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DISTRIBUTION AND ORIENTATION OF CAMPANIFORM SENSILLA
ON THE ABDOMEN OF THE COCKROACHES
PERIPLANETA AMERICANA AND BLABERUS CRANIIFER

A Thesis

Submitted to

the Department of Biology

Kansas State Teachers College, Emporia, Kansas

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by

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February, 1973

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335161

ACKNOWLEDGEMENT

I express sincere thanks and gratitude to Dr. Edward C. Rowe for his invaluable assistance, advice, prompt attention, and extreme patience in all directions throughout the course of study. A special note of appreciation and gratefulness goes to Dr. Katherine N. Smalley and Dr. Gaylen Neufeld who rendered assistance in preparing this paper. I thank Mrs. Cynthia Brown for letting me use the histological slides.

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INTRODUCTION

A sensillum can be defined as a sense cell or group of sense cells associated with a sense organ. In insects sensilla often occur in association with specialized cuticular structures. Sensilla are more easily classified in insects by their structure than according to their function and many structural types have been distinguished (Snodgrass, 1935).

Among the classified sense organs are campaniform sensilla (Latin campana = bell) which derive their name from their bell- or dome-shaped cuticular part. They are often seen in groups of 2 to 20 on the legs according to Pringle (1938) and up to 72 on the wings according to Gettrup (1965). Pringle (1938) was able to record electric discharges from the nerve associated with the campaniform sensilla of the cockroach while creating pressure in the neighborhood of the sensilla. He thus demonstrated that campaniform sensilla are cuticular stress receptors. Since the receptors he studied are arranged so they respond to changes in loading on the legs, it is appropriate to consider them as proprioceptors. He further showed that stimulation of these receptors triggers an antigravity response similar to the mammalian stretch reflex (Pringle, 1940).

The distribution of campaniform sensilla on legs, wings, halteres and palps has been established (Pringle, 1938; McIndoo, 1914; Gettrup, 1965; Pringle, 1948) but relatively little is known about the distribution, much less the function, of campaniform sensilla on the abdominal segments of insects. The main question asked in this

research was - where are the campaniform sensilla located in the cockroach abdomen and what function or functions can be inferred from this distribution?

MATERIALS AND METHODS

ANIMALS

Adult cockroaches (Periplaneta americana and Blaberus craniifer) were raised in 31 by 47 by 20 cm steel cages in the laboratory. Their food consisted of sliced apples, dog food, oatmeal and water supplied twice a week.

WHOLE MOUNTS OF CUTICLE

The wings, legs and head were removed from a living specimen. It was then pinned dorsal side up on a paraffin-filled petri dish. The abdomen was opened and most of the internal organs were discarded. After boiling 10 to 15 minutes in 10% KOH to digest the soft tissue, the remaining chitinous cuticle was rinsed thoroughly in water. It was then dehydrated by two changes of 100% alcohol before being cleared in xylene for 15 to 30 minutes and in clove oil for two to thirty days. Usually the preparations were mounted in Permount before being observed under the microscope. An ocular micrometer was employed in measuring distances between the campaniform sensilla and other nearby cuticular structures.

HISTOLOGICAL PREPARATIONS

For histological studies, Mallory-stained transverse, sagittal, and frontal sections were observed carefully and repeatedly under light microscope. (These were prepared by Mrs. Cynthia Brown for Kehler's 1968 Thesis).

METHYLENE BLUE WHOLE MOUNTS

To find out which nerve branches carry the sensory information from the abdominal campaniform sensilla to the central nervous system, methylene blue-stained whole mounts were prepared using the techniques of Stark, Smalley and Rowe (1969). Reduced methylene blue solution (0.2 to 0.5 ml) was injected into the body cavity of the cockroach. To stop the staining process and to fix the methylene blue, ammonium picrate solution was injected 30 to 60 minutes later and the animals were dissected to uncover the nerves in the neighborhood of the campaniform sensilla. The preparation was flooded one-half to two hours later with ammonium molybdate solution. After 12 to 48 hours, the unwanted tissues were removed and the preparation was rinsed in distilled water, given two 30 minute changes in tertiary butyl alcohol, cleared in two 15 minute changes of xylene, and mounted in Permount.

NERVE AND MUSCLE TERMINOLOGY

In referring to the abdominal nerves and muscles of Periplaneta the numbering and naming system of Shankland (1965) has been followed. In referring to the corresponding structures of Blaberus, the independently devised but similar system of Smalley (unpublished dissertation, 1963) has been followed.

RESULTS

Appearance of the abdominal campaniform sensilla:

In the KOH-treated cuticle mounts, the thinned out domes of campaniform sensilla appeared as slightly oval bright spots on a darker background (Fig. 1 & 2). Under 450 x magnification, a distinct inner ring could be seen (Fig. 1 & 2B). These were particularly obvious when viewed with dark-field illumination. The dimensions of the oval domes are approximately 8.5 x 11 microns in Periplaneta. In Blaberus, the sensilla are larger and more oval (approximately 13 x 17 microns).

Distinguishing campaniform sensilla from empty hair sockets:

Initially there was difficulty in positively identifying campaniform sensilla, since cockroaches have large numbers of abdominal hairs and some were inevitably broken off at their bases to yield an oval transparent area, some of which are about the same size as the campaniform sensilla. McIndoo (1914) and Snodgrass (1935) have mentioned the same difficulty. Both the campaniform sensilla and the hair sockets possess an inner and outer ring (Fig. 3A - 3E), but the resemblance ends here. When the campaniform sensillum is viewed with transmitted light, the area between two rings is noticeably brighter than either the center of the dome or the cuticle around the sensillum (Fig. 1, 2, & 3A). Also in the campaniform sensillum there is a point, along the long axis in oval sensilla, where the inner and outer rings appear to join. Many of the hairs are tilted at an angle from the

