THE ULTRASTRUCTURE OF THE ROSTRAL SENSORY ORGANS OF THE
WATER BUG, CENOCORIXA BIFIDA (HUNGERFORD), (HEMIPTERA).

by

S. ESTHER LO

B. Sc. (General) The University of Hong Kong, 1964

B. Sc. (Special) The University of Hong Kong, 1965

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Zoology

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

June, 1967

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver 8, Canada

Date 29th June, 1967.

Abstract

The sensory organs in the transverse grooves of the dorsal labium of the water bug, Cenocorixa bifida, (Hungerford) (Hemiptera) were studied with the electron microscope. It was found that each sense organ is supplied by a single, bipolar neuron, which, together with its sheath cell, forms a sensory unit. The dendrite of the neuron is modified into various structures along its length; it has a root system, two basal bodies, and an axial filament complex. These structures are characteristic of many mechanoreceptors and chemoreceptors in insects. The sheath cell surrounding the dendrite possesses many characteristic fine structures, such as the desmosomes and the microtubules.

According to their ultrastructure and their location near the mouth opening, it is most likely that these sensory organs are chemoreceptors. The significance of the presence of the ciliary regions in the dendrites of these organs is suggested to be related to the regeneration of the distal portion of the dendrite which may be torn off during the process of moulting. The axial filament complex may also serve as an internal support in the dendrite.

Table of Contents

	page
Abstract	i
List of Diagrams	ii
List of Figures	iii
Introduction	1
Materials and Methods	5
Results	
1. Terminology (a) The Integument	7
(b) The Sensory Unit	9
2. Ultrastructure of the sensory unit	
(a) The soma and axon	14
(b) The root system	14
(c) The basal bodies	15
(d) The ciliary region	16
(e) The sheath cell	17
(f) The neurofilament region	19
(g) The end organ	20
Discussion	23
Summary	39
Literature cited	40
List of symbols used in the figures and diagrams	47
Figures 1A to 14C with explanations	48

List of Diagrams

Diagrams	page
IA Dorsal view of a typical heteropteran head.....	2
IB Dorsal view of the labium of <u>C. bifida</u>	2
IIA & B Distribution of the sensory organs in the rostrum (after Benwitz 1956).....	4
III Diagrammatic longitudinal section through a group of sensory neurons.....	9a
IV Diagrammatic longitudinal and transverse sections through the sensory unit in the epi- and exo- cuticle.....	11
V Diagrammatic longitudinal and transverse sections through the sensory unit in the endocuticle.....	12
VI Diagrammatic longitudinal and transverse sections through the sensory unit in the epidermis.....	13

List of Figures

Figures	page
1A. Cuticular structure of the dorsal labium	48
1B. Cuticular structure of the ventral labium	49
2A. Longitudinal section of a sensory unit in the epidermis	50
2B. Section through a dendrite emerging from the epidermis into the cuticle	51
3A. Section through a group of neurons	52
3B. Section through a group of axons	53
4A. Longitudinal section through the dendrite	54
4B. Section through the rootlet region	55
4C. Transverse section through the rootlets	56
5A & B Transverse sections through the distal basal body	57
5C. Longitudinal section through the proximal basal body	58
5D. Transverse section through the proximal basal body	59
6A. Transverse section through the cilium	60
6B & C Transverse sections through the cilium	61
7A. Section through the nucleus of the sheath cell ..	62
7B. Section through the sheath cell enclosing neurofilaments	63
7C. Section through sheath cell enclosing cilia	63
8. Transverse section through the neurofilaments ...	64
9A. Transverse section showing characteristic structure of the cuticular sheath	65
9B. Longitudinal section showing characteristic structure of the cuticular sheath	66

Figures		page
10A.	Dendrites emerging from epidermis into the endocuticle	67
10B.	Longitudinal section of neurofilaments in endocuticle	68
11A.	Longitudinal section through the terminal portion of the sensory organ	69
11B.	Section showing the structure at the base of the peg	70
11C.	Longitudinal section through the end of the sensory organ	71
11D.	Transverse section through the end organ	71
12A.	Longitudinal section through the end organ	72
12B.	Transverse section through the cuticular sheath.	73
12C.	Transverse section through a labial sensory groove, showing rows of dendrites in the exocuticle	74
13A.	Section through the ciliary region of a sensory unit near the mouth opening	75
13B.	Section through the basal body of a dendrite in the same region	75
14A.	Transverse section through a sense organ made up of a group of three dendrites	76
14B.	Transverse section through a similar type of sense organ	76
14C.	Transverse section through a sense organ made up of a group of five dendrites	77

Acknowledgment

I would like to thank Dr. A.B. Acton for his encouragement and assistance during the course of this study and in the final thesis preparation. Thanks are also extended to Dr. G.G.E. Scudder for his generous supply of living specimens of the water bug, Cenocorixa bifida, and for his advice in this study.

I would also like to express my appreciation and gratitude to Mr. L. Veto for his guidance, advice and suggestions in the techniques in electron microscopy throughout this project.

Introduction

Cenocorixa bifida is a corixid which is truly aquatic all through its life. Most members of the aquatic heteropteran families, or Hydrocorisae, are predacious, possessing raptorial forelegs. However, the corixids differ considerably from the typical Hydrocorisae: they are detritus feeders, ingesting both fluid and particulate matter, their head and mouthparts being modified accordingly.

The mouthparts of insects are composed of three gnathal somites, the mandibular, maxillary and labial segments. In biting insects the jaw-like mandibles and maxillae are paired, while the labium, serving as a lower lip, is unpaired, broad and flat, and formed from the union of two maxilla-like appendages. In the Hemiptera the mouthparts are modified for a fluid diet. The mandibles and maxillae form long, slender, unsegmented stylets. The stylet bundle, which is supported and directed by a highly modified, beak-like labium (Diag. 1A), pierces the tissue of the plant or animal upon which the insects feeds.

The corixid labium is much shortened and broadened, lacking a distinct four-part segmentation. Dorsally it bears a deep, closed stylet groove flanked, in C. bifida, by a series of transverse sclerotized bands and grooves (Diag. 1B).

In the Corixidae the rostrum is densely covered with sensory organs. Weber (1930) was among the first to describe some of these organs. Hsu["] (1937) described the sensory organs in the dorso-lateral labial grooves in greater detail. Benwitz (1956)

Diagram 1A Dorsal view of a typical heteropteran head
(after Parson, 1966).

Four segments (I, II, III, IV) are present,
a median stylet groove (SG) is also present.

Diagram 1B Dorsal view of the labium of C. bifida. The
labium is shortened and broadened, lacking a
distinct 4-part segmentation. Dorsally there
is a deep stylet groove (SG) flanked by a
series of transverse sclerotized bands (TG).
Two fleshy lobes (FL) surround the distal apical
plate (DA).

DIAG. IA

IB

distinguished four or five different sensory organs in the grooves, and ten or more near the protruded stylets and other areas on the rostrum. However, all of the works mentioned above deal only with the terminal portion of the sensory organ in the cuticle of the insect. Because of the limited resolving power of the light microscope, it is difficult to study the structure of the rest of the sensory organ in the epidermis, and hence relate it to the cuticular portion. With the electron microscope it is now possible to study the ultrastructure of the entire sense organ, both cuticular and epidermal regions. Without accurate determination of the structure of the sense organs, little or no progress is possible on the studies of their function.

In the present study, special attention was directed to the sensory organs in the labial grooves. Those in the other areas of the rostrum will be only briefly reviewed. Each transverse band on the dorsal labial surface is in fact a much thickened sclerotized ridge with an associated groove of thin, soft cuticle. Each of these grooves has three to four rows of sensory organs (Diags. IIA & B). Since they are located near the mouth opening, the suggestion of their role as chemoreceptors by Benwitz (1956) is an easily understandable one. However, their orderly arrangement in transverse rows may suggest that they have other functions besides that of chemoreception related to feeding. It was thus intended that by studying the ultrastructure of these sensory organs, it would be possible to add new information to that we already possess and to support or correct earlier interpretations.

Diagram II Distribution of the sensory organs in the
 rostrum (after Benwitz, 1956)

A. Sensory organs around the mouth M, and those
 in the first and second transverse grooves
 (1 & 2) are shown.

B. Sensory organs in one of the transverse
 grooves.

DIAG. IIA

I I B

Materials and Methods

Cenocorixa bifida (Hungerford) was collected from White Lake, in the B.C. interior -- the Green Timbers Plateau. They were transported to the laboratory in one-gallon thermos jugs half full of lake water. They were then kept at 10°C. in constant temperature cabinets until needed. In all cases, specimens were used within three weeks of capture.

The head of the water bug was fixed in 6% glutaraldehyde in phosphate buffer (pH 7.5). This was followed by fixing in OsO₄ (pH 7.3). The fixed material was rinsed in 70% ethanol and dehydrated rapidly with ethanol. It was then embedded in Epon 812 according to the method of Luft (1961). Some heads were also embedded in Araldite. Sections were cut with a Porter-Blum microtome, and stained with uranyl acetate and lead citrate, each for a period of 3-5 minutes. Some sections were cut at a thickness of 0.5 to 1.0 μ , and were studied under the phase contrast microscope.

