A COMPARATIVE ANATOMICAL STUDY OF THE STERNAL GLAND IN ARIZONA TERMITES (ISOPTERA)

by

Roger Stanley Stasiak

A Thesis Submitted to the Faculty of the

DEPARTMENT OF ENTOMOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

MASTER OF SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

1 9 6 8

STATEMENT BY AUTHOR

This thesis has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Roger S. Stasiak

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

William L. Nutting
WILLIAM L. NUTTING
Professor of Entomology

February 28, 1968
Date

ACKNOWLEDGMENTS

The author wishes to express his sincere appreciation and thanks to Dr. William L. Nutting for his invaluable assistance during the course of this study, particularly for supplying preserved specimens of various termites from his collection.

To Michael Lindsey, for his willing assistance in collecting *Zootermopsis*, and John Beard for supplying living soldiers and workers of *Heterotermes aureus*, I am most grateful.

The author wishes to acknowledge that this research was made possible through National Science Foundation Graduate Traineeship 5702-800-652-606.

Lastly to my wife, Ann, for her loving encouragement and patience throughout the course of this work go my unending gratitude and thanks.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

ABSTRACT

The position, size and cellular arrangement of the sternal gland in eight species of termites, representing the four families found in Arizona, were studied using stained serial sections and vitally stained, living specimens. The gland, which is responsible for trail following behavior, can be placed in one of four basic cellular arrangements according to family.

In the Hodotermitidae, *Zootermopsis laticeps*, *Z. nevadensis*, and *Z. angusticollis* have the sternal gland in the fourth abdominal sternite, and divided in a dorso-ventral arrangement of secretory and columnar cells, covered with a striated cuticle. Campaniform sensilla are present, with processes going vertically through the gland and terminating in the cuticle.

The gland in *Marginitermes hubbardi* and *Pterotermes occidentis*, kalotermitids, is in the fifth abdominal sternite, and has secretory, intercalary, and sensillar cells intermixed above a cuticle which is striated only along the posterior margin of the gland.

Reticulitermes tibialis and *Heterotermes aureus*, representing the Rhinotermitidae, have the gland in the fifth abdominal segment with secretory cells anteriorly

and a concentration of campaniform sensillar processes posteriorly. A concave depression or space is present between the ends of these processes and the cuticle, which is striated over the entire surface of the gland.

In Gnathamitermes perplexus, a termitid, the gland is in the fifth abdominal segment and is composed of intermixed glandular and sensillar cells. The cuticle is striated over the entire surface of the gland.

INTRODUCTION

The principal purpose of this study was to examine several species of termites found in Arizona to determine if they possessed sternal glands and, if so, to describe the position, size, and cellular arrangements of these glands. A secondary objective was to examine additional representatives of the genus *Zootermopsis* in order to verify the position of the sternal gland in this genus. Stuart (1964) reported that the sternal gland in *Z. nevadensis* (Hagen) is located in the fifth abdominal sternite.

Stuart (1963) has identified the sternal gland as the source of the trail-laying substance in both *Z. nevadensis* and *Nasutitermes corniger* (Motschulsky). He also (Stuart, 1964) did the first detailed morphological work on the sternal gland, using the hodotermitid, *Z. nevadensis*. Satir and Stuart (1965) continued with the detailed microstructure of the gland in this species and reported finding a new organelle, an apical microtubule, in the cells of the gland. Noirot and Noirot-Timotheé (1965a) described the morphology of the sternal gland in *Kalotermes flavicollis* (F.), a kalotermitid, using electron microscopy, and found it to be similar in structure to that in *Z. nevadensis*.

Smythe and Coppel (1966) reported on the morphology of the gland in the Rhinotermitidae when they studied the sternal gland in Reticulitermes flavipes (Kollar). While the gland is similar in its location to that of K. flavicollis, its morphology is markedly different. The primary difference involves the concentration of campaniform sensilla-like processes which comprise the posterior portion of the gland in R. flavipes.

Among the Termitidae the gland has been studied by Pasteels (1965) in Nasutitermes lujae workers, by Moore (1966) in N. exitosus (Hill), N. walkeri (Hill), and N. graveolus (Hill), and in various other genera by Noirot and Noirot-Timothée (1965b). Moore (1966) isolated the scent pheromone of N. exitosus and identified it as a diterpenoid hydrocarbon with a molecular weight of 272.

MATERIALS AND METHODS

The species of termites used in this study were chosen so as to include representatives of each of the four families in Arizona. Also of importance was the fact that the sternal glands of these species had not been studied previously.

Zootermopsis laticeps (Banks), the southwestern rotten-wood termite, is the only representative of the Hodotermitidae (damp-wood termites) in Arizona. The inclusion of this species was desirable as Stuart's work (1963, 1964) was done with a closely related species, *Z. nevadensis* (Hagen). *Z. laticeps* is the largest termite in the United States, with an alate body length of 12 mm. It is easily maintained in the laboratory. Soldiers and nymphs were collected from injured willow trees along the San Pedro River near Hereford, Cochise County, Arizona. Alates were obtained as they appeared in laboratory colonies. Specimens of *Z. nevadensis* and *Z. angusticollis* (Hagen) were obtained from the collection of Dr. W. L. Nutting.

Two species in the Kalotermitidae (dry-wood termites) were studied: *Pterotermes occidentis* (Walker), the large, primitive dry-wood termite; and *Marginitermes* *hubbardi* (Banks), the light, western dry-wood termite. Nymphs and soldiers of *P. occidentis* were collected from dead palo verde branches on the Santa Rita Range Reserve near Sahuarita, Pima County, Arizona. Alates were collected as they appeared in laboratory colonies. Additional alates were provided by Dr. W. L. Nutting from his collection. Nymphs and soldiers of *M. hubbardi* were collected in the skeleton of a saguaro cactus near Soldier's Trail in the vicinity of Tucson, Pima County, Arizona. Alates were collected at light traps in Tucson, Arizona.

Alates of *Heterotermes aureus* (Snyder), the desert subterranean termite, were collected from light traps in Tucson, Arizona, while soldiers, nymphs and workers were collected from pieces of buried timber in the same location. Soldiers, nymphs and workers of *Reticulitermes tibialis* (Banks), the arid land subterranean termite, were collected in a dead pine stump near Rose Canyon Lake, on Mt. Lemmon, in the Santa Catalina Mts., Pima County, Arizona. Alates were obtained from the collection of Dr. W. L. Nutting. Both *Heterotermes* and *Reticulitermes* are representatives of the Rhinotermitidae (subterranean termites).

