristles running across the top of the rostrum. On the back of the head capsule, the short fine bristles show the typical corixid arrangement.

7 ridges with sense organs are present on the third labial segment, though the upper ridge has an incomplete row of sense organs. Sense organs present on the fourth labial segment are grouped round the labial orifice.

Pores of dermal glands are very numerous on the gena, and some are also present on the ventral vertex.

Forelimb, fig. 315

The fine basal bristles are restricted to a small area on the wide femur. On the inner edge of this segment are a variable number of long strong bristles. Numerous short strong bristles form a variable and irregular diagonal row.

The tibia has a distal comb of bristles and some longer stronger bristles along its inner edge.

The tarsus is long and thin with short paleal bristles. In the upper paleal row there are only 4 bristles restricted to the basal end; in contrast 13 bristles of the lower row extend the full length of the tarsus. There are approximately 13 short, strong upper palm bristles, and a large number of fine curved inner palm bristles which are shorter distally. The claw is long and thick, with a basal bristle about a quarter of its length.

The male fore femur differs from that of the female, showing a small

group of strong bristles on the inner edge of the fine basal bristles.

Again, in contrast to the female ^{the male} trochanter has a number of strong bristles and pegs. The female tibia has no comb and fewer strong bristles. The tarsus has 3 upper paleal bristles, 10 - 12 lower paleal bristles, about 16 upper palm bristles, and a row of 24 pegs, one of which is illustrated in detail (fig. 3.15E). The claw is thick and stubby but no basal bristle is found. The difference in size between the male and female claws is not mentioned for any species of this genus in previous work (Hungerford, 1948).

3.47 Corixa punctata (Illig.)

A detailed study of the head of this species was carried out by Benwitz (1956a).

The Head, figs. 3.16 and 3.17

The head, 3.8 - 4.2 mm. wide, has few bristles on the frons and clypeus and lorai plate, and the majority of the long bristles of this group are on the edge of the area covered by them, and link up with the 14 - 15 long bristles on the lateral edge of the anteclypeus. The curvature of the more dorsal of the lateral anteclypeal bristles follows the edge of the head and the ventral bristles curve downwards.

The complex arrangement of bristles on the back of the rostrum is shown diagrammatically in fig. 3.17. The bristles of the outer row on the third labial segment are dense, the anterior bristles curving inwards strongly, those behind sticking out almost at right angles to the labial surface. The middle row of rostral bristles ^{which} is densest near the mid line, extends round the edge of the third segment, and 14 long bristles

near this mid line stick out backwards and curve downwards (see plate). The inner row of rostral bristles is represented in this species by a lateral tuft of fine bristles and a row of strong bristles sticking straight out. The bristles on the fourth labial segment are dense. The fine bristles of the rostrum and ventral head capsule are shown on layer D. fig. 3.17.

The third labial segment has 6 ridges with sense organs, whereas the sense organs on the fourth segment are arranged in groups.

Pores of dermal glands are numerous on the gena and loreal plates as well as being present on the vertex and frons. These areas also have irregular^{ly} shaped microsculpture.

The male head has a slight depression in the front of the head capsule which extends upwards between the eyes (plate /).

Forelimb, Figs. 3.18, 3.19, and 3.20.

On the femur, the basal bristles extend about half its length, with those on the outer edge the longest. The diagonal row of strong bristles is short and there are a few larger distal bristles.

The short tibia has some scattered strong bristles and distally a comb of 5 - 6 strong bristles.

The tarsus has 16 thin curved bristles in the upper paleal row and 18 strong curved bristles in the lower paleal row. Approximately 36 short upper palm bristles and the many thin inner palm bristles point distally. The slender claw has a serrated base, and the basal bristle is less than one quarter its length. In both the male and female the claw is either straight, or curves slightly either inwards or outwards.

Pores are found on the femur and on the outer edge of the tibia in both sexes, and scale-like ~~ceriseous~~ microsculpture is found on the femur, tibia, and tarsus.

Some of the inner basal bristles on the femur in the male are thicker and arranged in rows as part of the sound producing mechanism (von Mitis 1935). There is no comb on the tibia, but the bristles at the distal end are arranged in two groups, an outer group of 5 to 6 strong straight bristles, and an inner group which varies in arrangement between individuals. The upper paleal row is composed of 16 bristles, the lower paleal row of 21 bristles and the upper palm row of 29 - 30 bristles. There is also a row of 28 - 29 short pegs on the pala curving inwards distally. The distal pegs are hooked. The detailed structure of these pegs is shown in fig. 3.20 B.

3.48 Sigara falleni (Fieb.)

The Head, figs. 3.1 and 3.2

The head, 2.0 to 2.2 mm. wide, has few long bristles on the front of the head capsule. Only short bristles are found on the central anteclypeus, but there are 12 to 13 long bristles along each lateral edge which are arranged as in C.punctata.

The outer and middle rows of rostral bristles are also arranged as in C.punctata, though the group of 16 strong bristles of the middle row is more easily distinguished. The inner row has a lateral tuft of fine bristles, and is represented centrally by a diffuse row of short strong bristles. Short fine bristles are found on the same areas of the rostrum and head capsule as in C.punctata.

The third labial segment has 6 ridges with sense organs, whereas, on the fourth segment, the sense organs are arranged in groups round the labial orifice. Pores of dermal glands are found on the vertex, frons, post-clypeus and are most numerous on the gena and loreal plate. Micro-sculpturing is present all over the head capsule, with the exception of the clypeus. The markings are polygonal on the vertex and frons, but scale-like on the side of the head. Scale-like markings are also found on the posterior exposed area of the anteclypeus.

The male head has a shallow depression in front.

Forelimb, figs. 3.3, 3.4, and 3.5

On the outer edge of the femur, at the distal end of the basal group of fine bristles, is a row of long thin bristles. The diagonal row of strong bristles is long.

The short curved tibia has scattered small strong bristles and a distal comb of 3 - 4 bristles.

On the tarsus are 9 thin curved upper paleal bristles, and 23 stronger lower paleal bristles. There are approximately 32 short strong curved upper palm bristles, ^{and} those of the inner palm are numerous and long. The slender claw has a serrated base and a basal bristle about one quarter of its length. Like C. punctata, the male femur has an inner area of strong basal bristles used in sound production. The tibia is short and curved and the bristles form two groups: an upper group of thin bristles and a lower group of strong bristles forming a comb. The tarsus is flattened and enlarged, an extreme form of the male pala modified to accommodate short pegs. There are two groups of pegs, a distal group of

4 to 6 hooked pegs on the upper edge of the pala, and a basal longer row of about 30 pegs. Both types of pegs are illustrated in detail in fig. 3.5. There are 8⁻⁹ thin curved upper paleal bristles along the edge of the pala, and 1 or 2 bristles near the basal group of pegs. The typical palm structure is seen with 23 lower paleal bristles, 38 upper palm bristles, and many long thin inner palm bristles.

The pores on the forelimb of both sexes are found at the distal end of the femur, and on the outer side of the tibia. Scale-like micro-sculpture is found on the femur and tibia in the male, and on all segments of the female limb. The upper surface of the male tarsus is rugose.

3.49 Other species of Corixidæ

3.491 Sigara dorsalis (Leach)

This species, head width 2.2 to 2.3 mm., is similar to S.falleni. Longer bristles found on the central anteclypeus extend dorsally to join those on the postclypeus. The inner row of rostral bristles is represented by a continuous row of thin bristles. ~~Laterally,~~ These bristles are longest and most numerous ~~laterally~~

The femur of the female has an inner patch of strong basal bristles, but not as strong as the homologous bristles of the male. Unlike S.falleni, there is a short diagonal row of strong bristles.

The tibial comb is composed of 6 strong bristles.

The tarsus has 11 upper paleal bristles, 22 lower paleal bristles, and about 32 upper palm bristles. The inner palm bristles are long like those of S.falleni; in contrast however the slender claw does not have a serrated base in either sex.

Like S. falleni, the male fore tibia has two distal groups of bristles, an upper group of thin bristles and a lower group of strong bristles.

The tarsus has 11 upper paleal bristles, 22 lower paleal bristles. There are about 38 upper palm bristles; the curvature of the row is slightly distorted. Distally, some of the inner palm bristles are arranged to form a second upper palm row. There are two curved rows of pegs which do not greatly distort the shape of the pala from that of the female. The arrangement of the pegs of this and other British corixids is illustrated by Macan (1965).

3.492 Sigara nigrolineata (Fieb.)

This is a small species of corixid, head width 1.65 to 1.75 mm. The front of the head capsule has very few long bristles. The bristles on the lateral edge of the anteclypeus, and the inner row of rostral bristles, are well developed however. The third labial segment has 6 ridges with sense organs. The depression ^{on} the male head is terminated ^{dorsally} by a transverse ridge at the level of the lower margin of the eyes.

The female front leg has 14, ²⁵ ~~25 and about 28~~, upper, and ^{about 28} lower paleal bristles and upper palm bristles ~~respectively~~, and thin, short, curved, inner palm bristles. The slender claw has no serrated base.

The ~~male~~ ^{of the male insect} fore-femur has an inner patch of basal bristles slightly stronger than the other basal bristles, although sound production is not claimed for this species. The lower group of distal bristles on the tibia form ^s a comb.

The tarsus has 9 ²⁴ ~~and 24~~ upper and lower paleal bristles, and a row of

28 pegs which curve^s inwards distally. Two or 3 of the distal pegs are much longer than the others.

3.493 Sigara lateralis (Leach)

A small species, head width 1.55 to 1.70 mm., with numerous long bristles on the front of the head. The bristles of the lateral anteclypeus, and those of the inner row on the rostrum, are especially well developed. The male head has a long frontal depression. The tarsus has 12 ~~and 21~~²¹ upper and lower paleal bristles ~~respectively~~ in the female and 10 to 11 and 23 in the male. There are approximately 30 upper palm bristles in each sex. Numerous fine and short inner palm bristles and other forms of roughness are found on the palm. The male has a single row of about 31 pegs which are longer ~~at the~~ distally. In both sexes the base of the claw is serrated.

3.494 Arctocorisa germari (Fieb.)

A medium-sized corixid, head width 2.3 to 2.5 mm., which lives in deep water. On the front of the head capsule, the bristles are dense and long. On the rostrum, the inner row of bristles is complete and runs across the rostrum about half way down the third labial segment. The middle row of bristles is represented centrally by 16 long bristles, and the bristles of the outer row are relatively long and are denser ventrally.

The female fore tarsus has 9 ~~and 15~~¹⁵ upper and lower paleal bristles respectively, and the inner palm has a few short curved fine bristles. The tibia has a distal comb and two long thin bristles which form a continuation of the upper paleal row. Both sexes have a slender claw.

The male has a patch of strengthened basal bristles on the femur for sound production. The pegs on the tarsus form an irregular row and are longer distally.

3.495 Glaenocorisa propinqua (Fieb.)

A deep water species belonging to the tribe Glaenocorisini. The head, 2.3 to 2.4 mm. wide, has numerous long bristles on the front which extend down the central anteclypeus. Bristles are absent from the lateral extensions of the anteclypeus except at the edge of the head capsule. The long bristles of the outer rostral row are not as dense as in C.punctata or S.falleni. Centrally, the middle row has 16 long curved bristles. The inner row runs across the top of the rostrum and has lateral tufts of long thin bristles and another tuft of thin bristles on the mid line.

The third labial segment has 6 ridges with sense organs and on the fourth segment the sense organs are grouped round the labial orifice.

Pores of dermal glands are found on the vertex, gena, and on the loreal plate, even among the bristles.

The male head has a frontal depression.

On the fore femur, the basal bristles are restricted to a small area, and there is a long irregular row of strong bristles. The tibia has an irregular distal comb and 3 long bristles forming an extension of the upper paleal row. On the female fore tarsus, the paleal bristles are long and widely spaced, and of equal strength with 9 to 10 upper and 12 lower paleal bristles. There are about 40, relatively long, upper palm bristles. The ~~adjacent bristles~~^{of the row} are close together. The short inner

palm bristles are few in number. In both sexes the claw is slender with a basal bristle about a quarter its length.

The male tarsus has an upward 'kink' in the upper palm row of bristles and the row of pegs (Macan 1965 fig. 47a). Distal to the 'kink', the upper palm bristles are longest and the pegs take the form of upper palm bristles. The pegs proximal to the 'kink' are relatively long and pointed compared with those of Corixa punctata. The upper paleal bristle row is interrupted by the 'kink', there are 7 distal and 3 proximal to it.

In both sexes, pores of dermal glands are found on the distal end of the femur only.

3.496 Micronecta poweri (Douglas and Scott)

A small species, head width 0.75 to 0.78 mm. wide, with small eyes (Walton 1938). The clypeoloral cleft is straight, except for a small upward curve at the inner end. There are long bristles on the front of the head capsule. Some of these form ^a definite row on the anteclypeus just below the clypeoloral cleft which connects with the long bristles on its lateral edge.

The front of the rostrum has only 4 ridges on the third labial segment. On each side of the third and fourth segments, 18 to 20 and 4 to 5 short curved bristles form the outer rows. 10 long bristles form the middle row and there is an inner row of bristles running across the top of the rostrum. There are short fine bristles on the rostrum and maxillary plate. As in all members of the sub-family Micronectinae, the antenna has 3-segments.

The forelimb of the female has a long, thin femur with the fine basal bristles restricted to a small area and two strong basal bristles represent the diagonal row. On the outer distal edge is a long, very thin bristle with many branches. The tibia and tarsus are fused, and there are a few strong bristles in the tibial region. The pala has 4 to 5 thin upper paleal bristles, and about 15 strong lower paleal bristles, while the upper palm row has 10 short, strong bristles. The claw is slender with a small basal bristle. In contrast, the male tibia and tarsus are not fused together, and ^{of the male insect} the claw ~~which~~ is wide and spatulate and normally folds behind the tarsus. A small basal bristle is present, and on the outer side at the base of the claw there is a strong bristle similar to one of the lower paleal bristles.

Pores are found only on the gena^e and loreal plates of the head and on the femur.

3.497 Tenagobia selecta White

This species, one of the largest in the genus is illustrated in O'Deay (1935).

The head, 1.55 to 1.65 mm. wide and the front legs are very similar in structure to those of Micronecta poweri. There is, however, no row of bristles ventral to the clypeoloral cleft on the anteclypeus, but the 4 - 6 lateral anteclypeal bristles are multipointed. On each side of the third labial segment, there are 10 short bristles in the outer row and approximately 10 long strong bristles on each side of the middle row of rostral bristles which extends round the edge of the third labial segment. The inner row is represented laterally by dense long fine

bristles which, on both sides, extend over a quarter of the way across the top of the rostrum.

The rostrum has 4 ridges and one incomplete ridge with sense organs on the third labial segment.

3.5 Notes on Corixid nymphs

In the first instar nymphs of the Corixini, the bristles on the front of the head capsule are arranged similarly to those of the adult. The rostrum has, however, only three ridges with sense organs, and the few bristles in the outer row are restricted to the base of the fourth labial segment. The middle row^{is} represented by long bristles on the ventral edge of the third labial segment. The fifth instar head and forelimb are similar to those of the adult, with these exceptions which are common to all nymphs: there are only 3 antennal^{and} segments; the tibia and tarsus are fused.

The forelimb has a well developed pala with a slender claw and a very small basal bristle. The inner palm bristles are few in number, and there are many rounded projections in the palm.

Pores are found on the femur of each leg, and on the abdomen, but are absent from the head of the first instar. Scale-like microsculpture mainly with microsetae covers most of the corixid nymph.

In Cymatia, the first instar nymph has relatively large eyes and a pala and rostrum similar to the adult structures.

3.6 Notonecta glauca Linn.

The head, 3.4 to 3.5 mm. wide, has two large eyes and a stout four-segmented rostrum (fig. 3.21, see also Macan 1965). The labrum, attached

to the anteclypeus, overlaps part of the short first and second labial segments. The edges of the labial groove are fused medianly in segments 3 and 4, except at the tip of the fourth labial segment. At the tip of this segment are a group of sense organs borne at the tip of two lateral lobes and two sets of tactile bristles. Other bristles and sense organs are also present on the rostrum.

Dense long bristles are found on the posterior side of the second labial segment and on the sub-occiput.

3.71 Structures associated with the air bubble (c.f. section 2.21)

The air bubble occupies the space between the head and pronotum, and its spread on to the rostrum is limited by the inner row of rostral bristles. In Diaprepocoris and Stenocorixa, these bristles are long and thin and lie on the surface of the bubble. In most other corixids, long thin bristles are restricted to a dorsolateral tuft. The rest of the inner row bristles are short and strong and run straight across the top of the rostrum, e.g. Glaenocoris or close to the middle row, e.g. Corixa. In some species, e.g. Cymatia^{spp.}, the inner bristle row is absent and the air bubble is limited by the middle row.

On the dorsal edge of the head are long bristles which lie on the surface of the air bubble, these ^{bristles} are particularly numerous in Cymatia.

The numerous fine bristles covering large areas of the posterior head and rostrum may have a tactile function, or they may help to maintain the position of the air bubble either when it becomes very small or during movements of the head and forelimb. Fine bristles on the edge of the maxillary plate extend over the space behind and prevent the air

bubble coming into contact with the anteclypeus and so allowing the cephalic gland, which opens into this space, access to external water.

The forelegs protrude from the air bubble, which extends on to the area of the femur which is covered by fine basal bristles. These bristles may be restricted to a small basal area, e.g. Cymatia, or cover up to half the segment. The fore femur of most corixids show^s, on the upper and lower surfaces, distal extensions of the basal bristles, ~~These distal extensions of the basal bristles are the~~ areas of the fore-femur that are pressed close to those parts of the head and pronotum which are covered by the air bubble. The outer basal bristles, particularly those on the distal edge, are often long and form a definite row in some species, e.g. Cymatia^{spp.} and Sigara falleni. ~~These long~~ *They* bristles lie on the surface of the air bubble and probably prevent the bubble coming into contact with other parts of the leg.

3.72 Structures associated with cleaning (c.f. section 2.22)

Observations show that the front of the head ventral to the eyes and the posterior rostrum are cleaned by the forelimb. The forelimbs also rub each other, and one is rubbed by the hind leg while the middle leg is being cleaned. This ~~latter~~^{last} procedure may be concerned with spreading the secretion of the gland which opens at the base of the fore and hind legs, the limbs most concerned with cleaning (Benwitz 1956b).

^{When} *The* fore femur rubs against the posterior surface of the rostrum, the diagonal row of bristles of the fore femur is used to clean the rostral bristles. The diagonal row of bristles, which is always distal to the air bubble, may be short and simple as in Corixa punctata, or very complex

as in Neocorixa. This variation is probably related to several factors, including the length and shape of the forelimb segments, the shape of the rostrum, and the relative position of the rostral bristles.

It is not possible to determine which of the strong bristles on the fore femur of Cymatia clean the few rostrum bristles, although the arrangement of fore femur bristles is variable, there are always two short strong basal bristles to which this function may be ascribed.

The tibia and tarsus^{are} rubbed against the front of the head ~~and~~ the rostral bristles. The tibial bristles, in particular the distal comb, may clean the rostral and lateral anteclypeal bristles, but the main cleaning structure for the front of the head is the upper palm row of bristles on the tarsus.

The tibial distal comb of bristles is replaced in the male Corixinae by two irregular groups of bristles. This results from the modification of the insertion of the tarsus depressor muscle to enable the effective use of the male pegs on the tarsus for gripping the female during copulation. Distal groups of tibial bristles are not present in Diaprepocoris, Micronecta, Tenagobia or Cymatia.

The curved shape of the upper palm row of bristles fits the curvature of the head. The bristles of this row are short and strong and the adjacent bristles are usually very close together. ~~The~~ Variation amongst the species is not associated with the density of bristles on the head capsule, for example, both Diaprepocoris barycephala and Neocorixa have widely spaced upper palm bristles, but only Neocorixa has very dense bristles on the head capsule. The upper palm bristles are modified to

cope with the depression on the male head in Corixa and Sigara. In the male Sigara dorsalis, some of the inner palm bristles reinforce the upper palm bristles, and in the male Glaenocorisa, the distal pegs have the form of upper palm bristles.

In Cymatia, instead of the palm structure, are 2 - 3 rows of short strong bristles, which, as well as being used in feeding, clean the front of the head.

It was not determined which bristles were involved in the mutual cleaning of the fore tibia and tarsi. On the back of the tibia and tarsus are some very long thin bristles which were present in all species examined and were occasionally numerous; their function is unknown.

3.73 Structures associated with reproduction (cf. section 2.23)

The male forelimb is usually modified for reproductive functions.

Only Diaprepocoris was found to have the same forelimb structure in both sexes, ^{with} where the tibia and tarsus are fused and there is a stout, wide, terminal claw, similar to the ^{that} ~~male claw~~ of Stenocorixa and Cymatia used by the male ^{animals} ~~of these genera~~ to hold the female during copulation. The claw of Diaprepocoris is suitable for the male to use during copulation and for use by both sexes for digging during feeding, cf. female Neocorixa.

In the sub-families, Stenocorixinae, Cymatiinae, and Micronectinae, the male claws are modified for gripping the female hemielytra during copulation. In Stenocorixa and Cymatia, the male claw is stout and wide, ^{that} whereas ~~the male claw~~ of Micronecta and Tenagobia is relatively long and wide, and when it is not used for gripping the female, it is carried folded back behind the pala.

In most Corixinae, the claws of the male and female are similar, but Neocorixa snowi of the tribe Graptocorixini shows sexual dimorphism, the female claw ^{being} long and wide and the male claw short and 'stubby'.

A characteristic of the sub-families Heterocorixinae and Corixinae is the row of pegs between the palm and upper paleal bristles on the male fore tarsus. The varied arrangements of these pegs are shown by Hungerford (1948) and Macan (1965). ^{Their} ~~The function of these pegs in~~ the British Corixini and an explanation of some of the variation in their arrangement ~~of the pegs~~ and the corresponding distortion of the pala is given by Popham (1961). During copulation, the male holds on to the female's back, gripping the base of the hemielytra with the front legs, the pegs of the male tarsus hooking on to the two lateral ridges on the female hemielytra.

In C.punctata, the hooked distal pegs hold on to the ventral ridge, while the other pegs grip the second ridge of the hemielytra. The tibia of C.punctata is straight, but that of S.falleni is curved, thus, if the male pegs of S.falleni ^{had} retained ~~retained~~ the same form as C.punctata, their effectiveness in holding on to the female would be greatly reduced (Popham 1961). Associated with the change of shape of the tibia, the pala is broadened and the pegs are separated into two groups, so that an effective grip on the female can be maintained. S.falleni (fig. 3.5) represents an extreme of this trend. The shorter claw of the male Neocorixa and the row of pegs function in a similar way, the claw gripping the base of the female hemielytra and the pegs hook^{ing} on to the upper ridge.

The male pegs have distinctive surface patterns (figs. 3.5, 3.15,

and 3.20) which are derived from the longitudinal ridging found on most strong bristles on corixids. It is claimed that the male pegs are represented in the female by a row of short fine bristles found between the upper paleal and upper palm bristles (Popham 1961). But ^{in C. punctata} similar fine bristles are found ^{on the tarsus of} ~~in the male C. punctata~~ ^{the tarsus} between the pegs and the upper paleal bristles, and also, on both the male and female of Stenocorixa (figs. 3.11 and 3.12) and Cymatia (fig. 3.14). This evidence supports the view that the male pegs are derived from a duplication of the upper palm bristles. ^{the male has} In ~~the male~~ Glaenocoris, ~~the~~ distal pegs ~~have~~ with the form of upper palm bristles.

The male pegs or the large claw may modify the shape of the tarsus, but the palm and lower paleal bristles retain the form found in the female of the species.

The tibia of the male Corixinae differs from that of the female in the arrangement of the bristles and shape of the distal end. This is because of a difference in articulation with the tarsus which enables the tarsus depressor muscle of the male to cause the pala to grip the female hemielytra effectively with the male pegs. In the male Stenocorixa, an outer distal projection on the tibia prevents the tarsus from being bent back too far. ^{In the micronectinae} ^{the} The tibia and tarsus of male Micronectinae are distinct segments, but in the female the two segments are fused, cf. Diaprepocoris. This is also the typical nymphal condition.

The most common modification of the fore femur is the presence of an inner patch of basal bristles which have been strengthened and arranged in regular rows. These structures are used for sound production. (von Mitis 1935).

head of the
The male head of Diaprepocoris and Stenocorixa differ^s slightly
in the vertex from that
from the female head in the dorsal vertex region between the eyes.

The head of both the male and female Cymatia has a long depression in the clypeus and frons, which is deeper in the male. In contrast, only the head of the male Corixinae is flattened or concave in front. There is considerable variation between species in this feature. When the male mounts the female, the head and thorax of the female is pressed into the head depression. This means that short front legs will suffice to grip the female, and it is noticeable that the males of several British species are smaller than the females.

3.74 Structures associated with feeding (cf. sections 2.24 and 2.25)

In all the methods of feeding, the food material is brought by the forelimbs to the head, usually first in the region of the anteclypeus and then over the rostrum to the labial orifice. The food may be gathered by digging in the substratum and by netting swimming animals. The typical corixid forelimb (fig. 3.3, S.falleni, female) is suitable structurally for both methods of feeding, but from the evidence of the form of the pala in each case, and from direct observations of Cymatia only, some corixids have specialized in one or other of these methods of feeding, i.e. Diaprepocoris barycephala and Neocorixa in digging, and Cymatia and Glaenocoris in netting.

The digging corixid is searching for animals, dead or alive, or other concentrations of suitable organic matter, such as algae. In the typical corixid the lower paleal bristles, especially the distal ones, are strong, closely spaced and suitable for digging, or, at least,

scooping up detritus, but the long slender claw is not suitable for digging, cf. Neocorixa. The forelimb of Neocorixa is probably specialized for digging up large animals such as oligochaets or dipterous larvae. The tarsus is slender and has short, strong, widely spaced, lower paleal bristles and only a few basal upper paleal bristles, so that presumably there is reduced resistance to movement through the substratum. There is also a long powerful claw in this species. The upper palm bristles are short and ^{widely} spaced, with the short, strong bristles on the tibia and the long strong bristles on the femur, are adapted for holding struggling prey. (cf. Cymatia). The main features of this adaptation upon the form of the tarsus, are shown by Diaprepocoris barycephala, but not in the other two species of this genus. However, this form of the pala is characteristic of both Neocorixa and Graptocorixa which form the tribe Graptocorixini. (Hungerford 1948).

The upper paleal bristles of the typical corixid are relatively weak and are widely spaced. They help to hold the material which has been scooped up, as well as being used with the lower paleal bristles when swimming animals are caught. Cymatia which specializes in catching large swimming animals has a few very long, strong, widely spaced paleal bristles on the sub-cylindrical tarsus, (fig. 3.14). There are the same number of upper and lower paleal bristles, and they all have the same general form, though the lower paleal bristles are longer. The female claw is also long and slender. This form of the pala allows it to be moved through the water with much less resistance than the typical corixid pala, while covering a wider area. The wide spacing of the paleal

bristles, however, limits the minimum size of the prey that can be caught. The long bristle on the upper tibia and the long bristles on the upper and lower sides of the femur, and in particular the short strong 'palm' bristles on the tarsus, help to hold the prey.

The palae of Glaenocorisa has the corixid 'palm', but the paleal bristles (of both rows) are very long and widely spaced. On the tibia are three long bristles which form an extension of the upper paleal row. Whilst not exhibiting the extreme form of the Cymatia tarsus, the Glaenocorisa tarsus shows definite adaptations for catching swimming prey, rather than for digging.

It will be seen from table 3.1 that there are more lower paleal than upper paleal bristles, and that, compared with length of the palm, there are relatively more lower paleal bristles in the smaller corixids, whilst the number of upper palm bristles compared with the length of the palm is very variable.

The upper paleal bristles and the space between them and the palm is often modified in the males. The form of the palm and the lower paleal bristles, however, is usually the same in both sexes, which emphasizes their importance in feeding.

The lower paleal bristles of Stenocorixa have near their base small projections, Fig. 3.11D which during the manipulation of food material may help to give extra grip.

The inner palm bristles show an interesting progression from the stubby pegs of Diaprepocoris (fig. 3.9) through the short stout bristles of Stenocorixa (fig. 3.10) to the thin curved bristles of other corixids

(fig. 3.19, C.punctata). They are particularly long in S.falleni and S.dorsalis, but in Glaenocorisa they are short and sparse. In S.lateralis the palm also has some rounded cuticular projections similar to those of corixid nymphs. Bristles and any roughness within the palm help with the manipulation of food material. The thin inner palm bristles may also have a tactile function.

In some of the corixids examined, the base of the inner edge of the claw is serrated; the significance of the presence or absence of this serration is unknown. The serration may, together with the basal bristle, which is found in all species except Cymatia, help with the manipulation of small animal prey.

Corixids have large compound eyes. The number of ommatidia and the field of vision in S.distincta, a species similar to S.falleni, was measured by Popham (1953). He found that in the horizontal plane, the visual field of each eye is 304° with a common field of 56° . In the vertical plane, the visual field of each eye was 200° . The eyes are notably much more protuberant in Cymatia, but less so in Glaenocorisa, suggesting that the field of vision of each eye is greater, and that the common field of vision is also greater. A larger common field of vision and greater distance perception are consistent with specialization for feeding on swimming prey. The eyes of the first instar nymphs are very small, although in Cymatia they are larger than ⁱⁿ other species; the size of the eyes, compared with the head width, increases through the nymphal stages to adulthood. The eyes of the small adult Micronecta are small relative to the size of the head.

The rostrum and the lateral extensions of the anteclypeus provide a large flat area against which material gathered by the front legs can be held and manipulated. The numerous sense organs on the rostrum, particularly those arranged in ridges on the third labial segment, can presumably assess the nature of the food material. In both Cymatia and Neocorixa, the rostrum is small and the anteclypeus is short. These features are associated with feeding on larger animals, which can be easily held over the labial orifice while the stylets are inserted.

The bristles of the outer and middle rows of the rostrum and the lateral anteclypeus enlarge the area against which food can be manipulated, and provide 'side walls' to prevent the material escaping. The dense bristles of the fourth labial segment form a 'shelf' ventral to the labial orifice against which small objects can be held. Cymatia (fig. 3.12), which only feeds on large swimming animals, has a few long rostrum bristles; the lateral anteclypeal bristles are poorly developed and only a few short bristles are found around the labial orifice. The ~~last~~ ^{last} ~~latter~~ probably have a tactile function. The ridges with numerous sense organs on the third labial segment are a characteristic of corixids, and are described by Benwitz (1956a). There are usually 6 ridges in the Corixinae, but Diaprepocoris and the Micronectinae have only 4 ridges, and the first instar nymphs of the Corixinae 3 ridges. Cymatia is noticeable for not having transverse ridges with sense organs, ^{and} the rostrum is smooth with a few scattered sense organs (fig. 3.12). Corixids other than Cymatia will catch swimming animals, but also spend a lot of time searching through detritus or mud. The mud and any

objects in it are brought to the ventral head capsule, and then on to the rostrum, where it is analysed by the numerous sense organs, presumably chemoreceptors, on the broad third labial segment. The corixids become particularly 'excited' by animals which they find, but have been observed to feed on pure cultures of algae (section 2.33). In Cymatia which does not actively search for food, but seizes swimming prey, the eyes are presumably the most important sense organs for detecting the prey. The absence of ridges with sense organs on the rostrum of Cymatia is further evidence for the suggested olfactory function of these organs.

It is difficult to form any clear idea as ^{of} the significance of the variation in numbers and arrangement of the bristles on the front of the head capsule. Some species have very many bristles, e.g. Cymatia, while in others they are sparse, eg. Corixia punctata, ^{and} there seems to be no consistent pattern in relation to the known methods of feeding.

These bristles do have a tactile function; when they are lightly stimulated the forelimbs scrape down over the stimulated area, often rapidly and repeatedly. Thus, when an animal or other food material caught by the front legs, is brought to the head in the region of these bristles, its presence can be detected. There is no evidence to suggest that these bristles can be used to detect the movement of prey by vibrations in the water.

3.75 Other structures

Some of the lateral anteclypeal bristles of Diaprepocoris zealandiae and Tenagobia selecta have multipointed ends of unknown significance (fig. 4.6C). There is a pair of similar bristles on D. barycephala, but

they are not found on other corixids. Diaprepocoris and M. poweri have a continuous row of long bristles on the anteclypeus just below the clypeoloral cleft (fig. 3.6.) Descriptions and illustrations of other Micronecta species do not mention these bristles on the front of the head, so that it is not known whether this row is a generic character as it is in Diaprepocoris. These bristles have not been found in other corixids. The anterior edge of the Diaprepocoris anteclypeus has a row of short flat bristles (fig. 4.6C).

On the lateral edge is a group of short, strong bristles (fig. 4.6A), which could be used for cleaning the front leg. On the Micronecta poweri femur, at the distal end, is a long, thin, many branched bristles. This bristle is also described on many of the Micronecta species (Lundbad 1935). It is not found on T. selecta and its significance is not known.

Large dermal gland-pores with a radial surface pattern are found on the head, and the femur and fore tibia of all the adult corixids examined except Cymatia. The exact distribution of the pores is variable, and they are not usually found in areas covered with dense bristles, and are not found on the anteclypeus. Pores are seen on the head of only the fourth and fifth instars of C. punctata (Benwitz 1956a) and on the dorsal and ventral abdomen of the nymphs. Pores on the abdomen of the Micronecta nymphs are described by Walton (1938). The function of these glands is unknown and their absence in Cymatia is significant.

The significance of the various kinds of microsculpture which covers large area of the corixid is unknown. As well as the microsculpture described on the head and front legs of the corixids examined, there is

usually a variety of scale-like markings, sometimes with micro-setae on the middle and hind legs. The nymphs are covered with similar microsculpture on the abdomen and thorax.

3.76 Notonecta (cf. section 2.32)

The rostrum of Notonecta (fig. 3.21) is long four segmented and very mobile. On the tip of the fourth segment are long tactile bristles, and on the two terminal lateral lobes are sense organs similar to those on the terminal segment of Corixa punctata, (Benwitz 1956a).

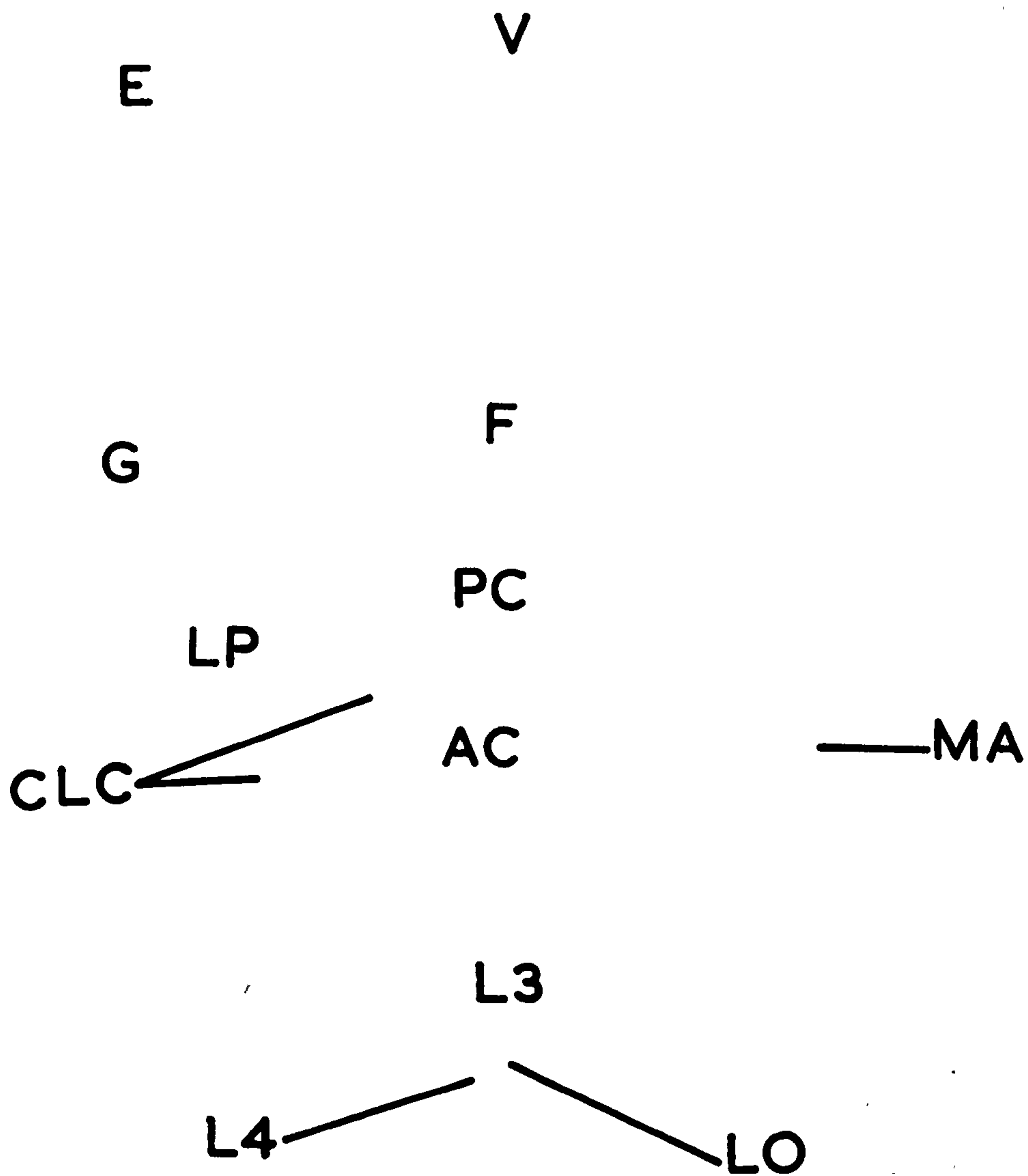
The first two pairs of limbs are of a generalized type, not the highly specialized form of the limbs of corixids or the raptorial type of forelimb of Nepa. These limbs which catch and hold the prey are long and thin, and each has a pair of claws. The prey is held at the base of the legs, while the tip of the rostrum moves over the prey, finding a suitable place for the stylets to be inserted.

<u>Species.</u>	Length of palm (mm.)	Lower paleal row	Upper paleal row	Upper palm row
<u>C.punctata</u>	1.6	18	16	36
<u>A.germari</u>	1.2	15	9	32
<u>S.protusa</u>	0.96 - 1.0	17 - 18	6 - 7	17
<u>S.dorsalis</u>	0.8	22	11	32
<u>S.falleni</u>	0.8	23	9	32
<u>D.zealandiae</u>	0.8	24	12 - 14	16
<u>S.lateralis</u>	0.56	21	12	30
<u>S.nigrolineata</u>	0.48	25	14	28
<u>M.poweri</u>	0.11	15	4 - 5	10
<u>G.propinqua</u>	1.1	12	9 - 10	40
<u>C.bonsdorffi</u>	0.96	7	7	
<u>C.coleontrata</u>	0.64	6	6	
<u>N.snowi</u>	0.8	13	3	13
<u>D.barycephala</u>		12	7 - 8	12

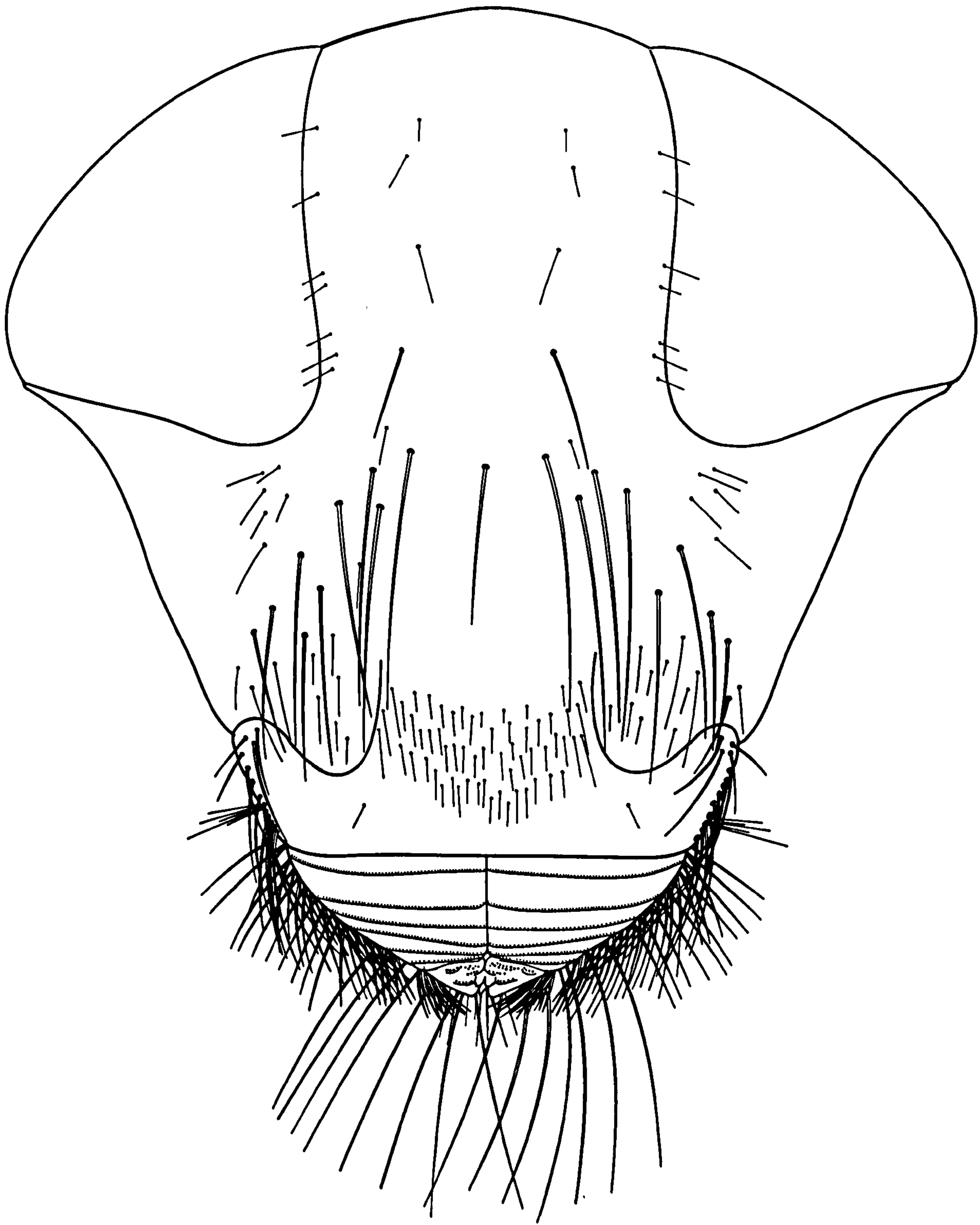
Table 3.1

The number of bristles in the upper and lower paleal rows and the upper palm row compared with the length of the 'palm' in female corixids.

Fig. 3.1. Sigara falleni, female;
front of the head.



1mm



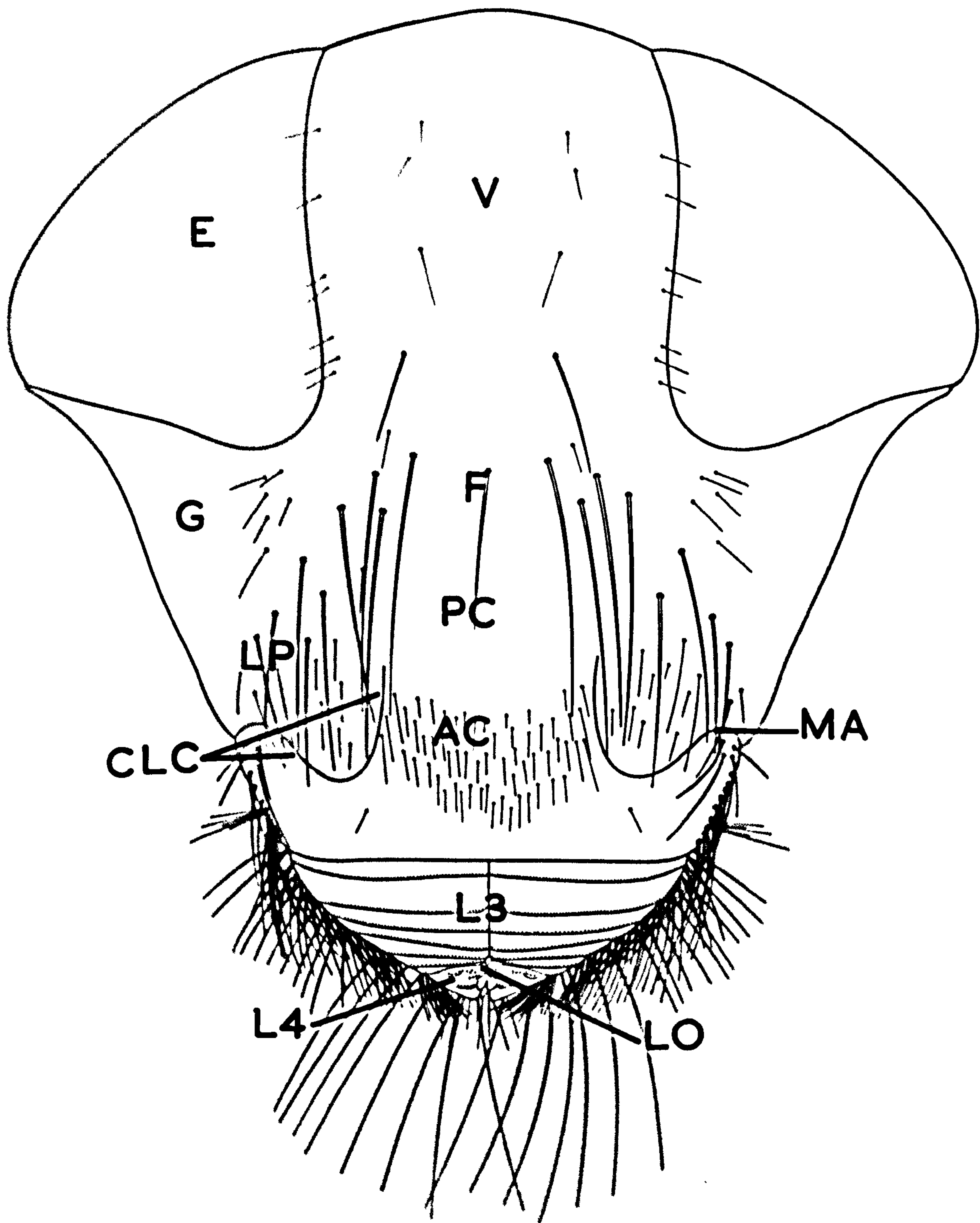


Fig. 3.2. Sigara falleni, female; posterior of the head. See fig. 3.17 and the text for a description of the rostrum bristles. The bristles on each antennal segment are not illustrated.

E

V

—R

A

FO > PR

O

MXPL —
AC —

SO

—GR

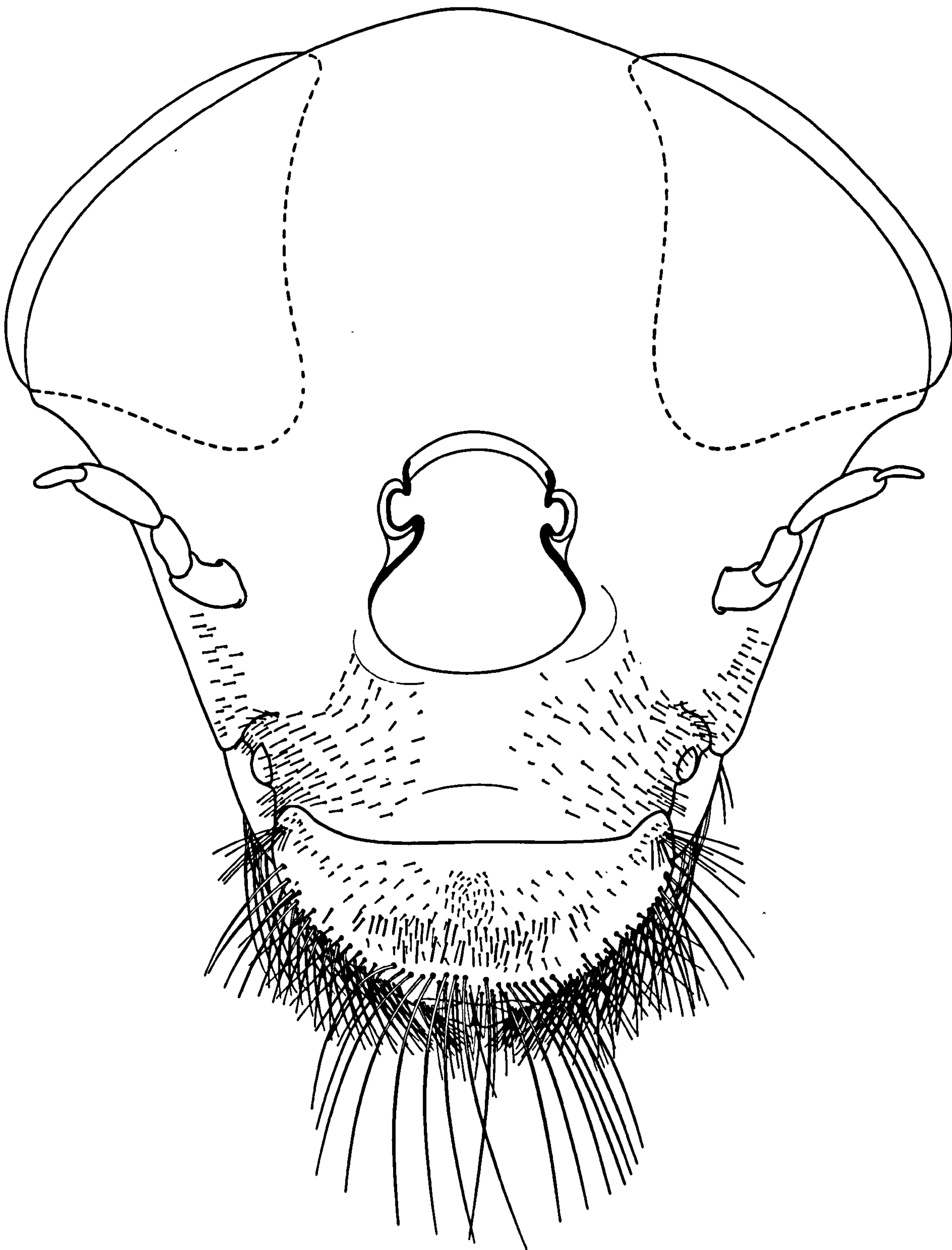
—MA
—CGO

L3

L4

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1 mm



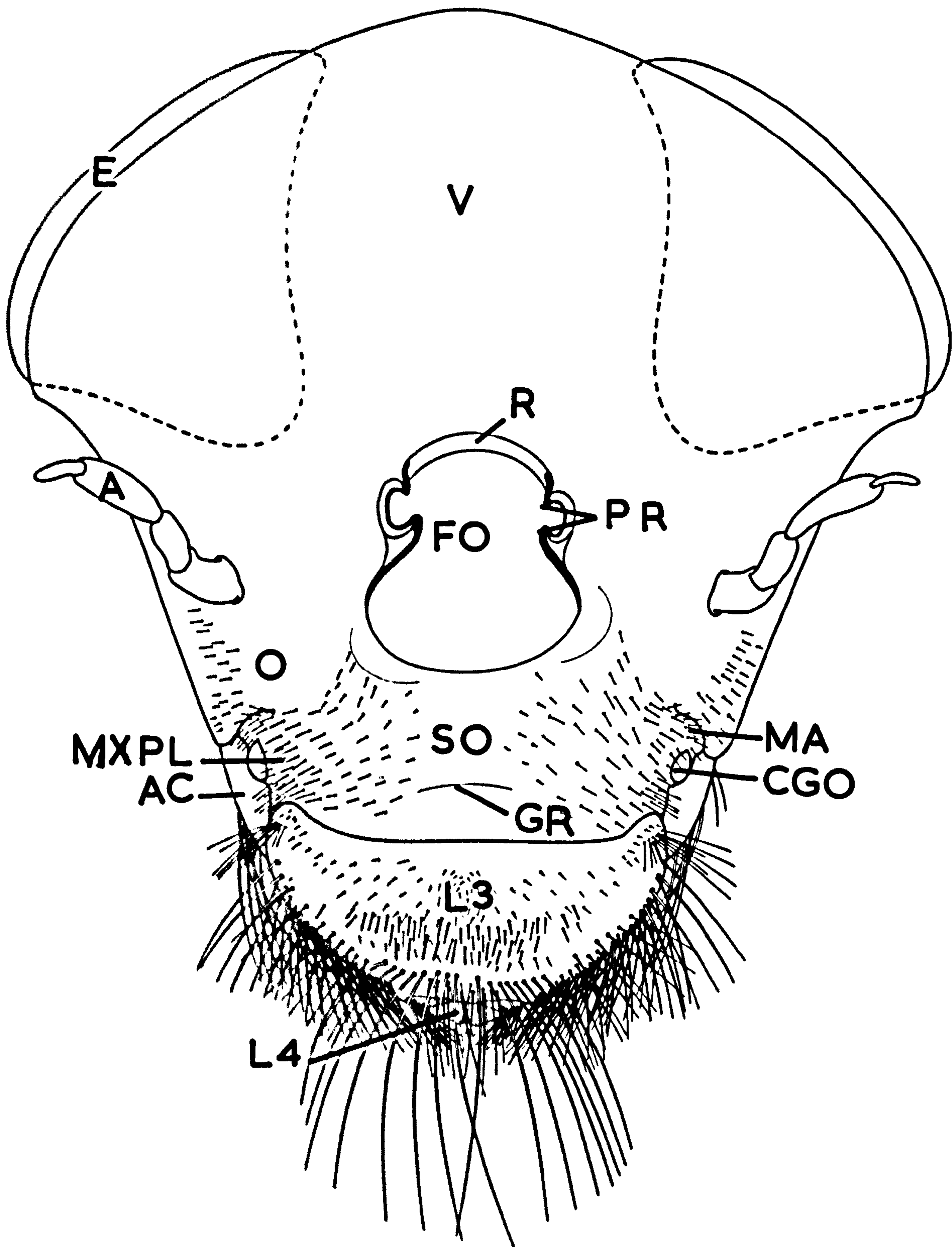
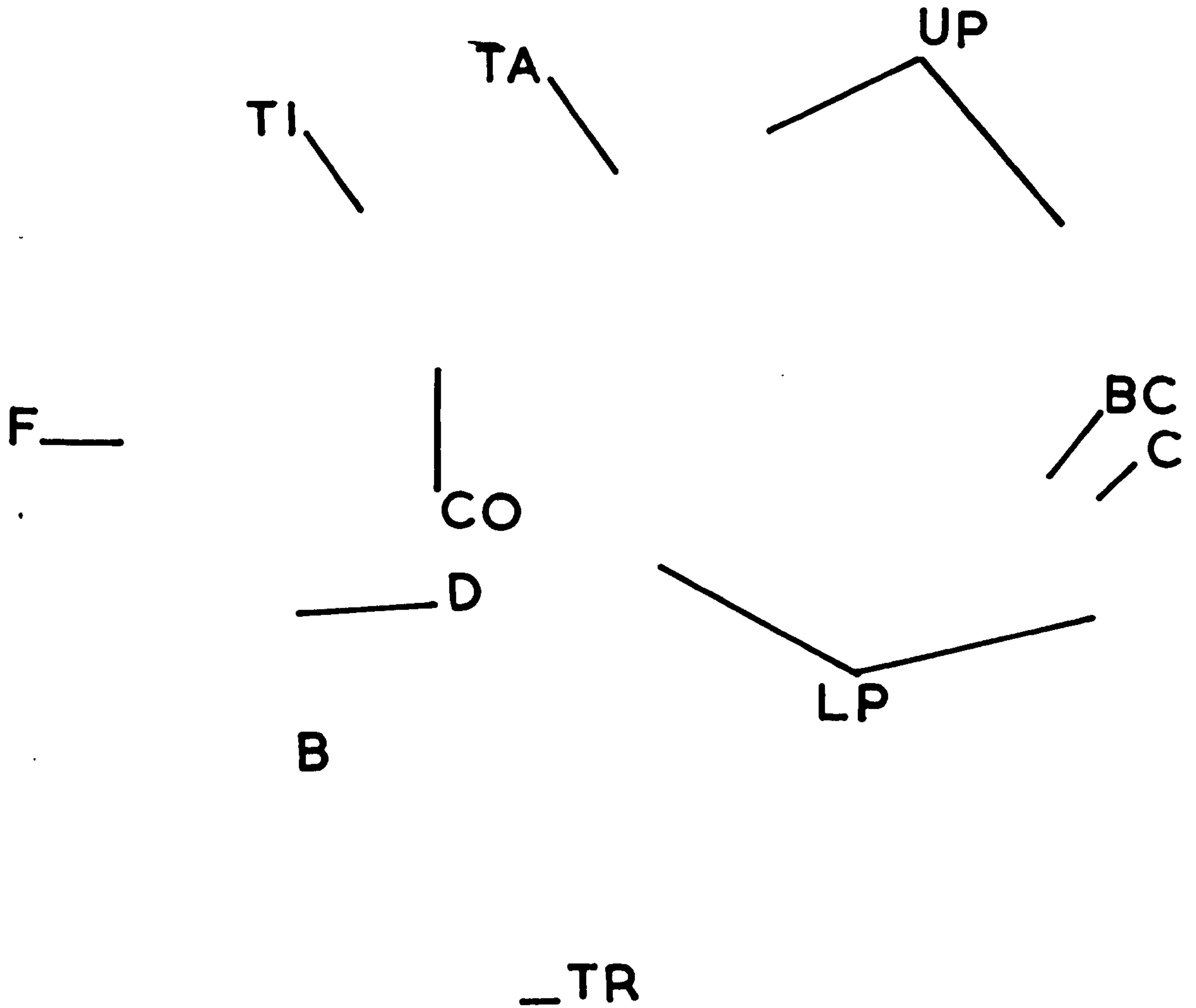
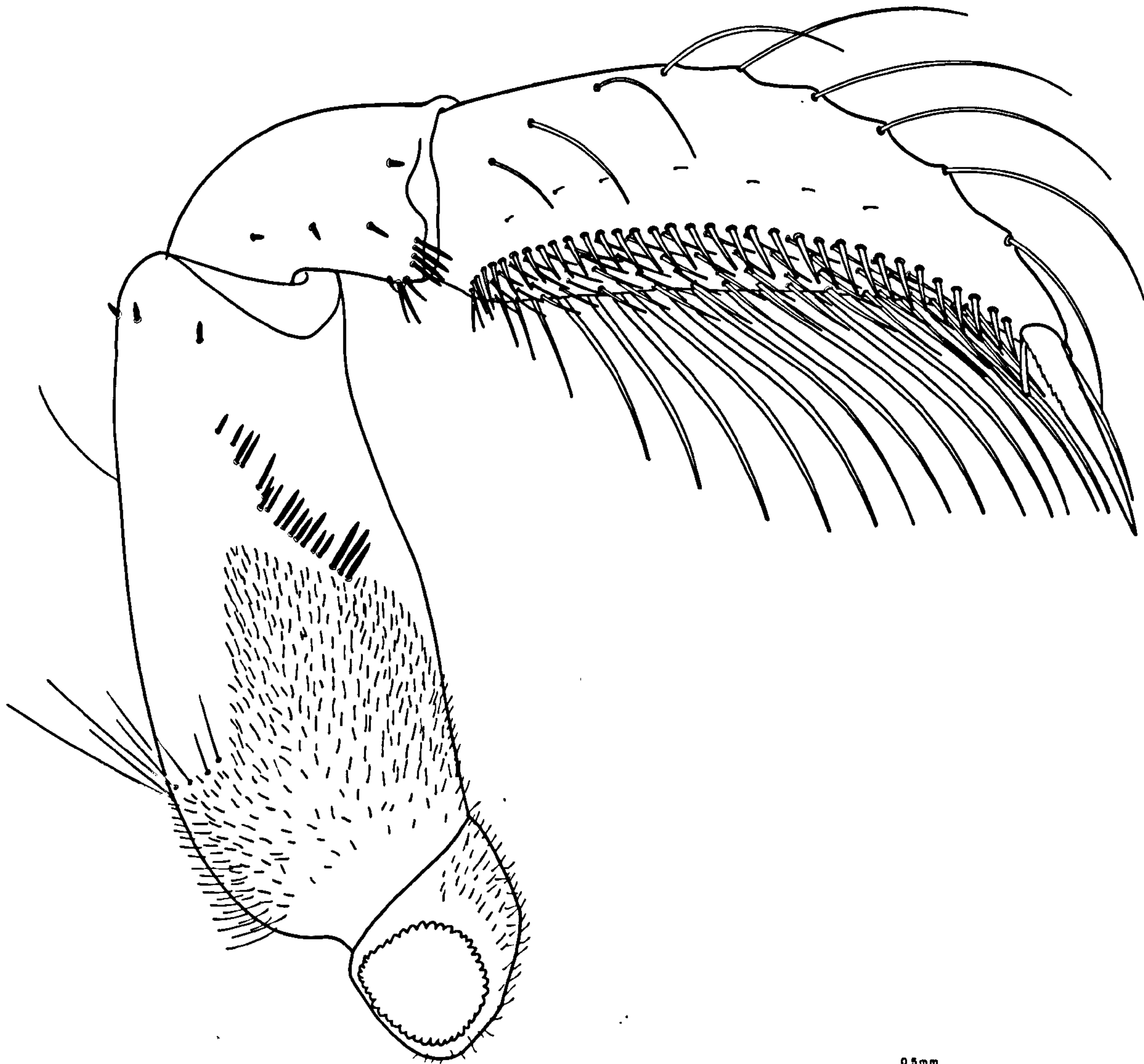
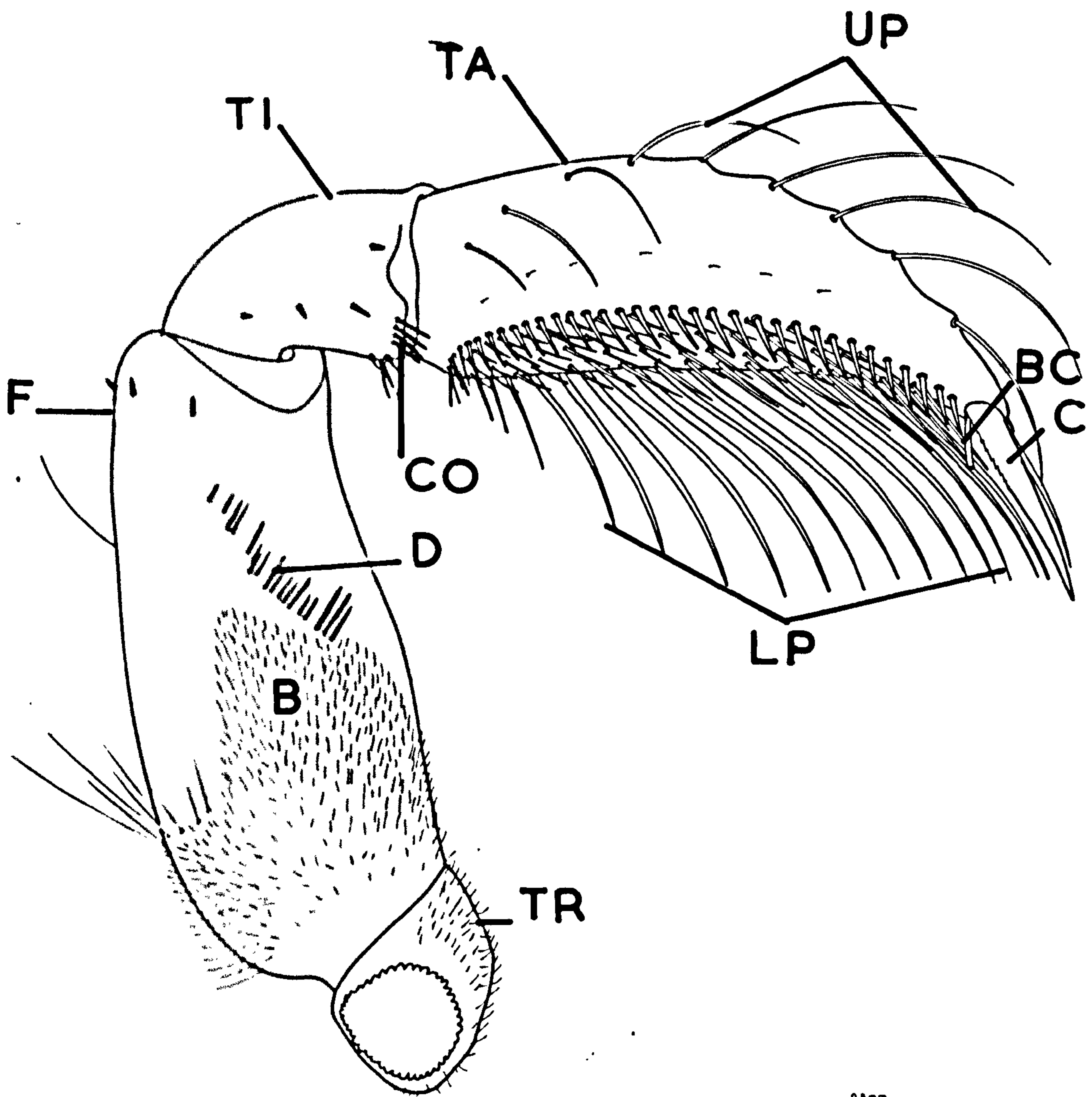


Fig. 3.3. Sigara falleni, female; forelimb.