The main difficulty in studying the rostral sensory organs is in sectioning, since there is little affinity of the cuticles for the embedding medium, and the two always break apart. In studying the rostrum of *C. bifida*, there has been many attempts to overcome this problem: a very hard embedding medium has been used, and also the period of infiltration at lower temperatures has been greatly lengthened. After dehydration and passing through propylene oxide, the tissues were embedded in Epon. These were left at room temperature overnight, and then for another day at 37°C. The tissues were finally transferred to 56°C. until polymerization was complete. However, this procedure did not completely overcome the problem

of separation between cuticle and embedding medium, though the chance of separation was decreased. Carbon-coated grids were used all through the study and they prevented, in most cases, the drifting apart of the already separated cuticle from the embedding medium.

Owing to the separation, it can be easily seen that if hairs or fine projections were present in the insect rostrum, cutting through one of these when no embedding medium surrounds it will be quite impossible. Thus in the following study, only a few sections through the part of the hair-like structures terminating the sense organs were obtained. Interpretation of these few sections, however, gave a clearer picture of the structure of the terminal portion of the sensory organ.

Results

1. Terminology

(a). The integument

Before describing the structure of the sensory organs it is important to clarify the terminology used for the insect integument. According to Lower (1956), the term integument denotes the unicellular layer with its internal limiting membrane and its outer secreted covering. The internal limiting membrane is termed the basement membrane, and the cellular layer is the epidermis or hypodermis. The external secreted part of the integument is the cuticle. The latter can be divided into two principal layers -- an inner, relatively thick, procuticle and a thin outer epicuticle. The procuticle is composed essentially of protein and chitin. The epicuticle does not contain chitin but consists of lipoprotein, polyphenol and wax, and a cement layer (Hackman 1964). Protein in the epicuticle, and sometimes also in the outer layer of the procuticle, is sclerotized, that is, it becomes after each moult hard, dark and insoluble in water. When the outer region of the procuticle becomes sclerotized, the hard, dark layer so formed is known as the exocuticle, and the remaining inner soft portion is known as the endocuticle. The endocuticle is made up of a number of lamellae whose appearance is due to the orderly arrangement of chitin-protein fibrils. However, the endocuticle next to the epidermis has no lamellate structure. Schmidt (1956) called this endocuticle the subcuticular layer and thought of it as a cement holding the cuticle to the cells. But according to Locke (1961) it is more probably newly secreted endocuticle in which fibres are not yet arranged in

order, and thus have a granular appearance under the electron microscope.

The cuticle is not uniform over the entire insect. Various parts of it differ from one another in appearance and in other physical properties. Generally, unsclerotized procuticle and soft cuticles have only two regions, the epicuticle and endocuticle. But in the regions where it is thick and hard, the cuticle shows distinctly three layers, the epi-, exo- and endo-cuticle. The dorsal wall of the labium of C. bifida has the three layers present (Fig. 1A). In this region the exocuticle is thick and homogeneous in appearance, with no evidence of lamellae. Only pore canals and sensory extensions through the cuticle interrupt this layer. This is true of all insects in regions where greater mechanical strength is necessary, for example, areas of the limbs, antennae, furcula, and area in the head capsule. A fully sclerotized exocuticle is absent from the ventral wall of the labium of C. bifida (Fig. 1B).

Below the dorsal labial wall in C. bifida, the epidermis is much thicker than the ventral epidermis of the labium. This thickening of epidermis appears to be associated with the presence of transverse ridges on the dorsal labium. I have also studied with the light microscope the heads of two other corixids Hesperocorixa laevigator and Callicorixa audeni which have sensory grooves on their labial surfaces. Both were found to have a thickened epidermis dorsally. Cymatia americana, which lacks transverse rostral grooves, was also examined by me under the light microscope, and sections show few sensory organs and no thickening of the epidermis, that is, the dorsal epidermis is virtually identical with the ventral rostral epidermis.

DIAG. III A GROUP OF SENSILLA

This examination suggests that the presence of rostral grooves is correlated with the presence of a thickened epidermis. Further, there are more sensory organs present in these insects with rostral grooves.

(b). The sensory unit

Though a number of structures which appear to be sensory are found near the mouth, most of the work which is reported below concerns the sensillae of the transverse labial groove. The reasons for choosing these from the variety available were their preponderance and uniformity of structure.

A detailed description of the ultrastructure of the sensillum will be found below, but to appreciate the general arrangement of the parts, one should refer to Diag. III, which gives only the barest outline. For convenience of description, the sensillum is divided into three regions: (A) the terminal region lying in the exo- and epi-cuticle; (B) the central region lying in the endocuticle; and (C) the epidermal region in the epidermis. A more detailed structure of each of the three regions can be found in Diags. IV, V & VI.

Each sensory unit in the labial groove is made up of a single bipolar neuron with a short distal process and an axon which enters the central nervous system (Diag. III). The cell body or soma, that part of a neuron containing the nucleus and surrounding cytoplasm, lies in the epidermis. It is thus termed a superficial sensory nerve cell, in contrast to the deep-lying cell body and long branching distal process of the higher invertebrates and the vertebrates. The axon is a process of a neuron specialized to distribute or conduct nerve impulses, generally over a considerable

distance (Bullock and Horridge, 1965). The distal process extends out through the cuticle to enter into the terminal cuticular structure. It is termed the dendrite and is specialised for receiving an excitation. Since the nerve cell is itself a receptor, it is also known as a primary sensory neuron.

Along its length the dendrite is differentiated into various regions. The portion of the dendrite lying in the exo- and endo-cuticle has neurofilaments along the whole length (Diags. IV & V). The part of the dendrite lying in the epidermis has four distinguishable regions; a rootlet region, a basal body region, a ciliary region and a neurofilament region (Diag. VI).

Rootlets extend from the proximal end of the basal body down into the cell and end freely in the vicinity of the nucleus (Diag. VI). When examined in longitudinal sections the fibres of the rootlets show prominent cross-striation of definite periodicity. There are two basal bodies, a proximal and a distal one. They are cylindrical structures formed by nine triple outer fibrils. The distal end of the basal body is continuous with the axial filament complex. The latter has nine pairs of peripheral fibrils, and two or more fibrils may be present in the central region. As the cilium enters the open inner end of a tubular cuticular sheath, the peripheral and central fibrils are replaced by numerous neurofilaments. The cell body and the portion of the dendrite in the epidermis are surrounded by additional sheath cells.

The sensory unit terminates in a peg, which is a cuticular specialization. This peg lies in a sunken pit in the transverse groove on the dorsal labium of the insect and surrounds the dendrite of the receptor neuron. The structure of the cuticle where the peg

Diagram IV Diagrammatic longitudinal sections and transverse sections through the distal dendrite in the cuticle. The end organ is composed of a short, stumpy peg, with a modified cuticular base structure. The socket consists of a rim (R) and pad (P) enclosing an inner cylinder of cuticle which in turn surrounds the cuticular sheath. Lamellae of soft cuticle (LS) connect the socket rim to the inner cylinder. (Terminology adopted from Noble-Nesbitt 1963).

DIAG. IV

Diagram V Diagrammatic longitudinal and transverse sections through the sensory unit in the endocuticle. Neurofilaments (NF) are enclosed in the cuticular sheath (CS). Around the sheath, the orderly arrangement of the fibrils in the lamina breaks up and the sheath is surrounded by granules and some longitudinal fibrils (FI). Finger-like projections of the epidermis (F) are present, jutting into the Schmidt layer (SL).

DIAG. V

Diagram VI Diagrammatic longitudinal and transverse sections through the sensory unit in the epidermis.

Transverse sections:

A--through neurofilament region (NE)

B--through ciliary region (CI)

C--through the distal basal body (B)

D--through the root apparatus (RA)

Desmosomes (D) between the plasma membranes of the neuron and the sheath cell (S) are characteristic of this region.

E--through rootlet region (RL)

showing rootlets of the dendrite enclosed in the sheath cell, whose nucleus (NUS) is also shown.

The axon (AX) and the nucleus (NU) of the neuron are also shown in the drawing.

is located is different from the remainder; the dendrite is surrounded by an inner cylinder and an outer rim of cuticle, with a pad in between the two (Diag. IV). The following is a detailed description of the various regions of the sensory unit.

2. Ultrastructure of the sensory unit

(a). The soma and axon

The soma or perikaryon is that part of a neuron containing the nucleus. The cell body is limited by a thin membrane and is surrounded by the sheath cell (Fig. 3A). The cell cytoplasm shows a matrix of low electron density. Usually groups of nerve cell nuclei can be distinguished from the rest of the epidermal cells.

The axons lie in groups below the epidermis. Each axon contains a large number of microtubules, and is ensheathed by interlocking cells (Fig. 3B).

(b). The root system

From the inner end of the basal body, rootlets extend down to near the nucleus of the neuron (Fig. 4A). A root system is found in many invertebrate and vertebrate motile cilia. In all cases they have been observed to have cross striations with a periodicity of 500-700 Å. In *C. bifida* there is a major periodicity of 600-700 Å.

