The Internal Anatomy of the Reproductive Systems of Young Primary Reproductives of the Formosan Subterranean Termite, *Coptotermes Formosanus* Shiraki (Rhinotermitidae: Isoptera)[1, 2]

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The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, is probably the most important insect pest locally, costing home and building owners of Hawaii several millions of dollars each year in repairs and application of control measures. This oriental species was first discovered in Honolulu by Perkins in 1907 or possibly earlier (Zimmerman, 1948). Since then it has spread to all the major islands of the State and continues to spread through commerce to other parts of the world, including parts of the southern continental United States.

Over the past 20 years, copious information has been published on preventive and chemical control measures of *C. formosanus,* but because of its cryptic and sheltered nature, little information regarding its biology and ecology is available.

The successful initiation and maintenance of incipient colonies of *C. formosanus* in the laboratory made possible investigations into some aspects of the biology of colony foundation over a two-year period. As a result of these investigations, a study of the internal anatomy of the reproductive systems of young primary reproductives was made possible. Interest in this aspect was stimulated by the tremendous reproductive potential of this insect which has a characteristic, primitive panoistic type of ovary. To illustrate the reproductive potential of this insect, Bess (1970) reported that approximately 10,000 eggs were observed from a field-collected carton containing a single physogastric queen as the sole reproductive form.

The literature concerning the reproductive systems of termites is limited to very few species. Child (1934) gave a gross description of the reproductive systems of the drywood termite, *Zootermopsis angusticollis* Hagen. Imms (1957) conducted a similar study with *Archotermopsis* sp. Geyer (1951) reported on morphological and histological studies of several species of South African termites. The most comprehensive single

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piece of study was presented by Weesner (1955), on *Tenuirostritermes tenuirostris* (Desneux) (Termitidae). In this work, she gave detailed descriptions of the structures and tissues which make up the reproductive systems of the primary reproductives. Weesner (1956, 1965) also presented gross descriptions of the reproductive systems of *Reticulitermes hesperus* Banks. In one of her most recent contributions, Weesner (1969) included a comprehensive discussion of the structures of the reproductive systems of termites in general, citing the works of investigators who have contributed knowledge over the years.

In particular, the present study considered the descriptions of the genital chamber, the accessory structures, the oviducts, and the ovaries of the female system; and the ejaculatory duct, vasa deferentia, accessory glands, and the testes of the male system.

Materials and Methods

The specimens used in this study were essentially young primary reproductives which were obtained from light-trap collections in June 1968 and colonized in the laboratory. All of the termites were collected in a funnel trap illuminated by a 15-watt blacklight bulb at one location in the vicinity of the Insect Toxicology Laboratory on Maile Way, on the University of Hawaii, Manoa Campus. The trapped alates were sexed (Fig. 1) and placed in moist containers to induce dealation. Each pair of the dealated reproductives was placed in an eight dram vial which was prepared with the following materials: water saturated layer of cotton set at the bottom of the vial, plaster of paris powder sprinkled over the wet cotton to provide a surface of about 3 mm in thickness, and a piece of wood about 6.4 x 1.5 x 1.5 cm placed on the plaster of paris to serve as food and nesting material for the termite pair and its ensuing brood. After the pair was introduced, the vial was tightly stoppered with a wad of cotton. The high moisture content required by *C. formosanus* was maintained by periodically wetting down the bottom layer of cotton with a hypodermic syringe with a long needle.

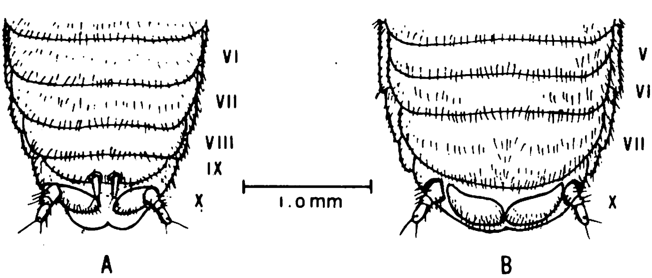


FIG. 1. Posterior ventral portion of the abdomen of primary reproductives; A, the male, B, the female. Note the enlarged seventh sternite (VII) of the female and the presence of style on the ninth (IX) sternite of the male.

Information on the internal anatomy of the reproductive systems was obtained from serial sections of a number of reproductives representing different age groups from sacrificed colonies ranging from one month to 24 months in colonization. The specimens were fixed in Carnoy's fixative for six to 12 hours and preserved in 70 percent ethanol in six dram screw-top vials until time for embedding.

The preserved specimens were prepared for serial sectioning by the N-butyl alcohol embedding technique of Smith (1943). Staining was done primarily with Patay's triple stain as outlined by Gray (1964). After staining, the serial sections were mounted in Canada balsam, covered with 20 x 50 mm cover slips and dried on the slide warmer for at least 10 days at 36° C.

In regards to the terminology used to describe the various structures of the reproductive systems, the interpretations of Snodgrass (1935) and Weesner (1955, 1969) were used.

The Reproductive Systems

The Female System. General Layout.—The ovaries of a young female appear as a pair of conspicuous organs lying laterally along the alimentary canal. Posteriorly, they originate at about the level of the midgut and incline in an anterodorsal direction over and above the midgut where they eventually join to form the median ligament in the dorsal posterior thoracic region. The left and right oviducts are short tubes which continue posteriorly and meet medially, ventral to the rectum, in a short common oviduct which is directly connected to the genital chamber. Arising from the anterior region of the genital chamber are the spermatheca, a conspicuous fingerlike tube extending dorsally and having a recurved tip, and the accessory gland which is characterized by a series of convoluted tubes, also extending dorsally.

The Genital Chamber.—The genital chamber is formed by the overlapping of the eighth and ninth sternites by the elongated seventh sternum (Fig. 2). The seventh sternum therefore, forms what Weesner (1955) referred to as the subgenital plate. The floor of the chamber is formed by the enlarged intersegmental membrane between the seventh and eighth sternites. The roof of the genital chamber consists of the sternites of the eighth and ninth segments. Weesner (1955) reported that there were two lateral scerotized and pigmented plates, connected medially by a membranous sheet of chitin, on the eighth and ninth sternites of *T. tenuirostris*. These plates appear to be rather vague in *C. formosanus*.