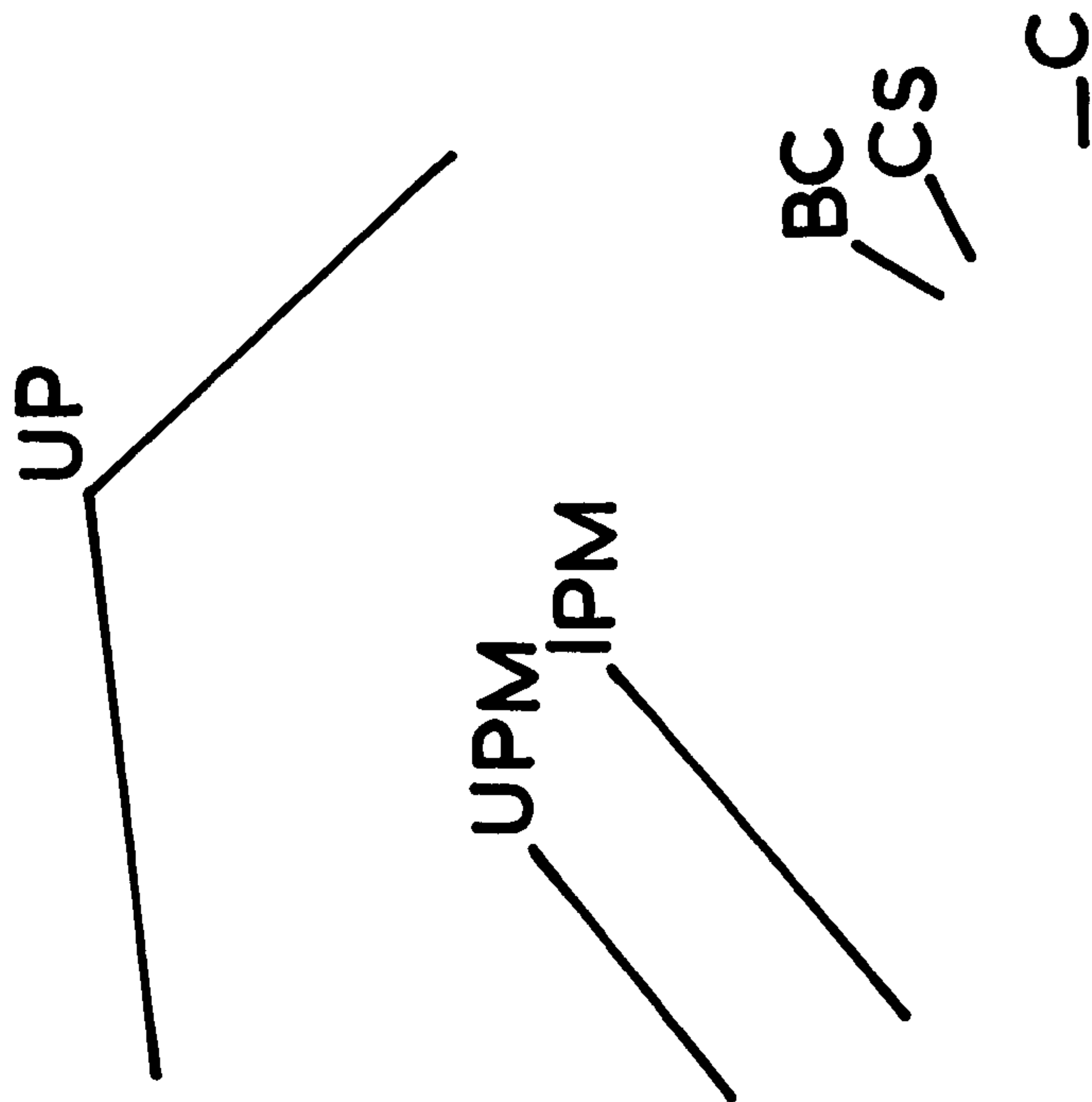






0.5mm

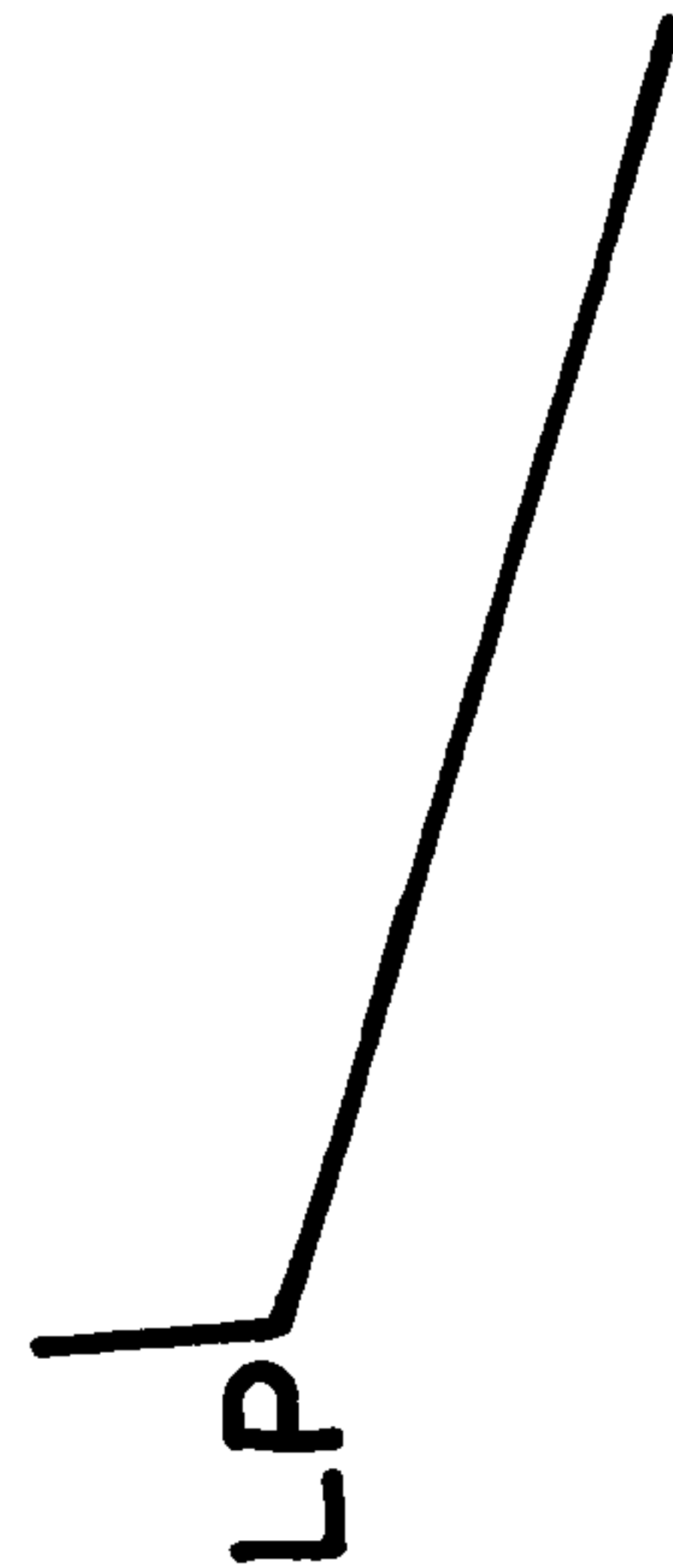
Fig. 3.4. Sigara falleni, female; fore tibia and fore tarsus.



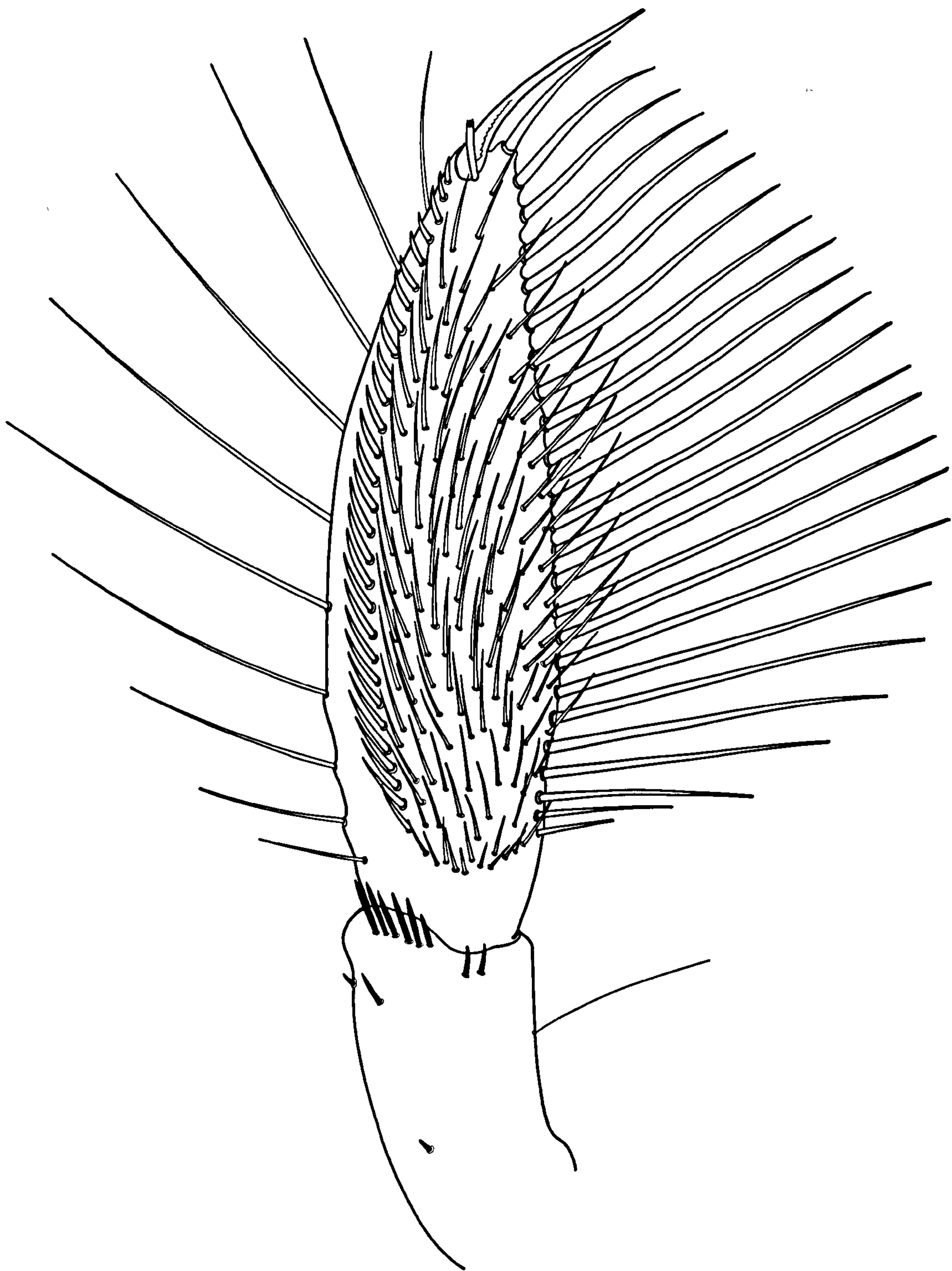
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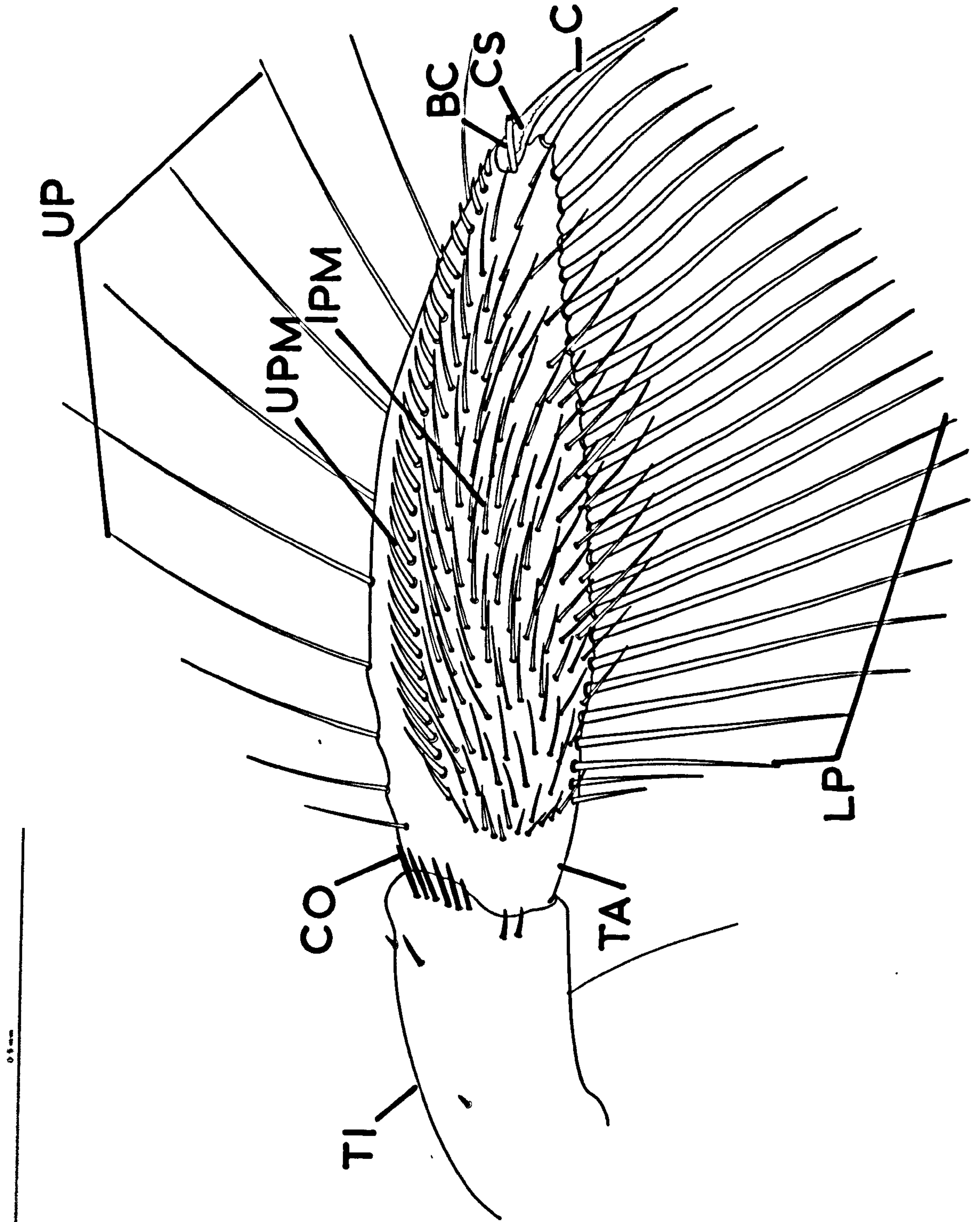
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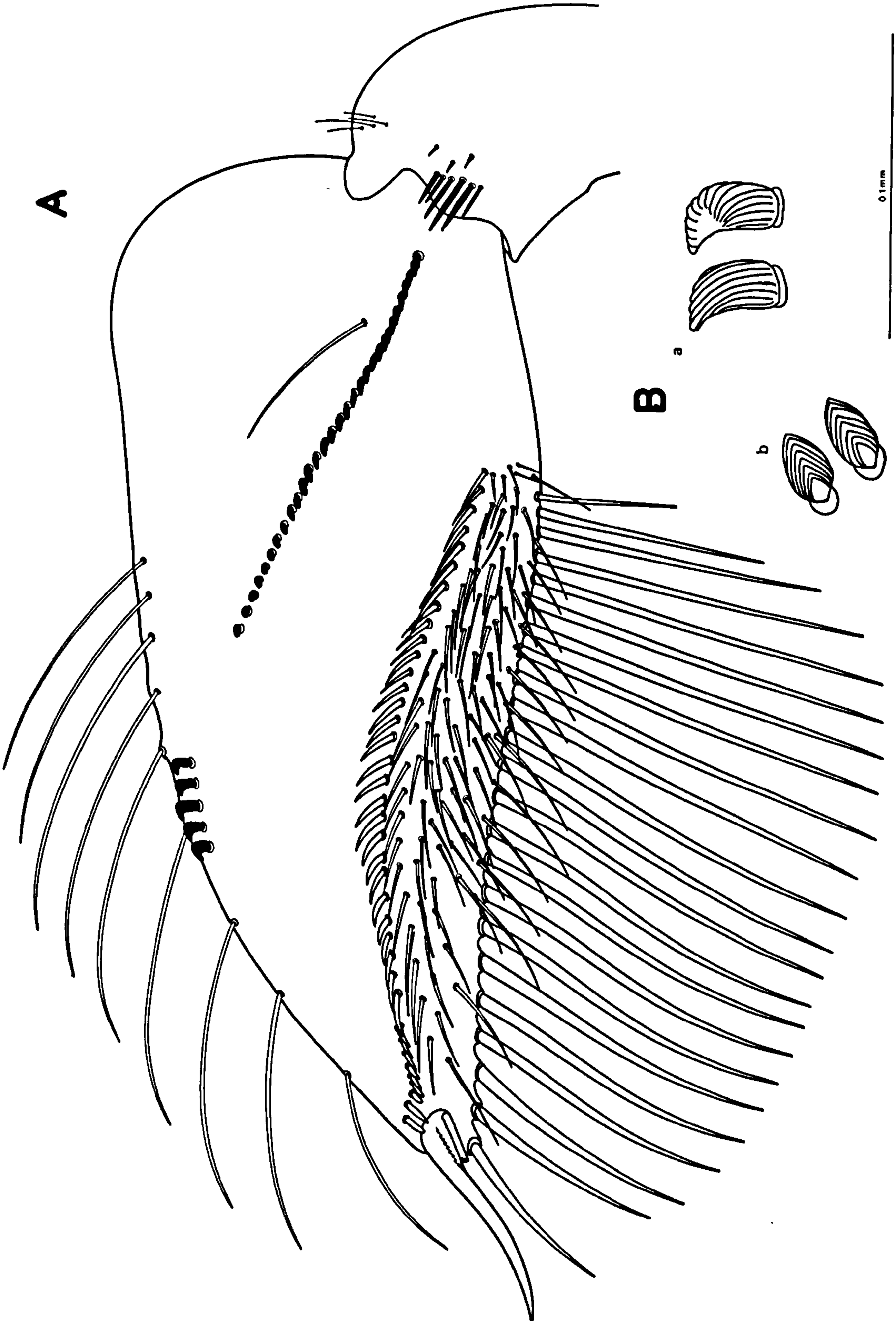




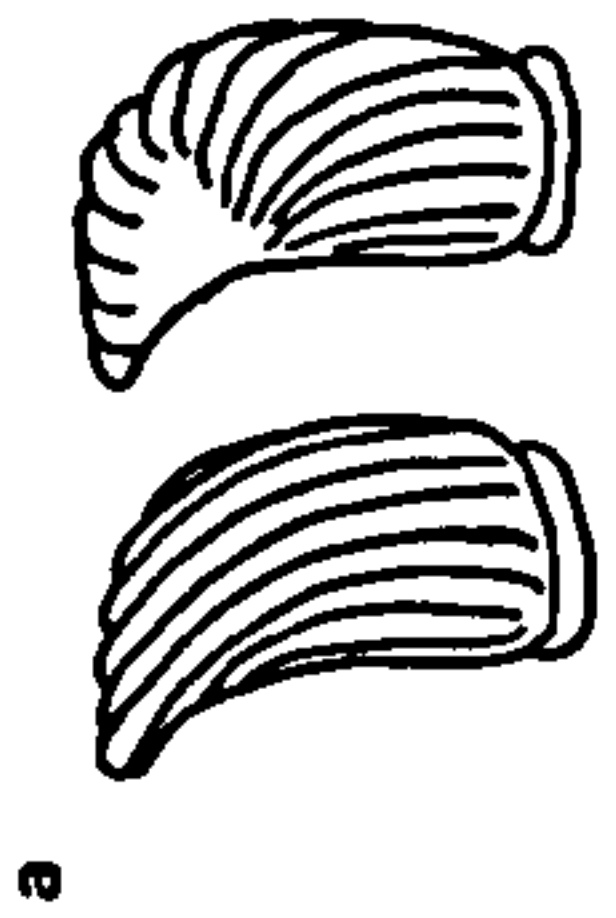
Figs. 3.5. Sigara falleni, male; fore tibia and fore tarsus. A, between the upper paleal and upper palm bristles (see fig. 3.4) are the two rows of male pegs, a short distal row and a long basal row. B, the detailed structure of the male pegs; a, the hooked distal pegs; b, basal pegs.

0.5 mm

A



B

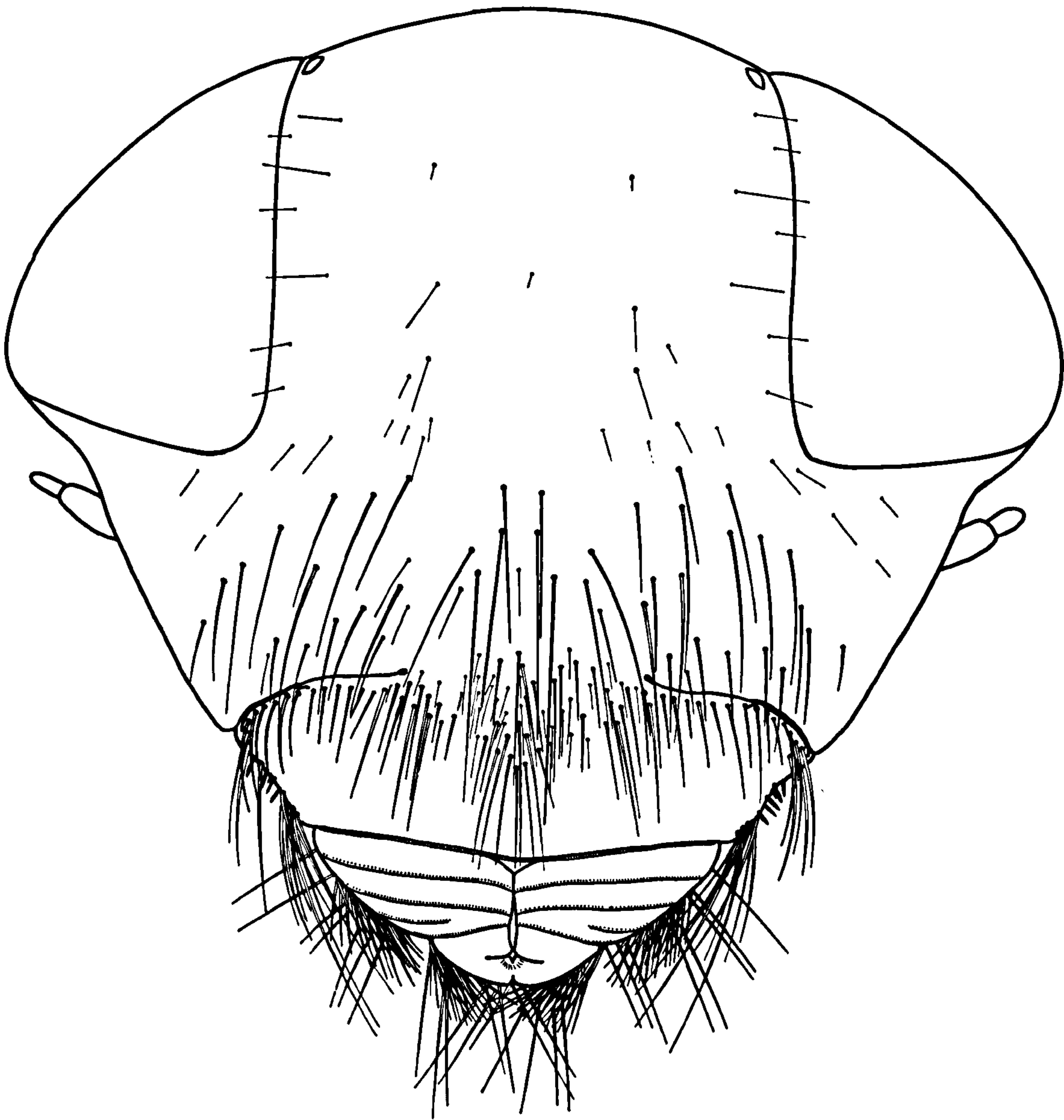


0.1 mm

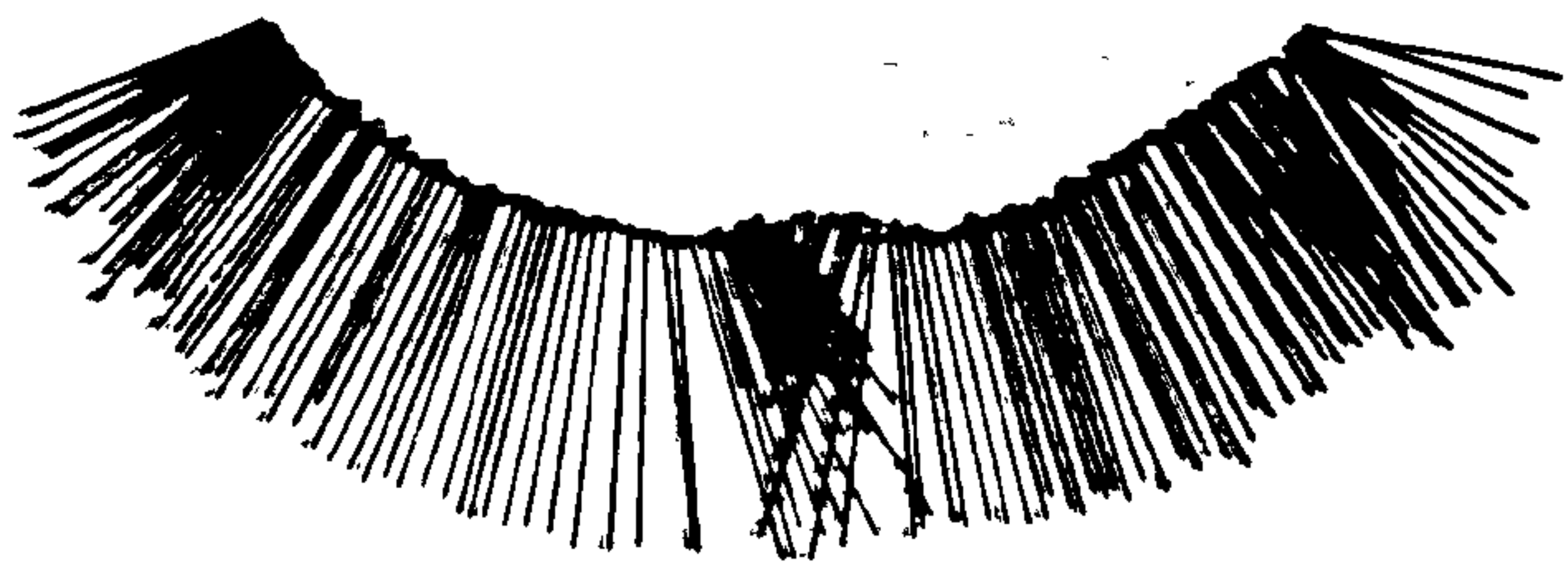
Fig. 3.6. Diaprepocoris zealandiae, female; front of the head.

Diaprepocoris has ocelli on the dorsal vertex adjacent to the compound eye. See fig. 3.1 for the names of the parts of the head.

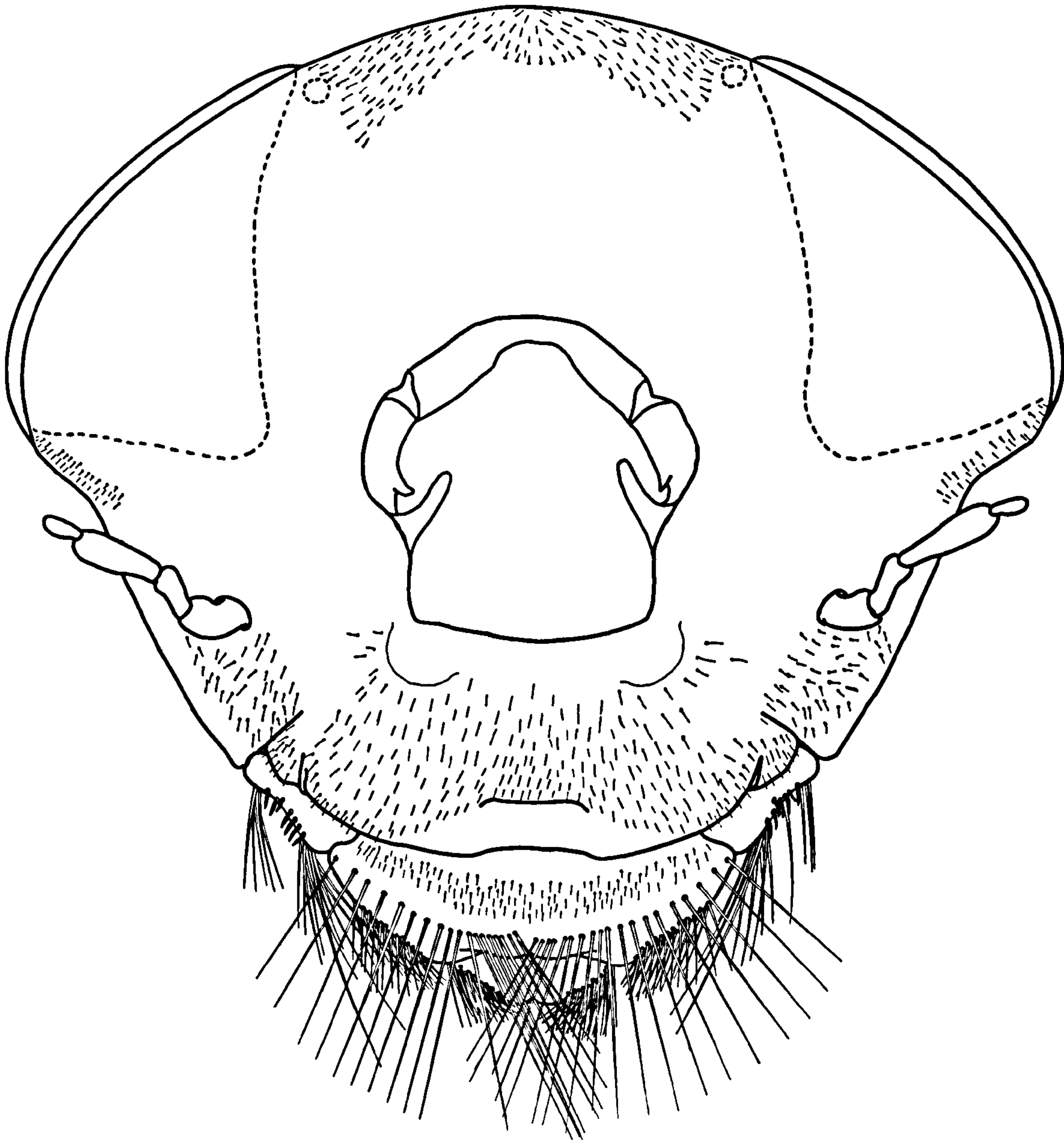
1 mm



Figs. 3.7 Diaprepocoris zealandiae, female; posterior of the head. The inner row of rostrum bristles on the third labial segment are shown on the transparency. See fig. 3.2 for the names of the parts of the head.



1mm



1mm

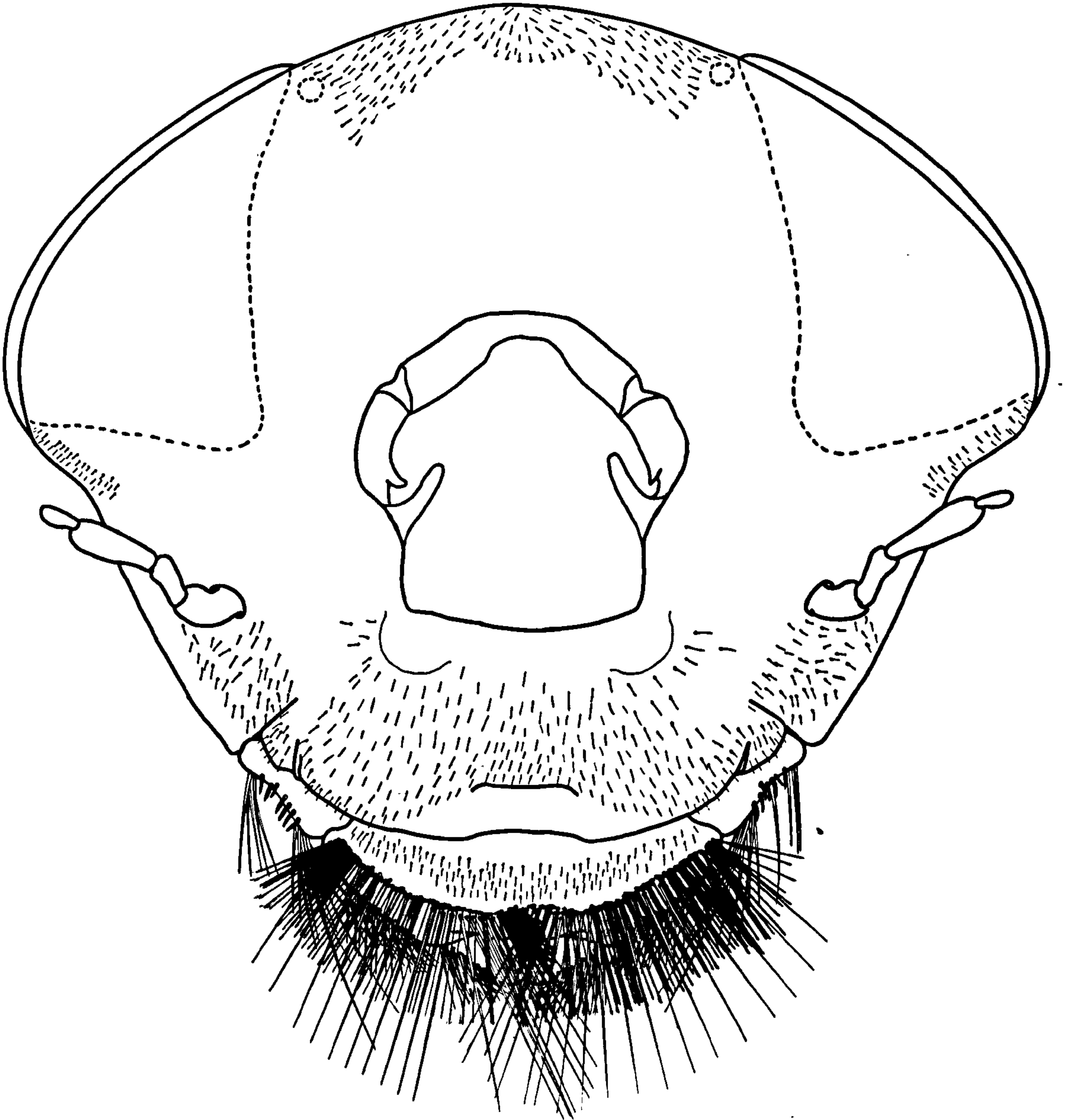


Fig. 3.8. Diaprepocoris zealandiae, female; the forelimb in which the tibia and tarsus are undivided. See figs. 3.3 and 3.4 for the names of the parts of the leg.



0.5 mm

Fig. 3.9. Diaprepocoris zealandiae, female; the fore tibia-tarsus.

See fig. 3.4 for the names of the parts of the leg.

0.5 mm

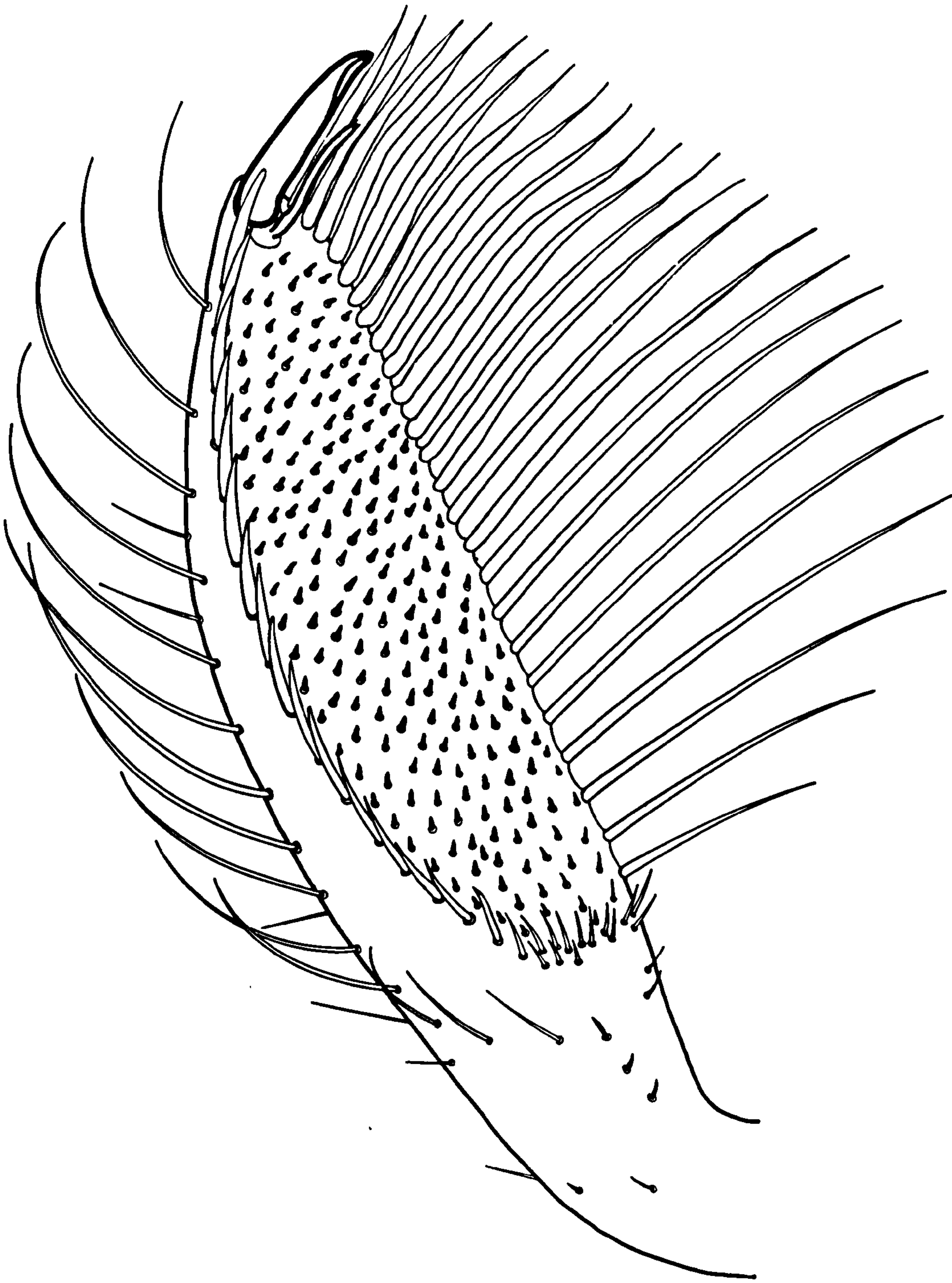


Fig. 3.10 Stenocorixa protrusa, female; the forelimb. Details of the basal region of the lower paleal bristles are shown in fig. 2.11 D. See figs. 3.3 and 3.4 for the names of the parts of the forelimb.

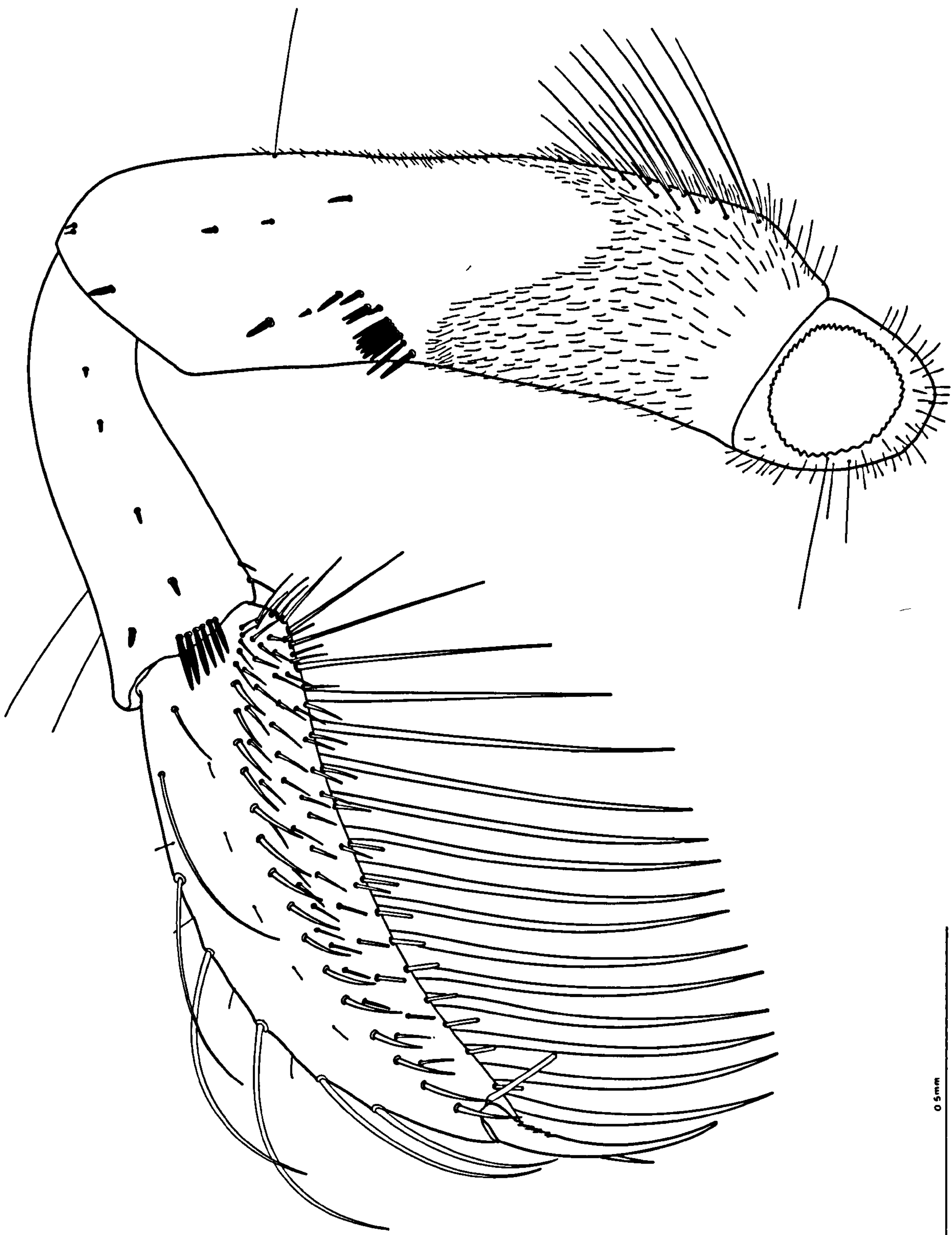


Fig. 3.11. Stenocorixa protrusa, adult, forelimb; A, the male fore tibia and fore tarsus; B, male and C, female, distal end of the tarsus showing the effect of the claw, represented by dotted lines, on the shape of the tarsus and the arrangement of the bristles; D, an enlargement of the base of the lower paleal bristles showing the small projections on the bristles, see fig. 3.4 for the names of the parts of the leg.

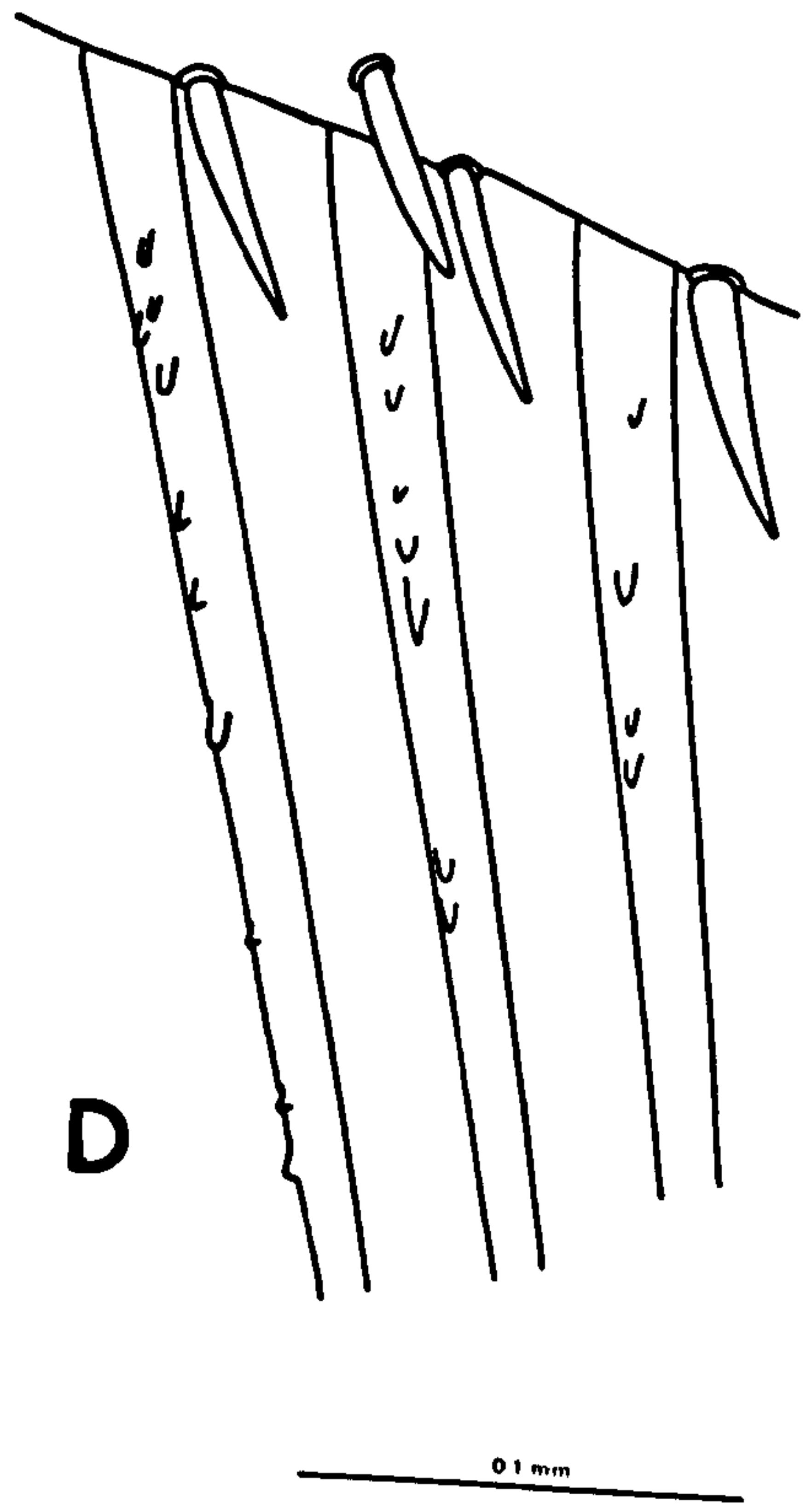
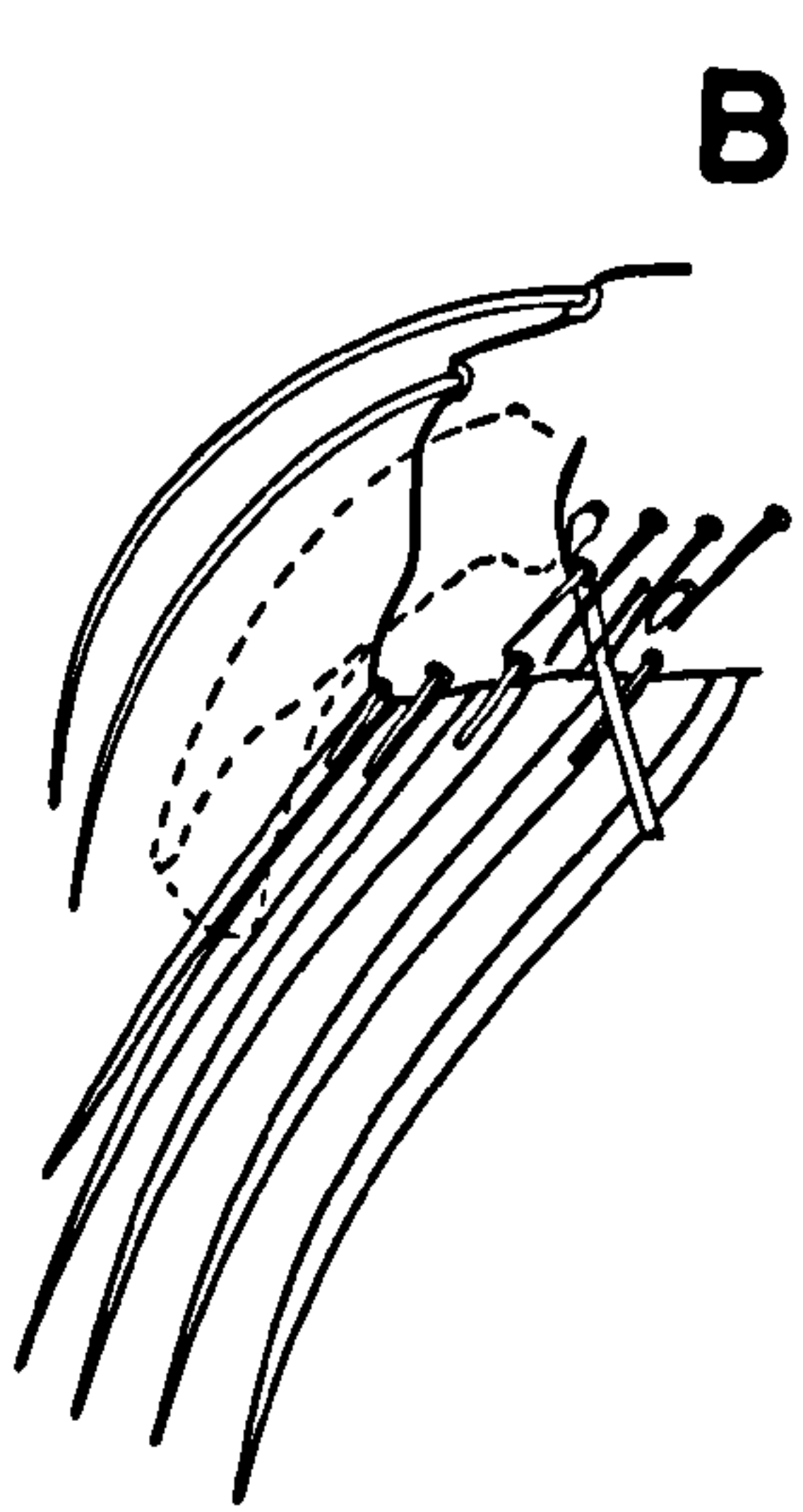
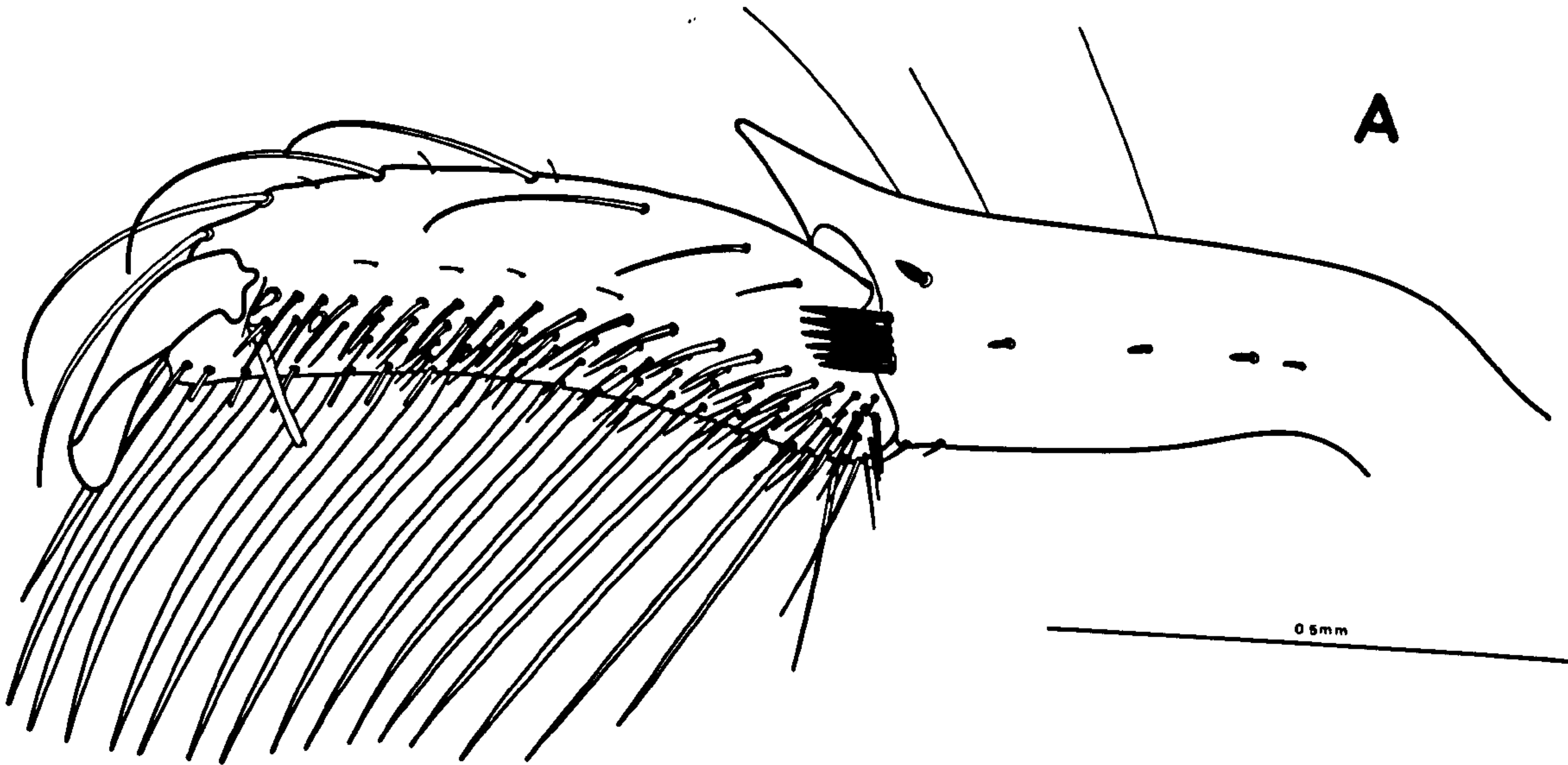


Fig. 3.12. Cymatia bonsdorffi, female; front of the head. See fig. 3.1 for the names of the parts of the head, and note that there are no transverse ridges on labial segment 3.

1mm

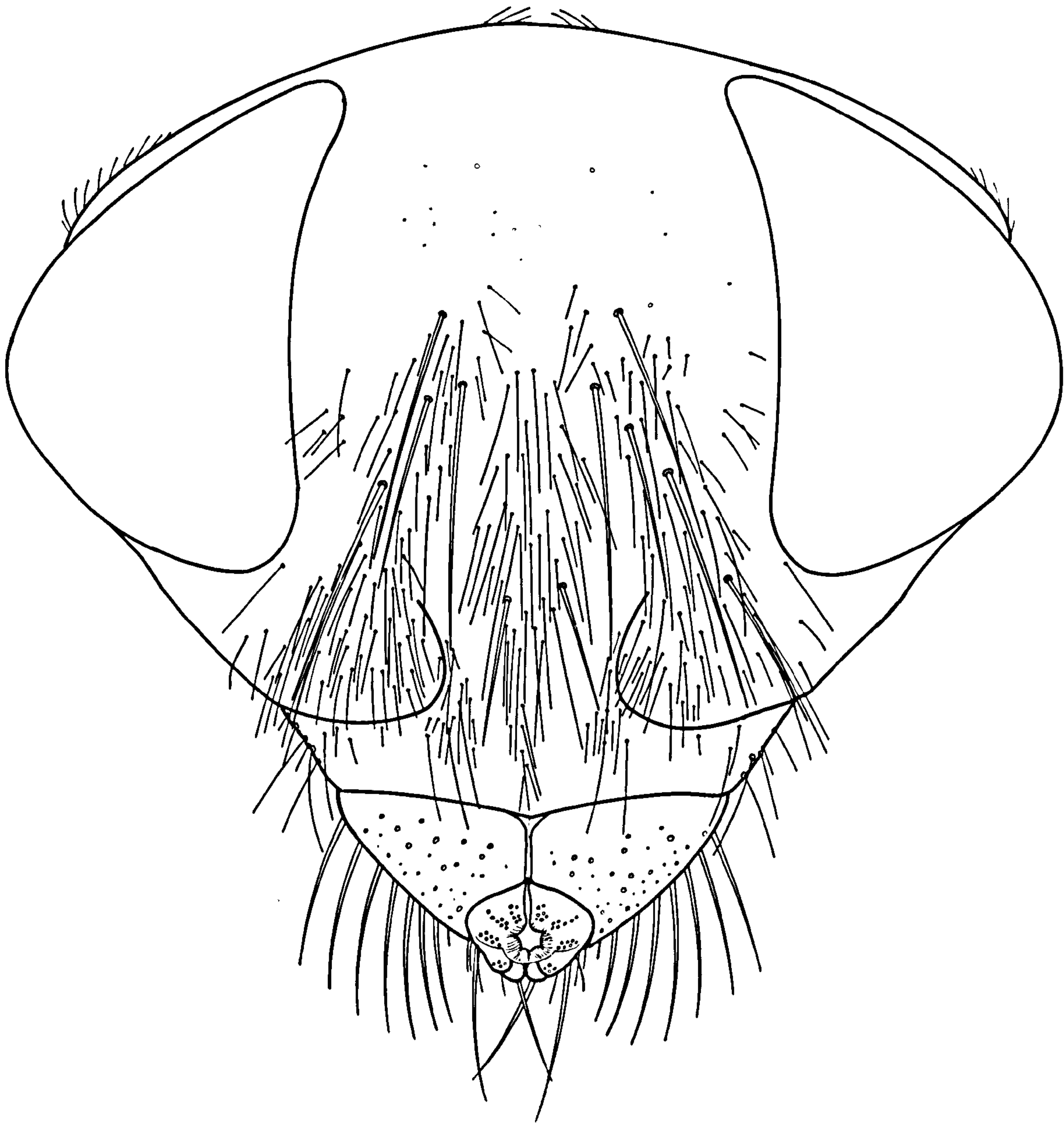


Fig. 3.13. Cymatia bonsdorffi, female; posterior of the head. See fig. 3.2 for the names of the parts of the head.

