The Morphology and Histology of the Genital Organs of Leucophaea maderae (Fabr.) (Blattidae, Orthoptera).

By

L. E. Van Wyk
Department of Entomology, University of Pretoria

CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>4</td>
</tr>
<tr>
<td>TECHNIQUE AND MATERIAL</td>
<td>4</td>
</tr>
<tr>
<td>THE GENITAL ORGANS OF MADERAE</td>
<td>5</td>
</tr>
<tr>
<td>A. Morphological studies</td>
<td>5</td>
</tr>
<tr>
<td>1. Internal genitalia</td>
<td>5</td>
</tr>
<tr>
<td>i. Female</td>
<td>5</td>
</tr>
<tr>
<td>The ovaries</td>
<td>6</td>
</tr>
<tr>
<td>The lateral oviducts</td>
<td>7</td>
</tr>
<tr>
<td>The oviductus communis</td>
<td>7</td>
</tr>
<tr>
<td>The genital chamber</td>
<td>9</td>
</tr>
<tr>
<td>The vestibulum</td>
<td>10</td>
</tr>
<tr>
<td>The spermatheca</td>
<td>11</td>
</tr>
<tr>
<td>Spermathecal glands</td>
<td>11</td>
</tr>
<tr>
<td>Accessory glands</td>
<td>12</td>
</tr>
<tr>
<td>ii. Male</td>
<td>13</td>
</tr>
<tr>
<td>The testes</td>
<td>14</td>
</tr>
<tr>
<td>Vasa deferentia</td>
<td>15</td>
</tr>
<tr>
<td>Accessory glands</td>
<td>15</td>
</tr>
<tr>
<td>Vesiculae seminales</td>
<td>17</td>
</tr>
<tr>
<td>Ductus ejaculatorius</td>
<td>19</td>
</tr>
<tr>
<td>Phallic gland</td>
<td>20</td>
</tr>
<tr>
<td>2. External genitalia</td>
<td>20</td>
</tr>
<tr>
<td>i. Female</td>
<td>20</td>
</tr>
<tr>
<td>ii. Male</td>
<td>25</td>
</tr>
<tr>
<td>B. Histological studies</td>
<td>28</td>
</tr>
<tr>
<td>i. Female</td>
<td>28</td>
</tr>
<tr>
<td>The ovaries</td>
<td>28</td>
</tr>
<tr>
<td>The lateral oviducts</td>
<td>31</td>
</tr>
<tr>
<td>Oviductus communis</td>
<td>32</td>
</tr>
<tr>
<td>The genital chamber</td>
<td>32</td>
</tr>
<tr>
<td>Vestibulum</td>
<td>33</td>
</tr>
<tr>
<td>The spermathecal glands</td>
<td>36</td>
</tr>
<tr>
<td>The accessory glands</td>
<td>37</td>
</tr>
<tr>
<td>Spermathecae</td>
<td>35</td>
</tr>
<tr>
<td>ii. Male</td>
<td>39</td>
</tr>
<tr>
<td>The testes</td>
<td>39</td>
</tr>
</tbody>
</table>

* Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Entomology in the Faculty of Science, University of Pretoria, November, 1951.
In this paper the results are given of studies made on the genital organs of Leucophaea maderae (Fabr.). The internal and external genital organs of adult males and females were studied morphologically and compared with other cockroaches found in South Africa. Sections were also made through the internal genital organs of adult males and females and the histological structure of the organs studied. In addition the development of the external genitalia in the nymphal stages was observed.

INTRODUCTION

The cockroach, Leucophaea maderae (Fabr.), that forms the subject of this paper belongs to the subfamily Panchlorinae. Species such as Periplaneta americana L. and Blattella germanica L. are more commonly found in South Africa than maderae, but this latter insect differs from them in that the females are viviparous. It is of African origin (Rehn, 1937), but has been distributed over a considerable portion of the tropical and subtropical parts of the world. In Africa it is found in Natal, Portuguese East Africa, Kenya, Uganda, Angola, Belgian Congo, French Equatorial Africa and parts of Northern Africa.

