THE REPRODUCTIVE SYSTEM OF YOUNG PRIMARY REPRODUCTIVES OF *TENUIROSTRITERMES TENUIROSTRIS* (Desneux)

by

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The reproductive systems of various Isoptera have been the subject of a number of investigations during the past fifty years. These studies have varied greatly in scope and approach, from generalized descriptions of gross morphology to considerations of microanatomical and cytological details. The variations which have been reported by different authors for the same or different genera suggest that further studies are warranted in an effort to obtain a better picture of the apparent variations which occur within the order.

The interest in the termite reproductive system has probably been stimulated to a large extent by the tremendous reproductive potential of a group of insects which have a primitive panoistic ovary. The mature queens of many of the tropical Termitidae become extremely physogastric and deposit many thousands of eggs per day. The only queen of *Tenuirostritermes tenuirostris* which was collected from a well developed colony in the field (Weesner, 1953) was but slightly physogastric. This individual deposited approximately 300-400 eggs over a twelve hour period. Unfortunately, this queen died in culture and was destroyed by the workers. No information has been obtained regarding the internal anatomy of the fully matured reproductives, which are difficult to find in the subterreanean workings of this species. The alates, on the other hand, were readily obtained and are functional at the time of flight.

The young primary reproductives begin depositing eggs within a few days after pairing and as many as 55 eggs may be deposited by a single queen during the first ten days (Light and Weesner, 1955). This pattern of egg deposition indicates that some of the eggs must be well developed at the time the young primaries leave the parent colony. Furthermore, it seemed probable that there are a larger number of functional ovarioles than are usually attributed to young queens. A superficial examination of the ovaries showed that whereas well developed eggs are present at the time of flight, only a limited number of ovarioles are functional, as will be evident from the subsequent descriptions.

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METHODS AND TERMINOLOGY

The specimens which were utilized in this study were preserved in 70 % ethanol during the initial investigation of the mature and incipient colonies in 1946. The present study was not anticipated at that time and little hope was held regarding the histological preservation and staining qualities of the material after such simple fixation and storage until 1954. Actually the material sectioned well in paraffin, was receptive to stains and there was no appreciable distortion.

Forty two individuals were prepared in serial sections at 8 microns. These included brachypterous nymphs, alates and young primary reproductives which had deposited the initial group of eggs. Most of the sections were stained with Alum Hematoxylin and Eosin, a few with Heidenhain's Iron Hematoxylin and others with Mallory's Triple Stain. In addition, carmine-stained whole mounts were prepared of dissections of both male and female reproductive tracts and a number of dissections were made without the preparation of permanent mounts.

Counts of the number of ovarioles were made in four individuals (primary reproductives after the initial egg laying period) by noting the origin of each ovariole, section by section, along the length of the oviduct. In one instance a camera lucida drawing was prepared of each section, so that the fate of each ovariole could be traced. This is the ovary which was utilized in the preparation of figure 4, *b*, *c* and *d*.

In considering the subsequent descriptions, especially as regards the morphology of the ovary, it must be borne in mind that the individuals utilized were functional but had not reached their full reproductive development. The descriptions refer to the structure of the young imagoes unless otherwise specified.

Snodgrass (1935) has been taken as the standard for terminology. This usage is fairly consistent throughout the termite literature except for the terms sternum, sternite and venter. Sternum refers to a major, ventral, segmental, sclerotized plate. Sternite refers to a subdivision of a sternal plate. Venter refers to the ventral body surface, or the ventral surface of a particular segment.

The term genital chamber, as it is used here, does not follow the strict definition which Snodgrass (1933) uses in which he distinguishes between a vestibulum and a genital chamber. This distinction depends upon the situation of the pouches above the seventh or eighth venters respectively, with the vestibulum enclosing the genital chamber. Comparable regions will be referred to here as the inner and outer genital chamber. Geyer (1951) uses the term vestibulum and, occasionally, genital chamber, for the same structure. Most other workers have used the term genital chamber or genital cavity (Browman, 1935). Where certain structures are not mentioned by Snodgrass, an effort has been made to use preexisting terms on the basis of priority.

In the absence of developmental studies it is not possible to establish with certainty the line of demarkation between ectodermally and mesodermally derived structures, especially as regards the oviduct in the female and the ejaculatory duct in the male. The terminology which is applied to these regions, therefore, is based upon the apparent structures in the adult and should not be considered necessarily indicative of their origin. Likewise, the actual limits between segments seven, eight and nine in the female are indicated by various adult characteristics (musculature, scleritization, etc.) and cannot be considered final without developmental information.

THE FEMALE REPRODUCTIVE SYSTEM

1. — The Genital Chamber.

The genital chamber of the female is formed by the overlapping of the eighth and ninth venters by the somewhat elongated seventh sternum (fig. 1). As in other Isoptera, therefore, the seventh sternum forms the sub-genital plate. The floor of the chamber is formed by the enlarged intersegmental membrane between the seventh and eighth venters. The roof of the chamber consists of the venters of the eighth and ninth segments. Both the eighth and ninth venters bear two lateral scleritized and pigmented plates, connected medially and to each other by a membranous sheet of chitin. These sternites bear numerous large and minute bristles on their exposed portions, as does also the seventh sternum. The chitinous membrane lining the chamber lacks bristles. The lateral coria are densely setigerous but bear only large bristles.

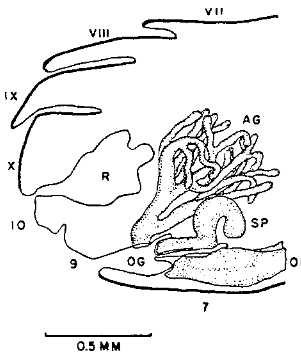


Fig. 1. — Schematic reconstruction from serial sections of the posterior abdomen of a young primary queen. VII-X, tergites; 7, 9, 10, venters; AG, accessory gland; OD, oviduct; OG, outer genital chamber; R, rectum; SP, spermatheca.

The genital chamber includes two regions: an outer, open chamber posteriorly, and an inner, more restricted chamber, anteriorly. The outline of the outer chamber corresponds to the shape of the seventh sternum as it overlaps the ninth venter and the lateral portions of the eighth. At the medial, anterior portion of the ninth venter is the orifice of the duct from the accessory gland. This orifice is partially enclosed ventrally by the posterior projection of two lips from the eighth venter (fig. 2, *a*). These apparently represent the ventral valves. Anteriorly, between the bases of these two valves, appears the opening of a deep, heavily chitinized groove (fig. 2, *b*) running along the medial ventral line of the eighth venter. This is the spermathecal furrow ("samerrine" of HOLMGREN, 1909).