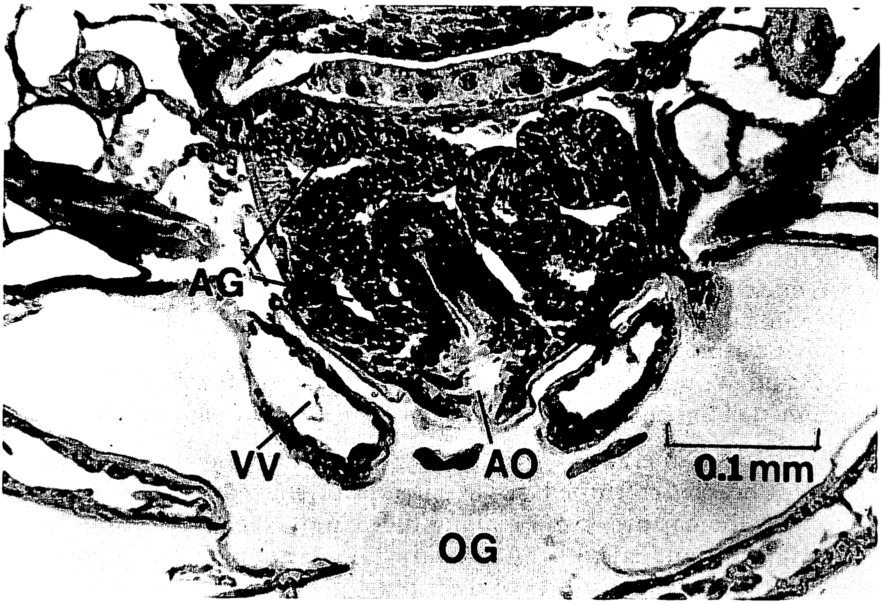
The genital chamber is composed of two regions; an outer, open chamber posteriorly, and an inner, somewhat flattened and more restricted chamber, anteriorly. This distinction was first made by Weesner (1955). The outer chamber occupies the space outlined by the shape of the seventh sternum as it overlaps the ninth and the lateral portions of the

FIG. 2. Sagittal section through the genital chamber. (AG) Accessory gland; (AO) Accessory gland orifice; (IG) Inner genital chamber; (IS) Intersternal fold; (OD) Oviduct; (OG) Outer genital chamber; (P) Pouch at inner end of genital chamber; (R) Rectum; (SF) Spermathecal furrow; (SP) Spermatheca; (7, 9, 10) Sternites.

eighth. At the medial, anterior portion of the ninth sternite is the orifice of the duct of the accessory gland. This orifice is partially enclosed ventrally by the posterior projection of the two lips of the ventral valve of the eighth sternite (Fig. 3A). Anteriorly, between the bases of the ventral valves, there is the opening of a deep, heavily chitinized groove (Fig. 3B) along the medial ventral line of the eighth sternite. This is the spermathecal furrow of Weesner (1955). From the very beginning point of the spermathecal furrow, the genital chamber is restricted ventrally by a fold of the intersegmental membrane between the seventh and eighth sternites. This is the intersternal fold, first reported by Browman (1935). The posterior limits of these two structures, the spermathecal furrow, above, and the posterior lip of the intersternal fold, below, mark the posterior boundaries of the inner genital chamber.

The inner genital chamber is markedly compressed dorso-ventrally as is shown in Figs. 3C and 3D. Posteriorly, it is about 0.45 mm wide and tapers anteriorly to about 0.30 mm. It is approximately 0.24 to 0.30 mm long. The spermathecal furrow extends slightly past the midpoint in the chamber as an open groove in the roof. Further anterior to the anterior limit of the open furrow is the posterior limit of the opening of the common oviduct or gonopore, which opens through the floor of the chamber. The gonopore is a laterally compressed opening and runs in an anterior-posterior direction (Fig. 3E).

In Fig. 2, a blind pouch (P) is shown. According to Weesner (1955) this pouch forms the anterior wall of the inner genital chamber and the



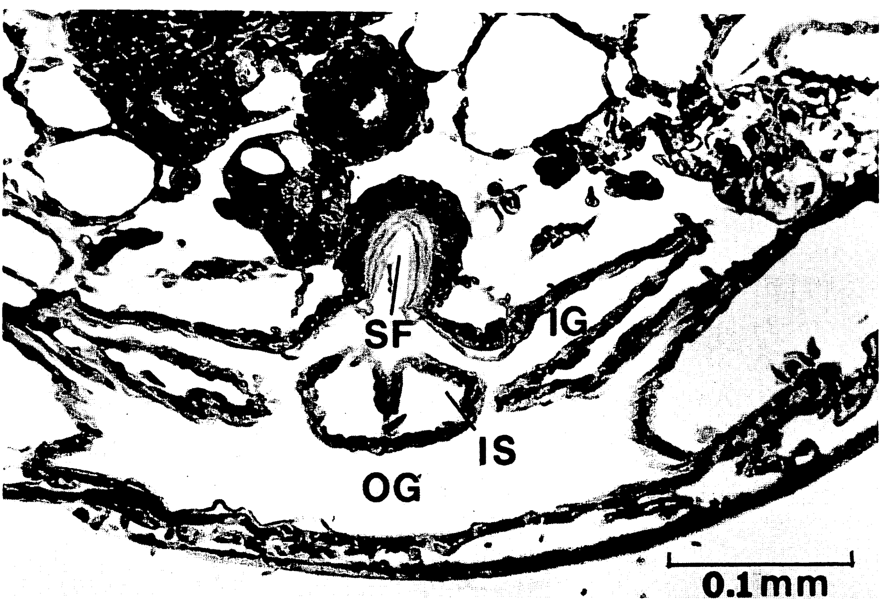


FIG. 3. Successive transverse sections (posterior to anterior) through the female outer genital chamber, inner genital chamber, gonopore, medial oviduct, lateral oviducts and their associated structures. *A*, Medial portion of the outer genital chamber at the level of the accessory gland orifice of a 3 month old reproductive; (AG) Accessory gland, (AO) Accessory gland orifice, (OG) Outer genital chamber, (VV) Ventral valve of eighth venter. *B*, Posterior limit of the inner genital chamber (IG), showing the spermathecal furrow (SF), and grooved intersternal fold (IS).