1mm

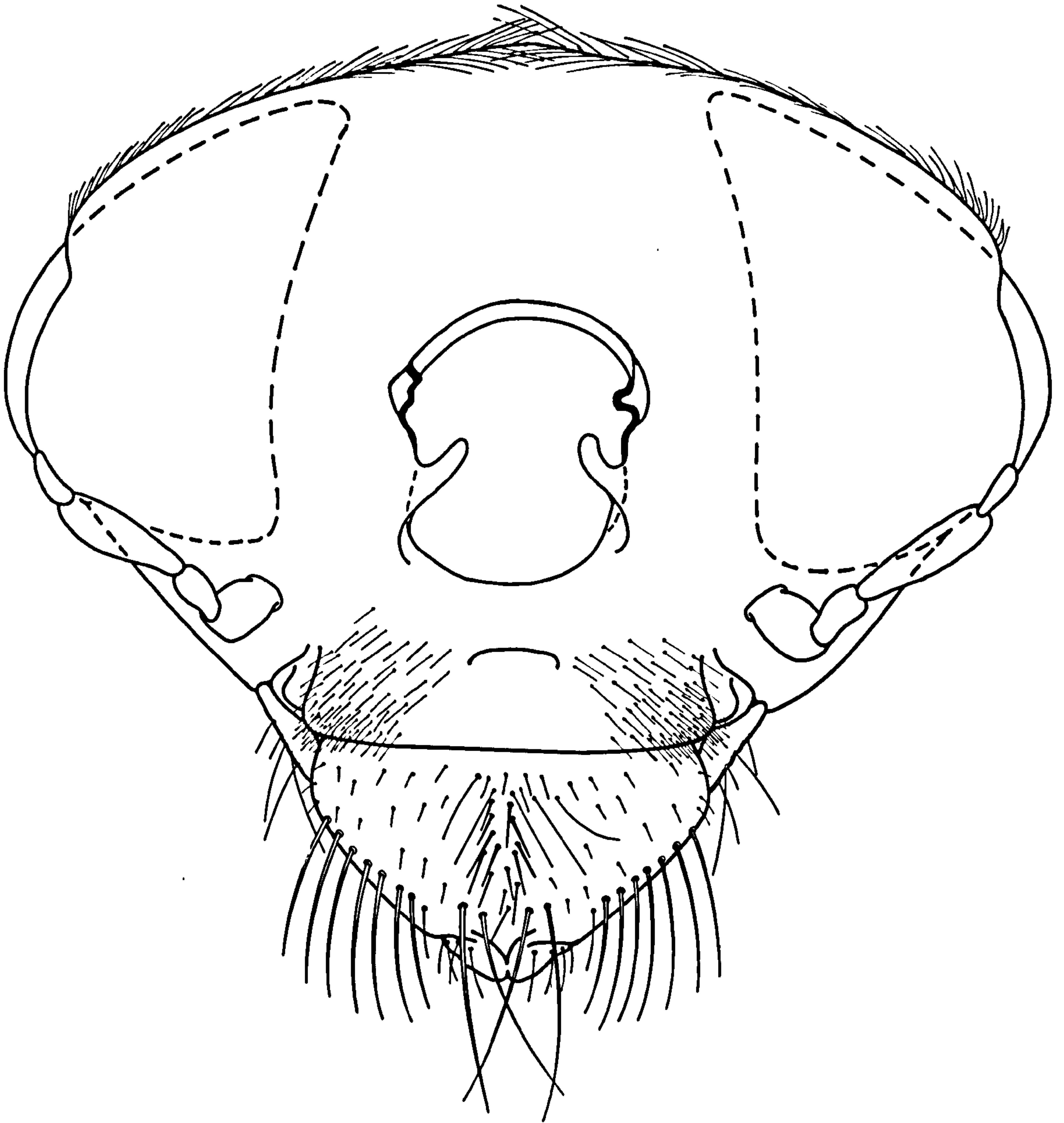


Fig. 3.14. Cymatia bonsdorffi, female; forelimb. The typical palm structure on the tarsus is absent and there are long strong bristles on the femur. See figs. 3.3 and 3.4 for the names of the parts of the forelimb.

0.5 mm

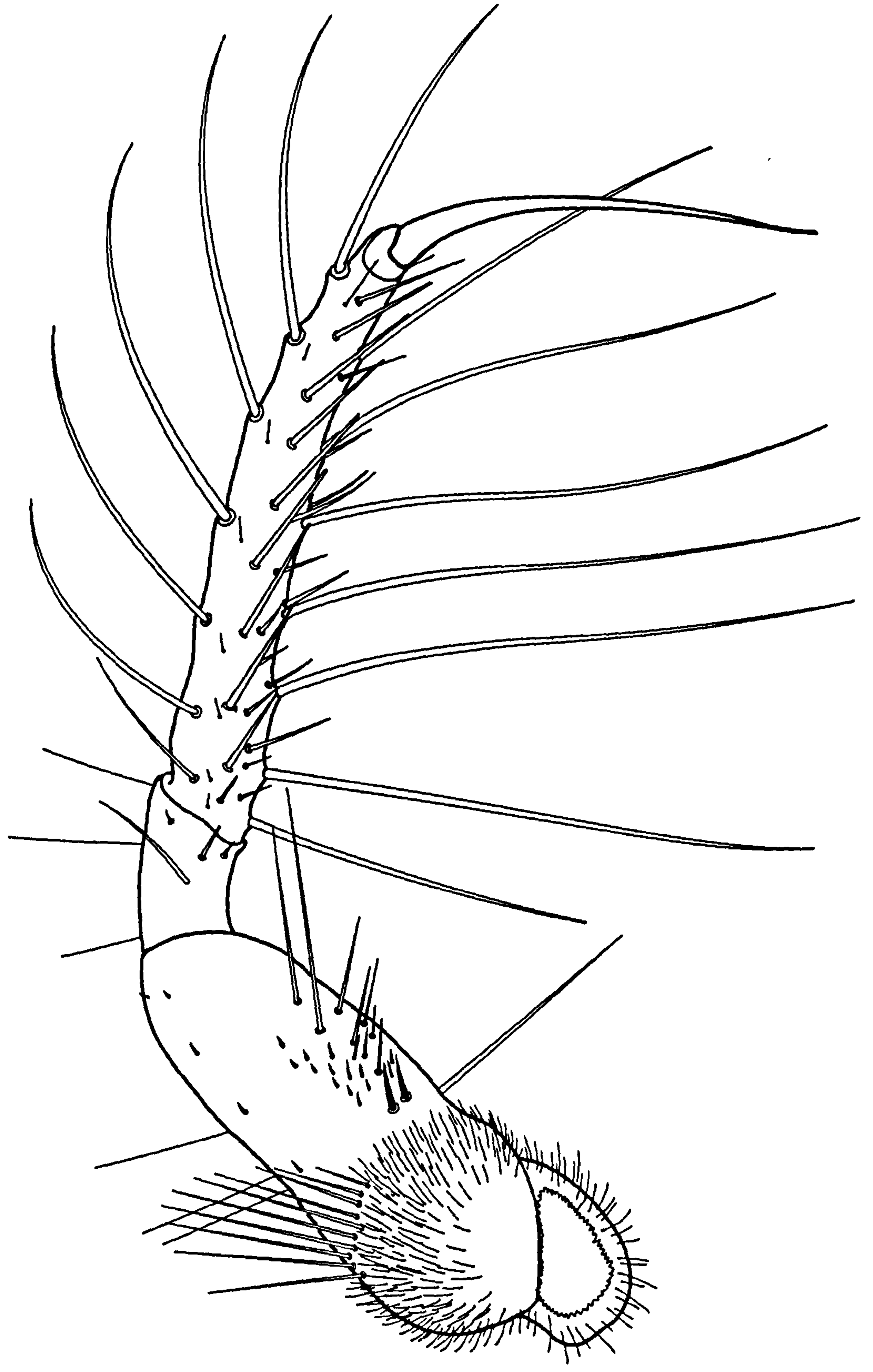
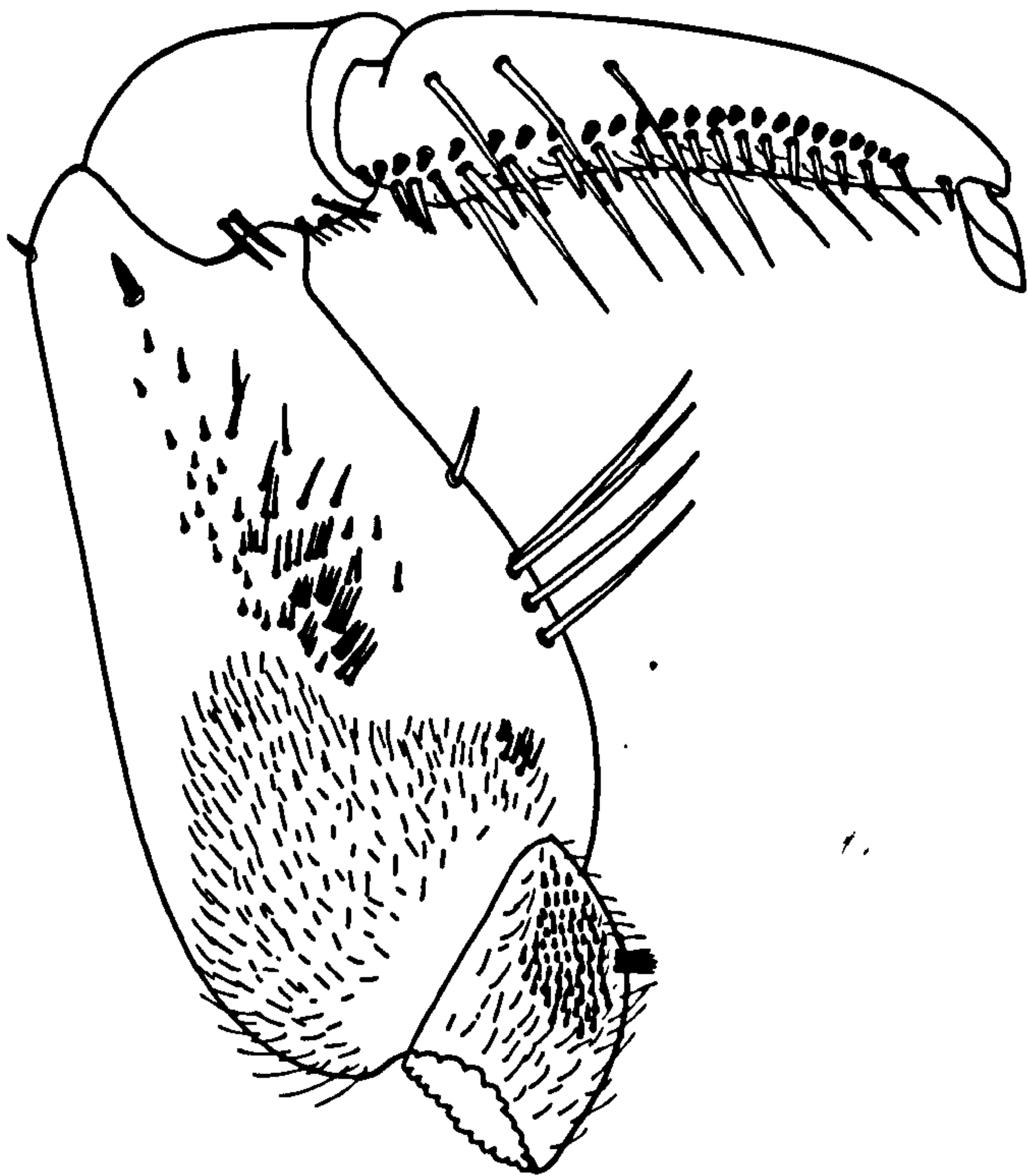
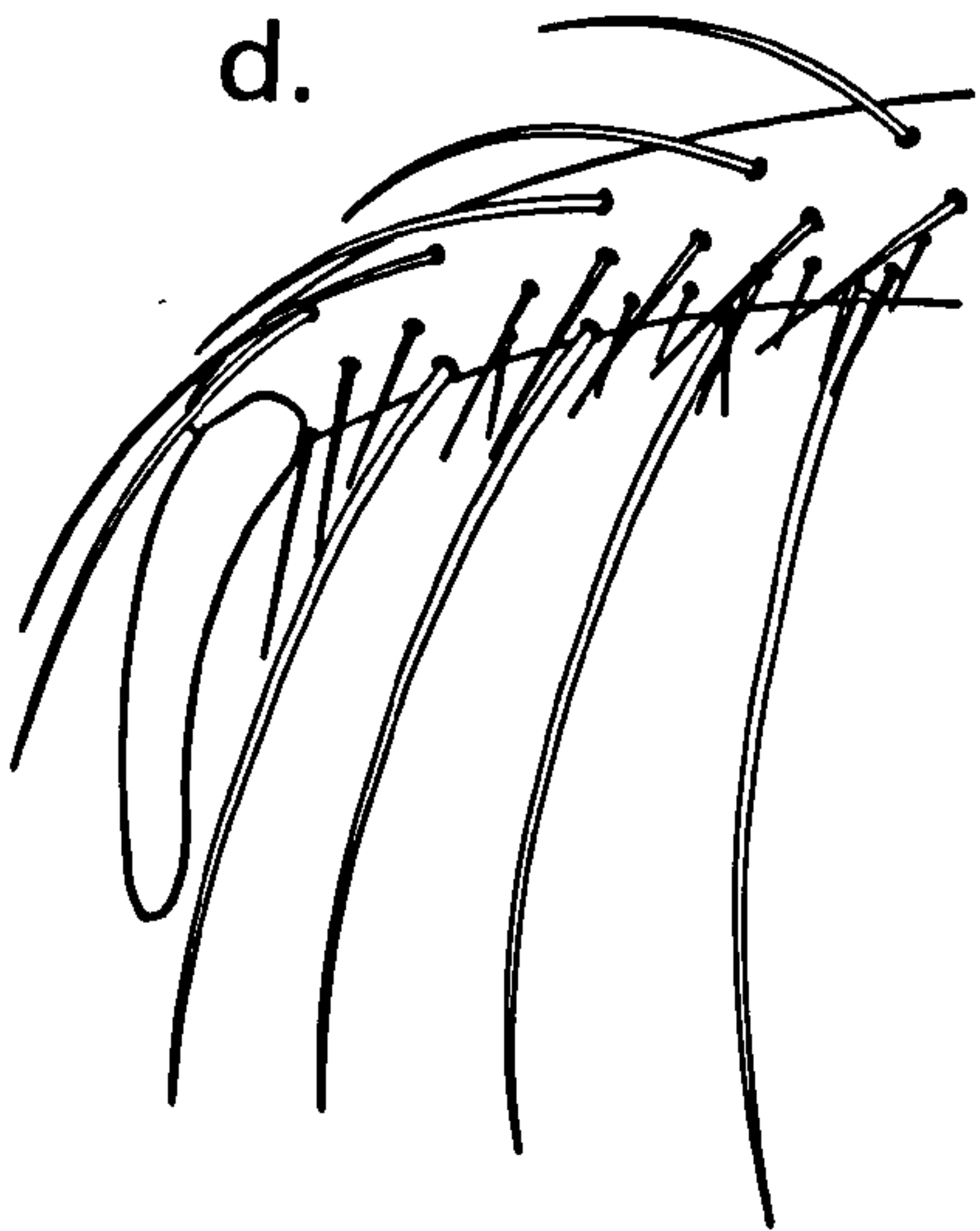
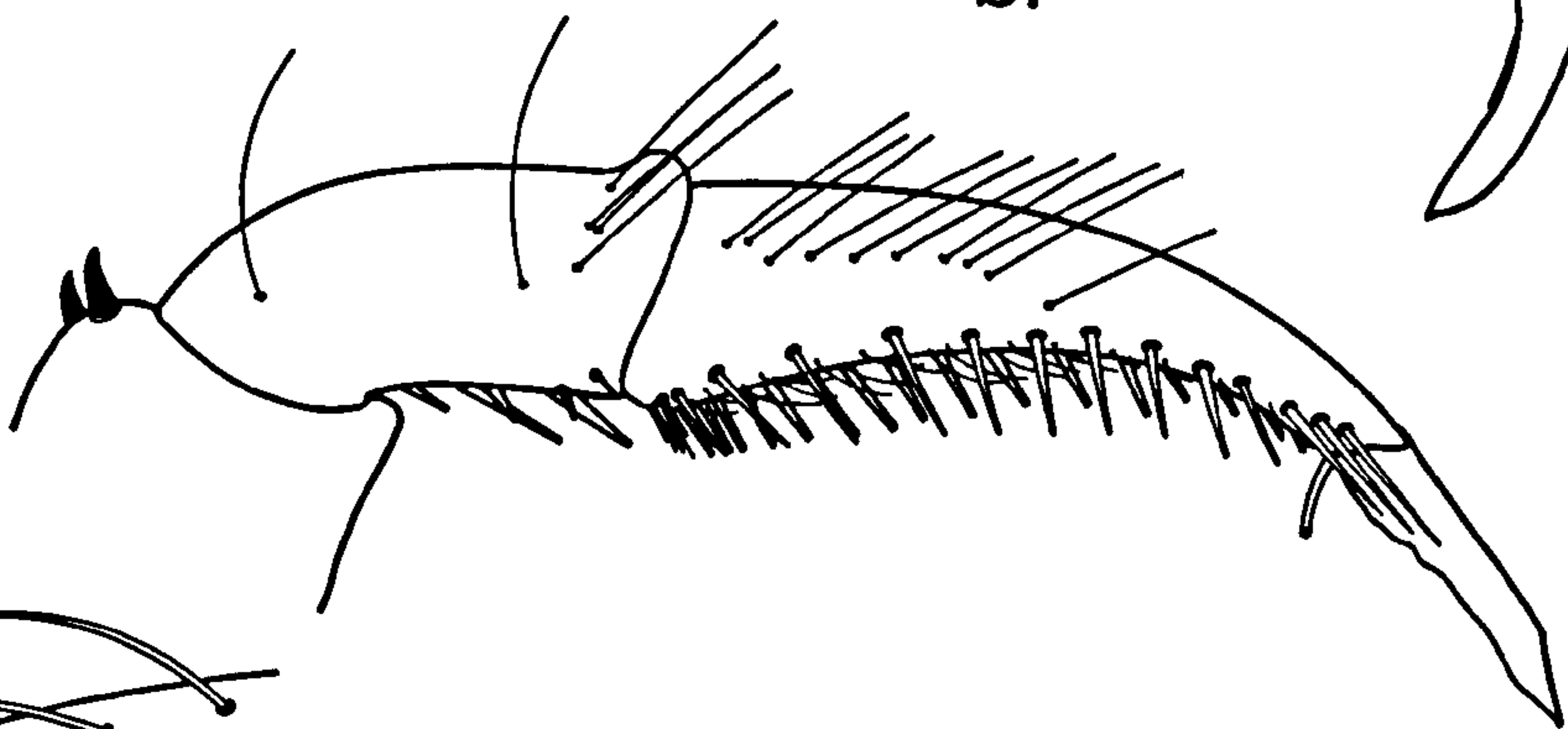
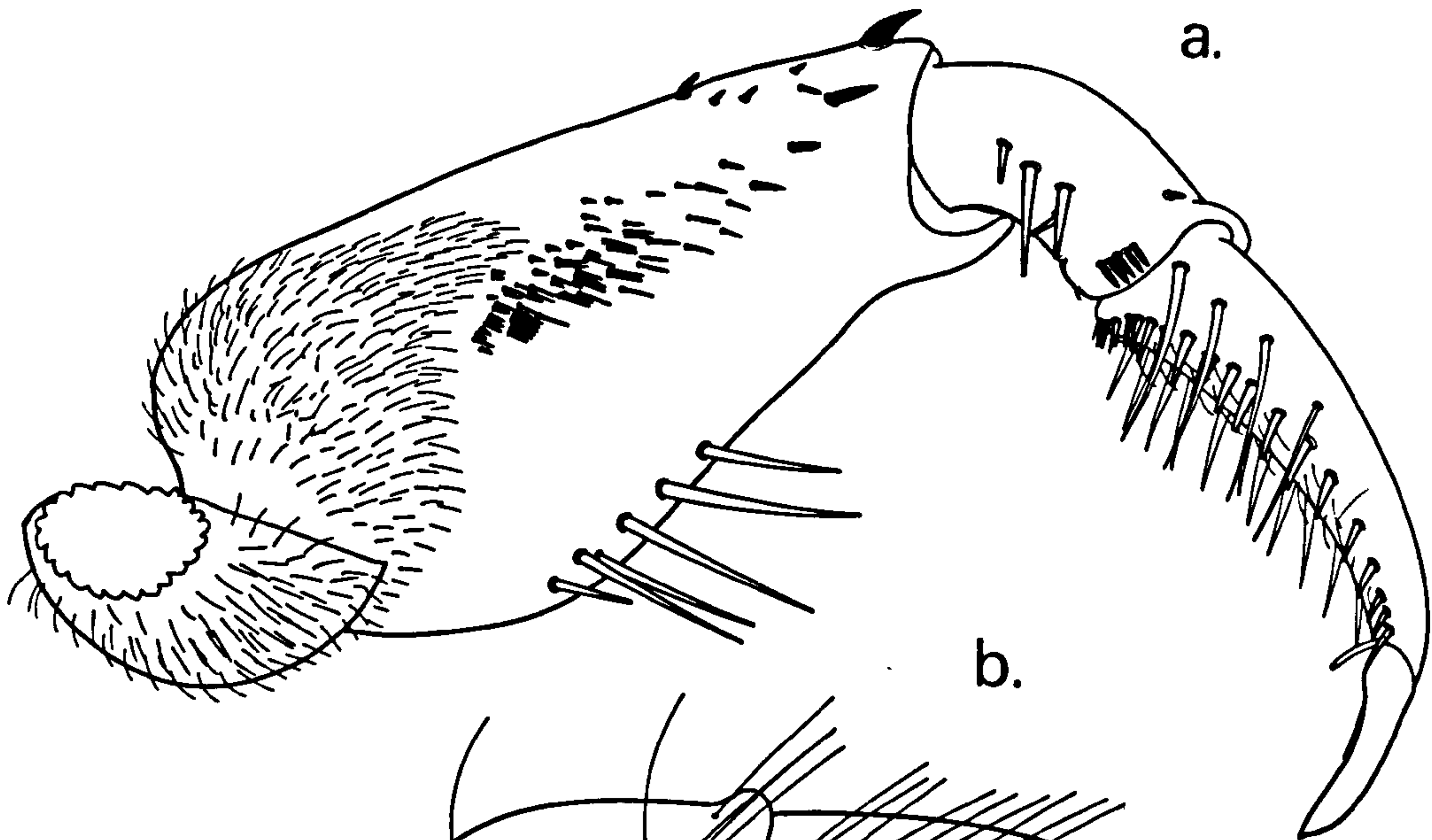


Fig. 3.15 Neocorixa snowi, adult; forelimb: A, female, upperside;
B, female, lower side; C, male, upper side; E, enlargement of a male
peg.

D, Cymatia bonsdorffi, male; distal end of fore tarsis and claw.

See figs. 3.3 and 3.4 for the names of the parts of the forelimb.



e.



Fig. 3.16. Corixa punctata, female; front of the head. See fig. 3.1
for the names of the parts of the head.

1 mm

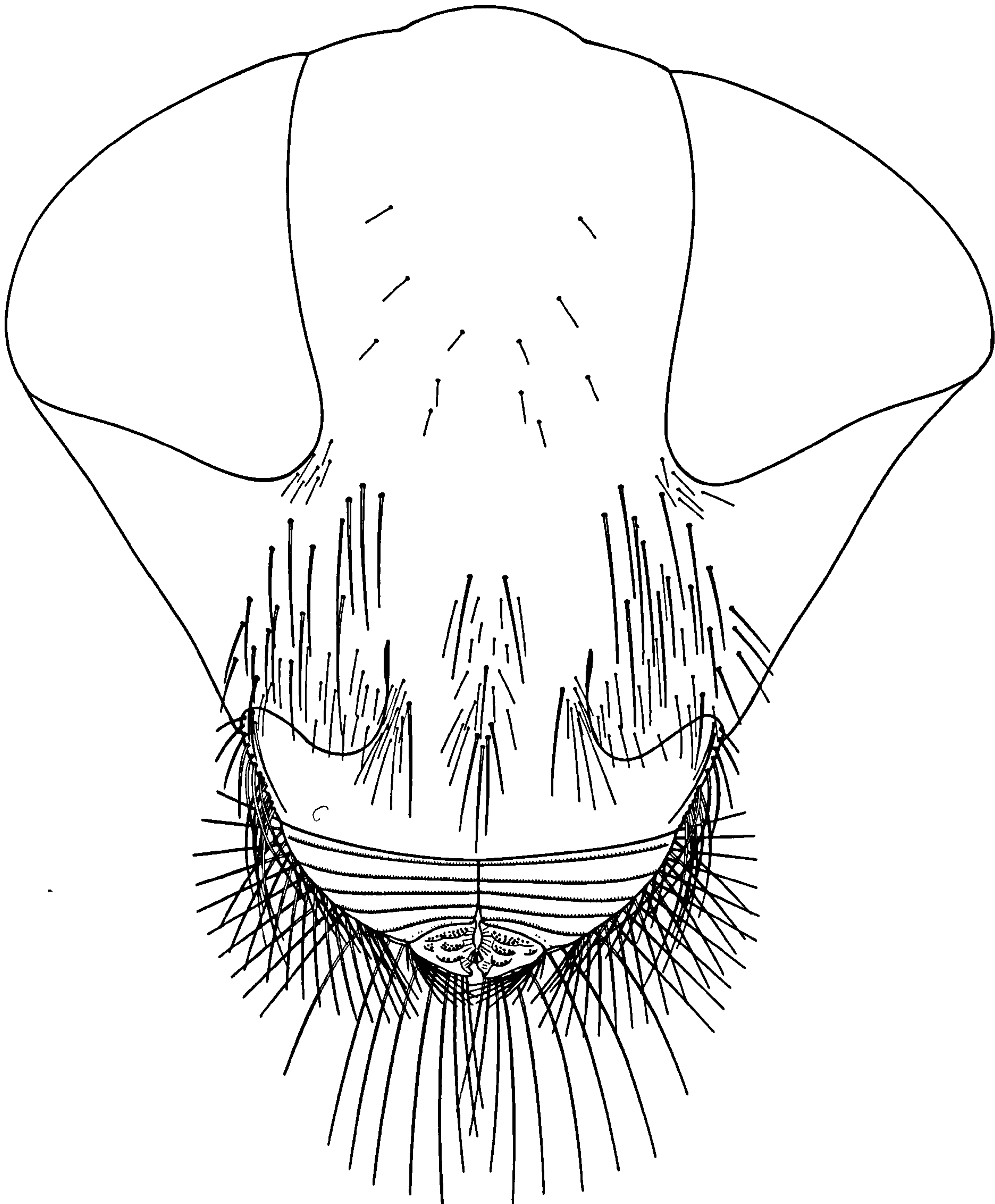


Fig. 3.17 Corixa punctata, female; back of head, ventral region.

The bristles of this region have been separated into 4 layers;

A, outline of the ventral head capsule and the rostrum, (see fig. 3.2 for the names of the parts), and the bristles of the lateral anteclypeus and the fourth labial segment;

B, the anterior bristles of the outer row on the third labial segment;

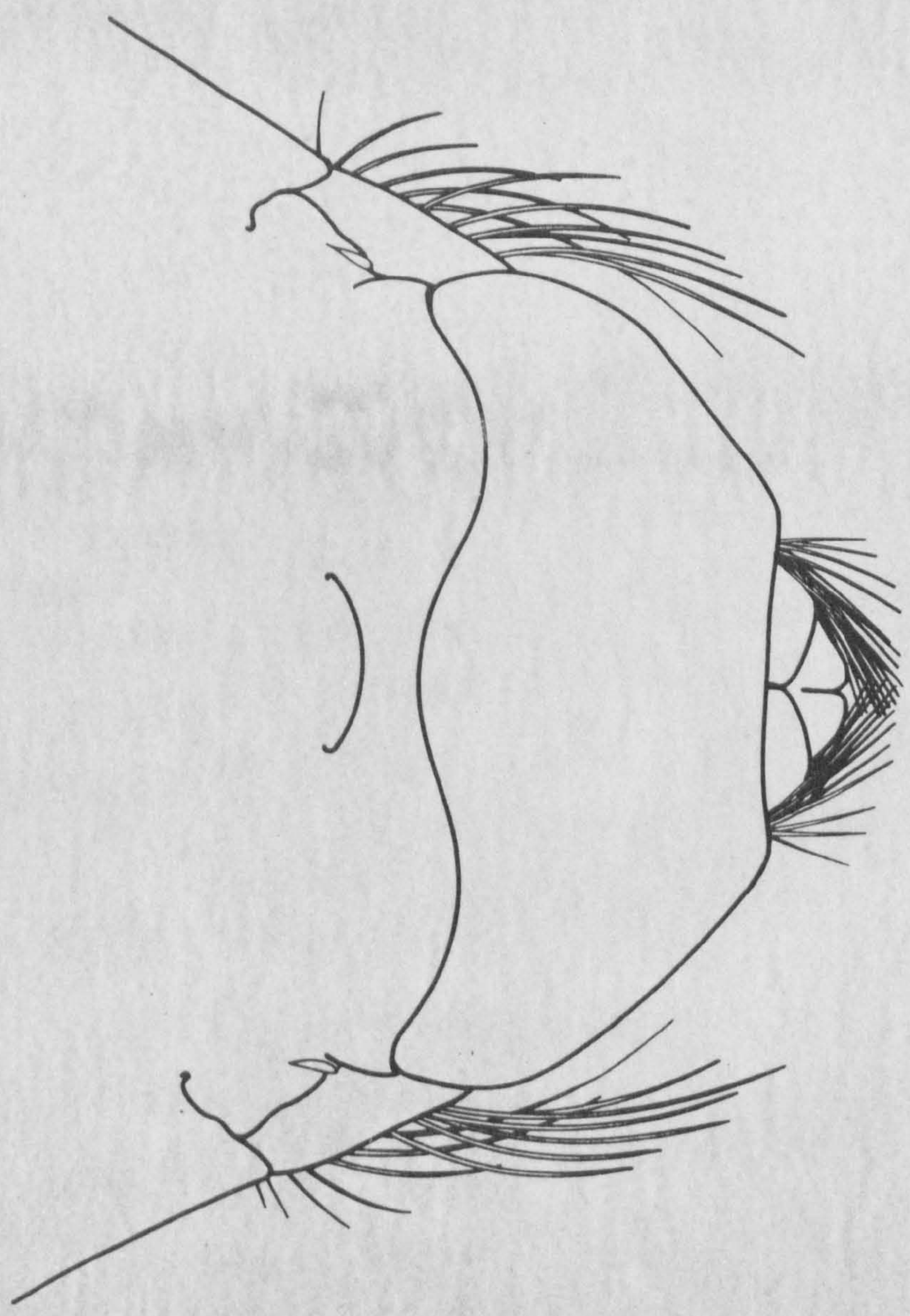
C, laterally the posterior bristles of the outer row on the third labial segment, and medianly the finer median bristles of the middle row on the third labial segment;

D, the middle row of long bristles, the inner row of short bristles with a lateral tuft of finer and longer bristles, and fine short bristles on the rostrum and ventral head capsule.

The arrangement of the bristles in the outer row on the third and fourth and labial segments is simplified and those of the third segment have been reduced to 6 layers.

1 mm

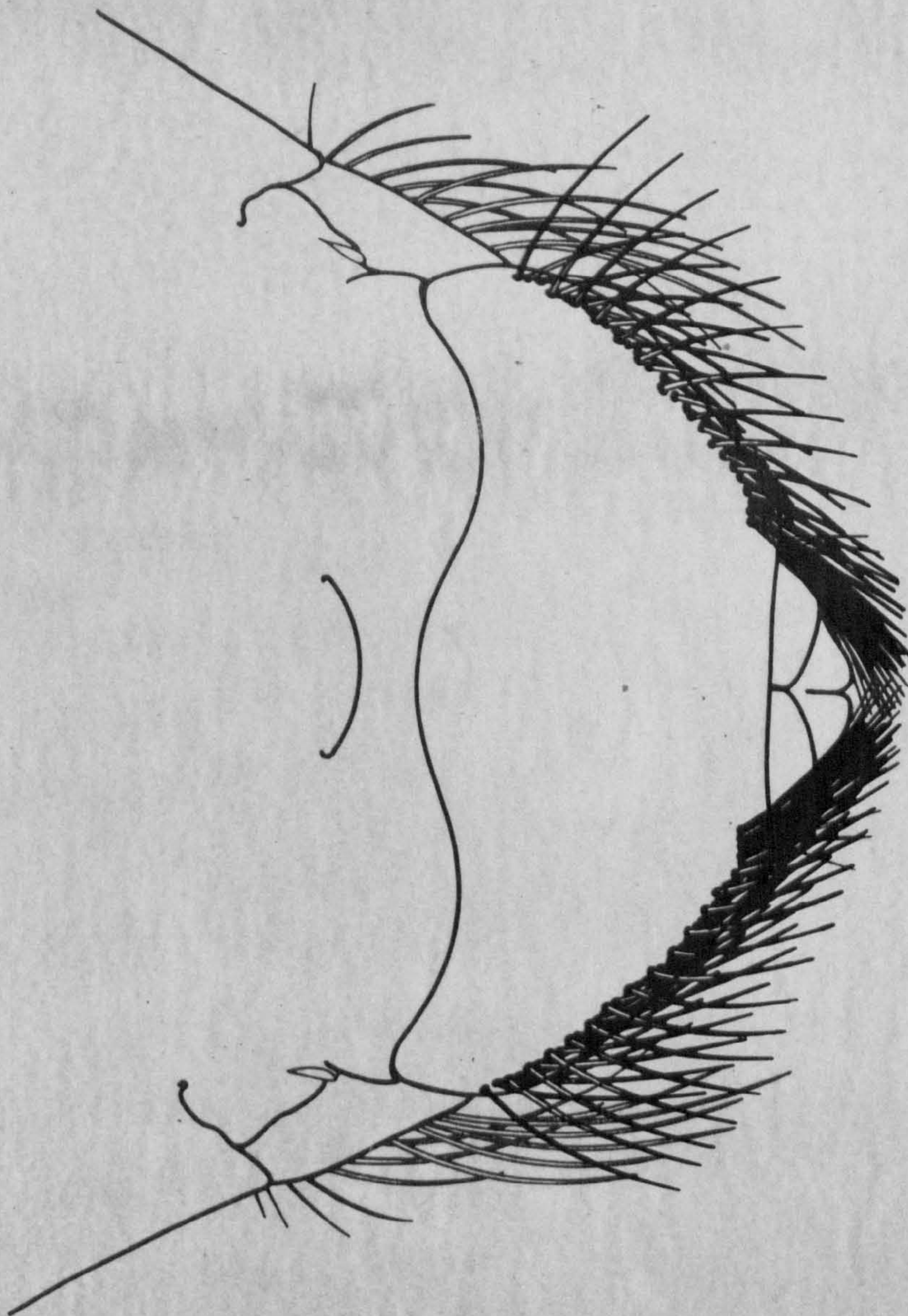
A.



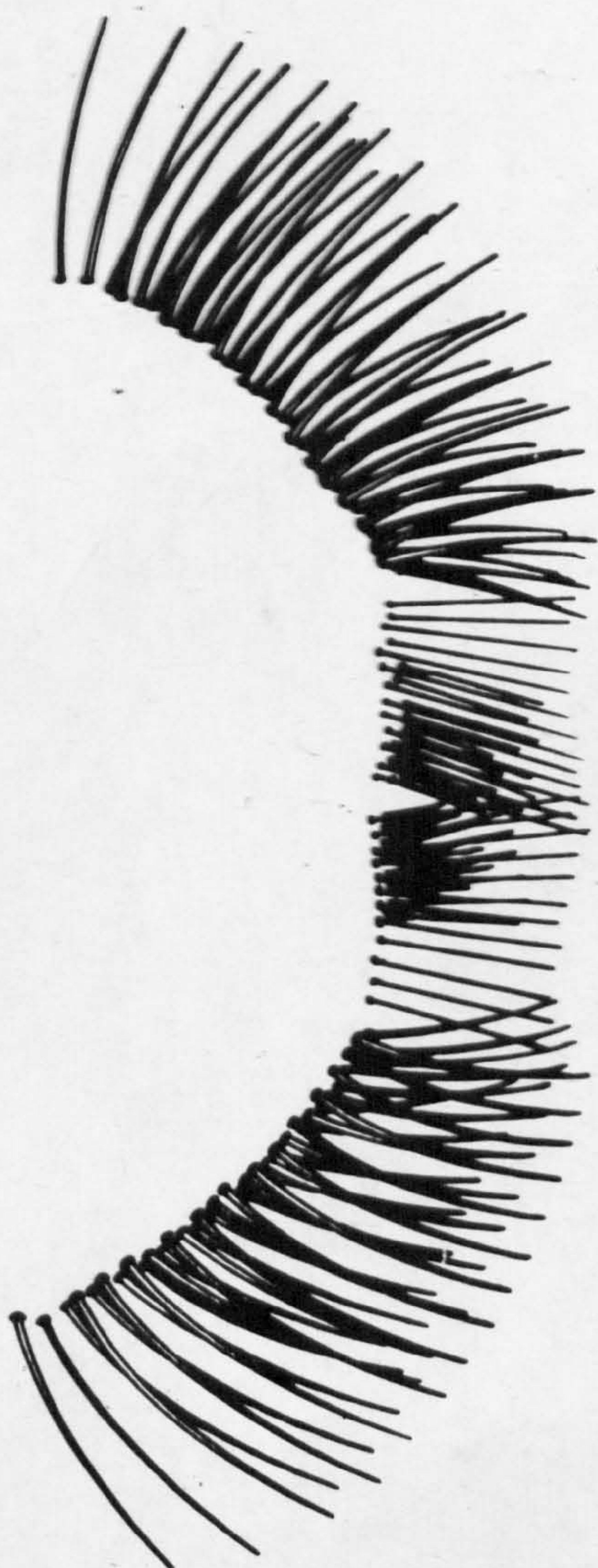
B.



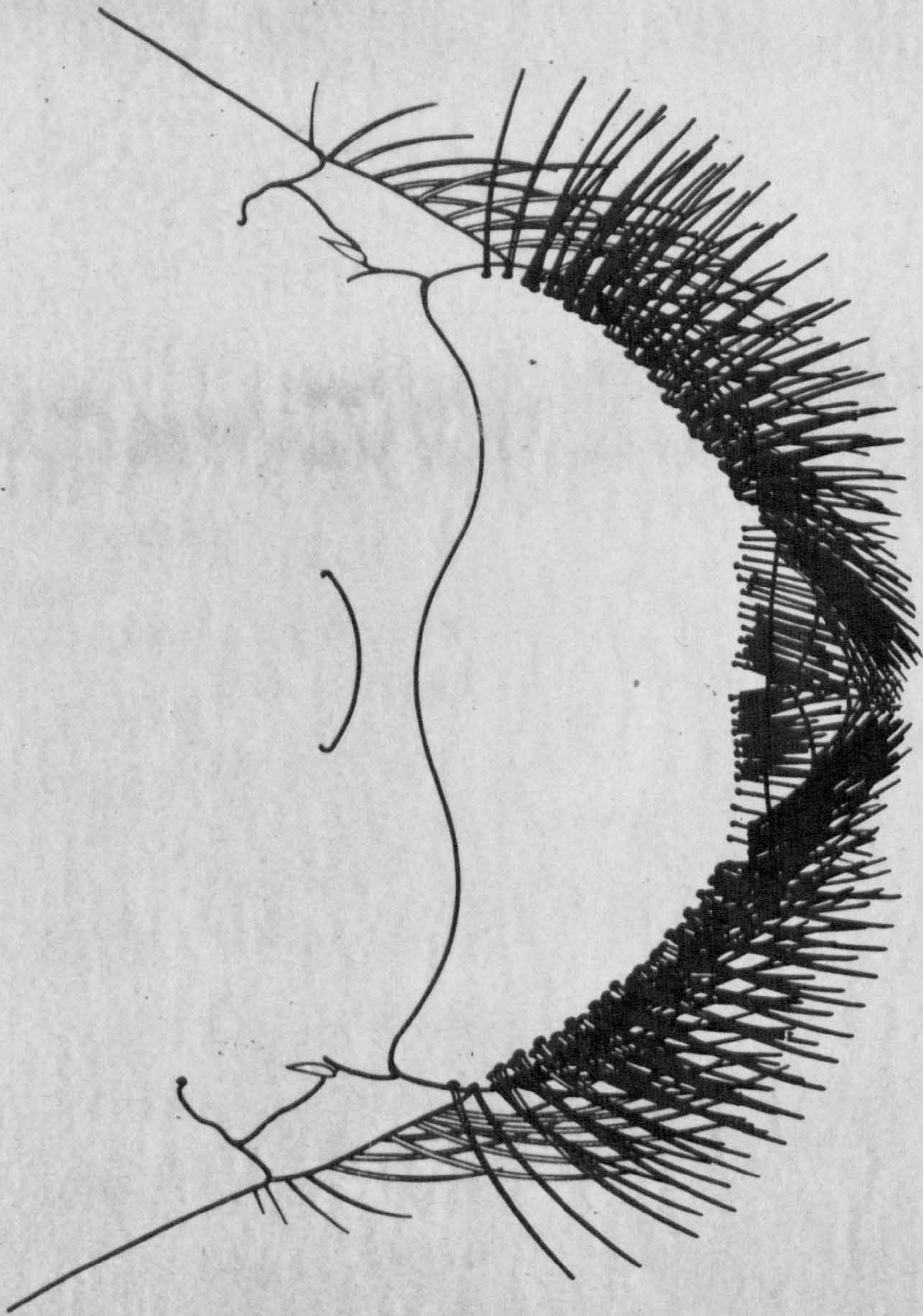
1mm



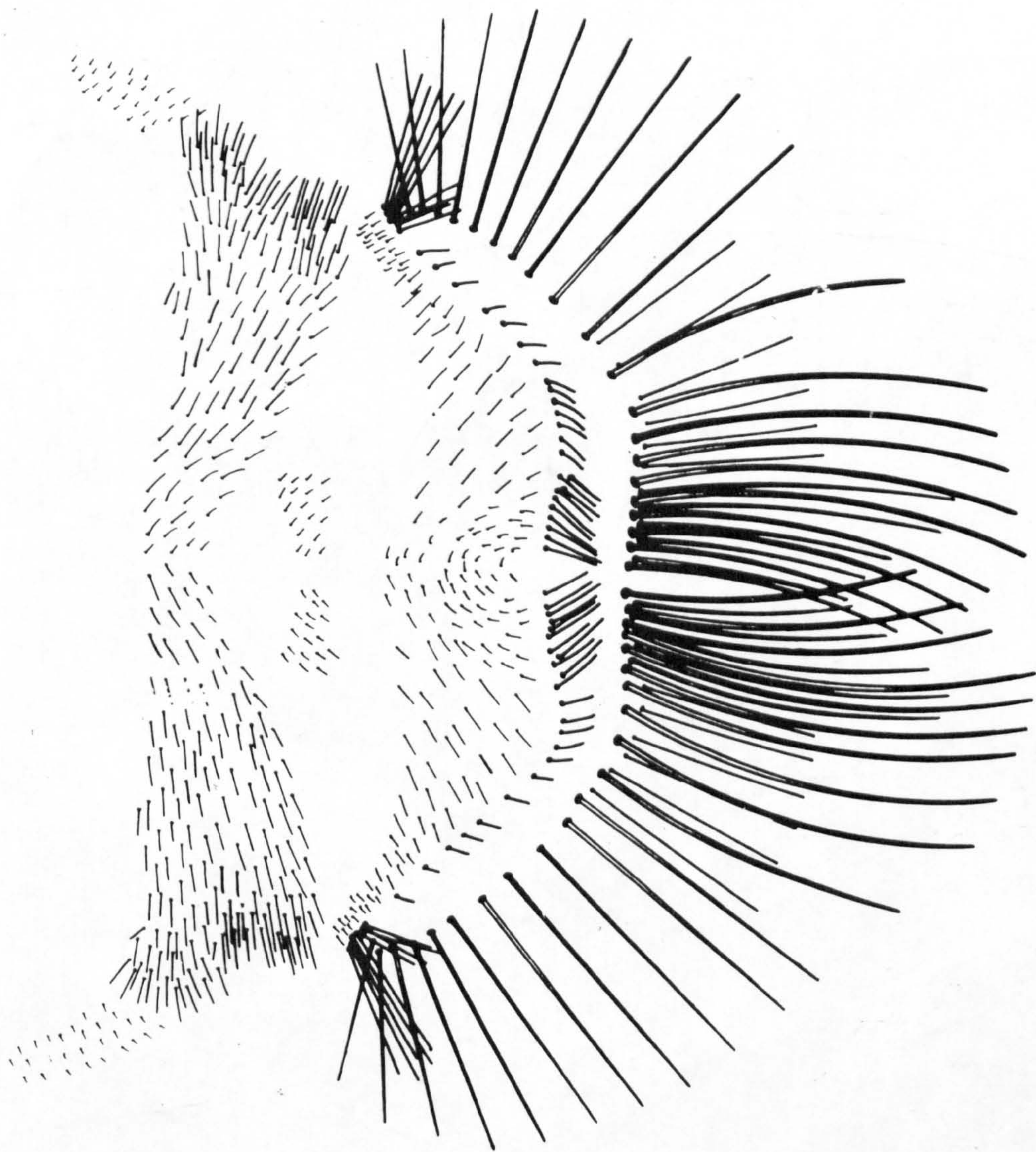
A. B.

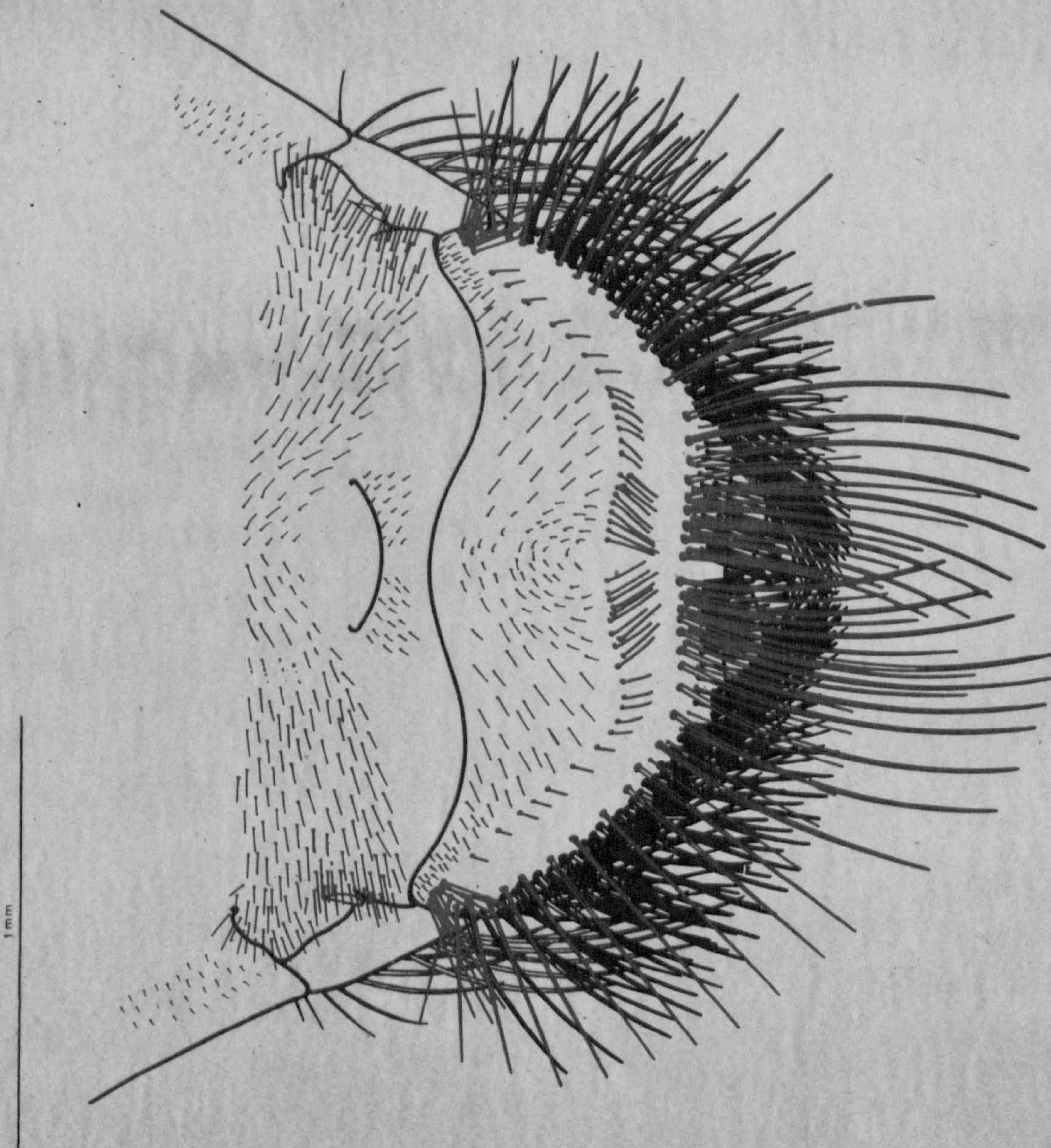


1 mm



A. B. C.





A. B. C. D.

Fig. 3.18. Corixa punctata, female; the forelimb. See figs. 3.3 and 3.4 for the names of the parts of the forelimb.

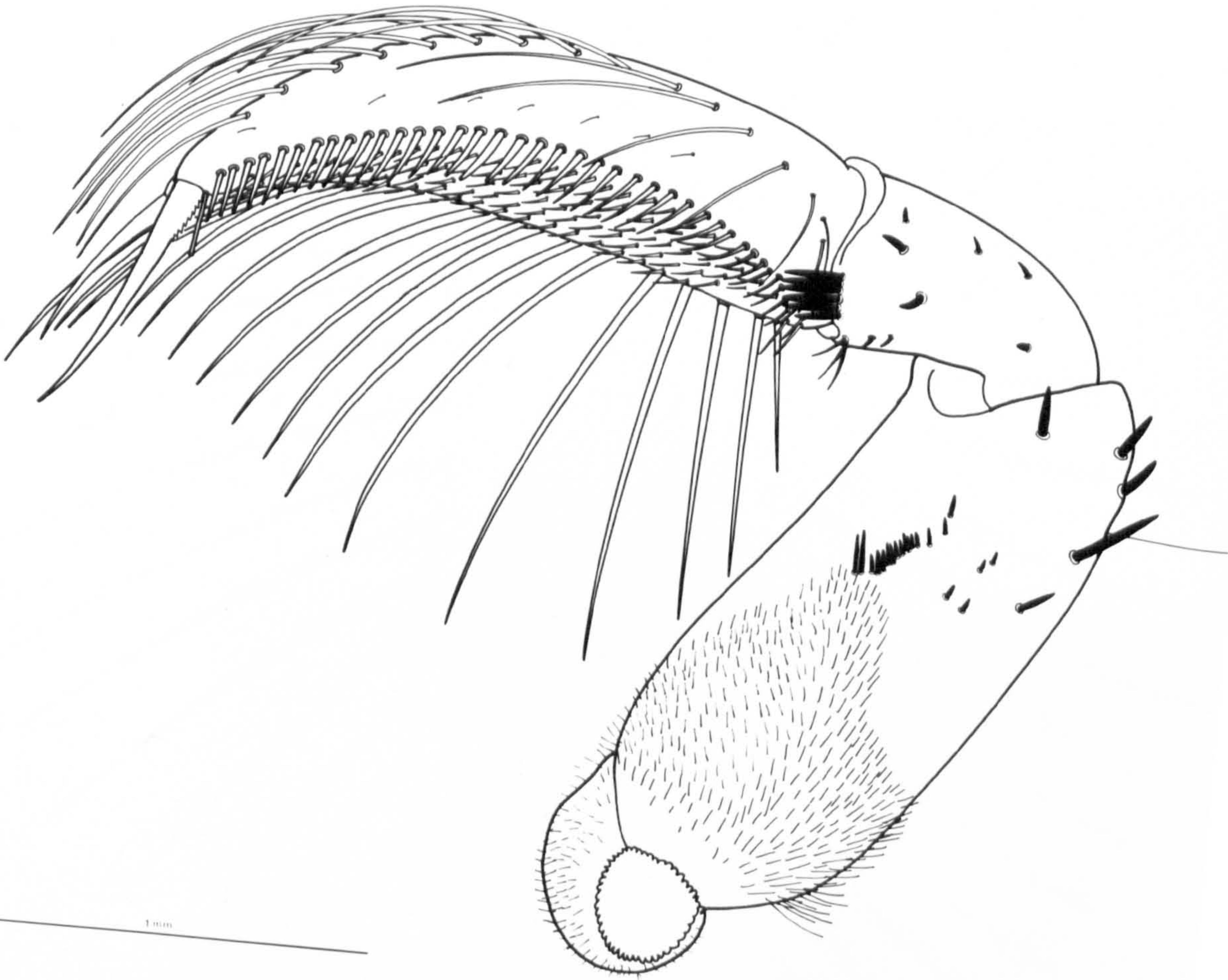


Fig. 3.19. Corixa punctata, female; fore tibia and fore tarsus. See
fig. 3.4 for the names of the parts.

1 mm

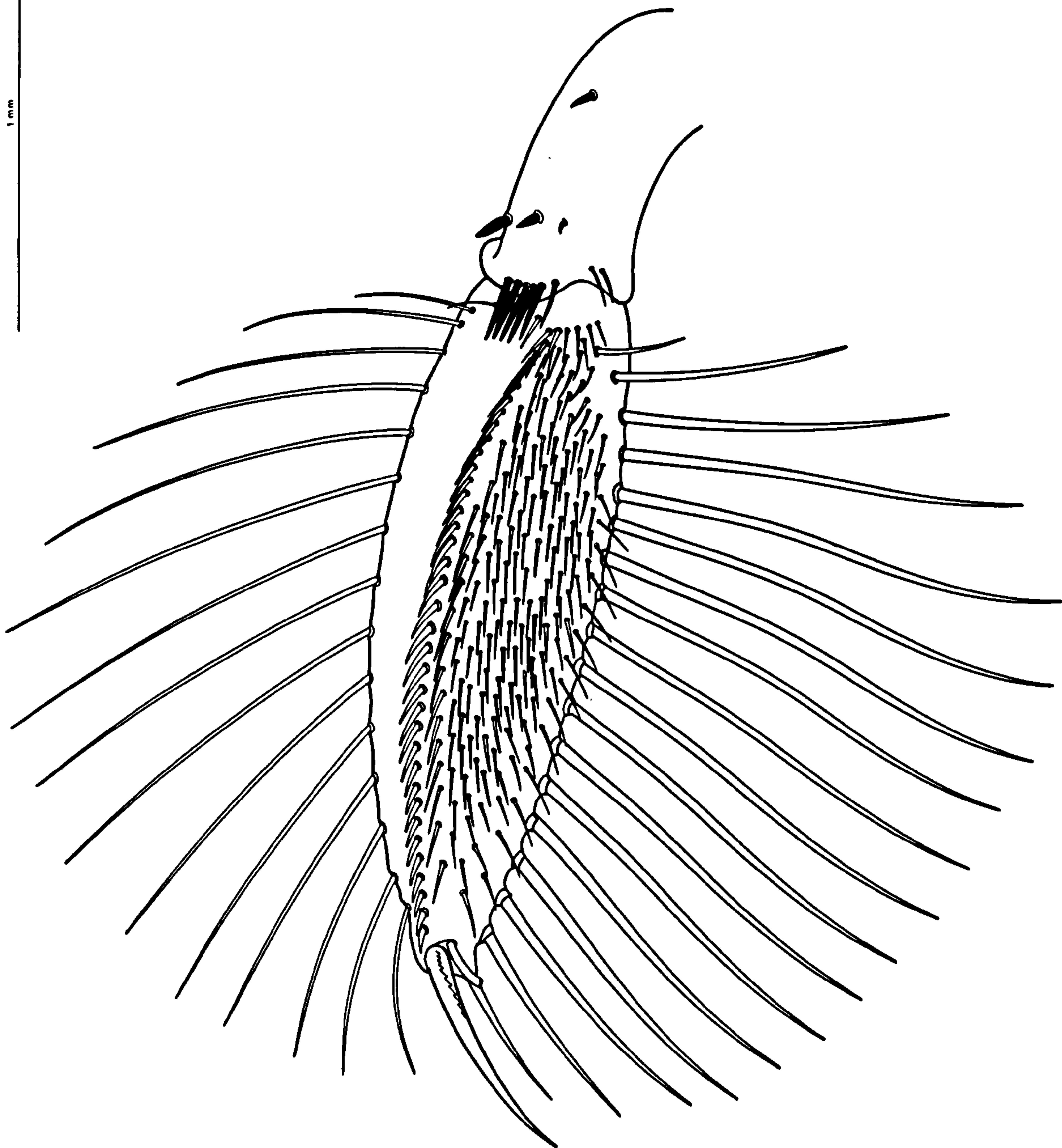


Fig. 3.20. Corixa punctata, male; the fore tibia and fore tarsus.

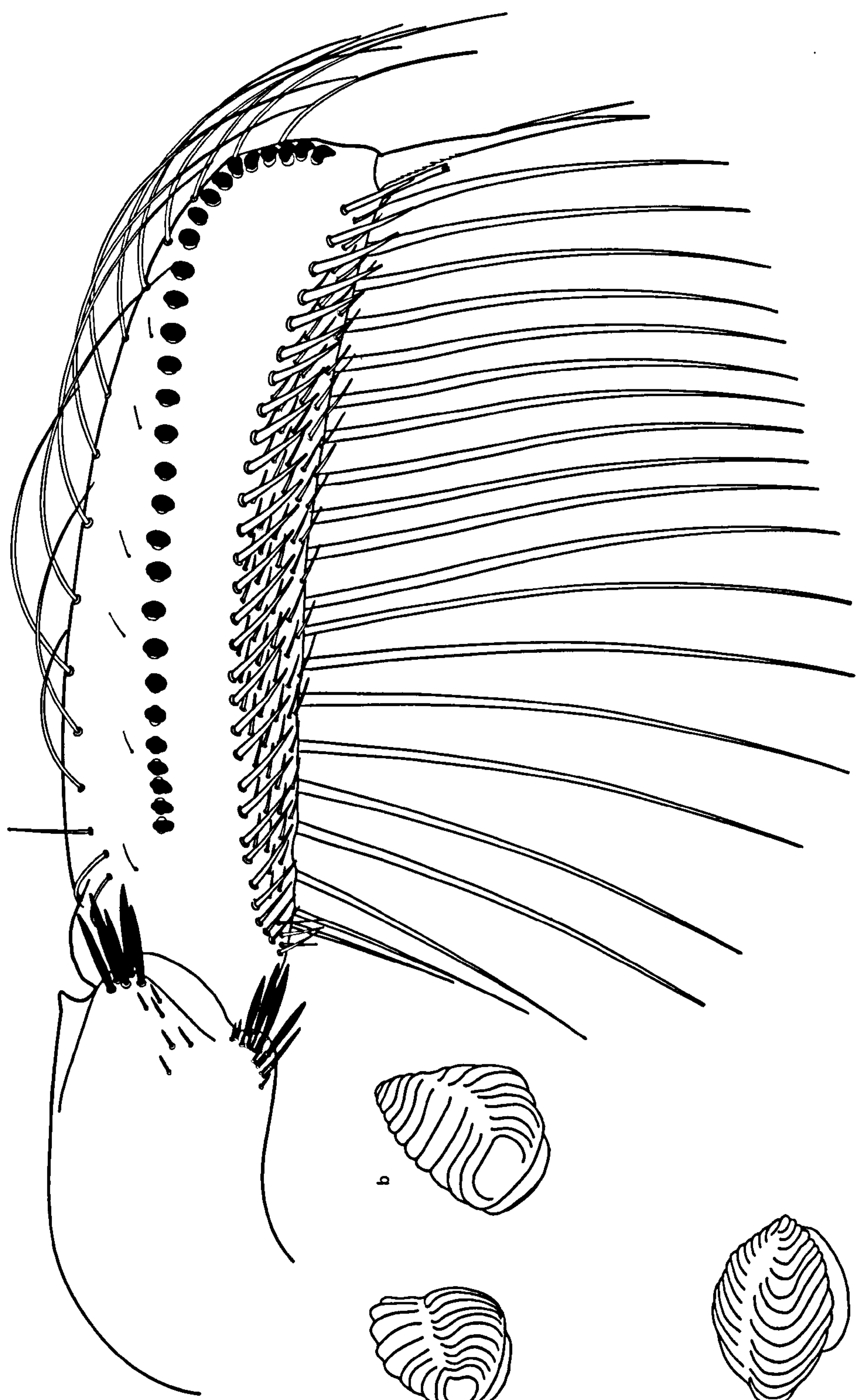
A, shows the single row of male pegs between the upper paleal and upper palm bristles;

B, the detailed structure of the pegs; side view of peg from middle of the row, a, and distal end of the row, b; and top view of a peg from the middle of the row, c.

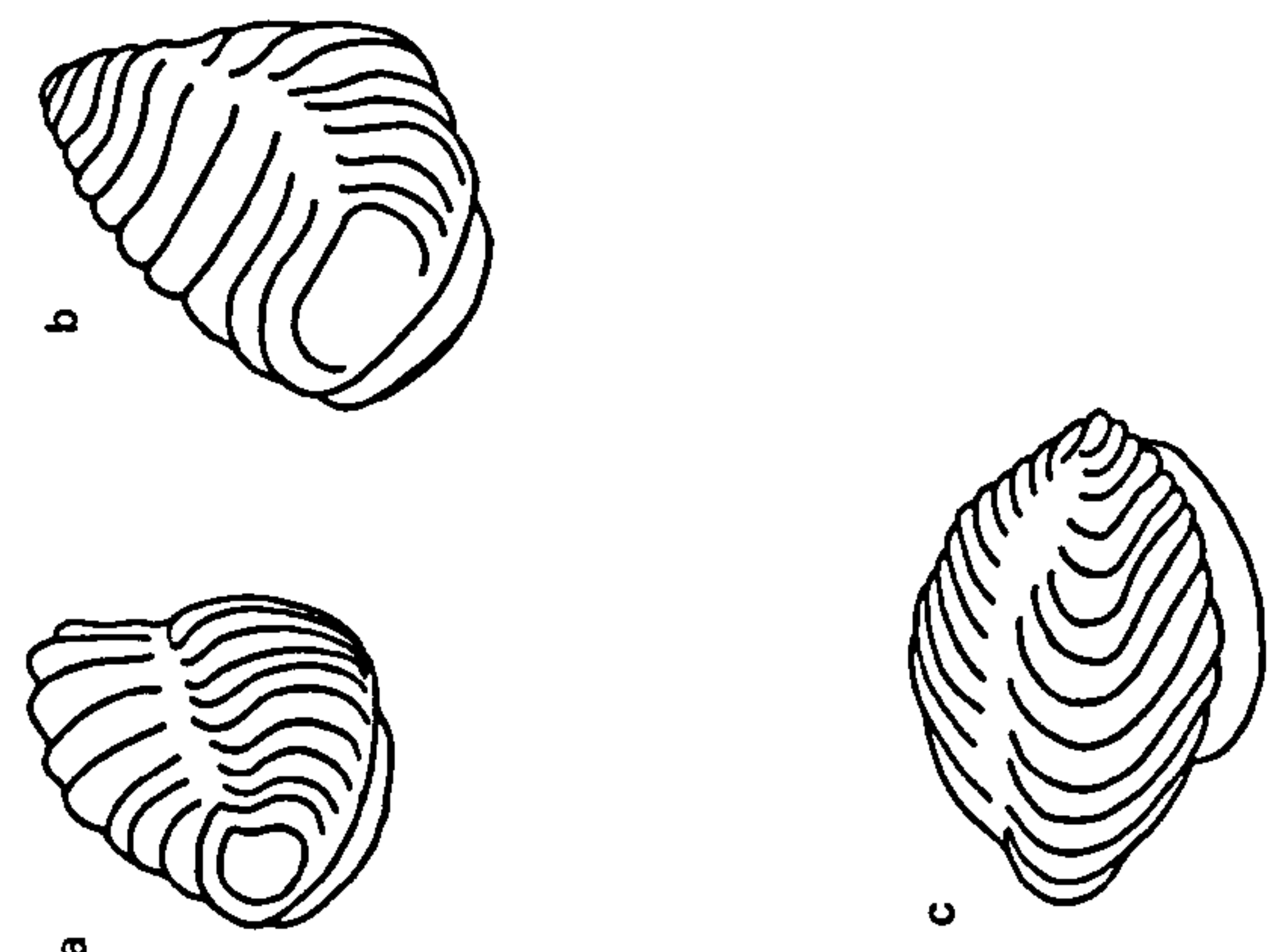
See fig. 3.4 for the names of the parts of the forelimb.