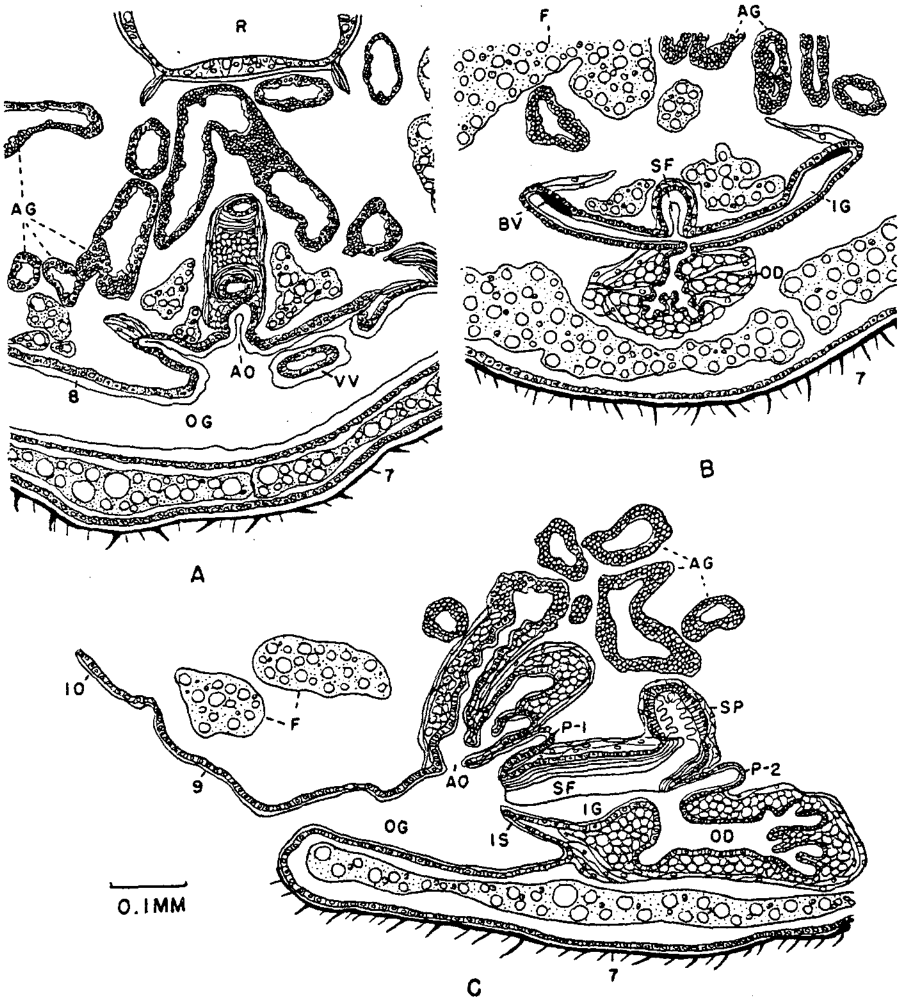


Fig. 2. — Sections through the female genital chamber and associated structures. *a*. Transverse section through medial portion of the outer genital chamber at the level of the accessory gland orifice. *b*. Transverse section through the inner genital chamber at the anterior limit of the spermathecal furrow and the posterior limit of the gonopore. *c*. Sagittal section through the genital chamber. AG, accessory gland ; AO, accessory gland orifice ; BV, basivalvula ; F, fat body ; IG, inner genital chamber ; IS, intersternal fold ; OD, oviduct ; OG, outer genital chamber ; P-1, pouch between venters 8-9 ; P-2, pouch at inner end of genital chamber ; R, rectum ; SF, spermathecal furrow ; SP, spermatheca ; VV, ventral valves ; 7, 8, 9, 10, venters. Camera lucida drawings.

At the point where the spermathecal furrow begins, the genital chamber is restricted ventrally by a fold of the intersegmental membrane between the seventh and eighth venters. BROWMAN (1935) designates this as the "intersternal fold". The posterior origin of the spermathecal furrow, above, and the posterior lip of the intersternal fold, below, mark the posterior limits of the inner genital chamber.

The inner genital chamber is compressed laterally as well as dorsoventrally (fig. 2, *b*). Posteriorly it is about 450 microns wide and tapers slightly anteriorly to about 400 microns. It is approximately 240 to 280 microns long. The spermathecal furrow extends to the midpoint in the chamber as an open groove in the roof. Immediately opposite the anterior limit of the open furrow is the posterior limit of the gonopore which opens through the floor of the chamber (fig. 2, *b* and *c*). The gonopore is slit-like and runs in an anterior-posterior direction. At the upper, lateral margins of the inner genital chamber are two narrow, sleritized bars (fig. 2, *b*) which apparently represent the basivalvulae.

There are two distinct blind pouches in the genital chamber. The first lies anterior to the orifice of the duct from the accessory glands and above the spermathecal furrow (fig. 2, *c*). The upper wall of this pouch forms the attachment point for two bundles of muscles, right and left, which run to the outer lateral margins of the ninth sternites. This pouch apparently marks the limit between the eighth and ninth venters. The second pouch forms the anterior wall of the inner genital chamber. The ventral, anterior surface of this pouch forms the attachment point for muscles running to the anterior margin of the seventh sternum. Thus, as was indicated earlier, the floor of the inner genital chamber appears to be formed by the intersegmental membrane between the seventh and eighth venters.

2. — The Accessory Structures.

The duct leading to the accessory gland divides, usually into anteriorly and posteriorly directed trunks, from which arise the tubules of the gland (fig. 1). These tubules are more or less convoluted and are usually bifurcated. The duct itself is provided with a muscular wall which is absent from the tubules. These tubules are composed of minute and densely crowded cells surrounding a central lumen and enclosed by an epithelial sheath. The function of these glands in the Isoptera has not yet been determined.

The spermathecal furrow consists of a heavily chitinized groove, roughly horseshoe shaped in tranverse section, with the narrow opening along the ventral line. The thickened inner wall is concentrically laminated and is continuous with the thin chitinous intima of the inner genital chamber (fig. 2, *b*). The furrow is enclosed dorsally and laterally by an epithelial layer, resting on a basement membrane, which, in turn, is enclosed by a muscular wall. Although this furrow is present in the pre-imaginal nymphs, the thickened chitinous lining does not appear except in the imago.

At its posterior end the furrow opens directly into the outer genital chamber. At its anterior end it is continuous with a closed duct (fig. 3, *b*, *c*) lined with a smooth, concentrically laminated chitinous wall overlying an epithelial layer and enclosed dorsally and laterally by a muscular coat. This duct is attached throughout its length to the upper, inner surface of the inner genital chamber. The spermathecal duct leads into the sper-

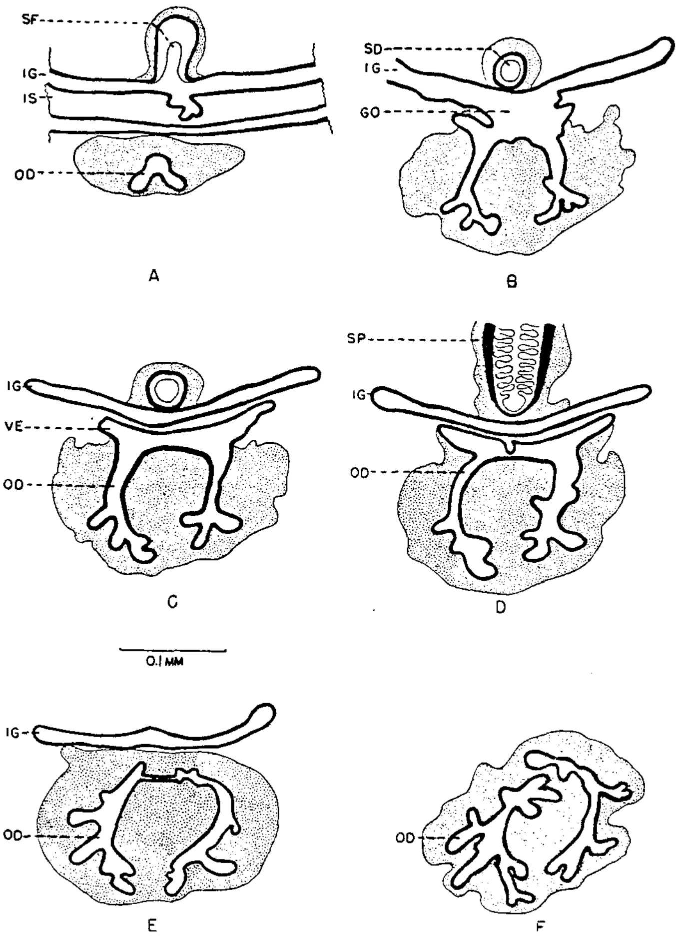


Fig. 3. — Transverse sections through successive areas (posterior to anterior) of the inner genital chamber, gonopore and medial oviduct. *a*. Section through the posterior portion of the inner genital chamber (IG) showing the spermathecal furrow (SF), grooved intersternal fold (IS) and the posterior projection of the medial oviduct (OD). *b*. Section at the level of the gonopore (GO), showing the spermathecal duct (SD) above the inner genital chamber (IG). *c*. Section anterior to the gonopore, showing the thin walled vestibule (VE) below the inner genital chamber. *d*. Section at the level of the spermatheca (SP) showing the dorsal-medial fold in the wall of the vestibule. *e*. Section posterior to the vestibule, the oviducts still interconnected at the dorsal mid-line. *f*. Section of the medial oviduct, internally divided into right and left oviducts. Solid black indicates epithelium; stippled areas denote muscular mass. Diagrammatic, drawn with the aid of a camera lucida.

matheca which usually arises at a right angle to the duct (fig. 1 ; 2, *c* ; 3, *d*) and runs dorsally.