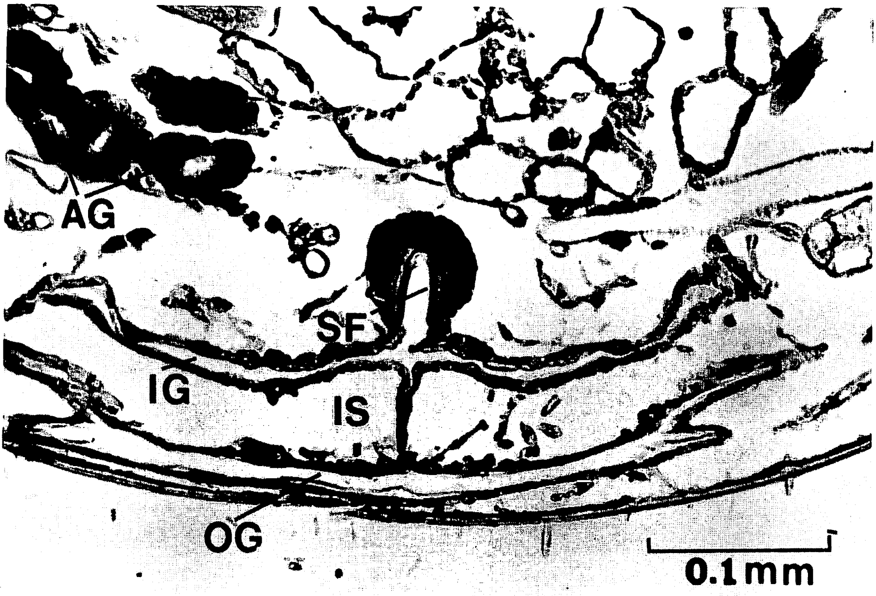
attachment point for muscles running to the anterior margin of the seventh sternum. She further describes a second pouch, associated with the outer chamber, which lies anterior to the orifice of the duct of the accessory gland and above the spermathecal furrow, and which marks the limit between the eighth and ninth sternites. This second pouch, however, has not been observed in *C. formosanus.*

The Accessory Structures.—The duct leading to the accessory gland from the roof of the anterior aspect of the ninth sternite is a short, common, muscular canal which bifurcates into two trunks, each of which divides into a number of narrow convoluted tubules. The exact function of this gland is not known, but a number of investigators, including Imms (1957) and Weesner (1969), believe that there is a secretory function and the lumen of the tubules may be more or less filled with a clear coagulum.

The spermathecal furrow, which is 0.16 to 0.20 mm in length, consists of a heavily chitinized groove, horseshoe-shaped in transverse section, with the narrow opening along the ventral line. The furrow is enclosed dorsally and laterally by an epithelial layer of cells. At its posterior end the furrow opens directly into the outer genital chamber. At its anterior end it is continuous with a relatively short (0.05 to 0.10 mm) but closed duct, the spermathecal duct (Figs. 3D and 3E) which is lined by a smooth and laminated chitinous wall lying over an epithelial layer of cells. This duct is continuous with the upper, inner surface of the inner genital chamber. The spermathecal duct leads into the spermatheca which usually arises at a right angle to the duct. The general form of the spermatheca is that of a thick blind tube with a recurved end. The inner wall is composed of a fibrous network beneath which lies a dense layer of epithelial cells on which continues a rank of tall columnar cells. Weesner (1969) believes that these columnar cells have a secretory function.

The Oviducts.—The lateral oviducts join to form a short common oviduct which opens posteriorly via the gonopore, a laterally compressed opening through the floor of the inner genital chamber (Fig. 3E). Posteriorly, where it opens, the gonopore is continuous with the medial groove in the intersternal fold. This groove lies opposite the spermathecal furrow, and probably permits expansion of the chamber when the egg is extruded from the gonopore. Below the intersternal fold lies a posterior projection of the oviduct (Fig. 3F), which is joined at the apex to form an inverted *U* in transverse section.

Anterior to the gonopore of the common oviduct there is a thin-walled vestibule or cavity (Fig. 3G), which opens into the oviduct. More anteriorly, the left and right oviducts become distinct although they are still interconnected at their midline (Fig. 3H). Finally the two oviducts separate completely from each other and proceed to extend laterally and dorsally, in a nearly vertical plane on either side of the gut (Fig. 3I). The