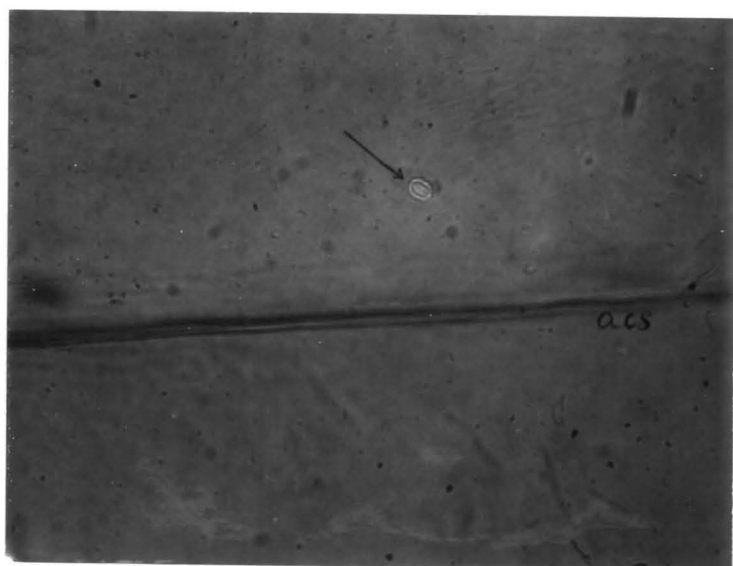


Fig. 1. Campaniform sensillum (arrow) of Periplaneta just anterior to the antecostal suture (acs). Note the orientation of the receptor; the long axis is angled slightly towards the mid dorsal line of the body (towards upper left in photograph). Photographed at 450 x.



Fig. 2A. Campaniform sensillum of Blaberus. Photographed at 100 x.

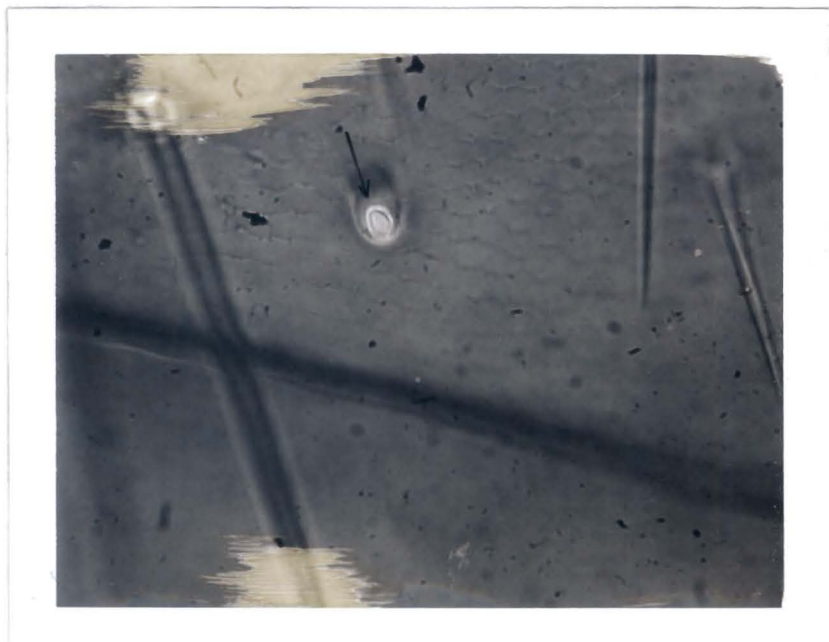


Fig. 2B. Same campaniform sensillum. Photographed at 450 x.

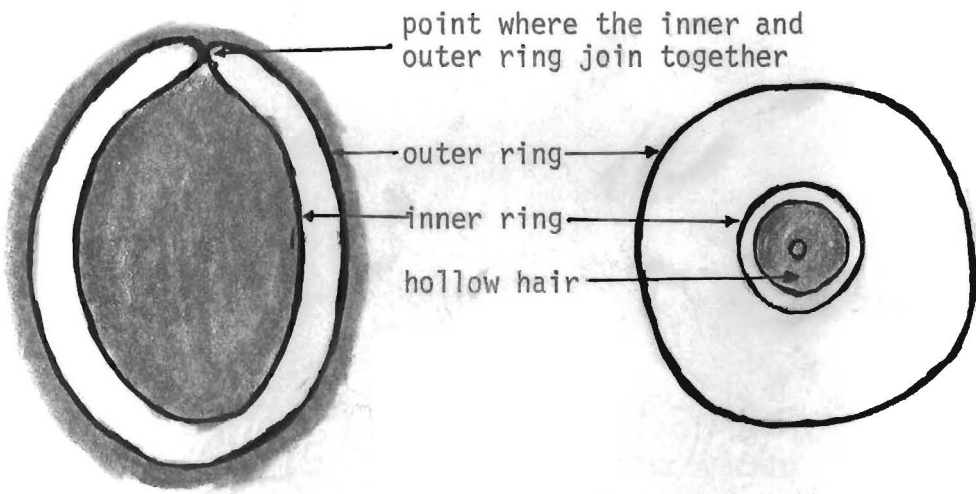


Fig. 3A. Diagram of appearance of campaniform sensillum.

Fig. 3B. Diagram of appearance of a hair socket containing stump of hair. (See photograph in Fig. 3D.)

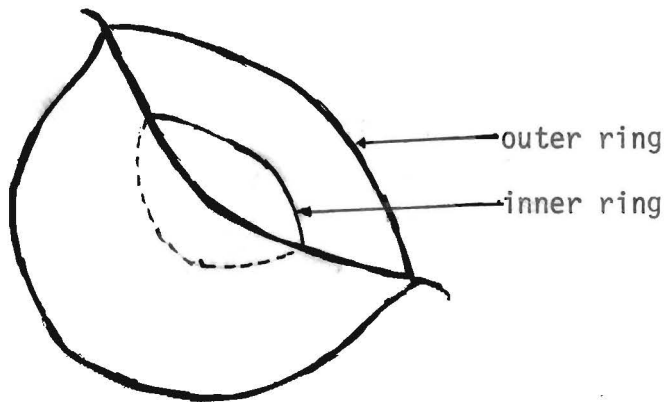


Fig. 3C. Diagram of an empty socket of tilted hair. (See photographs in Fig. 3E.)