Gnathamitermes perplexus (Banks), the tube-building desert termite represents the Termitidae in this study. Soldiers, workers and nymphs were collected from partially buried timber and alates were collected from light traps, both located in Tucson, Arizona.

In general, standard histological techniques were followed in making stained, serial sections of the termites. Living insects were fixed in aqueous Bouin's solution after being cut between the metathorax and mesothorax to allow better penetration. Specimens from alcoholic collections were placed directly in absolute alcohol. The abdomens were then dehydrated, embedded in Tissuemat[R] and sectioned at ten or twelve microns. Sections were stained with hematoxylin-eosin-orange G for cellular detail or Mallory's triple stain for cuticular details. Living specimens of *Zootermopsis* and *Pterotermes* were also injected with aqueous acid fuchsin. When examined under a dissecting microscope the position and lateral extent of the sternal gland could be distinguished as a milky white area against the red background of the acid fuchsin in the body.

Drawings were made by tracing the outlines from projected photographic negatives and from the projected images of the stained sections in a Rayoscope micro-slide projector.

RESULTS

Hodotermitidae - *Zootermopsis laticeps*, *nevadensis* and *angusticollis*

Morphology of the Gland

In *Zootermopsis laticeps* the sternal gland was found in all three forms studied: alates, soldiers and nymphs. The gland lies in the anterior part of the fourth abdominal segment, ventral to the third abdominal ganglion (Fig. 5). As viewed externally in a vitally stained specimen (Fig. 1) the gland is about three times broader than long and is thickest in the midline. The gland is composed of modified epidermal cells of the fourth abdominal sternite, which are arranged in three distinct layers: a layer of columnar cells bordering the endocuticle; a middle layer of lightly staining, irregularly shaped, vacuolated cells; and a basal layer of darker staining secretory cells adjacent to the basement membrane. The cuticle covering the surface of the gland is striated with many fine, parallel lines running from the gland toward the outside, perpendicular to the plane of the cuticle. Stuart (1964) found similar striations in the endocuticle of the gland of *Z. nevadensis* and suggested that these were pore canals which might facilitate passage of a substance from

Fig. 1. Hodotermitidae: ventral aspect of abdomen. Position and lateral extent of the sternal gland in male alate of _Zootermopsis laticeps_. (Key to abbreviations on page 30)

Fig. 2. Kalotermitidae: ventral aspect of abdomen. Position and lateral extent of sternal gland in male alate of _Pterotermes occidentis_. (Key to abbreviations on page 30)

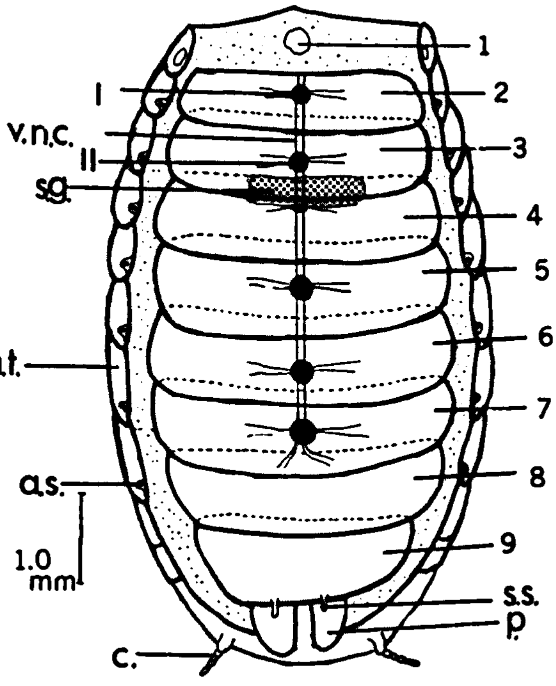

Fig. 1. Hodotermitidae: ventral aspect of abdomen

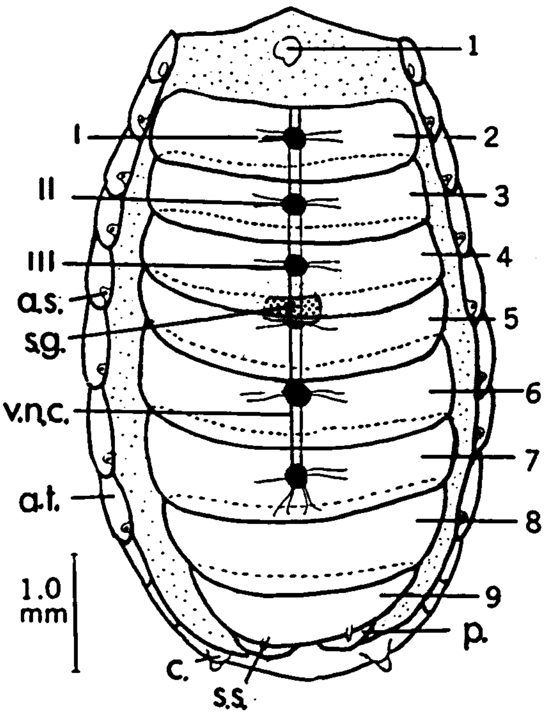

Fig. 2. Kalotermitidae: ventral aspect of abdomen

Fig. 3. Rhinotermitidae; ventral aspect of abdomen. Position and lateral extent of sternal gland in male alate of *Heterotermes aureus*. (Key to abbreviations on page 30)

Fig. 4. Termitidae: ventral aspect of abdomen. Position and lateral extent of sternal gland in male alate of *Gnathamitermes perplexus*. (Key to abbreviations on page 30)