For the purpose of this paper the terminal abdominal sternites and the genitalia of maderae were studied. For the sake of comparison studies were also made on americana, germanica and Blatta orientalis L.

In this paper the full names of the cockroaches are given once only (including generic, specific and author), thereafter the specific name only is given. At the end of this paper a list of abbreviations used in the figures and a glossary of terms are given.

TECHNIQUE AND MATERIAL

Specimens of maderae were obtained from Durban, Natal, and reared in cages at a constant temperature of approximately 30°C and
at room temperature. The moisture content of the air does not play an important part in the growth and development. The insects were fed on dog biscuits, tomatoes and bread. They are relatively inactive, eat little during the daytime and attain maturity in approximately nine months.

For the morphological studies of the external genitalia and organs of ectodermal origin associated with them, and the terminal abdominal sterna, the last four segments of the abdomen were detached and immersed in a 10% aqueous solution of sodium hydroxide for a few days. When the tissues were softened the material was washed in distilled water and transferred to 70% alcohol. All the tissues not required for study were removed. A dorso-longitudinal cut was made through the tergites to dissect out the genitalia. The sterna were then pinned down to expose the genitalia for morphological studies. Before they were mounted on a slide the genitalia were placed in a weak aqueous solution of acid fuchsin until sufficiently stained, then dehydrated, cleared and mounted in Canada balsam. Drawings were made with the aid of a projection apparatus.

In order to study the internal genital organs of adult males and females, dissections were made from fresh material by cutting along the medio-dorsal line of the abdomen and pinning down carefully. The organs were studied in *in situ*, then removed and preserved in 70% alcohol.

For the histological studies of the internal organs cockroaches were killed in a cyanide killing bottle and the required organs dissected out. They were placed in Bouin's fixative for 24 hours and then washed in 70% alcohol until most of the yellow stain was removed. After this the organs were dehydrated, imbedded in paraffin wax and serial sections 10µ thick were cut by means of a microtome. Haematoxylin and Eosin were used for staining and also Pasini's method, consisting mainly of Anilin Blue (Wasserblau) and Orcein. The sections were mounted on slides in Canada balsam.

A few chemical tests were made to determine the nature of various secretions in the male and female genitalia and glands associated with them. In order to preserve the secretions, the insects were anaesthetised with ether and the required portions dissected out and their secretions tested.

### THE GENITAL ORGANS OF MADERAE

#### A. Morphological studies

1. **Internal genitalia**

   i. **FEMALE.** An interesting relationship exists between the female genital apparatus of the Isoptera and that of the orthopteroid families Blattidae and Mantidae. This relationship was studied by Snodgrass (1933) and the following observations were made by him: "In each of the three families the eighth abdominal sternum of the female is reduced and the seventh sternum
is prolonged backward as a large subgenital plate concealing the eighth sternum and in the Blattidae the entire ovipositor as well. In the mantids the seventh sternum forms a troughlike structure with mobile, valvular terminal lobes for manipulating the material of the egg-case. In the blattids the lobes of the seventh sternum enclose a large distensible vestibular chamber in which the ootheca is formed and retained a varying length of time."

The ovipositor has many points of resemblance in the Mantidae, Blattidae and Isoptera, such as the following: It is of small size as compared with the usual ovipositor of orthopteroid insects and in some respects it appears to be degenerated, while at the same time it shows unusual specializations that obscure the generalized structure of the organ.

Shelford (1906) in his studies on the methods of reproduction amongst the Blattidae, classifies these as follows:—

(a) *Oviparous species*: The eggs are enclosed in a "chitinous" ootheca and carried by the female for a short period of time only; e.g. species of *Ectobia*, *Blatta* and *Periplaneta*.

(b) *Ovo-viviparous species*: (i) The eggs are enclosed in a "semichitinous" capsule protruding from the abdomen and is carried by the female during the greater part of the embryonic period. This is the case in *germanica*.
   (ii) The eggs are carried by the female for the greater part of the embryonic period, but are enclosed in a transparent membrane, as in species of *Temnopteryx*.