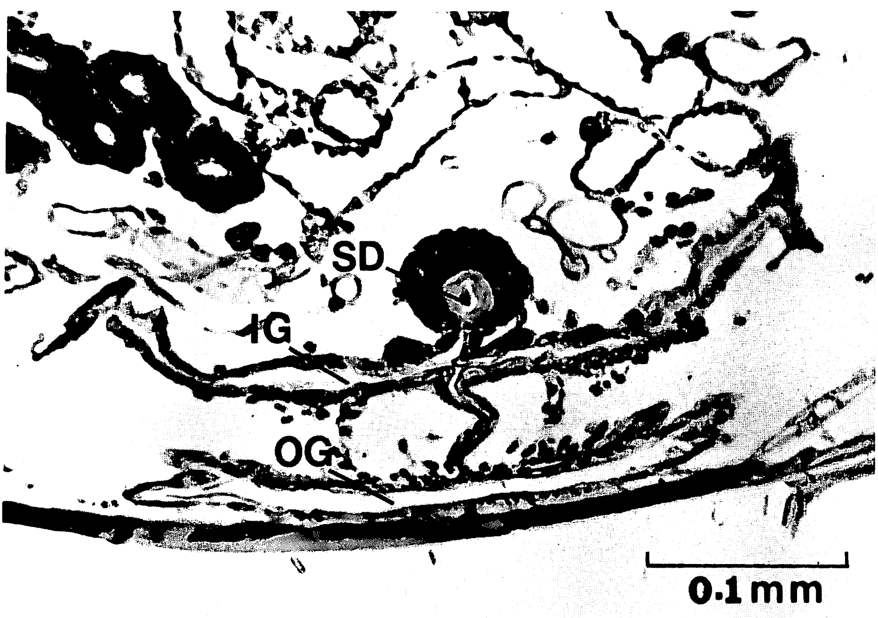
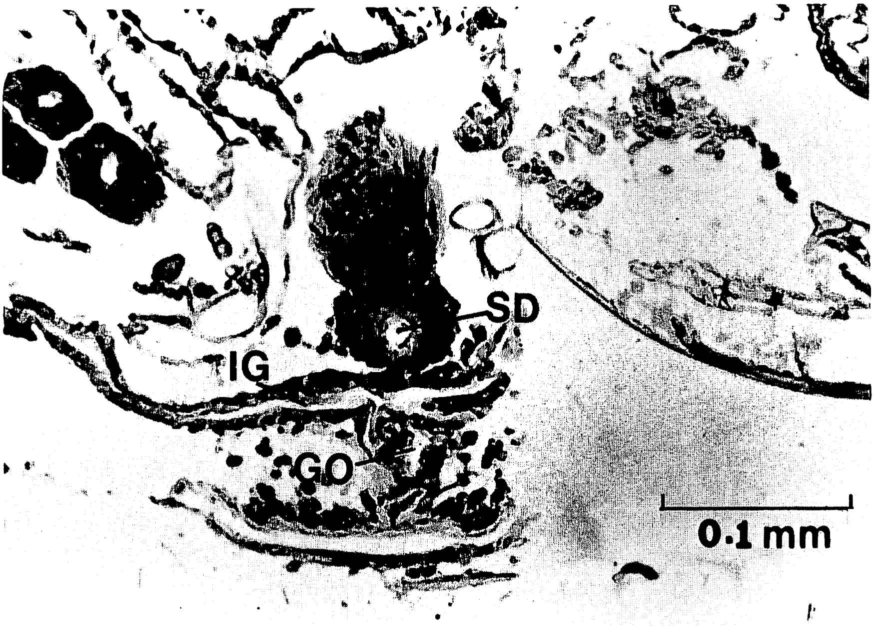


FIG. 3. *(Continued)* *C*, Posterior aspect of the inner genital chamber showing its width (approximately 0.45 mm). *D*, At the level of the spermathecal duct (SD), just anterior to the spermathecal furrow.



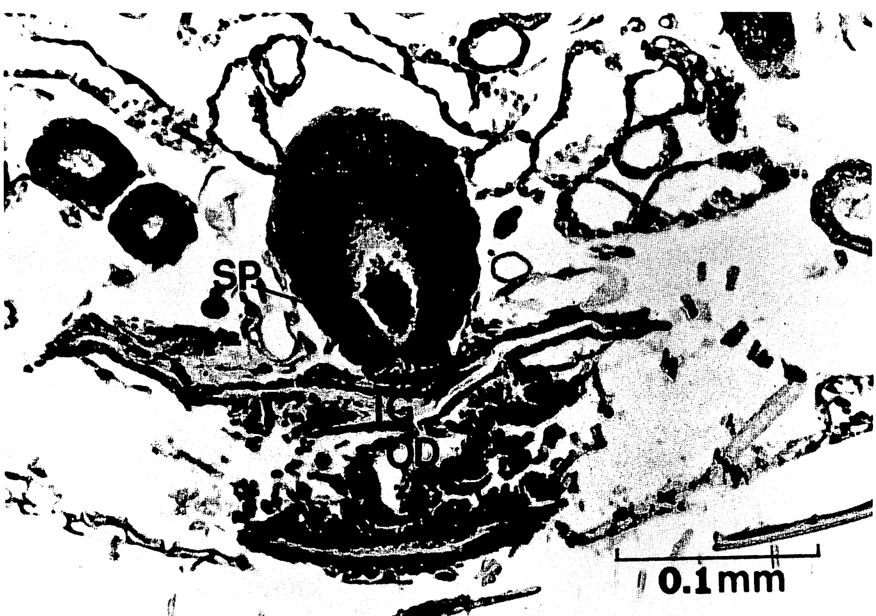


FIG. 3.*(Continued) E*, At the level of the gonopore (GO), showing the spermathecal duct lying above the inner genital chamber. *F*, At the posterior portion of the spermatheca (SP), showing the posterior portion of the common oviduct (OD), just anterior to the gonopore.