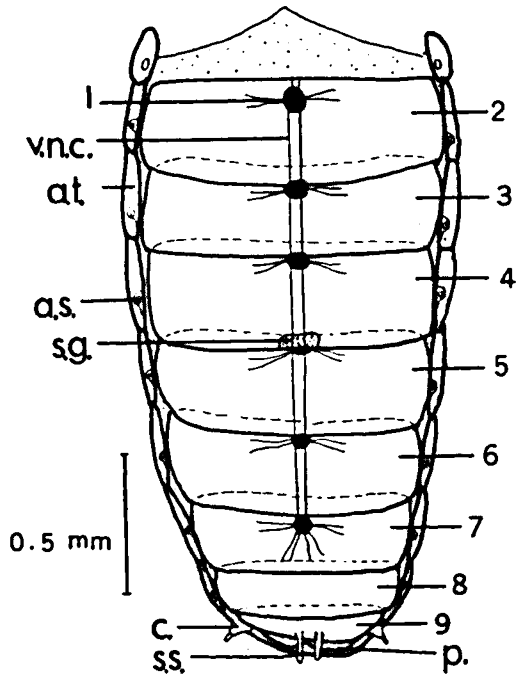

Fig. 3 Rhinotermitidae: ventral aspect of abdomen

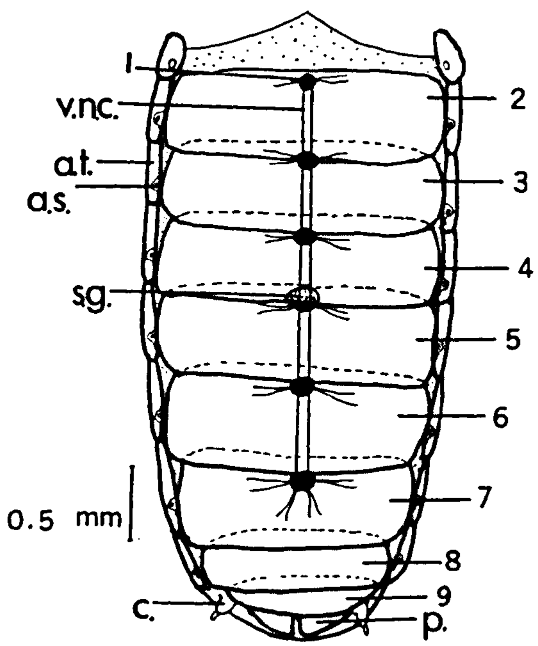

Fig. 4 Termitidae: ventral aspect of abdomen

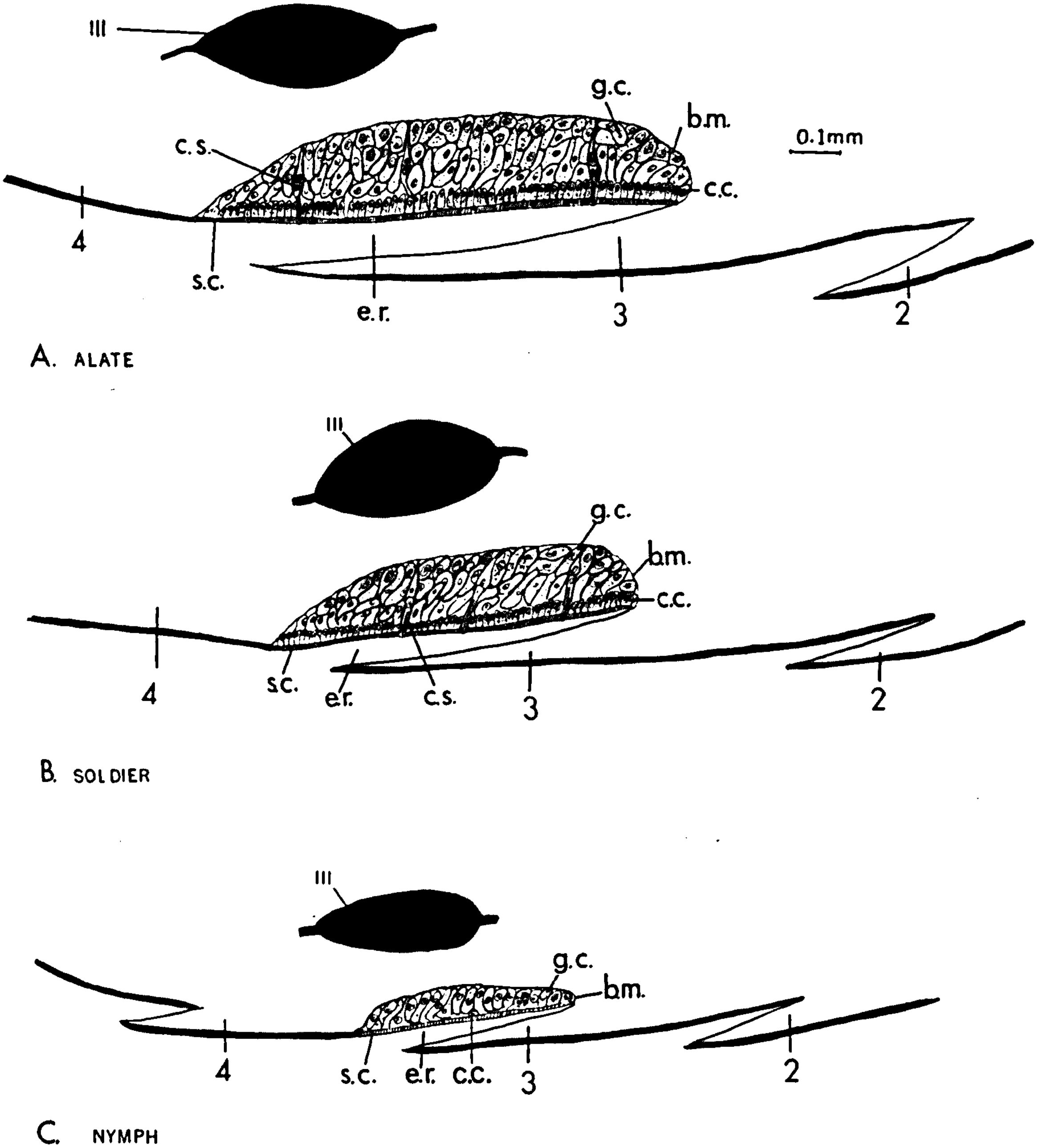

Fig. 5. Hodotermitidae: Zootermopsis

Parasagittal view of ventral wall of abdomen of A., alate, B., soldier, and C., nymph, showing position and cellular composition of sternal gland. (Key to abbreviations on page 30) the gland to the outside. In any case, this striated condition of the cuticle is not seen in any other sternite and suggests a possible relationship with the functioning of the gland. The third abdominal sternite overlaps the gland-bearing (anterior) portion of the fourth segment and the space formed between the third sternite and the cuticle overlying the gland may thus form an external reservoir for the secretion of the gland.