The general form of the spermatheca is that of a thick blind tube with a recurved end. The inner wall is composed of finger-like projections of chitin beneath which lies a dense eosinophilic layer underlaid by a zone of nuclei. Beneath these lies a rank of tall colymnar cells which are vacuolated and evidently secretory in function. These rest upon a basement membrane which is invested by a muscular tunic. The chitinous lining of the spermatheca is penetrated at 4 to 5 micron intervals by the opening of the intracellular canals ("Ausfuhrgang" of AHRENS, 1935). These canals lead from the lumen of the spermatheca, through the eosinophilic layer and into the columnar epithelium. The canals appear to be invaginations of the chitinous intima and are 1 to 1.5 micron in diameter. They may be as much as 20 microns long, running at various angles from the surface into the epithelium. Both the finger-like chitinous projections and the intracellular canals are lacking in the pre-imaginal nymphs.

All of the females which had been combined with males in culture had sperm present in the spermathecal duct and the spermatheca. In a few instances sperm were also present in the spermathecal furrow.

3. — THE OVIDUCTS.

Superficially, the lateral oviducts appear to join to form a medial duct opening via the gonopore through the floor of the inner genital chamber (fig. 1). A consideration of serial sections, however, reveals a more complex situation. A section through the most posterior portion of the gonopore (fig. 2, *b*) shows a duct having the form of an inverted Y. The stem of the Y represents the gonopore and the two arms represent the extensions of the right and left oviducts. Posteriorly the gonopore is continuous with a medial groove in the intersternal fold. This groove lies opposite the spermathecal furrow (fig. 3, *a*), 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 oviducts which are joined at the apex to form an inverted V in transverse section. They are surrounded by a muscular and connective tissue mass.

Anterior to the posterior edge of the gonopore, the aperture is widened (fig. 3, *b*) and leads into a thin-walled vestibule into the floor of which open the right and left oviducts which are separated and enclosed by a muscular mass. Anterior to the gonopore, the upper, thin-walled vestibule persists (fig. 3, *c*) lying immediately below the inner genital chamber. More anteriorly, at the level of the origin of the spermatheca (fig. 3, *d*) a fold appears in the medial, dorsal wall of the vestibule and the lower arms of the chamber are enclosed by extensions of the muscular wall surrounding the oviducts. At the level where the inner genital chamber ends, the vestibule has disappeared, the right and left portions being continuous with the right and left oviducts and the whole being surrounded by a muscular mass. Although the right and left oviducts are distinct, they are still interconnected at the dorsal medial line (fig. 3, *e*). Finally, the right and the left oviducts are completely separated from one another internally (fig. 3, *f*), although surrounded by a common muscular mass.

The two ducts separate completely to form the right and left oviducts which extend laterally and then dorsally, in a nearly vertical plane on either side of the gut. The vertical arms of the oviducts lie within the limits of the seventh segment.

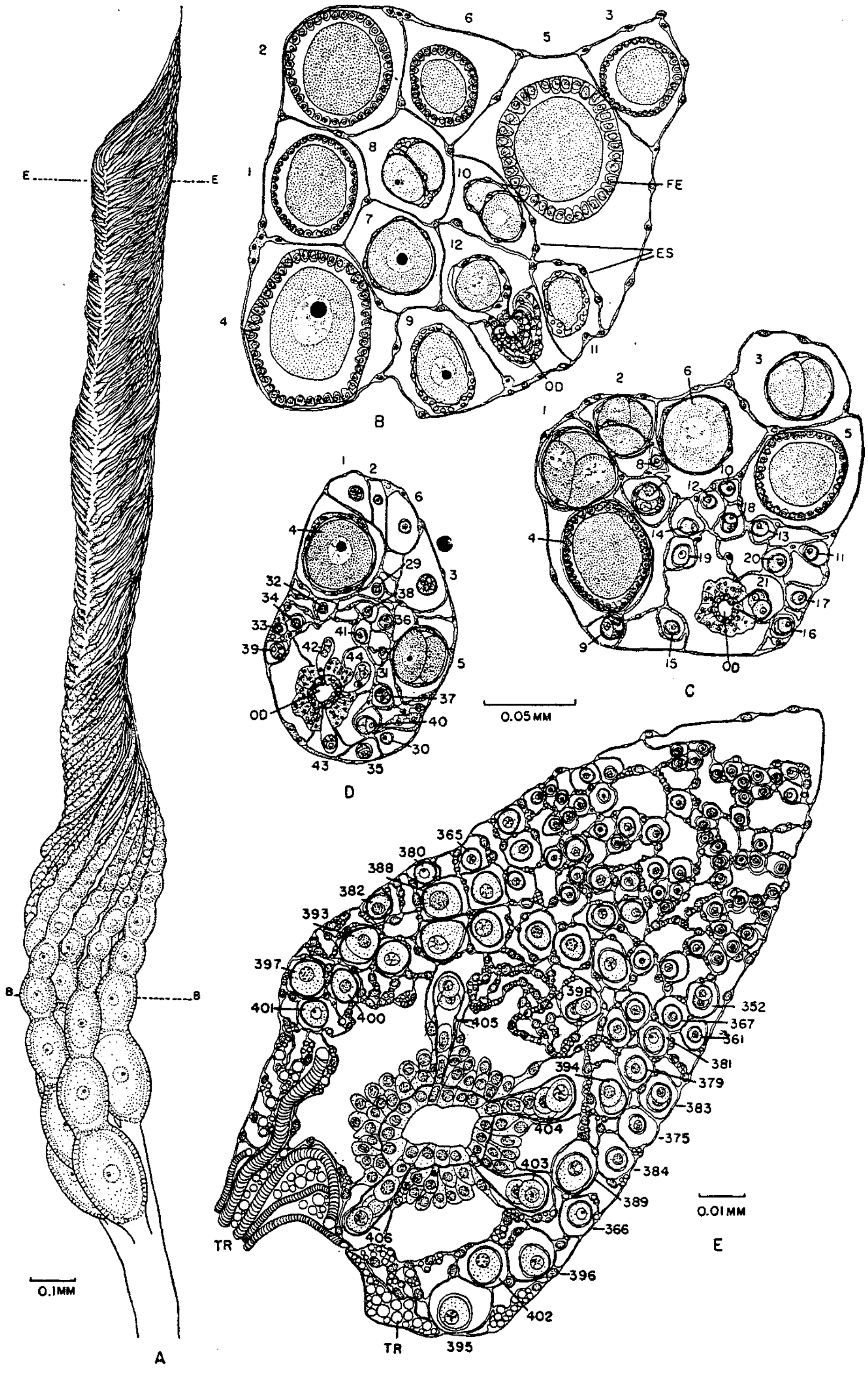
Immediately above the level of the gut, the first ovarioles are inserted into the oviducts. The oviducts extend anteriorly, maintaining a fairly constant level dorsal to and on either side of the gut. At their anterior ends they are slightly more dorsal and medial than at their posterior ends. The oviducts persist for almost the full length of the abdomen, terminating at the level of the first or second abdominal segments. Anteriorly the oviducts lack a muscular wall, the lumen of the duct being surrounded by an epithelial layer and this is enclosed by a mass of connective tissue. A distinct basement membrane underlies the epithelium.

4. — The Ovary.

Each ovary (fig. 4, *a*) is composed of a large number of ovarioles, arising along the entire length of the oviduct anterior to the vertical arms. The ovarioles arise from all sides of the oviduct (fig. 4) and extend anteriorly and towards the dorsal mid-line of the body from their point of insertion on the oviduct. The total number of ovarioles, as counted in serial sections of one ovary in each of four individuals, was found to be 408, 413, 415 and 450, respectively. Of this large potential, between 800 and 900 per individual, only 5 to 8 are functional in each ovary at the time of flight. The most mature ovarioles are those inserted at the posterior portion of the oviduct.