(c) *Viviparous species*: (i) The eggs are enclosed in a "chitinous" ootheca which is retained in the brood sac of the mother, e.g. *Oxyhaloa saussurei* Borg. and *Blabera* species. (ii) The eggs are enclosed in a transparent membrane which is retained in the brood sac of the mother. The membrane is complete in the case of *Molytria* species, *Panchlora viridescens* L., *Epilampra burmeisteri* Guér, *Panesthia javanica* Serv. This was also found to be the case in *maderae* by the writer. The membrane is incomplete as in *Panchlora viridis* Burm.

The terms "chitinous" and "semichitinous" used in the above classification are, strictly speaking, incorrect, owing to the fact that no chitin is present in the ootheca. The ootheca consists of tanned protein (Pryor, 1940).

Viviparity occurs in at least six of the eleven subfamilies of the Blattidae, namely in *Epilamprinae*, *Panchlorinae* (to which *maderae* belongs), *Blaberinae*, *Oxyhaloinae*, *Perisphaerinae* and *Panesthiinae*. It is possible that the embryonic development in viviparous genera may differ from that of oviparous genera (Shelford, 1906).

The internal genital organs of female cockroaches have been studied by Deegener (1911), Packard (1909), Kolbe (1893), Nel (1929), Snodgrass (1931, 1933, 1939, 1940), Chopard (1950) and others.

The internal female genital organs of *maderae* consist of the following:—

Two ovaries, two lateral oviducts, oviductus communis, genital chamber, vestibulum, two spermathecae, two spermathecal glands, and two groups of branched accessory glands, also called the collereral glands.

*The ovaries*: Each ovary consists of a group of approximately fifteen to twenty ovarioles that open together at the anterior end of the oviductus
Van Wyk: Genital Organs of Blattids

lateralis. Each ovariole has a beaded appearance and in it a number of oocytes in different stages of development are found, enclosed in follicular chambers. In the terminal chamber, or germarium, a large number of nucleated cells are found. The protoplasm of these cells form a network. The oocytes develop in the succeeding chambers. Between the last formed egg chamber and the germarium new chambers are added by a rapid multiplication of the follicular cells in this region. These cells are formed to supplement those which collapse when the oocytes move into the oviductus lateralis. In this way it seems as though the oocytes move backward in the ovariole. In reality the ovariole collapses at its posterior end and new cells are formed near the anterior end. Before the oocytes leave the ovariole, a mass of follicle cells forms a plug that closes the opening of the egg tube into the oviductus lateralis. This plug degenerates just before the ova move into the oviductus lateralis.

The anterior terminations of the ovarioles are prolongations of the walls of the ovarioles and they are named the terminal filaments. In maderae they form elastic bands and serve to attach the ovaries to (i) the body wall, and, in the embryo to (ii) the splanchnic wall of the coelom. (iii) The terminal filaments are also joined to the dorsal diaphragm.

When a female of the viviparous cockroach Blabera sp., is carrying an ootheca containing fertilized eggs, the ovarioles are small and contain no ova (Holmgren in Deegener, 1911). In the ovarioles of maderae females, however, eggs in all stages of development were observed including "ripe" eggs, while the ootheca was carried by the female. The ovaries are situated in the fourth to sixth abdominal segments.

The lateral oviducts: In maderae, as in other blattids, the lateral oviducts are simple tubes through which the mature eggs are transported to the oviductus communis. The anterior ends of these ducts, where the posterior ends of the ovarioles converge, are slightly dilated to form the egg calyces, into which the eggs are emitted by the ovarioles. The lateral oviducts are situated between the sixth and eighth abdominal segments. In the eighth segment they curve forward, then backward, and open at the anterior end of the genital chamber into the oviductus communis or median oviduct (see figure 1).