It seems appropriate to point out here an error made by Stuart in reporting the position of the sternal gland in *Z. nevadensis* (Stuart, 1964). He stated that the gland is in the fifth abdominal sternite, ventrally adjacent to the third abdominal ganglion. To resolve this apparent discrepancy specimens of all three species of the genus were sectioned and compared to determine the exact location of the gland. The gland in all three species of *Zootermopsis* lies in the fourth abdominal sternite, adjacent to the third abdominal ganglion. Child (1934, pp. 80-81), in his description of the internal anatomy of *Z. nevadensis*, placed the third abdominal ganglion dorsal to the fourth abdominal sternite. It is thus evident, in order to be consistent with the location of the abdominal ganglia, that the gland lies in the fourth abdominal sternite, not in the fifth. Further support for placing the sternal gland in the fourth sternite in *Zootermopsis* may be gained by considering the positions of the eight abdominal spiracles (Fig. 1 and Light, 1934, p. 56). These spiracles are on the first eight segments of the abdomen and appear in line with their corresponding tergites and sternites. The gland in all three species is in line with the fourth abdominal spiracle, and therefore belongs with the fourth abdominal sternite. In counting the abdominal sternites in Zootermopsis the first sternite appears only as a small, raised, sclerotized area which is in line with the first abdominal spiracle. No ganglion is present in this first abdominal segment (Child, 1934, pp. 80-81). The second and succeeding abdominal sternites are large, well-developed structures. The six abdominal ganglia lie dorsal to these, in the second to seventh abdominal segments. Thus, it seems extremely likely that Stuart mistook the fourth abdominal sternite for the fifth when he reported the position of the sternal gland in Z. nevadensis.

Variations in the Gland

The sternal glands of the alates and soldiers of Z. laticeps are very similar except for size. In the alates, the gland is slightly larger, in both relative length and thickness, than the gland in the soldier. It averages about 0.90 mm in length by 0.175 mm in thickness, while the sternal gland of the soldier measures 0.75 by 0.15 mm.

In nymphal forms the gland appears in the youngest individuals as a single layer of cells (Fig. 5, C). The sternal gland in each of the instars appears larger and more developed until, in the brachypterous stages, the glands are just slightly smaller than those in the soldiers and alates.

The sternal glands in *Z. nevadensis* and *Z. angusticollis* are identical in structure to that in *Z. laticeps*.

Kalotermitidae - Pterotermes occidentis and Marginitermes hubbardi

Morphology of the Gland

A sternal gland was found in all forms of *M. hubbardi* and *P. occidentis* examined. The gland lies in the anterior part of the fifth abdominal sternite, ventral to the fat body, longitudinal muscles, and the fourth abdominal ganglion. Three types of cells make up the gland: secretory cells, intercalary cells, and campaniform sensilla, all of which are intermixed in a layer between the cuticle and the basement membrane (Fig. 6). The secretory cells are globose and vacuolated, and have deeply staining nuclei, while the intercalary cells are tall, thin and columnar. The sensilla have processes terminating in the cuticle. The cuticle is striated, but only along the posterior portion of the gland (Fig. 6).

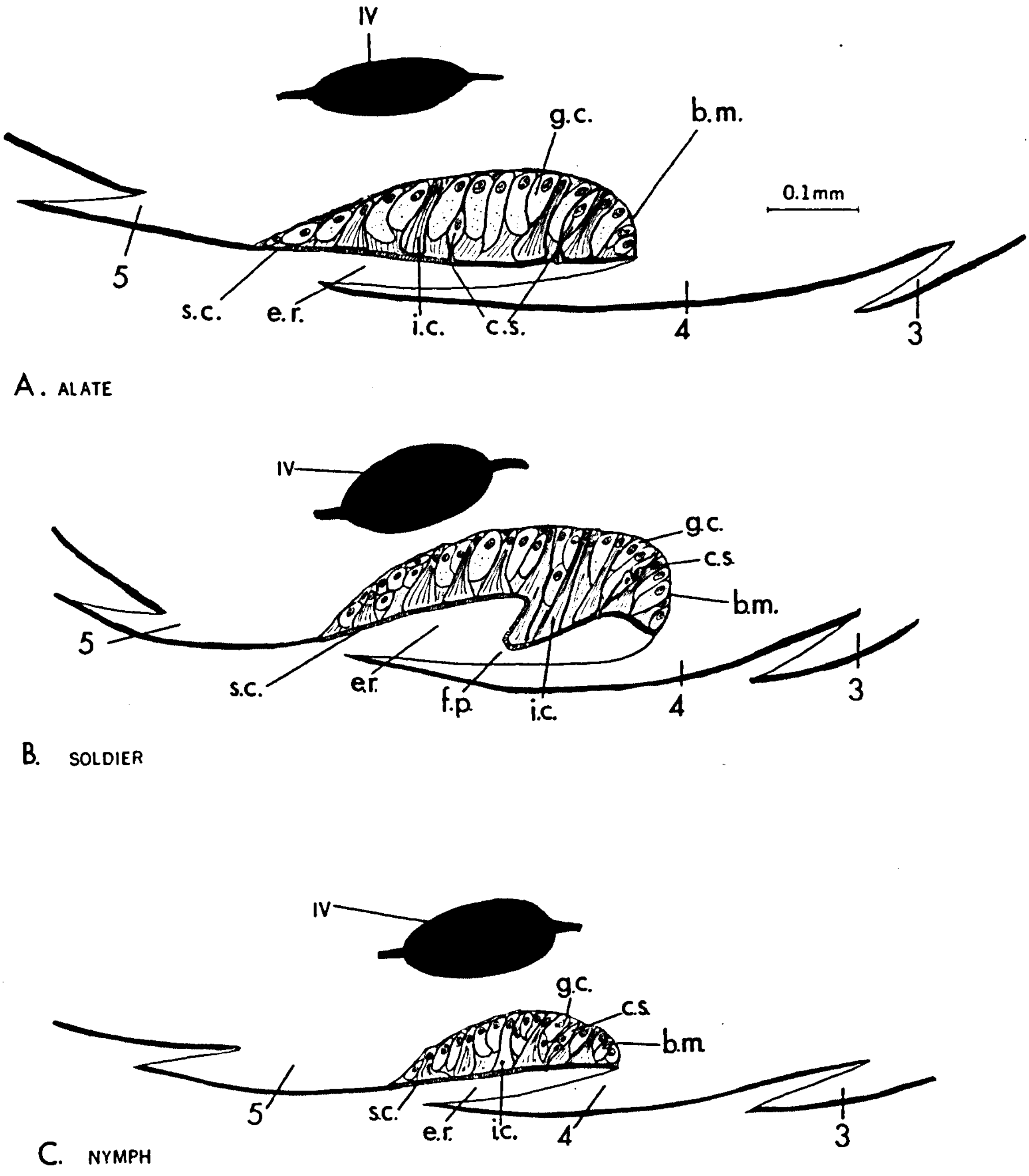

Fig. 6. Kalotermitidae: Marginitermes

Parasagittal view of ventral wall of abdomen of A., alate, B., soldier, and C., nymph, showing position and cellular composition of sternal gland. (Key to abbreviations on page 30)