0.5 mm

A



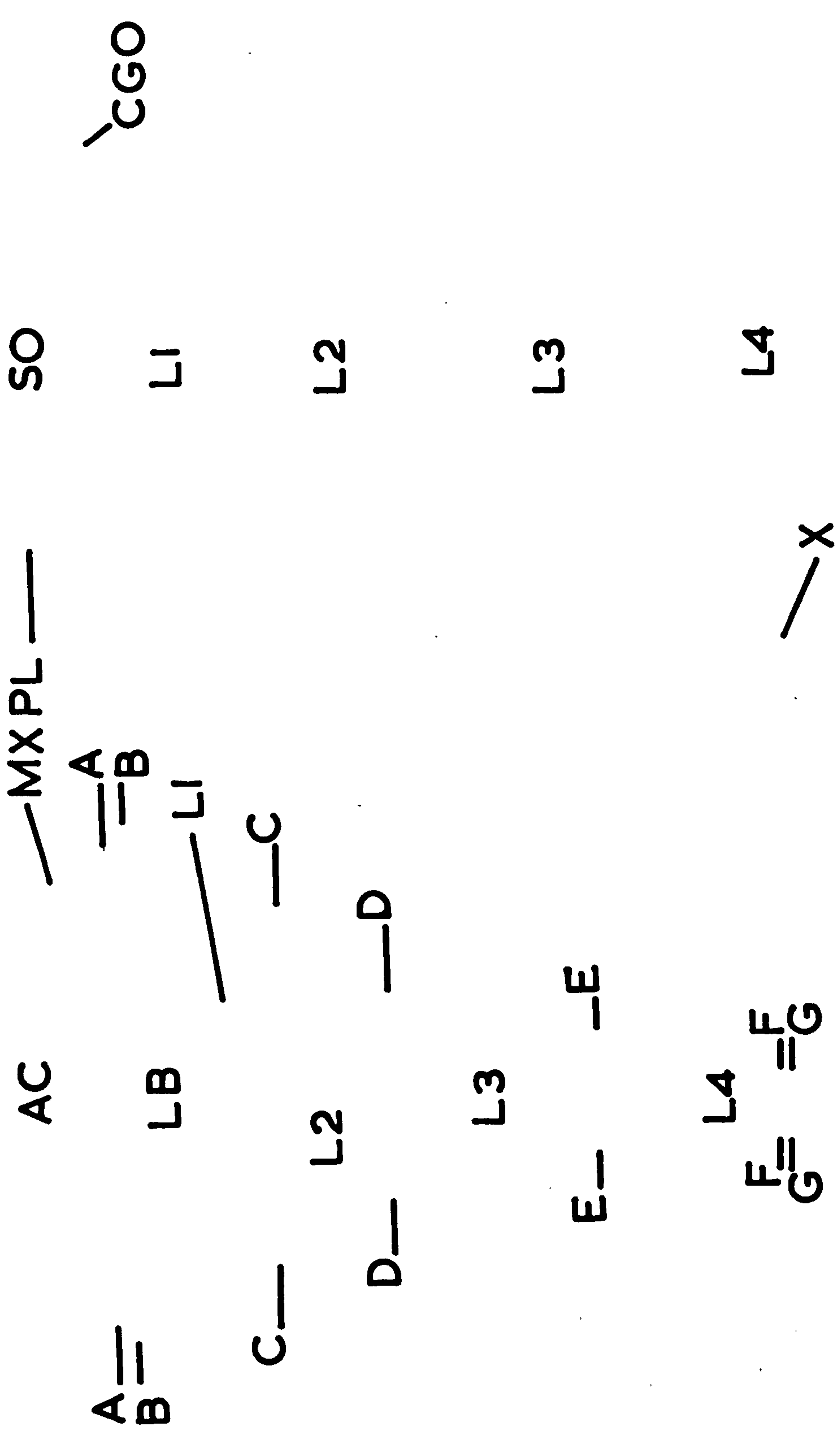
B



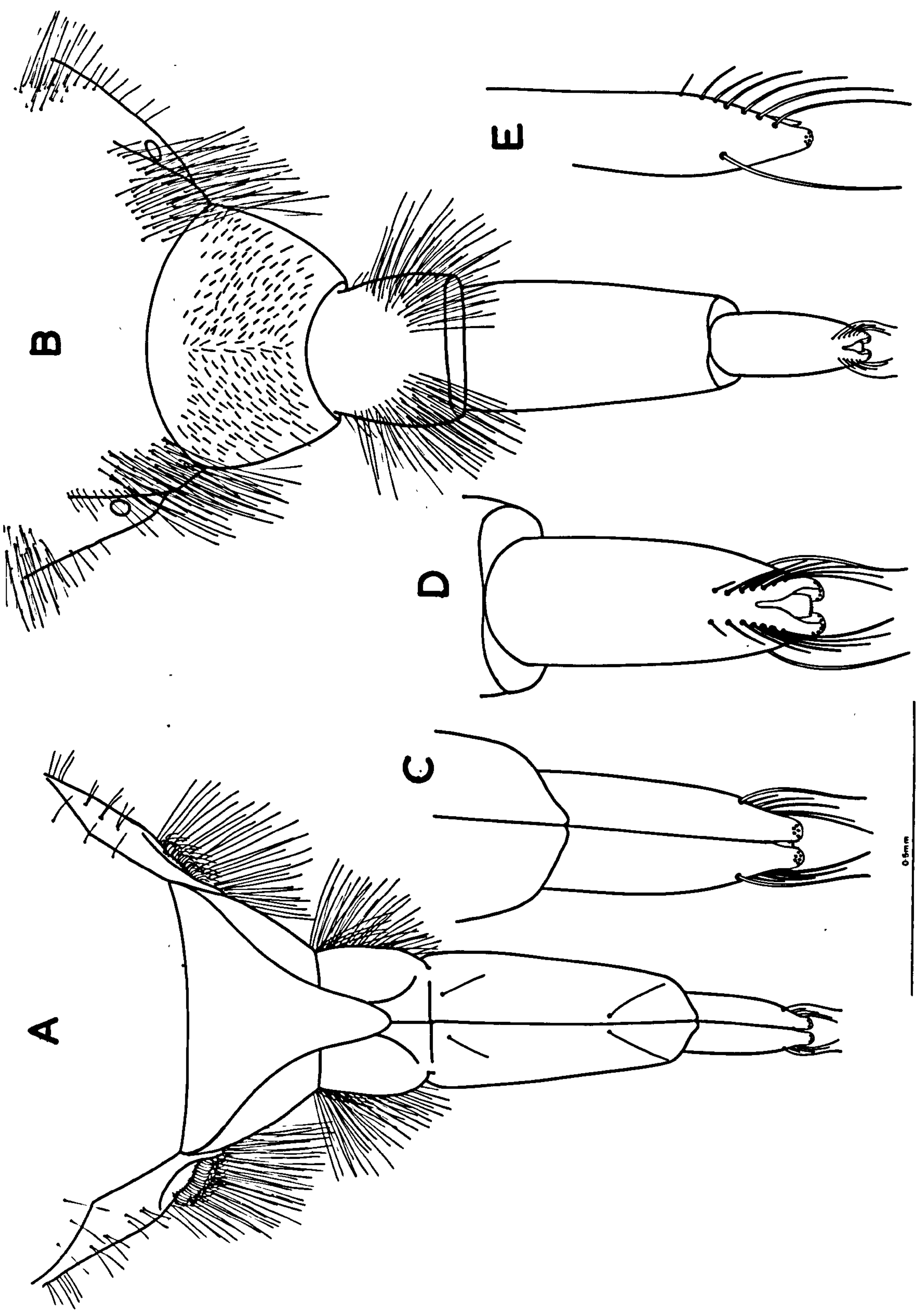
0.1 mm

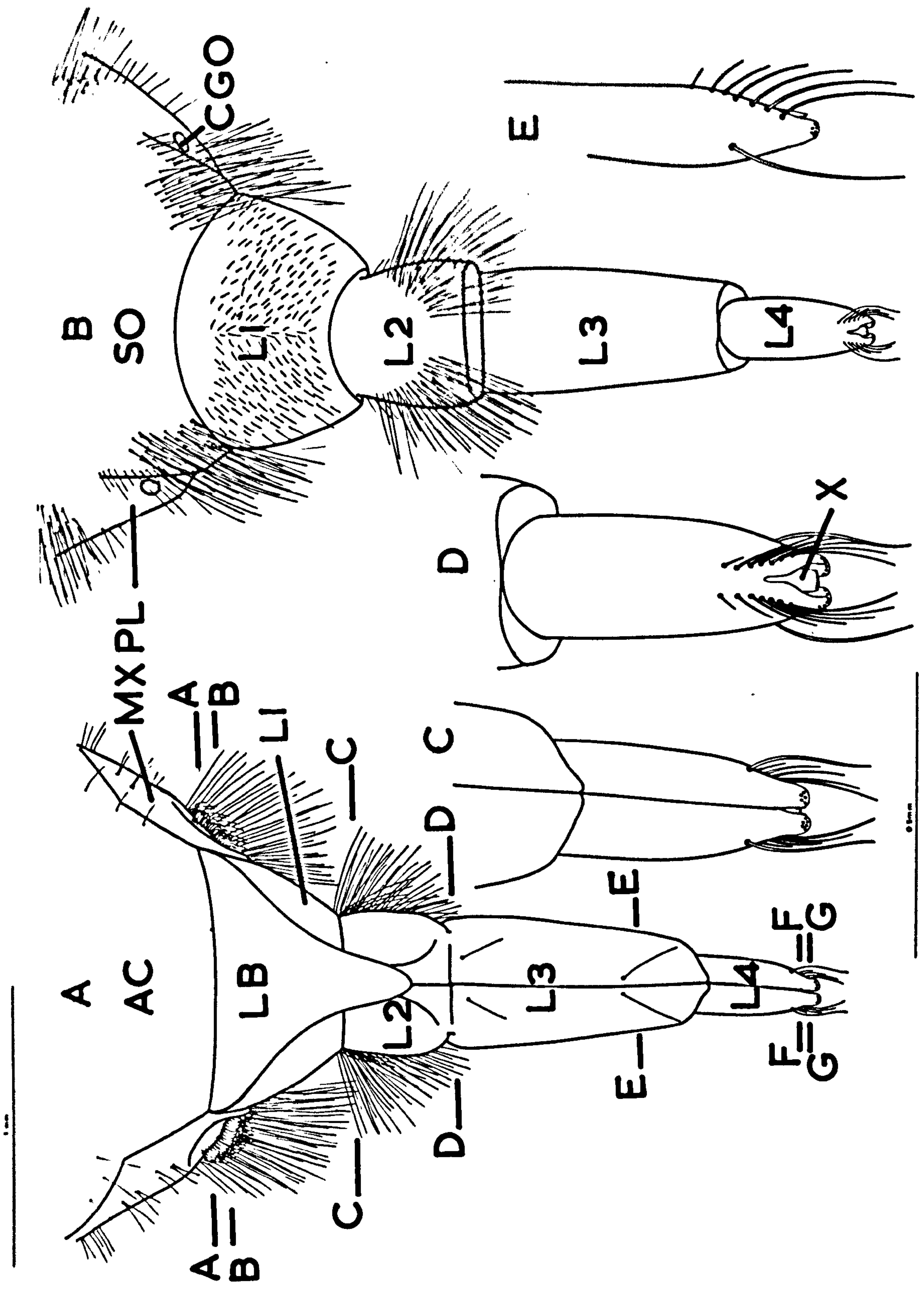
Fig. 3.21. Notonecta glauca, adult; the rostrum and part of the head capsule, A, anterior, and B, posterior view; and enlargement of the fourth labial segment to show the structure and the arrangement of the bristles and the position of the terminal sense organs, C. anterior, D, posterior, and E, side view.

In fig. A, A-A to G-G are the positions of the transverse sections of the stylet bundle illustrated in fig. 4.3. A-A is equivalent to fig. 4.3A, etc.



1 mm





SECTION 4.

The Internal Anatomy of the Head.

4.1 Introduction

With ^{the} exception of species in the sub-family Diaprepocorini^{ae}, the internal structures of the head, foregut, and associated organs in corixids show a marked uniformity in design.

4.2 Materials and methods

The masticatory mechanisms of all the species described in section 3 were examined from whole mounted specimens. The food pump of Diaprepocoris zealandiae, Sigara falleni, and Corixa punctata, and also the stylets of these and other species, including Cymatia bondsdorffi, Neocorixa snowi, Micronecta poweri, and Tenagobia selecta were dissected out.

In the histological studies, adults of each species were used, and in some cases, the first instar nymphs. The type species used was Corixa punctata, but Sigara falleni, S. nigrolineata, Callocorixa praeusta, Cymatia bondsdorffi, Micronecta poweri, and the New Zealand species, Diaprepocoris zealandiae were also examined.

The British specimens were fixed in alcoholic Bouin's solution, and all the material was sectioned transversely and longitudinally, using the Peterfi's technique, and stained with Mallory's triple stain.

For comparison, histological material of Notonecta glauca was prepared in the same way, and the stylets of both N. glauca and Nepa cinerea investigated.

From a functional point of view, the types of cuticle which form the structures of the head are important. The cuticle is divided into three main layers (Wigglesworth 1965); the epicuticle, the very thin surface

layer; the exocuticle, where present, lies beneath the epicuticle and is a rigid non-staining layer usually amber coloured, but is sometimes black pigmented; and the endocuticle of which two types are distinguished by their staining reactions with Mallory's triple stain (Schatz^{-e} 1952), cuticle staining red is termed mesocuticle and cuticle staining blue, endocuticle.

In corixids and Notonecta, the exocuticle is usually white or pale amber coloured. One type of exocuticle, however, which forms the stylets and many of the epipharyngeal teeth in the middle region of the food pump, is brown but in sections it appears bright yellow. From its position it may be inferred this type of cuticle is harder than the pale exocuticle. Black pigmented exocuticle is found on the posterior vertex and the dorsal surface of the pronotum, and also in some internal structures, for example, the ventral layer in the hypopharynx of the middle region of the food pump and the anterior end of the hypopharynx. This black exocuticle is probably harder than the paler forms. From their position it can be inferred that all types of exocuticle are harder than both endocuticle and mesocuticle. Contradictory to Wigglesworth (1965), the exocuticle does not always lie directly beneath the epicuticle.

The endocuticle is very soft material, normally staining deep blue, differences in the intensity of the staining reaction in various areas of the same preparation reflecting variations in the density of the cuticular material.

Two types of mesocuticle are distinguished. One type, a pale orange staining cuticle which frequently forms a thick layer with distinct

lamellae, is associated with many of the areas of exocuticle, for example, the anterior wall of the head capsule. It is convenient to call both types of cuticle where they occur together, 'sclerotized' cuticle.

The second type of mesocuticle stains a bright uniform red. Its staining reaction and its position in many structures, for example, the roof of the food pump, are consistent with it being resilin, a type of cuticle with rubber-like properties. (Anderson and Weis-fogh 1964).

Other cuticular areas distinct from those outlined above are referred to in conjunction with specific structures.

4.3 The stylets (figs. 4.1, 4.2, 4.3, and 4.4)

The stylets of Nepa and Notonecta are very much longer than those of corixids and the maxillae are longer than the mandibles in Nepa, Notonecta, and Cymatia. Measurements made on the maxillae of Nepa during feeding showed the maximum length the maxillae stuck into the prey was 1.45 mm., compared with a difference in length of the mandibles and maxillae of 1.2 mm.

The mandibles of Nepa have thin, wide, distal ends, with 4 small backward-pointing barbs on the outer side. The lateral edges have small forward-pointing spines extending 0.4 mm. to 1.3 mm. from the tip of the mandible.

In Notonecta, the mandibles are stronger and carry 5 blunt projections distally, with 12 longer backward-curving spines. On a thin flange there are a few small forward-pointing spines, 0.5 - 1.0 mm. from the tip of the mandible.

The mandibles of all corixids are much stronger and blunter, with 5 - 6 blunt projections similar to the distal projections on the Notonecta mandibles. These barbs on the mandibles of Neocorixa and Cymatia are more prominent than in the other corixids.

In the Heteroptera, the maxillae join together to form two separate channels, a dorsal food channel up which food is ingested, and a ventrally situated saliva channel through which saliva is ejected. The two maxillae have different distal ends; in Nepa they both have sharp pointed ends and long spines on the ventral edge, those of the left maxilla curving round the outside of the right maxilla and those of the right maxilla curving round the inside of the left maxilla. Proximal to the long spines on the left maxilla are some short fine hair-like spines, and on the dorsal edge of both maxillae, extending back for 0.7 mm., are small forward-pointing spines. These small spines are part of the interlocking mechanism which hold the two stylets together, whilst allowing them to move in and out relative to each other. The inner edge of the saliva channel on the left maxilla ends in a short curved spine.

The end of the left maxilla of Notonecta is sharply pointed, but has no long spines. On the ventral side of the saliva channel are two groups of short fine hair-like spines, one group of which are at the distal end of the channel. The inner edge of the saliva channel has eight blunt forward-pointing spines, and ends in a short blunt spine. On the dorsal side of the left maxilla, small forward-pointing spines extend back for about 3 mm. The right maxilla has a blunt inward^{ly} curving tip and a ventral row of long spines which lie against the inner edge of the left maxilla in

the region of the saliva channel but distal to it. The spines are smaller proximally and extend back for about 3 mm. On the dorsal side a row of long sharp spines extends back for only 1.25 mm.

Fig. 4.3 shows the ~~inter~~-relationship between the various structures along the length of the rostrum in Notonecta. At the proximal end of the rostrum, the stylet bundle lies in a shallow dorsal groove of the first and second labial segments, ^{while} the labrum extends over these segments covering the stylet bundle, (fig. 3.21). In the middle of the second labial segment, the dorsal groove is very shallow in the distal region of the segment. However, the stylet bundle is enclosed within this groove which is sealed along the midline. Distally, the stylets protrude from the tip of the fourth labial segment which is split into three parts: two lateral lobes each of which bear numerous sense organs and a projection derived from the ventral wall of the labial groove.

In each stylet is a cavity which contains the epithelial cells from which the cuticle of the stylets are derived. The diameter of this cavity becomes smaller distally and disappears near the tip of each stylet.

The mandibles fit closely against the maxillae for most of their length. They have two flanges, a dorsal flange which is widest distally, and a narrower ventral distal flange.

At the basal end of the rostrum, the interlocking mechanism of the maxillae is simple, but becomes more complex distally, especially those parts associated with the saliva channel. This channel is formed equally by both maxillae at the basal end of the rostrum, but it becomes enclosed distally within the left maxillae to open into the food channel near the

tip of the stylet. In this region the long spines of the right maxilla project into the food channel. Despite changes in shape, the food and saliva channels maintain a constant cross-sectional area throughout their length, except at the distal end where the food channel is enlarged, reflecting the greater width of the left maxilla distal to the saliva channel, (table 4.1).

The maxillae differ little in form among the corixid species examined, (fig. 4.2), only those of Neocorixa and Cymatia showing obvious modifications. All corixid maxillae are much smaller than those of Nepa and Notonecta. The left maxilla is narrower than the right except at the blunt tip where its dorsal edge is greatly expanded. The wide right maxilla is pointed at the tip, with single central and ventral teeth, the ventral edge also bears a row of small forward-pointing spines.

In Neocorixa snowi, the left maxilla is similar, except for a few small terminal teeth. The right maxilla is, however, modified to include a large terminal tooth, a row of 4 small sharp spines on the ventral edge, and 5 larger pointed spines on the dorsal edge.

The most noticeable feature in Cymatia bondsdorffi is the great length of the maxilla compared with the mandibles; this^{is} in marked contrast to other corixids, including Neocorixa, where the maxillae and mandible are about the same length. The tip of the left maxilla is similar to that of other corixids but has a small barb on its outer side. The right maxilla has a large terminal tooth and a smaller distinct dorsal tooth, but on the ventral edge only the terminal tooth is prominent. It is noticeable that, although the mandibles of Cymatia bondsdorffi and Sigara

falleni are of similar dimensions, the longer maxillae of Cymatia are distinctly narrower.

Fig. 4.4 shows the inter-relationship between the various structures along the length of the rostrum in Corixa punctata. The stylets lie in a sealed, dorsal groove in the labium of a short rostrum and protrude through the labial orifice. The area of the cellular cavity within each stylet becomes smaller and disappears near the tip. In the left maxilla, the cavity splits distally into three parts.

The stylets are composed of amber-coloured cuticle, but both maxillae show long strips of resilin along their outer walls. The right maxilla also has resilin associated with the dorsal edge and an inward projection, which serve to occlude the food and saliva channels.

The distal ends of the maxillae have a slightly more complex series of dorsal grooves and projections, which in Cymatia are well developed, associated with the greater length of the maxillae protruded from the labial orifice.

The difference between the cross-sectional area of the food and saliva channels of all the corixids examined is much greater^{than} in Notonecta, table 4.1. Also, in contrast to Notonecta, the saliva channel passes from the left maxilla into the right maxilla.

4.4 The food pump and other structures of the head.

Dissections of Sigara falleni and Diaprepocoris zealandiae are illustrated, (figs. 4.5 and 4.6). The much larger Corixa punctata was also dissected, but showed little difference from S.falleni.

The most convenient corixid for histological study is the large

Corixa punctata, ^{though} little difference other than that associated with size is found between this species and Sigara falleni. The illustrations, figs. 4.4 and 4.7 - 4.15, are of C. punctata and Diaprepocoris material.

Descriptions of the layers and pockets of the integument and of the food pump are given by Benwitz (1956a) and Parsons (1966) respectively. The food pump formed by the epipharynx and hypopharynx is both cibarial and pharyngeal in origin. For convenience, the epipharynx is regarded as the dorsal side of the pump.

In the typical corixid, the epipharyngeal plates lie beneath the lateral extension of the anteclypeus, which anteriorly takes the form of a median lobe-like projection (AC! figs 4.5, 4.7, and 4.8) lying within the labial groove. At the tip of the anteclypeus is the reduced labrum. The clypeal epipharynx forms the trough shaped roof of the anterior region of the food pump, the sides of the trough extending dorso-laterally to join the anteclypeus (AC fig. 4.5 and 4.8). The hypopharynx which forms the floor of the pump, as well as the saliva pump, extends dorsolaterally to join the loral plate (LP fig. 4.8) ('mandibular plate' of Benwitz). The loral plate and anteclypeus are separated by the clypeoloral cleft (CIC fig. 4.5 and 4.8), but at the posterior end of this cleft, the epipharynx and hypopharynx are united laterally, their junction forming a thickened ridge (HE, fig. 4.5) running from the wall of the head capsule to the middle region of the food pump. The lateral edges of the anterior region of the food pump are marked by a longitudinal ridge (LR, fig. 4.5 and 4.8). A typical corixid food pump has a long anterior region, a short complex middle region, and a

very short posterior region which opens into the pharynx (PH, fig. 4.5 and 4.7).

The muscles of the food pump of corixids are difficult to homologize with those in the other Hydrocorisa, and the system of naming of the muscles which has been adopted, is an extension of the system used by Parsons (1966). The muscle group 1 is cibarial, originating on the anteclypeus and postclypeus and inserted on to the tendons of the anterior region of the food pump, (M1 and T1, figs. 4.5 and 4.7). Muscle group 2, also cibarial, originates on the postclypeus and attaches to a thick tendon at the beginning of the pump's middle region, (M2 and T2, figs. 4.5 and 4.7). Muscle group 3 is pharyngeal, lying behind the frontal ganglion and originates on the frons. It inserts on to the tendon at the posterior end of the pump's middle region (M3 and T3, figs. 4.5 and 4.7). Muscle group 4 is again pharyngeal originating on the frons, and inserting directly on to the pump's posterior region, (M4, figs. 4.5 and 4.7).

The pharynx has a layer of circular muscle and, where it passes through the occipital foramina, a pair of dorso-lateral and ventro-lateral dilator muscles (DP, fig. 4.7; muscles 18 and 19 of Parsons).

4.41 Corixa punctata and Sigara falleni

General features (fig. 4.7)

Longitudinal sections show the cap-like shape of the corixid head the ^{of which} concave posterior surface, closely fits on to the pronotum which, in turn, is also concave posteriorly, fitting on to the mesonotum. Those areas of the cuticle of the pronotum, which are in contact with the

air bubble, and covered by very short and fine nonstaining filaments, are strongly hydrophobic. The corixid head and pronotum is an unpigmented pale amber colour, ^{but} the posterior vertex behind the eyes, ~~however~~, and the dorsal pronotum have black pigmented exocuticle. The pigment of the dorsal pronotum is restricted to distinct patches which correspond to the transverse stripes seen in the whole animal. The thin posterior extension of the pronotum has small cuticular struts joining the dorsal and ventral layers of the integument.

The labium (figs. 4.4, 4.7, and 4.8)

Adductor and depressor muscles allow slight movement of the corixid rostrum. The muscles (IA and ID) are attached to the labial shaft (IS) and a second group of adductors inserted on to the dorsal side of the third labial segment. The labial orifice dilator muscles (IOD) are attached by a tendon to the lateral end of each labial orifice lever (IOL) near the base of the fourth labial segment.

The labial orifice (IO) extends from the fourth transverse ridge on the third labial segment to the anterior end of the fourth labial segment. The sides of the labial orifice are very flat, but in some regions have complex sockets and projections of endocuticle (fig. 4.4B) which make a good seal when the orifice is closed. The labial orifice levers articulate with the dorsal fusion of the sides of the labial groove (IG), and run anteriorly along each side of the orifice. They expand laterally to the point where they are attached to the tendon of the labial orifice dilator muscle. The muscle opens the orifice and it is closed by the elasticity of the levers and the bars of hardened cuticle which run from the levers to the sclerotised base of the labial

groove. - The soft endocuticle of the inner sides of the groove is closely applied to the stylets.

The different types and arrangement of some 3,500 sense organs on the third labial segment and the types and arrangement on the fourth segment are described by Benwitz (1956a). Between each transverse ridge of sense organs, within the integument, are bars of sclerotised cuticle, which are narrower anteriorly.

The junction between the maxillary food channel and the food pump (figs. 4.4 and 4.5)

At the junction of the food channel and the food pump, the dorsal edges of the maxillae separate in the region of the labrum. Here the epipharyngeal endocuticle presses down on to the maxillae to seal the food channel. Lateral epipharyngeal rods of sclerotised cuticle, some of which are black pigmented, support the region. Centrally, the epipharynx projects into the food channel. This projection has thin endocuticular walls and a median rod of resilin, it widens posteriorly into the food pump proper and the median rod connects with the first tendon of the food pump dilator muscle. Posterior to the tendon, the epipharynx is entirely formed of resilin. The tendon originates behind the anterior epipharyngeal sense organ (ASO) which has 4 pairs of pores in Sigara falleni and 5 pairs in Corixa punctata. Between the second and third tendons of the food pump dilator muscle, is the posterior epipharyngeal sense organ (PSO) and this has two separate lateral rows of 4 pores each.

The black pigmented anterior projection of the hypopharynx separates

the ventral edges of the maxillae and extends to below the anterior epipharyngeal sense organ. Part of this projection within the food channel widens posteriorly to form a trough which expands to envelope the stylets. In the region of the first tendon of the food pump dilator muscle, the hypopharynx joins laterally with the epipharynx to form the food pump.

The efferent saliva duct projects into the saliva channel of the maxillae.

The Corixinae food pump

Within the Corixinae, the form of the food pump is very constant. The pump is described from named species of 4 genera. These are Corixa (Corixa sp., Elson (1937); C.punctata (Illig.) and C.panzeri (Fieb.), Sutton (1951); C.punctata (Illig.), Benwitz (1956a); Hesperocorixa (H.linnei (Fieb.), Poisson (1924); H.escheri (Heer), Marks (1958); H.interrupta (Say), Parsons (1966); Sigara S.striata (Linn.), Giese (1883); S.striata (Linn.), S.falleni (Fieb.), S.distincta (Fieb.), S.semistriata (Fieb.), Sutton (1951); S.lateralis (Leach), S.falleni Fieb., Benwitz (1956a); S.ornator (Abbt.), Parsons (1966); S.dorsalis (Leach), Elliott and Elliott (1967); Arctocorixa sp., and Ramphocorixa acuminata (Uhler), Griffith (1945). In this present work, the food pump ^{was examined} in the following species ~~was examined~~, Corixa punctata (Illig.), Sigara falleni (Fieb.), S.dorsalis (Leach), S.nigrolineata (Fieb.), and Callixorixa praeusta (Fieb.).

The anterior region of the food pump, (figs. 4.4, 4.5, and 4.7 to 4.10)

In the anterior part of this region, the food pump is strongly

V-shaped in cross-section, but posteriorly it becomes wider and rounded, and then flat-bottomed, posteriorly. There is a constriction about half way along its length, and here the epipharynx is covered by fine backward-pointing spines. On the posterior half of this region of the pump, the spines are restricted to the lateral edges.

The roof of the anterior region of the pump is formed from resilin and attached laterally for most of its length to the epipharyngeal longitudinal ridge. The epipharynx and hypopharynx are closely applied to each other in the region of the longitudinal ridge and extend dorsolaterally to the clypeoloral cleft, where it is present. A strengthened vertical ridge (HE) curves from the posterior end of the clypeoloral cleft to the posterior end of the anterior region of the food pump.

The hypopharynx forms the floor of this region of the food pump, and is of sclerotised cuticle with an inner, dorsal, layer of red staining cuticle.

The tendons of the muscle group 1 become stronger posteriorly, and the muscle fibres inserted on to each tendon extend posteriorly and laterally to the clypeus. The fibres nearest to the mid line extend furthest back. The most anterior tendon and muscle are very strong, and have the same form as the other anterior group 1 muscles, (cf. labrum abductor muscle, Benwitz 1956a).

Middle region of the food pump, the masticator, (figs. 4.5, 4.7 and 4.9-11)

The middle region of the food pump ('masticator' of Griffith (1945) and 'Kauapparat' of Benwitz (1956a)) is regarded as one of the most

complex masticating and filtering devices found in Heteroptera (Parsons 1966). It is formed from both cibarial and pharyngeal regions in corixids.

An epipharyngeal transverse fold (TF) separates the middle region of the food pump from the area just described. This transverse fold is more pronounced laterally where the ventral surface is covered by numerous fine bristles.

For convenience, the epipharynx of the masticator can be divided into three zones. Zone (1) (zones I and II of Parsons 1966), lies between the transverse fold and transverse groove (TG) and is divided by a median groove (MG. fig. 4.5). The tendon, T2, inserts at the junction of the transverse and median grooves. On either side of this tendon, a dorsal transverse ridge (TR and TRE) joins the vertical^(HE) and longitudinal^(LE) ridges. ~~(HE and LR, respectively)~~. A row of strong, amber-coloured, closely packed, hexagonal teeth lie ventral to the transverse ridge, and is interrupted by the median groove. These teeth form a chisel-shaped edge, the central ones are longer with prominent points. Dorsal to the teeth is a pale-blue staining cellular structure with exocuticular cell walls. From this structure, a thin strip of exocuticle extends through the transverse ridge to the hypopharynx, and longitudinal and vertical^a ridges. Resilin forms most of the transverse ridges and endocuticle forms most of the zone (1) where it bulges into the transverse fold.

Zone (2) (zone III of Parsons), posterior to the transverse groove, consists of resilin with ventral rows of exocuticular teeth. The zone

narrows posteriorly, and there is a median gap between the hindmost teeth. The anterior teeth are arranged in regular rows, and their form progressively changes from short, strong, pointed teeth to thin, long, double-pointed teeth at the posterior limit of this zone, (fig. 4.11).

Zone (3) (zone IV of Parsons) comprises two pads of resilin on either side of the endocuticle to which the tendon, T3, is attached. Posteriorly laterally the zone is formed by exocuticle.

The black pigmented exocuticle of the strong bowl-shaped hypopharynx of the masticator is restricted to a single ventral layer found beneath the denticulate pad beneath zones (1) and (2). Beneath zone (1) are strong, backward-pointing spines which are laterally finer and more numerous. Under zone (2) there are very fine spines. All these spines are exocuticular; however, the cuticle forming most ^{of the} ~~the~~ denticulate pad has a fibrous appearance and stains both red and blue. In the posterior hypopharynx there is a thin dorsal layer of resilin, separated by a pale-blue staining cuticle from the ventral layer of sclerotised cuticle which forms the posterior transverse ridge (TRH).

Posterior region of food pump, (figs. 4.5, 4.7, 4.9, and 4.11).

This is a very short region where a small dilator muscle, M4, attaches directly to the epipharynx. Here the walls of the pump are of endocuticle, except for a slightly strengthened region at the muscle insertion. The pharyngeal wall is also strengthened at the point of attachment of the pharyngeal dilator muscles (DP).

Salivary pump, (fig. 4.7)

The corixid salivary pump is similar to, but relatively smaller than, those of other Heteroptera.

Glands, (fig. 4.8)

a. Dermal glands. The cell bodies of these glands are filled with densely staining material, usually a dark purple in colour, (Benwitz 1956a), and open to the exterior via pores described in sections 3.3 and 3.75.

b. Hypopharyngeal glands. A pair of small elongated glands ('Druse der Hypopharynxflügel' of Benwitz) open into a channel in the hypopharyngeal wings, and connect with the space around the stylets.

c. Cephalic glands. The cephalic glands (CG) ('Maxillary gland' of Benwitz) are the largest glands in the corixid head and lie between the compound eyes. They consist of vacuolated epithelial cells which contain a blue staining material, ^{and} completely surround a large central cavity within which similar substance is found. These glands open behind the anteclypeus and in front of the bristles of the maxillary plate.

d. Labial glands. The labial glands (LG) appear as rounded structures on each side of the labial groove. The secreting cells are arranged around the edge of a blue staining area connecting them to a small central lumen which, in turn, connects to the space surrounding the stylets and to the gap between the labium and anteclypeus.

Corixinae nymphs

In the first instar nymphs of Corixa punctata the food pump is essentially the same as that of the adult, although the masticator is less powerfully constructed.

4.42 Diaprepocoris zealandiae, (figs. 4.6 and 4.12 to 4.15)

This species differs from other corixids in that the clypeolateral

cleft extends laterally and shows no tendency to curve anteriorly or to run posteriorly. Also, unlike other corixids, the vertical ridge (HE) is straight.

The anterior region of the food pump changes shape evenly, with no central constriction and there the epipharynx lacks bristles.

The middle region of the food pump is not as complex or powerful as that of the Corixinae. The epipharynx consists of resilin which forms radiating struts on the dorsal surface. The exocuticular teeth are similar in form and arrangement to those of zone (2) in Corixa. In Diaprepocoris there is a median epipharyngeal groove. Muscle group 2 is inserted on to tendon (T2), originating from the anterior roof of the masticator. In contrast, muscle group 3 inserts directly on to the posterior roof of the masticator.

The hypopharynx of the masticator shows similarities to Corixa, but is simpler. It is formed mainly of sclerotised cuticle ~~mesocuticle~~, but in the posterior part of the masticator there is an area of endocuticle and resilin which extends into the posterior region of the food pump. Anteriorly there are dorsal longitudinal ridges which fit between the epipharyngeal teeth.

The posterior region of the food pump is long, becoming narrow posteriorly and changes from a V-shaped trough with a sclerotised hypopharynx and an epipharynx of resilin to a membranous endocuticular pharynx. The muscle group 4 insert^s directly on to the epipharynx.

The labial and cephalic glands differ from the homologous structures in other corixids. The labial glands are tubular with the glandular

epithelium adjacent to the central canal. The thin glandular epithelium of the cephalic glands only partially surrounds the large central cavity in this species.

4.43 Micronecta poweri

The food pump of Micronecta and another member of the sub-family, Micronectinae, Tenagobia selecta, is basically the same as that of the Corixinae.

The anterior region of the food pump, like that of Diaprepocoris, shows neither constriction nor epipharyngeal bristles. Also there is no transverse fold.

The epipharyngeal teeth of the middle region of the food pump have the same basic arrangement as ⁱⁿ the Corixinae. There are only two rows of large bluntly pointed teeth in zone (1), the teeth of each row arise alternately, (see Walton 1938). In contrast, the teeth of zone (2) are finer than those of the Corixinae, but the basic arrangement and type of teeth is the same.

Except for the exocuticular teeth, the epipharynx of zones (1) and (2) is formed of resilin, connected directly to the sclerotised lateral walls of the hypopharynx. Zone (3) is composed of exocuticle, except for the thin endocuticular region posterior to tendon, (T3). This endocuticle extends into the short, posterior region of the food pump where it is slightly thickened at the insertion of the small muscle, M4.

Two tendons arise at the junction of the median and transverse grooves. The large anterior tendon, T2, forms the attachment for many muscle fibres, whereas the smaller posterior tendon has only a single

median muscle fibre, (Walton 1938). This median muscle passes behind the frontal ganglion and is, therefore, pharyngeal in origin, unlike the muscles of group 2 which are cibarial. Functionally, however, the median muscle is part of muscle group 2.

The hypopharynx ^{of the} middle and posterior regions of the food pump has several distinct zones which are referred to in relation to the epipharyngeal structures above them. The first zone, lying anterior to the epipharyngeal teeth, is formed entirely of endocuticle with several rows of dorsal bristles which are long, strong, and point backwards. This zone is separated by a small transverse groove from a darkly pigmented exocuticular region with a row of blunt teeth which oppose the epipharyngeal teeth of zone (1). Beneath the epipharyngeal zone (2) is a region of resilin with fine, dorsal posterior pointing spines. Posterior to this zone is a ventral layer of exocuticle which extends into the posterior region of the food pump. Between the exocuticle and a dorsal layer of resilin is endocuticle. The lateral hypopharyngeal walls of the middle and posterior regions of the pump are mainly of sclerotised cuticle.

4.44 Cymatia bonsdorffi

In contrast to other corixids the dorsal surface of the third labial segment is not ridged, (see section 3.44 and fig. 3.12). It is composed posteriorly of sclerotised cuticle and anteriorly of resilin and endocuticle. In contrast to the usual arrangement of sockets, there is a set of overlapping flaps which, when closed, seal the labial orifice. Surrounding the labial orifice there are large 'frilly' lobes

of endocuticle.

The most numerous sense organs of both the third and fourth labial segments have tactile sense organs with fine hair-like bristles. Other types of sense organs are also found on the terminal segment.

The form of the food pump is basically the same as that in the *Corixinae*, however, the musculature has in addition a set of dorsal transverse muscles on either side of the small muscle group 4.

The anterior region of the food pump has no constriction, but in the posterior quarter of this region there are fine, backward-pointing bristles covering the ventral surface of the epipharynx. The dorsal surface of the epipharynx bears a median strip of endocuticle.

The middle region of the food pump has no black pigmented cuticle, and is less massively constructed than that in Corixa. The transverse fold in the epipharynx has laterally numerous fine bristles.

In zone (1), the teeth are similar to those of the *Corixinae*, but above them, instead of the cellular structure, is a rod of exocuticle with a small central hole. This exocuticle is continuous with the thin strip in the transverse ridge and joins the lateral longitudinal and vertical ridges of the anterior region of the food pump. Resilin forms the bulk of the transverse ridge which is very tall laterally. Anterior to the transverse ridge an endocuticular bulge projects into the transverse fold.

The teeth of zone (2) are similar to those of Corixa and Sigara. The teeth of the anterior row are large and rounded, but the other teeth are fine. On top of the resilin is a layer of endocuticle.

Zone (3) is composed of resilin attached to the hypopharynx and has an extensive ventral layer of exocuticle.

The hypopharynx forming the sides of the middle and posterior regions of the food pump is of sclerotised cuticle. Under zone (1), the hypopharynx is exocuticular and bears a transverse row of blunt teeth with laterally a large number of fine backward-pointing spines. In the mid-line, the exocuticle is continuous with the posterior transverse ridge. Beneath zone (2) the dorsal layer of resilin has long, fine backward-pointing bristles which become smaller posteriorly and are replaced by small spiny tubercles. Laterally, in this region is a ventral area of endocuticle, whilst dorsal to the exocuticular transverse ridge is endocuticle surmounted by a layer of resilin (cf. Corixa fig. 4.11). This arrangement of cuticle extends into the posterior region of the food pump.

4.45 Stenocorixa protrusa

Again, the food pump is similar to that of the Corixinae. Prominent hypopharyngeal teeth are seen in a transverse section, probably through the anterior of zone (1), Poisson and Jaczewski (1928).

4.46 Notonecta glauca

In Notonecta, the transition between the food channel of the stylets, to a channel formed by the epipharynx and hypopharynx, and then to the food pump, is gradual. In the region of the junction between the labrum and anteclypeus, the maxillary stylets separate and later become widely separated by an anterior sclerotised projection of the hypopharynx. The efferent saliva^{ry} duct protrudes into the saliva channel of the maxillary

stylets (fig. 4.3). The hypopharynx widens posteriorly and becomes trough-shaped before joining the epipharynx laterally to form the food channel. The hypopharyngeal portion of this channel and in the anterior region of the food pump consists of sclerotised cuticle.

Where the stylets separate, the epipharynx consists of dorsal endocuticle and ventral resilin and presses down on to the stylets, sealing the food channel. In the part of the food channel formed by the hypopharynx and epipharynx, the latter forms the flat roof. The epipharynx is thin anteriorly and bears a median row of 10 pores, the openings of the anterior epipharyngeal sense organ. Behind these openings, a sclerotised transverse bar is followed by the food pump. The roof of the pump, which is composed of resilin, bulges forwards slightly and fills the whole of the hypopharyngeal trough when the dilator muscles are relaxed.

The first tendon of the dilator muscles is stronger than the nearby tendons of the muscle (cf. Corixa and Sigara). On either side of the space between the first two tendons is a row of three pores from the posterior labial sense organ. Between the second and fourth tendons on the ventral epipharynx are fine bristles which are restricted to the central area.

The food pump has again three regions including a complex middle region (Giese 1883 and Parsons 1966).

4.5 Structure and function

In some cases, direct observation has shown how a particular structure is used, e.g. the stylets, but in other cases the function of

some parts of the head is deduced from their structure, and it is necessary to pay particular attention to detail.

4.51 The stylets

In the species studied, only the barbed distal end of the mandible penetrates the prey during feeding. The function of the mandibles is solely to hold the prey (section 2.32). The sharp barbs of the mandibles of Nepa and Notonecta are obviously suitable for hooking into the integumentary tissues of the prey. Nepa, which has delicate mandibles, holds the prey in its powerful raptorial forelegs. The distal group of barbs of Notonecta mandibles are like the blunt projections of the corixid mandibles. These projections are most prominent in Neocorixa and Cymatia, which are known to feed on large swimming prey (section 2.25). Corixid mandibles are curved distally, and are capable of slight rotation (Benwitz 1956a). Both of these features increase their effectiveness as anchoring and manipulating organs.

The maxillae of Notonecta and Nepa are much longer than the mandibles and during feeding, they penetrate ^{more} deeply into the prey (section 2.32). The maxillae of Cymatia, which feeds on large prey, are also longer than the mandibles and they protrude from the rostrum further than the maxillae of other corixids. In all species, at least one maxilla has a sharp point. The maxillae are probably the stylets used first to penetrate the prey. Both maxillae have sharp points in Nepa, but only the left one is sharply pointed in Notonecta and the right one in corixids. The right maxilla of both Neocorixa and Cymatia has larger distal spines than other corixids. ~~Cymatia is known to feed on large animals.~~

Long curved spines are found on the distal end of both maxillae in Nepa, and on the right one in Notonecta, but are entirely absent in corixids. These long spines are also found in other Heteroptera (Belostomatidae, Quadri (1951); Gerris remigis Say (Gerridae), Cranston and Sprague (1961); Gelastocoris oculatus (F.) (Gelastocoridae), Parsons (1959); Saldula pallipes (F.) (Saldulidae), Parsons (1962); Limmogonus fossarum (F.) (Gerridae), Cheng (1967)). But in these other species, the arrangement of the spines is not sufficiently well known nor is their relationship to the opposite stylet known. There are two possible ways in which the long spines may function. They may help to hold the maxillae together (Quadri 1951), but this is unlikely because in both Nepa and Notonecta, the long spines of one maxilla lie inside the food channel when the tips of the maxillae are level. Alternatively, the long spines may filter the food (Parsons 1959). This seems to be their function in Notonecta. In the prey, the left maxilla moves relative to the right maxilla frequently and rapidly, but does not extend beyond the tip of the right maxilla. When the left maxilla is partly withdrawn, the long spines of the right maxilla are exposed, and as they almost complete the second side of the food channel, could act as a filter. The same procedure could operate in Nepa. The absence of a maxillary filtering mechanism in corixids must be associated with their ability to ingest large particles and membranes (section 2.33).

The maxillae of Nepa and Notonecta, and, in fact, all other Hemiptera except the corixids, form two sealed channels over a great length, at least 2 millimetres in Nepa, and yet are capable of independent extension

and withdrawal. In Notonecta, the maxillae have interlocking projections and grooves which are better developed at the distal end (fig. 4.3).

Also, at the distal end of the maxillae, and on the lateral edges, are numerous short forward-pointing spines which run in the grooves of the opposite maxilla. Similar spines are found in Nepa. In contrast, the grooves and projections of the short maxillae of corixids are very simple (fig. 4.4), but they are better developed in Cymatia where the longer maxillae are protruded further from the rostrum.

The mechanism for holding the maxillae together also seals the food and saliva channels. In many Heteroptera, including the Corixidae and Notonecta, the proportion that each maxilla contributes to the saliva channel varies along the length of the stylet bundle. In Notonecta, the saliva channel is formed equally by both maxillae proximally but distally the saliva channel is formed entirely by the left maxilla and opens into the food channel just before the tip of the stylet. A similar condition is found in Saldula pallipes (F.) (Saldulidae) (Parsons (1962)). This peculiar condition in Notonecta and Saldula would ensure the saliva mixing with the ingested food. However, external digestion of the prey occurs (section 2.31) presumably by proteases from the saliva which is ejected into the prey. It is possible that the movements of the left maxilla, which contains the saliva channel, are associated with the injection and spread of the saliva within the prey.

In Notonecta, resilin is only found at the basal end of the maxillae, along the ventral edges. These are the edges which have to maintain the sealed saliva channel and to accommodate the efferent

saliva duct which is inserted into the saliva channel.

Resilin is much more important in the sealing mechanism of the food and saliva channels in the maxillae of corixids. The edges of the stylets are pressed together by their own elasticity and by the labium, and a seal is achieved by the strips of rubber-like cuticle.

In all corixids examined, the food channel is proportionately wider and the saliva channel narrower than the equivalent structures in Notonecta. The width of the food channel, and hence the maxilla, in Notonecta is limited by the need for flexibility as wide maxillae are structurally resistant to bending. The narrow saliva channel in corixids is associated with their small saliva pump. A wide saliva channel in Notonecta may also be associated with the need to reduce the resistance to the flow of saliva down the great length of the stylets.

4.52 Labium

The long, mobile rostrum of Notonecta and the short, almost totally immobile rostrum of the Corixids have similar sense organs on the tip of the terminal segment and both have a sclerotised ventral projection from the labial groove (figs. 4.3 and 4.4). Unlike Notonecta, the labial orifice of the corixids can be closed and sealed when the stylets are retracted into the rostrum. Also, the labial groove is lined with endocuticle which, by pressing against the stylets, can seal the groove even when the stylets are extended. As Corixa has a higher uptake of water through the cuticle than Notonecta (Staddon 1966), any mechanisms such as the ability to seal the labial groove which prevents inflow of water, are significant.

4.53 The junction between the stylets and the food pump

This anatomical area in

In Notonecta there are three functional regions; one, the transition from the food channel of the maxillae to the food channel formed by the epipharynx and hypopharynx; two, a sensory region with the anterior epipharyngeal organ in the food channel and the posterior epipharyngeal organ near the tip of the food pump; three, the food pump itself.

In corixids, all these functional regions overlap, for example, the flexible epipharyngeal roof and the sense organs project into the 'food channel' which is still largely formed by the maxillae.

4.54 The food pump

The corixid food pump is divided into three regions; anterior and posterior pumping regions and a middle masticatory region.

The long anterior region of the food pump sucks the food material up through the food channel in the stylets and pushes it into the middle region. The roof of the anterior pump is actively raised by the dilator muscles, but returns to its normal position by the elasticity of the resilin of which the roof is composed. This movement ^ucases food to be pumped into the animal. The fine backward-pointing bristles in the Corixinae and Cymatia must prevent particles passing forwards.

The middle and posterior regions of the food pump in the Corixinae form ^{the} most powerful masticatory apparatus known in the Heteroptera (Parsons 1966). A mode of working is described by Elliot^t and Elliot^t (1967), but fuller knowledge of the structures is now available.

From the position of the masticator in different specimens, the

muscles, M2 and M3 appear to work in opposition to each other. When the muscle, M2 contracts zone (1) and the anterior ^{part} of zone (2) of the epipharyngeal roof are raised and the posterior end of zone (2) is pulled forwards slightly. The roof bends along the median groove, and transverse groove at the junction of zones (2) and (3) and along the junction of zones (1) and (2) with the hypopharynx. The transverse ridge of zone (1), composed of resilin and the strip of exocuticle, is twisted. It is the untwisting of the transverse ridges which probably provides the greatest force returning the anterior roof of the masticator to its original position when the muscle, M2, relaxes. The teeth of zone (1) strike against the anterior teeth of the hypopharyngeal denticulate pad. The 'cellular' structure supporting the epipharyngeal teeth of zone (1) probably has great resilience and is able to absorb the strains incurred when the tooth row descends sharply on substances of differing hardness. The mesocuticle forming the bulk of the denticulate pad probably also possesses great resilience. Zone (2) is pushed back as well as down and the teeth of this zone grind and scrape against the posterior region of the denticulate pad.

The contraction of muscle, M3 raises zone (3) and the posterior end of zone (2) and probably pulls the anterior end of this zone backwards, causing the teeth to grind against the hypopharynx. The epipharynx bends most along the junction of zones (2) and (3) and the junction of zone (3) with the hypopharynx. It is returned to its starting position by the elasticity of the roof, with a large part of the force possibly being provided by the thin exocuticle which joins the posterior

epipharynx and hypopharynx (figs. 4.11 D and E).

The probable sequence of events in the masticator are as follows.

It is convenient to start with muscle M2 relaxed and muscle M3 contracting, so that suction is occurring in the posterior half of the masticator and with the particle laden liquid being pushed into the masticator by the anterior food pump. The liquid passes across and through the transverse fold, and reaches the posterior part of the masticator through the zone (1) teeth and the anterior denticulate pad of the hypopharynx. Probably a large part of the liquid passes laterally through the filter of fine bristles, the large particles being left in the region of the transverse fold.

The anterior food pump roof is now pressed against the hypopharynx and the muscle M3 relaxes and the posterior region of the masticator roof descends, pushing the liquid and crushed particles into the posterior food pump and pharynx. At this point, the posterior muscles of muscle group 1 and the muscles M2 and M3 are relaxed.

Muscle, M2 now rapidly contracts and relaxes, raising the anterior roof of the masticator and allowing it to snap back. When the anterior roof of the masticator is raised, the particles and liquid accumulated in the transverse fold and between the masticator and anterior food pump are brought into the space under the teeth of zone (1) and anterior zone (2), where they are crushed. The teeth of zone (1) towards the midline are most sharply pointed, and are probably used to pierce food particles, the central region being the place where the largest food particles will be gathered, and the greatest force developed by the masticator. Laterally, where the zone (1) teeth are blunter and are

moved less, they probably grind material against the anterior denticulate pad. When the anterior roof of the masticator is raised, the posterior raking teeth of zone (2) are against the posterior part of the denticulate pad, and when the anterior roof of the masticator snaps down the teeth of zone (2), scrape and grind against the posterior part of the denticulate pad. Towards the end of this movement, the muscle M₃ contracts, starting to raise the roof of the posterior masticator, an action which probably intensifies the grinding by the anterior teeth of zone (2). It may be that the raising of the posterior roof of the masticator both pulls back and then pushes zone (2) forwards, and this activity may also affect the action of the teeth of zone (1). The cycle now begins again, and with the contraction of muscle M₃ and the activity of the anterior food pump, liquid is now flushed through the filters of the anterior masticator and over the posterior denticular pad, washing out the crushed material.

It is not known what volume of liquid passes through the masticator in each cycle and how much remains to go through the procedure again. It would be possible for a closed system to be set up for a thorough maceration of material if the circular muscles of the pharynx remained contracted, and from an examination of the contents of the midgut, it is known that the masticator is very efficient at breaking up material as resistant as algal cells, though some unbroken material and membranes do get through (section 2.33).

The masticator of Cymatia is less powerfully constructed than in the Corixinae, but probably functions in a similar way. The hind part

of the masticator and the posterior region of the food pump, form a powerful pumping unit. The dorsal transverse muscles in the posterior region of the pump are a most notable feature.

The masticator of Micronecta is again essentially similar to that of Corixa but it is less powerful. Instead of the transverse fold and fine backward-pointing epipharyngeal bristles, long, fine backward-pointing hypopharyngeal bristles act as a filter.

In Diaprepocoris, the middle and posterior regions of the food pump are different. There is a simple middle region with epipharyngeal teeth and the roof slightly stronger than the rest of the pump. Unlike Corixa, there are no filtering or particle guiding mechanisms. Also in contrast to Corixa, there is a long posterior pump.

The muscles, M2, and M3, probably act alternately, muscle M2 raising the anterior end of the masticator roof which bends along the median groove, the posterior teeth remaining in contact with the hypopharynx. When this muscle relaxes, the strengthened resilin roof brings the teeth down against the hypopharyngeal ridges and pushes the posterior teeth backwards, scraping up any food particles present. At this point, the muscle M3 probably contracts, raising the posterior end of the masticator roof and dragging the anterior end with its strong teeth backwards, grinding the food particles against the hypopharynx ridges. With the relaxation of muscle M3 the grinding action of the teeth is continued as the masticator roof returns to its original position. The pumping action of these movements of the masticator are probably synchronized with the pumping activities of the anterior and

posterior region of the food pumps.

4.55 Glands

Corixids contain many different and prominent glands in the head, their functions are still subject to speculation. Some differences between the glands of different corixids have been noticed.

No dermal glands at all are found in Cymatia whereas these prominent glands are found on all the other corixids examined. The dermal glands may be associated with the other corixids' greater activity and their searching in the detritus for food where they have increased contact with bacteria and organic matter. This activity increases the chance of organisms becoming attached to the corixid, and the dermal glands may contain a substance which deters the adhesion of these organisms.

All corixids have large cephalic (maxillary) glands which open directly to the exterior. These glands in Diaprepocoris have a thinner epithelium than the other species examined.

There is also a difference between the labial glands of Diaprepocoris and the other corixids. In Diaprepocoris, they are tubular, but in the other corixids they are very compact. The labial glands open into the space round the stylets and into the space between the anteclypeus and labium (fig. 4.13), and these glands may produce a bacteriacide to keep these spaces clean.

The thin elongated glands of the hypopharynx wings also connect with the space surrounding the stylets and may produce a substance with similar properties, and a lubricant.

4.6 Discussion of the variation of the food pump in the Corixidae

Stages in the development of the Corixinae food pump from a type similar to that of the present day Diaprepocoris, can be seen in both Micronecta and Cymatia, though all three genera have structures which show divergence from the main evolutionary line.

The form of the Diaprepocoris food pump, with the long anterior and posterior regions and the short complex middle region immediately behind the clypeoloral cleft, is similar to that of four other Hydrocorixae families, i.e. Notonectidae, Naucoridae, Ochteridae and Gelastoteridae. The food pump in these families is almost entirely cibarial in origin, in contrast to the food pump of Diaprepocoris, which is half pharyngeal. In the other sub-families of corixids, the posterior region of the food pump with its muscle M4 is very reduced. This reduction is associated with a more complex middle region of the food pump with a posterior pumping area. This change is also associated with the lengthening of the anterior region of the food pump and the corresponding posterior extension of the clypeoloral cleft. The cleft also has an anterior extension in Stenocorixa, Cymatia, and the Corixinae, giving better support to the anterior and middle regions of the food pump.

The epipharyngeal teeth of Diaprepocoris and their relationship to muscles M2 and M3 are remarkably similar to the teeth of zone (2) in other corixids (cf. figs 4.11 and 4.15). The large epipharyngeal teeth of zone (1) can easily be derived from those anterior to tendon T2 and the absence of a median groove in zone (1), gives the form of epipharyngeal teeth found in Micronecta. The development of the transverse ridge in

zone (1) and of the transverse fold with fine epipharyngeal teeth which extend into the anterior region of the food pump, is seen in both Cymatia and the Corixinae. In the Corixinae, the transverse ridge is more powerfully developed, and has a transverse 'cellular' exocuticular structure. The distribution of the epipharyngeal bristles in the anterior region of the food pump is, however, more elaborate.

The form of the hypopharynx of the posterior part of the masticator is similar in all the corixids except that in Cymatia and the Corixinae there is, in addition, a transverse ridge. The hypopharynx of the anterior part of the masticator is much more variable. In Diaprepocoris there are exocuticular ridges, but in the other sub-families there are exocuticular teeth and spines beneath zone (1). There are also finer backward-pointing spines beneath zone (2), though the arrangement and form of the teeth and spines is peculiar to each sub-family. In Micronecta there is also an anterior group of long backward-pointing spines which act as a filter. In Cymatia and the Corixinae, bristles of the transverse fold and lateral hypopharyngeal spines have a similar filtering function (section 4.54).

There are other structural features which indicate divergence from the main line of evolution, an example of this in Diaprepocoris being the dorsal struts of resilin in the masticator. More obvious are the dorsal transverse muscles of the posterior region of the food pump in Cymatia, associated with the powerful activity of the masticator in this sub-family.

The significance in Micronecta of the small pharyngeal muscle

associated with the muscle M2 may only be determined after examination of Tenagobia, the other large genus of the sub-family. Histological material was not available.

In Cymatia, the differences in the structure of the food pump from that of the Corixinae are largely related to their diet of large swimming animals and because they do not ingest material with hard silica parts such as algae.

Species	Number of the diagram	Food channel	Saliva channel
<u>Notonecta</u>	4.3 b	360	80
<u>glaucia</u>	c	410	50
	d	410	35
	e	360	40
	f	410	40
	g	730	
<u>Corixa</u>	4.4 e	1550	30
<u>punctata</u>	f	1550	20
	g	1690	15
<u>Diaprepocoris</u>			
<u>zealandiae</u>		260	4
<u>Cymatia</u>			
<u>bonsdorffi</u>		200	4
<u>Sigara</u>			
<u>falleni</u>		330	4
<u>Micronecta</u>			
<u>poweri</u>		40	2

Area of the efferent saliva duct; N.glaucia, $70 \mu^2$ C.punctata, $16 \mu^2$

Table 4.1, Shows the area (μ^2) of the food and saliva channels of the maxillae and the area of the distal end of the efferent saliva duct of Notonecta glaucia and several species of corixid. The diagram of the section, from which the measurements are taken is indicated.

Fig. 4.1 Stylets of female Hydrocorisae. Distal end of mandibles and maxillae; Neocorixa snowi, a. left mandible, b. right maxilla; Nepa~~cin~~ereae c. left maxilla, d. right maxilla, f. and g. mandible; Notonecta glauca, h. left maxilla, i. right maxilla, j. left mandible; k-m. Mandible (MD) and Maxilla (MX), k. Neocorixa, l. Nepa, m. Notonecta. Figs. a-j. and k-m. are to the same scale as the equivalent structures in Fig. 4.2.