Each ovariole is surrounded along its entire length by a closely applied, non-cellular layer, the *tunica propria*. Anteriorly, the *tunica propria* encloses three or four elongated epithelial cells, forming the terminal filament (fig. 5). The terminal filament is attached to adjacent cells of the epithelial sheath and the tracheal mass with which the ovary is richly

Fig. 4. — The ovary of a young primary after the initial egg laying period. *a*. Ovary as observed in a whole mount. b-b and e-e indicate approximate levels of sections *b* and *e*, respectively. *b*. Transverse section through ovary at level where the twelfth ovariole arises from the oviduct. *c*. Transverse section through the last section in which the twelfth ovariole is visible. *d*. Transverse section through the last section in which the first ovariole is visible. *e*. Transverse section through the anterior portion of the ovary. Numbers refer to successive ovarioles as they arise from the oviduct from posterior to anterior. ES, epithelial sheath ; FE, follicular epithelium ; OD, oviduct ; TR, trachea. Trachea have not been shown in figures a, b, c and d. Camera lucida drawings.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provided. The terminal filament may be extended into a thin prolonged strand, or may be pleated and recurved as shown in figure 5. Posteriorly, the *tunica propria* appears to be continuous with the basement membrane of the epithelium lining the oviduct. This relationship is best demonstrated in sections prepared with Mallory's Triple Stain.

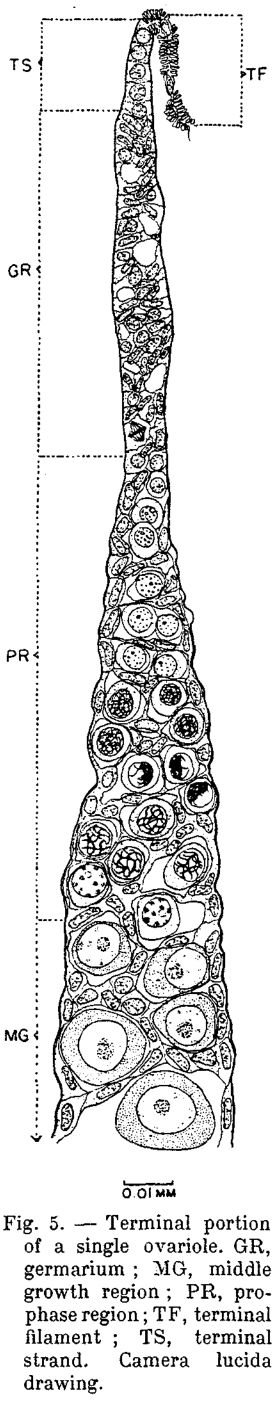

Fig. 5. — Terminal portion of a single ovariole. GR, germarium ; MG, middle growth region ; PR, prophase region ; TF, terminal filament ; TS, terminal strand. Camera lucida drawing.

In the case of young primary reproductives which have deposited the initial group of eggs, the stalk or peduncle of each functional ovariole is enclosed by a greatly folded sheet of *tunica propria.* A similar structure has been described by Ahrens (1935) in *Odontotermes redemanni.* Apparently the *tunica propria* persists as a continuous layer, although the cells of the follicular epithelium disintegrate after the deposition of the fully developed eggs. The presence of this folded *tunica propria* is helpful in recognizing ovarioles which have released eggs.

Beyond the *tunica propria*, each ovariole is enclosed by loose epithelial sheath of flattened cells (fig. 4, *b*, *c*, *d* and *e*). These cells are continuous basally with the epithelium surrounding the oviduct. In crowded regions of the ovary the epithelial sheath may be in contact with the *tunica propria* but they do not have any mutual structural continuity. The epithelial sheaths appear to extend anteriorly to form the ovarian ligaments which usually remain separated on the right and left sides until immediately before their attachment in the dorsal portion of the meta-thorax.

The mature ovariole tapers anteriorly and has a typical panoistic organization, lacking specialized nurse cells and provided posteriorly with a well developed follicular epithelium. In addition to the terminal filament, mentioned above, the mature ovariole usually includes five structural areas which are fairly sharply defined from one another. As will be indicated later, the proportion of each region varies from ovariole to ovariole. These areas include: the terminal strand; germarium; prophase or initial growth region; middle growth region; and the terminal growth region. The areas may be defined as follows:

a. *The terminal strand.* Immediately posterior to the terminal filament lies a strand of small cells with round nuclei (fig. 5). These cells are arranged in a linear series and measure about 4 microns in transverse section. They fill the entire ovariole at this level and are enclosed by the *tunica propria.* Their number varies from as few as four in well developed ovarioles to sixteen in the immature ovarioles. In a few instances, this area could not be distinguished in the most posterior ovarioles, the terminal filament arising directly from the germarium. The origin, function and fate of these cells has not been determined.

b. *The germarium.* Posterior to the terminal strand is an area in which the cells and their nuclei are flattened and closely crowded (fig. 5). In immature ovarioles, these cells may be arranged in a linear series, the nuclei being oriented with their long axes across the ovariole. In mature ovarioles, the diameter of the ovariole may increase suddenly from 4 microns (of the terminal strand) to 8 or 10 microns and the cells are arranged at random within the *tunica propria.* Dividing cells are frequently observed within the germarium, especially in the posterior third.

c. *The prophase region.* The posterior limit of the germarium is marked by the appearance of small round oöcytes surrounded by smaller, elongated epithelial cells (fig. 5). These oöcytes, which are 5 to 6 microns in diameter, mark the anterior limits of the prophase or initial growth region. The oöcytes increase gradually in size until they are 10-14 microns in diameter. The epithelial cells increase slightly in number, but maintain their relatively small size and squamous form. The most distinctive character of this region, as implied by the name, is a conspicuous rearrangement of the chromatin material within the nuclei of the young oöcytes. The most anterior oöcytes have a reticulated chromatin network with a small nucleolus. The latter disappears and the chromatin material is arranged in fine, elongated threads, at first diffuse and then concentrated to one side of the nucleus. Subsequent nuclei contain shorter, thicker chromatin threads, distributed throughout the nucleus. Finally, the nucleoli reappear and the nuclei contain about twenty peripheral clumps of basophilic material which appear to represent clumped chromatin threads. This series of transformations corresponds closely to the typical pregrowth meiotic prophase. Throughout the prophase region, the cytoplasm of the oöcytes is eosinophilic and the chromatin strongly basophilic. The nuclei in the posterior oöcytes reach a diameter of 7.5 to 9 microns and the nucleoli a diameter of 2 to 2.5 microns. The overall cross-sectional diameter of the ovariole increases from about 21 microns anteriorly to about 34 microns posteriorly.

d. *The middle growth region.* Posterior to the prophase region, the oöcytes increase rapidly in size and the cytoplasm becomes basophilic. The developing oöcytes are crowded within the ovariole, either side by side, or in a staggered series, expecially towards the posterior end. They are usually ovoid or tetrahedral in shape. The large round germinal vesicle contains a conspicuous nucleolus and peripheral clumps of chromatin material which become diffuse and oxyophilic. Posteriorly, the nuclei reach a diameter of 14 microns and the nucleoli have a diameter of 5 microns. Each oöcyte is enclosed in a thin sheet of follicular epithelium whose nuclei tend to be grouped in clumps between adjacent oöcytes.

TABLE 1.