The oviductus communis: This duct is a short, simple tube which opens by means of the gonopore into the genital chamber. The lateral oviducts converge and open at the anterior end of the median oviduct. In the immature stages of many insects the genital ducts, receptaculum seminis, genital chamber and the unpaired glands are paired (Kolbe, 1893). According to Kolbe (t.c.) the genital openings such as the openings of the lateral oviducts were also originally paired, but in most insects there is a secondary single invagination of the body wall on the eighth abdominal sternum and it replaces the paired openings. This forms the unpaired median oviduct. The paired lateral oviducts are therefore

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).
Van Wyk: Genital Organs of Blattids

of mesodermal origin, while the median oviduct is ectodermal. Kolbe (1893) states: "Bei den Larven mancher Insekten (Mallophagen, Blattiden, Culiciden) sind die Ausführungsgänge im Keime paarig; auch der Penis, das Receptaculum seminis, der Uterus (Eigang) und die unpaarigen Drüsen sind bei diesen paarig angelegt. Jedenfalls sind wir jetzt völlig klar darüber dass die Fortpflanzungsorgane eigentlich paarig ausmünden, bei den meisten Insekten aber nach Ausbildung eines einfachen Ausführungsgänges durch Einstülzung der Körperhaut von diesem letzteren aufgenommen werden. Diese Einstülzung (D. ejaculatorius beim Männchen, Vagina beim Weibchen) ist bei entwickelten Wasserjungfern und bei Heuschreckenlarven kurz; die Samenleiter münden direkt in diese Einstülzung."

The genital chamber: In the Blattidae there is a large invagination of the body wall above the seventh sternum, namely the vestibulum. The ventral parts of the succeeding segments are also drawn into the body to form the genital chamber. These segments, namely the eighth and ninth, are membranous in structure and the sclerotized sternites seen in the nymphs of maderae cannot be distinguished as such in the adult female.

The genital chamber includes the bulbous portion into which the spermathecae and spermathecal glands open as well as the portion caudad of the oviporus. The term "vestibulum" refers to a secondary invagination above the seventh sternite anterior to the ovipositor and ventrad of the bulbous part of the genital chamber. This invagination will be described later.

The genital chamber can therefore be homologized with the genital chamber of mantids, while the vestibulum is an additional invagination above the seventh sternum. The vestibulum forms a mould and container for the ootheca.

The posterior opening of the median oviduct, the gonopore, lies on a fold of the eighth sternite and is surrounded by slightly sclerotized and corrugated areas, which represent rudiments of the eighth sternum. The spermatheca, or receptaculum seminis, opens posterior to the gonopore, namely between the gonopore and the spermathecal gland. (Fig. 2). The accessory glands discharge the substance that forms the ootheca into the genital chamber. Their common opening is situated at the bases of the inner valves of the ovipositor. Strictly speaking the cavity into which the accessory glands open is part of the vestibulum.

---

Fig. 1.—maderae female. Internal and external organs. Semi-diagrammatic.
Fig. 2.—maderae female. Sagittal, dorsoventral section through the terminal segments of the abdomen. Diagrammatic.
Fig. 3.—Development of the three pairs of valvulae from the limb bases of the eighth and ninth sternites. Diagrammatic. (From Snodgrass, 1933.)
Fig. 4.—maderae female. External genitalia with right ventral valve removed. Ventral view. Semi-schematic.
Fig. 5.—maderae male. Internal genital organs. Ventral view. Semi-schematic.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).
but in the literature it is often referred to as the genital chamber.

Nel (1929) mentions the gonopore of *germanica* as being situated on the eighth intersternal membrane, i.e. the membrane between the seventh and eighth sternites. Snodgrass (1933) however concluded that, although the gonopore is situated mesially on the reflexed inner surface of the eighth intersternal membrane, it is virtually borne on the eighth sternum. This was verified by the writer. A longitudinal groove connects the spermathecal opening or spermora with the gonopore, thus furnishing a passage along which the sperms move to the gonopore.

In *maderae* there are relatively few sclerotized areas in the genital chamber and the whole structure is simpler than that of *americana*. It is difficult to recognise sternites eight and nine which form the inner surface of the chamber. On the whole the genital chamber gives the impression of being a simple, muscular and membranous sac into which open the median oviduct, the spermathecae and the spermathecal glands. The accessory glands open into the vestibulum at the base of the ovipositor.