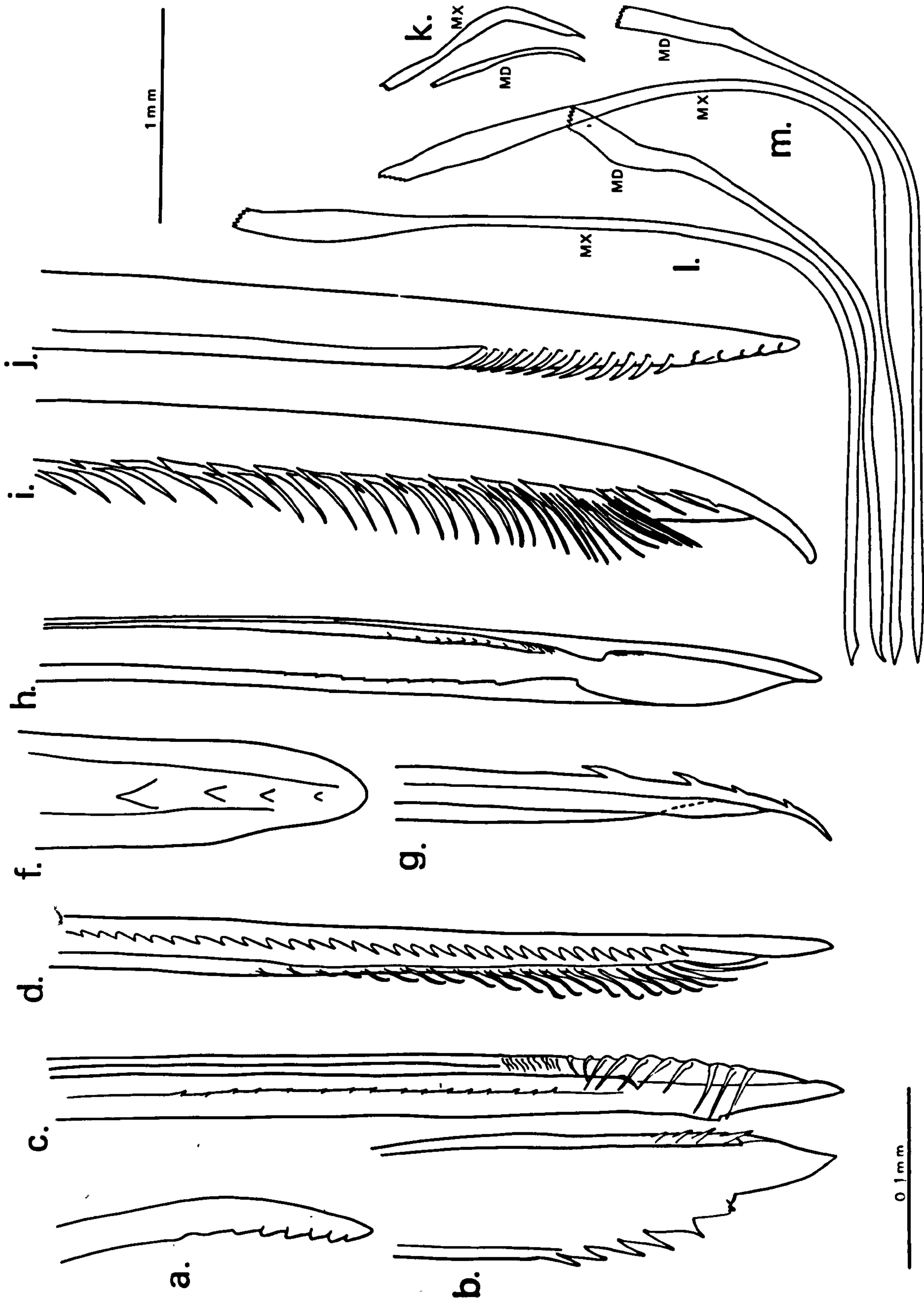


Fig. 4.2 Stylets of Corixidae. Distal end of mandibles and maxillae; Cymatia bonstorffi, a. left maxilla, b. right maxilla, c. left mandible; Corixa punctata, d. left maxilla, e. right maxilla, f. left mandible; Sigara falleni, g. left maxilla, h. right maxilla, i. left mandible, j-m. mandible (MD) and Maxilla (MX); j. Neocorixa snowi, k. Cymatia bonsdorffi, l. Sigara falleni, m. Corixa punctata. Figs. a-i. and j-m. are to the same scale as the equivalent structures in Fig. 4.1. The left maxilla, except that of C. bonsdorffi, becomes twisted when dissected out of the head.

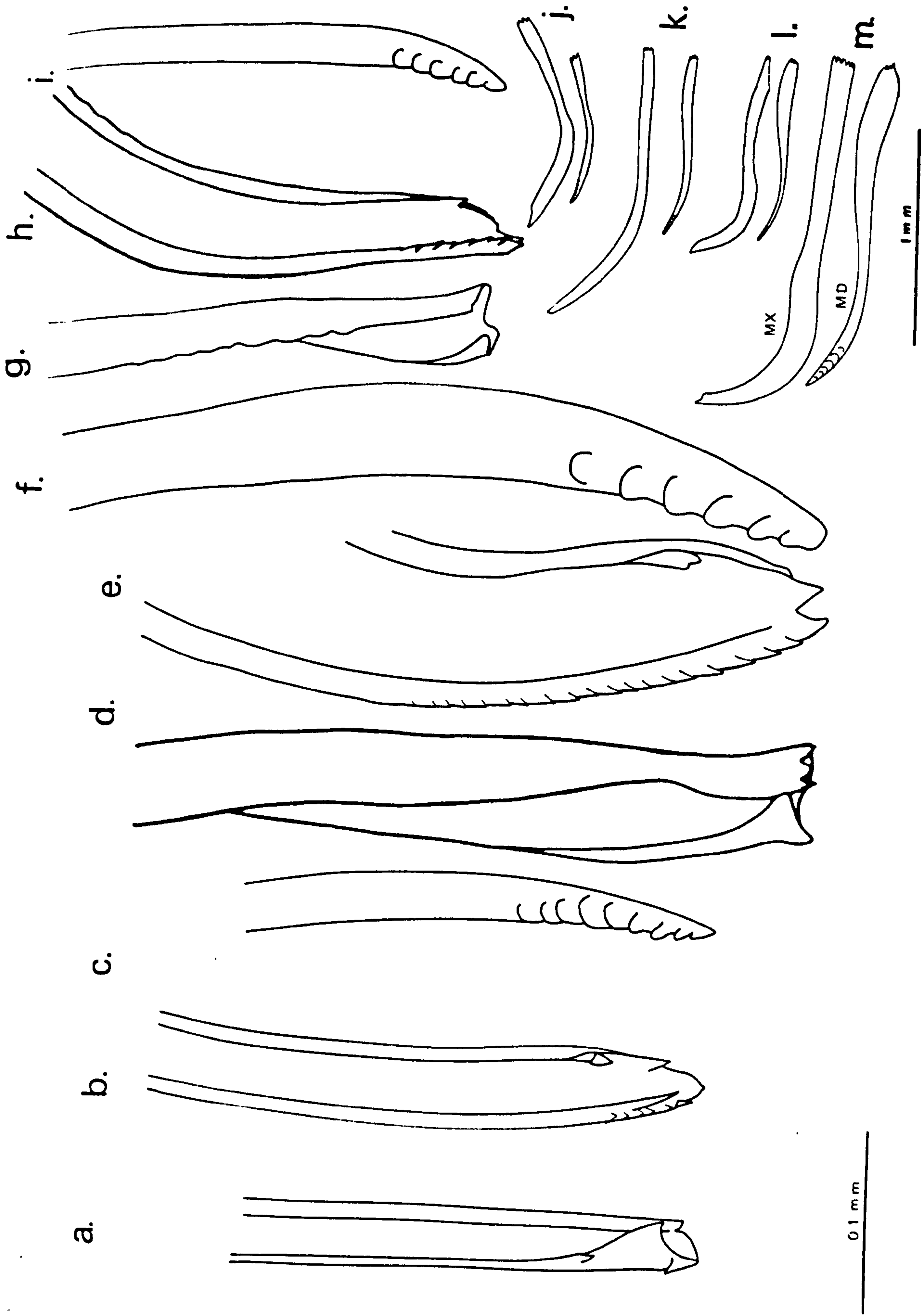


Fig. 4.3 Notonecta glauca, adult; transverse sections through the stylets and rostrum (see also fig. 3.21)

a. distal end of clypeus - illustrating the relationship of the hypopharynx and maxillae in this region.

b. proximal end of labrum, the projection of the left maxilla into the saliva channel gradually changes position so as to form part of the ventral groove in fig. C.

c. proximal end of second labial segment.

d. proximal end of third labial segment.

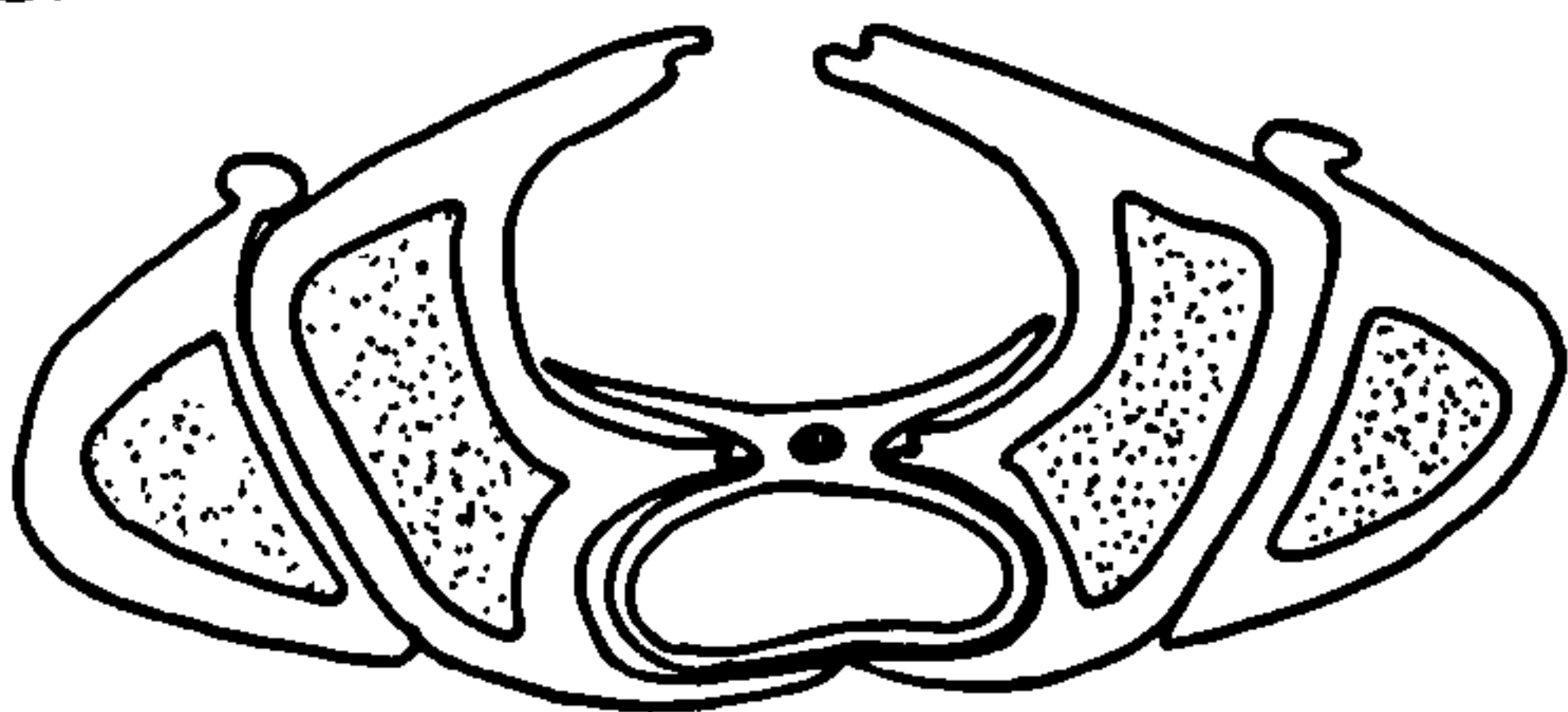
e. distal end of third labial segment.

f. and g. distal end of fourth labial segment - illustrating the relationship of the maxillae and mandibles to the distal labial lobes and sense organs; x - sclerotized projection of the ventral side of the labial groove. Fig. f. shows long spines of the right maxilla penetrating the saliva channel.

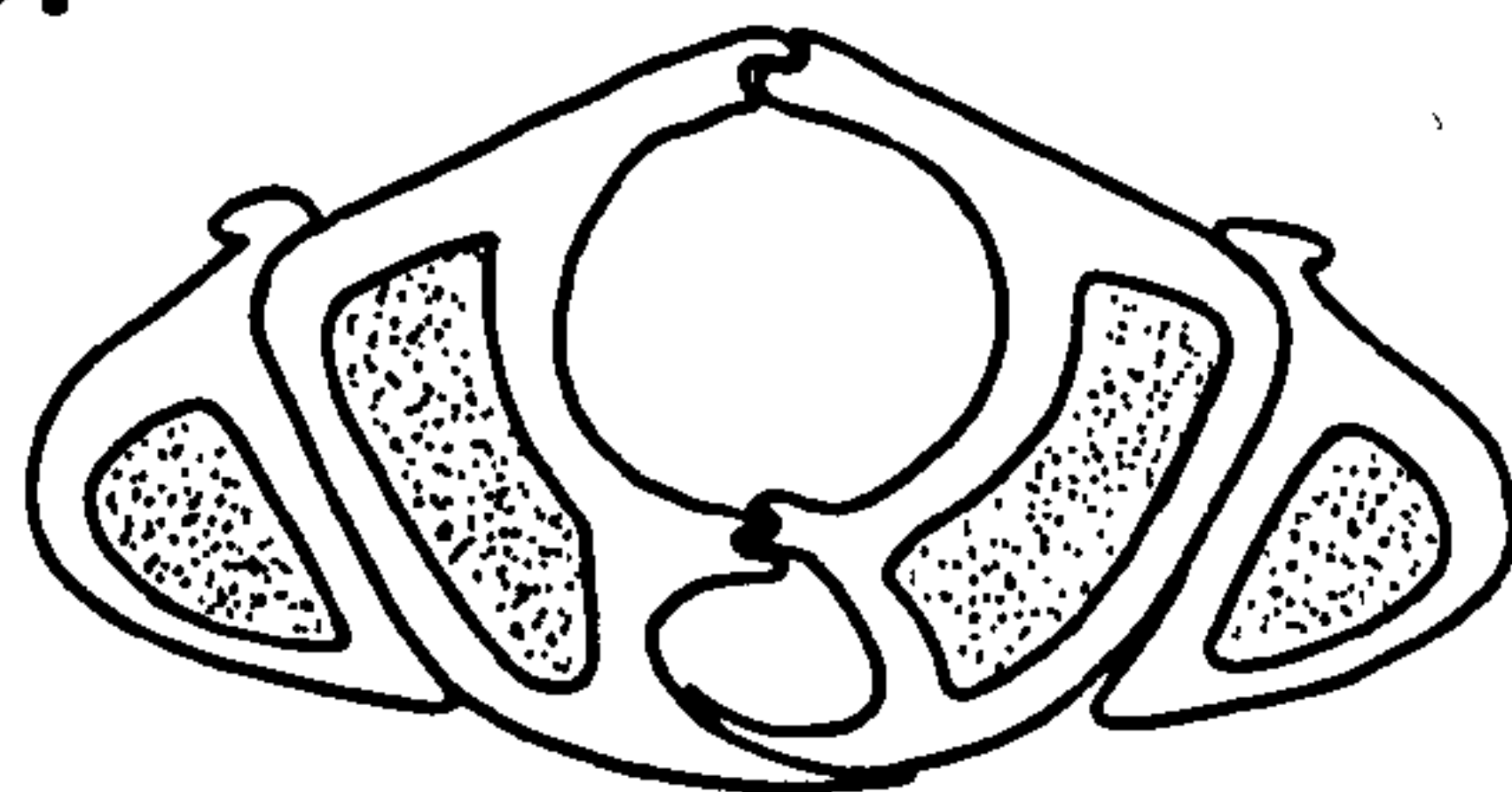
The mandibles end near the distal end of the fourth labial segment (fig. f.). The maxillae end just beyond the tip of the rostrum. The two stylets join to form the large dorsal food channel and the narrower saliva channel. The cuticle forming the ventral walls of the saliva channel in figs. a. and b. stains red, the cuticle of the rest of the stylets is non-staining. The way in which the food and saliva channels are sealed, changes gradually from the proximal to distal end of the maxillae.

Fine stippled areas indicate the cellular cavity within the stylets and hypopharynx, coarse stippled areas the non-cuticular labium.

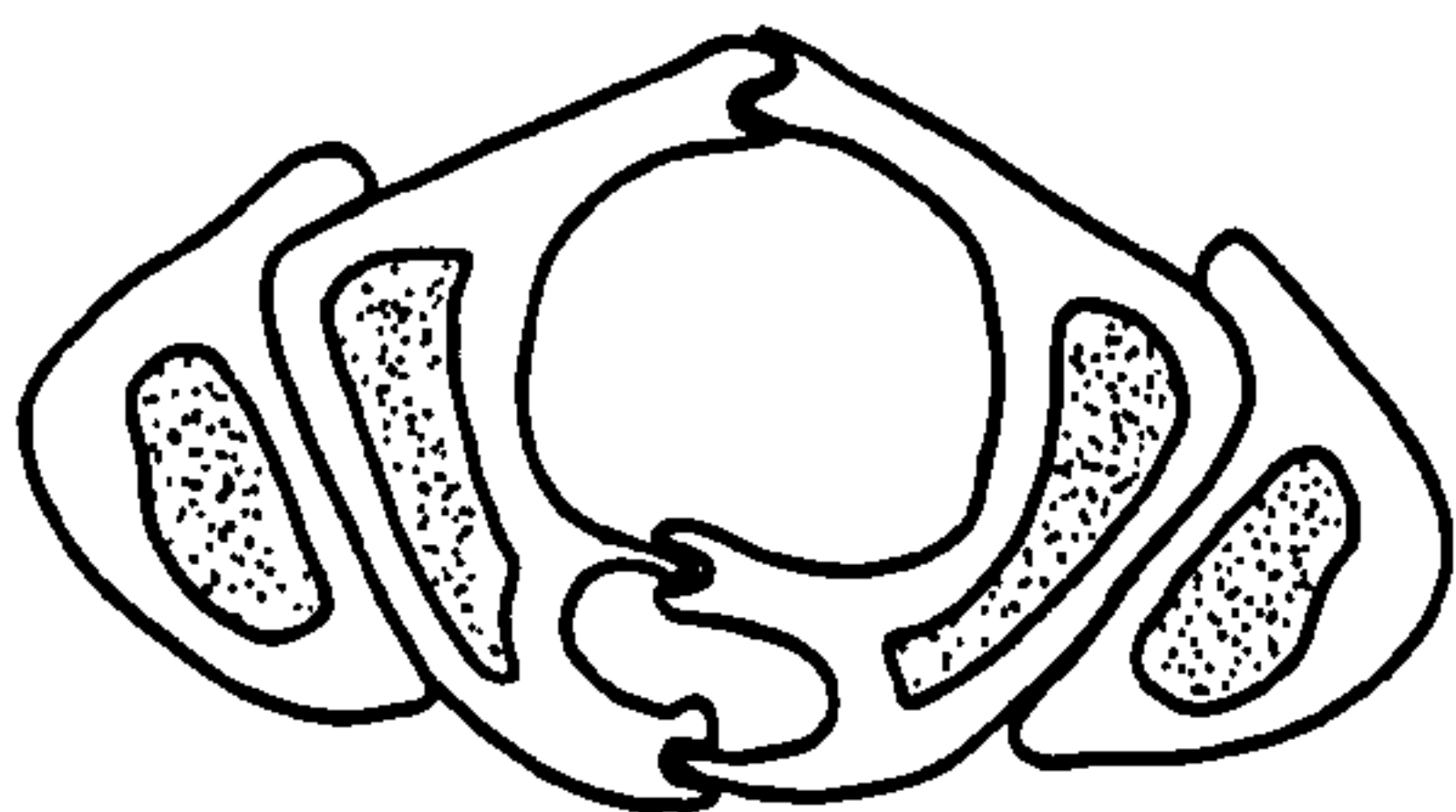
a.



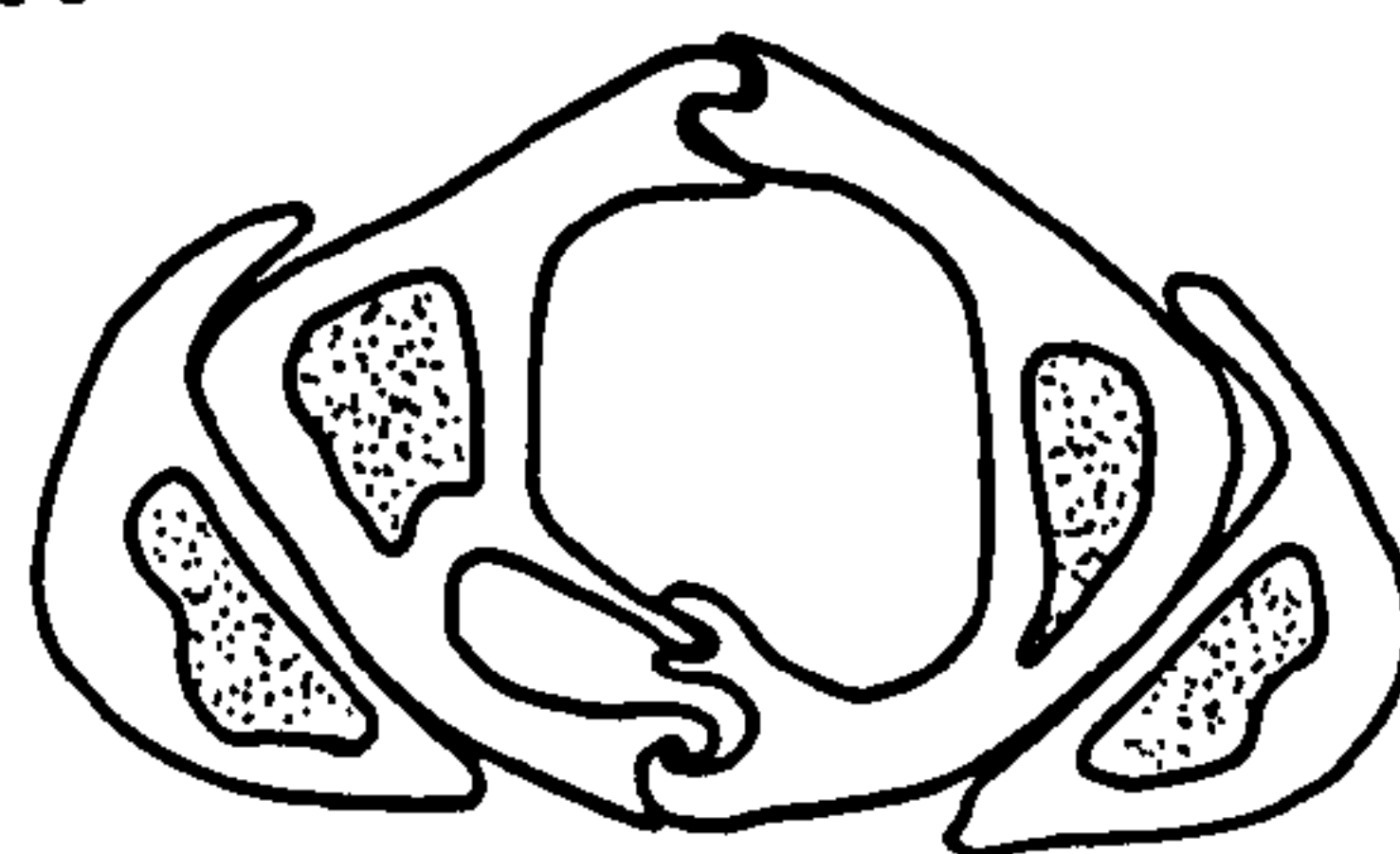
b.



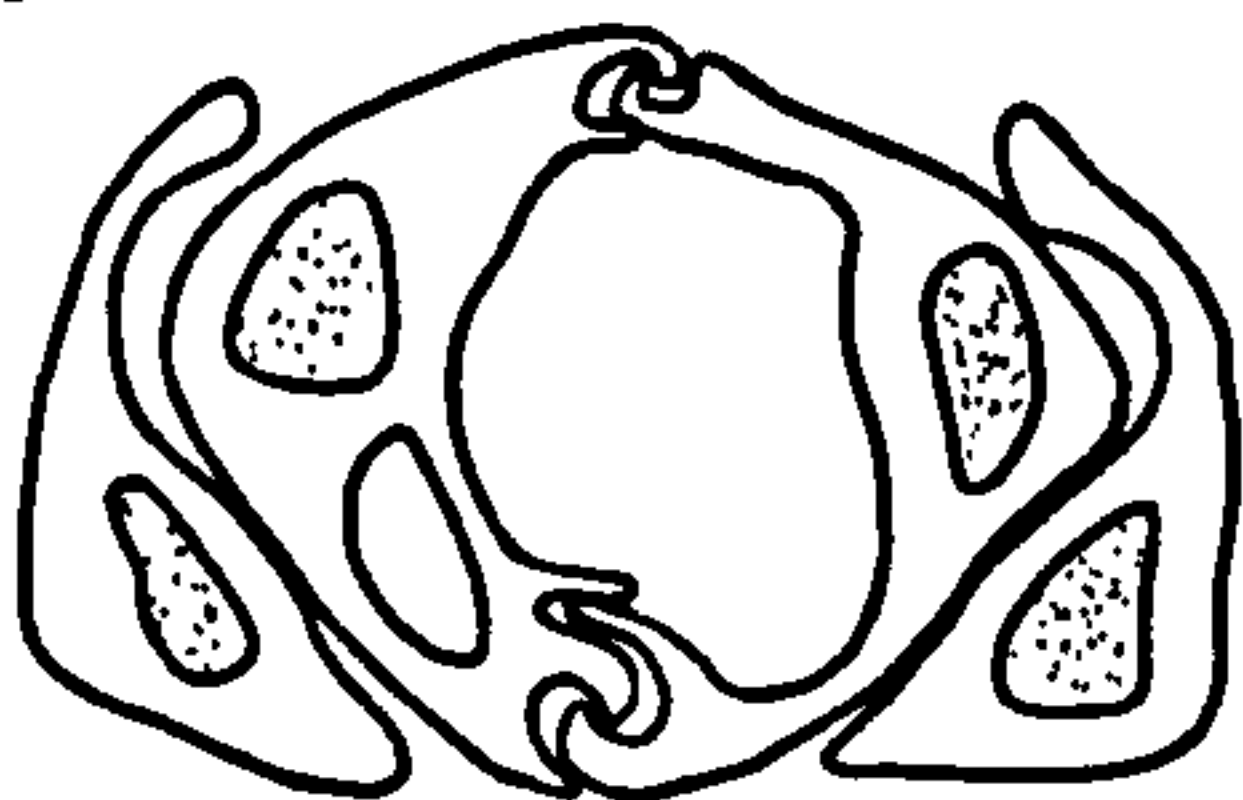
c.



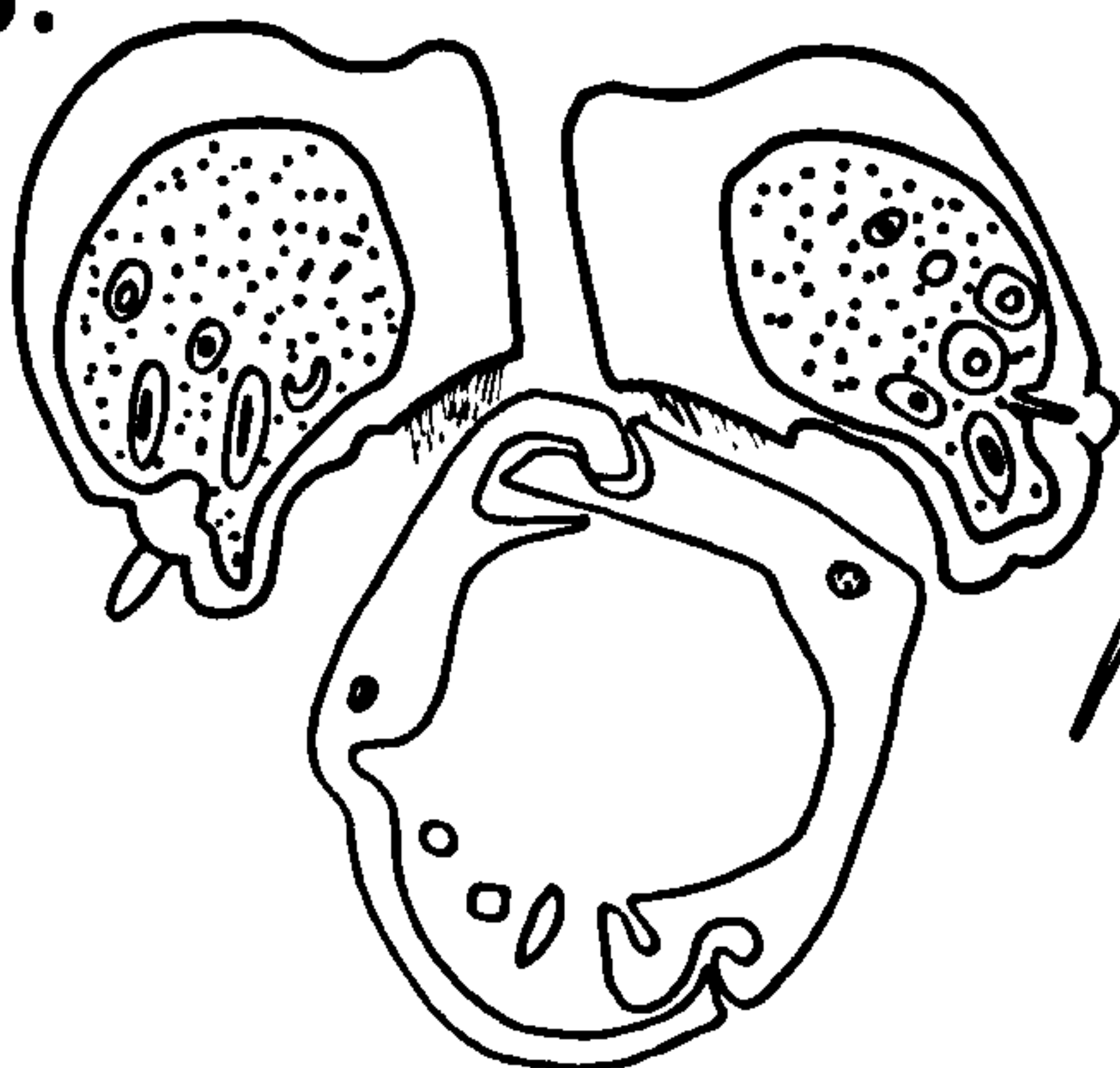
d.



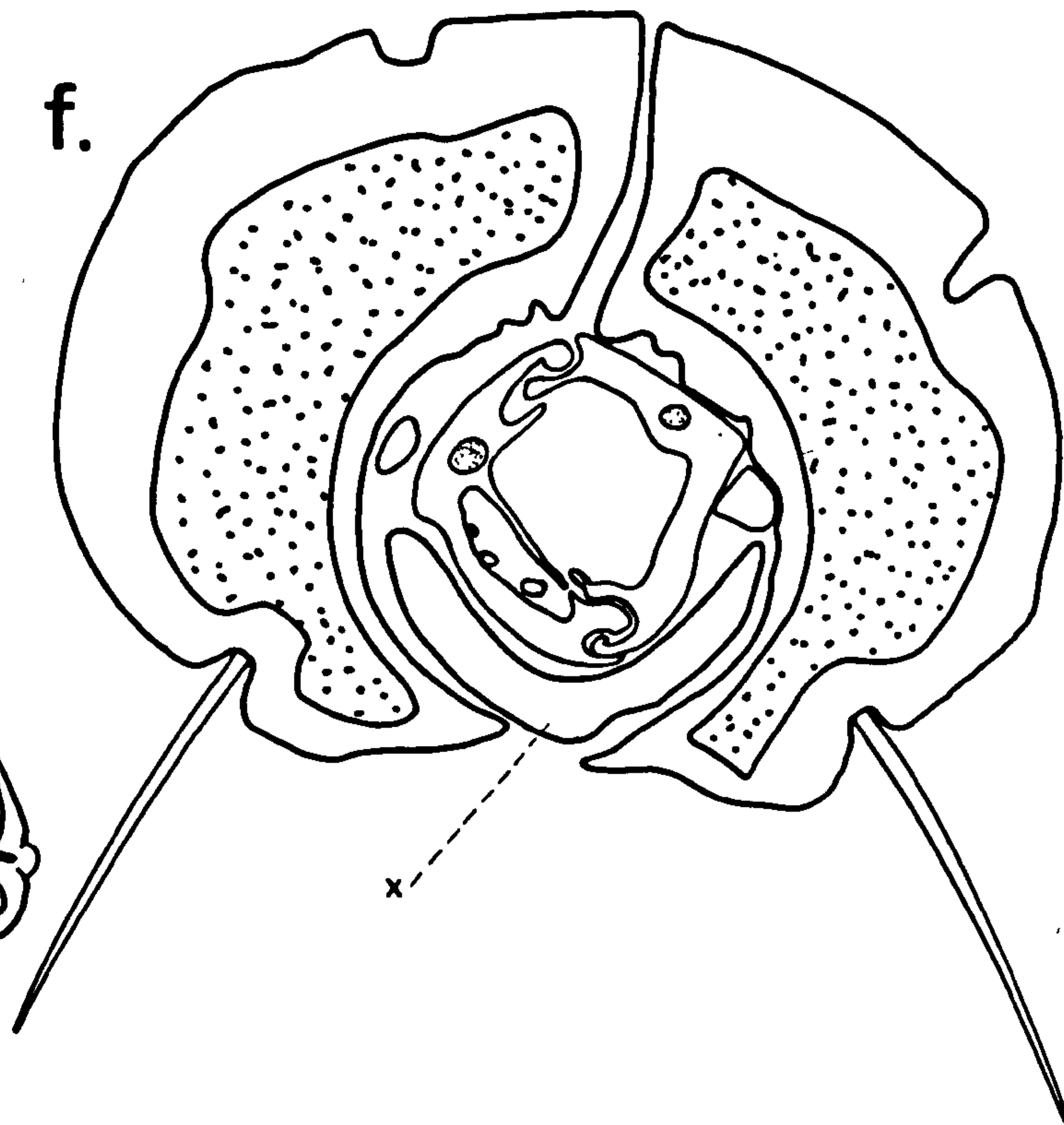
e.



g.



f.



0.1 mm

Fig. 4.4 Corixa punctata, adult, sections through the rostrum and stylets.

Transverse sections; A. through the anterior epipharyngeal sense organ (ASO), illustrating the relationship between the maxillae, hypopharynx, and epipharynx; B. through the labial orifice lever (LOL) illustrating the relationship between the stylets and the labial groove.

Frontal sections (see fig. 4.7 for the position of the sections);

C. through the labial orifice, illustrating the relationship of the stylets to the labial orifice (cf. fig. 4.3f), x - sclerotized projection of the ventral labial groove.

D to G show the changes in the maxillae and food and saliva channels. E is an enlargement of section C.

The stylets in the specimen from which the transverse sections are made, are withdrawn into the labial groove. The maxillae in the specimen from which the frontal sections are made, protrude from the rostrum and the mandibles remain within the labial groove.

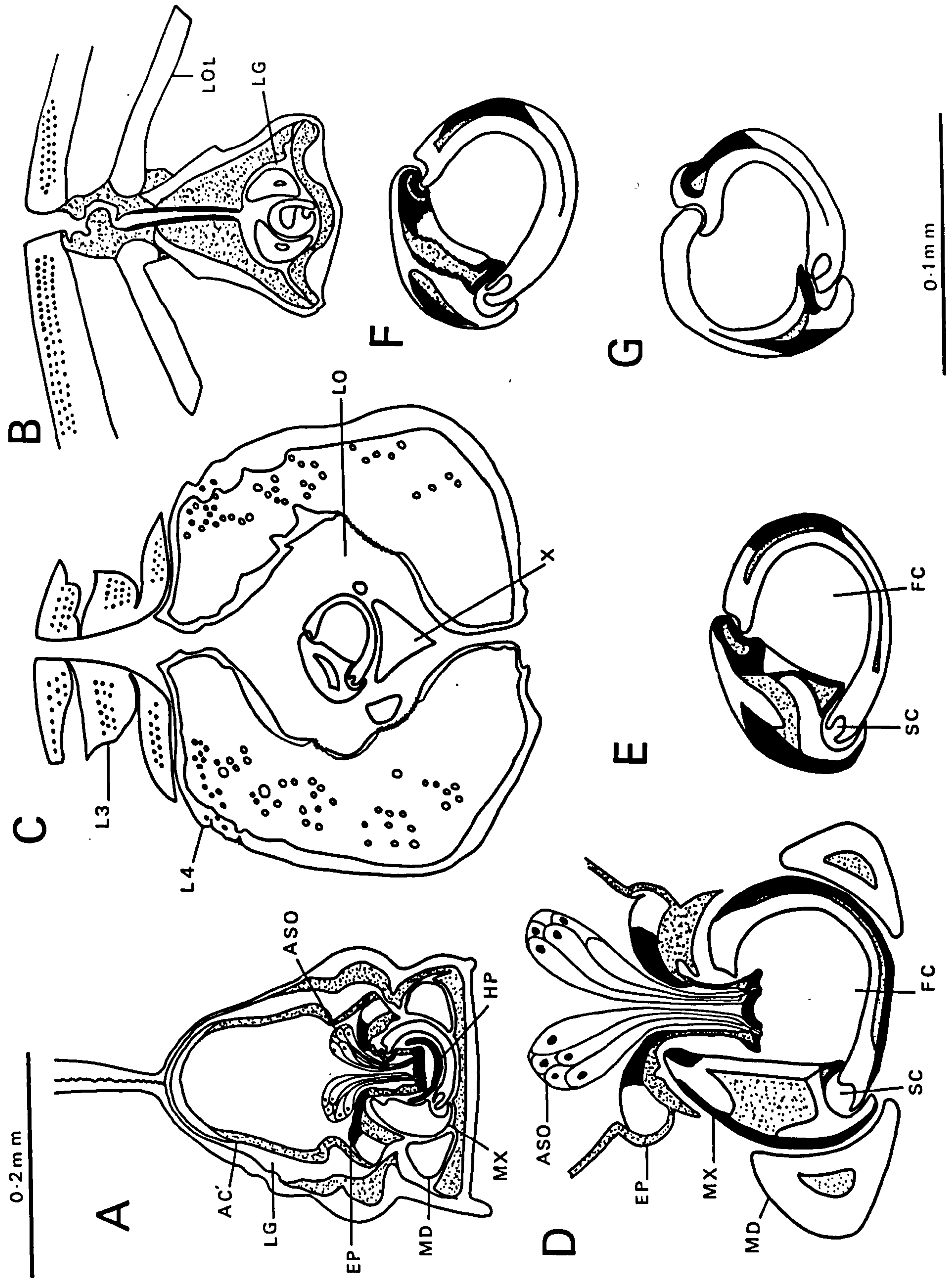


Fig. 4.5. Sigara falleni, female. The ventral surface of the epipharynx, which forms the roof of the food pump, exposed by removal of the rostrum, ventral (posterior) surface of the head capsule, the hypopharynx and associated muscles.

PH
M4
T3

(3)
(2)
(1)
ET

HE
LR

MA

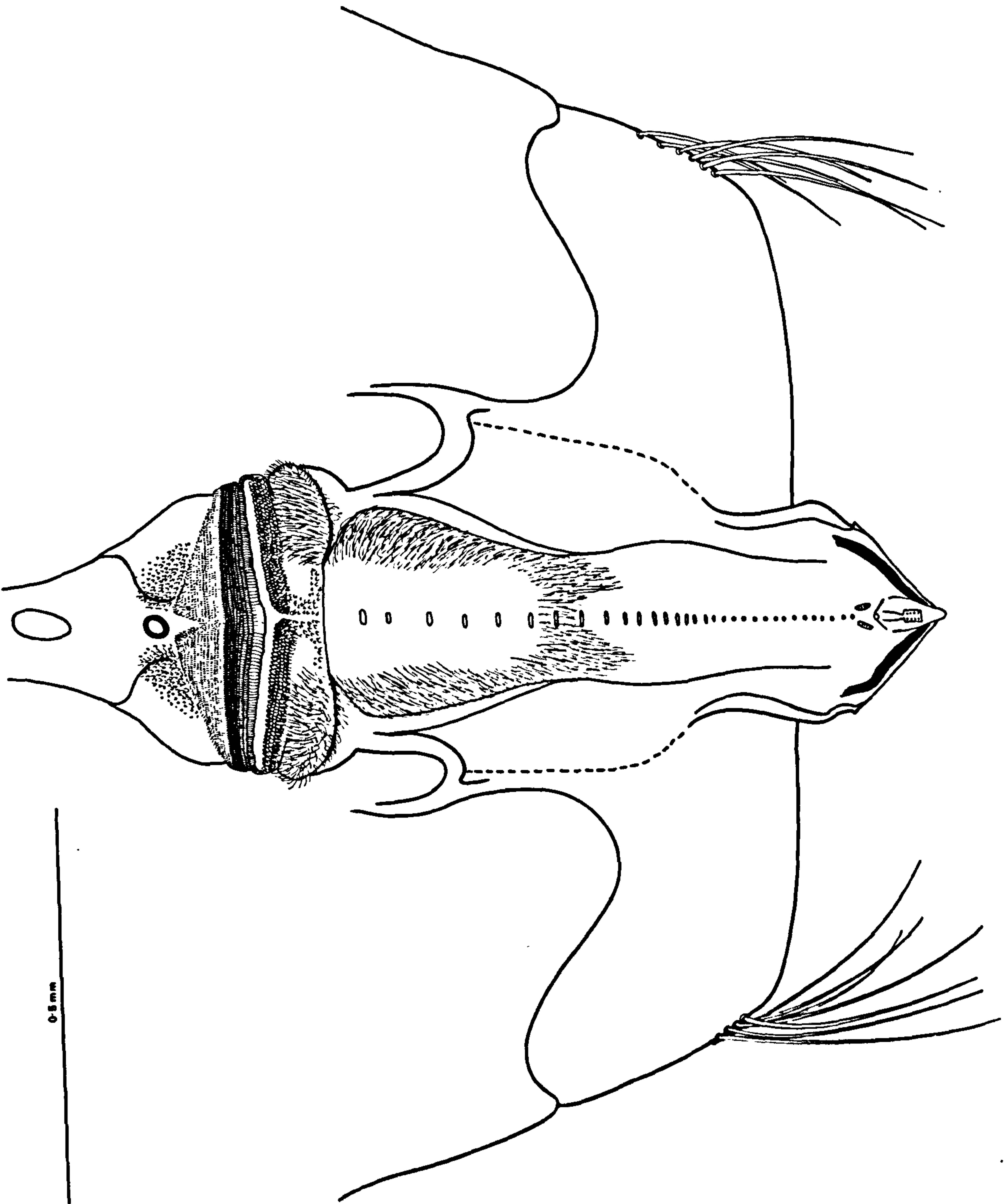
TG
MG
TF
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CLC
LP

EP

TI
AC
EPL

PSO
ASO
AC'
LB



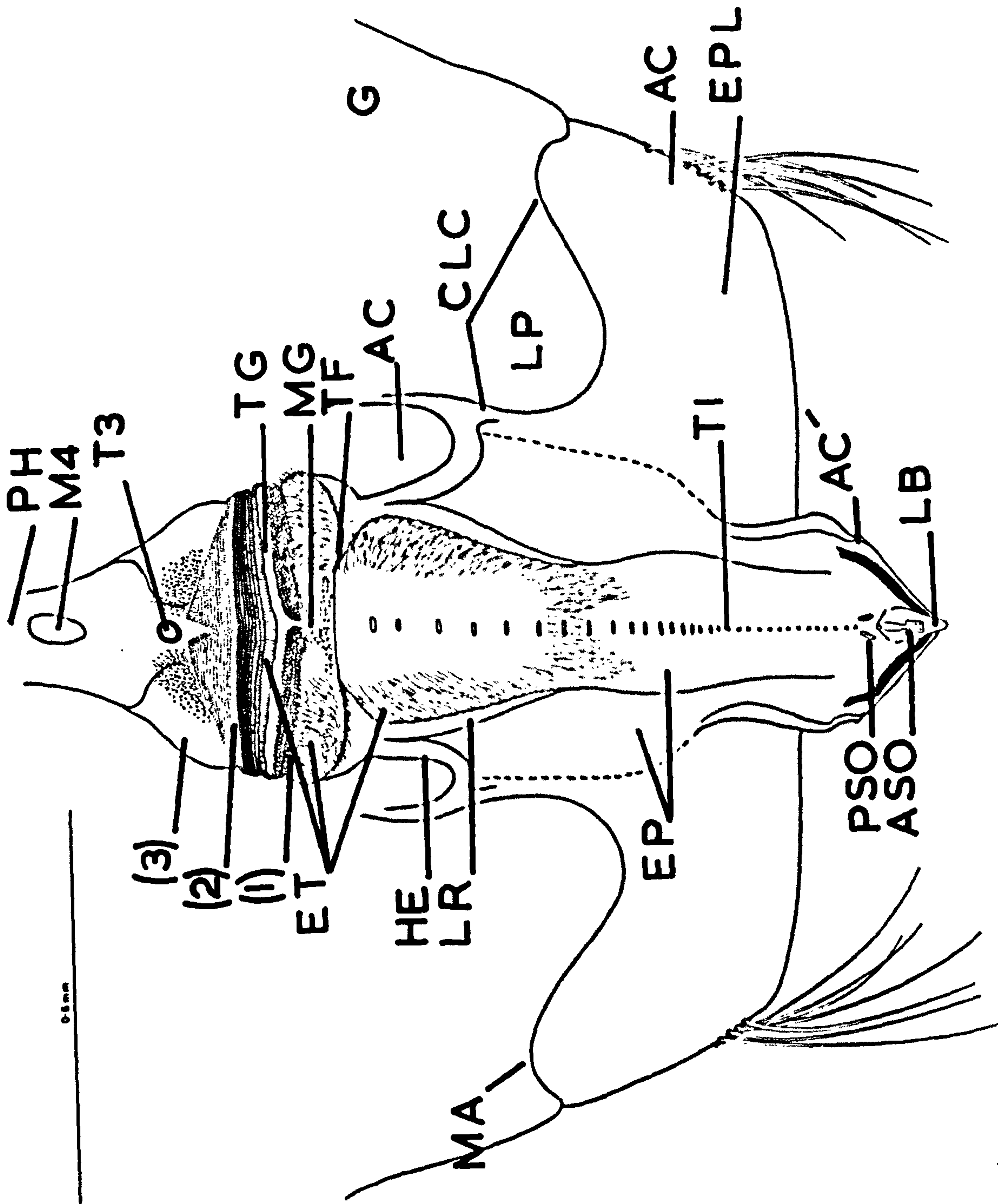


Fig. 4.6 Diaprepocoris zealandiae, female.

A. dissection of the food pump, see fig. 4.5 for details. The anterior extension of the loral plate is shown on the right side.

B. shows the position of the struts on the dorsal surface of the epipharynx, with the hypopharyngeal ridges superimposed.

C. enlargement of anteclypeal bristles; a, b. and c. tips of the long ventrolateral bristles; d. and e. flat bristles on flattened anterior edge, d. median bristles, e. lateral bristles.

Stippled areas indicate the areas between the dorsal epipharyngeal struts of the middle region of the food pump.

—M4

—M3

—ET

TI

LP

—MA

—AC

HR

HE

LR

CLC

~144~

Fig. 144

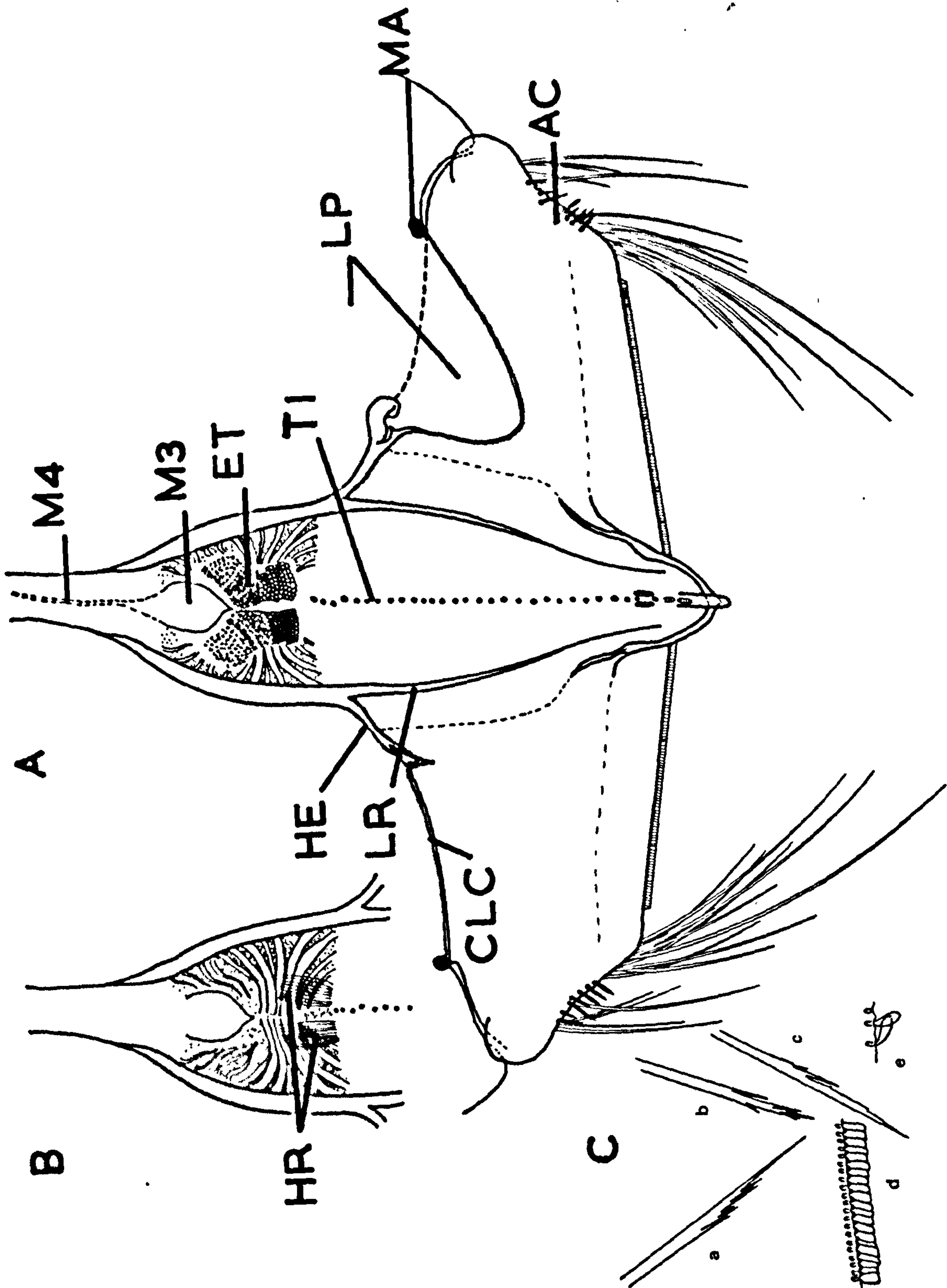


Fig. 4.7 Corixa punctata, female; saggital section of the head showing the cuticular structures, muscles, nerve ganglia, and the epipharyngeal sense organ. The position of dorsal pharyngeal dilator muscles is shown. The labial abducta and labial dilator muscles are shown as they appear in a parasaggital section.

A-A and B-B, the position of the transverse sections in fig.4.8.

C-C to G-G, the position of the frontal sections in fig. 4.4.

D

C
B

// A

B

A

D
C
F G

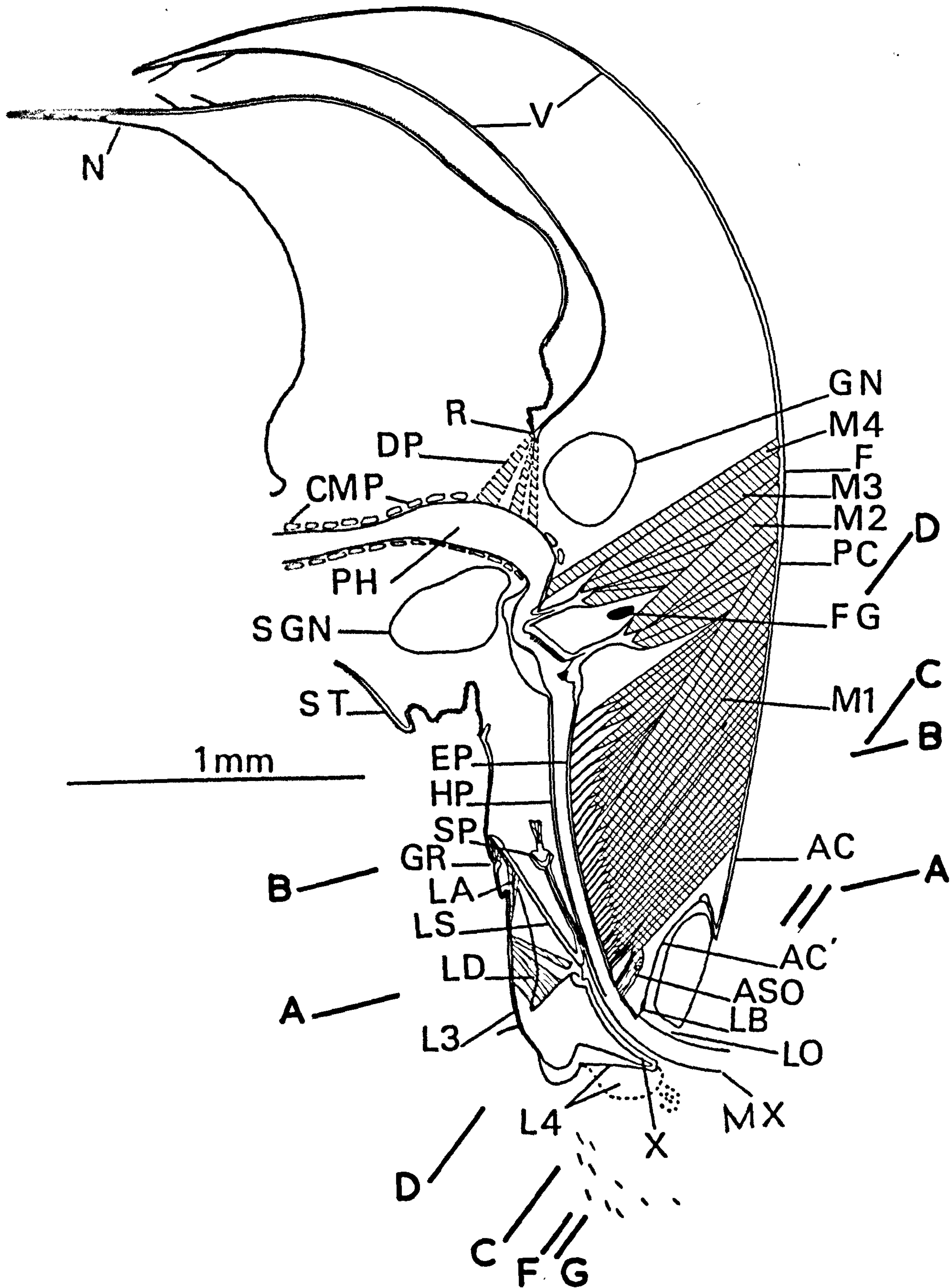
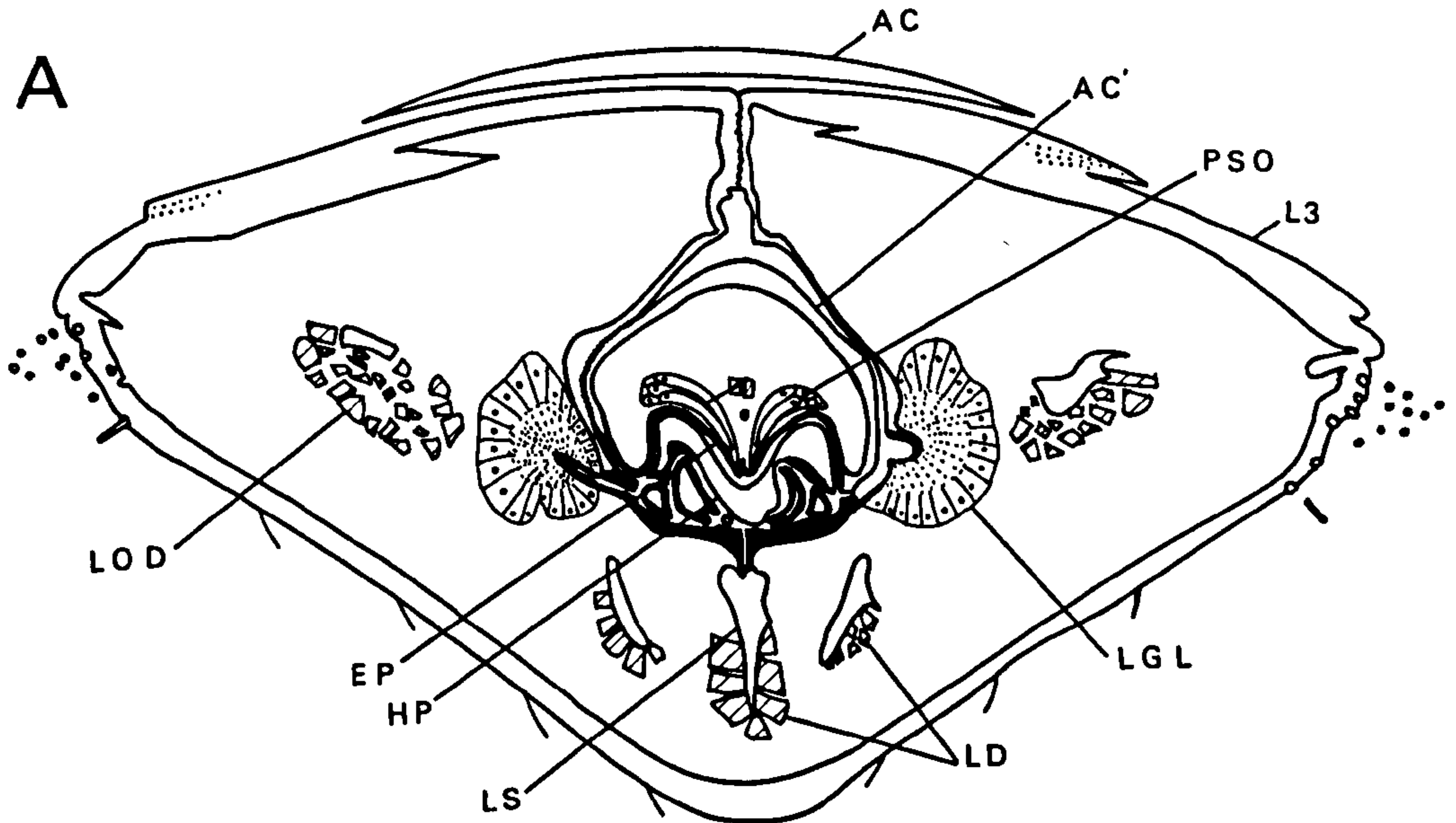


Fig. 4.8 Corixa punctata, female; transverse sections of the head at the levels A. proximal end of the third labial segment, B. anterior food pump, indicated in fig. 4.7.