Dimensions of Oöcytes in the Terminal Growth Region of Five Ovarioles in a Young Queen.*

OOCYTE **.	FIRST ovariole.	SECOND ovariole.	THIRD ovariole.	SEVENTH ovariole.	NINTH ovariole.
1	210 × 107	252 × 175	210 × 122	120 × 45	48 × 40
2	88 × 59	140 × 70	122 × 70	55 × 70	30 × 36
3	77 × 52	112 × 59	105 × 63	42 × 32	30 × 36
4	77 × 49	112 × 59	73 × 56	25 × 32	27 × 36
5	63 × 45	80 × 58	59 × 49	18 × 32	
6	49 × 45	63 × 52	49 × 49	15 × 32	
7	38 × 45	52 × 49	28 × 42	15 × 32	
8	31 × 42	38 × 42	28 × 42		
9	22 × 42	31 × 42			
10	21 × 38	31 × 35			
11	28 × 38				
12	24 × 31				

* Dimensions given in microns. First figure in each pair is greatest dimensions of oöcyte on the long axis of the ovariole. Second figure is greatest transverse dimension.

** Oöcytes and ovarioles numbered from most posterior to most anterior.

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

The general size and shape of successive oöcytes in the terminal growth region is indicated by the examples in table 1. These measurements were taken from sections of a young primary reproductive which had deposited the initial group of eggs. The first six ovarioles on either side of this individual each contained one fairly well developed, yolky egg. Judging by the presence of a pleated *tunica propria* at the base of the peduncles, there were seven functional ovarioles in this ovary. The ninth ovariole, therefore, although containing a few oöcytes in the terminal growth region, was still immature.

The germinal vesicle increases gradually in size and maintains a central position in the oöcyte until the latter have reached a length in excess of 200 microns. The largest central nuclei have a diameter of 24 microns. In oöcytes exceeding 200 microns it was usually impossible to distinguish the nucleus. In a few instances an irregular nucleus, usually with two large, irregular nucleoli could be observe at the periphery of the larger, yolky oöcytes. No maturation spindles were observed, although an effort was made to find them.

The largest contained oöcyte in any of the primary reproductives which were sectioned was 754 by 232 microns. This oöcyte possessed a well developed chorion. The three succeeding oöcytes in this same ovariole were 464 by 233, 406 by 202, and 348 by 174 microns, respectively. This was the first (most posterior) ovariole in an alate taken from the colony workings on the day when alates first appeared in the field colonies, more than a month before the first flight occurred.

As has been indicated earlier, the presence and proportion of the various regions varies from the mature to the immature ovarioles. The bulk of the anterior ovarioles consist only of an elongated germarium, 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 10 or 11 in young primaries, include a terminal growth region. Only 5 to 8 of these latter are actually functional at the time of flight. Frequently, the most posterior ovarioles lack the middle growth region. In these, the terminal region immediately adjoins the prophase region. This condition, as well as the presence of rather distinct areas of development in all of the ovarioles, suggests a rhythmic rather than a continuous production of oöcytes.

5. — The Follicular Epithelium.

The development of the follicular epithelium is comparable to that described by Ahrens (1935) in *Odontotermes redemanni*. I was unable, however, to distinguish with certainty between follicular and germinal cells in the germarium. The first recognizable follicular cells lie in the anterior portion of the prophase region. These cells are squamous and contain an elongated nucleus with a reticulated chromatin network. Throughout the prophase and middle growth regions, the follicular epithelium is composed of flattened and irregular cells, separating the oöcytes from one another and from the *tunica propria.* Dividing follicular nuclei are frequently observed through these areas.

At the anterior portion of the terminal growth region, the epithelial cells separating the oöcytes from the *tunica propria* become more numerous and assume a flattened cuboidal and, later, a cuboidal form. The cells which separate adjacent oöcytes are squamous in form. By the time the oöcyte reaches a dimension of about 170 by 80 microns, and before active yolk formation occurs, the follicular epithelium is columnar, with a rounded inner surface (fig. 6, *a* and *b*). At this time the cells are frequently binucleate, the nuclei being arranged one above the other. By the time the chorion is deposited, the cells of the follicular epithelium are enlarged and once again flattened, being compressed between the egg and the *tunica propria.* They may be bi- or uni-nucleate, the former cells being appreciably larger than the latter (fig. 6, *c* and *d*).

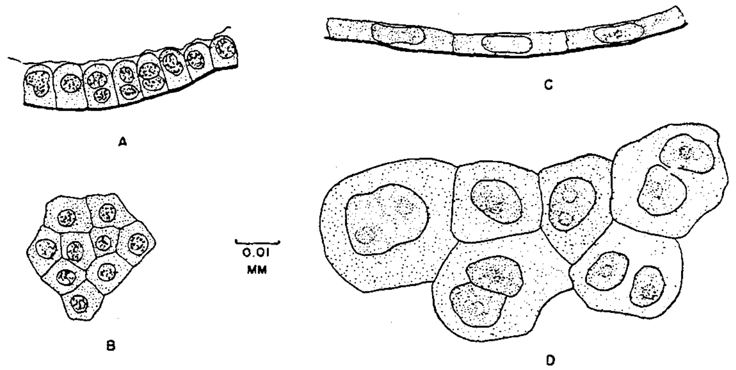

Fig. 6. — Follicular epithelial cells. *a*, section and *b*, surface view of follicular epithelium from an oöcyte of 170 × 80 microns. *c*, section and *d*, surface view of follicular epithelium from an oöcyte having a chorion. Black line in sectional views represents the *tunica propria.* Camera lucida drawings.

Subsequent to the deposition of the egg, the follicular epithelium disintegrates and is apparently resorbed. As has been indicated earlier, the *tunica propria* persists as a tremendously pleated sheet, connecting the oviduct with the next follicule. No yellow pigment granules are observed in the area of disintegrating follicular cells, as have been described for various species (Bugnion and Popoff, 1912; Ahrens, 1935).

THE MALE REPRODUCTIVE SYSTEM

The seventh sternum of the male reproductive is not elongated as it is in the female. It has the same general form and size as the preceeding sterna, being about 2.4 mm. wide by 0.64 mm. deep. Unlike the divided plates in the female, the eighth and ninth sterna of the male are entire, although they are smaller than the seventh. The eighth sternum is about 1.89 mm. by 0.45 mm., and the ninth, 1.31 by 0.22 mm. The seventh, eighth and ninth sterna are all scleritized, pigmented and densely setose. As in the female, the setae include both a large and minute series on the sterna, whereas the lateral coria bear only large setae. No styli are apparent on the ninth sternum.

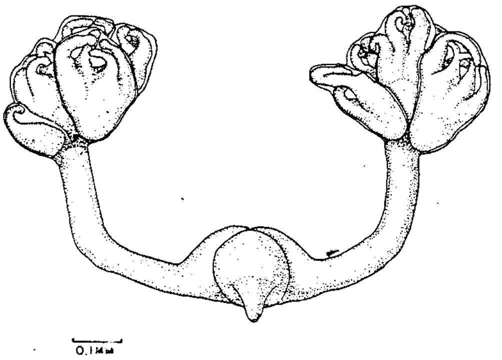

Fig. 7. — The male reproductive system, from a whole mount.

The external gonopore lies medially in the intersegmental membrane between the ninth and tenth sterna. In sectioned material this opening can be observed to lie within an invaginated membranous sheath which probably represents a small, distendable penis. The gonopore is continuous with a short, muscular ejaculatory duct which terminates in a round bulbous portion (fig. 7) into which open the right and left vasa deferentia.

The vasa deferentia open into the ejaculatory bulb via two small openings situated anterior-laterally and slightly dorsal of the midline on either side of the bulb. The basal portion of each vas deferens is slightly enlarged to form a chamber, roughly triangular in form, which evidently serves as a point of sperm storage. Beyond the enlarged basal portion, each vas deferens runs laterally and then dorsally in an almost vertical plane on either side of the rectum to join the testicular lobes.

The testes are minute and lie laterally on either side of the rectum. Each testis (fig. 7) consists of 6 to 8 compound testicular lobes. Each lobe may include 1 to 6 spermatic tubes which are united at the base and open into a chamber, which might be considered the vas efferens, and which empties into the vas deferens. Each sperm tube has a free end distally which is usually recurved and is occasionally bifurcated.