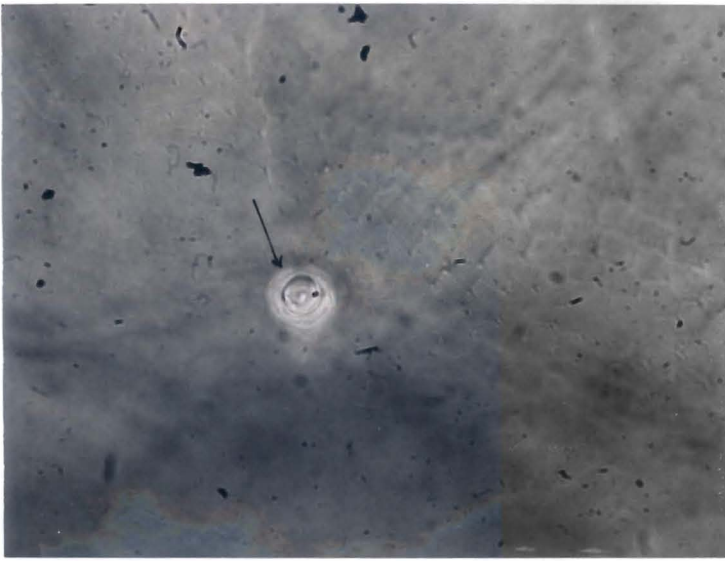


Fig. 3D. A hair socket (arrow) containing a hair broken off near its base. Photographed at 450 x.



Fig. 3E. Empty hair sockets (arrows). Photographed at 450 x.

plane of the cuticle surface (Fig. 3C & 3E), and these are quite easy to distinguish from the campaniform sensilla. Hair sockets (Fig. 3D & 3E) may also be oval and possess inner and outer rings but there is no point where the inner and outer rings join and the space between the rings does not appear brighter than the surrounding cuticle.

Campaniform sensilla on the dorsal surface of the abdomen:

On each of the abdominal segments from 1 through 9, there are two campaniform sensilla on the dorsal surface, one near each lateral edge (Fig. 4). The term dorsolateral campaniform sensilla (DLCS) is hereby suggested for those receptors. In Periplaneta they lie 0.63 ± 0.14 mm from the lateral edge and 0.072 ± 0.027 mm anterior to a transverse intrasegmental ridge of cuticle ("antecostal suture" of Snodgrass, 1935). The long axes of the sensilla incline 25 to 60 degrees from the long axis of the body, with the anterior ends pointing in toward the midline (as diagrammed in Fig. 4).

Three types of cuticle preparations were made: whole dorsal surface, whole ventral surface, and flattened lateral region. This last preparation was made by cutting animals parasagittally about 2 mm in from the lateral edge. After digesting soft tissue with KOH, the cuticle of the lateral edge was made into a flattened whole mount so that both the ventral and dorsal structures in the region of the pleural fold could be viewed in the same plane. The photomicrograph of Fig. 5 shows the area around a single DLCS in such a preparation. The diagram of Fig. 6 shows the relationship between the DLCS and adjacent structures in several segments.

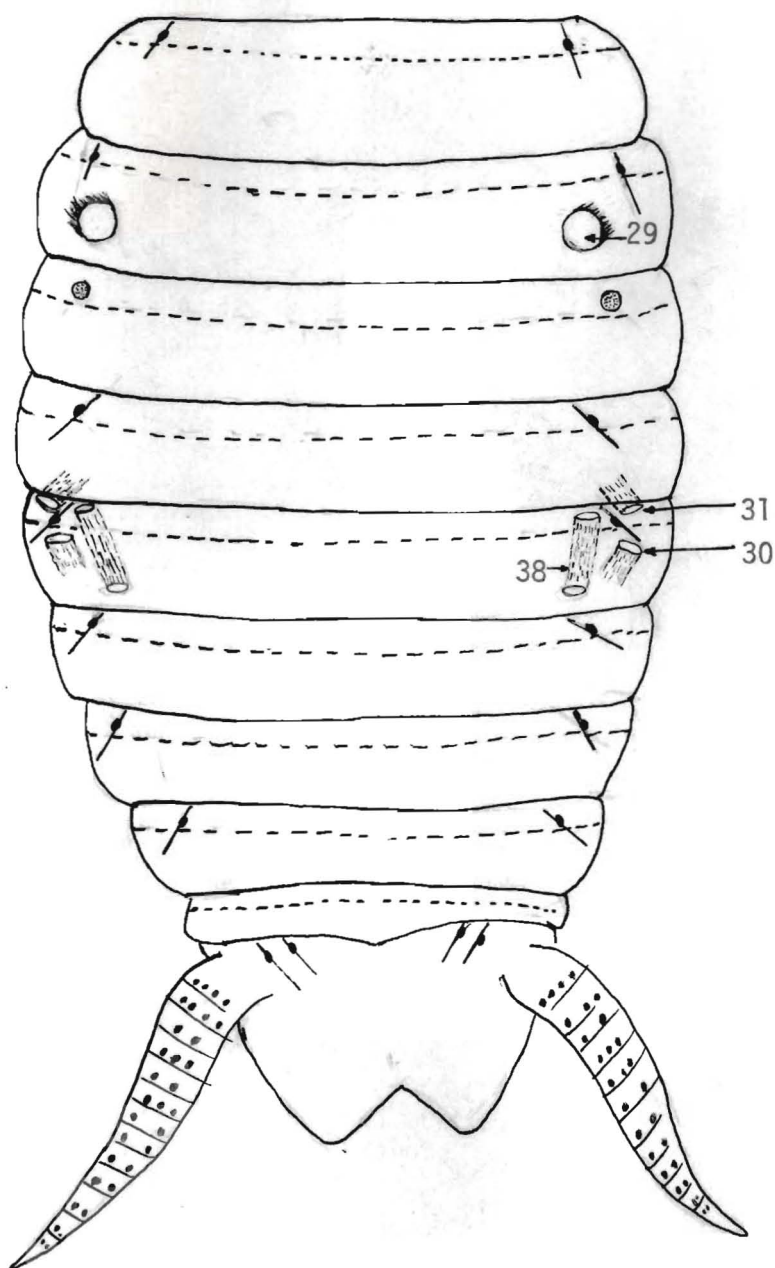


Fig. 4. Distribution of dorsally located abdominal campaniform sensilla of *Periplaneta americana*. Campaniform sensilla are indicated by dots. Lines through the dots indicate long axes of DLCS. Dashed lines indicate antecostal sutures. The following structures are segmental, but are shown only in a representative segment: 29 (see segment 2) = zones of dorsal attachment of large tergo-sternal muscles. 30, 31, and 38 (see segment 5) = dorsal attachments of 3 smaller muscles; dotted area (see segment 3) = region of cuticle involved in catch mechanism. Numbers from Shankland, 1965)



Fig. 5. Flattened whole mount of Periplaneta showing campaniform sensillum (arrow) and nearby structures, including spiracle opening (sp) and antecostal suture (acs). See Fig. 6 for diagram which shows orientation of these structures within a larger area of the abdominal cuticle. Note large number of (tactile?) hairs, especially along margins of tergites and sternites. Photographed at 100 x.