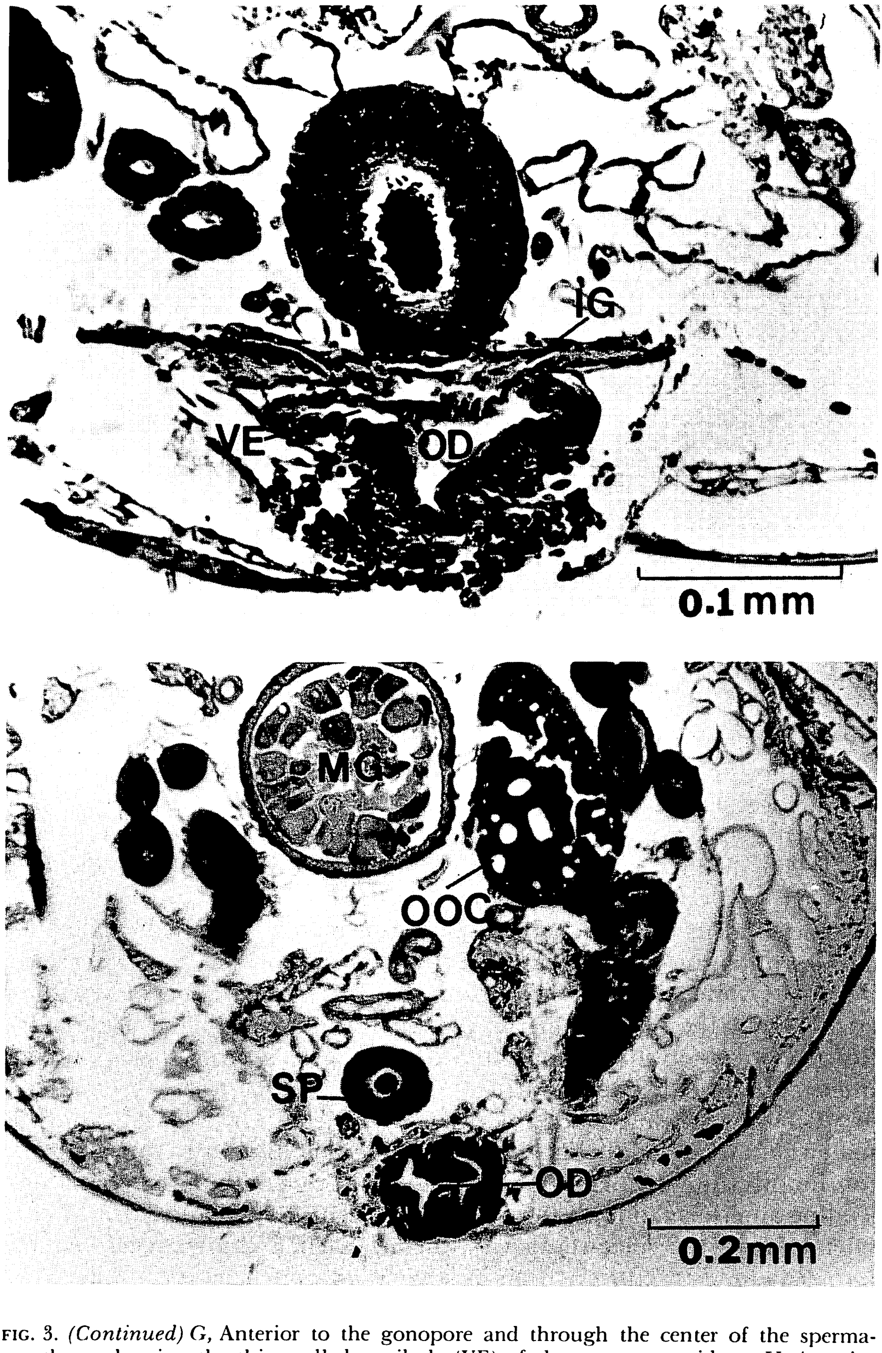
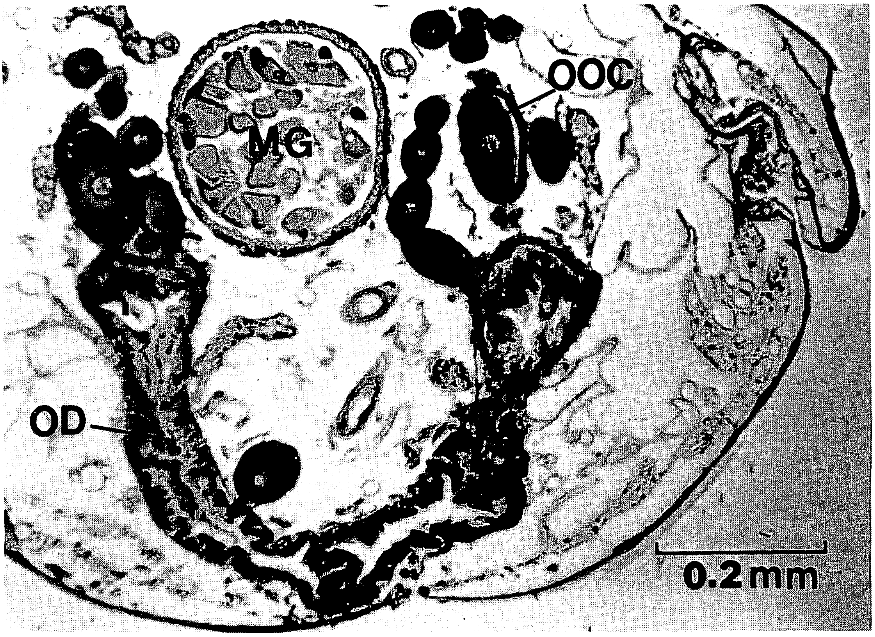


FIG. 3. *(Continued) G,* Anterior to the gonopore and through the center of the spermatheca, showing the thin walled vestibule (VE) of the common oviduct. *H,* Anterior limit of the common oviduct just before separating into the lateral oviducts; note maturing oocyte (OOC) and relative size of midgut (MG).



I, Lateral oviducts; note the vertical arms of the oviducts terminating at the ventral level of the midgut.

vertical arms of the oviducts appear to lie within the anterior limit of the seventh segment.

At the level of the midgut, the first ovarioles are inserted into the oviducts. The oviducts extend anteriorly, maintaining a fairly constant level dorsal to and on either side of the gut. In the most mature females, it becomes evident that the oviducts persist for a good length in the abdomen, terminating in the vicinity of the second segment.

The Ovaries.—Each ovary is composed of a large number of ovarioles, arising along the oviduct anterior to the vertical arms. The ovarioles arise from all points on the oviduct and extend anteriorly from their points of insertion on the oviduct.

Each ovary is surrounded along its entire length by a loosely applied, somewhat elastic, epithelial sheath. The epithelial sheath appears to be continuous from the oviducts through the entire length of the ovaries extending anteriorly to form the ovarian ligaments which attach in the dorsal region of the meta-thoracic segment. Each ovariole, itself, is surrounded along its entire length by a closely applied, non-cellular layer, the tunica propria. Anteriorly, the tunica propria ends by forming the terminal filament (Fig. 4). The terminal filament is apparently attached to adjacent cells of the epithelial sheath and the tracheal mass with which the ovary is richly provided.