*The vestibulum*: The vestibulum is a secondary invagination of the body wall and is formed by the extension of the seventh sternite beyond the eighth and ninth.

Nel, (1929) who studied the cockroach *germanica*, stated:—

“...The inner surface of the subgenital plate, i.e. the seventh sternum, is strikingly modified, having to carry the oötheca; it is thrown into folds and fold-like invaginations possessing areas of glandular cells. In cross-section two main lateral folds are seen rising up on either side of the ovipositor lobes situated dorsally on the roof of the genital cavity.”

The vestibulum is much larger than the genital chamber and is expansible to a large degree. The oötheca is contained in the vestibulum and the latter extends cephalad as the former increases in size. The oldest eggs are therefore situated at the anterior end of the vestibulum. The small, bulbous genital chamber is then borne dorso-posteriorly on the large vestibulum.

Shelford (1906) studied viviparity amongst the Blattidae. This method of reproduction was observed by him in *viridis* and *Panchlora nivea* L. These two species belong to the same subfamily as *maderae*, namely the Panchlorinae. The specimens of *viridis* and *nivea* studied, contained an egg-cluster of crescentic form, the eggs being arranged in a double row on top of one another, as in *maderae*, and the egg-mass was contained in a thin-walled “brood-sac” or vestibulum. In *Eustegasta micans* Sauss. and Zehntn., the oötheca splits open whilst still in the vestibulum and the young nymphs emerge in pairs from the mother. In *javonica* Serv. the egg-mass, which is 18 mm. long and is contained in a thin-walled brood-sac, lies on the left side of the abdomen and extends as far forward as the third abdominal sternite. The number of eggs varies from 36 to 40 and are retained in the vestibulum until they are ready to hatch. *L. maderae* is a typical viviparous species, in which the approximately forty eggs are arranged in a double row to form an oblong mass covered with a thin membranous oötheca and enclosed in the
sheath-like vestibulum. The eggs hatch in pairs in the ootheca while it is still in the vestibulum and the young immediately leave the mother. It seems likely that each ovariole sets an egg free at the same time. Forty eggs are then enclosed in an ootheca simultaneously and will therefore hatch at approximately the same time. The remains of the ootheca and the chorion of each egg are thrown out by the mother after all the eggs have hatched, and the vestibulum is apparently reduced in size.

The spermatheca: According to Nel (1929) the spermatheca in germanica is represented by four small bulbous bags lying internally in the body cavity, two on each side of the common oviduct. Sections of a female of germanica which had copulated showed all four filled with spermatozoa. The spermathecae of germanica open directly into the genital cavity. A short duct leads from the opening of each spermatheca to open into a short dorso-longitudinal groove on the fold carrying the gonopore. The ducts from the two spermathecae on either side of the oviductus communis have one common opening. According to Snodgrass (1940), however, there are two spermathecae in germanica and one each in orientalis and americana. In these species each spermatheca opens separately into the genital chamber. The two openings are located, adjacent to one another in the dorsum of the genital chamber. In addition to the functional spermatheca, each spermatheca has a glandular branch. In these species each spermatheca is thus a two-branched structure, one branch of which is usually thicker than the other, or enlarged apically. This branch is the true sperm receptacle, the other being a glandular accessory.

In maderae there are two spermathecae, each consisting of a tubular white sac. They open separately into the genital chamber just posterior to and dorsad of the opening of the median oviduct. (Fig. 2.) Each spermatheca is a simple, curved sac and no sign was seen in maderae of a glandular branch corresponding to that found by Snodgrass in orientalis and americana.

Spermathecal glands: In maderae there are two strongly-divided glands that open into the genital chamber posterior to the openings of the spermathecae. Packard (1909) and Shelford (1906) called these glands the colleteral glands, but it has been shown by Snodgrass (1933), Nel (1929) and others that the colleteral glands open on the ninth sternite at the base of the ovipositor. It may therefore be possible that these large glands opening separately into the genital chamber correspond with the spermathecal glands of orientalis and americana.