Vitally stained nymphs and alates of Pterotermes showed that the sternal gland does not extend so far laterally as that of Zootermopsis, but is roughly as broad as long ventrally (compare Figs. 2 and 6). The posterior portion of the fourth abdominal sternite forms what may be considered an external reservoir for the secretion of the gland.

Variations in the Gland

The sternal glands of the alates, soldiers and nymphs of Pterotermes, and alates and nymphs of Marginitermes, appeared identical in structure, with the only difference being one of size. Approximate sizes of the glands are as follows (length x width in mm): Pterotermes - alate, 0.4 x 0.1; soldier, 0.4 x 0.08; large nymph, 0.35 x 0.1; Marginitermes - alate, 0.3 x 0.075; soldier, 0.3 x 0.1; large nymph, 0.3 x 0.05. The only structural variation in this family was seen in the soldier caste of Marginitermes, in which the gland has a median, finger-like projection (Fig. 6, B) directed into the external reservoir.

Rhinotermitidae - Heterotermes aureus and Reticulitermes tibialis

Morphology of the Gland

A sternal gland was found in all of the castes examined: alates, soldiers and worker-nymphs. The gland is located in the anterior part of the fifth abdominal sternite, ventral to the fat body, longitudinal muscles and adjacent to the fourth abdominal ganglion. The gland extends laterally only a short distance from the midline of the termite and is only slightly wider than the fourth abdominal ganglion (Fig. 3). It is composed of two parts, the anterior being made up of irregularly shaped, vacuolated cells, with deeply staining nuclei. From the basal area of these secretory cells many long, thin processes arise from darkly staining, flattened nuclei, and curve posteriorly along the basement membrane and ventrally to the endocuticle, to form the posterior portion of the gland. These resemble the processes of campaniform sensilla in the sternal gland of Reticulitermes flavipes (Kollar), as described by Smythe and Coppel (1966). The cuticle is striated over the entire surface of the gland.

A cup-shaped, concave space is present at the juncture of the sensillar processes and the endocuticle at the posterior part of the gland in both Reticulitermes and Heterotermes (Fig. 7, A). The fourth abdominal sternite forms an external reservoir where it covers the area of the gland in the fifth sternite, as in the kalotermitids.

Variations in the Gland

Since the sternal glands of Reticulitermes and Heterotermes are identical in structure, varying only in relative size, only drawings of the gland of Heterotermes are presented (Fig. 7). The approximate length and width of the glands in the alates are: Reticulitermes, 0.10 x 0.045 mm; Heterotermes, 0.11 x 0.05 mm. The gland in the worker-nymphs is identical to that in the alate except for a slight enlargement at the anterior apex of the gland. In the glands of the soldier the cup-shaped space is much larger than it is in either the alate or the worker-nymph (Fig. 7, B).

Termitidae - Gnathamitermes perplexus

Morphology of the Gland

The sternal gland in G. perplexus is located in the anterior part of the fifth abdominal sternite, adjacent to the fourth abdominal ganglion (Fig. 4). The gland is composed of two types of cells, glandular and sensory. The glandular cells are very uniform in height, staining density, and position of nuclei (Fig. 8), except for a few which are more highly vacuolated. This condition is similar to that reported by Pasteels (1965) in the gland of the workers of Nasutitermes lujae. Intermixed with these glandular cells are campaniform sensillar processes. The cuticle is striated over the entire surface of the gland. The fourth abdominal sternite forms an external reservoir where it overlaps the gland in the fifth abdominal sternite.