The root region is enclosed in a much folded sheath cell which has a characteristic structure. The apposed cell membranes have septate desmosomes throughout. Islands of cytoplasm surrounded by cell membranes are exceptionally abundant and ^{may} group together to form lamellae (Fig. 4B). These structures of the sheath cell will be described later.

(c). The basal bodies

The distal basal body is a cylindrical structure at the inner end of the cilium (Fig. 4A), about 0.4μ long and 0.2μ in diameter. The wall is composed of nine triple fibrils arranged parallel to its longitudinal axis (Fig. 5A). From the triple fibrils spoke-like structures radiate out (Fig. 5B). It is from the inner end of this basal body that the rootlets arise. At a short distance below their origin, the rootlets surround another cylindrical structure, which closely resembles the distal basal body in size, shape, and structure. No rootlets, however, originate within this cylinder. This, according to Slifer and Sekhon (1964) in their work on the antennal olfactory sense organs of the grasshopper, is the proximal basal body. In longitudinal section (Fig. 5C) electron-dense substances are located outside the cylinder of the proximal basal body, with the rootlets closely surrounding them. In cross section (Fig. 5D) the inner cylinder is surrounded by an outer ring of electron dense material which is in turn encircled by the rootlets.

The two basal bodies are in fact very similar to those in the auditory units in the locust (Gray, 1961). However, instead of the distal and proximal basal bodies, they are termed the ciliary base and the root apparatus respectively, since no triple tubules are found in either structure. Two basal bodies are also found in the antennal sense organs of the milkweed bug (Slifer & Sekhon 1963), but the proximal basal body lies not directly below the distal one but to one side. In the dendrite of C. bifida a distal basal body is evident, but it is difficult to decide whether the term proximal basal body or root apparatus should be used for the second structure below the distal one. Triple fibrils are never found in cross

sections of this region, although it has a very similar structure to the distal basal body in longitudinal section. This will be discussed later.

(d). The ciliary region

The ciliary region is about 1.1μ long and the diameter increases from base to apex. In the axial filament complex one can identify nine peripheral double fibrils, each containing two sub-fibrils. At the base the diameter is approximately 0.2μ and the nine pairs of peripheral fibrils appear to be joined up in a ring of electron dense substance (Figs. 6A & B). Two or more fibrils may occupy the central region of the axial filament complex. It is interesting to note that departure from the usual number of fibrils in cilia and flagella has been reported in many cases, both in vertebrates and invertebrates.

Near the apex of the ciliary region the diameter increases to 0.3μ by the spreading out of the peripheral fibrils (Fig. 6C).

At the junction of the axial filament complex and the distal basal body, the cell membrane of the dendrite is closely applied to the cylinder formed from the peripheral fibrils, so that a structureless region is formed between the plasma membranes of the nerve cell and the surrounding sheath cell. Nearer to the base of the dendrite, the two membranes are apposed to each other with a gap of approximately $75-100\text{\AA}$. Distally, this widens out to the structureless region which, however, is filled with fine granules (Figs. 6A, B & C). The cuticle which forms the cuticular sheath is deposited in this granular region close to the membrane of the sheath cell. At the lower level of the ciliary region, the cuticle is discontinuous, and thus seems to be the region where the cuticular sheath

just begins (Fig. 6B). Higher up in this region, the cuticle is thicker and the wall of the sheath is almost continuous in outline (Fig. 6C). Groups of microtubules are abundant just outside the wall in the cytoplasm of the sheath cell (Figs. 6B & C).

(e). The sheath cell

The soma of the neuron as described above is surrounded by a simple sheath cell, but the dendrites, on the other hand, are bounded by a loosely folded system which may represent the membranes of a single rolled-up sheath cell folded as in vertebrate myelinated nerve, but with many indentations. In Fig. 7A, a single dendrite containing rootlets is wrapped around by a sheath cell. In some cases, two dendrites, both containing cilia or neurofilaments, may be enclosed in a common sheath cell. (Figs. 7A & B).

In sections the membranes are seen to be double. Due to the fact that when the membrane rolls itself around the single nerve the plasma membranes become apposed to form pairs. Each unit membrane shows the characteristic triple layer described by Robertson (1959), that is, two parallel dense lines and a clear intervening layer. Each pair of membranes is separated by a space containing material of higher density than the surrounding cytoplasm of the sheath cell. The relationship between adjacent units of the invaginated membrane is essentially as has been described by Edwards and his co-workers and also by Gray (1961). Similar membrane structure is also found in the peripheral nerves of Tenebrio (Smith, 1960).

Very often the spaces between the adjacent membranes are transversed by fine bars. These are the septate desmosomes first described by Wood (1959) in a study of Hydra. In C. bifida, septate desmosomes are found in great abundance in the rootlet region (Figs.

4B & 4C). They are not only found between the apposed membranes of the sheath cell, but also between membranes of the nerve cell and its surrounding sheath cell. The distribution of the septate desmosomes suggest that they are structures primarily concerned in adhesion.

In all sections through the dendrites and the sheath cells there are present also small islands of cytoplasm surrounded by cell membranes. Some of these may be arranged in lamellae. These are most abundant in the root region as mentioned previously. They are in fact sheet-like and finger-like extensions of the sheath cells, so that two neighbouring sheath cells become interdigitated. These are presumed to provide sites of firm attachment between the loose folds of the sheath cell and also between two neighbouring sheath cells.

Another aspect of the relation of sheath cell to nerve cell that deserves comment is the presence of desmosomes on their apposed surfaces. This is restricted to the region of the basal bodies (Figs. 5C & D). Each desmosome consists of localized areas of thickening of the cell membrane, on the cytoplasmic sides of the limiting membranes.

The most profuse sheath cell inclusion consists of microtubules, which can be seen in varying concentrations in all regions of the cell, including the dendrite. They have an overall diameter of 220-270Å; the wall is about 55Å, and the hollow core about 100-140Å thick. Their lengths are indeterminate, some probably well in excess of 1µ. These microtubules are oriented primarily along the long axis of the nerve fibres, but others may be arranged in any direction.

(f). The neurofilament region

The ciliary structure of the dendrite finally loses its peripheral fibrils and the only elements now recognisable within the dendrite are delicate neurofilaments. These neurofilaments are enclosed by an irregularly shaped cuticular sheath, which is in turn enclosed by a much folded sheath cell (Fig. 8). Where the axial filament complex changes into neurofilaments, the structureless region filled with fine granules is still evident outside the plasma membrane of the dendrite. But at a greater distance above this, the granular substance disappears, and the cell membrane of the dendrite is now closely apposed to the cuticle of the sheath (Fig. 9A). The latter has a very characteristic structure, with a much folded wall. These finger-like projections may give the cuticular sheath a firmer grip in the cytoplasm of the sheath cell.

When the neurofilaments begin to emerge from the epidermis to the Schmidt layer, the sheath cell disappears and the neurofilaments are enclosed in the smooth cuticular sheath only (Fig. 10A). As the cuticular sheath traverses the endocuticle (Fig. 10B), the orderly arrangement of the fibrils in the lamina breaks up and the sheath is here surrounded by granules. This region becomes more pronounced in the exocuticle, where a large area of these granules surrounds the cuticular sheath containing the neurofilaments (Figs. 11A & 12C).

The cuticular sheath is believed to be an invagination of the cuticle from the peg of the sensory organ. This is present in all of the antennary sense organs of many insects described by Slifer and co-workers.

(g). The structure of the sensory end organ

The cuticular sheath in the outermost region of the exocuticle bordering the epicuticle becomes very narrow and the neurofilaments inside it are reduced to a few, and run up into the peg (Fig. 11B). The structure of the cuticle where the peg is inserted is modified.

A very similar structure has been seen in the setal insertions of the insect, Podura aquatica (Noble-Nesbitt, 1963). The terminology used in the following description is adopted from that used by Noble-Nesbitt (1963). In C. bifida a socket is present which consists of a rim surrounding an inner pad, overlain by an epicuticular 'articular membrane'. Structurally the rim is made up of hard cuticle which resembles exocuticle. It has a tapering connection to the base of the inner cylinder which enclosed the cuticular sheath. This gives a solid foundation from which the peg juts out. The pad consists of lamellated cuticle running from the socket rim to the inner cylinder. In Fig. 11C these lamellae have a different pattern from those of the endocuticle. According to Noble-Nesbitt (1963), the lamellae in the socket of the seta stain differently in Mallory when compared to the lamellae of the endocuticle. This suggests a chemical difference between these two types of lamellae in the cuticle. The structural as well as chemical differences could well be associated with different mechanical properties such as elasticity. The rim is further connected to the peg by means of the epicuticle which presumably is a tough, inelastic membrane giving an additional suspension at this level between the peg and the socket rim (Fig. 12A).

In spite of many attempts to section the mouth parts of the water bug, it proved difficult to obtain a longitudinal section through one of these pegs which includes at the same time the walls, the cuticular sheath, and the neurofilaments enclosed within. Thus it is impossible to describe how nerve endings are arranged and their subsequent fate in the peg. The following account is an attempt to guess the possible structure from the micrographs.