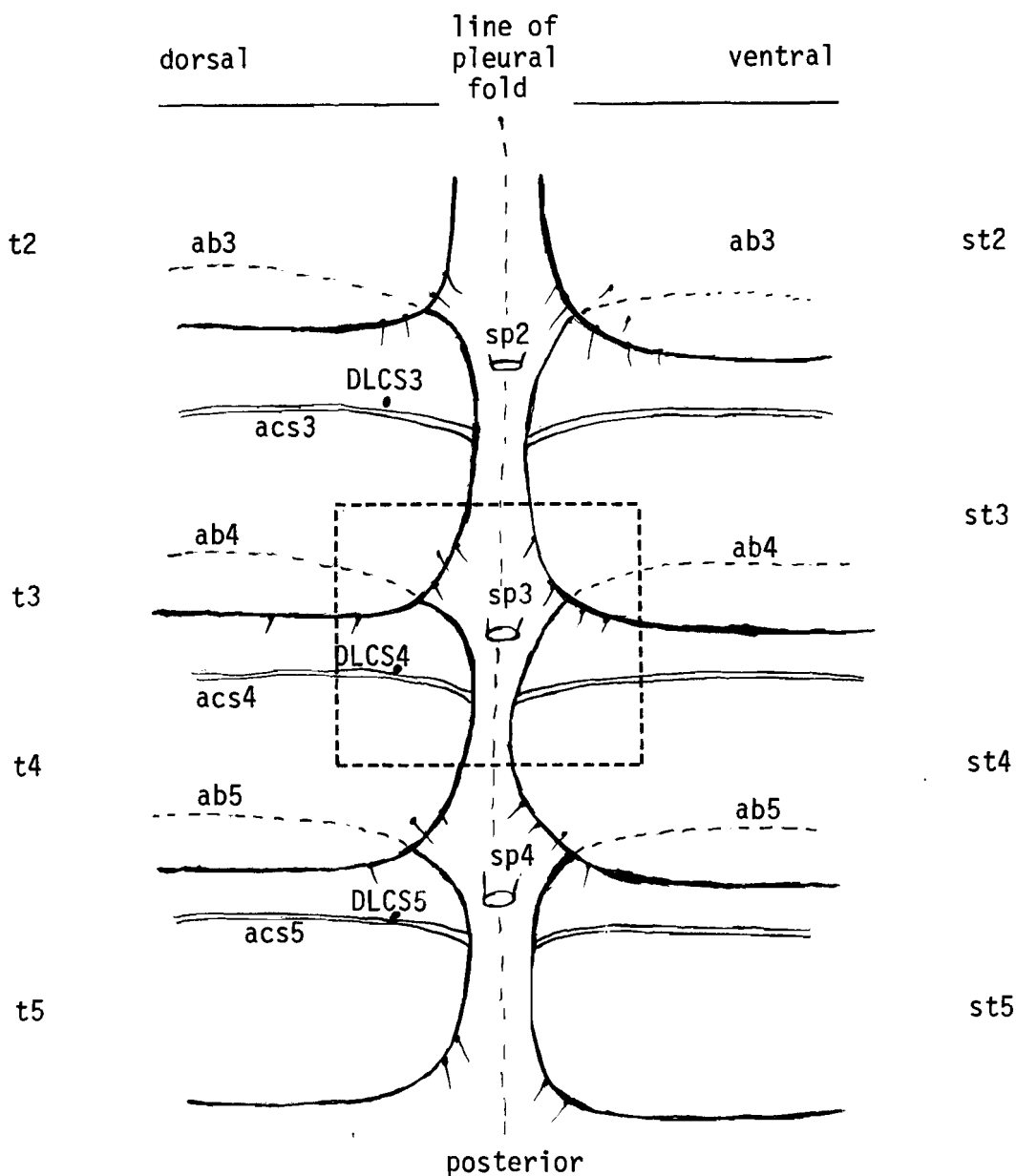


Fig. 6. Diagram of dorsolateral campaniform sensilla in relation to nearby structures. Drawn from flattened whole mounts of lateral cuticular structures. Area surrounded by dashed lines represents field of micrograph of Fig. 5. acs = antecostal suture; t = tergite; st = sternite; sp = spiracle; ab = anterior boundary of tergite or sternite; DLCS = dorsolateral campaniform sensillum. Numbers refer to abdominal segment.

Campaniform sensilla on the ventral surface of the abdomen:

Observations on the ventral surface of the abdomen showed one to four campaniform sensilla are located on each segment (Fig. 7). In Periplaneta sensilla lie within a 2.5 mm wide midventral band and within 0.08 mm anterior or posterior to the antecostal suture. In contrast to the DLCS, none lie close to the lateral edge. The term ventromedial campaniform sensilla (VMCS) is hereby suggested for these receptors. The orientation of the long axes of the VMCS varies somewhat from animal to animal. Fig. 7 shows how they were oriented in one particular specimen of Periplaneta. In general the long axes of the receptors point in toward the midline.

The situation is similar in Blaberus (Fig. 8) except the anterior ends of the campaniform sensilla on the first few segments point laterally rather than toward the midline and the sensilla were always found anterior to the antecostal suture.

The observations showed that the VMCS are more variable in distribution and orientation than the DLCS.

Other abdominal campaniform sensilla:

In addition to the repeating DLCS and the VMCS there are four dorsal and four ventral campaniform sensilla on the terminal segment, in pairs near the base of each cercus (Fig. 4 & 7). In addition, each cercus has approximately 35 individual campaniform sensilla, most occurring laterally in pairs at folding points in the cerci.