It was found that the larger branch of the spermatheca of orientalis is traversed by a “narrow axial canal with strongly sclerotic walls, from which are given off numerous canaliculi into the cells of the thick glandular epithelium.” (Snodgrass, 1940.)

Chopard (1950) studied a cockroach of the subfamily Perisphaerinae, namely Gromphadorina laevigata Sauss. and Zehntn., and he found only one spermatheca, opening into the uterus or genital chamber, with two accessory glandular tubes, slightly branched and whitish in colour.

The lumina of the spermathecae of orientalis and americana after copu-
lation, are filled with spermatozoa and fine granules of secretion. The spermathecal glands are supposed to secrete a substance that stimulates the spermatozoa into entering the spermathecae. (Khalifa, 1950).

Nel (1929) concluded that the spermathecae of *germanica* are formed on the eighth intersternal membrane, while the spermathecae of other Orthoptera arise from invaginations on the eighth sternite. His theory was that the original spermatheca of the eighth segment became atrophied in the last nymphal stages and a secondary spermatheca was formed on the eighth intersternal membrane. This conclusion was proved to be incorrect by Snodgrass (1933), who showed that the spermathecae of all Orthoptera are formed on the eighth segment.

**Accessory glands**: The accessory glands in female cockroaches consist of a number of long tubules borne on a single basal tube which opens into the genital chamber at the base of the ovipositor on the ninth segment. They are also called colleterial glands and they secrete the substance which forms the oötheca in which the eggs are encased. The formation of an oötheca is typical of the Mantidae and Blattidae and, as indicated above, can assume various forms.

Packard (1909) called the accessory glands that open at the base of the ovipositor of *orientalis* "cement glands" and mentioned the accessory glands as being situated on the genital chamber. The author, however, studied specimens of *maderae* and *orientalis* and came to the conclusion that the "cement glands" described by Packard are in reality the accessory glands of these insects as described by Snodgrass (1933), Nel (1929) and Shelford (1906).

According to Packard (t.c.) the secretion of the accessory glands is a substance consisting of chitin and large crystals of oxalate of lime. Subsequently, however, it was proved by Pryor (1940) that the oötheca is free from chitin. In *maderae* the oötheca is a transparent yellowish, membranous sheath in which the eggs are enclosed.

In *germanica* the accessory gland tubules are glistening white until the time of oviposition approaches, when they assume a yellowish tint (Packard, 1909). The glands are paired in *germanica*, the tubules from each pair of glands leading into a short common duct which joins its fellow from the other side to open by a common pore at the base of the ovipositor.

In *viridis* the oötheca is not horny, but is a fine membranous sheath enclosing only the basal half of the egg-mass. Without dissecting this cockroach, Shelford (1906) assumed that the accessory glands are absent or reduced.

Pryor (1940) studied the secretions of the accessory glands in *orientalis* and found that the two branches of the gland open separately on the dorsum of the vagina or genital chamber. Although these branches are morphologically left and right, they are not of equal size. The left gland is much the larger of the two and its tubules surround those of the right gland. Both glands consist of a large number of branched tubules, opening into a common duct, but they differ in their histological structure and in the nature of their secretions. According to Pryor (t.c.) in fresh dissections the left gland appears
white and slightly opalescent and secretes a white fluid containing a water soluble protein and crystals of calcium oxalate. The greater part of the ootheca was found to be formed from the secretion of this gland. The right gland is slightly more compact in structure than the left, and is transparent. The secretion, which contains a dihydroxyphenol, forms a clear solution in water and serves to stick the eggs together at the time of their inclusion in the ootheca as well as stabilizing the protein of the latter.

"The ootheca is composed of a structural protein, the hardening and stabilizing of which occurs as the result of the addition of a quinonoid substance which acts by cross-linking the protein molecules. Protein is derived from the left colleterial gland and the right gland secretes the precursor of the o-quinone, in the form of an o-dihydroxyphenol derivative, which was enzymatically oxidized to the quinone." (Brunet, 1951.) The secretions of the accessory glands of *maderae* were not analysed and it is therefore not certain whether they consist of the same substances as was found in the case of *orientalis*.