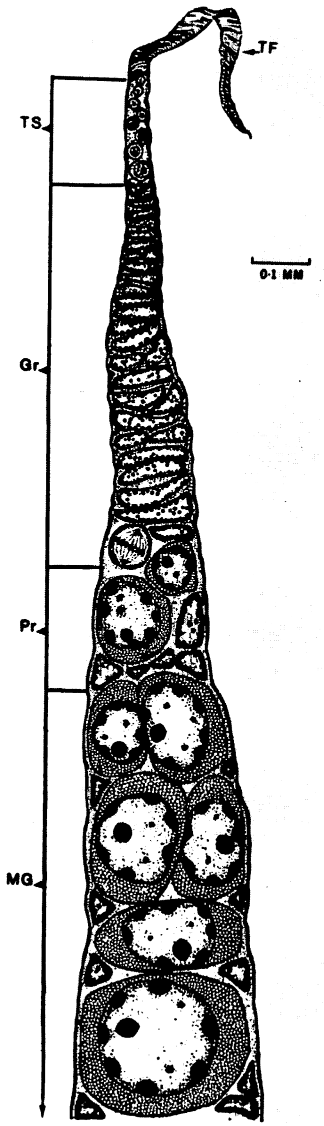


FIG. 4. Terminal portion of a single ovariole: (TF) Terminal filament; (TS) Terminal strand; (Gr) Germarium; (Pr) Prophase region; (MG) Middle growth region.

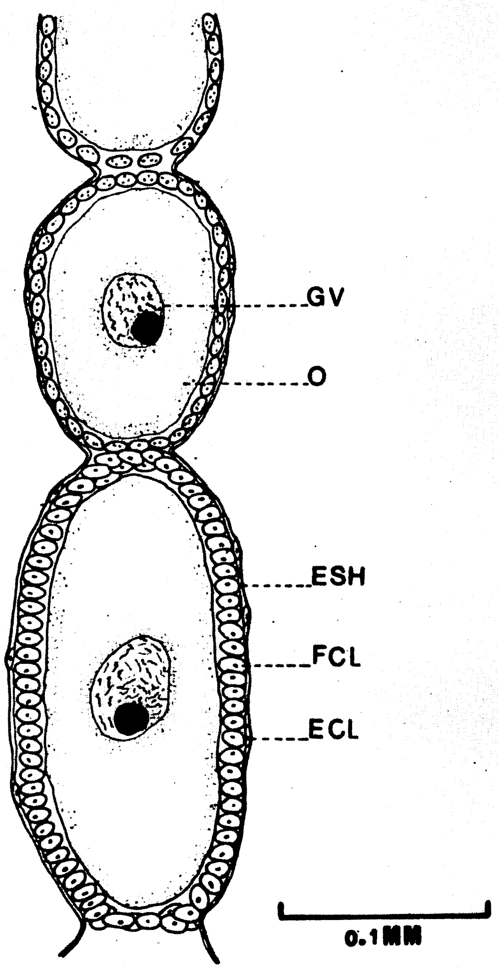


FIG. 5. Sagittal section through the terminal growth region of a maturing ovariole: (ECL) Epithelial cell; (ESH) Epithelial sheath; (FCL) Follicular Epithelium; (GV) Germinal vesicle; (0) Oocyte.

The mature ovariole tapers anteriorly and has a typical panoistic organization, lacking trophocytes or nurse cells and provided posteriorly with a well developed follicular epithelium. Besides the terminal filament, the functional ovariole usually includes six structural areas which are fairly well defined from one another. These areas may be described as follows:

1. The terminal strand.—Immediately posterior to the terminal filament lies a strand of small circular cells with round nuclei (Fig. 4). These cells are arranged in a linear series, nearly occupying the entire space of the ovariole at this point. According to Weesner (1955) their number varies from a few in mature ovarioles to many in immature ones.

2. The germarium.—Posterior to the terminal strand is an area in which the cells and their nuclei are flattened and closely arranged (Fig. 4). Cellular division may be frequently encountered, especially in the posterior portion.

3. The prophase region.—The posterior limit of the germarium is marked by the appearance of small round oocytes and the first appearance of epithelial cells (Fig. 4). These oocytes are the beginning of the prophase or initial growth region. Here the oocytes and epithelial cells continue to grow. The most distinctive characteristic of this region, as implied by the name, is a conspicuous rearrangement of the chromosomes and other chromatin material within the nuclei of the young oocytes. There is, however, no cellular division in this region.

4. The middle growth region.—Posterior to the prophase region, the oocytes increase rapidly in size and become crowded within the ovariole, either side by side, or in a staggered series. They are usually ovoid or tetrahedral in shape (Fig. 4). There is a considerable increase in the size of both the oocyte and germinal vesicle and the nucleolus becomes increasingly more conspicuous.

5. The terminal growth region.—The final growth phase includes a number of oocytes arranged in a linear series and enclosed in a well defined wall of follicular epithelium. The most anterior oocytes may be round or frequently flattened across the ovariole, so they may be wider than long. The oocytes gradually become elongated in the plane of the long axis of the ovariole.

6. The pedicel.—The stalk or pedicel of the ovariole is considered a portion of the ovariole. Each pedicel has a lumen communicating the ovariole with the lateral oviduct, but in an immature ovariole, the passageway is closed at its upper end, just beneath the first oocyte by a "plug" of several layers of epithelial cells. At the time the first egg is ready to be laid the cells of the "plug" are dissolved, opening the passageway through the pedicel from the egg tube into the oviduct. The wall of the pedicel consists of epithelial cells which appear to be comparable to that of the oviduct proper.

At the time of flight each of the immature ovarioles consists primarily of an elongated germarium, a terminal strand and the terminal filament. More posteriorly, subsequent ovarioles include a definite prophase region. Posterior to these, the ovarioles also include a middle growth region, and finally, the last five to eight include a terminal growth region.