In Fig. 12A, it is evident that a peg has been present and that the cuticular sheath opens into it. In other sections not shown here, a broken and indistinct peg whose length is about that of the narrow cuticular sheath is often seen in the region of the end organ. In the thin-walled basiconic peg of the grasshopper (Slifer and Sekhon 1964), the cuticular sheath opens to the outside by a single pore at the base of the peg. Numerous neurofilaments enter into the lumen of the peg, pass through openings in the wall of the cuticular sheath and open to the outside through many small pores in the peg wall distal to the single opening through which the cuticular sheath opens. This arrangement is unlikely in the pegs of the water bug, since enough detail can be seen to make it clear that they are dissimilar.

The lumen of the cuticular sheath is so narrow that only one or a few of the neurofilaments can pass through (Fig. 12B). It seems to be more likely that the cuticular sheath runs into the lumen of the peg and opens to the outside through a pore at the tip. This situation is present in the thick-walled basiconic peg of the grasshopper (Slifer et. al., 1957).

The structure of the sensory unit described above

represents a typical sense organ found in the transverse grooves. Each sensory organ is innervated by a single bipolar neuron, with its own sheath cell. However, in the region anterior to the grooves at the tip of the labium near to the mouth opening, other varieties of sensory organs are found. Basically their dendrites have the same structure, with a root region, basal bodies, and an axial filament complex (Figs. 13A & B), but each sense organ may be innervated by two or more neurons. In Figs. 14A & B, two or three neurons are present. They have a different cuticular sheath structure and microvilli are present in the sheath cell. In general, dendrites in this region are much larger in diameter. In Fig. 14C, groups of five dendrites are enclosed in a common cuticular sheath. All these sensory organs at the tip of the labium will be known as the apical rostral sensory organs, as distinct from those sensory organs located in the labial grooves. Benwitz (1956) can identify (light microscope) ten or more different types of apical sensory organs in Corixa punctata.

Discussion

Earlier workers regarded the sensory organs found in the rostral area as olfactory organs (Benwitz, 1956). Receptor cells sensitive to chemicals are among the most important components of the insect's sensory system. Such cells are designated as chemoreceptors, and the physiological processes which occur in these cells upon chemical stimulation are termed chemoreception. Insect chemoreception is generally divided into two categories, analogous to olfaction and gustation in vertebrate animals (see Hodgson 1964). Olfactory sense is defined as that mediated by chemical stimuli in a gaseous state at relatively low concentrations, and gustation, or contact chemoreception, as that mediated by chemical stimuli acting as liquids or solutions at relatively high concentrations on contact (Dethier & Chadwick 1948). However, this distinction into olfaction and gustation must be regarded as a matter of convenience, rather than a critical one. There is still a third chemical sense, involved in reactions to high concentrations of chemicals, such as the so-called irritating compounds, and which mediate avoidance reactions.

The principal methods for investigating the chemical senses are many. They can be studied from observations on the behaviour of intact animals in the field, or under simulated field conditions in the laboratory. The studies of von Frisch (1938) are an example of this approach. The behavioural experiments reached a new level during the 1940's when Dethier and Chadwick (1948) carried out large-scale experiments defining the relationship between molecular structure and the effectiveness of chemicals applied to the tarsal chemoreceptors of the blowfly, Phormia regina.

During the 1950's, a more precise measurement of the

responses of chemoreceptor cells using electrophysiological techniques was achieved. The first successful application of the electrophysiological methods was an analysis of the function of single chemoreceptor cells in the labellar lobes of the blowfly, Phormia regina (Hodgson et al., 1955). Electrophysiology now provides an indispensable aid in the study of single receptor cells, and even large populations of cells (Schneider, 1957).

Another method of studying insect chemoreceptor is by the detailed anatomy of the sensory cells involved. Development of the electron microscope and other superior histological techniques gave more detailed information about the anatomy of chemoreceptors. In this present study, full attention is given to the anatomy of the receptor organs in the rostrum of the water bug. It is apparent that anatomy alone cannot provide us with a definite function for a particular sensory organ. However, the structure of a sense organ can be compared with that whose function has already been established, and a probable function can be arrived at for this new organ. In C. bifida, the rostral sensory organs have a very similar structure to the typical gustatory receptors in insects. The best known gustatory receptors are those found in the longer labellar hairs of the flies. These have unbranched, tapering dendrites about 0.1 μ in diameter at their distal end. Receptor cells thought to function as chemical sensilla have dendrites of relatively simple structure (Slifer et al., 1957). Dendrites of olfactory receptors are more complex in structure. Receptors for the detection of food and water by the grasshopper (Slifer & Sekhon 1964) have dendrites which divide into several branches.

Sutton (1951) has studied the behaviour of feeding

corixids. The first pair of legs of the corixids bear upon their surfaces a variable number of stiff setae, or palar pegs. These create a current of water containing detritus which passes ventrally, in an antero-posterior direction. When a large piece of food reaches the rostral apex, the palae hold it there for a few seconds, after which the current is retarded. Food is held close to the mouth, thus facilitating the insertion of the stylets. Frequently after detrital feeding has ended, the palae clean the rostrum by removing small food particles which have been trapped by the rostral hairs. These are scraped by the palae and are then held against the mouth and the adhering food particles sucked into the alimentary canal. From the above account, it is highly probable that the apical rostral sense organs of the water bug are truly gustatory receptors.

However this is unlikely to be the function of the sensory organs placed further up on the head and somewhat protected within the grooves. The association of the abundance of these sense organs with the presence of the rostral grooves and the possession of an elaborated dorsal epidermis would seem to indicate some alternative function. At the present time this function is unknown.

There is some indication that the thickened dorsal epidermis is associated with osmotic and ionic regulation (Scudder & Jarial, unpublished). If this is the true nature of the rostral epidermis in C. bifida, it then seems quite likely that the sensory organs in the rostral grooves have an associated function.

The labellar hairs of the blowfly, Phormia regina, are the most intensively investigated and well-known receptors. At the

present time it is certain that there are four neurons supplying each hair: one neuron is specifically sensitive to sugars, one is sensitive to monovalent salts, a third one is sensitive to mechanical stimuli, and a fourth one is a water receptor (Dethier, 1963). It is possible that the sensory organs located in the labial grooves may be sensitive to different concentrations of various compounds.

By the lengths of the cuticular end organs of the sensilla in the labial grooves of Corixa punctata, Benwitz (1956) distinguished three or four types of sensilla. In studying the ultrastructure of the sensilla located in the same area in C. bifida there is no distinction into various types, but the terminal portions are difficult to study with the electron microscope. This does not necessarily mean that they have identical function. Dethier (1961) shows that some labellar hairs of Phormia respond more vigorously to bending or to water than the others. He concludes that even though the labellar hairs may be supplied with the same four or more neurons they are not equally sensitive to all compounds. It follows that the sensilla in the labial grooves of C. bifida, though of the same structure, may react differently to various ionic concentrations.

It is now generally agreed that chemoreceptor cells of insects are modified epithelial cells, and that the central axon of the receptor is formed by the ingrowth of an extension process towards the central nervous system, that is, they are primary sensory cells. Wigglesworth (1953) studied the sensory neurons in Rhodnius prolixus (Hemiptera) and found that the four cells which together make up a sensory hair, the tormogen, trichogen, neuron and sheath cell, are the granddaughter cells of a single epidermal cell. The inwardly growing process from the sense cell forms the axon which joins the first sensory nerve it meets so that impulses can now

pass to the central nervous system. However, in C. bifida, of the four cells which usually make up a sensory unit in other insects, only the neuron and its sheath cell are clearly evident.

The presence of the cuticular sheath surrounding the distal dendrite is common to all cuticular sense organs in insects. According to Slifer et al. (1959), this cuticular sheath is secreted by the trichogen cell. The principal function of this sheath is suggested to be a mechanical one. It serves to protect the dendrite from sudden movement of the internal organs which might tear it loose from the body wall to which it is attached. And in the more complex olfactory sense organs, where numerous neurons innervate a single sense organ, the sheath serves to hold the distal dendrites together. There is general agreement in the literature that the so-called cuticular sheath is of a cuticular nature. This is based on the observation that it is shed with the cuticular exuvium at ecdysis, that it stains the same way as does the cuticle, and that it appears to be continuous with the cuticular covering of the sensillum. Hsü (1933), based on the fact that it resists treatment with sodium hydroxide, concluded that the cuticular sheath is of a chitinous nature. However, in more recent studies, it has been found that the cuticular sheaths of the wireworms resist treatment with a weak solution of potassium hydroxide (Zacharuk 1962). In this latter work the cuticular sheaths of the wireworm are observed to be strongly chromophilic to methylene blue when administered intra-vitally, unlike the surrounding layer of the cuticle.