Figure 8 presents a camera lucida drawing of a section transecting two testicular lobes. The terminal portion of each tube consists of a germarium and contains small, closely packed cells among which division figures may occasionally be observed. Histologically the germarium of the testis resembles the germarium of the ovary. Below the germarium, the cells are enlarged and regular in shape and are arranged in groups or cysts. The nuclei show a reticulated chromatin network. Below this lies an area in which the cells are undergoing prophase phenomena and meiotic divisions. All of the cells within a given cyst divide synchronously. Finally, immediately adjacent to the vas efferens, lie cysts containing spermatids and spermatazoa.

In the upper portion of the vas deferens the sperm are frequently clumped into groups, although not enclosed within a cyst. The spermatazoa in the upper portion may be surrounded by an eosinophilic cytoplasmic mass, which is absent from the sperm in the lower portion of the vas deferens. The sperm, as observed in the testis and vas deferens of the male and the spermatheca of the female, are apparently non-flagellated.

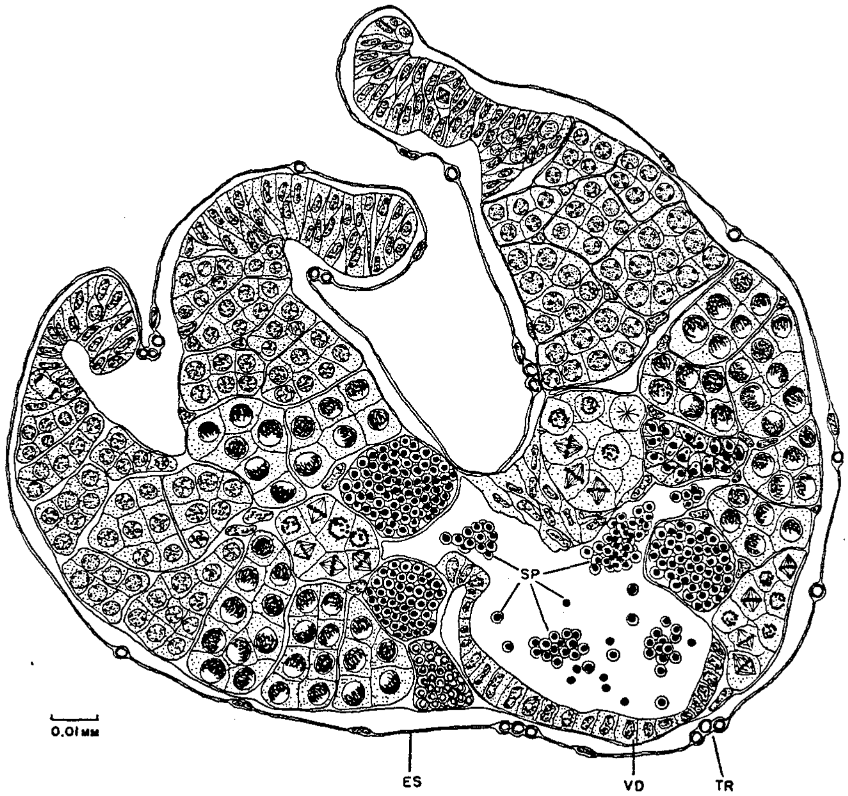

Fig. 8. — Section through two testicular lobes, showing two spermatic tubes on the left ; the terminal portion of one and the basal portions of three spermatic tubes on the right. ES, epithelial sheath ; SP, sperm ; TR, trachea ; VD, vas deferens. Semi-diagrammatic ,drawn with the aid of a camera lucida.

The sperm are minute round bodies, staining intensely with hematoxylin or acid fuchsin. Under high magnification they give the appearance of small ring-like structures with a dark periphery and a more lightly staining central portion. They are about 1.5 to 1.75 micron in diameter. There are also present, in smaller numbers, sperm which are 2.5 to 3.5 microns in diameter, which frequently retain their cytoplasmic envelope. In these cells the basophilic portion is usually irregular and vesiculated. Such "sperm" are probably abortive and apparently disintegrate, since they are not usually encountered in the spermatheca of the female.

GEYER (1951) describes micro- and macrosperm in *Macrotermes natalensis*, but in this species the larger sperm apparently represent the normal elements and are present in large numbers. The larger cells observed in *T. tenuirostris* may be comparable to the sperm nutritive cells which JUCCI (1924) describes in *Kalotermes flavicollis* and *Reticulitermes lucifugus*. STELLA (1938) also observed these cells in the same two species. Both Jussi and Stella conclude that these cells may represent abortive germinal elements which serve a nutritive function for sustaining the matured sperm in the vas deferens and the seminal vesicle.

DISCUSSION

Perhaps the most difficult discrepancy to resolve in the existing literature on the termite reproductive system is the occurrence of a spermathecal furrow. The only description of such a structure, to my knowledge, is that by HOLMGREN (1909) in *Heterotermes* (=*Leucotermes*) *tenuis*. There is reason to believe, however, that such a structure is present in some of the other genera which have been described but that various authors have not made a distinction between a simple pore or spermora and an elongated furrow. AHRENS (1935, *b*) states that the spermatheca and the accessory gland of *Odontotermes* species and *O.* (=*Termes*) *redemanni* open posterior to the oviduct. His figures, however, indicate that the opening of the spermatheca lies at the same level as the opening of the oviduct and is extended posteriorly as a furrow. The presence of a furrow is also suggested in BROWMAN's (1935) figure of *Pseudacanthotermes militaris* and it is almost certainly present in *Macrotermes natalensis*, *M. swaziae* and *Odontotermes* (=*Termes*) *angustatus* as illustrated by GEYER (1951). On the other hand, the figures which both of these authors present for species from the lower families of termites do not suggest any prolongation of the spermathecal aperture. Indeed, the sagittal section of *Neotermes zuluensis* shown by GEYER, clearly indicates that the opening of the spermathecal duct is a simple pore in this species.

The spermathecal furrow appears to represent an elongation of the spermora which it resembles histologically. GEYER's transverse sections of the "proximal portions" of the "spermora" of *M. natalensis* and *N. zuluensis* show a striking similarity to one another and to a similar section of the spermathecal furrow of *T. tenuirostris*. However, no scleritization occurs between the thickened chitinous intima and the epithelial layer of the furrow in *T. tenuirostris*, as it does in the "spermora" of the other two species. I have examined sections of *Reticulitermes hesperus* (BANKS) and in this species the spermora also shows the same general histological organization and has a sclerotized arch. The size of the aperature in *R. hesperus*, however, does not exceed 40 microns as compared with the elongated (120-140 microns) structure in *T. tenuirostris*. HOLMGREN (1909) does not state the length of the furrow in *Heterotermes tenuis*, nor does GEYER (1951) indicate the actual size of the "spermora" in any of the species which he considered.

Functionally, the long spermathecal furrow, opening directly into the outer genital chamber, would seem advantageous in transmitting sperm into the spermatheca. At the same time, the actual opening of the spermathecal duct is maintained opposite the gonopore. The presence of such a furrow is apparently correlated with a long inner genital chamber. In *R. hesperus*, for example, the inner genital chamber is relatively shallow and the spermora relatively small. HOLMGREN (1909) illustrates the oviducts of *H. tenuis* as opening posterior to the termination of the spermathecal furrow. HEBERDEY (1931), in considering HOLMGREN's description, suggests that the spermathecal furrow aids in the transfer of sperm from the anteriorly situated spermatheca to the posteriorly situated gonopore. This, of course, is a perfectly good functional relationship, provided that HOLMGREN's description is correct. Regarding the position and opening of the oviduct, HOLMGREN remarks: ,,Ich bemerke, daß bei *Leucotermes tenuis* ist dies Verhältnis an meinen Präpparaten nicht besonders deutlich sehen. Da aber bei anderen Termitenpraparaten das Verhältnis sehr deutlich hervortritt, so wage ich es auch so für *Leucotermes* zu deuten." It seems possible, therefore, that he was mistaken regarding the position of the gonopore, relative to the position of the spermathecal furrow. A re-examination of this species would certainly be desirable.