Follicular Epithelium.—Weesner (1955) indicated that with *T. tenuirostris* the first recognizable follicular cells occur in the anterior portion of the prophase region. In *C. formosanus* it appears that follicular cells first can be recognized in the posterior portion of the prophase region (Fig. 4). Here they are small, irregular in shape and loosely scattered. In the middle growth region, they can be seen quite regularly along side and near the edges of the ovariole. They are uninucleate, but often in these young cells the nuclei are not easily recognizable. In the terminal growth region the epithelial cells separate the oocytes from the tunica propria. Anteriorly, they are flattened and occur sparsely around the oocytes. Posteriorly, in more developed oocytes, the cells become ovoid or cuboidal in shape and appear to join in a single row around the oocytes. In fully developed oocytes in the most posterior region of the ovariole, the follicular cells are more numerous and often enlarged, maintaining their cuboidal or ovoid shape, and pack around the enlarged oocytes, forming enclosed egg chambers (Fig. 5). In both the middle growth and the terminal growth regions, these cells have been observed undergoing division. In the basal egg chamber, subsequent to the deposition of the egg, the follicular epithelium apparently disintegrates and much of it is probably resorbed (Snodgrass, 1935). The ovariole is apparently somewhat shortened at that point as the succeeding oocyte becomes the most posterior oocyte. However, as the ovariole shortens posteriorly by the degeneration of each emptied chamber, it continually increases in length anteriorly by renewed growth and accommodates the newly forming oocytes.

The follicular epithelium of the ovarioles in insects, is generally believed to be derived from the mesodermal sheath of the primitive gonad and to arise either from the terminal cells closing the ovariole or from the ovarian pedicel. As far as termites are concerned, because there are no specialized nurse cells associated with their ovarioles, most investigators conclude that the follicular epithelium is the immediate source of the nutrients which enables the rapid development of the oocytes and deposition of yolk in the terminal growth region (Weesner, 1969).

The Male System. General Layout.—Unlike the female, the seventh sternum of the male is not elongated and the eighth and ninth sterna are entire (Fig. 1). These sterna are all sclerotized, pigmented, densely setose, and a pair of styli are present on the ninth sternum.

The external opening or gonopore lies medially in the intersegmental membrane between the ninth and tenth sterna. Weesner (1956) reported that in sectioned material of *R. hesperus* this opening can be observed to lie within an invaginated, membranous sheath which probably represents a small, distensible "penis." Geyer (1951) reported that the gonopore of the alate male of the African harvester termite, *Hodotermes mossambicus* (Hagen) is associated with the membranous projection on the ninth sternite, which is probably the penis. In *C. formosanus,* a similar situation probably exists, the "penis" being a simple, distensible, and membranous structure, because sections through the ejaculatory duct showed no evidence of any sclerotized organ which would indicate the presence of a complex copulatory organ. The gonopore apparently is continuous with a short, muscular ejaculatory duct into which open the right and left vasa deferentia. Arising from the ends of the paired vasa deferentia are a pair of testes. Unlike the ovaries, the testes of a young male are rather small and inconspicuous organs lying laterally in the eighth sternite amidst fatty tissue of the abdominal cavity. Arising also from the anterior region of the ejaculatory duct are a pair of conspicuous and convoluted tubules of the accessory glands.

Vasa Deferentia.—The vasa deferentia open into the ejaculatory duct via small, elliptical openings situated anterodorsally in either side of the duct (Fig. 6). From their points of insertion into the ejaculatory duct, the vasa deferentia run laterally and then dorsally to either side of the rectum to join the testes.

The Accessory Glands.—As noted earlier the accessory glands are simple, paired, elongated and somewhat convoluted tubules arising from the anterior margins of the ejaculatory duct. Their openings internally into the ejaculatory duct are adjacent and ventral to the openings of the vasa deferentia (Fig. 6). The function of these glands may be secretory as suggested by Imms (1957), although this has not been ascertained. It is unlikely, however, that these glands function as areas for sperm storage, as have been reported from certain species by Springhetti and Gelmetti (1960), because serial sections through several specimens, representing various age groups, have shown the tubules to be clear and free of sperm.

The Testes.—The testes are enclosed in a sheath of flattened epithelial cells and consist of a number of testicular lobes which are borne in a tight cluster at the ends of the paired vasa deferentia. There are between 10 and 15 lobes per testis, each becoming more prominent with increasing maturity of the male. According to Snodgrass (1935), within each testicular lobe can be distinguished successive regions according to the state of development of the germ cells. These regions are as follows: (1) the germarium or upper part containing the primary spermatogonia; (2) zone of growth or zone of spermatocytes where primitive germ cells undergo repeated division to form spermatocytes which are often enclosed in cysts; (3) zone of meiosis and maturation where the encysted spermatocytes divide, first a meiotic (reduction) division followed by

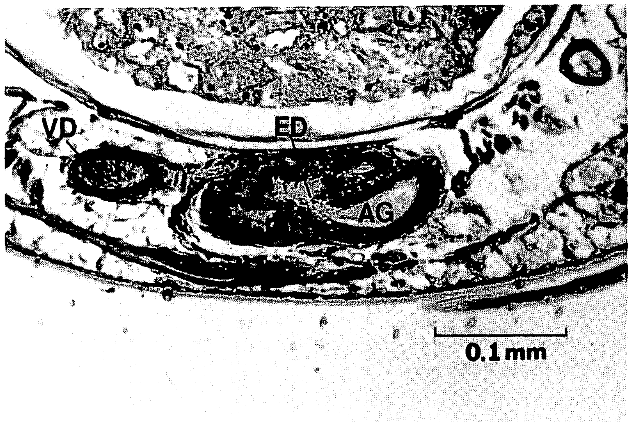


FIG. 6. Transverse section through the abdomen of a nine-month old male, showing the bases of the vas deferens (VD) and the accessory gland (AG) from the ejaculatory duct (ED). Note sperm in vas deferens.

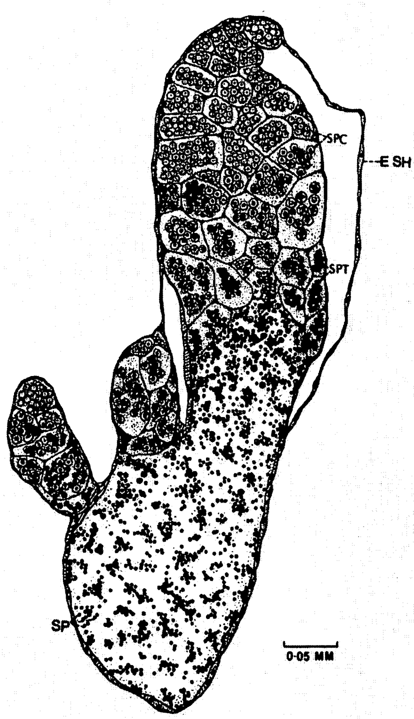


FIG. 7. Sagittal section through a large testicular lobe of a 24 month old male reproductive: (ESH) Epithelial sheath; (SP) Sperm; (SPC) Spermatocytes; (SPT) Spermatids.

mitosis, which form encysted spermatids (immature sperm); and (4) zone of transformation in which spermatids are converted to sperm.