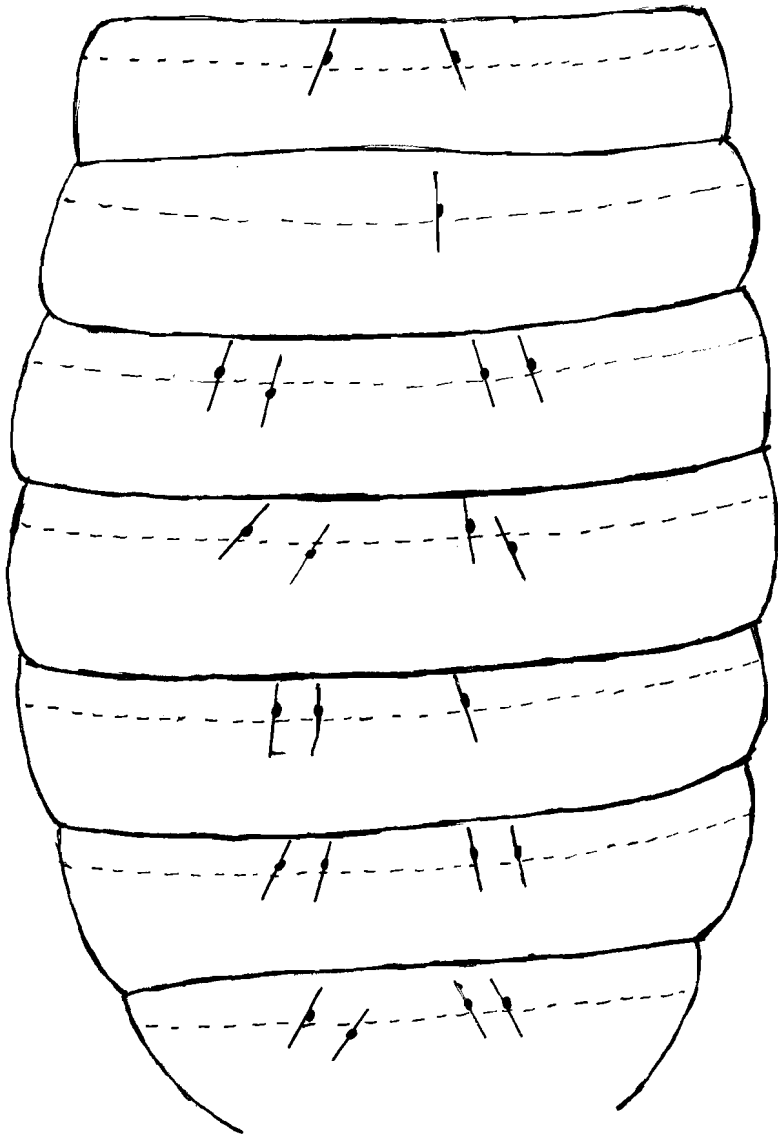


Fig. 7. Diagram showing orientation of ventromedial campaniform sensilla (VMCS) on sternites of a specimen of Periplaneta.

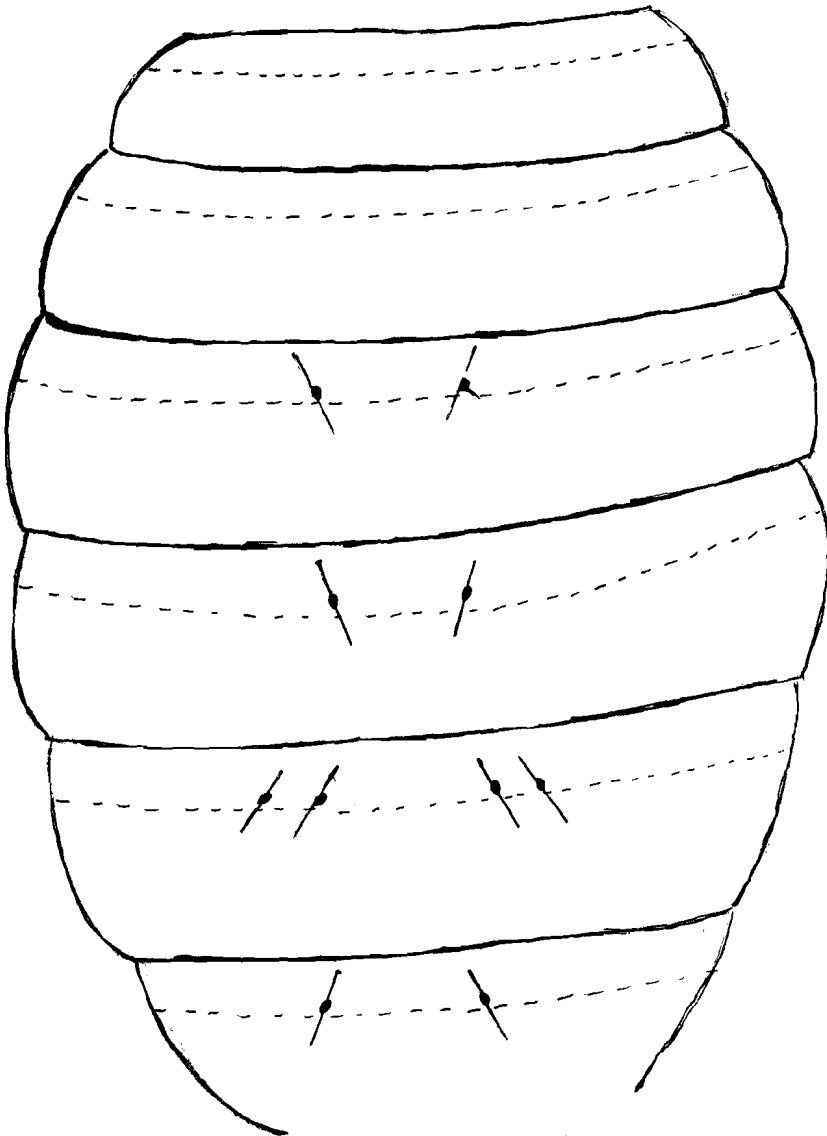


Fig. 8. Diagram showing orientation of ventromedial campaniform sensilla (VMCS) on sternites in a typical specimen of Blaberus. Note: campaniform sensilla were not found in first two segments.