In the sensory cells of C. bifida this difference in property of the cuticular sheath from the ordinary cuticle is confirmed. In figures showing these sheaths (Figs. 10B, 11A, B & D),

it can be seen that they stain more darkly than the surrounding cuticle. The sheath just outside the apex of the ciliary region, where it originated, shows a characteristic, much folded outline (Figs. 6A, B & C). These characteristic sculptures of the wall of the sheath have not been described by any other authors studying insect sensilla. The cuticular sheath, besides having the mechanical function of holding the dendrite in place, may also serve as a selectively permeable membrane, which 'insulates' each neuron, or units of neurons, from the other, and also from the other tissues and fluid in the body.

During the process of moulting, the sense cell retains its connection with the sensillum on the old cuticle. It is suggested that the filaments enable the old sense organ to function until an advanced stage in moulting. Richard (1952) observed in termites a period shortly before moulting during which the sensitivity of the insect is greatly reduced, and this may be ascribed to the rupture of the distal filament. It is also seen that the sensory cell areas are more resistant to moulting fluid. This may be due to the protection given by the cuticular sheath. Although the process of moulting of C. bifida has not been studied, it is probable that in this insect the cuticular sheath surrounding the dendrite protects the latter from the action of the moulting fluid until late in the moulting cycle.

A surprising finding of several recent studies of sense organs is that the dendrite of the neuron frequently contains a modified ciliary structure. These are now known in many different kinds of receptors, such as photoreceptors, mechanoreceptors and chemoreceptors. In a hydromedusan, Polyorchis penicillatus, studied

by Eakin and Westfall (1962), the photoreceptor cell has a ciliary structure, with nine pairs of peripheral fibrils and two single ones at the centre. In the vertebrate eye, a cilium pushes outward at the growing point of the embryonic rod cell and develops a row of vesicles along its side. Eakin and Westfall (1959) also concluded that the reptilian third eye, or the parietal eye, is evolved from a ciliary structure.

Sensory organs for the reception of vibration or pressure, generally known as mechanoreceptors, show various ciliary modification too. Illustration of this can be cited in the auditory sense organ of the locust (Gray 1961). The chordotonal sensillum in the antenna of Drosophila melanogaster (Uga & Kuwabara 1965) has a structure very similar to that of the locust auditory sense organ.

Many chemoreceptors in insects show ciliary modifications also, e.g. in the plate organ of the honey bee antenna (Slifer & Sekhon 1960), in sensory organs on the antennal flagella of the milkweed bug (Slifer & Sekhon 1963), in grasshopper (same authors, 1964), and in aphid (1964), as well as in the fleshfly (1964). The presence of a cilium in the dendrite in sensory organs of C. bifida indicates that it also belongs to this category of typical sensory structure.

In all these sensory organs, nine pairs of peripheral fibrils are always present. However there is some variation in the presence or absence of the central pairs and their number.

Barnes (1961) reviewed types of cilia and concluded that many sensory cilia, in particular light receptors, lack the two central fibrils common to motile cilia. This type is usually associated with two centrioles or basal bodies. The 9+2 system is usually associated with a single basal body. However it is now obvious that

not all sensory dendrites can be included in the above classifications only. In the photoreceptors of ctenophores (Horridge 1964), cilia of both 9+0 and 9+2 patterns are found. There is only one basal body present. In the study of the aesthetasc hairs (chemoreceptors) of the decapod crustacean Panulirus argus (laverack & Ardill 1965), the number of the central fibrils varies between 1 and 4, and these may be single or paired.

In many of the insect chemoreceptors mentioned above, the central two fibrils are absent, but in the fleshfly, some dendrites have two single fibrils and an extra paired fibrils in the centre, in addition to the nine peripheral pairs. In the thin-walled peg of the grasshopper antenna, vesicles of various sizes are present in the centre. In the present study, the dendrites in the sensory organs have 1-4 central fibrils in the cilia (Fig. 6B). In some sections, two fibrils are present in the central areas of the cilia, however, these fibrils are smaller in diameter than the peripheral ones (Fig. 6C).

A sensory dendrite with a 9+0 ciliary pattern could characterize a structurally primitive cilium, which, having failed to develop the structure associated with motility, still retains a primitive sensory or conducting capacity. Equally well, this pattern could characterize a structurally degenerate form, which, having lost its ability to move, has been functionally modified in the direction of sensory reception. The latter seems more probable. Those sensory neurons which have a 9+2 axial unit system, such as those of C. bifida may represent the fact that the central pair, for some reason or other, has not degenerated.

Ciliary structure in the dendrite is generally associated with structures such as the root system and the basal bodies. In C. bifida, these two structures are present. The rootlet in this insect has a major periodicity of 600-700 Å. This is similar to that found in the sensory organ of the locust ear (Gray 1961) with a periodicity of 650-700 Å, as well as that of the antennal sensory organ in the milkweed bug (Slifer & Sekhon 1963), the periodicity of which is 750 Å. As suggested by Fawcett (1954), the striated character of these rootlets places them in the category of protein fibres, and they may perform a mechanical or contractile role in the cell. The variation in the period length could conceivably result from different degrees of stretching. In studying ciliary movement in a protozoan, Roth (1958) suggested that rootlet fibrils play a major role in ciliary co-ordination by functioning as electrical conductors.

In C. bifida, two structures similar to the basal bodies are present. The distal one, at the inner end of the cilium, has triple fibrils in the wall of the cylinder, as typical of other basal bodies. It seems justified to call this structure the distal basal body. Triple fibrils, on the other hand, are never found in the proximal structure, but in longitudinal sections this is very similar to the distal one. Two similar structures are present in the auditory sense organ of the locust (Gray 1961), and in the chordotonal sensillum in the antenna of D. melanogaster (Uga & Kuwabara 1965), and the authors named them the ciliary collar and the root apparatus respectively. It is left undecided whether the proximal structure in the dendrite of C. bifida should be termed the root apparatus or the proximal basal body. In most cases in this

study, the term root apparatus is used.

In C. bifida the sheath cell surrounding the dendrite in the epidermis has many characteristic structures, as found in the sheath cells in other insects. Of these structures, the most pronounced ones are the double membrane system, the normal desmosomes, the septate desmosomes, and the cytoplasmic microtubules.

As described above, the double membrane in the sheath cell of C. bifida is formed when the sheath cell membrane rolls itself around the nerve, and the plasma membranes become apposed to form pairs. Very often the spaces between the adjacent membranes are traversed by fine bars. These, according to Wood (1959), are the septate desmosomes. These are also found in a large number of insect tissues: they are present in the plasma membranes of the epithelium below the cuticle of the greater wax moth, the yellow mealworm, and the boney bee (Locke 1961). Similar structures are also noted in the dendrites of the milkweed bug and the grasshopper (Slifer & Sekhon 1963, 1964). Septate desmosomes are also found in annelids (Hama 1959), anemones (Grimstone et al. 1958), and in echinoderm embryos (Balinsky 1959). In fact they are probably universally present in the invertebrates. Wood (1959) defines them as an adherent region between two plasma membranes which are joined together by parallel arrays of lamellae arranged at right angles to the surface. But by means of sections tangential to the surface of these desmosomes, it is now suggested (Locke 1965) that the septa are arranged in a hexagonal network. The walls of the spaces are formed from three arrays of septa oriented at 120° to one another, giving an almost perfectly symmetrical pattern. Wiener (1964) studied the epithelial cell junctions of Drosophila salivary glands

and found that the junctional surfaces or septate desmosomes of these epithelial cells may be concerned with the permeability properties of the cell attachment area.

Another structure present in the sensory unit of C. bifida, which is also present in a large number of invertebrates, is the desmosome in the region of the basal bodies of the dendrite (Figs. 5C & D). Desmosomes are present in the dorsal giant fibres of the earthworm Eisenia foetida (Hama 1959), and in the sheath cells encapsulating the neurons in the eighth nerve ganglion of the goldfish (Rosenbluth & Palay 1961). They are also present in the interdigitating neuroglial cells in barnacle photoreceptors (Fahrenbach 1965). Such specialization of the surface has generally been interpreted as a device for maintaining cohesion of adjacent cells. Since they usually join cells of the same type, it has been speculated that they might be the morphological basis for the well known selective cohesion of like cells, which has been extensively studied by embryologists (e.g. Overton 1962). So the formation of a desmosome seems to involve the co-operation between cojoined cells, and it has been considered likely that initiation of a half desmosome in one cell would induce the formation of the complementary half in an adjacent cell of the same kind (Fawcett 1962). In the study of a leech nervous system (Coggeshall & Fawcett 1964), desmosomes are found to be present on the apposed surfaces of the glia or sheath cells and the neurons, as in those of C. bifida. This fact makes it necessary to modify our views as to the type specificity of this mechanism of cell attachment.

In C. bifida, microtubules are abundant in the sheath cell, as well as in the dendrite. Electron microscope studies of a

variety of invertebrate and vertebrate cell types have supported the postulate that the microtubules is a universal cellular organelle. Microtubules are found to occur in the axoplasm of many animals, including coelenterates, annelids, arthropods, and vertebrates. When present in the axoplasm, microtubules are termed neurotubules by Bullock and Horridge (1965).