Pryor, Russell and Todd (1946) also made studies on the ootheca of *orientalis* and inferred that it was the same phenolic substance that was responsible for the hardening of the exocuticle of insects that caused the hardening of the ootheca. This substance was isolated by them from the ootheca of *orientalis* and identified as protocatechuic acid (3:4 dihydroxybenzoic acid).

In *javanica* according to Shelford (1906), the left accessory gland is absent but the right is well developed. He also states:—

"It is remarkable to find that on one side at least they are well developed in a species whose eggs are enclosed in a thin membrane."

In *maderae* approximately forty eggs are also enclosed in a thin yellowish oothecal membrane, although the accessory glands are well developed. This phenomenon, namely the presence of a thin, membranous ootheca, may be considered as an adaptation to the reproductive habits of the species. In species such as *americana*, where the ootheca is deposited before the eggs hatch, the thick, strong ootheca is necessary as a protective covering of the eggs. In species with a membranous ootheca it is retained in the body of the female until shortly before the eggs hatch, e.g. *javanica* and *viridis*. Probably in such cases as *maderae*, the membranous ootheca demonstrates a more advanced stage of development than that encountered in *americana*.

The accessory glands of *maderae* consist of two branched structures, apparently uniting just before they open into the genital chamber at the base of the ovipositor. The two glands are of approximately the same size, although the left gland appears whitish and more opaque and the tubules are slightly thicker, while the tubules of the right gland are thin and transparent.

According to Chopard (1950) *laccigata* has three groups of "very branched tubules" forming the colleterial glands. The median group is more slender and whiter in colour than the lateral groups.
the more highly developed families of Tettigoniidae and Acrididae the male copulatory organ is a highly developed phallic organ. It is formed by three or more lobes of the wall of the genital chamber. In these families the phallus is specially adapted to the formation of a spermatophore. The phallus of Mantidae and Blattidae is not so well developed. It consists chiefly of three lobes forming the three phalomeres. The phalomeres are outgrowths of the body wall and can assume various shapes.

The relation between the orthopteroid families of Blattidae, Mantidae, Tettigoniidae, Gryllidae and Acrididae can be seen in the structure of the accessory glands in the males (Snodgrass, 1940). They appear to arise from the anterior end of the ductus ejaculatorius, but are outgrowths of the mesodermal ampullae that lose their identity in the adult insect.

Closely associated with the above-mentioned families by the same feature are the Termitidae, Embiidae, Grylloblattidae, Phasmidae and Zorotypidae. (Snodgrass, t.c.).

In the Orthoptera the definitive median genital exit passage, or ductus ejaculatorius is a composite structure. It is formed by a posterior ectodermal part which opens on the external genitalia, and an anterior mesodermal part into which the vasa deferentia discharge the spermatozoa. The outgrowth of diverticula from the mesodermal part is characteristic of all Orthoptera, as was mentioned above. These outgrowths include the tubular accessory glands of various lengths producing material for the formation of spermatophores, and the saclike vesiculae seminales serving as storage places for the spermatozoa.

The internal genital organs of different species of Blattidae resemble one another. The writer studied specimens of orientalis, americana, germanica and maderae. The internal organs of maderae consist of the following:— Two testes; two vasa deferentia; three groups of accessory glands; two vesiculae seminales; ductus ejaculatorius and phallic gland (Fig. 5).

The testes: Each testis consists of a group of sperm tubes, corresponding in their origin to the ovarioles of the female. The sperm tubes, or testicular follicles can assume various forms. In many insects the sperm tubes open serially into the vas deferens by means of the small stalk-like vasa efferentia. Each tube can be separate or they can be enclosed in a common peritoneal sheath. The number of sperm tubes in a testis is generally less than the number of ovarioles in the ovary (Snodgrass, 1935).