Innervation of the dorsolateral abdominal campaniform sensilla:

Using methylene blue techniques, whole mounts of flattened lateral region were prepared to find out which nerve branch innervates the DLCS in Periplaneta. A branch of nerve A3 (Shankland, 1965; see Fig. 2 in appendix) innervates the DLCS region in Periplaneta and a branch of nerve DN3 (Smalley, 1963; Kehler, 1968) innervates DLCS in Blaberus.

Electrophysiology of the dorsolateral abdominal campaniform sensilla:

Using the information reported here on the location of the DLCS, Smalley (Personal Communication, 1973) has found it possible to record activity from a mechanoreceptor which is probably the DLCS. After cutting all but the branch of nerve DN3 which serves the area in Blaberus, gentle prodding of the tergal cuticle resulted in responses from two or three fibers, as seen in the spikes marked by dots in Fig. 9A and 9B. In addition, spikes of a much greater amplitude (marked by X's) could be recorded under the following special conditions which suggest that the DLCS was stimulated. In each tergite in the area surrounding the DLCS there is a circular region (dotted area in Fig. 4) which, when depressed with gradually increasing pressure, noticeably "buckles" downward, and when released buckles back up into position. When the cuticle pops downward (or occasionally when it pops upward) the large amplitude spikes are produced. The behavior of the cuticle around the DLCS suggests a "catch" mechanism such as has been described for the movement of insect wings. The possible significance of this observation will be left for the discussion.

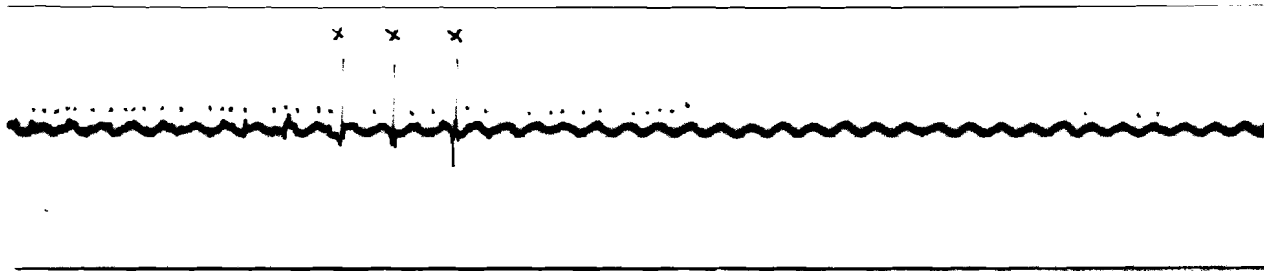


Fig. 9A.

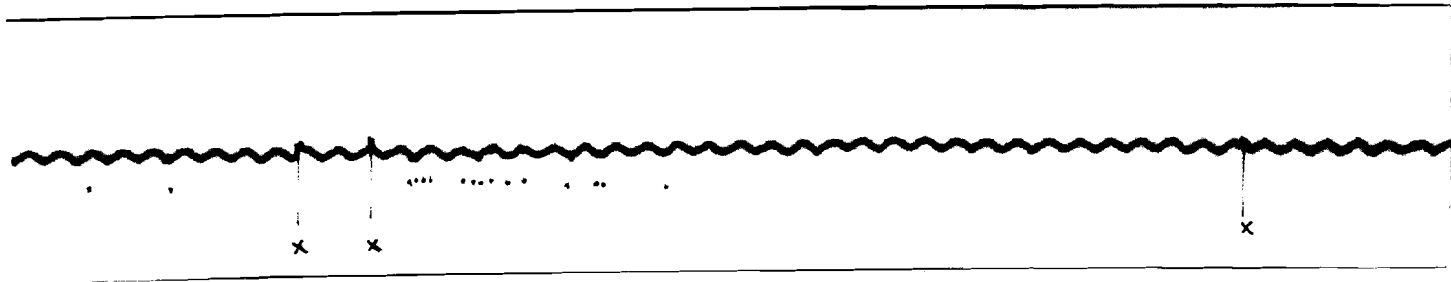


Fig. 9B.

100 μ Sec.

Fig. 9A & 9B. Two records showing responses from DN3 in Blaberus to pressure applied to area surrounding DLCS. The large amplitude spikes (marked by x's) occurred when cuticle buckled. Small spikes (marked by dots since they are hard to detect in the 60 cycle interference) occurred in response to gentler prodding as well as in response to buckling. Records courtesy of Dr. K. N. Smalley.

Study of cross sections:

Even after an extensive search of the available cross sections no evidence could be found of the DLCS. It is very difficult to get consistently good sections of cuticle and it is probable that the crucial sections were lost in preparations. However, a typical campaniform sensillum was found during histological examination of cross sections of the midventral region (Fig. 10A and 10B). There could be seen a dome-shape body, the cap of which is surrounded by cuticle. The thread-like distal process of the sense cell could be seen to run down through a transparent canal. The structure is very similar to those described by Snodgrass (1935, see diagram, Fig. 10C). It was not possible to trace the distal process of the sense cell to any one of the cell bodies shown in the photograph.



Fig. 10A. Cross section of the mid-ventral campaniform sensillum of Blaberus. Photographed at 450 x magnification.



Fig. 10B. Same as Fig. 10A, photographed at 1000 x magnification.