Cytoplasmic microtubules in both animal and plant cells have the same dimensions as the flagellar and ciliary tubules. The spindle fibres of the mitotic apparatus (Kane 1962) also are tubules with a diameter of 180-220 Å, very close to that of the microtubules in C. bifida, 220 Å. Studies on the fine structure of both the fibrils of cilia and flagella (Pease 1963, Phillips 1966), and the cytoplasmic microtubules (Gall 1966, Ledbetter & Porter 1964), indicate that subunits are present in the two kinds of tubules. This suggests that these two different organelles may have a similar function, that is, they are contractile organelles. Another possible function of the microtubules is that they may serve for intracellular conduction. Rudzinska (1965) studied microtubules in the feeding tentacles of a suctorian, and suggested that these organelles form a structural basis for the passage of microwaves of contraction which serve to conduct food material down the tentacle. Fukuda and Koelle (1959) suggested that acetylcholinesterase in the neuron is synthesized within the endoplasmic reticulum, then transported by means of the microtubules to the surface of the cell. It is still not certain if microtubules are hollow structures (Winston et al. 1966), and it is possible that intracellular conduction takes place in the manner described by Rudzinska. A third possible function is that microtubules may serve as intracellular supports. Since in C. bifida,

microtubules are abundant in the sheath cell cytoplasm, they may serve all the different functions.

From the above discussion, it is obvious that the sheath cell in C. bifida serves to separate or to protect the epidermal region of the dendrite from the surrounding tissues or fluids. The characteristic structures of the sheath cell, such as the septate and conventional desmosomes and the microtubules serve various other functions in supporting or promoting the activity of the dendrite. Horridge and Bullock (1965) suggested that there is a linear relationship between the number of the sheath cells and the length of the nerve axon or dendrite. The data were interpreted as indicating that the sheath cells are indeed 'nurse cells' or 'auxiliary metabolic units'. It was proposed that the neuron, being incapable of hypertrophy, recruits sheath cells as auxiliary metabolic units whenever the demands for maintenance of the cell processes are increased by reason of their length, ramification, or excessive activity. Recent studies on the neurons and sheath cells suggested that the two components should be thought of as forming a single functional metabolic unit.

After discussing the ultrastructure of the sensory organ of C. bifida, I shall now speculate on its possible function. In 1960 when Gray gave a detailed description of the fine structure of a ciliary region in the dendrites of the locust ear, it seemed logical to suppose that dendrites with a ciliary process would be restricted to structures which were receptors of vibration or pressure. Since both receptors would be directly concerned with movement or stretching of the neurons, this would account for the presence of the cilium. Ciliated dendrites were then reported for many other sensory

organs in insects, which by previous experimental work were proved to be chemoreceptors. It is thus possible for the dendrites of insect chemoreceptors also to have a ciliary region. The presence alone of a cilium in a sensory neuron cannot therefore suggest the function of the organ.

It is now certain, at least in the sensory organs of some species of Hemiptera, Isoptera and Diptera (all works by Slifer and co-workers), that the dendritic endings of chemoreceptors are freely exposed to air. Whether a chemoreceptor may function when completely covered by cuticle, even specialized types of cuticle, is still not certain. Thus, opening of dendrites to the outside seems a more reliable criterion for identifying chemoreceptors.

Hence in C. bifida, a ciliary structure in the dendrite provided no evidence about its function as a chemoreceptor or a mechanoreceptor. A longitudinal section through one of the sensory pegs which includes the walls, the cuticular sheath and the dendritic endings is very difficult to obtain. However, a possible structure can be constructed from the electron micrographs. In Figs. 11B, 11C and 12A, it is obvious that the cuticular sheath continues to pass into the peg, and as shown in the results section (page 21), it is most probable that this opens at the tip of the peg. However, whether the dendritic endings continue into the narrow cuticular sheath and become exposed to the outside at the tip of the peg is doubtful. In most sections (Figs. 11B & 12A) it appeared that the dendrite stops at the region where the cuticular sheath becomes narrow, and a few supportive or connective fibres serve to hold the dendrite close to the outer opening.

Now that the presence of cilia in nerve cells of both vertebrates and invertebrates is now well established, it is obvious that one question will be asked. What is the function of the ciliary structure in some of the neurons? The role of the cilium in the rods and cones of the vertebrate eye has been discussed by Brown, Gibbons and Wald (1963). They suggest that the ciliary process may be mainly concerned with the development of the outer segments of the embryo rod cell, and their regeneration in the adult. The basal body is necessary for the regeneration of the axial filament complex, while the latter is required for the regeneration of the outer segment of the rod. According to Slifer and Sekhon (1964), need for a centre from which regeneration could start would be apparent when applied to the process of moulting in insects. During the earlier stages of the moulting cycle the distal processes of the dendrites may be retracted into the sheath, and they will grow out later to make contact with the new sensory peg. On the other hand, it is possible that the dendrites are not retracted at the time of moulting, and are torn off. New processes would be required to grow out from the stumps of the old ones.

Since in the sensory unit of C. bifida, the cuticular sheath originates from around the ciliary region, it may be possible that during moulting in the nymphal stages, the axial filament complex is torn off. The basal body would then regenerate a new complex and the neurofilaments distal to it. If only the neurofilaments are lost during moulting, the cilium could be necessary for the regeneration of the distal process of the dendrite. For species of insects which do not moult again after acquiring their sensory pegs, the

basal body and cilium would be needed for the development of the dendrites in the first place.

Another possibility is that cilia in neurons may serve as skeletal or supporting elements. The dendrites are delicate fibres, and to have them stand erect in the cuticle, even if the cuticular sheath is present, some skeletal supports would be needed. With the presence of cilia, these delicate structures might be able to remain intact during the violent changes in internal pressure which occur in an insect during locomotion, respiration, moulting and other normal activities.

Since it is apparent that a cilium in the dendrite does not in itself lend any weight to the acceptance of a particular function for the sense organ, can these organs which are found in the rostrum of C. bifida be mechanoreceptors? According to Horridge and Bullock (1965) each mechanoreceptor has only one bipolar sensory neuron. This is just the case observed in the rostral sense organs. However, from the structure of the short, stumpy peg, it would be a very inefficient receptor for pressure or vibration. So, if they are chemoreceptors, what is the functional significance of their arrangement in rows on the rostrum? No adequate answer is available to this question at present, but the abundance of a single type of sense organ in a certain area in insects may be used to explain the sensitivity of these insects to chemical stimuli, since they may be the anatomical basis for summation effects.

Summary

The sensory organs in the transverse grooves of the dorsal labium of the water bug, Cenocorixa bifida were studied with the electron microscope. It was found that each organ is innervated by a single bipolar neuron. The dendrite of the latter is modified into various structures along its length; it has a root system, two basal bodies and an axial filament complex. The last structure is unusual, consisting of nine pairs of peripheral fibrils and one to four central fibrils, as compared to the 9+0 or 9+2 system in the dendrites of other insect sense organs. Neurons are surrounded by their own sheath cells, which possess many characteristic fine structures, such as 'normal' and septate desmosomes, and microtubules. Other sensory organs having a modified ciliary region in the dendrites are reviewed. Since the dendrite appears to open to the outside through a pore in the sensory peg, it seems most likely that the sense organs in the grooves are chemoreceptors.

Sensory organs, other than the type found in the transverse grooves, are located at the tip of the rostrum nearer to the mouth opening. These apical rostral sense organs are likely to be gustatory organs in the feeding of the insect. These structures are only briefly reviewed.

Literature cited

Balinsky B. 1959

An electron microscope investigation of the mechanism of adhesion of the cells in a sea urchin blastulas and gastrula.

Exp. Cell Res. 16: 429

Barnes B. G. 1961

Ciliated secretory cells in the pars distalis of the mouse hypophysis.

J. Ultra. Res. 5: 453-67

Bensitz G. 1956

Der kopf von Corixa punctata Ill. (Hemipter)

Zoll. Jahrb. 75: Heft 3

Blatchley W.S. 1926

Heteroptera of Eastern North America.

Nature Pub. Co. Indianapolis.

Brown P.K., I.R. Gibbons & G. Wald 1963

The visual cells and visual pigments of the mud puppy.

J. Cell Biol. 19: 79-106

Dethier V.G. 1954

The physiology and histology of olfaction in insects.

Ann. N.Y. Acad. Sci. 58: 139-58

Dethier V.G. 1955

The physiology and histology of the contact chemoreceptors of the blow fly.

Quart. Rev. Biol. 30: 348-71

Dethier V.G. 1961

Behavioural aspects of protein ingestion by the blowfly.

Biol. Bull. 121: 456-70

Dethier V.G. 1963

The physiology of insect senses.

Methuen, London.

Dethier V.G. & L.E. Chadwick 1948

Chemoreception in insects.

Physiol. Rev. 28: 220-58

Dethier V.G. & M.L. Wolbarsht 1956

The electron microscopy of chemosensory hairs.

Experimentia 12: 335-37

Doolin P.F. & Bridge W.J. 1966

Ultrastructure of cilia and basal bodies.