05mm

A



B

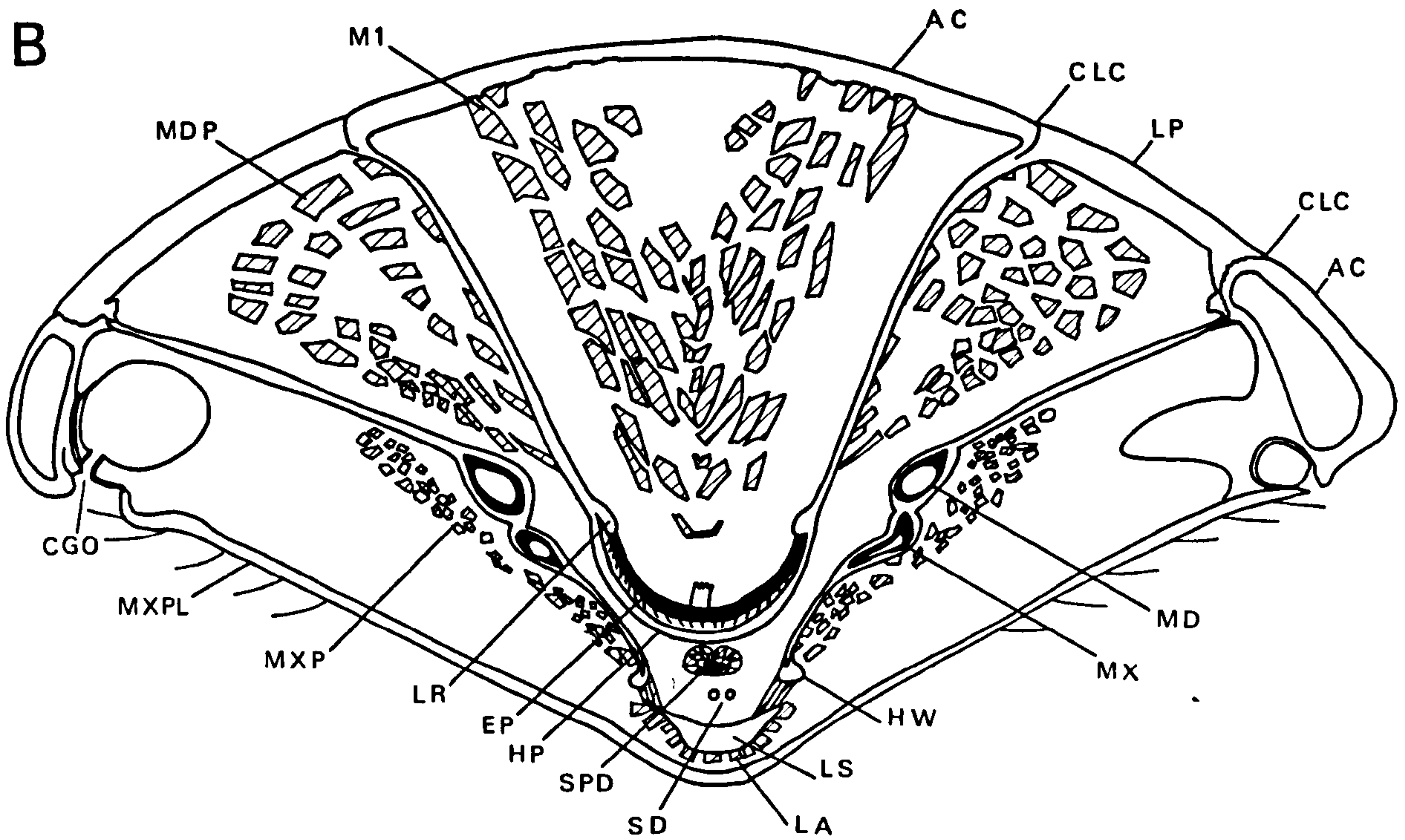
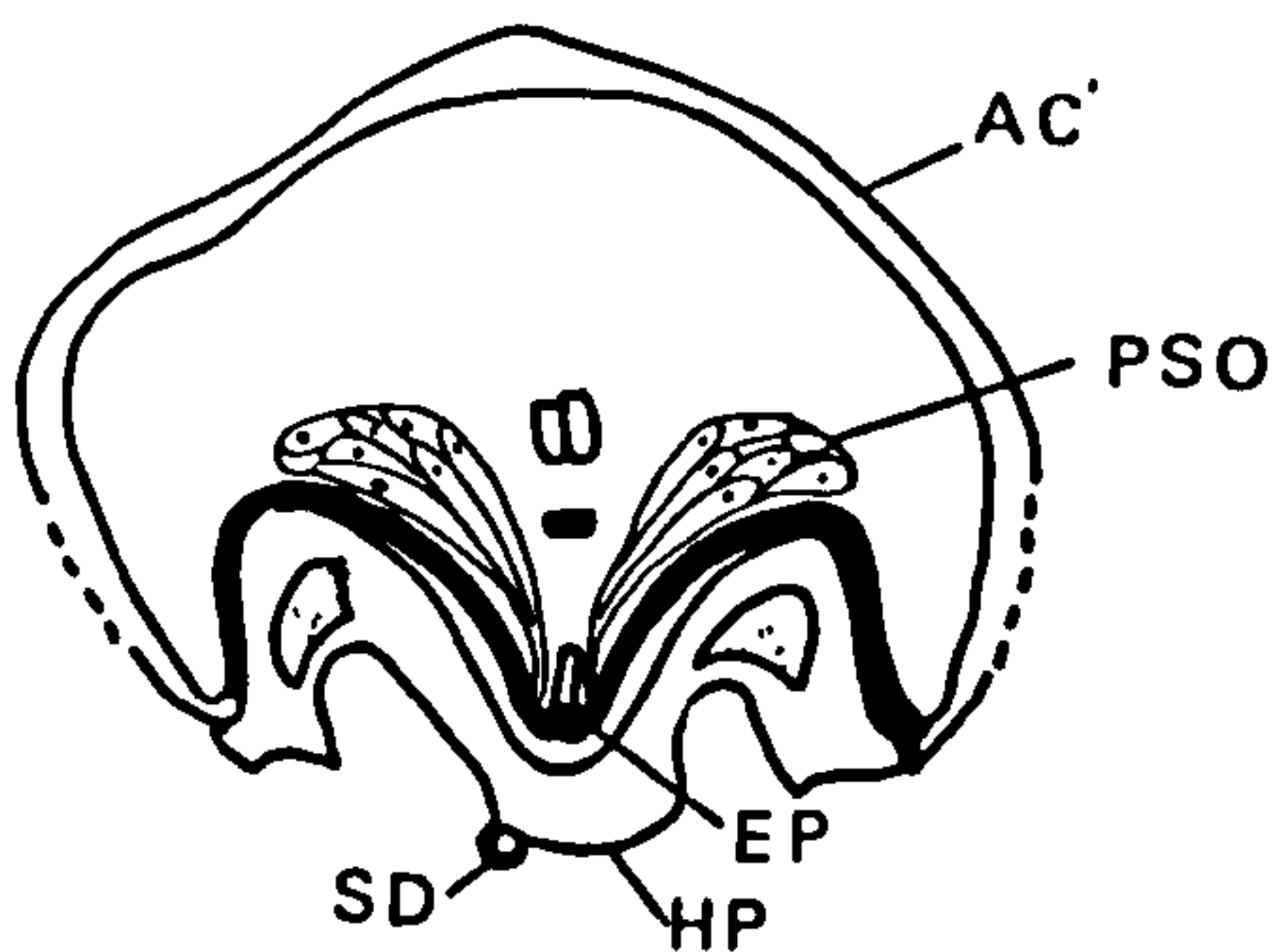


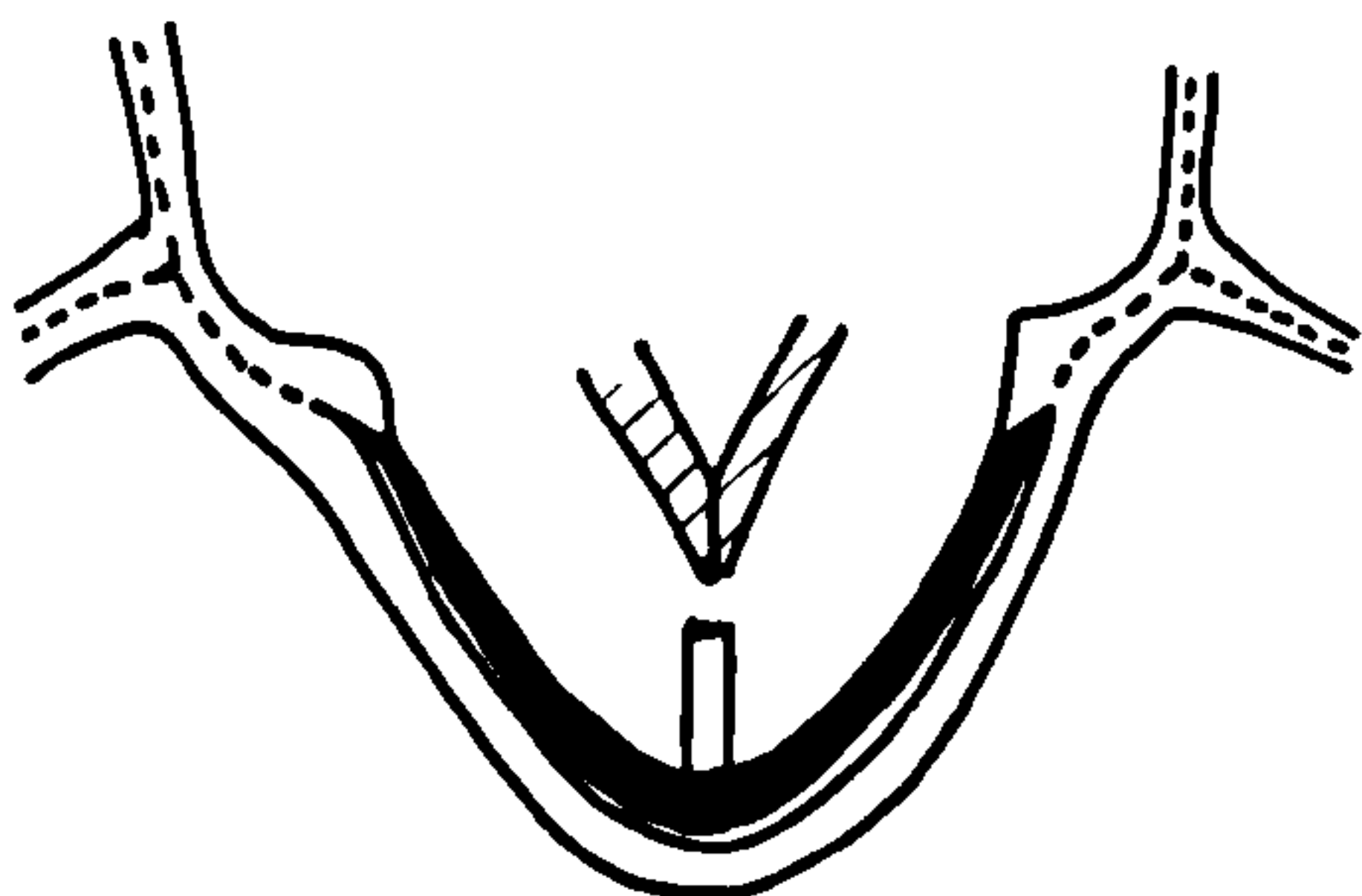
Fig. 4.9. Corixa punctata, adult, transverse sections of the food pump; A-D, anterior region of the food pump. A. is an enlargement of food pump in Fig. 4.9A, D. is through the constriction in the anterior region of the food pump (see fig. 4.5). Note the epipharyngeal teeth; I-K. middle region of the food pump; L. posterior region of the food pump. Non-cuticular and non-muscular structures except the posterior epipharyngeal sense organs have been omitted. Shading: clear, non-staining or orange staining cuticle; black, red staining cuticle; fine stippling, blue staining cuticle; large stippling, black pigmented cuticle; diagonal lines, muscles. See Fig. 4.10 for E-H.

0.5 mm

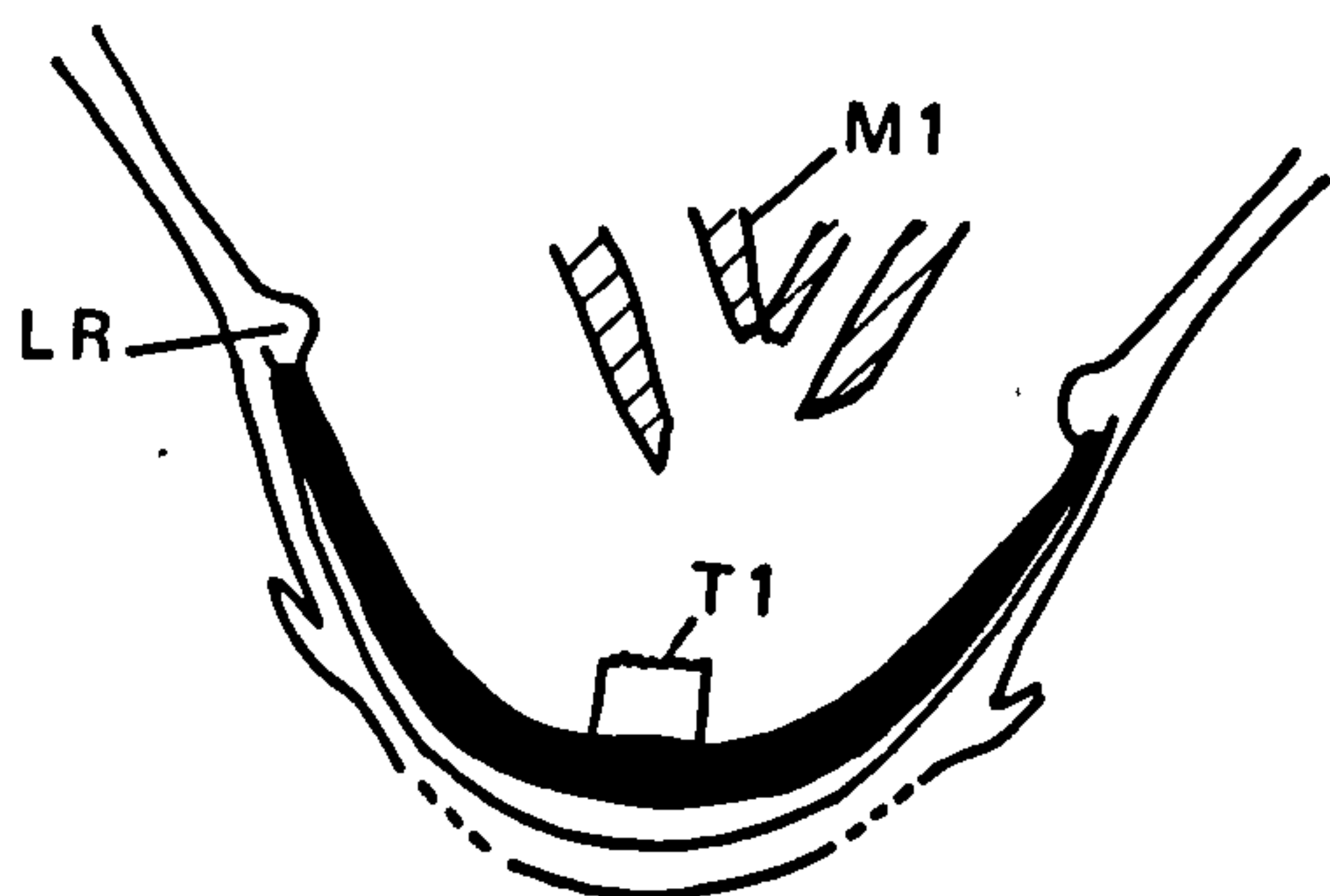
A



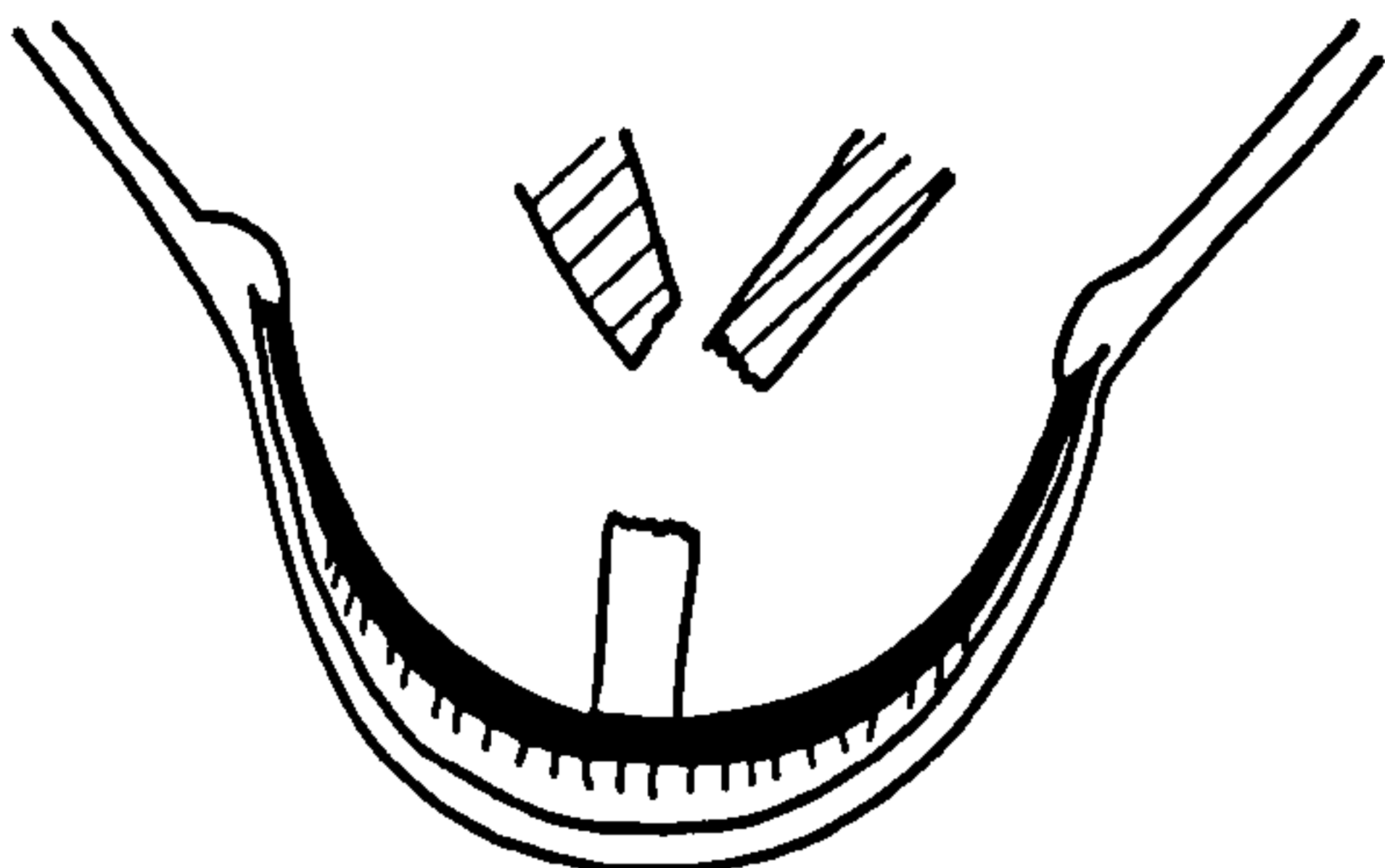
B



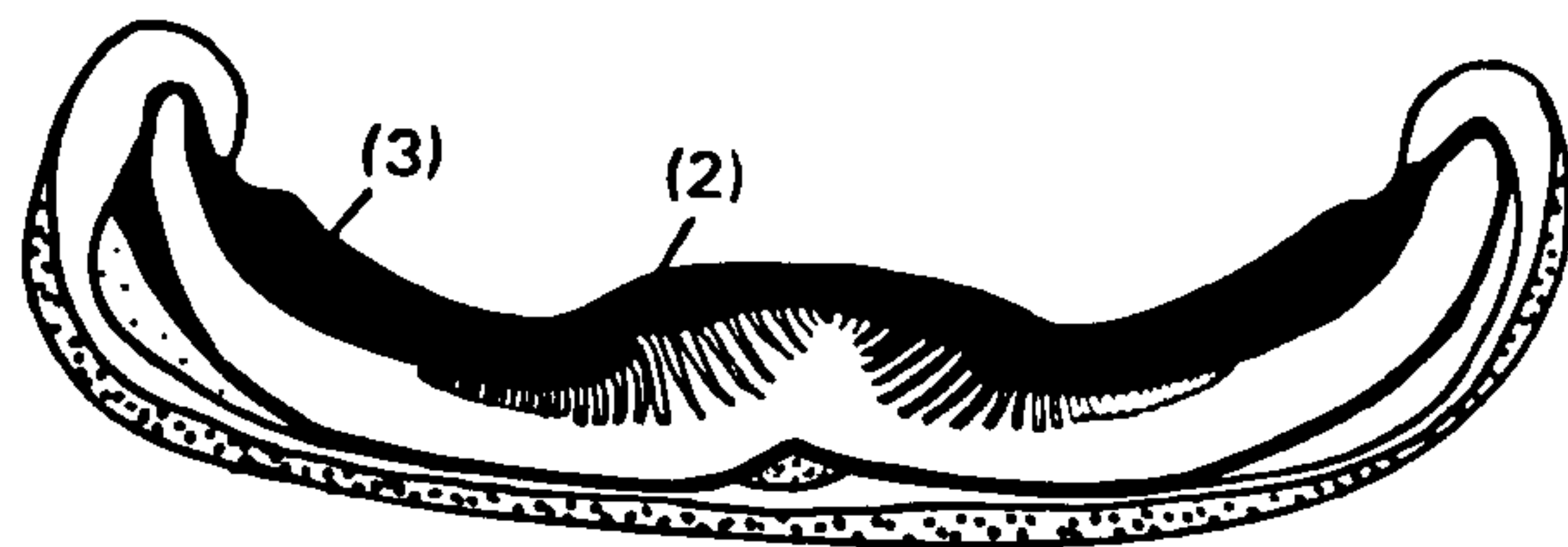
C



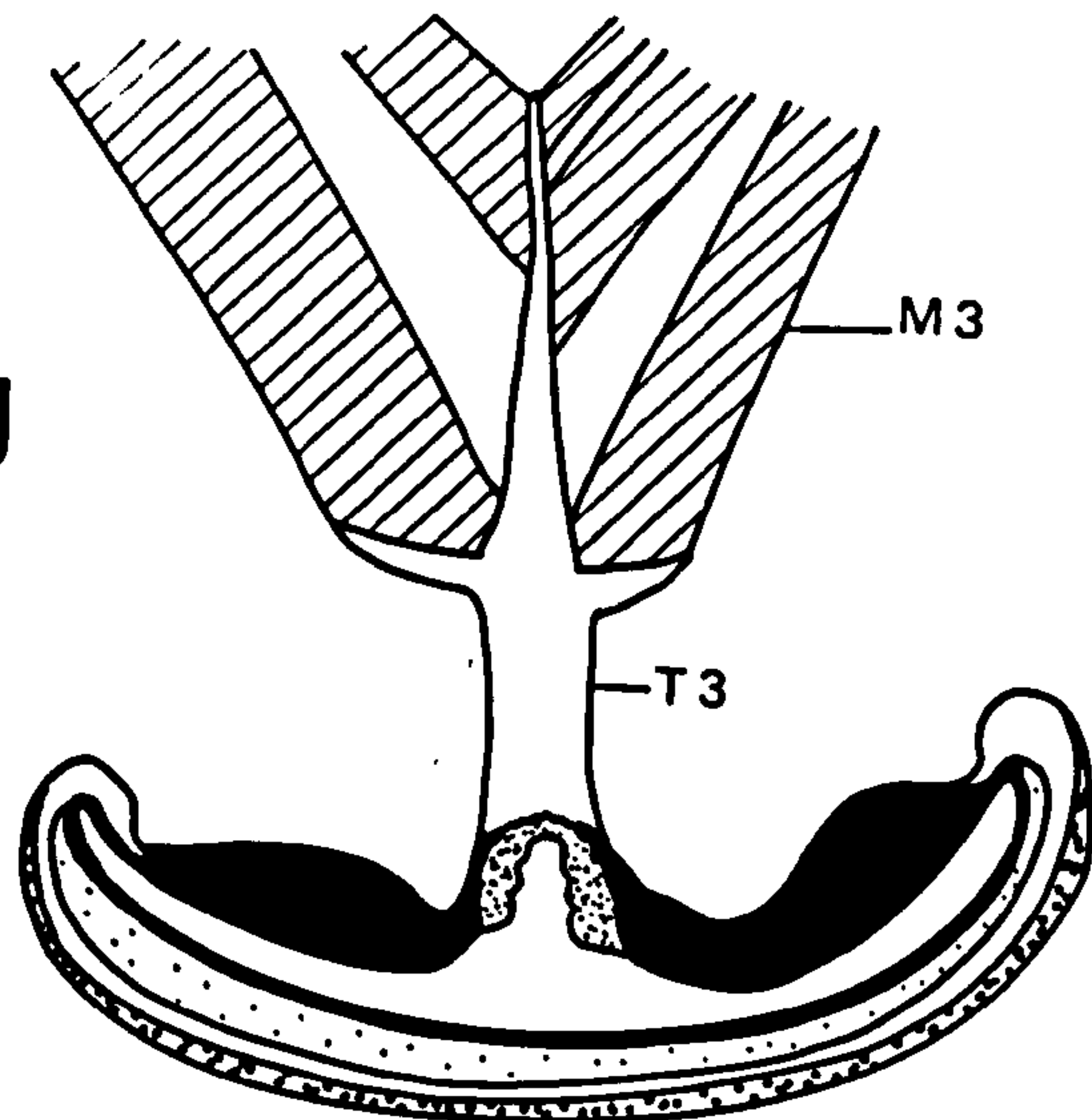
D



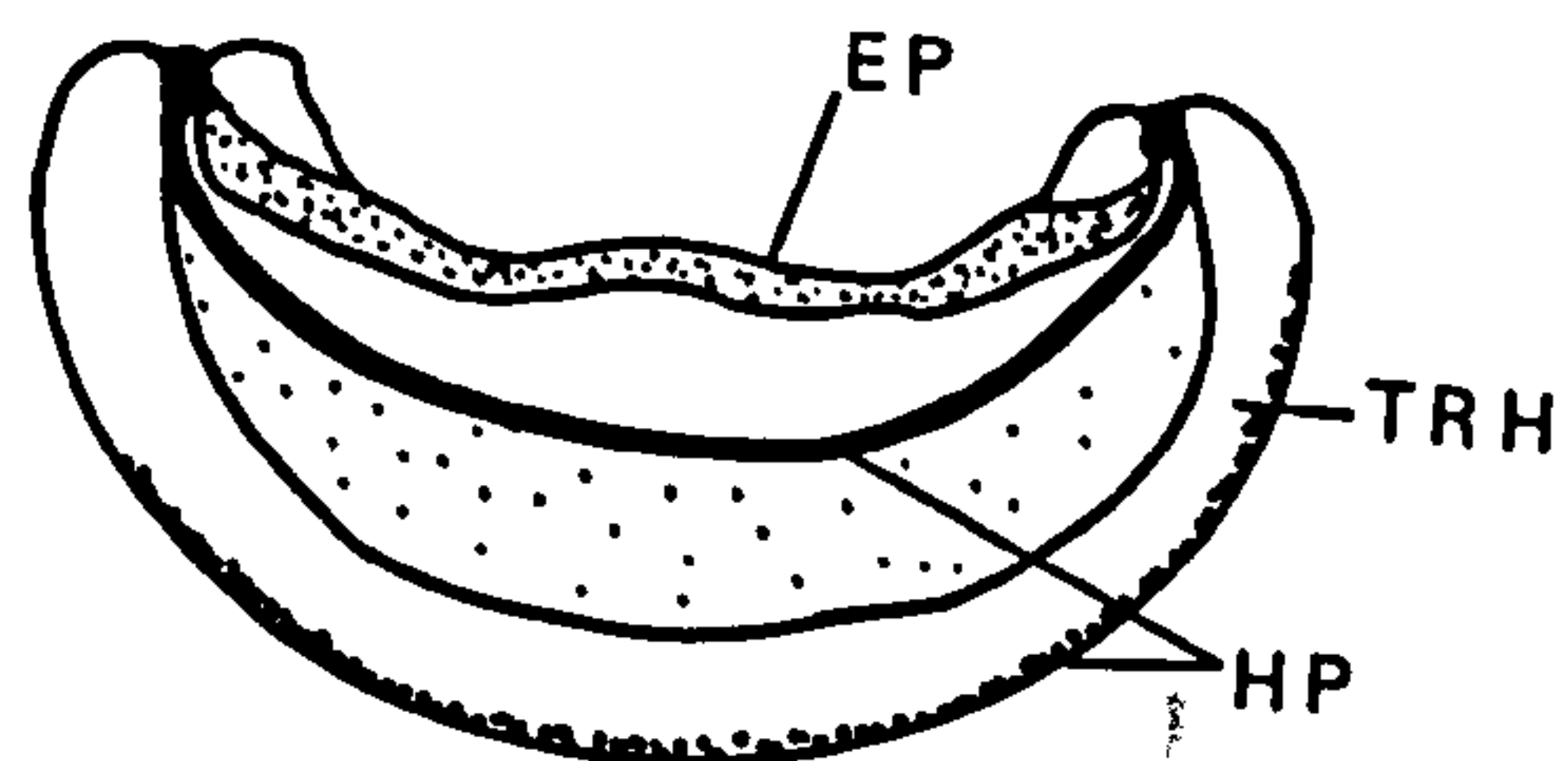
I



J



K



L

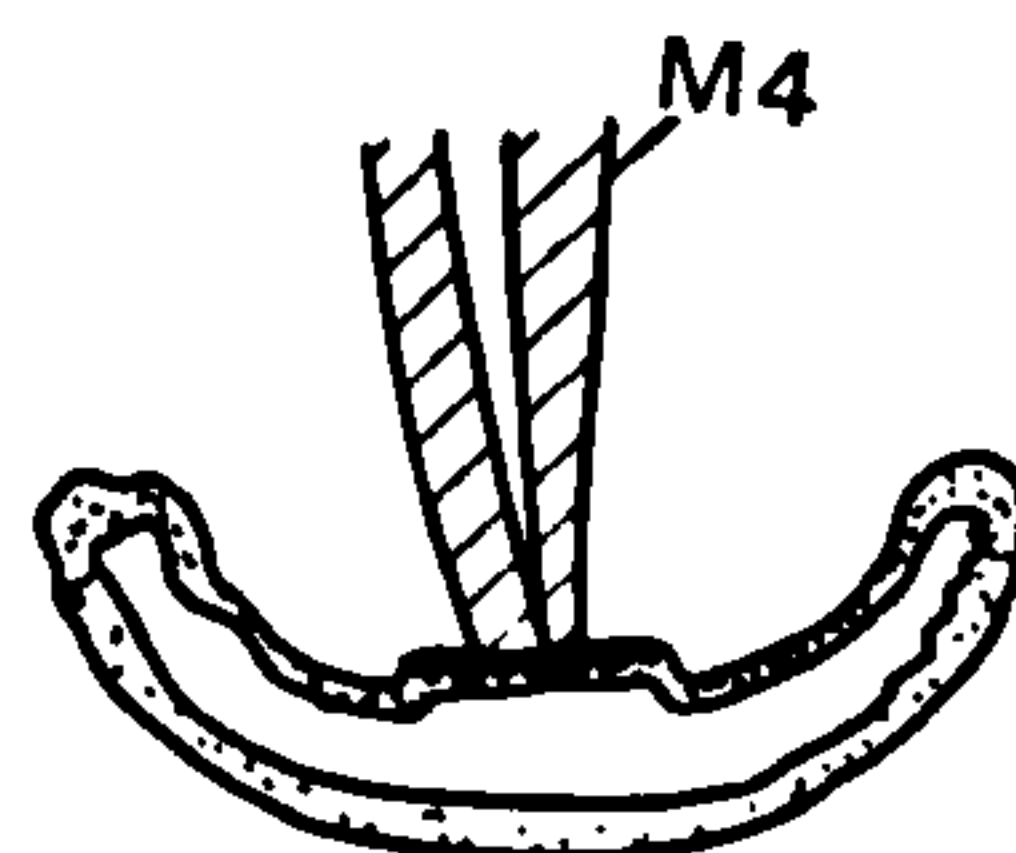
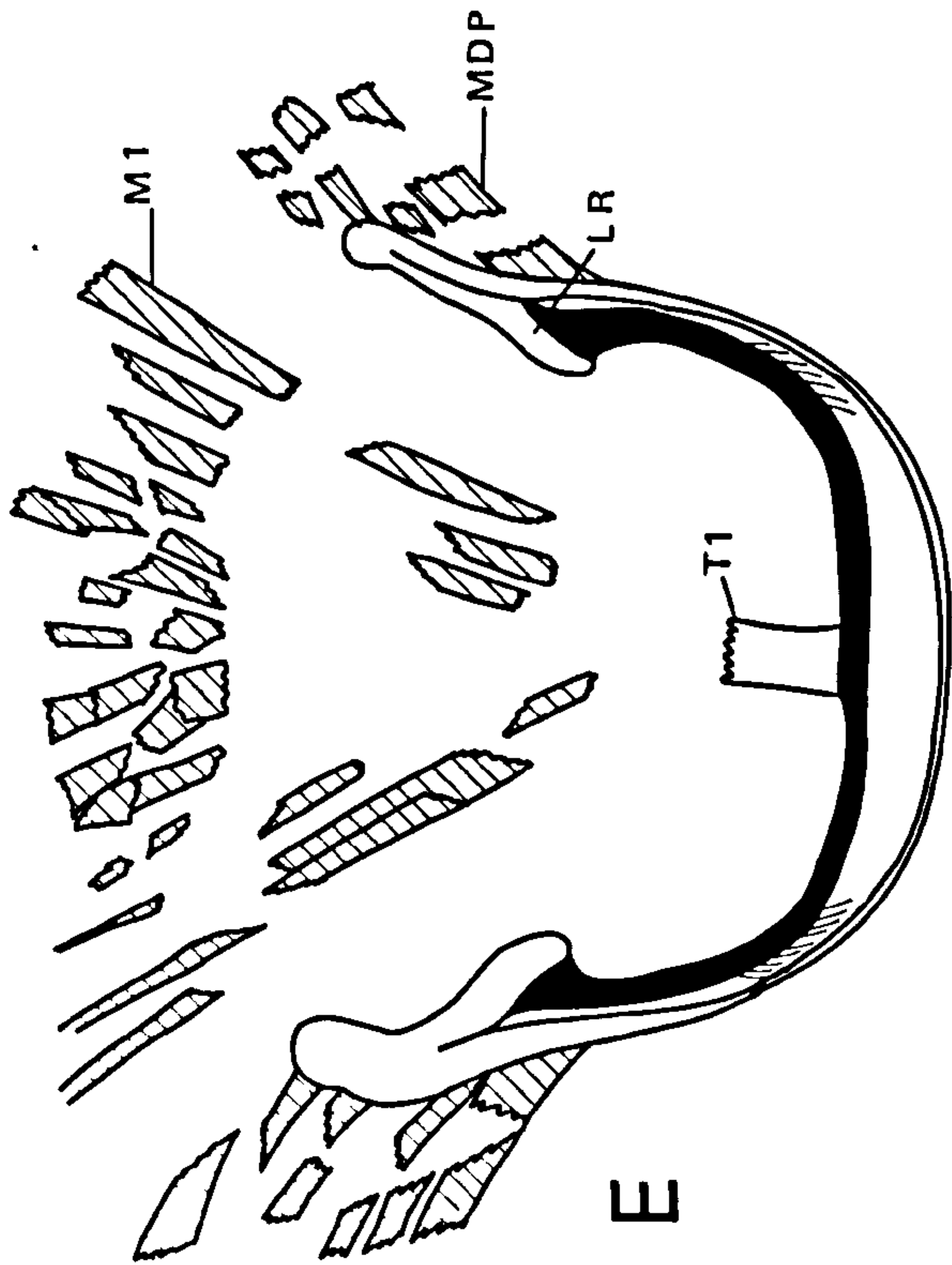
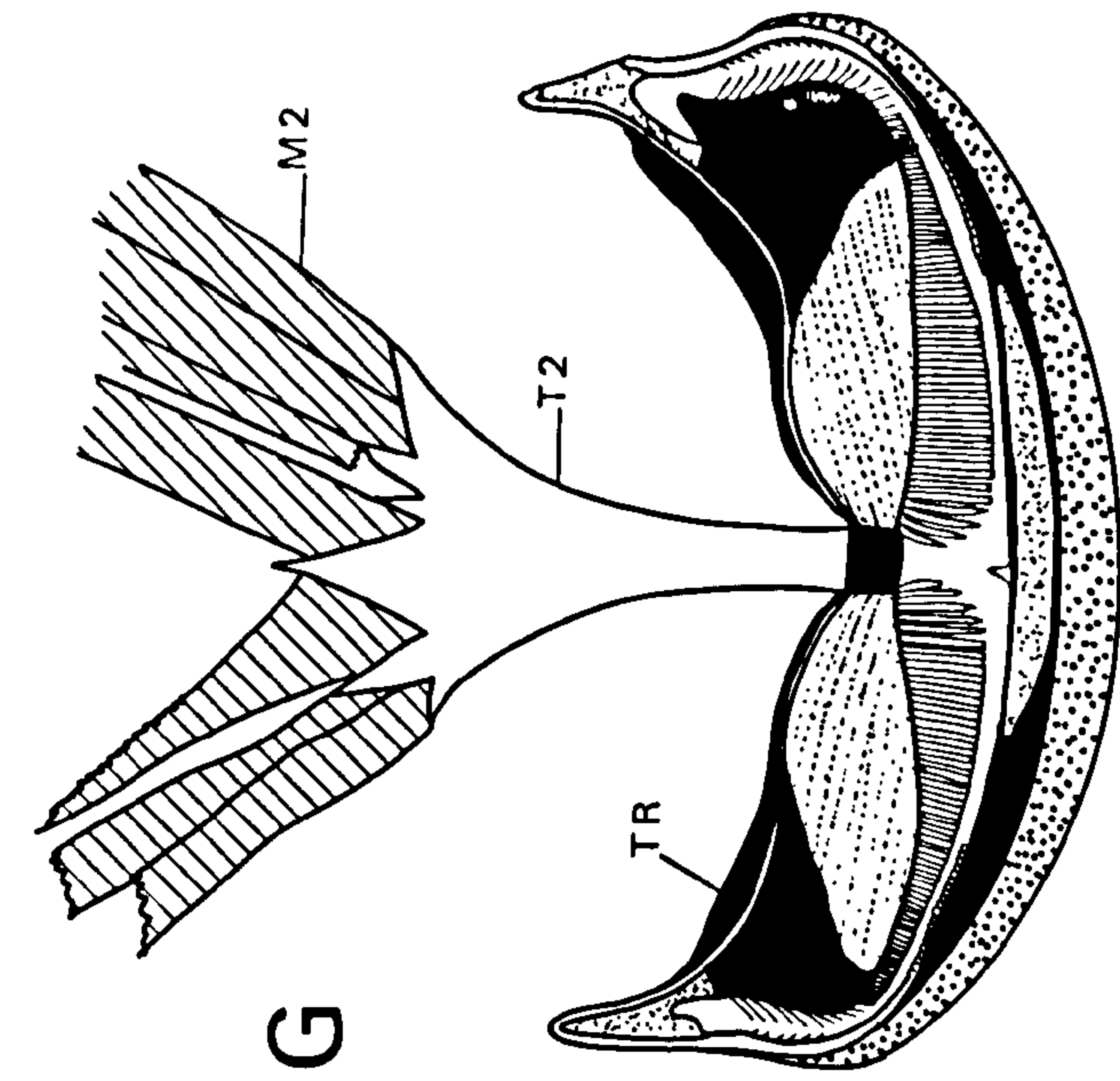
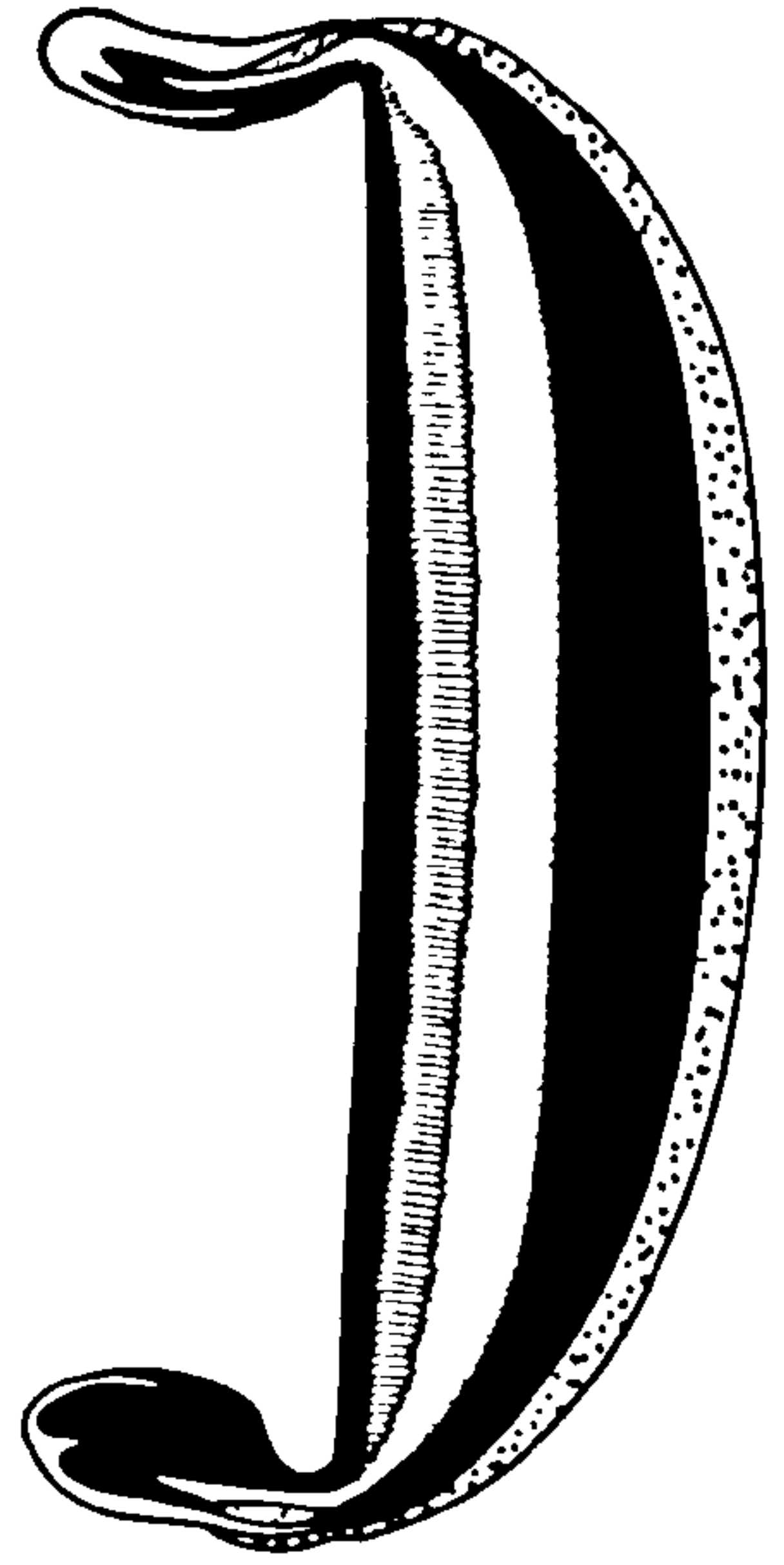


Fig. 4.10 Corixa punctata, adult; transverse sections of the food pump; E. anterior region of the food pump, just before the middle region of the food pump; F-H. middle region of the food pump; F. and G. through Zone (1) of the epipharynx; F. first posterior to the transverse fold; G. first anterior to the transverse groove; H. through Zone (2) of the epipharynx, first posterior to the transverse groove. See fig. 4.9 for A-D. and I-L. and for an explanation of the shading.



H



0.5mm

F

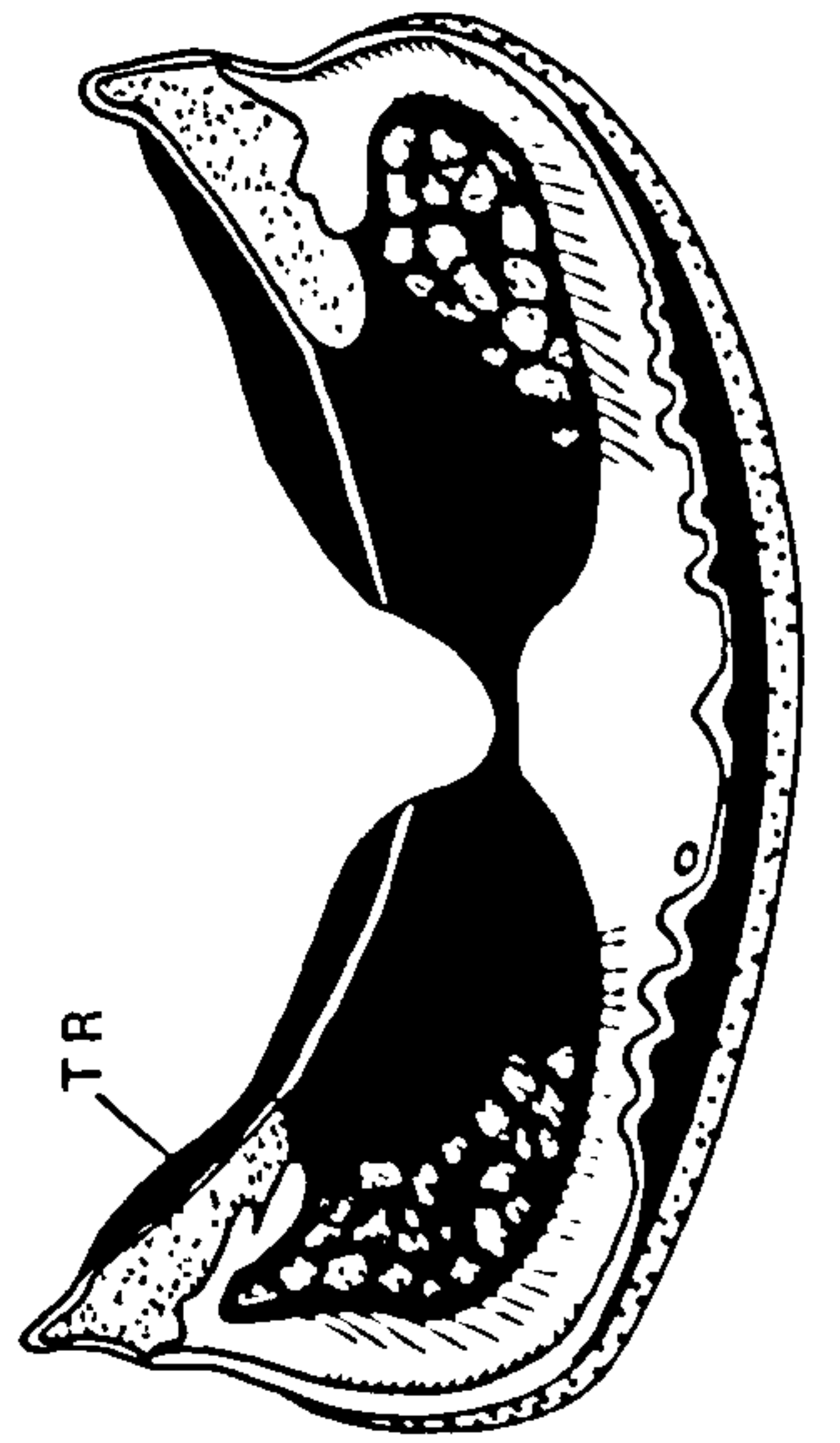


Fig. 4.11 Corixa punctata, adult; longitudinal sections through the middle and posterior food pump. A. sagittal and B-E. parasagittal sections; F. enlargement of the epipharyngeal teeth. See fig. 4.9 for explanation of the shading.

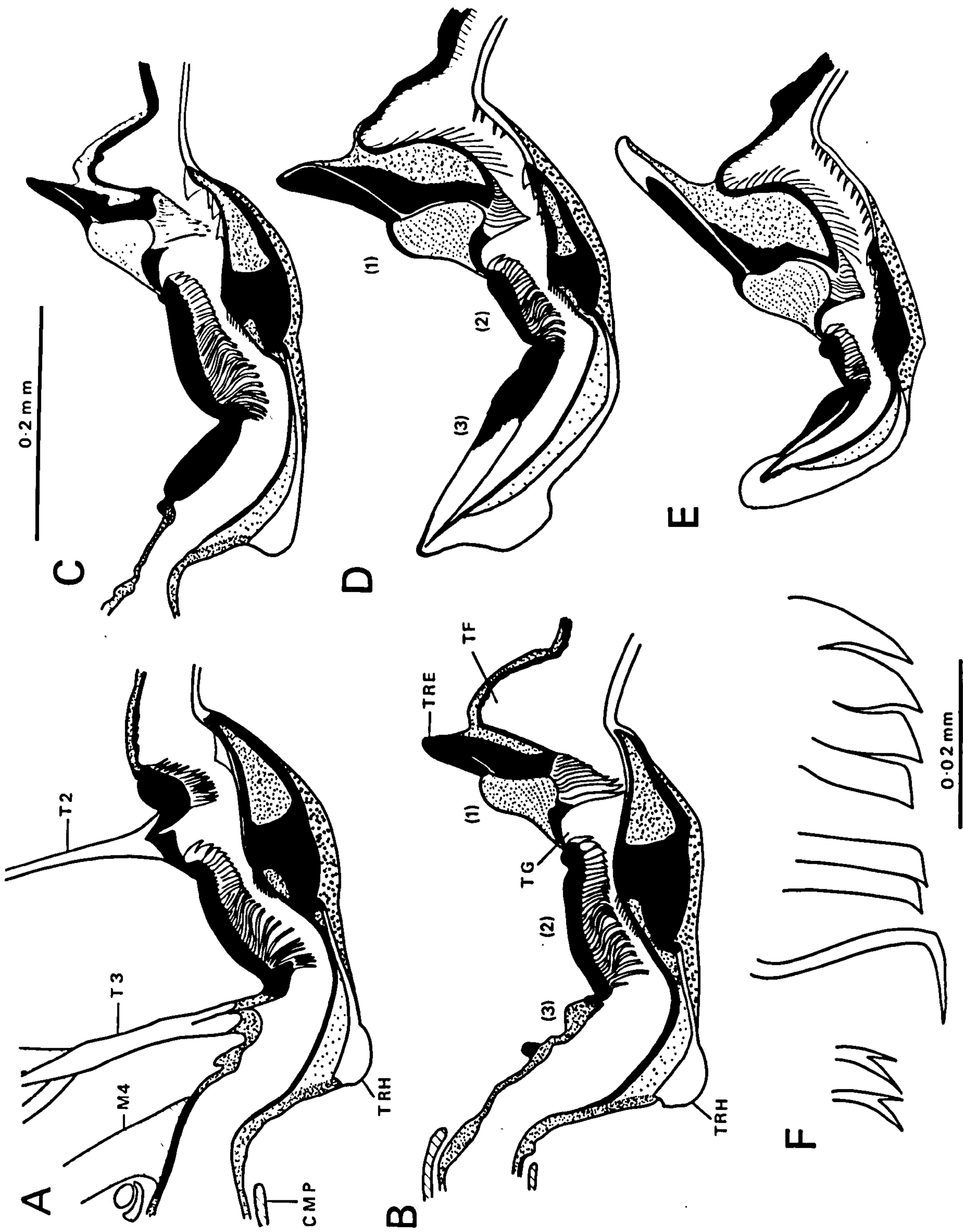


Fig. 4.12 Diaprepocoris zealandiae, female; sagittal section of head showing the cuticular structures, muscles, nerve ganglia and the anterior epipharyngeal sense organ. The position of the dorsal pharyngeal dilator muscles is shown. The labial abductor and labial dilator muscles are shown as they appear in a parasagittal section.

A-A and B-B, the position of the transverse sections in fig. 4.13.

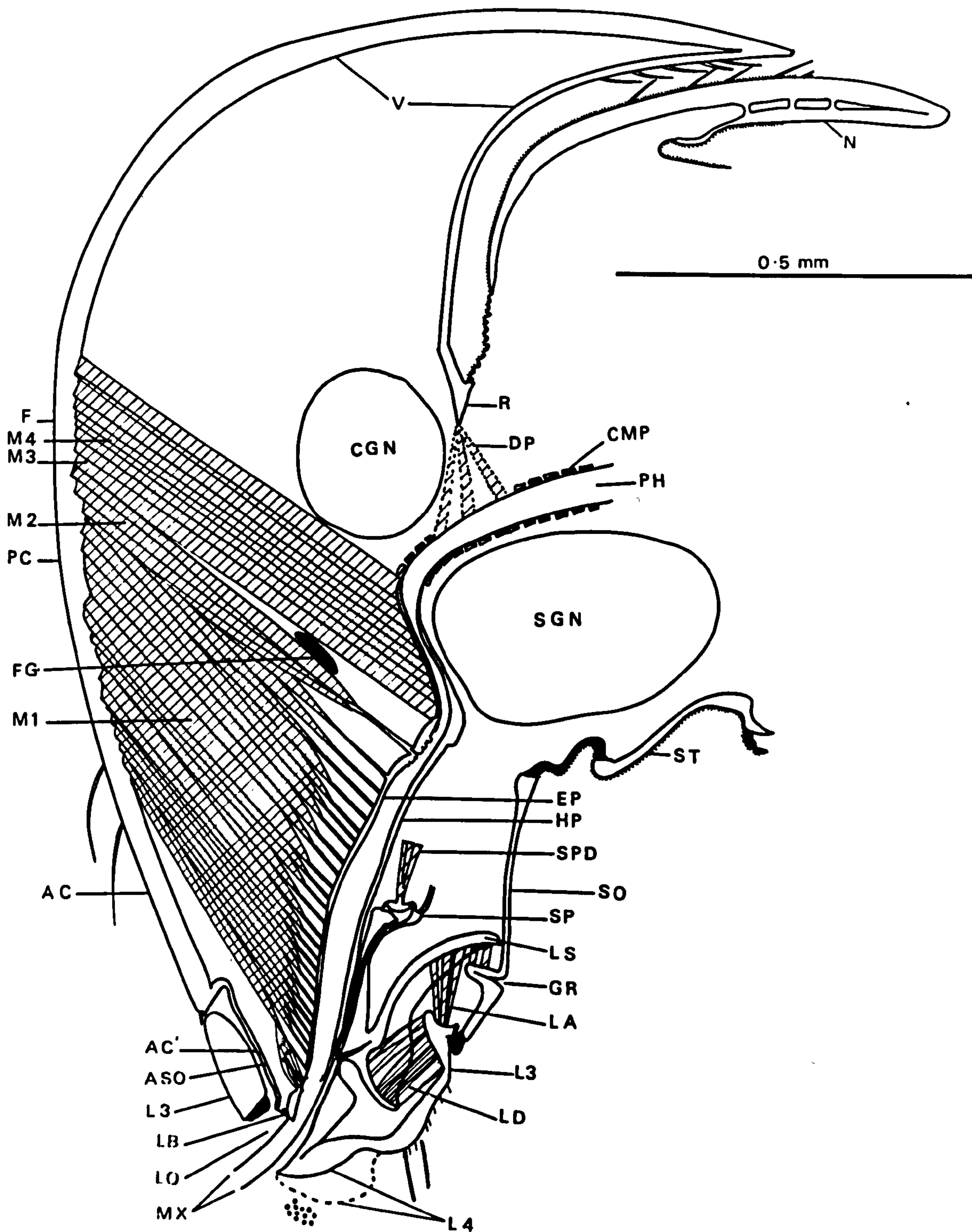
1. 2. 3. 4. 5. 6. 7. 8. 9. 10. 11. 12. 13. 14. 15. 16. 17. 18. 19. 20. 21. 22. 23. 24. 25. 26. 27. 28. 29. 30. 31. 32. 33. 34. 35. 36. 37. 38. 39. 40. 41. 42. 43. 44. 45. 46. 47. 48. 49. 50. 51. 52. 53. 54. 55. 56. 57. 58. 59. 60. 61. 62. 63. 64. 65. 66. 67. 68. 69. 70. 71. 72. 73. 74. 75. 76. 77. 78. 79. 80. 81. 82. 83. 84. 85. 86. 87. 88. 89. 90. 91. 92. 93. 94. 95. 96. 97. 98. 99. 100.

A_

B_

A

B



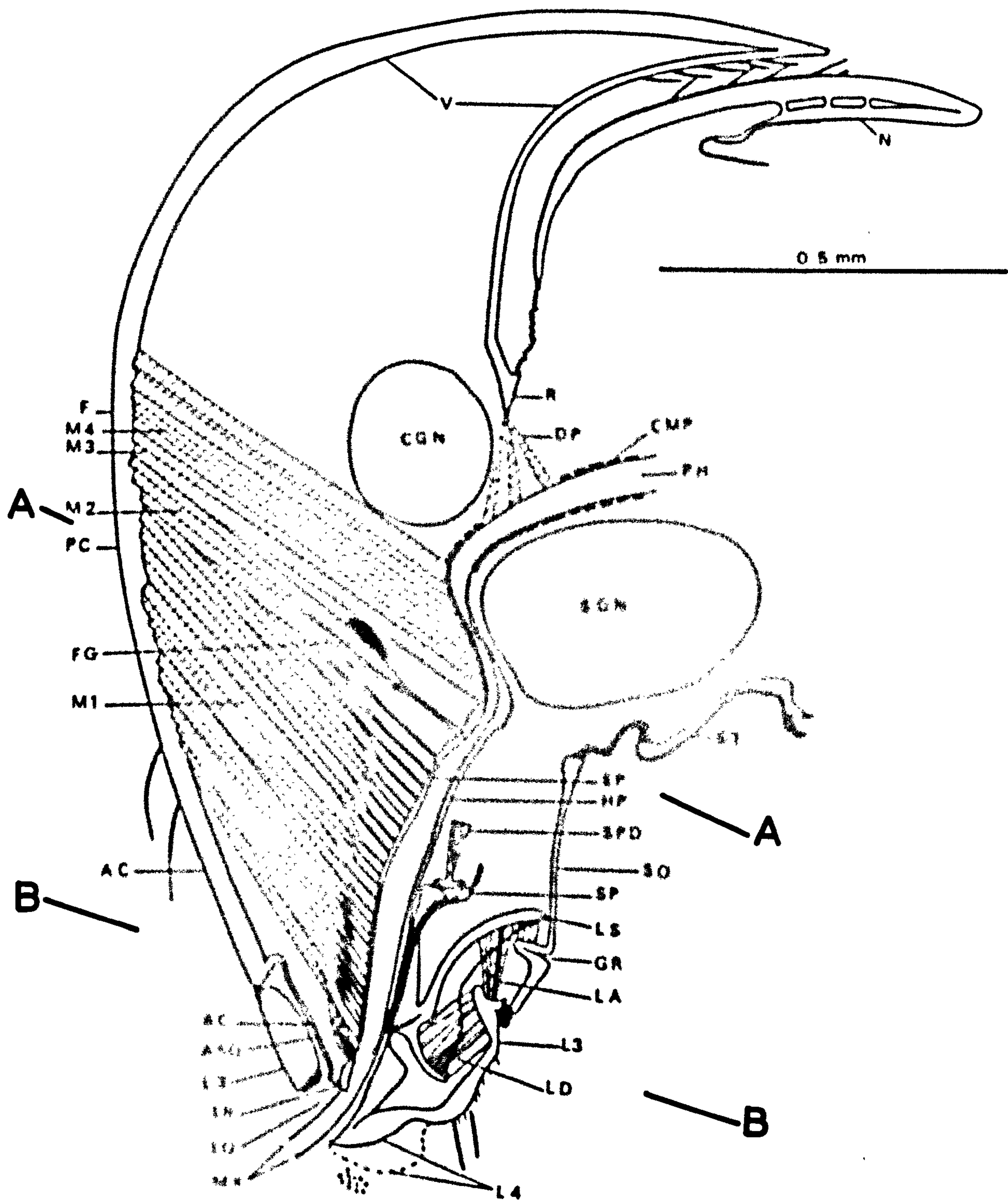


Fig. 4.13 Diaprepocoris zealandiae, female, transverse sections of the head at the levels A. middle region of the food pump, B. Labium and anterior projections of the anteclypeus, indicated in fig. 12.

0.5 mm

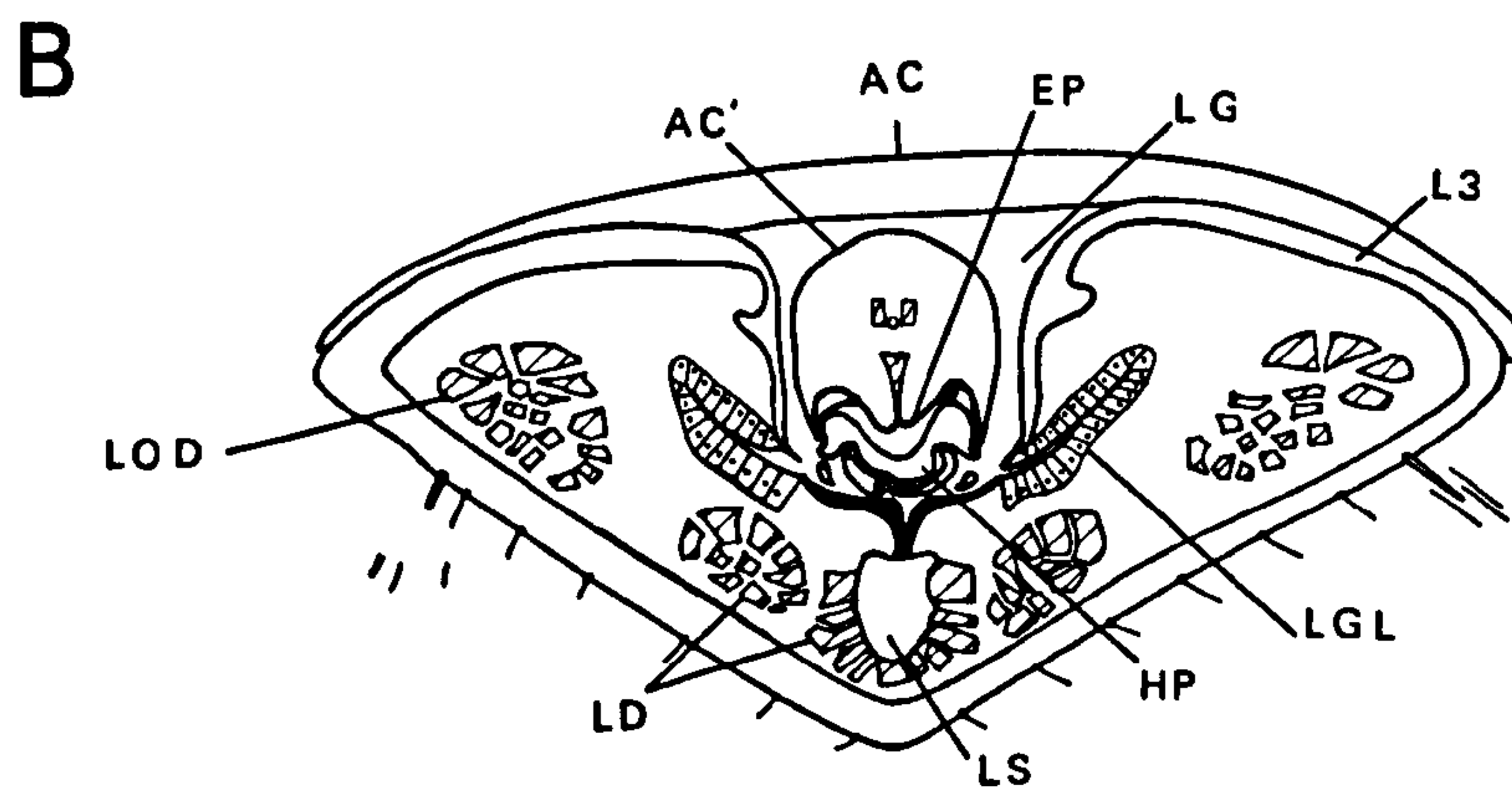
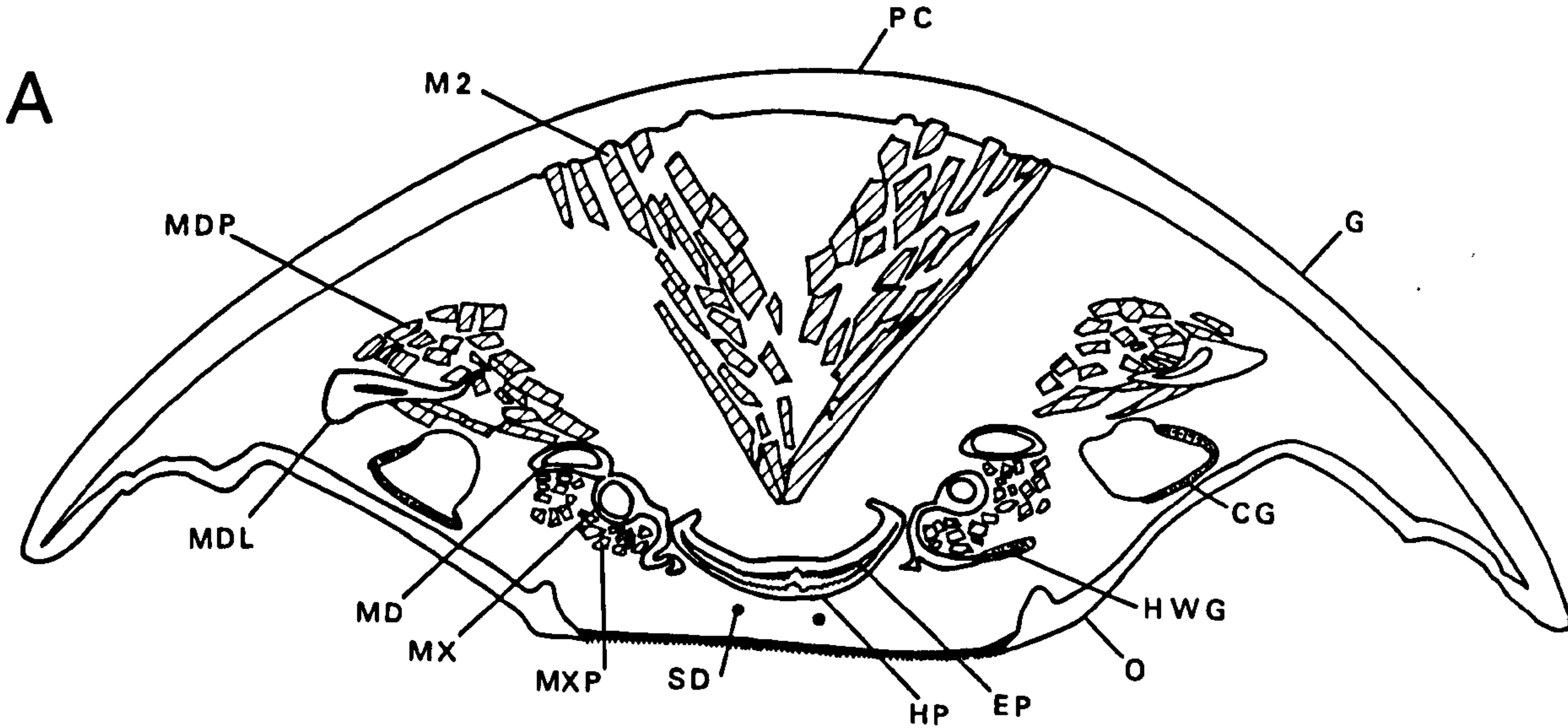


Fig. 4.14 Diaprepocoris zealandiae, female; transverse sections of the food pump. A. and B. anterior region of the food pump; C-F. middle region of the food pump; G-I posterior region of the food pump. See fig. 4.9 for explanation of the shading.