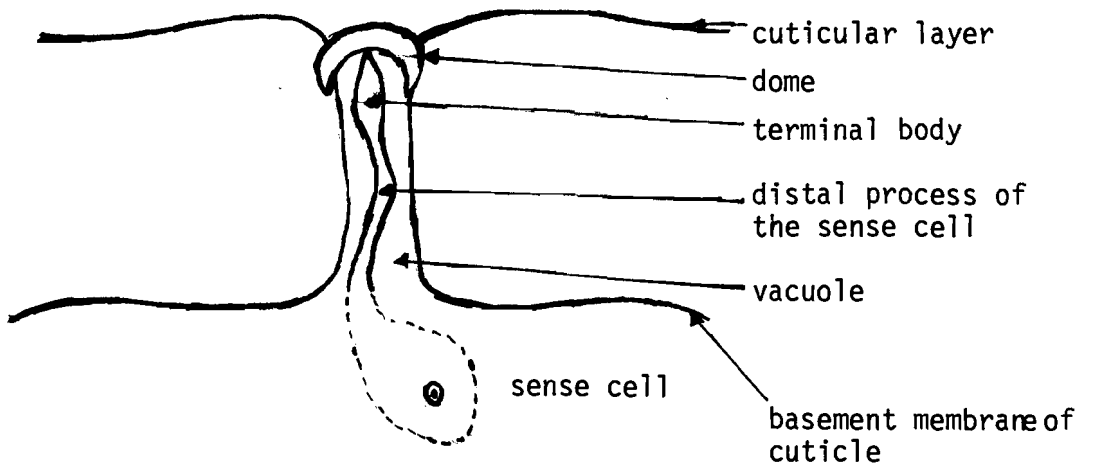


Fig. 10C. Diagram of the structures seen in Fig. 10A & 10B. Parts labeled as in similar diagram of Snodgrass (1935).

DISCUSSION

A. Distribution of the campaniform sensilla in the cockroach abdomen.

Compared to previously described campaniform sensilla, the DLCS and VMCS of cockroach are somewhat unusual in their distribution since they are found as single, isolated receptors. Isolated campaniform sensilla have been described but it is more common for campaniform sensilla to be found in groups in areas where compressions and stresses are most likely to occur (Pringle, 1938, 1948). In contrast to the small numbers of sensilla reported here, McIndoo (1914) mapped very large numbers of campaniform sensilla on the honey bee. On the drone, he found 1,998 on the wing bases and 606 on the legs. On the worker bee he found 1,510 on the wings, 658 on the legs, and 100 on the sting. On the queen bee he found 1,310 on the wings, 450 on the legs, and 100 on the sting.

Having small numbers of receptor cells in insects is not entirely unprecedented, the best example being the moth ear with only two sense cells per ear (Roeder and Treat, 1961). But having only single receptors eliminates one possibility for handling the range of possible stimulus strengths, that of having several receptors with different thresholds. This suggests that whatever may be the specific function of these receptors, they are not able to report detailed information on stimulus intensity.

B. Orientation of abdominal campaniform sensilla.

The DLCS and VMCS are also unusual in that their long axes showed (with a little variability) a definite pattern of orientation (see Fig. 4, 7, and 8) so they are probably selectively responsive to shearing stresses applied in specific directions. This does not fit with an earlier conclusion of Pringle (1948) who found that where single isolated campaniform sensilla are found in the cockroach leg they tend to be circular rather than oval. This suggested that isolated campaniform sensilla are non-specific as to the direction of mechanical deformation they detect.

C. Position with respect to the antecostal suture.

The campaniform sensilla studied here are closely associated with the antecostal suture, being found within 0.08 mm of the suture in the case of the VMCS and 0.03 mm in the case of the DLCS. The "suture," which is a narrow, transverse structure providing strength to the tergites and sternites might be better termed a rib. When forces are put on the cuticle, maximum bending could occur just anterior or posterior to these transverse stiffeners. The VMCS lie under longitudinal muscles and might be activated by their contractions, which cause telescoping movements of the abdomen (Fig. 11A). The DLCS lie close to the attachments of several muscles which compress the abdomen dorsoventrally (Fig. 11B). None of these muscles seems ideally situated to trigger a response in the DLCS. However, 31 has an attachment close by, and 29, though somewhat more distant, is the strongest of the abdominal muscles and its contractions might well

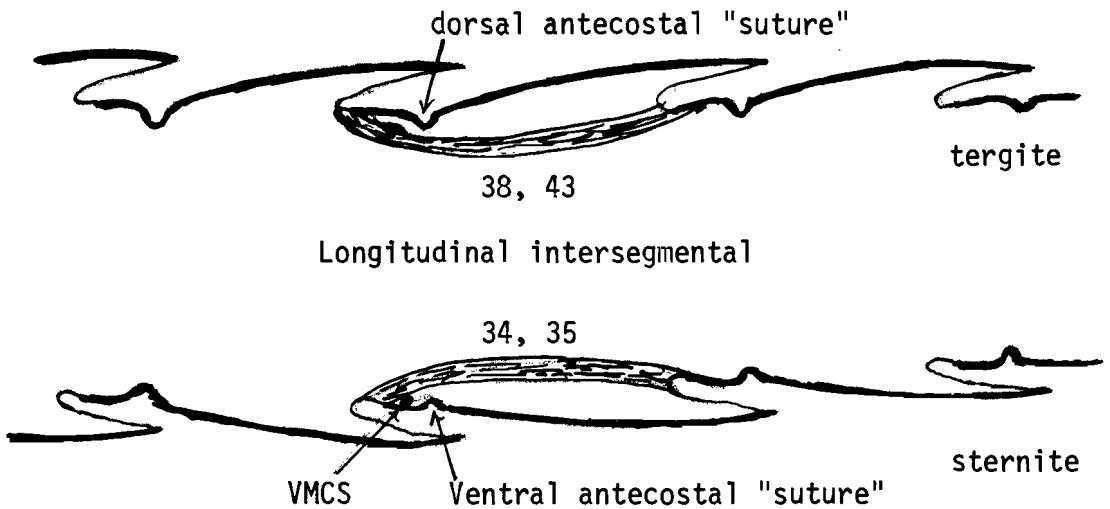


Fig. 11A. Diagram to show how VMCS might be activated by contractions of longitudinal intersegmental muscles. Diagram represents tergites and sternites cut sagittally near the midline.