J. Cell Biol. 29: 333

- Dorey A.E. 1965
The organization and replacement of the epidermis in
acoelous turbellarians.
Quart. J. Micr. Sci. 106: 147-72.
- Duvall A.J., Flock A. & Wersall J. 1966
Ultrasturcture of sensory hairs.
J. Cell Biol. 29: 497
- Eakin R. M. & Westfall J. A. 1962
Fine structure of photoreceptors in Hydromedusan,
Polyorchis penicillatus.
Proc. Nat. Acad. Sci. 48: 826
- Farquhar M.G. & Palade G.E. 1963
Junctional complexes in various epithelia.
J. Cell Biol. 17: 375
- Fawcett D.W. 1961
Intercellular bridges.
Exp. Cell Res. suppl. 8: 174-87
- Fawcett D.W. 1962
Physiologically significant specializations of the cell
surface.
Circulation 26: 1105-25
- Fawcett D.W. & Porter K. R. 1954
Fine structure of ciliated epithelia.
J. Morph. 94: 221
- Gall J.G. 1966
Microtubule fine sturcture.
J. Cell Biol. 31: 639-43
- Gray E.G. 1960
The fine structure of the insect ear.
Phil. Trans. Roy. Soc. Lond. B 243: 75-94
- Grimstone A. V., Horne R.W., Pantin C.F.A. & Robson E.A. 1958
The fine structure of the mesenteries of the sea anemone.
J. Micr. Sci. 99: 523
- Hama K. 1959
Some observations on the fine structure of the giant
nerve fibres of the earthworm.
J. Biophys. Biochem. Cyto. 6: 61-66
- Hilton W.A. 1933
Nervous system and sense organs.
J. Ent. Zool. 23: 31.
- Fahrenbach W.H. 1965
The morphology of some simple photoreceptors.
Z. Zellforsch. 66: 233-54

- Hodgson E.S. 1955
Problems in invertebrate chemoreception.
Quart. Rev. Biol. 30: 331-47
- 1958
Chemoreception in arthropods.
Ann. Rev. Ent. 3: 19-36
- 1964
Chemoreception in the Physiology of Insecta.
M. Rockstein (ed.) Academic Press. N.Y.
- Horridge G.A. 1964
Presumed photoreceptive cilia in a ctenophore.
Quart. J. Micr. Sci. 105: 311-17
- Horridge G.A. & Bullock T.H. 1965
Special relations and components of nervous tissue
in Structure and function in the nervous systems of
invertebrates.
Freeman & Co.
- Kane R.E. 1962
The mitotic apparatus
J. Cell Biol. 15: 279-83
- Lansing A.I. & Lamy F. 1961
Fine structure of the cilia of rotifers.
J. Biophys. Biochem. Cyt. 9: 799-812
- Laverack M.S. & Ardill D.J. 1965
The innervation of the aesthetasc hairs of Panulirus
argus.
Quart. J. Micr. Sci. 106: 45-60
- Edbetter M.C. & Porter 1964
Morphology of microtubules of plant cells
Sci. 144: 872
- Locke M. 1961
Pore canals and related structure in insect cuticle.
J. Biophys. Biochem. Cyt. 10: 589-618
- 1964
The structure and formation of the integument of insects.
in the Physiology of Insecta
Academic Press, N.Y.
- 1965
The structure of septate desmosomes.
J. Cell Biol. 25: 166-69
- Loewenstein W.R. & Kanno Y. 1964
Study on an epithelial cell junction.
J. Cell Biol. 22: 565

- Lower H. F. 1956
Terminology of the insect integument.
Nature 178: 1355-56
- 1957
A comparative study of the cuticular structure of
three female mealy bugs.
Biol. Bull. 113: 141-59
- Luft J.H. 1961
Improvement in epoxy resin embedding method.
J. Biophys. Biochem. Cyt. 9: 409
- Miller N.C.E. 1956
The biology of the Heteroptera
Leonard Hill Ltd. Lon.
- Noble-Nesbitt J. 1963
The fully formed intermoult cuticle and associated
structure of Podura aquatica (Collembola).
Quart. J. Micr. Sci. 104: 243-70
- 1963
The cuticular and associated structures at the moult.
Quart. J. Micr. Sci. 104: 369-91
- Overton J. 1962
Desmosome development in normal and associating cells
in the early chick blastoderm.
Develop. Biol. 4: 532-48
- 1963
Intercellular connections in the outgrowing stolon of
Cordylophora.
J. Cell Biol. 17: 661
- Parson M.C. 1966
Labial skeleton and musculature of the Hydrocorisae
(Heteroptera).
Can. J. Zool. 44: 1050-84
- Pease D.C. 1963
The Ultrastructure of flagellar fibrils.
J. Cell Biol. 18: 313
- Phillips D.M. 1966
Substructure of flagellar tubules.
J. Cell Biol. 31: 635
- Reese T.S. 1965
Olfactory cilia in the frog.
J. Cell Biol. 25: 211
- Richards A.G. 1952
Studies on Arthropod cuticle III. The antennal cuticle
of the honeybee.
Biol. Bull. 103: 201

- Robertis E. 1956
Morphogenesis in the retinal rods.
J. Biophy. Biochem. Cyt. suppl. 2: 209-18
- Robertson J. D. 1959
The ultrastructure of cell membranes and their derivatives.
Biochem. Soc. Sym. 16: 3
- Rosenbluth J. & Palay S. L. 1961
The fine structure of nerve cell bodies and their myelin sheaths in the eighth nerve ganglion on the goldfish.
J. Biophy. Biochem. Cyt. 9: 853-77
- Roth L.E. 1958
Ciliary co-ordination in Protozoa
Exp. Cell Res. suppl. 5: 573-85
- Rudzinska M. A. 1965
Tentacle structure in suctoria.
J. Cell Biol. 25: 459
- Satir P. 1962
On the evolutionary stability of the 9+2 pattern.
J. Cell Biol. 12: 181
- 1965
Studies on cilia
J. Cell Biol. 26: 805
- Schmidt. E. L. 1956
Observations on the subcuticular layer in the insect integument.
J. Morph. 66: 211
- Shigekazu Uga & M. Kuwabara
On the fine structure of the chordotonal sensillum in the antenna of D. melanogaster
J. of E. M. 14: 173-81
- Slautterback D.B. 1963
Cytoplasmic microtubules I. Hydra
J. Cell Biol. 18: 367-88
- Slifer E.H., Prestage J.J. & Beams H.W. 1957
The fine structure of sensory pegs of grasshopper.
J. Morph. 101: 359
- 1959
The chemoreceptors and other sense organs on the antennal flagellum of the grasshopper.
J. Morph. 105: 145

- Slifer E.H. & Sekhon S.S. 1960
The fine structure of the plate organs on the antenna
of the honeybee.
Exp. Cell Res. 19: 410-14
- 1961
The fine structure of the sense organs of the antennal
flagellum of the honey bee.
J. Morph. 109: 351
- 1963
Sense organs on the antennal flagellum of the small
milkweed bug.
J. Morph. 112: 165
- 1964
Fine structure of the sense organs on the antennal
flagellum of a flesh fly.
J. Morph. 114: 185-208
- 1964
Olfactory dendrites of the grasshopper
J. Morph. 114: 393-410
- & Lees A.D. 1964
The sense organs on the antennal flagellum of aphids.
Quart. J. Micr. Sci. 105: 21-29
- Slifer E.H. 1961
The fine structure of insect sense organs.
Intern. Rev. Cyt. 11: 129-59
- Smith D. S. 1960
Innervation of the fibrillar flight muscle of an insect.
J. Biophys. Biochem. Cyt. 8: 487
- Southwood T.R.E. & Leston D. 1959
Land and water bugs of the British Isles.
Frederick Warne & Co. Ltd. London & N.Y.
- Sutton M.S. 1951
Food and feeding in Corixidae
Zool. Societ. Lond. Proc. 121: 465
- Trujillo-Cenoz O. 1959
Studies on the fine structure of the central nervous
system of Pholus laburscoe (Lepidoptera).
Z. Zellforsch. 49: 432-446
- Wiener J., Spiro D. & Loewenstein W. 1964
Studies on an epithelial cell junction
J. Cell Biol. 22: 587

Wigglesworth V.B. 1953

The origin of sensory neurons in an insect
Quart. J. Micr. Sci. 94: 93-112

----- 1959

The histology of the nervous system of an insect
Rhodnius prolixus (Hemiptera).
Quart. J. Micr. Sci. 100: 285-98

Winston A.A., Weissman A. & Ellis R.A. 1966

A comparative study of microtubules in some vertebrate
and invertebrate cells.
Z. Zellforsch. 71: 1-13

Wood R.L. 1959

Intercellular attachments in the epithelium of Hydra
J. Biophy. Biochem. Cyt. 6: 343

Zacharuk R.Y. 1962

Sense organs of the head of larvae of some Elateridae
(Coleoptera).
J. Morph. 111: 1-35

----- 1962

Exuvial sheaths of sensory neurons in the larvae of
Ctenicera destructive
J. Morph. 111: 35-48

List of symbols used in the diagrams and figures

AM	articular membrane
AX	axon
B	basal body
C	cuticle
CI	ciliary region
CS	cuticular sheath
D	desmosome
ED	epidermis
EPI	epicuticle
EXO	exocuticle
F	finger-like projections of the epidermis
FI	fibrils in endocuticle outside the cuticular sheath
FS	fibrous structure in exocuticle
G	granular cylinder surrounding cilium
IE	inner cylinder
IS	island of cytoplasm enclosed in double membrane
L	lamellae of sheath cell
LS	lamellae of soft cuticle at the base of the sensory peg
MT	microtubules
NE	neurofilaments
NU	nucleus of sensory neuron
NUS	nucleus of sheath cell
P	pad
PC	pore canal
PG	sensory peg
R	rim
RA	root apparatus
RL	rootlet
S	sheath cell
SD	septate desmosome
SE	sensory end organ
SL	Schmidt layer

Fig. 1A Cuticular structure of the dorsal labium:
Epi-, Exo- and Endo-cuticle are present.
A sensory end organ (SE) is present in the
exocuticle. Pore canals (PC) traverse this
region.

x 17,600

Fig. 1B Cuticular structure of the ventra labium. A
very thin epicuticle is present: there is
no exocuticle. Pore canals (PC) are present.
x 12,500

Fig. 2A Longitudinal section of a sensory unit.