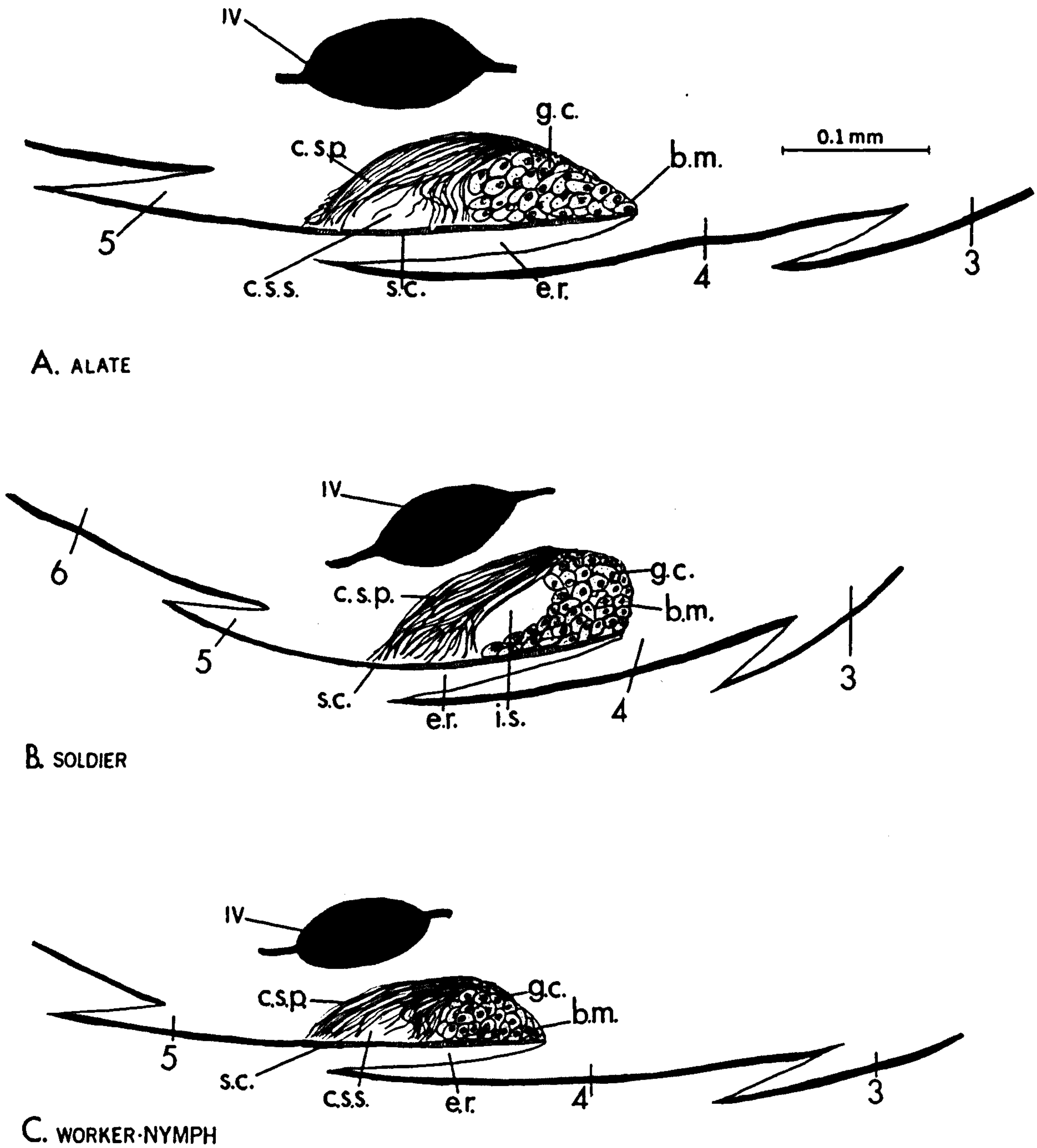

Fig. 7. Rhinotermitidae: Heterotermes

Parasagittal view of ventral wall of abdomen of A., alate, B., soldier, and C., worker-nymph, showing position and cellular composition of sternal gland. (Key to abbreviations on page 30)

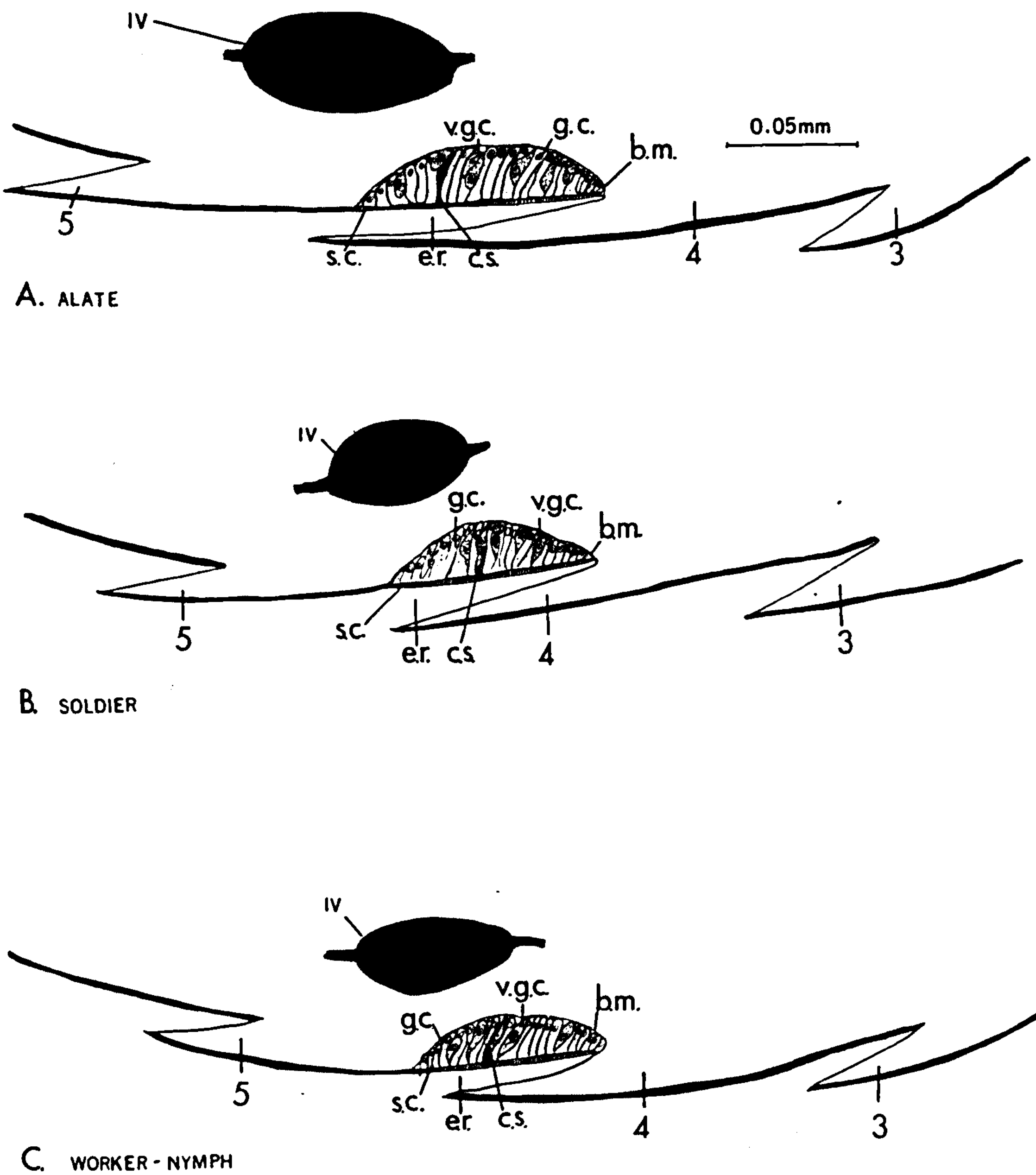

Fig. 8. Termitidae: Gnathamitermes

Parasagittal view of ventral wall of abdomen of A., alate, B., soldier, and C., worker-nymph, showing position and cellular composition of sternal gland. (Key to abbreviations on page 30)

Variations in the Gland

The glands of the three castes are identical in structure, varying only in size. The gland of the alate is about 0.10 x 0.04 mm; of the soldier, 0.09 x 0.04; and of the worker-nymph, 0.09 x 0.04 mm.