HOLMGREN does not show any structure comparable to the intersternal fold. IMMS (1919) shows a highly developed intersternal fold in *Archotermopsis wroughtoni*. HEBERDEY (1931) felt that IMMS was mistaken regarding the presence of this structure and regarded it as a possible fixation artifact. Subsequent work by BROWMAN (1935) on *Masototermes* and *Zootermopsis*, shows the presence of a well developed intersternal fold in these two primitive genera. In both of these the intersternal fold bears scleritized areas. BROWMAN remarks that "the intersternal fold is greatly reduced in practically all the other termites studied". AHRENS (1935, *b*) shows a distinct intersternal fold in *Odontotermes redemanni*. It seems probable, therefore, that IMMS' description of *Archotermopsis* is correct and this genus resembles the other primitive genera described by BROWMAN. Likewise, it is possible that HOLMGREN did not recognize the intersternal fold in *Heterotermes tenuis*, since in this species it is probably reduced and membranous.

As regards segmentation, I agree with KNOWER (1901), HEBERDEY (1931), BROWMAN (1935) and GEYER (1951), in placing the accessory gland opening on the ninth venter, the spermatheca on the eighth and the gonopore on the intersegmental membrane lying between the seventh and eighth. These structures, therefore, have maintained their primitive positions segmentally, although there has been a shifting anteriorly of the medial portions of the eighth and ninth venters and a shifting posteriorly of the seventh segment. HOLMGREN (1909) concludes that the spermatheca, accessory glands and the oviducts of *Heterotermes tenuis* all open through the intersegmental membrane between the seventh and eighth segments. In *Archotermopsis*, IMMS (1919) considers the intersternal fold and the floor of the inner genital chamber as the eighth segment and the entire roof of the chamber, including the apertures of the accessory gland and the spermatheca, as the ninth. These differences are more probably differences of interpretation rather than actual differences between the various genera.

The presence of a large number of ovarioles, arising along the entire length of the ovary, is in agreement with earlier observations on various Termitidae. BUGNION and POPOFF (1912) in their study of *Odontotermes* (=*Termes*) *obscuriceps*, counted 2,420 ovarioles in one ovary of a mature queen. GEYER (1951) remarks that in *Macrotermes natalensis* "the ovaries consist of a large number of ovarioles, probably several thousand in each ovary" of the young alates. The relative degree of development of the ovarioles of the young queens, as observed in *Tenuirostritermes tenuirostris* also agrees with GEYER's observations that of the large number present in *M. natalensis*, at the time of flight only the last six are well developed. In view of the large number of ovarioles which are present in these young primaries, some reconsideration must be made of the hypothesis of ovariole augmentation which has been suggested (GRASSÉ, 1949) to explain the tremendous development of certain queens and the discrepancies in the counts of the number of ovarioles in the same species as reported by different authors. In examining the young primary reproductives it is easy to misjudge the number of ovarioles, even in serial sections. In the well developed primaries on the other hand, all of the ovarioles are conspicuous and give the impression of an increased total number. BUGNION and POPOFF (1912), for example, counted the ovarioles of the mature queen by removing them one by one from the oviduct. In the serial sections of *T. tenuirostris*, on the other hand, it was necessary to use high magnification in order to distinguish the point at which each of the many immature ovarioles arose from the oviduct.

Although meiotic spindles have not been observed, all the information now at hand suggests that maturation occurs either after the deposition of the egg, or only after the oöcyte is in the final phases of development. No meiotic division figures, nor any indication of such phenomenon were found in any of the many ovarioles examined. In view of the consistent observation of mitotic figures in the germarium and various prophase stages in the initial growth region, it is difficult to feel that the process of maturation was not observed if it occurs as described by STELLA (1938). In *Kalotermes flavicollis* and *Reticulitermes lucifugus*, STELLA describes the meiotic divisions from the more anterior oöcytes of the terminal growth region. According to her descriptions and figures, such oöcytes were still surrounded by a flattened epithelial sheath and did not contain true yolk. STELLA considered the large, central nuclei, encountered in the posterior oöcytes, as the female pronucleus. After a careful consideration of her descriptions and figures and an examination of *T. tenuirostris* and also of *Reticulitermes hesperus*, I cannot but feel that STELLA was mistaken. Certainly some confusion exists regarding her figures 3 and 4 in Plate 2, which according to the legend show the first meiotic spindles of *K. flavicollis* and *R. lucifugus*, respectively. A careful comparison of these two figures shows that figure 3 is a photograph at higher magnification of a portion of the same field shown in figure 4. In the text, STELLA refers both figures to *K. flavicollis* and later refers the fourth figure to *R. lucifigus*. In my opinion, the figures show a dividing follicular epithelial cell, overlying a young primary oöcyte in the anterior portion of the terminal growth region. The large nucleus which appears in Stella's figure 4 and which she considers a pronucleus is a typical germinal vesicle of a developing oöcyte prior to yolk formation. The occurrence of a later maturation is indicated in the present observations by the persistence of a large, central germinal vesicle until long after yolk formation and by the peripheral position of an irregular nucleus in the largest yolky eggs in which a nucleus could be observed.

The structure of the testis of *Tenuirostritermes tenuirostris* resembles that of *Macrotermes* (=*Bellicositermes*) *natalensis* as described by BONNEVILLE (1936) in that the spermatic tubes are arranged in groups which empty into extensions of the vas deferens. In the case of *M. natalensis*, BONNEVILLE found that the spermatic tubes are reflexed upon themselves to form a U-shaped structure. The arch of the U is broad, and narrows towards the germarium on the one side and the basal portion on the other. The basal portions of adjacent spermatic tubes open separately into a common vas efferens. The testis is composed of a number of such clusters of spermatic tubes draining into vasa efferentia arising from the vas deferens. In *T. tenuirostris*, on the other hand, only the terminal portion of the germarium of each spermatic tube is reflexed. The basal portion of each tube is broad and the basal portions of all spermatic tubes within a testicular lobe are fused at the base. In *M. natalensis*, as in *T. tenuirostris*, there are no accessory structures associated with the male reproductive system. The sperm are apparently stored in simple enlargements of the basal portions of the vasa defferentia.

GEYER (1951) describes the male reproductive system of *Macrotermes natalensis*. According to present synonymies (A. E. EMERSON, personal correspondence), *Bellicositermes natalensis* is a synonumn of *Macrotermes natalensis*. That is, the species studied by BONNEVILLE (1936) is synonymous with that later considered by GEYER. The descriptions of the male reproductive systems, however, are extremely dissimilar. GEYER does not describe the form of the individual spermatic tubes. He states that the testes are "irregular structures, hollow in the centre. The testicular tubules open into these cavities and the vasa deferentia also originate from the posterior third of the testes." As regards the basal portions of the vasa deferentia, GEYER describes basal, anteriorly directed pouches arising from the vasa deferentia. He considers these pouches to be "simple saccular mesadenia" which have "attained the secondary function of vesiculae seminales since the primary vesiculae seminales are absent". These pouches were also present in *M. swartzi* as well as in the more primitive *Neotermes zuluensis* and *Kalotermes durbanensis.* GEYER does not make any direct comparisons between his observations and those of BONNEVILLE although he mentions the latter work. It is not possible, on the basis of the information now available, to resolve the differences in the descriptions by these two authors for what is reported to be the same species.

In the case of those reproductives of the Termitidae which have been described, there are a larger number of generative elements in the testis and the ovary than are encountered in those species described from the more primitive families. In the latter, the ovarioles do not usually exceed 50 in each ovary and there are usually only six to ten spermatic tubes in each testis. In the Termitidae, at least 400-500 ovarioles are present and there may be as many as several thousand in each ovary in some species. Likewise, the number of testicular elements has increased to 40 or more spermatic tubes.

Summary.