This lies in the epidermal region, and the dendrite distal to the nucleus (A) is differentiated into a root region (B), a ciliary region (C), and a neurofilament region (D)

Fig. 2B Dendrite in the form of neurofilament (NF) emerging from the Schmidt layer (SL) into the endocuticle (END). The neurofilaments are enclosed in a cuticular sheath (CS).

In the immediate vicinity of the sheath, the orderly arrangement of the fibrils into endocuticular laminae changes, so that the sheath is either surrounded by some cytoplasmic granules or long fibrils running parallel to the axis of the dendrite (FI).

x34,000.

Fig. 3A Section through a group of neurons.

The nuclei (NU) of the neurons are grouped together
as distinct from the surrounding spidermal cells.

x8750.

Fig. 3B Section through a group of axons.

A group of axons (AX) enclosed in sheath cells
close to the soma of the neuron in the epidermis
of the insect. NU is the nucleus of the neuron.

x 50,000.

Fig. 4A Longitudinal section through the dendrite, showing the origin of the rootlets from the inner end of the distal basal body (B). They then encircle the proximal basal body or root apparatus (RA). Just above the distal basal body the dendrite assumes the structure of a cilium (CI), and the latter is soon broken down into neurofilaments (NF). Desmosomes (D) are characteristic of the region of dendrite containing the basal bodies.

x 58,000.

Fig. 4B Section through the rootlet region showing a much folded sheath cell. Septate desmosomes (SD) and microtubules (MT) are abundant. Lamellae (L) representing interdigitation with neighbouring sheath cell are also present.

x 50,000.

Fig. 4C Transverse section through the rootlet region.

A double membrane system is evident in this section.

Each is formed from a pair of unit membranes closely

apposed to each other, leaving a gap of about 75-100 Å

in between. This gap is filled with material of higher

density than the surrounding cytoplasm. A double

membrane is not only formed between the membranes

of the folded sheath cell, but also between the latter ~~one~~

and that of the nerve cell.

x 57,600.

Fig. 5A Transverse section through the distal basal body. Triple fibrils are clearly distinguishable. This section also cut through the structureless region filled with very fine granules (G). This shows that it is cut through a region near the axial filament complex.

x 62, 400

Fig. 5B Transverse section through the distal basal body, at the level slightly below that in Fig. 5A.

Dense materials are condensed outside the fibrils and radiate out like the spokes of a wheel.

The cuticular sheath (CS) is not continuous in outline.

x 55,000

Fig. 5C Longitudinal section through the proximal basal body or root apparatus (RA). It has a structure and size very similar to that of the distal one. However no rootlets arise from its inner end. Desmosome (D) is present between the apposed membrane of the dendrite and the sheath cell. x 57,000.

Fig. 5D Transverse section through the proximal basal body or root apparatus (RA). There is a dense inner ring which is surrounded by an outer ring of electron dense material. RL represents one of the rootlets encircling the root apparatus.

x 50,000.

Fig. 6A Transverse section through the ciliary region.

This shows different regions of the insect integument, the epidermis (ED), the finger-like projections (F) from the epithelium into the Schmidt layer (SL) and the endocuticle (END) above it. The cilium lies in a structureless region filled with fine granules (G), and the cuticular sheath (CS) is discontinuous.

x 36,500.

Fig. 6B Transverse section through the ciliary region.

Nine peripheral paired fibrils and three central ones are evident. Of the three at the centre, two are together to form a pair and the third one is a single one by itself. Microtubules are abundant around the cuticular wall.

x 78,000.

Fig. 6C Transverse section through the ciliary region a short distance above the one in Fig. 6B.

Here the diameter of the axial filament complex is much increased, by the spreading out of the paired peripheral fibrils. Two central fibrils are present in this section, smaller in size than the outer.

In both sections, the cuticle (C) is deposited in the granular structureless region (G), next to the membrane of the sheath cell.

x 78,000.

Fig. 7A Section through the nucleus of the sheath cell (NUS).

The dendrite containing rootlets (R) is wrapped
around by a protrusion of the sheath cell.

The dendrite is lodged in the notch of the nucleus
of the sheath cell.

x 40,000.

7A

NUS

R

Fig. 7B Transverse section through the neurofilament region of the dendrite, showing two dendrites enclosed in a common sheath cell.

x 50,000.

Fig. 7C Transverse section through the ciliary region of the dendrite, showing two dendrites enclosed in a common sheath cell.

x 32,400.

Fig. 8 Transverse section through the neurofilaments.

The cuticular sheath becomes smoother in outline.

x 72,000.

Fig. 9A Transverse section through the neurofilament region. In the upper one the structureless region containing fine granules has completely disappeared. The wall of the cuticular sheath (CS) has many finger-like projections.

x 54,800.

Fig. 9B Longitudinal section showing the cuticular sheath
with characteristic structure. Microtubules are
abundant.

x 45,600.

Fig. 10A Longitudinal section showing the emerging of dendrite from the epidermis (ED) into the Schmidt layer (SL). Note that sheath cell is absent when the dendrite is in the Schmidt layer.

33,600.

Fig. 10B Longitudinal section showing neurofilaments in endocuticle (END). The formation of endocuticular laminae is inhibited, so that the cuticular sheath is surrounded by unorientated fibres or granules.

x 28,500.

Fig. 11A Longitudinal section through the terminal portion of the sensory organ.

The cuticular sheath becomes narrow when it enters the inner cylinder (IE). The socket consists of a rim (R) surrounding the inner pad. The rim has a tapering connection to the base of the inner cylinder. Lamellae of soft cuticle (LS) run from the socket rim to the inner cylinder.

x 15,500.

Fig. 11B Section to show the structure of the base of the
peg. Arim (R) surrounds an inner pad (P). The
narrow cuticular sheath is surrounded by an
inner cylinder (IE). Articular membrane (AM) is
present.

x 50,000.

Fig. 11C Longitudinal section through the end of the sensory organ, showing lamellae of soft cuticle running from the socket rim to the inner cylinder.

x 13,000.

Fig. 11D Transverse section through the end organ, showing that the innermost ring of the cuticular sheath is encircled by the inner cylinder (IE), the latter is in turn surrounded by the socket rim (R), with the pad (P) lying between them.

x 30,000.

Fig. 12A Longitudinal section through the end organ.

An articular membrane (AM) of epicuticle overlies the rim (R) and pad (P). The cuticular sheath opens into the peg (PG) which is broken off in this section. The size of the peg can be visualized.

x 40,000.

Fig. 12B Transverse section through the cuticular sheath.

The lumen of the sheath into the peg is so narrow that only a few neurofilaments would be able to pass through it to enter into the peg.

Refer to Fig. 11B for symbols.

x 42,000.

Fig. 12C Transverse section through a labial sensory groove, showing rows of dendrites (in the form of neuro-filaments NF) surrounded by granular substance in the exocuticle (EXO). The section also cut through a portion of the peg near the epicuticle (EPI). In this a cuticular sheath (CS) is surrounded by the peg wall.

x 18,000.

Fig. 13A Section through the ciliary region of a sensory unit near the mouth opening. Two cilia (CI) are present in a common cylinder of fine granules (G) surrounded by a cuticular sheath (CS).

x 64,000.

Fig. 13B Section through the basal body of a dendrite in the same region as above. It has a structure similar to the type found in the dendrite of the sensilla within the transverse groove. Microtubules are abundant both in the dendrite and in the sheath cell.

x 76,000.

Fig. 14A Transverse section through a sense organ made up of a group of three dendrites. The wall surrounding the dendrites is quite different from the cuticular sheath of the groove sensillum. Microvilli are abundant in the surrounding sheath cell.
x 16,000.

Fig. 14B Transverse section through a similar type of structure.
x 50,000.

Fig. 14C Transverse section through a sense organ made up of a group of five dendrites. These are enclosed in a common cuticular sheath (CS).