Operation of the Sternal Gland

That the sternal gland of *Zootermopsis* is responsible for the production of a trail-marking secretion has been firmly established by Stuart (1963) in *Z. nevadensis*. In his detailed study of the structure and function of the sternal gland he (Stuart, 1964) offered the following hypothesis for the operation of the sternal gland. The marking substance is produced by the secretory cells and transferred to the columnar cells, which pass it to the external reservoir. It is possible that what is produced by the secretory cells is a precursor and that synthesis is completed in the columnar cells. From the reservoir the marking substance is probably released as the insect presses the abdomen against the substrate. As the marking substance is applied an odor trail is laid. The campaniform sensilla in the gland would enable the termite to sense the amount of pressure being applied to the substrate, thereby giving it some control over the amount of secretion being released from the external reservoir.

The operation of the kalotermitid sternal gland is probably quite similar to the operation in the hodotermitid gland, except for the following differences. The marking substance, after production in the secretory cells, is passed to intercalary cells which are perhaps analogous to the columnar cells of the hodotermitid gland. Then, it probably passes to the external reservoir through the cuticle covering the posterior surface of the gland. Only this area of the cuticular surface in the kalotermitids is striated.

Smythe and Coppel (1966) suggested a method of operation for the gland in Reticulitermes flavipes which probably describes the operation of the gland in all the species of Rhinotermitidae studied so far. The trail marking substance is formed in the vacuolated cells in the anterior part of the gland where it passes through the cuticle to the external reservoir. The concentration of campaniform sensillar processes would give the termite better pressure sensitivity which would permit it to deposit the marking secretion very precisly.

The operation of the termitid gland is probably very similar to that in the kalotermitids, with the exception that the marking secretion could pass through the cuticle under the entire surface of the gland.

DISCUSSION AND CONCLUSIONS

Noirot and Noirot-Timothée (1965b) have determined that sternal glands are probably present in all termites. They have also presented a family-by-family summary of the position of the gland in relation to segmentation and the ganglia of the ventral nerve cord. A sternal gland was present in all of the species examined in each of the four families in this present study. However, an examination of Zootermopsis nevadensis showed the sternal gland to be in the fourth abdominal sternite and not in the fifth sternite as reported by Stuart (1963, 1964). This fact resolves the only apparent exception to the scheme of Noirot and Noirot-Timothée (1965b).

The structure and position of the sternal gland in the five living families of termites provides a character which can be used in a phylogentic consideration of the Isoptera. The most primitive living termite, Mastotermes darwiniensis Froggatt (Emerson, 1965), has separate sternal glands in three abdominal sternites, the third, fourth and fifth (Noirot and Noirot-Timothée, 1965b). Further, the glands are positioned above the middle of each sternite. This is important because only the anterior portion of each gland is overlapped by the posterior portion of the preceding sternite. Thus the sternites cannot serve as efficiently, if at all, as external reservoirs for the marking substance secreted by the gland. The endocuticle is striated over the entire surface of the sternal glands in Mastotermes, and campaniform sensilla are interspersed with secretory cells (Noirot and Noirot-Timothée, 1965b).

In the Hodotermitidae Zootermopsis has only one sternal gland, located in the anterior portion of the fourth abdominal sternite, representing a loss of the third and fifth glands in Mastotermes. This single gland in Zootermopsis shows another significant improvement over the mastotermitid gland in being displaced forward into the anterior portion of the segment. This position gains use of the posterior portion of the preceding sternite as an external reservoir. The trail-marking secretions of the gland in the hodotermitids can thus be stored outside the body of the insect and laid more precisely along the substrate.

Further development of the hodotermitid gland is shown in the dorso-ventral arrangement of the glandular and columnar cells. The campaniform sensilla are intermixed among the cells of the gland in Zootermopsis in the same manner as those of Mastotermes.

The Kalotermitidae, as represented by Pterotermes and Marginitermes, have one sternal gland located in the fifth abdominal sternite. This is most likely a retention of the posteriormost gland of the three occurring in Mastotermes. This consideration points to two distinct lines of evolution of the kalotermitids and the hodotermitids from a Mastotermes-like ancestor, rather than an ontological evolution from the Mastotermitidae directly through the Hodotermitidae to the Kalotermitidae. Considering the present positions of the sternal glands in these three groups, it is likely that both the kalotermitids and the hodotermitids evolved independently from a Mastotermes-like ancestor. However, the kalotermitid gland is in the anterior part of the gland-bearing sternite and gains use of an external reservoir in exactly the same manner as it does in the hodotermitids.

The cuticle covering the kalotermitid gland is striated only along its posterior half. This suggests that the trail-marking substance can pass into the external reservoir only through the posterior portion of the cuticle covering the gland. This modification is best seen in the soldiers, where a finger-like projection is directed into the posterior portion of the reservoir. The cellular arrangement shows a closer relationship to the mastotermitid gland than the hodotermitid gland, as the secretory and intercalary cells are intermixed rather than being arranged in distinct layers.

Heterotermes and *Reticulitermes*, rhinotermitids, have one sternal gland in the fifth abdominal sternite, which puts them in the kalotermitid line of evolution rather than the hodotermitid line. The reasoning is the same as that for separating the kalotermitid and hodotermitid lines: the retention of a gland in the same segment is more likely than a complete disappearance in one segment and reappearance in another. The cuticle covering the gland in this family is striated.

A significant advancement in the sternal gland of this family may be represented by the concentration of campaniform sensillar processes in the posterior portion of the gland. This concentration of pressure-sensitive processes would give these insects a more precise control over the release of marking substance from the external reservoir. Another modification is the antero-posterior division of the rhinotermitid gland. This arrangement is most apparent in the soldiers where a large space is present in the posterior portion of the gland. It is suggested that this space serves as an internal reservoir for collecting the secretion of the gland.

With the sternal gland present in the fifth abdominal sternite, *Gnathamitermes* (Termitidae) also falls in the kalotermitid line. The gland is in the anterior part of the sternite and thus has an external reservoir.

The endocuticle is striated over the entire surface of the gland and the glandular and sensillar cells are intermixed in a single layer. These features would seem to place the termitid gland on about the same level of development as it is in the Kalotermitidae.

The presence of campaniform sensilla in the sternal glands of all five families, with processes terminating in the cuticle, would suggest that utilization of pressure stimuli is important in the operation of the sternal gland. Such stimuli would result when the abdomen of the insect is pressed against the substrate for the purpose of opening the external reservoir and depositing an odor trail. The sensilla in all of the families are dispersed among the other cells, with the exception of the rhinotermitid gland where all of the sensillar processes are concentrated posteriorly.