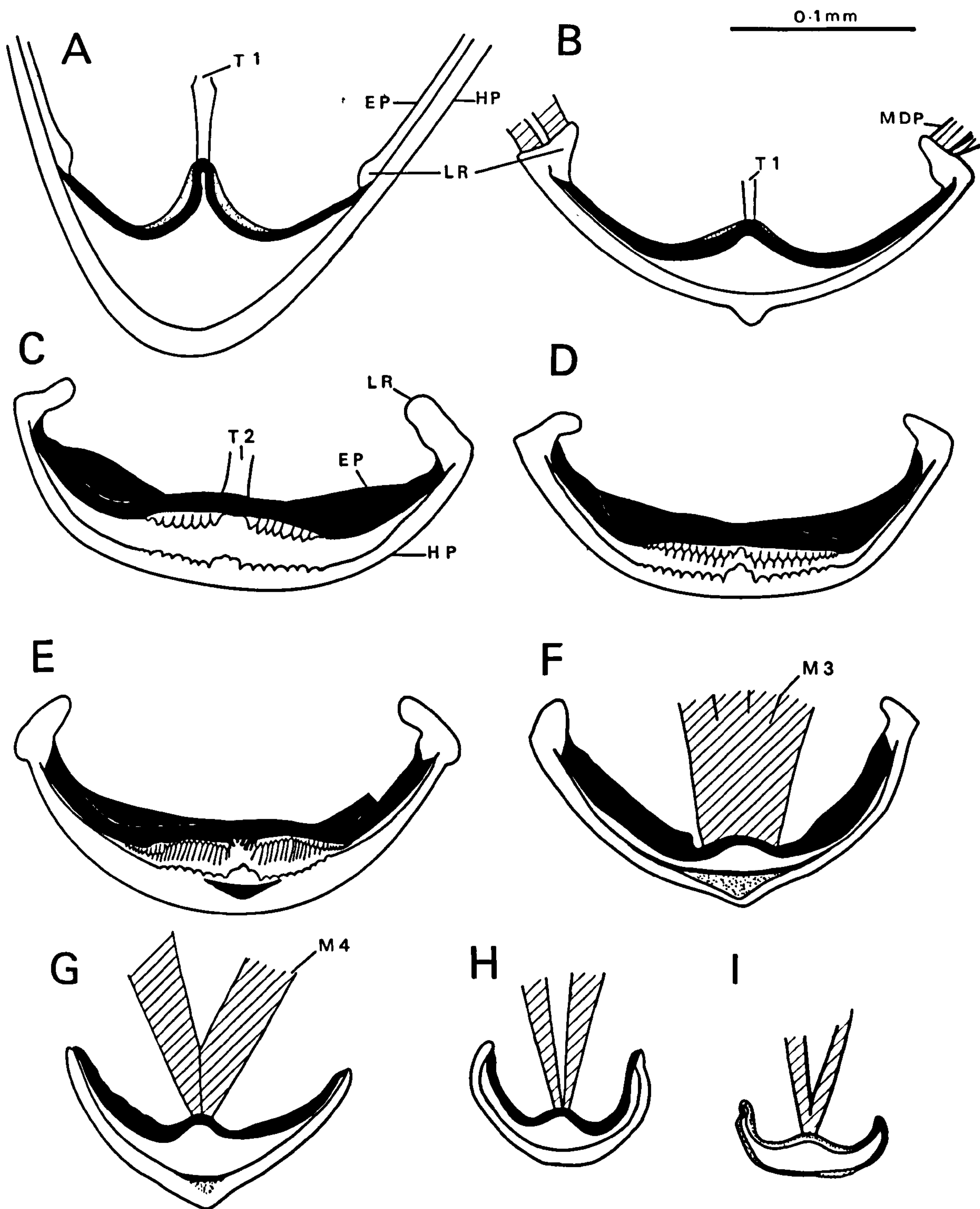
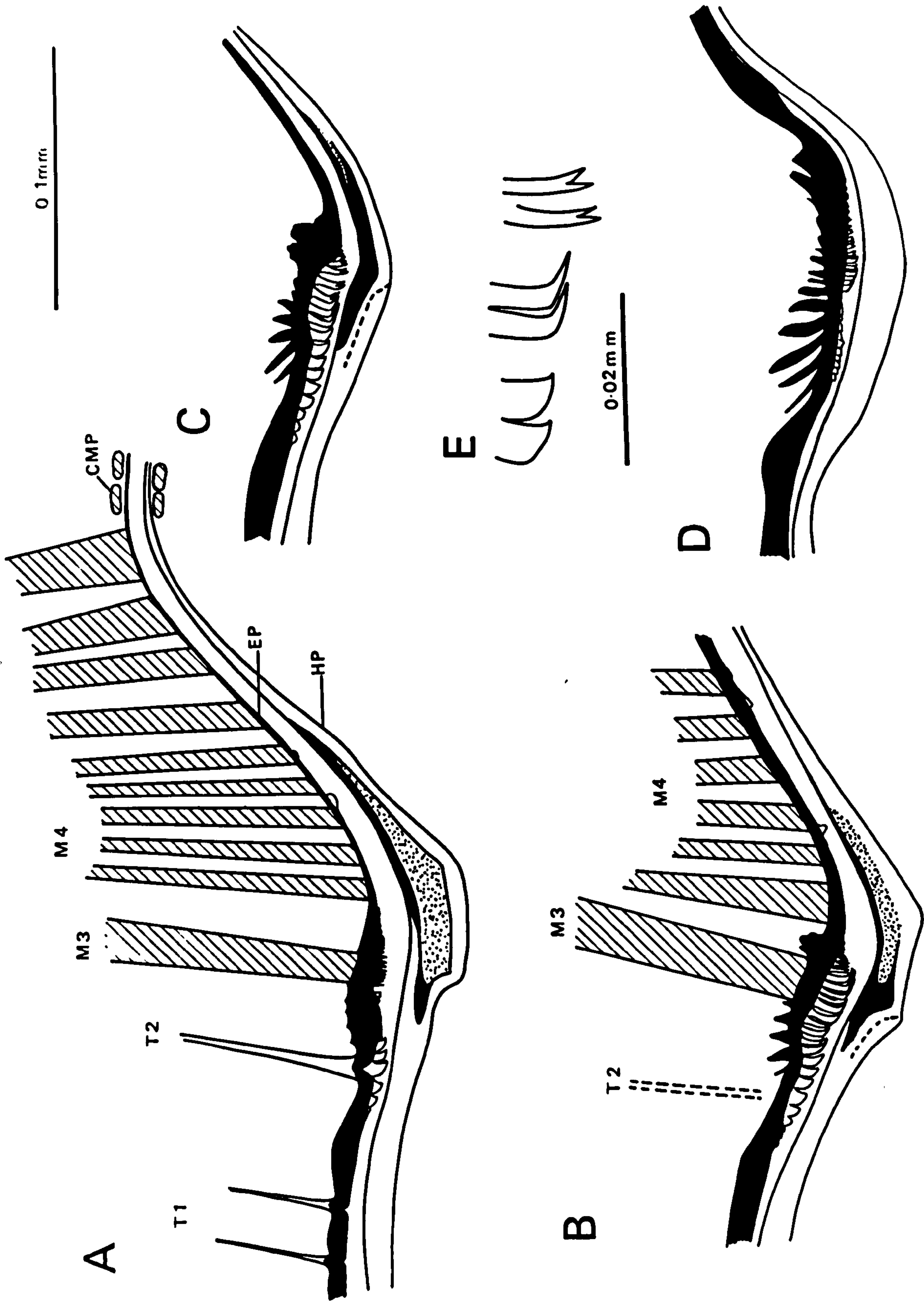


Fig. 4.15 Diaprepocoris zealandiae, female; longitudinal sections of the middle and posterior regions of the food pump. A. sagittal and B-D. parasagittal sections; E. enlargement of the epipharyngeal teeth. See fig. 4.9 for explanation of shading.



SECTION 5

The Corixid Habitat in Leicestershire.

5.1 Introduction

The fresh-water habitats of Leicestershire, together with some of the annual changes which occur in them are described. The temperature conditions, in particular, were investigated.

5.2 The Fresh-water habitat in Leicestershire

Running water was rarely investigated, and is usually very variable in both depth and rate of flow. The slower stretches of the larger rivers produce a habitat very similar to the canals. The Grand Union Canal is lined by reeds on at least one side, the bottom is generally muddy and covered by Juncus bulbosus, Elodea, Callitriche, and Nuphar lutea. On the bottom, where the canal passes by a wood, there is usually an accumulation of leaves. On the bottom of canals and rivers, the corixids have a patchy distribution unrelated to vegetation.

In Leicestershire, all the larger water bodies are artificial; either reservoirs, ornamental lakes, or flooded quarry workings. The large reservoirs are edged with reed beds which are exposed during the summer when the water level is low. Patches of Polygonum amphibium are found in the water, and it often covers large areas, as, for example, in Saddington reservoir. One large north-west facing bay of Swithland reservoir (Grid Reference SK/562141) is ringed by reed beds which consist mainly of Typha latifolia with patches of Carex sp. and Sparganium ramosum. To the north-east, trees grow by the shore. The bottom

shelves gradually and is covered by large areas of Polygonum amphibium, some of which is rarely exposed even when the water level is low.

Flooded quarries, including granite, limestone, and gravel workings, ornamental lakes and the remaining moats are variable, both in depth, topography, and vegetation.

The commonest type of standing water body in Leicestershire is the rectangular field pond. These ponds, many of which were dug at the time of the Parliamentary enclosures (Moon, personal communication), vary in size from 3 metres wide and 4 metres long, to 5 metres wide and 8 metres long. They have steep sides and are often over one metre deep. These ponds may be completely fenced round or have at least one side open to give cattle and sheep access to the water. The open side usually shelves gently into the water; in some ponds this shallow area is enlarged and in others a concrete ramp leads down into the water. The ponds are often overgrown with weed and overshadowed by trees and shrubs, and in varying stages of neglect. There are also the circular ^{or} field ponds which have shallow margins all round and ^{are} situated in shallow depressions in the ground. Their situation suggests that they are older than the Parliamentary enclosures. There are also village ponds which again have a different history.

Rectangular field ponds of all types are found both on the flat low ground and near the brows of hills. Some are fed by springs and ditches run into others.

The vegetation of the ponds includes Potamogeton sp., Elodea, Callitriche sp., Ranunculus sp., Lemna minor, and L. trisulca.

Glyceria fluitans is very common and in some ponds Chara and Fontinalis are occasionally found.

Another common, more or less temporary fresh-water habitat, is the concrete or galvanized iron cattle trough.

5.3 Changes within ponds

The access of both cattle and sheep to a fresh-water habitat can have several effects. First: the animals may indirectly affect the macro- and micro-flora and fauna as a result of their excreta. Second: cattle directly affect the vegetation in and around the water by eating and trampling it; for example, in several ponds and by the canal, the stands of Typha and Sparganium, grow away from the water's edge out of reach of the cattle. Third: areas of bare mud, often result from the tramplings of cattle. Bare areas of mud are also found where trees and bushes shade the water, or may be seasonal, for example, appearing in the winter and spring where plants have died down. Some corixids are associated with these vegetation-free areas.

The different species of water plants have various effects on the physical nature of the water body. Some plants, for example Ranunculus, die down, and most species are greatly reduced in the winter, though the stems of Potamogeton natans remain, however, and species such as Callitriche and Glyceria fluitans, maintain a large growth throughout the winter. The plant and plant remains provide shelter for animals and micro-organisms, and give support to algae which grow throughout the winter. The growth of algae throughout the autumn, winter, and spring, is a noticeable feature of Leicestershire fresh-water habitats. In

association with this growth, other organisms, Protozoa, rotifers, dipterous larvae, and oligochaetes, and in the sheltered parts of ponds cladocerans and copepods flourish throughout the winter.

In summer, the faster growing submerged plants are less encrusted with algae and some plant species form a dense surface layer shading the water below and preventing the continual growth of algae. When a thick surface covering occurs of, for example, Lemna minor, the corixids are faced with the physical problem of reaching the water surface to renew their air supply.

Changes in water level have been briefly mentioned already. These changes are very marked in streams and rivers, however. The ponds and reservoirs are full for most of the winter and show a gradual fall in level during the summer. The timing of the low water levels can vary from year to year (Appendix). The changes in water level recorded at Normanton House farm are shown in table A.1. In 1967, the water level remained high until late May, and the lowest levels were recorded in September. In 1968, following a dry spring, the water in the ponds was at its lowest point in mid-June. Differences in the timing of the changes in water level affect the duration of areas^{of} shallow water around the edge of the water body, and in ponds which dry up completely, the length of time they can support fresh-water life.

5.4 Temperature fluctuations within ponds

The small water bodies in which corixids are commonly found, frequently experience rapid and often large changes of temperature. Studies of temperature conditions in ~~similar-sized~~^{small} water bodies in

Indonesia shows that in shallow ponds, 0.6 metres deep, the water temperature closely follows that of the air, and that stratification occurred (Vaas and Sachlan 1953). A similar result was obtained in Brazilian ponds by Rakusa - Suszczewski (1964) who also showed that any vertical temperature gradient was related to water depth. A larger water body (0.44 ha. in area and up to 3 metres deep) in the English lake district, was studied by Macan and Maudesley (1966). A continuous temperature record of the water at a depth of 15 - 20 cm. for several years showed the effect of air temperature, wind and sunshine on the water temperature. In general, the average water temperature followed the average air temperature.

Method

As part of the routine procedure when visiting a pond, the temperature was measured with a maximum and minimum thermometer to the nearest half degree centigrade.

At Normanton House Farm, four Cambridge Instrument Company thermographs were arranged to record the water temperature at the bottom of the deep and shallow ends of two ponds. The thermographs were installed in pond D on 19 January 1967 and in pond B on 16 March 1967. During the summer of 1968, the thermograph from the shallow end of pond B was moved to pond D. First, to the shallow end to enable the temperature at the bottom to be recorded at three different depths in one pond 23 May to 13 June. Second, to the surface water of the deep end of the pond D, 13 June to October 1968. (Full details of the construction and history of these ponds will be found in the appendix).

The steel bulbs of the thermographs were laid on the bottom of the pond to record bottom temperature fluctuations, or held parallel to the surface of the water during surface measurements. Thermograph bulbs in the shallow water were protected from direct solar radiation by short lengths of iron drain pipe, or by cylinders of aluminium foil placed round all the steel bulbs. The bulbs were coated with black rubber as protection against rust.

An air temperature thermograph, housed in a small screen 75 cm. above the ground was sited near the ponds. Air temperature and weather records were also obtained from the weather station at Newtown Linford, seven miles north of Normanton House Farm.

For each thermograph, the temperature for each hour was estimated to the nearest degree centigrade, and the total number of degree hours for each week calculated. The mean temperature was then calculated to the nearest half degree centigrade by dividing the total number of degree hours by the number of hours in the week. These figures also give the mean monthly temperature.

Results

The water temperatures found in Leicestershire ponds were similar to those at Normanton House Farm under the same conditions.

The results show an annual cycle of temperature fluctuations corresponding to the season:

- 1, Period of increasing temperature March - May
- 2, Plateau of high temperature, June to August
- 3, Period of falling temperature, September to November
- 4, Period of low temperature, December to February.

Considerable variation is seen, however, between 1967 and 1968 corresponding with periods of hot weather which occurred at different times in the two years (figs. 5.1 and 5.2).

During the winter, there is very little variation of the water temperature both between ponds and within the same pond. At this time of year, the water temperature follows the fluctuations of the air temperature. The rate of change, however, is influenced by strong winds and by ice (fig. 5.3).

In the spring and autumn, the water temperature in ponds is more variable than in the winter, table 5.4.

In summer, however, water temperature is most variable. The most important external factor affecting the water temperature is the hours of sunshine per day, tables 5.1 to 5.3 and figs. 5.4 to 5.7, and at night the cloud cover is an important factor, affecting the water temperature. During long periods of cloudy weather, the air and water temperatures are more closely related.

The amplitude of the daily fluctuations of the water temperature within a pond also depends upon internal factors such as the clarity of the water, its depth, and upon the presence of vegetation. ^aQualitative measurements of the water clarity were made, during the period covered by tables 5.1 to 5.3 and figs. 5.4 to 5.7, the water was clear (Appendix).

At the bottom of the pond, ^{the} amplitude of daily temperature fluctuations is greater in shallow water, table 5.1 and fig. 5.4, and the amplitude of fluctuations is greater nearer the water surface than at the bottom of the pond, table 5.3 and fig. 5.6. At the deep end of the pond, the water becomes stratified during daytime, with the surface temperature

equal to the bottom temperature plus up to 6 degrees centigrade. At night, this stratification is occasionally inverted, and surface temperature equals the bottom temperature minus 1 degree centigrade. In the shallow parts of a pond and near the surface, the water temperature usually rises higher than the air temperature during the day, but does not reach air temperature minima at night.

A thick, surface layer of algae or other surface plants reduces the amplitude and rate of fluctuation in the water temperature, cf. tables 5.2 and 5.3 and figs. 5.5 and 5.6. The water temperature near the surface does not fall to the same minima when surface algae and plants are present, and is never inversely stratified (table 5.3 and fig. 5.6).

Discussion of temperature conditions

Variations in climatic conditions in 1967/8 are reflected in the water temperatures recorded in those years.

In the winter, the most important factor affecting the water temperature in ponds is the air temperature, whereas in the summer, the hours of sunshine per day becomes the dominant factor. Similar conclusions were reached by Macan and Maudsley (1966) working on Hodsons Tarn, a larger body of water than those examined during this present work.

In the winter, there is a general uniformity of water temperatures found in different ponds on the same day. The maximum temperatures recorded for the winter months were similar to those from Hodsons Tarn. In summer, however, there is great variability in the water temperature both within a pond and between ponds, and changes of water temperature may be rapid (fig. 5.4). On a sunny day, there are consistent features

in the water temperature distributions within a pond. Maximum temperatures of 25 - 32 degrees centigrade are recorded during the day in very shallow water (0 - 3 cm. deep). In slightly deeper water (10 - 15 cm. deep) and in the surface layers to a depth of 10 cm. over water 60 cm. deep, maximum temperatures of 20 - 26 degrees are recorded. The minimum temperatures recorded at night in very shallow water is rarely less than 10 degrees centigrade. In the surface water the minimum temperature recorded is not less than the bottom temperature minus 2 degrees centigrade.

Floating algal masses and surface plants reduce the amplitude of the temperature fluctuations in the pond and increase the difference in temperature between surface and bottom water. Similar observations were made by Rakusa - Suszczewski (1964) in tropical ponds. Emergent vegetation also reduces the amplitude of temperature fluctuations (Muirhead-Thompson 1951).

In very shallow water, temperature fluctuations of up to 19 degrees centigrade can occur in a day. At the bottom of a pond 70 cm. deep, the greatest daily fluctuation recorded was 3 degrees centigrade. Greater daily fluctuations were recorded at equivalent depths in tropical ponds (Vaas and Sachlan 1953 and Suszczewski 1964).

| Depth and position of bulb. | | May 31st | June 1st | June 2nd | June 3rd | June 4th | June 5th | June 6th |
|-----------------------------|-----------|----------|----------|----------|----------|----------|----------|----------|
| 7 - 3 cm
(on bottom) | Min. | 11 | 11.5 | 14 | 14 | 16 | 15 | 13 |
| | Max. | 27 | 27 | 27 | 26.5 | 26 | 22 | 26 |
| | Amplitude | 16 | 15.5 | 13 | 12.5 | 10 | 7 | 13 |
| 18 - 14 cm
(on bottom) | Min. | 15 | 16 | 17 | 17 | 17.5 | 17.0 | 15 |
| | Max. | 22 | 22 | 22 | 21 | 21 | 20 | 21 |
| | Amplitude | 7 | 6 | 5 | 4 | 3.5 | 3 | 6 |
| 66 - 62 cm
(on bottom) | Min. | 17 | 17 | 18 | 18 | 18.5 | 18.5 | 17.5 |
| | Max. | 18.5 | 19 | 19.5 | 19 | 19 | 19 | 18.5 |
| | Amplitude | 1.5 | 2 | 1.5 | 1.0 | 0.5 | 0.5 | 1.0 |
| Air temperature | Min. | 1.5 | 1.5 | 8 | 8 | 11 | 10 | 9 |
| | Max. | 21 | 21 | 21 | 20 | 20 | 16 | 16 |
| | Amplitude | 19.5 | 19.5 | 13 | 13 | 9 | 6 | 7 |
| Hours of Sunshine | | 11.8 | 11.7 | 9.2 | 3.2 | 2.3 | 1.9 | 8.9 |

Table 5.1 The daily temperature changes recorded between 31.5.68 - 6.6.68 at three depths in pond D. Normanton House Farm.

Air temperature was recorded at Normanton House Farm. Hours of Sunshine were recorded at Newton Linford weather station. Temperature - degrees centigrade.

| Depth and position of bulb. | Aug. 2nd | Aug. 3rd | Aug. 4th | Aug. 5th | Aug. 6th | Aug. 7th | Aug. 8th |
|----------------------------------|----------|----------|----------|----------|----------|----------|----------|
| 6 - 3 cm Min. | 15.5 | 14 | 14 | 15 | 16 | 14.5 | 13 |
| (on bottom) Max. | 19 | 20 | 25 | 28 | 22.5 | 18 | 17 |
| Amplitude | 3.5 | 6 | 11 | 13 | 6.5 | 3.5 | 4 |
| 4 - 1 cm Min. | 16.5 | 15.5 | 15 | 16 | 17 | 16 | 15 |
| (below surface at deep end) Max. | 19 | 19 | 23.5 | 27 | 22 | 18 | 17 |
| Amplitude | 2.5 | 3.5 | 8.5 | 11 | 5 | 2 | 2 |
| 71 - 68 cm Min. | 15 | 15 | 15 | 15 | 15.5 | 16 | 15.5 |
| (on bottom) Max. | 15 | 15 | 15 | 15.5 | 16 | 16 | 15.5 |
| | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 |
| Air Min. | 10 | 11 | 9.5 | 11 | 13 | 12 | 11 |
| temperature Max. | 17 | 18 | 22 | 23 | 18 | 15 | 14 |
| Amplitude | 7 | 7 | 12.5 | 12 | 5 | 3 | 3 |
| Hours of sunshine | 0.6 | 0.1 | 3.0 | 4.5 | 0.0 | 0.0 | 0.0 |

Table 5.2 The daily temperature changes recorded between 2.8.68 - 8.8.68 at three depths in pond D. Normanton House Farm. Air temperature was recorded at Normanton House Farm. Hours of Sunshine were recorded at Newton Linford weather station. Temperature - degrees centigrade.

During this period there was a thick surface layer of algae at the deep end of the pond (c.f. table 5.3).

Temperature changes at the shallow end of pond D. during 2.8.68 - 8.8.68 when the greatest fluctuations were a lot less than at the deep end.

| Depth and position of bulb | | Sept. 6th | Sept. 7th | Sept. 8th | Sept. 9th | Sept. 10th | Sept. 11th | Sept. 12th |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|------------|------------|------------|
| 6cm (below surface at deep end) | Min. | 14 | 14.5 | 15 | 15 | 16 | 16 | 15 |
| | Max. | 20 | 19 | 18 | 21 | 21 | 17 | 19 |
| | Amplitude | 6 | 4.5 | 3 | 6 | 5 | 1 | 4 |
| 70 cm (on bottom) | Min. | 14.5 | 15 | 15 | 15 | 15.5 | 16 | 15.5 |
| | Max. | 15 | 15.5 | 15 | 15.5 | 16 | 16 | 16 |
| | Amplitude | 0.5 | 0.5 | 0.0 | 0.5 | 0.5 | 0.0 | 0.5 |
| Air temperature | Min. | 10 | 5 | 6 | 10 | 11 | 10 | 9.5 |
| | Max. | 23 | 20 | 18 | 22 | 23 | 14 | 19 |
| | Amplitude | 13 | 15 | 12 | 12 | 12 | 4 | 9.5 |
| Hours of Sunshine | | 8.4 | 3.7 | 0.2 | 8.2 | 2.5 | 0.1 | 7.2 |

Table 5.3

The daily temperature changes recorded between 6.9.68 - 12.9.68 at two depths in pond D. Normanton House Farm. Air temperature was recorded at Normanton House Farm. Hours of Sunshine were recorded at Newton Linford weather station. Temperature - degrees centigrade. During this period surface algae was removed from the pond (cf. table 5.2)

| | April 5th | April 15th | April 18th | April 25th | April 26th |
|---------------|-----------|------------|------------|------------|------------|
| Min. | 4 | 5 | 10 | 11 | 11 |
| Max. | 17 | 18 | 20 | 21 | 21 |
| Amplitude | 13 | 13 | 10 | 10 | 10 |
| Depth of bulb | 6 cm | 1 cm | 1 cm | 10 cm | 10 cm |

Table 5.4

Temperature changes at the shallow end of pond D. during April 1968 showing the greatest fluctuations record for the month.

Fig. 5.1. The monthly changes in water temperature of Pond D for 1967 and 1968; recorded from the bottom at the deep end; range, to the nearest degree centigrade; mean, to the nearest half degree centigrade; ————— 1967, - - - - - 1968; dates for the 4-weekly periods of 1967.

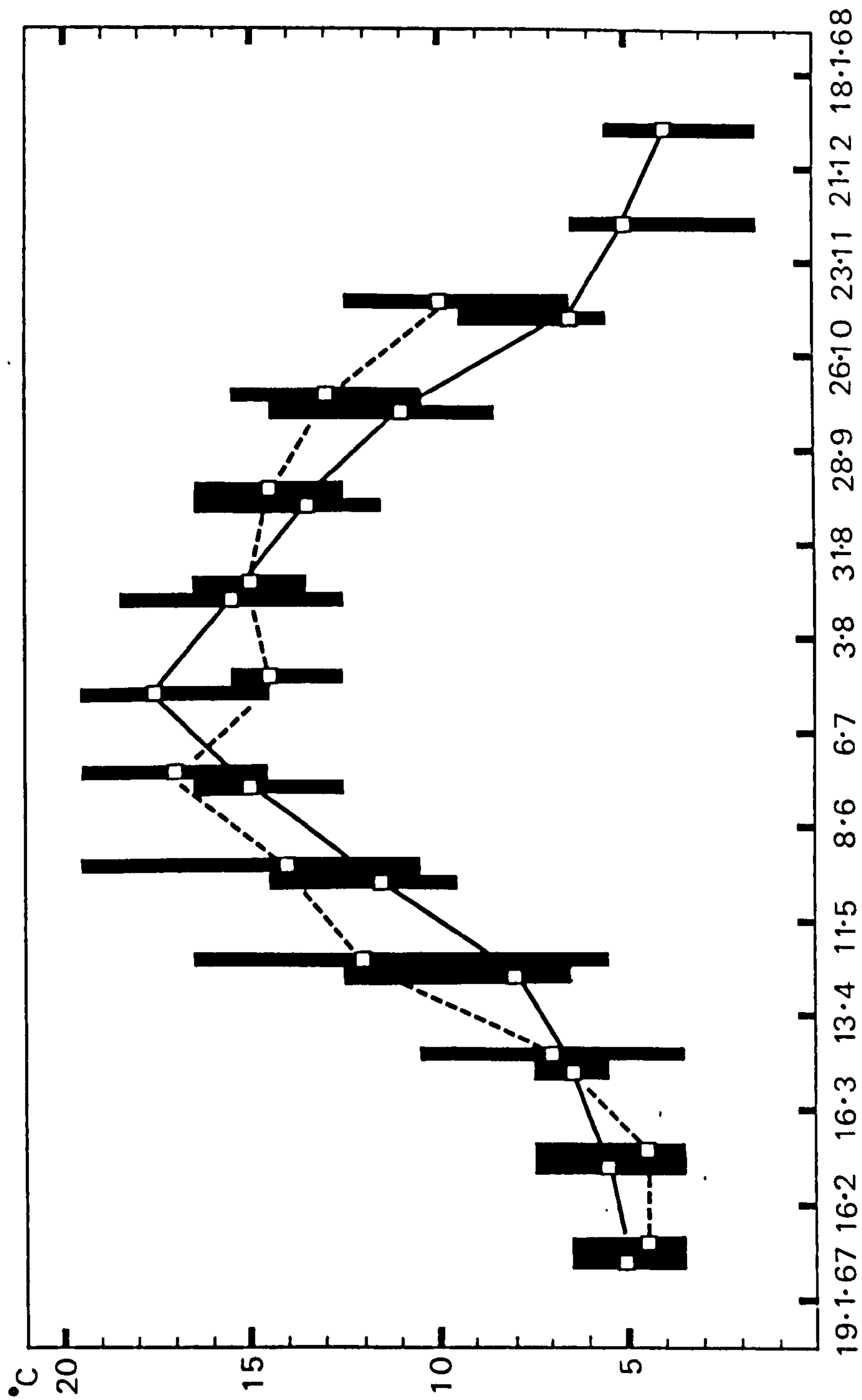


Fig. 5.2. The weekly changes in water temperature of Pond D for March until August in 1967 and 1968; recorded from the bottom at the deep end; range, to the nearest degree centigrade; mean, to the nearest half degree centigrade; ————— 1967, - - - - - 1968. The dates correspond to the 4-weekly periods in 1967 (see fig. 5.1).

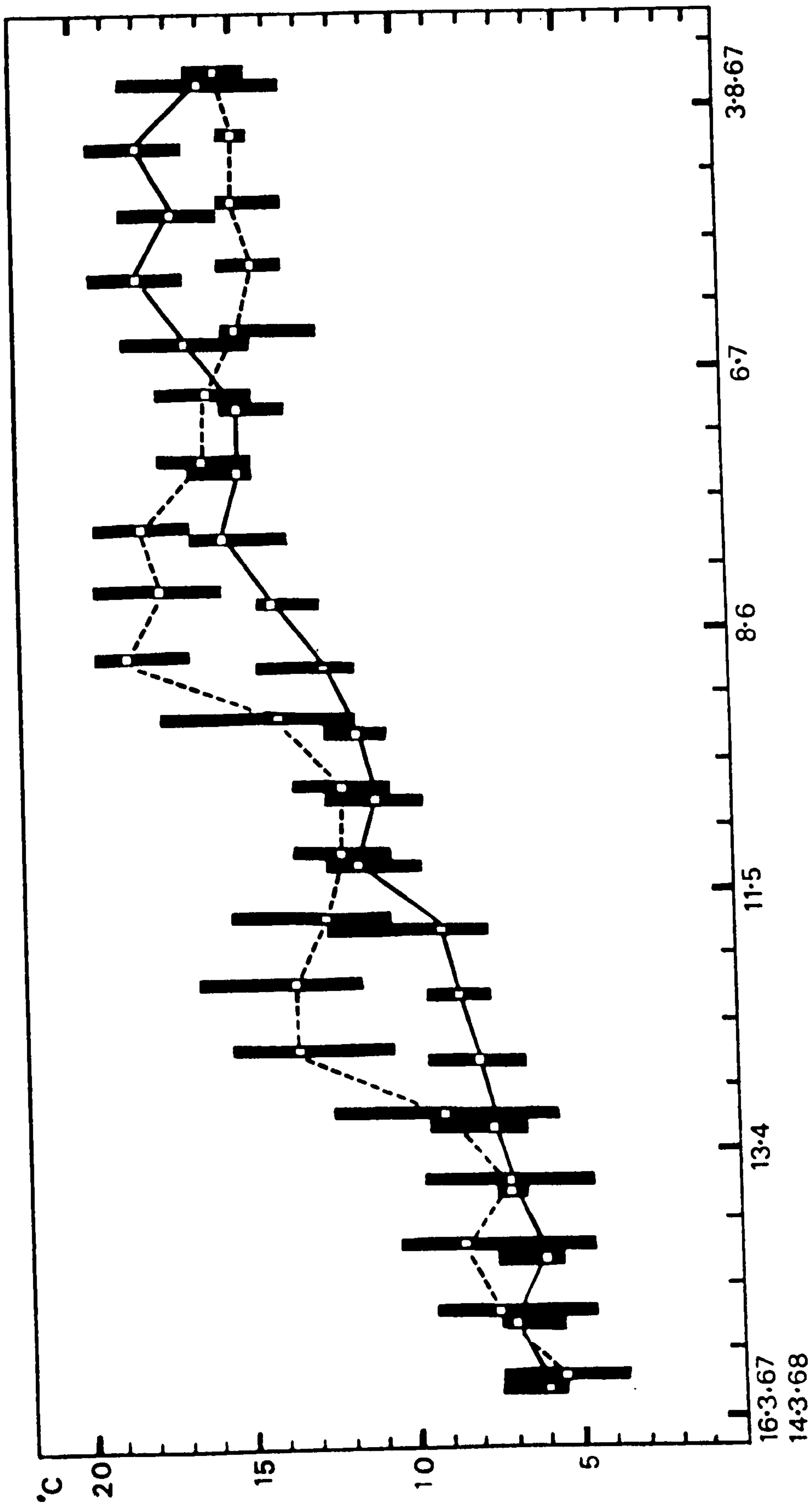


Fig. 5.3. Temperature changes in Pond B during 6-7 December 1967, top, and 21-22 December 1967, bottom. Temperature, in degrees centigrade, recorded at the bottom of pond, □. 30 cm. deep, and 0.10 cm. deep; *. air temperature, straight line joins maximum and minimum air temperatures; ▼. minimum ground temperature; the mean wind direction and force m.p.h. is shown at noon each day with hours of sunshine beneath; time in G.M.T. (Max. and min. air temp. shown at 6 and 12 hours and min. ground temp. at 6 hrs., as it is not known exactly when they occurred). Ice was present on the pond on 7 and 21 December.

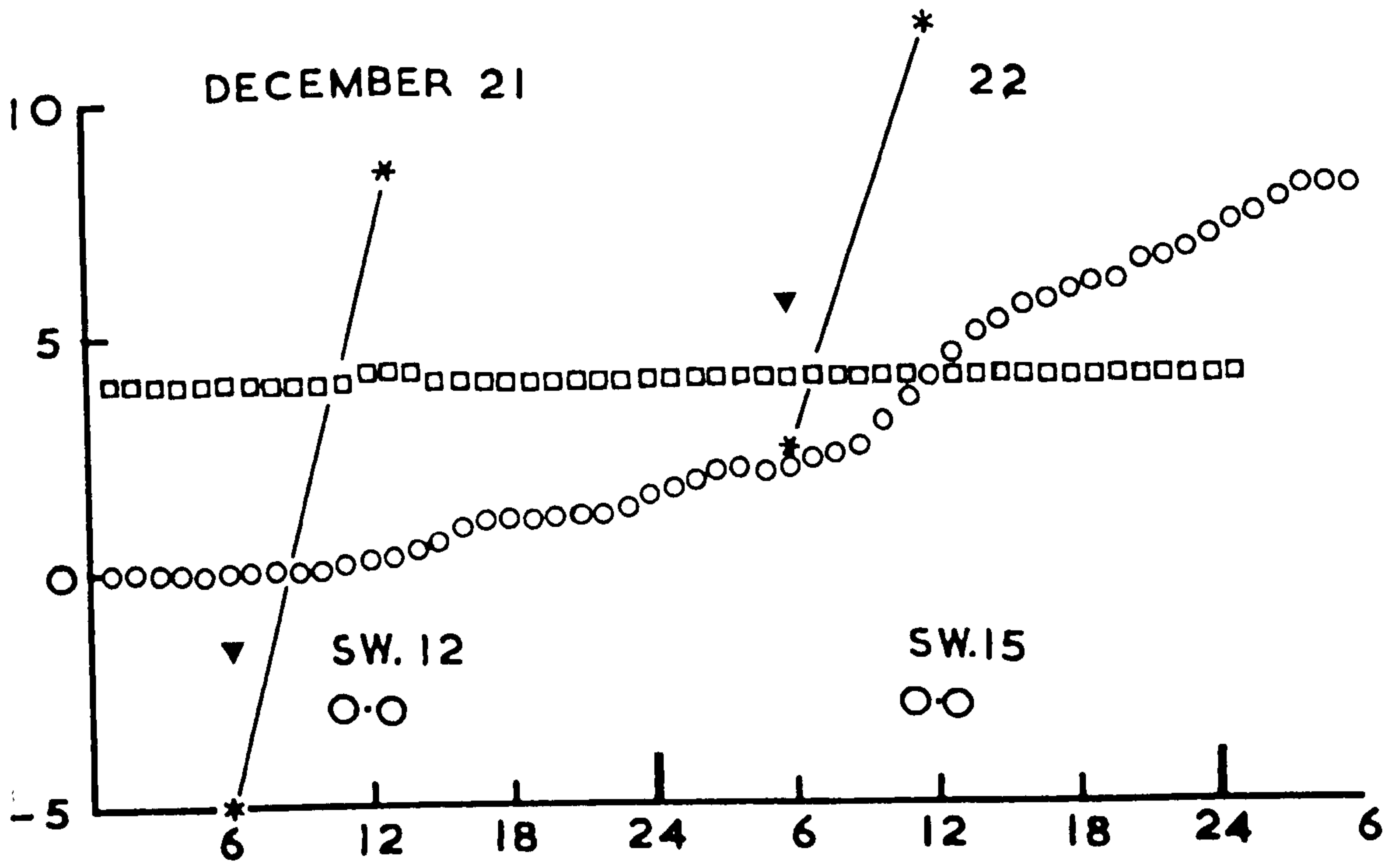
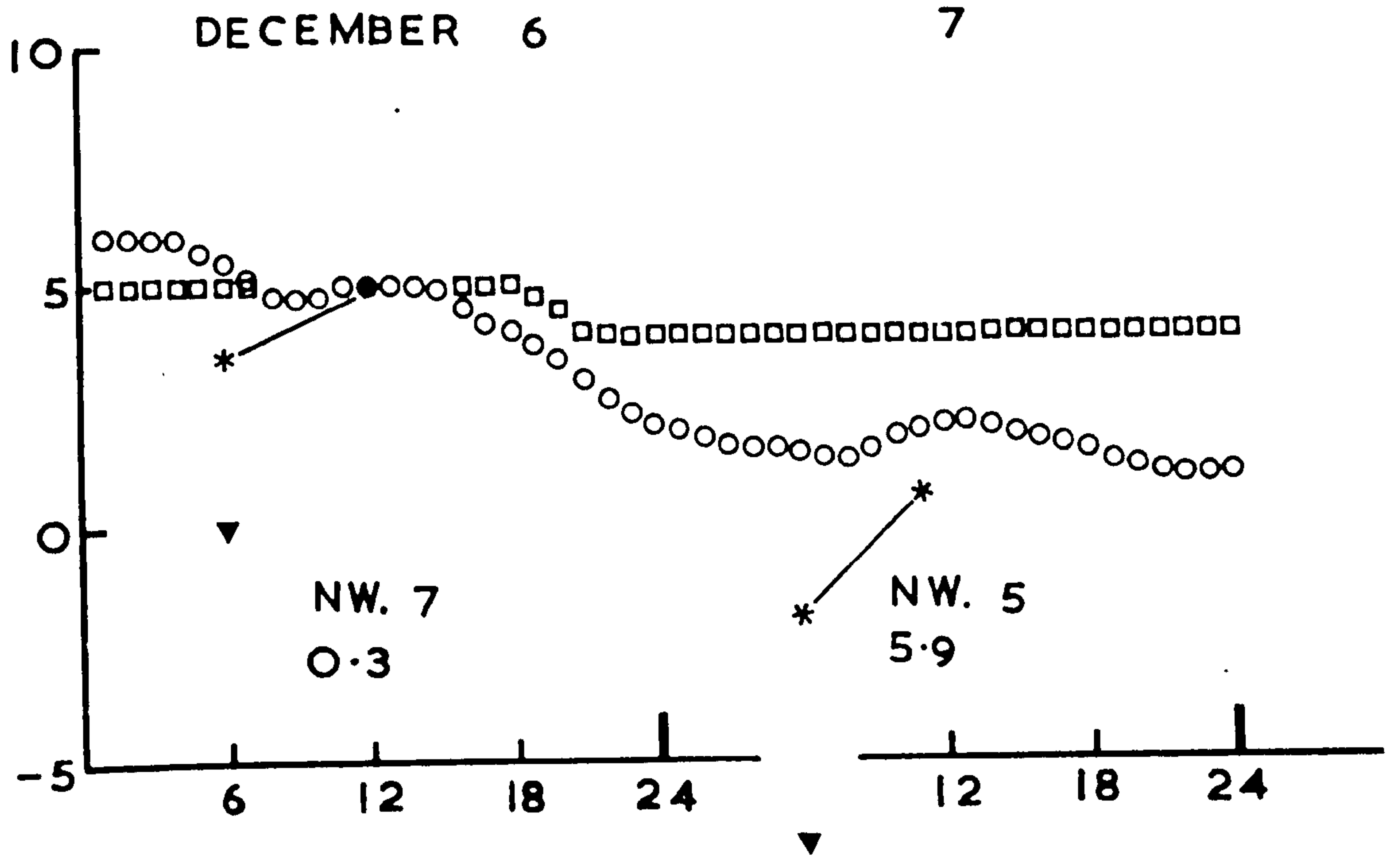


Fig. 5.4. Temperature changes in Pond D on 9 to 12 June 1968.

Temperature, degrees centigrade; water, recorded from the bottom of pond, \square . 60 cm. deep, \blacktriangle . 10-12 cm. deep, \circ . 0-2 cm. deep; air, $*$; hours of sunshine at the bottom of graph at noon each day; time B.S.T.

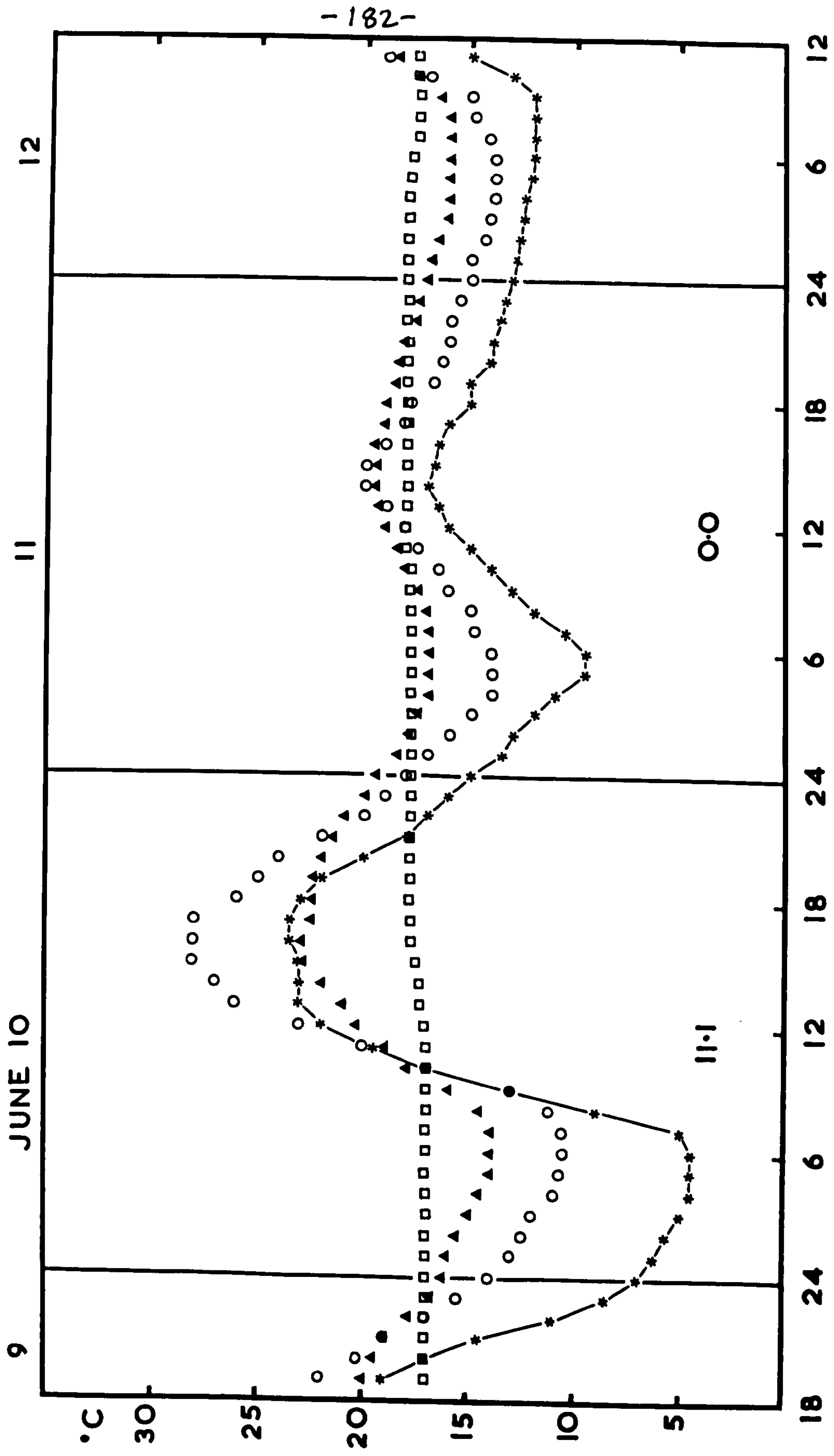


Fig. 5.5. Temperature changes in Pond D on 27-30 July 1968.

Temperature, degrees centigrade; water, recorded from the bottom of pond □ . 77-75 cm. deep, 0. 0-2 cm. deep and ▲ .
3-5 cm. below water surface at deep end; air * ; hours of sunshine at bottom of graph at noon each day; time, B.S.T. During this period algae covered the surface at the deep end of the pond (cf. fig. 5.6).

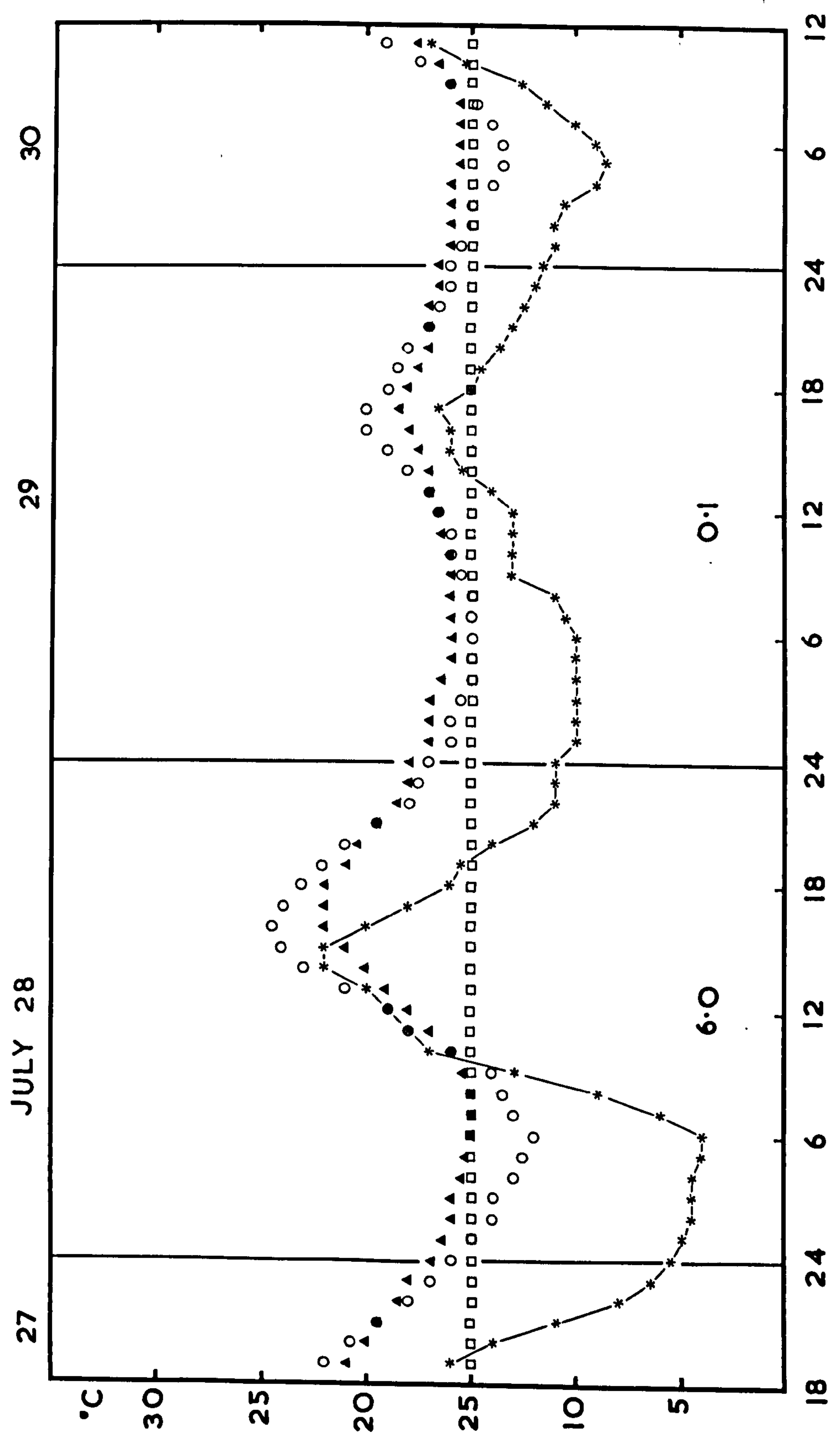


Fig. 5.6. Temperature changes in Pond D on 29 August to 1 September. Temperature, degrees centigrade; water, recorded from bottom of pond, \square . 68-70 cm. deep, and \blacktriangle . 4-6 cm. below water surface at the same place; air * ; hours of sunshine at bottom of graph at noon each day; time, B.S.T. During this period surface algae was removed from the pond (cf. fig. 5.5).

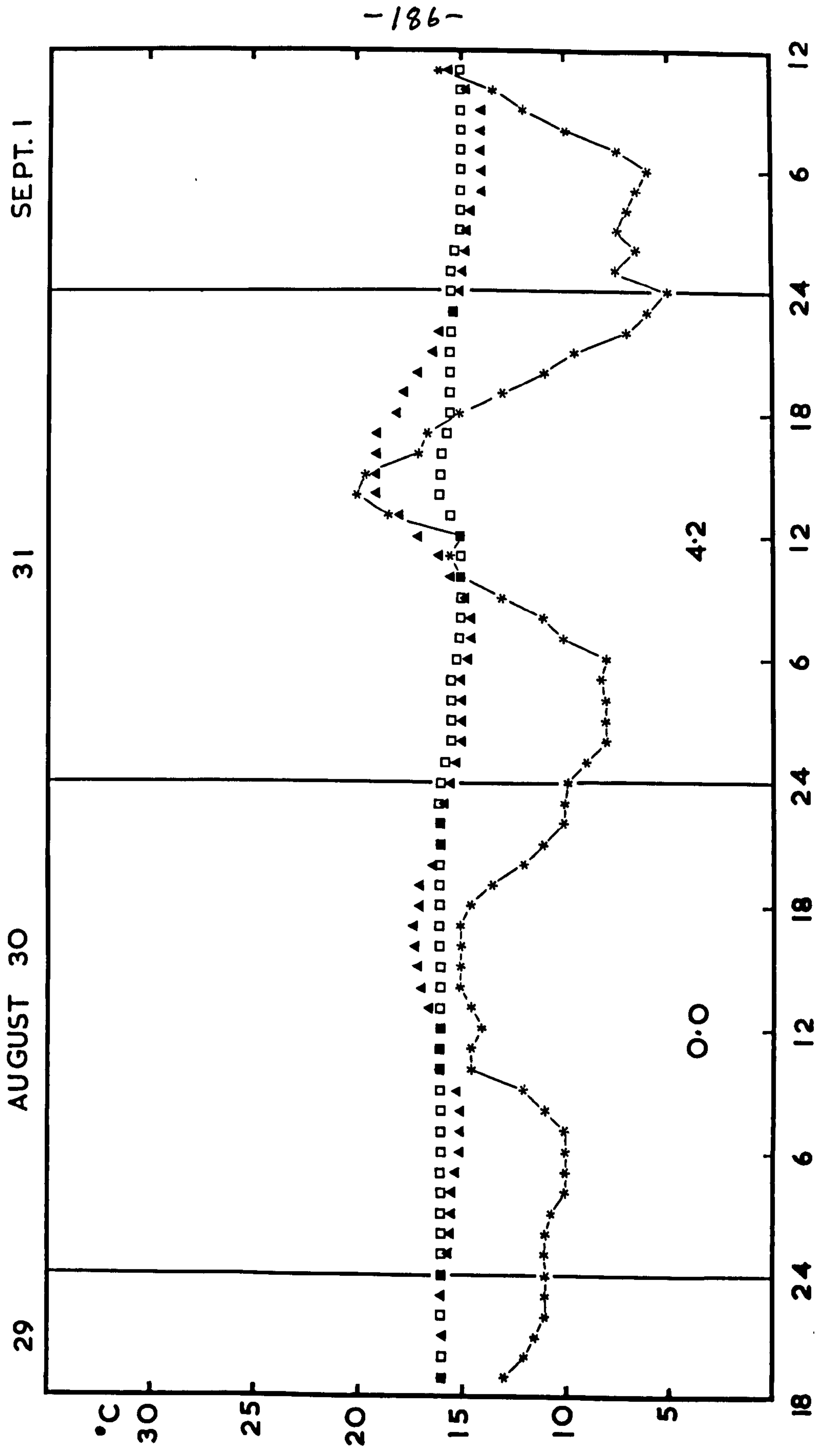


Fig. 5.7. The temperature changes in Pond D on A. 6-7 June 1968,
and B. 5-6 August 1968. Temperature, degrees centigrade; air, * ;
hours of sunshine at bottom of graph at noon each day; time B.S.T.

Water temperature;

A. on bottom, □ . 62 cm. deep, ▲ . 14 cm. deep, ○ . 3 cm. deep;

B. on bottom, □ . 69-70 cm. deep, ○ . 3-5 cm. deep, and ▲ . 1-3 cm.

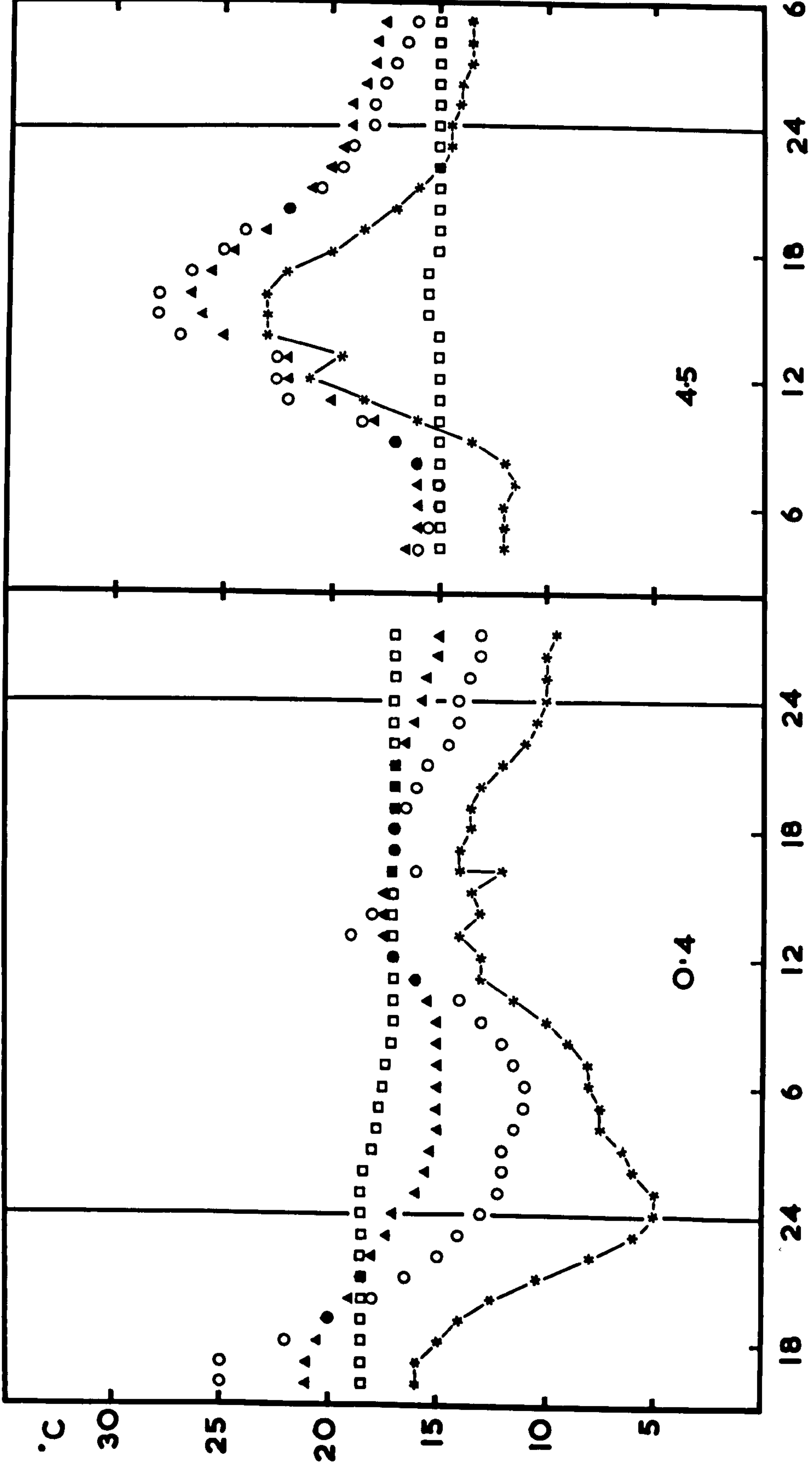
below surface at deep end. The diagrams show the rapid minor
fluctuations in air and water temperature during the day.

A

JUNE 7

B

AUGUST 5



SECTION 6

The Ecology of the Leicestershire Corixidae6.1 Introduction

The distribution and habitat of each species is described, but the various stages in the life cycle are ~~only~~^{only} examined in a few species. The effects of parasitism are described in a single population of corixids.

6.2 Distribution of the Corixidae

Descriptions of the types of habitat in which the British corixid species are found, are given by Macan (1954 and 1965) and Southwood and Ieston (1959). In Leicestershire a similar pattern of distribution is found and the various habitats of each species are described, some in detail. The relative abundance of each species is shown in table 6.1.

Micronecta poweri (D. and S.) was found in five localities; the dam wall of Thornton reservoir and on silt in streams and rivers. This species was particularly abundant in 1966 in a tributary of the river Welland in a large area of shallow water below a bridge at (Grid Ref. SP/751925) where the bottom was trampled and fouled by cattle. M. poweri was still abundant the following year, 1967, though the cattle were absent. In 1968, however, the corixid could not be found. The habitat had changed, the banks were covered with vegetation and the bottom with Elodea. In this environment, Sigara dorsalis had replaced M. poweri.

Micronecta minutissima (L.) was found only once, in the emergent vegetation of Eyebrook reservoir.

Cymatia bondsdorffi (Sahlb.) was found in large numbers in two habitats where both emergent and submerged vegetation were present. In one of these habitats, Kilby Bridge pond, a flooded limestone quarry (Grid. Ref.

SP/612970) where eighteen months previously no Cymatia species were found; three flightless individuals of C.bonsdorffi were found in the spring of 1967. In the same summer, the species was found over a large area of the pond, in association with Chara growing between the reed beds. It bred successfully that year and the following year 1968, when its distribution was similar. In contrast, C.bonsdorffi has disappeared from a pond at Market Bosworth. It was found in 1962 and 1963, but was not found in 1967. In two other habitats, both of which were frequently sampled, only single flightless specimens were found.

Cymatia coleoptrata (Fab.) was found in habitats with dense submerged water plants. In one habitat, Wistow Lake, the species has been taken many times since it was first found there in 1949. In Kilby Bridge pond, however, it was first found in the summer of 1968 and bred there that year and ⁱⁿ the following year it was restricted to a smaller area in that pond than C.bonsdorffi.

Corixa panzeri (Fieb.) was found ^{at} three localities, each characterized by Chara growing in large shallow areas. The flightless morph occurred in each locality.

Corixa dentipes (Thomson) was found breeding in reservoirs and ponds with deep water, but is always found amongst plants in shallow water. These insects were also collected from the unlikely shallow pond B at Normanton House Farm during 1967/8. They were probably autumnal immigrants.

Corixa punctata (Illig.) is a common species in Leicestershire. It is present in a few reservoirs and large numbers are often present in

ponds. It occurs in still shallow water, i.e. 15 to 60 cm. deep, amongst the vegetation. If Lemma minor covers a pond C. punctata may be the only corixid species present. In winter, this species is found in deep water in the ponds at Normanton House Farm and in Hallaton pond (Grid Ref. SP/790968) at this time of year it is most abundant in the vegetation where the water is 15 - 30 cm. deep.