A section of testis transecting a large lobe and part of two others from a two year old male is shown in Fig. 7. The round cells in the upper end, which are enclosed in cysts are apparently the spermatocytes of the zone of growth. Further down, these cells are shown undergoing various stages of division and multiplication which represent the zone of meiosis and maturation. Still further down the lobe are a group of encysted cells bearing large nuclei. These are the spermatids, which later mature into sperm. The sperm are found loosely within the vasa deferentia. However, in the upper portion of the vasa deferentia the sperm are frequently clumped into groups although not enclosed within a cyst. The sperm as observed in the testes, the vasa deferentia, and in the spermatheca of the female are apparently non-flagellated and do not appear to be motile. The sperm are minute bodies, staining intensely with hematoxylin or Feulgen. Under high magnification (1000 x) they give the appearance of small ring-like structures although many are irregular in shape and not at all circular as appear under low magnification. The sperm are about 1.5 to 3 microns in diameter.

SUMMARY

The present study was concerned with the internal anatomy of the reproductive systems of the primary reproductives of *C. formosanus.*

The genital chamber of the female reproductive system was found to be formed by the overlapping of the eighth and ninth sternites by the elongated seventh sternum. This chamber was found to be composed of an outer, open chamber posteriorly, and an inner, somewhat flattened and more restricted chamber, anteriorly. Associated with the genital chamber were the accessory gland, a series of thread-like, convoluted tubules which opened from the roof of the anterior aspect of the ninth sternite into the outer genital chamber, and the spermatheca, which was joined to the outer genital chamber via a short spermathecal duct and an extended spermathecal furrow, horseshoe-shaped heavily chitinized groove. Associated with the genital chamber anteriorly was a short common oviduct which opened via the gonopore into the floor of the inner genital chamber. From their points of insertion into the common oviduct, the lateral oviducts extended laterally, then dorsally, in a vertical plane on either side of the midgut.

The ovaries were found to be composed of a large number of ovarioles arising from all points on the oviducts, extending anteriorly from their points of insertion. Studies indicated that there was augmentation of ovarioles in the ovaries with age of the queens. The functional ovarioles had a typical panoistic organization, lacking specialized nurse cells, and provided posteriorly with a well developed follicular epithelium. The

functional ovariole consisted of six structural areas which are fairly well defined from one another. These were: the terminal strand, germarium, prophase region, middle growth region, and the pedicel.

In the male reproductive, the copulatory organ appeared to be represented by a simple, membranous "penis" which probably distended from the short, muscular ejaculatory duct, into which opened the paired vasa deferentia and the ducts of the accessory glands. The accessory glands consisted of a pair of elongated and convoluted tubules arising from the anterior margins of the ejaculatory duct. The function of these glands was not ascertained but it did not appear that they served to store sperm as is apparently the case in some termites. The vasa deferentia also arose from the anterior aspect of the ejaculatory duct and from their points of insertion, they ran laterally and then dorsally to either side of the rectum to join the testes.

The testes of young imagos were found to be a pair of small and inconspicuous organs lying laterally in the eighth segment amidst fatty tissue. Each testis consisted of 10 to 15 minute, testicular lobes which increased in size with age. From serial sections it was found that each of these lobes consisted of a germarium, a zone of growth, a zone of meiosis and maturation, and a zone of transformation. The sperm were observed to be non-flagellated, minute, circular bodies measuring 1.5 to 3 microns in diameter.

Acknowledgments

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Literature Cited

Bess, H.A. 1970. Termites of Hawaii and the Oceanic Islands. In "Biology of Termites," Vol. 2 (Krishna, K. and Weesner, F.M., eds.), pp. 449-476. Academic Press, Inc., New York.

Browman, L.G. 1935. The chitinous structures in the posterior abdominal segments of certain female termites. J. Morphol. **57:** 113-129.

Child, H.J. 1934. The internal anatomy of termites and the histology of the digestive tract. In "Termites and Termite Control." (C.A. Kofoid, ed.), 2nd ed., pp. 58-88. Univ. of California Press, Berkeley, California.

Geyer, J.W.C. 1951. The reproductive organs of certain termites with notes on hermaphrodites of *Neotermes*. Union S. Africa, Dept. Agr. Entomol. Mem. **2:** 232-325.

Gray, P. 1964. "Handbook of Basic Microtechnique," 3rd ed., McGraw-Hill, New York. 302 p.

Imms, A.D. 1957. "A General Textbook of Entomology," 8th ed., Dutton, New York. 886 p.
Smith, S.G. 1943. Techniques for the study of insect chromosomes. The Canadian Entomologist **72**(2): 21-34.
Snodgrass, R.E. 1935. "Principles of Insect Morphology." McGraw-Hill New York. 667 pp.
Springhetti, A., and Gelmetti, L. 1960. Sull' apparato genitale maschile di *Reticulitermes.* Insectes Sociaux **7**: 377-382.
Weesner, F.M. 1955. The reproductive systems of young primary reproductives of *Tenuirostritermes tenuirostris* (Desneux). Insectes Sociaux **2**(4): 323-345.
———. 1956. The biology of colony foundation in *Recticulitermes hesperus* Banks. Univ. California Publ. Zool., Vol. **61**: 253-315.
———. 1965. The reproductive system and egg production. "The Termites of the United States," A Handbook, The National Pest Control Association, Elizabeth, N.J. pp. 12-13.
———. 1969. The reproductive system. In "Biology of Termites," Vol. **2** (Krishna, K. and Weesner, F.M., eds.), pp. 125-150. Academic Press, New York.
Zimmerman, E.C. 1948. "Insects of Hawaii," Vol. **2**, pp. 1-475. Univ. of Hawaii Press, Honolulu.