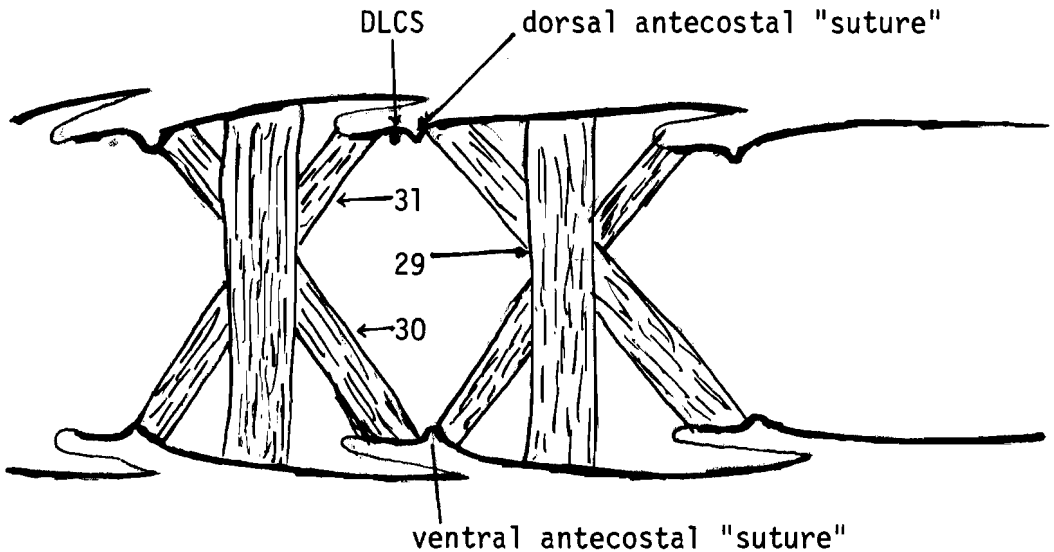


Fig. 11B. Diagram to show how DLCS might be activated by contractions of dorso-ventral muscles such as the large sterno-tergal muscle (29) or the smaller intersegmental muscles (30 or 31). Diagram represents tergites and sternites cut sagittally near lateral edge.

stimulate the DLCS. The orientation of some of these muscles is also shown in Fig. 4. Muscle 31 is particularly interesting since the orientation of its fibers is similar to that of the long axes of the DLCS.

D. Buckling of the cuticle; another possible catch mechanism.

The preliminary electrophysiological experiments on the DLCS (Fig. 9) suggested that it was necessary for the cuticle near the DLCS to undergo buckling before the receptor would fire. For this to happen, the cuticle would have to be depressed quite strongly, either by outside forces or by internal muscles. If it is true that this receptor fires only when the cuticle buckles, then the receptor has one very definite threshold. One possibility is that this receptor ordinarily tells the central nervous system when a critical level of dorsoventral compression has been achieved by contraction of a muscle such as muscle 29, the sternotergal muscle, an important muscle producing the ventilation movements.

E. Possible relationship of DLCS to ventilatory control system.

The last thoracic and the six abdominal ganglia comprise a respiratory control mechanism in cockroaches (Case, 1957; Smalley, 1963.) These central ganglia control the frequency and strength of contraction of muscles which pump air through the tracheal system. They also cause the spiracles to open and close in coordination with the compression movements so air is drawn in posteriorly and pumped anteriorly.

Not unexpectedly the cockroach respiratory control mechanism shows parallels with the vertebrate mechanism. The respiratory movements increase in frequency and depth in response to higher CO_2 concentrations (Case, 1957; Smalley, 1963). Also, the respiratory control mechanism is evidently influenced by feedback from a mechanoreceptor. Farley et al. (Farley, Case and Roeder, 1967; Farley and Case, 1968) recorded respiratory-induced activity from a peripheral mechanoreceptor and also showed that the frequency of the respiratory output could be modified by artificially increasing the input from the periphery. It is tempting to identify the receptor with the DLCS. However, Farley et al. recorded from a point near the base of the segmental nerve and did not identify the branch involved. Since there are several other mechanoreceptors, including the tonic stretch receptors (Finlayson and Lowenstein, 1958) and two sets of phasic receptors (Kehler et al., 1970; Florentine, 1967, 1968) additional recording will have to be done on the nerve branches to establish which of these receptors is the one Farley and Case (1968) found to be activated during ventilatory movements.

F. Relationship between the abdominal campaniform sensilla and internal stretch receptor organs.

Each of the campaniform sensilla described in this study lies close to another type of mechanoreceptor, a stretch receptor of the scolopophorous (chordotonal) type with sensory endings embedded in a strand of fibrous connective tissue. Near the VMCS lie the ventral attachments of a receptor (Kehler et al., 1970) called the ventral phasic receptor (VPR) because it responded phasically to displacements

of the abdomen. Near each DLCS lies a receptor called an abdominal vibration receptor by Florentine (1967, 1968) but recently called the lateral phasic receptor (LPR) by Smalley and Kehler (in preparation). Both the LPR and VPR respond phasically to stretching or bending of the abdomen. The LPR also responds to airborne sounds (Florentine, 1967, 1968) but the threshold levels for most specimens are so high as to suggest that sound reception is not their normal function.

Campaniform sensilla are also found in close association with chordotonal organs in the wing bases of many insects and in the halteres of flies (Zacwilichowski, 1933, 1934; cited in Pringle, 1957). It is tempting to think that these close associations of campaniform with chordotonal sensilla are of functional significance. One possibility is that these two kinds of receptors respond somewhat differently to particular mechanical inputs and that the central nervous system can compare the two inputs centrally. The vertebrate central nervous system is thought to make such a comparison between the output of the golgi tendon organs, which are responsive to muscle contraction and external stretch, with the output of spindle organs, which are responsive only to external stretch (Granit, 1955). However, until more is known about the response characteristics of both the abdominal campaniform sensilla and their associated chordotonal organs, this remains a highly speculative idea.

SUMMARY

Isolated campaniform sensilla were found on the abdominal tergites and sternites of the cockroaches, Blaberus craniifer and Periplaneta americana. On each side of each tergite a dorsolateral campaniform sensillum (DLCS) is found near the pleural margin. One to four ventromedial campaniform sensilla (VMCS) are found more centrally on each sternite. Both DLCS and VMCS are closely associated with the rib-like reinforcing structures ("antecostal sutures") of the tergites and sternites. The DLCS are at the edge of a region of cuticle which undergoes buckling movements. While there is little doubt that these are mechanoreceptors their function in the animal is not yet clear. It is possible that they function as receptors for muscle contractions, possibly providing sensory feedback for controlling ventilatory movements.

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