Hesperocorixa castanea (Thomson) was only found in association with the moss, Sphagnum.

Hesperocorixa moesta (Fieb.) was found breeding only once, in an unfenced field pond near Six Hills (Grid Ref. SK/633171).

Hesperocorixa linnei (Fieb.) was found breeding in only a few habitats; these had emergent vegetation and accumulations of dead plant material.

Hesperocorixa sahlbergi (Fieb.) is found in ponds where there are accumulations of organic matter in ponds, though large numbers of insects were only infrequently found.

Arctocorixa germari (Fieb.) is generally found in water at least 1 metre deep, (South wood and Ieston 1959). A few specimens were taken from reservoirs, ponds with deep water, and ponds with only shallow water.

Callicorixa praeusta (Fieb.) a common species was found in reservoirs, canals, and ponds, occasionally in large numbers, particularly amongst the plant debris and where pollution by animals occurred.

Sigara (Sigara) dorsalis (Leach) is found amongst vegetation in the shallow waters of rivers, reservoirs, and ponds, and is particularly

common in gravel pits.

Sigara (Subsigara) falleni is found in sheltered parts of habitats similar to those described above for S.dorsalis. It is locally abundant in canals and very common in reservoirs, particularly in one bay of Swithland reservoir described in section 5.2. In winter, the insects concentrated in emergent vegetation.

Sigara (S.) distincta (Fieb.), is a widespread, but not a numerous species. It was found breeding in a few ponds which have no obvious features in common.

Sigara (S.) fossarum (Leach), is usually associated with S.falleni in canals and ponds, where Elodea and emergent vegetation are present.

Sigara (Vermicorixa) lateralis (Leach), is found in shallow water areas free from vegetation, and with some organic pollution.

Sigara (V.) nigrolineata (Fieb.) is found in ponds where there are plant-free areas. This species is also found in small shallow ponds and breeds in large numbers in cattle troughs.

Sigara (V.) concinna (Fieb.) is widespread but numerous in only a few ponds, one pond being polluted by cattle.

Sigara (Retrocorixa) limitata (Fieb.) was found breeding in only a few ponds, one is a round field-pond in which S.distincta was breeding.

6.3 The life cycle

Butler (1923) outlines the life cycle of the British corixids. Detailed information is also available as a result of several recent investigations into the productivity of Arctocorisa germari in a ^NPenine, upland reservoir, (Crisp 1962 a and b), and into the flight polymorphism

of several species in southern England (Young 1965c).

The corixid over-winters as the imago. In the spring, the ovaries enlarge and egg-laying occurs in the spring and summer. The nymphs are found throughout the summer and the first adults of the new generation appear in mid-summer. Some of the new generation adults become reproductively active, and there is a partial second generation (Young 1965c). The ovaries of those females which produce eggs in late summer are inactive in the autumn and winter, but produce more eggs in the spring.

On the other hand, Micronecta over-winters as a nymph, usually a third instar nymph. In the south of England there are usually two complete generations per year (Walton 1938).

6.31 Sex ratio

There are no reports of corixid populations which do not have a 1:1 sex ratio in the winter and spring. In this present work, the same sex ratio was found in all large collections except those from the centre of a large bay in Swithland reservoir (section 5.2), where the Sigara falleni and S.dorsalis populations depart from this ratio. In all collections of S.falleni and most collections of S.dorsalis from the centre of the bay, a ratio of 30:70 is recorded (table 6.5 and 6.6), whereas collections of these species from other parts of this bay show the more usual 1:1 sex ratio.

6.32 Ovarian development

The condition of the ovaries was noted during the routine examination of the collections of corixids. The development of the ovaries and egg rudiments are divided into six arbitrary stages, based on the divisions

used by Young (1965c), whose stage 0 is equivalent to the Stage 1 used in this present work. These stages are: 0, teneral stage, the ovaries are very small; 1, 'over-wintering' condition, the ovaries are larger with a few egg rudiments differentiated in each ovule; II, egg rudiments up to mature egg size with yellow contents; III, egg rudiments of mature egg size but variable in shape; IV, egg rudiments with mature appearance with both chorion and pedicel; the chorion is usually opaque, within the ovule; V, mature egg, chorion shining within the lateral or common oviduct.

Each of the paired ovaries in the female, including Cymatia spp. contain seven ovarioles, cf. Walton (1943) and Southwood and Leston (1959). The smaller corixid species have fewer developing egg rudiments per ovariole than the larger species. The eggs of the small species are also smaller than those of the larger corixids but are large in relative terms.

Ovarian development and egg laying were investigated over two years in females from over-wintering populations in ponds, from many ponds throughout Leicestershire in the first year, but only from the ponds at Normanton House Farm in the second year.

The timing of the ovarian stages in each species of corixid was similar in the two winters. Most species overwinter with the ovaries at stage I, stage II, first appears in late February in insects in certain habitats, but is delayed until late March in corixids of other habitats. In the 'early' habitats, ovaries containing mature eggs are found in March and in all habitats most ovaries contain mature eggs by

the end of April. In Corixa punctata and Hesperocorixa sahlbergi, however, egg production starts much earlier in the winter than the other species in both 'early' and 'late' habitats.

Corixa punctata has only one generation per year (Young 1965c). In the late summer and early autumn, the ovaries of the insects are at stages 0 and I, but by late November, Stage II, is reached in some individuals. Development to Stages II and IV occurs in all insects during December, and in January, most females contain mature eggs and egg-laying may occur (Fernando 1959 and Young 1965c).

Hesperocorixa sahlbergi in contrast to C. punctata may have a second partial generation in the summer, but no mature eggs are found in the females in autumn. In winter, ovarian stage II is observed late in December and early January. In February, insects with mature eggs are found.

Ovarian development is delayed by cold conditions by as long as a month (Young 1965c). This suggests that the differences between early and late habitats may be due to the variation in the water temperature in these habitats. The exact timing of ovarian development is species specific. Young (1965c) found that Sigara dorsalis tended to start ovarian development earlier than the other Sigara species, and again that Callicocorixa paeusta started development slightly later than the other corixid species in the same habitat. These two observations were not repeated in Leicestershire.

Copulation is most frequently observed at the time when the first mature eggs are produced. In contrast to ^{the statement made by} Poisson (1933), Corixa

punctata and Hesperocorixa sahlbergi will copulate in water of 4 - 6 degrees centigrade and Arctocorisa germari copulates in water of 8 degrees (Crisp 1962b).

Observations made at Normanton House Farm ponds (see appendix) show the relationship of egg-laying and embryonic development in several species of corixid living in the same pond. In 1968, only the eggs of Corixa punctata were found at the end of March. In the middle of April eggs of Sigara falleni and S.dorsalis were also present. At this time, many of the eggs of C.punctata had reached the 'eyed' stage, and at the end of April, nymphs of C.punctata were found.

6.33 Temperature and embryonic development

40-100 freshly laid eggs of five corixid species; the large Corixa punctata; the medium-sized Sigara falleni and S.dorsalis; the small S.lateralis and S.nigrolineata were kept at different controlled temperatures. The time taken for the eggs to hatch at each temperature was the same for each member of the same size group, but, as can be seen from the table below, the eggs of the smaller species took a shorter time to hatch than those of the large species.

| Temperature:
degrees centigrade. | Time, in days, for 50% of eggs to hatch | | |
|-------------------------------------|---|-------------------|-----------------------|
| | <u>C. punctata</u> | <u>S. falleni</u> | <u>S.nigrolineata</u> |
| 25 | 7 | 7 | 5 |
| 20 | 11 | 11 | 9 |
| 15 | 20 | 19 | 19 |
| 10 | - | 55 | 53 |

Assuming that a minimum temperature (K) must be exceeded before development begins, it is possible to calculate for each species the threshold

value (K) and the number of degree days above this temperature required for complete development from the relationship:

$$d_1 (t_1 - K) = d_2 (t_2 - K)$$

where d_1 and d_2 are the time taken for the eggs to hatch at temperatures t_1 and t_2 respectively. The table below shows difference between the two extreme size groups of corixids examined.

| | Threshold temperature (K). | degree days $d_n (t_n - K)$ |
|------------------------|----------------------------|-----------------------------|
| <u>C. punctata</u> | 8 | 110 - 140 |
| <u>S. nigrolineata</u> | 9 | 90 - 120 |

Similar results were obtained for Arctocorisa germari by Crisp (1962b).

6.34 Flight polymorphism and teneral development

The presence of the teneral stages and the flightless morphs of corixids which are described by Young (1965a and b), provide positive evidence that the species has bred within a habitat. The nymphs of some species can also be identified. Teneral insects are easily recognized by their pliable cuticle, whereas, the flightless morphs are characterized by the small size of the wings or wing muscles and the lack of pigmentation on parts of the mesonotum. The size of the wing muscle must be examined in most species for a reliable determination of the morph, because of variation in the mesonotum pigmentation. A technique for measuring the diameter of the muscle fibres is described by Young (1963), but, in most cases, it is sufficient to open the mesonotum; in the normal morph, muscles fill the mesothorax, whereas,

in the flightless morph, there is a large cavity often filled with a fat body.

Table 6.2 shows the incidence of flight polymorphism found in Leicestershire, and includes two species with previously undescribed flightless morphs. H. castanea^{was} found in a pond in Bradgate Park, where a population of this species has been established for several years, and C. praeusta, probably the early flightless morph as the females^{was} contained mature eggs, taken from the lake in Market Bosworth in July 1963. Both new flightless morphs have unpigmented areas on the mesonotum.

6.35 Migration

There are two annual migrations, spring obligatory migration associated with ovarian development, and a summer/autumn facultative migration associated with a deterioration in the habitat (Young 1966). Both emigration and immigration were observed during September 1967 in conditions not previously described (Popham 1964 and Young 1966).

Emigration was observed at the Eyebrook reservoir. The water level was low, leaving an exposed shore line, with only a few patches of vegetation around which the corixids were concentrated. The water temperature at mid-day was 17 degrees centigrade, and rose slightly during the afternoon. There was a light south-westerly wind and an air temperature of 20 degrees centigrade. The corixids were observed to fly only when the sun was visible. They all flew down wind away from the sun, but some of the larger corixids (Corixa sp.) initially attempted to fly towards the sun.

Immigration into two neighbouring ponds was observed between 4 and

5 p.m. (BST.) on the same day. The weather was sunny, with only very light and variable winds. One pond was partly shaded and the corixids, which appeared to have been flying towards the sun, flew into that part of the pond exposed to the sun. They were probably attracted by the shiny water surface (Popham 1964). The indigenous species of this pond is Sigara nigrolineata. Those corixids which were caught flying into the pond were S.falleni. At the same time, some corixids of the same size were also leaving the pond, ^{and} one S.dorsalis was caught.

6.4 The effect of Hydracarina on corixids

Hydracarina are frequently found as ectoparasites of corixids (Fernando 1959). One species, probably Hydrachna c.cruenta reduces the fecundity but does not prevent the production of mature eggs in Corixa (= Sigara) scotti (D. and S.), (Crisp 1959).

Table 6.3 shows the species of corixids infected by Hydracarina nympho-chrysalids in Leicestershire. In most collections, no distinction was made between the two genera of immature mites (Jones 1965), but Hydrachna was frequently observed on Sigara nigrolineata and S.lateralis, and Eylais was often found on S.falleni and S.dorsalis.

A large population of S.falleni and S.dorsalis infected with Eylais sp. was investigated during 1968. The corixids were in the bay of Swithland reservoir described in section 5.2, and were taken from that part of the bay nearest the track. Approximately 200 individuals were caught with a pond net on each occasion. The following features of each corixid were noted: sex, flight muscle morph, condition of the ovaries, and the number, position, and size of the Hydracarina. The results are displayed in tables 6.4 - 6.10.

The composition of each collection is shown in table 6.4, a 1967 collection is included for comparison. Because of the variation found between collections, full details are given. When most of the collections were made, the corixids were concentrated in the shallow water amongst the emergent vegetation, but they swim towards the deeper water when disturbed, even when ice is present. On two occasions, the corixids were dispersed. On 26 January, there was strong wave action, and there was a slight concentration of corixids at the border of the emergent vegetation and the open water. But on 2 May, the water level had dropped below the emergent vegetation. On 31 May, the number of corixids in the bay appeared to be considerably reduced. These changes in distribution appear to affect the composition of the collections.

The sex ratio for Sigara falleni in this part of Swithland reservoir is 3 ♂: 7 ♀, table 6.6. A similar sex ration is also found in the larger collections of S.dorsalis, table 6.5 (see also section 6.31). Tables 6.4 - 6 show the incidence of the flight muscle morphs in the collections. In S.falleni there are significantly fewer normal flight muscle morphs in the females than the males, 20% and 30% normal morphs respectively, table 6.6. About 20 - 40% of S.dorsalis were normal morphs, table 6.5.

Nymphochrysalids of both Hydrachna and Eylais were found on S.falleni, S.dorsalis, and Callicocorixa praeusta. In 1968, $45.7 \pm 4.4\%$ S.dorsalis and $25.6 \pm 1.3\%$ S.falleni were infected with mites in the winter and spring, fewer S.falleni were infected in 1967 (Tables 6.5 and 6.6).

One red, large Eylais nymphochrysalid is numerous, usually attached

by the head near the lateral edge of the second abdominal tergite of the host, table 6.7. The size of the mite increased from January to May, and by the end of May, many mites have left the host.

There is usually only ^{one} Eylais nymphochrysalid per infected S.falleni and S.dorsalis, but up to seven were found on one S.dorsalis. The mean number of nymphochrysalids per host is greater, however, on S.dorsalis than on S.falleni (table 6.8), and a larger proportion of S.dorsalis are infected with mites (cf. tables 6.5 and 6.6). In S.falleni, there are more mites infecting the flightless morph than the normal flight muscle morph. This is significant at .5% level (see table 6.6).

The Eylais nymphochrysalids are randomly distributed amongst the individuals of each class of host except on the female flightless morphs of S.falleni in the collection of 14 March 1968 (tables 6.8 and 6.9).

Overwintering female corixids with readily visible nymphochrysalids of Eylais and Hydrachna tend to have smaller ovaries and fewer egg rudiments are differentiated in each follicle than the unparasitized female. Ovary development of parasitized females is delayed at stage I, however, when the mites leave the host, mature eggs are produced (table 6.10). The table also shows that the delaying effect on the ovary of the host is due only to those mites which had easily recognizable nymphochrysalids on the host during the winter.

Micronecta poweri (D. and S.), 4

M. minutissima (L.), 1

Cymatia bonsdorffi (Sahlb.), 5

C. coleotrata (Fab.), 4

Corixa panzeri (Fieb.), 3

C. dentipes (Thomson), 8

C. punctata (Illig.), 56

Hesperocorixa castanea (Thomson), 3

H. moesta (Fieb.), 5

H. linnei (Fieb.), 19

H. sahlbergi (Fieb.), 61

Arctocorixa^s germari (Fieb.), 7

Callicorixa praeusta (Fieb.), 7

Sigara (Sigara) dorsalis (Leach), 55

Sigara (Subsigara) falleni (Fieb.), 43

S. (S.) distincta (Fieb.), 34

S. (S.) fossarum (Leach), 14

S. (Vermicorixa) lateralis (Leach), 23

S. (V.) nigrolineata (Fieb.), 59

S. (V.) concinna (Fieb.), 10

S. (Retrocorixa) limitata (Fieb.), 10

Table 6.1. The Corixidae found in Leicestershire from 1945 to 1969, most collections were made in the last 10 years. The material from this work and of other collectors is deposited in Leicester Museum.

The number of 2 x 2 kilometer^s squares in which each species has been found, is given. This number reflects the relative abundance of each species within the county. Corixids were found in a total of 100 squares.

a) Wing muscle polymorphism

Corixa dentines (Thomson)

C.vanzeri (Fieber)

Hesperocorixa castanea (Thomson) *

Callicocorixa praeusta (Fieber) *

Sigara dorsalis (Leach)

S.falleni (Fieber)

S.distincta (Fieber)

S.concinna (Fieber)

S.fossarum (Leach)

b) Wing muscle and wing polymorphism

Cymatia bondsdorffi (Sahlberg)

C.coleoptrata (Fabricius)

Micronecta poweri (Douglas and Scott)

Table 6.2. The incidence of flight polymorphism in the
Leicestershire Corixidae. * flight polymorphism
not previously recorded in these species.

| <u>LIST OF SPECIES</u> | <u>HYDRACARINA</u>
(Water Mites) | <u>NEMATODES</u> | <u>CESTODE</u>
Cysticercoids
of a
Cyclophyllidae* | <u>PROTOZOA</u>
Gregarine
Cysts |
|------------------------|-------------------------------------|------------------|--|---------------------------------------|
| <u>C. coleoptrata</u> | X | | | |
| <u>C. punctata</u> | - | - | - | X |
| <u>C. praeusta</u> | X | X | - | X |
| <u>H. castena</u> | - | - | - | X |
| <u>S. falleni</u> | X | - | X | - |
| <u>S. dorsalis</u> | X | - | - | - |
| <u>S. nigrolineata</u> | X | - | - | X |
| <u>S. lateralis</u> | X | | | |
| <u>S. limitata</u> | X | | | |
| <u>S. fossarum</u> | X | | | |

Table 6.3

The parasites found infecting corixids in Leicestershire.

* identified by Miss J. Moody, Zoology Department,
University of Leicester.

DATES OF COLLECTIONS

| SPECIES | 2.2.67 | 26.1.68 | 29.68 | 14.3.68 | 2.5.68 | 31.5.68 |
|---|----------|----------|----------|-----------|---------|---------|
| S.falleni(a) | 61♂ 126♀ | 50♂ 121♀ | 49♂ 142♀ | 133♂ 429♀ | 33♂ 76♀ | 42♂ 80♀ |
| S.dorsalis(a) | 2♂ 2♀ | 9♂ 14♀ | 8♂ 6♀ | 9♂ 21♀ | 21♂ 41♀ | 5♂ 19♀ |
| C.praeusta(b) | 1♂ 1♀ | 2♂ 2♀ | 3♂ 3♀ | 5♂ 3♀ | 1♂ 4♀ | 2♂ 6♀ |
| C.dentipes(b) | - | - | 3♂ 3♀ | - | - | 1♀ |
| A.germari(b) | - | - | - | - | 1♀ | - |
| S.distincta(b) | 1♀ | - | - | - | - | - |
| S.concinna(b) | - | - | - | - | 2♂ 2♀ | - |
| C.bonsdorffi(c) | - | - | - | - | 1♂ | - |
| Temperature of
the Water degrees
Centigrade | 7° | 5° | 2° | 4° | 12° | 13° |

Table 6.4 List of species, and the numbers of each sex found in collections from Swithland reservoir in 1967 and 1968.

(a) Normal and flightless morphs, (b) normal morphs only found,
(c) flightless morph.

- 206 -

| Date | Sex
ratio,
per-
centage.

♂ ♀ | Percentage of
each flight
muscle morph
in each sex. | | Percentage of
each sex infected
by mites. | |
|---------|--|--|---------------|---|---------------|
| | | Male
N F | Female
N F | Male
m - | Female
m - |
| 2.2.67 | 50:50 | 0:100 | 0:100 | 50:50 | 50:50 |
| 26.1.68 | 39:61 | 11:89 | 21:79 | 67:33 | 57:43 |
| 29.2.68 | 57:43 | 37:63 | 66:34 | 62:38 | 50:50 |
| 14.3.68 | 30:70 | 22:78 | 19:81 | 66:34 | 48:52 |
| 2.5.68 | 34:66 | 33:67 | 37:43 | 48:52 | 27:73 |
| 31.5.68 | 21:79 | 0:100 | 16:84 | 0:100 | 0:100 |

Table 6.5. S. dorsalis; from Swithland Reservoir.

Analysis of sex ratio, flight muscle polymorphism and infection with mites.

Explanation of symbols.

N = Normal flight muscle morph.

F = Flightless morph.

m = Mite (Eylais sp) nymphochrysalid present.

- = " " " " " absent.

The sex ratio for 14.3, 2.5 and 31.5 differs significantly ($P > 5\%$) from 50:50 with t-test.

| Date | Sex
ratio.
per-
centage.

♂ ♀ | Percentage of
each flight
muscle morph
in each sex. | | Percentage of
males of each
flight muscle
morph infected
with mites. | | Percentage
of females of
each flight
muscle morph
infected with
mites. | |
|---------|--|--|---------------|--|----------|---|----------|
| | | Male
N F | Female
N F | N
m - | F
m - | N
m - | F
m - |
| 2.2.67 | 33:67 | 13:87 | 13:87 | 13:87 | 34:66 | 13:87 | 16:84 |
| 26.1.68 | 30:70 | 34:66 | 19:81 | 29:71 | 39:61 | 13:87 | 29:71 |
| 29.2.68 | 26:74 | 20:80 | 19:81 | 10:90 | 20:80 | 37:63 | 27:73 |
| 14.3.68 | 24:76 | 24:80 | 15:85 | 28:32 | 30:70 | 16:84 | 24:76 |
| 2.5.68 | 30:70 | 36:64 | 18:82 | 8:92 | 48:52 | 7:93 | 26:74 |
| 31.5.68 | 34:66 | 33:67 | 24:76 | 14:86 | 7:93 | 5:95 | 7:93 |

Table 6.6. *Sigara falleni*; Swithland Reservoir.

Analysis of sex, flight muscle polymorphism and infection with mites.

Explanation of symbols. see table 6.5.

Fewer normal flight muscle morphs in female than male

t-test (P<5%)

Fewer mites infecting normal morphs than flightless morphs

t-test (P<5%)

| <u>Date</u> | <u>Size of nymphochrysalid.</u> |
|-------------|---------------------------------|
| 26.1.68 | 2.3 - 2.8 mm |
| 14.3.68 | 2.4 - 35.0 mm |
| 2.5.68 | 3.1 - 14.8 mm |

Table 6.7 The size of Eylais sp. nymphochrysalids found on S.falleni in three collections.

The nymphochrysalid is approximately oval and in preserved specimens is flattened. The size is expressed as an area. The width of S.falleni abdomen at the first segment is 2.0 - 2.3 mm.

| Date | <u>S.falleni</u> | | Flightless morph | | <u>S.dorsalis</u> |
|---------|------------------|---------------|------------------|---------|-------------------|
| | Normal morph | | Male | Female | Male and Female |
| 26.1.68 | 0.29 | 0.13 | 0.51 | 0.31 | 1.23 |
| | (0.15) | (± 0.0) | (0.02) | (0.28) | (1.15) |
| 29.2.68 | 0.10 | 0.41 | 0.26 | 0.36 | 0.86 |
| | (± 0.0) | (0.22) | (0.08) | (3.62) | (± 0.0) |
| 14.3.68 | 0.34 | 0.19 | 0.34 | 0.31 | 0.87 |
| | (0.51) | (0.07) | (0.07) | (11.23) | (0.25) |
| 2.5.68 | 0.08 | 0.07 | 0.48 | 0.29 | 0.92 |
| | (± 0.0) | (0.0) | (1.02) | (0.03) | (0.04) |

Table 6.8

The mean number of Eylais sp nympho-chrysalids found on S.falleni and S.dorsalis. The observed and the expected random distribution of mites on the host is compared, χ^2 in brackets. With one degree of freedom and $P=5\%$, $\chi^2 = 3.84$, and $P=0.1\%$, $\chi^2 = 10.83$. In S.falleni more flightless than normal morphs are parasitised, significant at 5% level with t-test.

Male ; Normal morphs.

| No. of mites
per host. | O | E |
|---------------------------|----------|----------|
| 0 | 23 | 23 |
| 1 | 8 | 8 |
| 2 | - | 1 |
| 3 | 1 | - |
| <hr/> n | <hr/> 32 | <hr/> 32 |
| x | 11 | |
| \bar{x} | 0.343 | |

$$\chi^2 = 0.51$$

Male ; Flightless morphs

| No. of mites
per host. | O | E |
|---------------------------|-----------|-----------|
| 0 | 71 | 72 |
| 1 | 27 | 24 |
| 2 | 2 | 4 |
| 3 | 1 | - |
| <hr/> n | <hr/> 101 | <hr/> 100 |
| x | 34 | |
| \bar{x} | 0.336 | |

$$\chi^2 = 0.070$$

Female ; Normal morphs

| No. of mites
per host. | O | E |
|---------------------------|----------|----------|
| 0 | 54 | 53 |
| 1 | 8 | 10 |
| 2 | 2 | 1 |
| 3 | - | - |
| <hr/> n | <hr/> 64 | <hr/> 64 |
| x | 12 | |
| \bar{x} | 0.187 | |

$$\chi^2 = 0.075$$

Female ; Flightless morphs

| No. of mites
per host. | O | E |
|---------------------------|-----------|-----------|
| 0 | 276 | 266 |
| 1 | 64 | 83 |
| 2 | 22 | 13 |
| 3 | 2 | 1 |
| <hr/> n | <hr/> 364 | <hr/> 363 |
| x | 114 | |
| \bar{x} | 0.313 | |

$$\chi^2 = 11.23, p < 0.01\%$$

n = total number of hosts.

x = total number of mites.

\bar{x} = mean number of mites per host.

O = observed distribution.

E = Expected distribution.

Table 6.9 A comparison between the observed and expected random distribution of Eylais sp. nymphochrysalids on S. falleni from Swithland reservoir on 14.3.68. The distribution of the mites among the female flightless morphs is significantly non-random.

| Date. | Total number. | State of ovaries. | Hydracarina nymphochrysalids. - Genus and number per corixid. |
|---------|---------------|-------------------|--|
| 2.5.68 | 76 ♀ | 20 (I) | - { 1 with no mites
18 with mites - 13 with 1 large <u>Eylais</u> . |
| | | 1 (IV) | - no mites 2 with 2 large <u>Eylais</u> . |
| | | 55 (V) | - no mites 1 with 1 medium <u>Eylais</u> . |
| | | | 1 with 1 large <u>Hydrachna</u> on leg. |
| | | | 1 with 1 medium <u>Hydrachna</u> on leg. |
| 31.5.68 | 80 ♀ | 1 (I) | - 1 with 1 large <u>Eylais</u> . |
| | | 1 (II) | - 1 with 1 skin of <u>Eylais</u> . |
| | | 78 (V) | - 6 with 1 skin of <u>Eylais</u> . |
| | | | 1 with 1 small <u>Eylais</u> . |
| | | | 2 with 1 medium <u>Eylais</u> . |
| | | | 1 with 1 medium and 1 small <u>Eylais</u> . |
| | | | 3 with <u>Eylais</u> mite larvae. |

Table 6.10

S. falleni from two collections in Swithland Reservoir, showing the stage of development of the ovaries and the infection by Hydracarina of each corixid.

See section 6.32 for stages of ovary development; 0. teneral stage to V ovary with mature eggs.

SECTION 7

Discussion

One of the most important features in the ecology of the Leicester-shire corixids is their food and feeding mechanism. The results of this investigation support the view of Zwart (1965) that the species of the sub-family Corixinae, the group on which this study has concentrated, are predators. They do not depend mainly on detritus and algae as supposed by most other authors.

A close examination of the previous work on the group showed that in all cases where species of the sub-family had been kept successfully in the laboratory, other animals were available as food for corixids. These animals were either the only food available (Hale 1922) or were present in the detritus and silt of the aquarium (Hungerford 1919). Some of the authors who believed that corixids were primarily detritus feeders, actually described corixids catching and feeding on live aquatic animals, but they did not recognize the significance of this (Sutton 1951 and Benwitz 1956a). The present work has shown that not only are corixids predaceous, but a particular species is adapted for catching living animals in several ways. It can catch free swimming animals, ranging in size from minute copepods to large Cladocera, and it will search in the detritus for living animals. It can also find and feed on dead animals in the silt and debris, and even feed on its own eggs. Corixids will feed on algae but only where it is concentrated.

The reality of the predaceous habit is borne out by detailed observation of those parts of the head and forelimbs involved in feeding. The whole general arrangement and fine structure are adapted for feeding

on animals, either free in the water or concealed in the detritus.

These are not structures that would be expected for merely scooping up algae and silt.

In the forelimb, the long coxa which remains within the air bubble, and the long femur, support and give mobility to the tibia and tarsus. These two terminal segments, which are sometimes fused together, can be extended away from the head and be flexed so that they can brush down the front of the head in feeding and cleaning behaviour. The tarsus has a slender claw and two rows of long bristles, the upper and lower paleal bristles which form a net for catching smallswimming animals. The bristles of the lower paleal row are more numerous than the upper paleal row and much stronger, an adaptation for digging and scraping in the search for small animals in the detritus. There are also special structures on the tarsus for the manipulation of the small organisms on the rostrum to bring them to the labial orifice. These manipulative devices are the palm, with the upper row of short bristles and inner palm bristles and the basal bristle and the serrated inner basal edge of the claw. Helping to hold the organism on the short broad rostrum are the long dense bristles round the edge of the third labial segment and on the lateral edge of the anteclypeus, also the long tactile bristles on the head capsule. The dense group of bristles of the fourth labial segment forms a shelf below the labial orifice against which small food objects can be held. On the anterior surface of both labial segments are numerous sense organs, probably chemoreceptors (Benwitz 1956a), probably for the assessment of the collected food material.

The most significant adaptation of the corixid head for feeding on small animals is the short, broad, rostrum with the labial orifice opening on to this platform. The prey can be moved around on this flat surface by the manipulative devices at the terminal end of the fore tarsus and held over the labial orifice whilst the stylets are inserted into the prey. This is in contrast to the other aquatic Heteroptera, where the prey is held by the forelimbs and the mobile tip of the long rostrum searches over the prey for a suitable place for the insertion of the stylets. Also, in these Heteroptera, the maxillary stylets penetrate a long way into their large prey. The mandibular stylets are anchoring organs.

The simplicity of stylet structure, compared with other Heteroptera, is another argument used to support the view that corixids are algal and detrital feeders (Elson 1937, Quadri 1951, Sutton 1951 and others). The maxillary stylets' simple and unique mechanism for holding together and sealing the food and saliva channels is directly due to the shortness of the stylets, the small distance they protrude through the labial orifice, and because they do not bend. The maxillary stylets of corixids lack the long distal spines found in the stylets of other Heteroptera; if, as previously suggested, these spines act as a filter, their absence in corixids may be associated with the possession of a masticatory apparatus in the food pump. The only feature of the corixid stylets obviously associated directly with feeding on small organisms is the short distance which the stylets protrude from the labial orifice.

The presence of a complex masticatory apparatus in the food pump

of Corixids is used as another argument that corixids are detrital, and algal feeders (Griffith 1945, Sutton 1951, China 1955), but these workers have ignored the presence of complex masticatory and filtering devices in other families of the Hydrocorisa which are undoubtedly carnivorous, the Notonectidae, Naucoridae, Gelastocoridae, and Ochteridae (Geise 1883, Sutton 1951, and Parsons 1966). It is peculiar that such devices are found in so many aquatic and littoral Heteroptera, while a food pump masticatory or filtering device is only known from one terrestrial heteropteran, the phytophagous bug, Coridius janus (Fabr.) (Dinidoridae), (Rastogi 1965).

The shortening of the corixid head associated with the habit of holding the prey on the head and rostrum, has resulted in a few peculiarities of the food pump, notably the compressed transition from the maxillary food channel to the food pump, and the relationship of the food pump dilator muscles to the frontal ganglion. These peculiarities do not, therefore, provide evidence for the food of the corixids.

The versatility of the feeding mechanism of most corixids is emphasized by the different specializations found in a few species for digging (e.g. Neocorixa) and for catching swimming animals (e.g. Cymatia). These species also have a few structural peculiarities in common, which are adaptations for feeding on larger prey than the prey of other corixids of ^{the} same size.

In the Leicestershire Corixinae, there is little variation in the external and internal head and forelimb structures which are associated with feeding. The most extreme modifications in this group are found

in Arctocorisa germari which shows some external structural adaptations for catching large swimming animals. Differences between most species are restricted to minor details of unknown significance, for example, the variation in the density of bristles on the front of the head capsule, the length and density of the inner palm bristles. There are, of course, the modifications to the feeding structures in the males of each species, which, presumably, reduce the efficiency of this sex to find food. The males do not, however, have the burden of producing large quantities of eggs.

The adult corixids vary in size from 4 mm. long, e.g. Hesperocorixa castanea, to 13 mm. long, e.g. Corixa punctata, and there is an even greater size range amongst the nymphs of each species (Griffith 1945 and Sutton 1947). This wide size range is of particular significance in predators with the same type of feeding structure, because a particular predator is adapted structurally to feed on a particular size of prey (Holling 1964). If this applies to the corixids, then competition is reduced between different size groups feeding in the same area. The difference in size between the two Cymatia species, which feed only on swimming animals, may be why they are able to live in the same habitat, e.g. Kilby bridge pond (Section 6.2). It is also significant that the males of many species of corixid are smaller than the females. This probably reduces intra-specific competition for food, and increases the efficiency of the species in exploiting the available food resources.

While the species of the sub-family Corixinae were observed to feed

by both catching free swimming animals, and by searching through the detritus, some species showed^a tendency to adopt some particular method of feeding, for example, Sigara falleni was the species most often seen running the rostrum along plant stems. These behavioural differences also reduce competition between species living in the same habitat. Similar differences in behaviour between structurally similar species have been found for example in warblers (MacArthur 1958) and titmice (Betts 1955).

Some corixid species are adapted to extreme climatological, physical or chemical conditions. Callicorixa wollastoni and Arctocorisa carinata, for example, are found at high altitudes and northerly latitudes (Brown 1945). Corixid species have varying tolerance to salinity (Claus 1937, Lindberg 1948, and Scudder 1965). Sigara lugubris and S. stagnalis are British species characteristic of saline waters, though Sigara lateralis and S. dorsalis are among the Leicestershire species which are tolerant of low salinity (Lindberg 1948). Some species, for example Hesperocorixa castanea are found only in habitats with a low pH. (Macan 1938), and other species are associated with base-deficient waters, e.g. Sigara distincta (Macan 1954). These adaptations to extreme conditions suggest that some species are better able to live in the less extreme conditions found in Leicestershire ponds than other species.

In both oligotrophic lakes and tarns, there is a succession of corixid species associated with the increasing organic content of the substratum, that is, from a sandy and rocky shore to fens or bogs. (Macan 1954). This association of species with the organic content of

the substratum may only be coincidental, and that other features of the environment, which are reflected in the organic content of the substrata, are the real factors for the corixid species present. The exposure to wave action, plant life present and the nature of the substratum (that is particle size and type of plant litter) may well be the factors responsible for the species of corixid present. These factors all affect the type and abundance of animal life in the substratum, encrusting plant stems and the free swimming animals.

Micronecta poweri is found in exposed areas in lakes and rivers where there is a low percentage of organic matter in the substratum (Macan 1954). These places are characterized by a substratum of silt and limited plant growth. In one Leicestershire stream (section 6.2), the insect was abundant, although the environment was highly organic due to pollution by cattle. In a subsequent year, when there were no cattle present to trample the habitat, there was a growth of plants and Micronecta had disappeared.

Sigara falleni, one of the species in Macan's succession leading to corixids inhabiting fen pools, is found in habitats containing plants and areas of shallow open water. Another species in this succession, Hesperocorixa linnei, is found in habitats where there is an accumulation of plant material and emergent vegetation.

Pond species common in Leicestershire also have similar kinds of habitat preferences (section 6.2), for example, Sigara nigrolineata is found mainly in shallow plant-free areas, and Corixa punctata is associated with deeper water, often with dense vegetation.

In most Leicestershire ponds, several species of the sub-family occur together, and it is noticeable that there is usually a size pattern, Corixa punctata, a large species, at least one medium sized species, for example, Sigara dorsalis, S. falleni or Hesperocorixa sahlbergi, and at least one small species, for example, Sigara nigrolineata or S. lateralis (table A.2).

This size differences between species within one pond may, as previously suggested, help to reduce competition for food; but perhaps more important in reducing competition between the species, is their tendency to feed in different areas of the pond. Similarly, closely related species of warbler (MacArthur 1958) and titmice (Betts 1955) have been found to feed mainly in different parts of the same habitat and mainly on different organisms.

Two of the larger pond species, Corixa punctata and Hesperocorixa sahlbergi, show adaptations to the impermanence of their habitat, which also helps to reduce competition between them and the other species in the same habitat. The embryonic and nymphal development of the larger species takes longer than for small species under the same conditions (section 6.33 and Delsarte 1948), but both C. punctata and H. sahlbergi start ovarian development and lay eggs much earlier in the winter than the other smaller pond species, so that there is more time for development to be completed. These species are able to take advantage of the fluctuations of the water temperature above the threshold temperature for embryonic development, which is lower in the larger than in the smaller species. The adults of both C. punctata and H. sahlbergi are feeding in the winter at a time when other species are not, and the

nymphs are active before those of other species, so competition between these and other species in the habitat is reduced.

On the other hand, if a habitat is drying up, the smaller species with their higher rate of development, are better able to reach the post teneral stage and fly away before conditions become too difficult.

There is a reduction of the alary apparatus in all groups of aquatic insects, which suggests that it is advantageous, though few species of corixid are almost entirely flightless, e.g. Cymatia. No difference between flight muscle morphs in natural populations has been found in survival in winter, overall longevity and the onset and rate of ovarian growth in the spring (Young 1965c). He did find, however, that, under severe laboratory conditions, the flightless morph survived longer than the normal morph when starved, and that the females laid a greater number of eggs, suggesting that the flightless morph has some physiological advantage over the normal morph. Flightlessness also has the advantage of preventing the insects from leaving a suitable habitat in the obligatory spring migration. Though, of course, flightlessness does reduce the chance of a species finding new habitats. Flightlessness can be seen as an adaptation to favourable stable habitats and a large percentage of flightless insects in a population indicates that the conditions are close to the 'preferred' habitat of the species (Young 1965c). The converse, however, is not true for those species whose 'preferred' habitat tends to be unstable, for example, Corixa punctata and Hesperocorixa sahlbergi. Two of the small species, 'Sigara nigrolineata and S. lateralis, often, in temporary habitats, are both

able to produce eggs before developing flight muscles and then are able to grow flight muscles if conditions deteriorate (Young 1965c). These species are able to respond rapidly to changing circumstances. The large proportion of corixids able to fly in nearly all species reflects the general instability of the corixid habitat in Leicestershire, though the large populations present in many freshwater bodies shows that the different species are able to take advantage of favourable conditions.

The flying corixid cannot apparently select a favourable habitat from the air, but they will readily leave an unfavourable one (section 6.35). New habitats are rapidly colonized (Appendix), and species also respond rapidly to changes in older ponds. For example, the appearance and subsequent size of population of both species of Cymatia, a group in which flying morphs are rare, following the spread of Chara in the shallow water of Kilby bridge pond.

The efficiency of a population is increased if all the females can be inseminated by fewer than an equal number of males. An example of this was found in Swithland reservoir where both species in a large population of Sigara falleni and S. dorsalis had fewer males than females.

The efficiency of a population is also increased if the males successfully find or attract the females. The males of several species of British corixid can produce sounds which are part of their reproductive behaviour (section 2.23). Chemical attractants may also be used.

Both physical and chemical cleaning mechanisms appear to be important in corixids (sections 3.72 and 4.55). Another large gland, the metasternal gland, also produces a secretion with probable fungicidal and

bacteri~~cid~~idal properties (Pinder and Staddon 1965). It is possible that those species able to live in the more productive habitats, are also better able to keep clean and therefore feed efficiently than other species. The smooth stream-lined shape of corixid and the presence of the air bubble covering a large part of the under surface (section 2.31) aids the cleaning process.

A variety of parasites, internal and external, ^{is} are found on corixids (table 6.2). The effect of these on the insect is not usually known. Infection with gregarine protozoa does not appear to have any obvious ill effects (Crisp 1962b), but Nematodes and Hydracarina reduce the fecundity of the female corixid (section 6.4 and Crisp 1959). Corixid species are differentially infected by hydrachnids and because of the effect on the fecundity of the corixid the competition between two species in a habitat is affected.

This work has shown that several species of the structurally similar Corixinae, are able to live successfully in the same fresh water body by using the resources of the habitat in different ways.

S E C T I O N 8

Summary.

1. Corixids are frequently found in large numbers, often with several species occupying the same habitat. This thesis is concerned with the problem of how competition between structurally similar animals is reduced, by reason of differences in the food and feeding mechanism as well as differences in behaviour, life cycle and habitat preference.

2. Most previous workers have assumed that corixids are algal and detritus feeders, but, in fact, they are basically predators of very small animals. This is shown by a close study of the head and forelimbs of species from five sub-families and the function of these structures in feeding. It is also shown by comparison with the feeding behaviour and structures of known predators.

Notonecta and Nepa.

3. In the fore-tarsus, the upper and lower paleal rows of long bristles and the long slender claw form a net for catching small swimming animals. The bristles of the lower paleal row are stronger and more numerous than those of the upper paleal row, and are used for scraping and digging up animals and concentrations of algae.

4. The palm, the serrated basal inner edge of the claw and its basal bristle manipulate small organisms on the rostrum.

5. The numerous long bristles surrounding the flat anterior surface of the short, wide rostrum, help to prevent the escape of small animals. They are held over the labial orifice and against a 'shelf' formed by bristles of the fourth labial segment.

6. Organisms are brought by the forelimb to the head and passed over the rostrum where they are assessed by numerous chemoreceptors on the third and fourth labial segments.

7. The basic corixid pattern is modified for feeding on large swimming animals in Cymatia, Glaenocorisa, and Arctocorisa germari. It is also modified for digging up large animals in Neocorixa and Diaprepocoris barycephala.

8. A comparison between Corixids and Notonecta and Nepa shows that the short and simple corixid maxillary stylets have a unique interlocking and sealing mechanism involving the cuticular protein, resilin. There is a wide maxillary food channel and a very narrow saliva channel which is associated with the small saliva pump.

9. The prey of both Corixa and the acknowledged carnivore, Notonecta is digested externally and the partly digested material is ingested through the food channel of the maxillary stylets.

10. The labial groove in which the stylets lie can be sealed when the stylets are withdrawn completely into it or protrude through the labial orifice and so reduce inflow of water.

11. In Corixids, the junction between the maxillary food channel and the food pump is very compressed compared with the arrangement in Notonecta and several functional regions overlap.

12. The food pump of corixids, like that of Notonecta, can be divided into three regions, but, unlike Notonecta, the food pump is half pharyngeal and the complex middle region in corixids has only a masticatory function. The posterior region of the food pump in

Diaprepocoris is long like that of Notonecta, but this region is short in other corixids.

13. The method of functioning proposed for the middle region of the food pump is based on a consideration of the properties of the component cuticular elements.

14. The stylets of Cymatia and Neocorixa and the middle region of the food pump of Cymatia show modifications for feeding on large animals.

15. Some anatomical features of the head and forelimb show an evolutionary sequence from Diaprepocorixinae through the other sub-families to the Corixinae. For example, the food pump and clypeoloral cleft; and the claw and pegs of the male tarsus.

16. The fresh water habitats of Leicestershire, in particular the commonest habitat, the ponds, show considerable seasonal variation in the plant life and water level, as well as changes caused by trampling and pollution by cattle.

17. The fluctuations of the water temperature in ponds is much greater in the summer than in the winter, and on a sunny summer's day, there is considerable variation of the water temperature within the pond, with a maximum temperature of about 25 to 32 degrees centigrade in the very shallow water.

18. The distribution of the Leicestershire corixids is related to factors such as the depth of water, the type of substratum, and the form of the plants present, as well as animal pollution, and pH. All these factors affect the food of corixids, that is, the free swimming animals and the animals encrusting plants and in the detritus.

19. A large population of Sigara falleni with S.dorsalis present in smaller numbers had, for at least two years, fewer males than females instead of the usual 1:1 sex ratio..

20. Corixa punctata and Hesperocorixa sahlbergi, two of the larger species inhabiting ponds, start ovarian development and egg-laying in the winter at least a month earlier than other corixids.

21. The rate of embryonic development is slower in larger species than smaller species, but the threshold temperature is lowest in large corixids.

22. Observations on emmigration and immigration showed that, although corixids may enter an unfavourable habitat, they will rapidly leave if temperature conditions are still suitable for emmigration.

23. Flight muscle polymorphism was found in two species, Hesperocorixa castanea and Callicorixa praeusta, in which this condition had not been previously described.

24. The ectoparasitic Hydracarine, Eylais, infected the overwintering adults of Sigara dorsalis more severely than S.falleni in the same population. In S.falleni, more mites infect the flightless morph than the normal morph. The mite reduces the fecundity of the female corixids by delaying ovary development at Stage I, while it is on the host.

25. Some species are more efficient than others because of, for example, fewer males than females, and a higher proportion of flightless individuals in a population.

26. It is concluded that there is very little variation in the

feeding structures of the species of the subfamily, Corixinae, found in Leicestershire, and that competition between species in the same water body is reduced by:

- (a) differences in size of the corixids
- (b) differences in feeding behaviour and a tendency for species to feed in different areas of the habitat
- (c) differences in the occurrence and duration of ovarian, embryonic, and nymphal development.

SUMMARY

Corixids are found abundantly in freshwater habitats, usually several species living together. The competition between these species was investigated.

Corixids are generally believed to be algal and detritus feeders, but are shown to be predators. Observation of feeding behaviour and examination of feeding structures of British and foreign species representing five of the six subfamilies have shown that most corixids feed on small swimming animals and animals dug and scraped up from detritus. Some species, however, are specialised for feeding only on large swimming animals, e.g. Cymatia or only by digging up animals, e.g. Neocorixa. In contrast to other predatory aquatic heteroptera, the small prey of corixids is held on the short, wide rostrum and over the labial orifice. The short, simple stylets have a unique interlocking and sealing mechanism involving the cuticular protein resilin. A mode of functioning is suggested for the foodpump and the significance of the structural variation is discussed.

The freshwater habitats of Leicestershire, and in particular ponds, the commonest habitat, show considerable seasonal variation in the plant life and water level, as well

as changes caused by trampling and pollution by cattle.

An investigation into the fluctuations of water temperature in ponds showed that for example on a sunny summer's day 25 to 30 degrees centigrade is reached in very shallow water.

Competition between the closely related and structurally similar species of the corixinae inhabiting the same water body is reduced by differences in size and therefore in size of prey, differences in feeding behaviour and the areas of the habitat occupied and by variation in the occurrence and duration of ovarian, embryonic and nymphal development.

Some corixid populations may be more efficient than others because of a greater number of females than males, or a larger proportion of flightless individuals. Some species are more efficient because they are more resistant to attack by the ectoparasitic *Hydrocarina* which is shown to reduce the fecundity of the over wintering females.

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ABBREVIATIONS USED IN THE FIGURES OF THE CORIXID HEAD

| | |
|----------------|--|
| A | antenna |
| AC | anteclypeus |
| AC' | anteriormost part of anteclypeus |
| AF | anterior region of food pump |
| ASO | anterior epipharyngeal sense organ |
| CG | cephalic gland (maxillary gland) |
| CGO | cephalic gland (maxillary gland) orifice |
| CGN | cerebral ganglion |
| CMP | circular muscle of pharynx - clypeolateral cleft |
| DP | pharynx dilator muscle |
| E | compound eye |
| EP | epipharynx |
| EPL | epipharyngeal plate |
| ET | epipharyngeal teeth |
| F | frons |
| FC | food channel |
| FG | frontal ganglia |
| FO | occipital foramina |
| G | gena |
| GN | supra-oesophageal ganglion |
| GR | groove |
| HE | thickened line of union |
| HP | hypopharynx |
| HR | hypopharyngeal ridges |
| HW | hypopharynx wing |
| HWG | hypopharynx wing gland |
| L1, 2, 3 and 4 | labium segments 1, 2, 3 and 4 |
| LA | labium abductor muscle |
| LB | labrum |
| ID | labium dilator muscle |
| LG | labial groove |
| LGL | labial gland |
| IMX | left maxilla |
| LO | labial orifice |
| IOD | labial orifice dilator muscle |
| LOL | labial orifice lever |
| LP | loral plate |
| IR | longitudinal ridge of epipharynx |
| IS | labial shaft |
| M1, 2, 3 and 4 | dilator muscles of food pump, groups 1, 2, 3 and 4 |
| MA | mandibular articulation |
| MD | mandible |
| MDP | mandibular protractor muscle |
| MF | middle region of food pump |
| MG | median groove |
| MX | maxilla |
| MXP | maxillary protractor muscle |

| | |
|-------------|---|
| MXPL | maxillary plate |
| N | notum of prothorax |
| O | occiput |
| PC | postclypeus |
| EP | posterior food pump |
| PH | pharynx |
| PR | process |
| PSO | posterior epipharyngeal sense organ |
| R | ridge |
| RMX | right maxilla |
| SC | saliva channel |
| SD | saliva duct |
| SGN | suboesophageal and prothoracic ganglion |
| SO | subocciput |
| SP | saliva pump |
| SPD | saliva pump dilator muscle |
| ST | sternite of prothorax |
| T1, 2 and 3 | tendon of food pump dilator muscles of muscle groups 1, 2 and 3 |
| TF | transverse fold of epipharynx |
| TG | transverse groove of epipharynx |
| TR and | |
| TRE | transverse ridge of epipharynx |
| TRH | transverse ridge of hypopharynx |
| V | vertex |
| X | distal end of floor of labial groove |
| (1) | anterior zone of epipharynx in middle region of food pump |
| (2) | middle zone of epipharynx in middle region of food |
| (3) | posterior zone of epipharynx in middle region of food |

ABBREVIATIONS USED IN THE FIGURES OF THE CORIXID FORELIMB

| | |
|-----|--|
| B | basal fine bristles on femur |
| BC | basal bristle of claw |
| C | claw |
| CO | comb of strong bristles on tibia |
| CS | serrations at base of claw |
| D | diagonal row of strong bristles on femur |
| F | femur |
| IPM | inner palm bristles |
| LP | lower paleal bristles |
| TA | tarsus |
| TI | tibia |
| TR | trochanter |
| UP | upper paleal bristles |
| UPM | upper palm bristles |

A P P E N D I X

The Construction and Subsequent History of Ponds at Normanton House Farm,
Leicestershire.

so as to

Three ponds were dug, resemble the rectangular field pond common in Leicestershire. The ponds were constructed in order that; first, temperature recorders could be set up safe from interference, and in a body of water of known dimensions; second, large stocks of common corixid species could be kept so that the relations between species and the life cycles of the various species could be studied; third, the distribution of the corixid species in relation to depth and to temperature changes could be observed.

The ponds were constructed in a small field (0.32 hectares), 76 metres above sea level, on Normanton House Farm near Earl Shilton, Leicestershire (grid reference SP/485987). The shape of the field and the position of the ponds are shown in fig. A1. The field is at the foot of a steeper north facing slope and slopes slightly towards the stream. The neighbouring field is separated by an embankment about a metre high, with a hedge. The track and the hedge are also raised up on a causeway above the two adjacent fields. A hedge and ditch form the opposite (north-east) boundary. A large willow tree on the south side of the stream and other trees and shrubs on both sides of the stream give shelter to the field. On the southern edge of the field a small beech tree restricts sun from reaching parts of the ponds during the winter.

A small pond, A. (3 x 4 metres) was dug in July 1966 to see if the

subsoil, yellow clay with some rounded flints overlying a blue clay, would hold water. This pond is about half a metre deep at its maximum with a shallower region at its southern end.

The three large ponds, B, C, and D, dug in November 1966, each covering an area of 120 sq. metres (5 x 24 M.) which was considered large enough to hold sufficient animals to allow regular sampling. Some top soil was put into ponds B and C to create eutrophic conditions.

Two field drains were found, one crossing all three ponds, and, although the pipes were blocked, pond C continually leaked into pond B. The ponds, when full of water, were shorter than planned, and because of the wedge-shaped profile, the length varied with changes in the water level. Changes in the water level in each pond were recorded weekly, by noting the level of the water surface on centimetre marked posts. The pattern of water level changes showed significant differences between the two years, 1967 and 1968. The period of low water level occurring in September and June respectively, table A.1.

Thermographs were arranged in 1967 to record water temperatures in ponds B and D; the records are described and discussed in section 5.4.

An air temperature recorder was also used in 1968.

The water in all ponds contained a lot of suspended matter, particularly after rain. It was less cloudy during the summer of 1967, but pond B became rather black. The water of all ponds was clear for most of the following winter, spring, and summer, though after the flooding on 11 July 1968, pond D became cloudy.

Filamentous algae grew rapidly in all four ponds, forming the main

plant life, during 1967. In the autumn, a fresh growth of filamentous algae persisted throughout the winter, following spring and summer.

During 1967, grass extended from the edges of pond A into the water. In 1968, Juncus articulatus and Glyceria fluitans were present at the shallow end, and Glyceria fluitans was growing on the edge at the deep end. During the early part of the summer of 1968, the filamentous algae covered much of the ponds surface, but it died down later in the summer.

In pond B, a small plant of Potamogeton natans and several small growths of Callitriche were present in 1967, but in the following year, both species increased rapidly to cover almost the whole of the water surface by June 1968. At the shallow end of this pond grass, Juncus inflexus and Phalaris arundinacea were growing, and Juncus articulatus along the edge at the deep end.

In pond C, filamentous algae formed the main vegetation, and grew only on the bottom of the pond. In the summer of 1968, a few plants of Callitriche were present.

In pond D, filamentous algae again formed the main plant life, which, in the summer of 1968, formed an almost complete surface covering. Part of this cover was cleared temporarily, 12 August to October, from the deep end, while certain temperature measurements were being made (section 5.4). Some grass grew along the edge of the water and in the winter and spring, long, dead grasses bent over into the water.

Some corixid species were deliberately introduced and other freshwater animals accidentally came with them into ponds B, C, and D (table

A.2). The fauna of all the ponds was recorded, but of the insects, only the aquatic Hemiptera were identified to the species level.

Common frogs, Rana temporaria L. were seen near and in the ponds during both 1967 and 1968. In 1967, frogs spawned in pond C, and in 1968, in both ponds C and D. In 1968, metamorphosis was achieved by mid-June. Several smooth newts, Triturus vulgaris L. were seen in pond D in 1968, and numerous newt tadpoles were found from June onwards in ponds A and D. Three-spined sticklebacks, Gasterosteus aculeatus L. accidentally introduced into pond B with the corixids in March 1967 bred both years, increasing greatly in numbers. Some entered pond C through a temporary opening in the connecting field drain, and bred there in 1968. After the floods of 1968, sticklebacks also appeared in pond D.

The invertebrate fauna of pond A is of particular interest because no animals were introduced into it. The corixid fauna is listed in table A.2. The other aquatic Hemiptera Notonecta glauca and N. maculeata bred in 1967 and 1968. The Gerridae, (Hemiptera) and many beetles, including Gyrinus were numerous in both years. Dytiscus sp. was also present in small numbers. Ephemeropteran nymphs and dipterous larvae were also numerous, trichopteran larvae and odonatan (Zygopteran and Anisopteran) nymphs were present, but in smaller numbers. Cladocera and Copepods were also numerous but neither Asellus and Gammarus or any freshwater molluscs were found in this pond.

The insect fauna of the other three ponds was similar to pond A as described above, except that the Ephemeroptera nymphs were fewer in ponds B and C where the fish were present. Nepa (Hemiptera) was only found in pond B and was probably accidentally introduced.

The 14 species of corixids in the ponds, are shown in the table A.2. Those which were introduced and those which are known to have bred in the ponds, are indicated. The corixids were sampled regularly in the winter and spring of 1967/8 as part of an investigation into ovarian development (section 6.32).

The distribution of Notonecta and corixids in the winter was particularly interesting. All the species swam when disturbed, but showed a distinct pattern of distribution. The Notonecta species were found in the dead grass and other vegetation leaning into the water. Notonecta eggs were found in this situation. Corixa punctata was distributed in deeper water, usually in or around the Callitriche in pond C. The eggs of this species appear early in the year, from February onwards, and are laid on any vegetation or dead plant material available. During a dry spring, some of these eggs were exposed when the water level dropped. The smaller corixids, S.falleni, S.dorsalis, S.nigrolineata, and S.lateralis were mainly among the filamentous algae found in very shallow water. In spring, S.dorsalis and S.falleni in pond D, are found at the deep end and at the sides of the pond.

Assellus aquaticus was also accidentally introduced into pond B, and was also present in small numbers in ponds C and D. After the flood in July 1968, ^{ma}Gammarus pulex was found in pond B.

The molluses, Limnaea pereger, Planorbis spp. and Sphaerium were particularly numerous in pond B, and were also present in pond C.

| | Pond
A | Pond
B | Pond
C | Pond
D |
|---------------|-----------|-----------|-----------|-----------|
| January 1967 | 54 | 30 | 40 | 90 |
| May | 54 | 30 | 40 | 90 |
| June | 46 | 30 | 35 | 85 |
| September | 28 | 20 | 20 | 52 |
| October | 41 | 30 | 35 | 80 |
| November | 50 | 30 | 40 | 90 |
| December | 42 | 29 | 40 | 73 |
| February 1968 | 52 | 30 | 38 | 79 |
| March | 48 | 29 | 38 | 76 |
| April | 40 | 29 | 32 | 67 |
| June | 32 | 22 | 21 | 56 |
| August | 40 | 29 | 33 | 70 |


Table A.1; fluctuations of water level in 4 ponds at Normanton House Farm. The water level between January and May 1967 was lower than that recorded for the two months. The water level dropped slowly after 11 July 1968 when the stream flooded into ponds B, C, and D. Unit of depth, centimetres.

| Species | Pond A | Pond B | Pond C | Pond D |
|-----------------------|--------|--------|--------|--------|
| <u>C.punctata</u> | B | I,B | X | B |
| <u>C.dentipies</u> | - | X | - | - |
| <u>H.sahlbergi</u> | B | I,B | B | X |
| <u>H.linnei</u> | - | X | - | - |
| <u>H.moesta</u> | - | X | - | - |
| <u>S.dorsalis</u> | - | B | B | B |
| <u>S.falleni</u> | - | I,X | I,X | I,B |
| <u>S.distincta</u> | - | X | X | B |
| <u>S.fossarum</u> | - | - | - | X |
| <u>S.lateralis</u> | X | B | X | B |
| <u>S.nigrolineata</u> | X | B | B | B |
| <u>S.concinna</u> | - | - | X | - |
| <u>S.limitata</u> | - | - | X | X |
| <u>C.praeusta</u> | - | X | X | I,X |

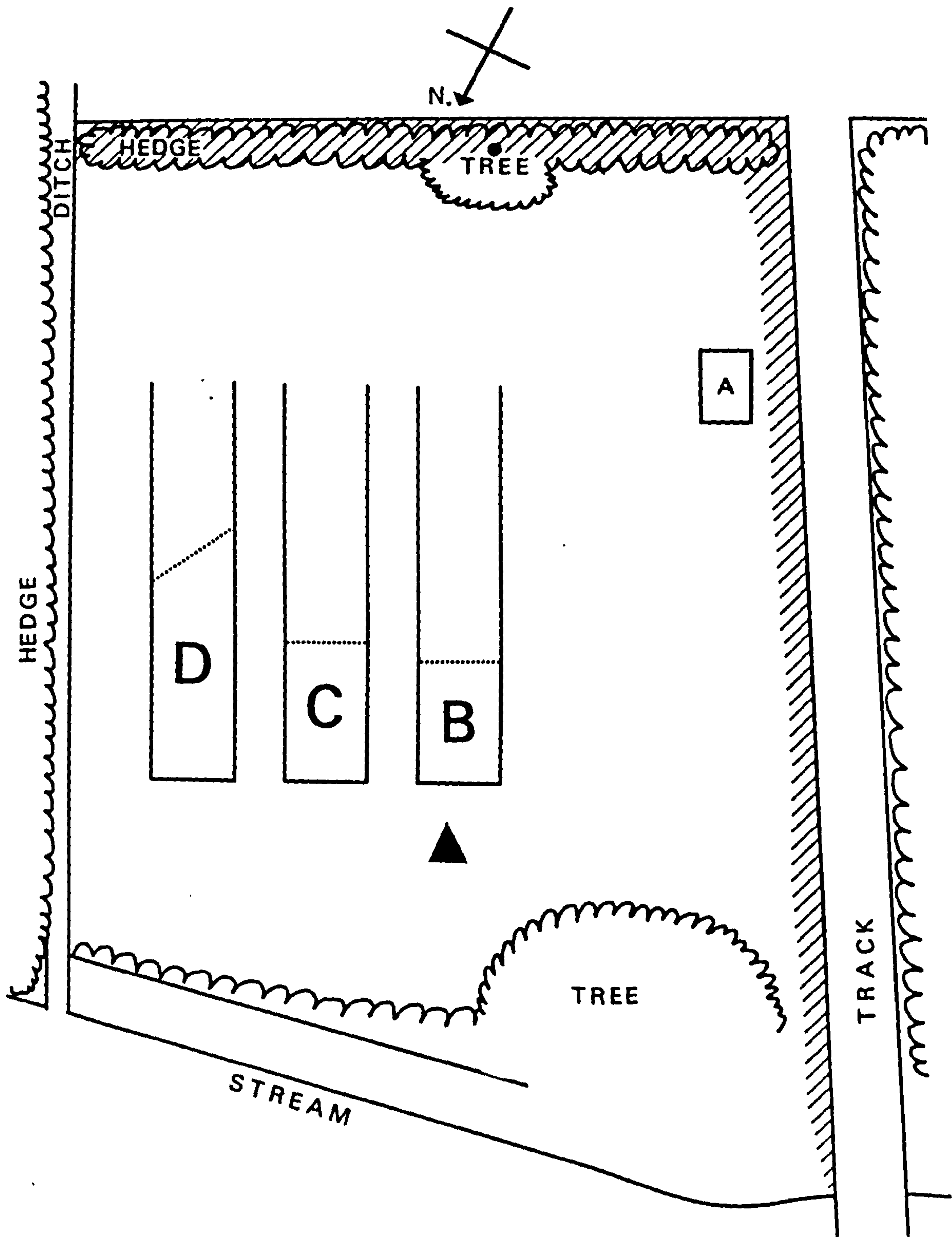
Table A.2. Corixidae found in ponds A, B, C, and D at Normanton House Farm, from their construction in 1966 to summer 1968.

I, species introduced into a pond in large numbers in March 1967;

B, species known to have bred in a pond during 1967.

Fig. A.1; position of ponds A, B, C, and D in a field at Normanton House Farm;  . air thermograph. The ponds, B.C and D. have a wedge-shaped profile, thus the length of each pond depends on the water level. The length and water level of these ponds in the diagram are as follows:-

| | length | water level |
|--------|--------------|-------------|
| Pond B | 7.3 metres | 30 cm. |
| Pond C | 8.5 metres | 35 cm. |
| Pond D | 12-15 metres | 70 cm. |



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