The fact that in all five families only the cuticle covering the surface of the sternal gland is thick and striated seems to point to some specialized function related to the operation of the gland. This function is most likely one of facilitating passage of the secretion of the gland through the cuticle.

Finally, the present study shows that the sternal gland is present in individuals of all castes of the termite species studied. The gland varies in size and complexity, but is present and probably functional in all stages of the various castes. This follows from the findings that even the youngest nymphal forms have all the cell types and that the cuticular striations are present. Thus, at least structurally, everything needed for the production, secretion, and deposition of the trail-marking substance is present.

This study also demonstrates some structural differences of the sternal gland in castes of a single species. Examples of these are the median projection in the gland of the soldier caste in the kalotermitidae and the internal space (reservoir?) in the glands of the soldier caste of the rhinotermitids.

SUMMARY

A histological study of the four families of termites in Arizona was undertaken to determine the presence, position, size and cellular composition of the sternal glands. All species examined had well-developed glands, with their positions matching those in the scheme presented by Noirot and Noirot-Timothée (1965b). It was determined that the sternal gland in all three species of *Zootermopsis* lies in the anterior part of the fourth abdominal sternite and not in the fifth as previously reported.

Four basic cellular arrangements within the gland are evident in the four families studied. The Hodotermitidae, as represented by the three species of *Zootermopsis*, have the glandular cells arranged dorsally and the columnar cells ventrally. Campaniform sensilla and a striated cuticle are present. The gland lies in the anterior part of the fourth abdominal sternite, which is covered by the third abdominal sternite to form an external reservoir.

In the kalotermitids, *Pterotermes* and *Marginitermes*, glandular and intercalary cells are intermixed in a single layer above the cuticle which is striated only over the

posterior portion of the gland. Campaniform sensilla are interspersed among the intercalary and glandular cells. The gland is located in the fifth abdominal sternite and covered by the posterior portion of the fourth sternite, which forms the external reservoir.

Heterotermes and Reticulitermes, in the Rhinotermitidae, have the gland in the fifth abdominal sternite. Glandular cells lie anterior to a concentration of campaniform sensillar processes. The cuticle is striated over the entire surface of the gland, and an external reservoir is formed by the overlapping of the fourth abdominal sternite.

The Termitidae, represented by Gnathamitermes, have the glandular and sensillar cells of the sternal gland arranged in a single layer above the striated endocuticle. The gland is in the anterior part of the fifth abdominal sternite and an external reservoir is formed where the fourth sternite overlaps the fifth.

The operation of the gland in all four families is probably very similar, with trail-marking substance being formed in glandular tissue, passed along columnar or intercalary cells, and out through a striated portion of the cuticle into the external reservoir. The sensilla sense the pressure of the abdomen against the substrate and thus provide a means of regulating the amount of marking substance which is released from the reservoir.

The sternal glands provide a character which indicates two separate lines of evolution from Mastotermes-like forms bearing glands in the third, fourth and fifth abdominal segments. The hodotermitid line has retained a gland in the fourth abdominal segment, while the kalotermitid-rhinotermitid-termitid line has retained that in the fifth.

The differences in the size and structure of the sternal glands in the various castes studied are shown along with the finding of well developed sternal glands in all stages of the various castes. The most marked variance in structure is present in the gland of the soldiers of the Kalotermitidae and Rhinotermitidae. In the kalotermitids the gland in the soldier has a median, finger-like projection directed into the external reservoir. The rhinotermitid soldiers have a large space in the posterior part of the sternal glands, presumably an internal reservoir for the marking substance.

KEY TO ABBREVIATIONS

1-9	abdominal sternites
I-VI	abdominal ganglia
a.s.	abdominal spiracle
a.t.	abdominal tergite
b.m.	basement membrane
c.	cercus
c.c.	columnar cell
c.s.	campaniform sensillum
c.s.p.	campaniform sensillar process
c.s.s.	cup-shaped space
e.r.	external reservoir
f.p.	finger-like projection
g.c.	glandular cell
i.c.	intercalary cell
i.s.	internal space
p.	paraproct
s.c.	striated cuticle
s.g.	sternal gland
s.s.	subanal stylus
v.g.c.	vacuolated glandular cell
v.n.c.	ventral nerve cord

LITERATURE CITED

Child, H. J. 1934. The internal anatomy of termites and the histology of the digestive tract, pp. 80-81. In Kofoid, C. A., et al. (eds.) Termites and Termite Control, 2nd ed., Univ. Calif. Press, Berkeley.

Emerson, A. E. 1965. A review of the Mastotermitidae (Isoptera), including a new fossil genus from Brazil. Amer. Mus. Novitates, no. 2236, pp. 1-46.

Light, S. F. 1934. The external anatomy of termites, p. 56. In Kofoid, C. A., et al. (eds.), Termites and Termite Control, 2nd ed., Univ. Calif. Press, Berkeley.

Moore, B. P. 1966. Isolation of the scent-trail pheromone of an Australian termite. Nature, 211:746-7.

Noirot, C., and C. Noirot-Timothée. 1965a. Ultrastructure de la glande sternale chez la termite Calotermes flavicollis. Proc. XII Int. Congr. Entomol., London (1964):129.

Noirot, C., and C. Noirot-Timothée. 1965b. La glande sternale dans l'evolution des termites. Insectes Sociaux, 12:265-272.

Pasteels, J. M. 1965. Polyethisme chez les ouvriers de Nasutitermes lujae (Termitidae, Isoptères). Biologia Gabonica, 1:191-205.

Satir, P., and A. M. Stuart. 1965. A new apical microtubule associated organelle in the sternal gland of Zootermopsis nevadensis (Hagen), Isoptera. Jour. Cell. Biol. 24:277-283.

Smythe, R. V., and H. C. Coppel. 1966. A preliminary study of the sternal gland of Reticulitermes flavipes (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Amer. 59:1008-1010.

Stuart, A, M, 1963. The origin of the trail in *Nasutitermes corniger* (Motschulsky) and *Zootermopsis nevadensis* (Hagen), Isoptera. *Physiol. Zool.* *36*:69-84.

Stuart, A. M. 1964. The structure and function of the sternal gland in *Zootermopsis nevadensis* (Isoptera). Proc. Zool. Soc. *London, 143*:43-52.