The reproductive system of *Tenuirostritermes tenuirostris* shows many of the features that have been attributed to other species of the Termitidae. In the female, the eighth and ninth sterna are reduced to lateral plates, connected by a chitinous membrane. The genital chamber is divided into two regions, a broad outer chamber posteriorly, and an inner, narrower chamber anteriorly. The accessory gland opens into the outer genital chamber via an unscleritized orifice at the medial, anterior portion of the ninth venter. Beneath and lateral to this aperture lie two unscleritized projections from the eighth venter, the ventral valves. At the base of the ventral valves lies the opening of a heavily chitinized groove, the spermathecal furrow. At this point the genital chamber is compressed laterally to form the inner genital chamber. The spermathecal furrow extends anteriorly for 120 to 140 microns to the mid-point of the roof of the inner genital chamber. It is continuous anteriorly with a closed duct which runs medially along the inner, dorsal wall of the inner genital chamber and joins the spermatheca. The spermatheca arises at right angles to the duct and runs dorsally. The inner wall of the spermatheca is perforated by numerous, minute, intracellular canals which extend into the secretory columnar epithelium. The spermathecal furrow, duct and the spermatheca all lie within the eighth segment. Dorsolaterally,

in the wall of the inner genital chamber, lie two narrow, scleritized bars, the basivalvulae. The floor of the inner genital chamber is composed of the intersegmental membrane between the seventh and eighth segments. This membrane is perforated by the gonopore, the posterior margin of which lies opposite the aperture of the spermathecal duct. The posterior ventral margin of the inner genital chamber is marked by an intersternal fold which is unscleritized. The seventh sternum forms the sub-genital plate. Each ovary includes 400-450 ovarioles, arising from all sides and along the entire length of the oviduct which extends anteriorly into the first or second abdominal segment. In the male, the eighth and ninth sternites are reduced but entire. There are no styli on the ninth sternum. No accessory structures are associated with the ejaculatory bulb or with the vasa deferentia. Each testicular lobe is a compound structure, including a number of spermatic tubes which are fused at the base but terminate individually in a recurved germarium.

Zusammenfassung.

Das Genitalsystem von *Tenuirostritermes tenuirostris* hat manche Eigenschaften, welche andern Termitidaen-Arten zugeschrieben worden sind. Im Weibchen sind die achte und neunte Sterna zu Seitenplatten reduziert und mit einer chitinösen Membran verbunden. Der Genitalraum ist in zwei Bezirke abgeteilt; davon ist der hintere Bezirk ein breiter, äußerer Raum, während der vordere Bezirk ein innerer, schmaler Raum ist. Die akzessorische Drüse öffnet sich in den äußern Genitalbezirk durch eine unsklerotisierte Öffnung am medialen vorderen Teil des neunten Sternits. Ventral und zugleich seitlich von dieser Öffnung liegen zwei unsklerotisierte Fortsätze vom achten Sternit, die Ventralklappen. An der Basis der Ventralklappen befindet sich die Öffnung einer stark chitinösen Rinne, die Samenrinne. An diesem Punkt ist der Genitalraum seitlich zusammengedrückt und bildet den innern Genitalraum. Die Samenrinne setzt sich um 0,120 mm bis 0,140 mm vorwärts bis zum Mittelpunkt des innern Genitalraumes fort. Diese Rinne setzt sich vorwärts in einen geschlossenen Kanal fort, welcher median an der inneren dorsalen Wand des innern Genitalraumes verläuft und sich an die Samenkapsel anschließt. Die Samenkapsel entspringt rechtwinkling zum Kanal und setzt sich dorsalwärts fort. Die innere Wand der Samenkapsel ist von zahlreichen kleinen intrazellulären Kanälchen durchbohrt, welche sich in das hohe Säulenepithel fortsetzen. Dorsolateral in der innern Wand des innern Genitalraumes liegen zwei schlanke sklerotisierte Bänder, die *Basivalvulæ*. Der Boden des inner Genitalraumes besteht aus der intersegmentalen Membran zwischen dem siebten und achten Segment. Diese Membran ist von der Geschlechtsöffnung, deren hinterer Rand der Öffnung des Samenkanals gegenüber liegt, durchbohrt. Der hintere ventrale Rand des innern Genitalraumes ist von einer unsklerotisierten Intersegmentalfalte begrenzt. Das siebte Sternit bildet die Subgenitalplatte. Jedes Ovar umfaßt 400—

450 Ovariolen, welche von allen Seiten und der ganzen Länge des Eileiters entlang entspringen. Der Eileiter setzt sich vorwärts bis in das erste oder zweite Abdominalsegment fort. Im Männchen sind das achte und neunte Sternit kleiner und ungeteilt. Am neunten Sternit befinden sich keine Styli. An den *Vasa deferentia* oder an der Ejkulationsblase finden sich keine akzessorischen Strukturen vor. Jeder Hodenlappen ist eine zusammengesetzte Struktur, welche eine Anzahl Samenröhrchen, welche an der Basis zusammen gewachsen sind aber individuell in einem gebogenen Germarium endigen, umfassen.

LITERATURE CITED.

1935 *a*. AHRENS (W.). — Die Entwicklung des ,,Corpus luteum" bei den Insekten. Nach Untersuchungen an *Termes redemanni* (*Zeitschrift für mikroskopisch-anatomische Forschung*, **37**, 467-500). — 1935 *b*. Monographie des weiblichen Geschlechtsapparates der Termiten (Nach Untersuchung an *Termes redemanni*) (*Jena. Z. Naturw.*, **70**, 223-302).

1936. BONNEVILLE (P. P.). — Recherches sur l'anatomie microscopique des termites (*Arvernia biol.*, Clermont-Ferrand, **15**, 1-127).

1935. BROWMAN (L. G.). — The chitinous structures in the posterior abdominal segments of certain female termites (*J. Morph.*, **57**, 113-129).

1912. BUGNION (E.), POPOFF (N.). — Anatomie de la reine et du roi-termite (*Termes redemanni, obscuriceps* et *horni*) (*Mém. Soc. Zool. Fr.*, **25**, 210-231).

1951. GEYER (J. W. C.). — The reproductive organs of certain termites with notes on hermaphrodites of *Neotermes* (*Union of South Africa, Dept. of Agri., Entomo. Mem.*, **2**, 232-325).

1949. GRASSÉ (P. P.). — Ordres des Isopteres ou Termites (in *Traité de Zoologie, Anatomi, Systématique, Biologie, Masson, édit., Paris*, IX, 408-544).

1931. HEBERDEY (R. F.). — Zur Entwicklungsgeschichte, vergleichenden Anatomie und Physiologie der weiblichen Geschlechtsausführwege der Insekten (*Ziet. Morpho. Okolo. der Tiere*, **22**, 416-586).

1909. HOLMGREN (N.). — Termitenstudien. 1. Anatomische Untersuchungen (*K. Svensk. Vet. Akad. Handl.*, **44**, 1-215).

1919. IMMS (A. O.). — On the structure and biology of *Archotermopsis*, together with descriptions of new species of intestinal Protozoa, and general observations on the Isoptera (*Philos. Trans. Roy. Soc.* B, **209**, 75-180).

1924. JUCCI (C.). — Su la differenziazione de le caste ne la Società dei Termiti (*Mem. R. Acc. Lincei Mem. Cl. Sci.*, V-**14**, 269-500).

1901. KNOWER (H. M.). — A comparative study of the development of the generative tract in Termites (*Johns Hopkins Hospital Bull.*, **12**, 135-136).

1955. LIGHT (S. F.), WEESNER (F. M.). — The incipient colony of *Tenuirostritermes tenuirostris* (Desneux) (*Insectes sociaux*, **2**, 135-146).

1933. SNODGRASS (R. E.). — Morphology of the Insect abdomen, Part II. The genital ducts and the ovipositor (*Smithsonian Miscellaneous Collections*, **89**, 1-148). — 1935. Principles of insect morphology (McGraw-Hill Book Co., Inc., New York, 1-667).

1938. STELLA (E.). — Richerche citologiche sui neutri e sui riproduttori delle Termiti italiane (*Calotermes flavicollis* e *Reticulitermes lucifugus*) (*Mem. R. Acc. Lincei Cl. Sci.*, VI-**7**, 3-30).

1953. WEESNER (F. M.). — The biology of *Tenuirostritermes tenuirostris* (Desneux), with emphasis on caste development (*Univ. Calif. Publ. Zool.*, **57**, 251-302).