The sperm tubes of insects do not have a true follicular epithelium such as that which forms the walls of the egg chambers in the ovary. Within each sperm tube there are successive regions according to the state of development of the germ cells. More attention is devoted to the cells of the sperm tube in a chapter below.

In germanica each testis consists of four round sacs opening radially at the anterior end of the vas deferens. In the blattid, Cryptocercus punctu-
Valt Wyk: Genital Organs of Blattids

latus (Scudd.) the testis consists of a large number of follicles attached to the vas deferens by means of the vasa efferentia (Snodgrass, 1940). In orientalis the testes are functionally mature at the end of the nymphal life. In the imago, however, they degenerate. (Snodgrass, 1940). Each testis is composed of an elongate mass of small globular sacs arising from the vas deferens.

In maderae each testis is a globular body formed by a mass of sperm tubes enclosed in a common peritoneal sheath. The testes are situated in the seventh abdominal segment. The sperm tubes converge upon the anterior end of the vas deferens, into which the spermatozoa move when they reach maturity.

Vasa deferentia: The vasa deferentia extend posteriorly from the testes to the rear part of the abdomen. In the tenth abdominal segment they turn mesially beneath the cercal nerves. They then go forward to open into the dorsal wall of the ductus ejaculatorius at the base of the accessory glands, in the ninth abdominal segment.

Heymons (1890) considers it to be of importance that, in the males of germanica, the vasa deferentia are not formed by the whole of the embryonic genital exit passage. According to him the distal portion of the embryonic exit passage degenerates. The functional vas deferens that joins the ectodermal ductus ejaculatorius is formed secondarily. The opposite is found in the case of the females. Here the whole of the primitive exit passage forms the oviducts with a few exceptions where the primitive oviducts are replaced by ectodermal tissue.

This view of Heymons (1890) is, however, contrary to that expressed by Snodgrass (1933): “The primitive mesodermal exit tubes of the gonads become the lateral oviducts in the females and the vasa deferentia in the males, except in so far as they may be partially replaced by branches of the ectodermal median duct.”

In maderae the vasa deferentia are simple narrow tubes that follow the course described above, and open at the base of the accessory glands. In orientalis however, a peculiar characteristic is found. Each vas deferens divides and re-unites at two places in its backward course. At the place where it divides, each vas deferens consists of two tubes running parallel for a short distance and then unite again. This structure is considered to be a remnant of the epididymis which is found in the Tettigoniidae. (Snodgrass, 1940).

Accessory glands: The accessory glands in Blattidae arise from the bifurcate anterior end of the ductus ejaculatorius. The bifurcate anterior end of the ductus ejaculatorius represents the embryonic mesodermal coelomic ampullae. The accessory glands arise from that part of the genital exit passage where the ectodermal ductus ejaculatorius joins the mesodermal vasa deferentia. The accessory glands can therefore be divided into two groups, according to their origin, namely mesadenia and ectadenia. The accessory glands of blattids are mesadenia. They arise from the mesodermal part of the median outlet duct. Included in this group are
the tubular accessory glands of various lengths and a pair of pyriform vesiculae seminales. The accessory glands and vesiculae seminales of Blattidae are therefore of mesodermal origin.

In other orders of insects the male accessory glands belong to the second group, i.e. they are ectadenia. These structures are formed by the ectodermal part of the ductus ejaculatorius and are therefore of ectodermal origin. (Snodgrass, 1940).

Ito (in Snodgrass, 1940) believes that the male accessory glands of orientalis secrete a spermatic fluid which stimulates the activity of the spermatozoa. Corresponding glands of other Orthoptera, however, furnish the material which, upon hardening forms the spermatophore. This capsule enclosing the spermatozoa was supposed to be absent in blattid males (Snodgrass, 1940) except in the case of orientalis. The presence of a spermatophore in various other species of Blattidae has, however, subsequently been proved by various authors (Khalifa, 1950). It is probable therefore, that the function of the accessory glands in male cockroaches is to produce material for the formation of a spermatophore.

In orientalis there are two groups of accessory glands, which form the different layers of the spermatophore. The inner layer is formed by the small median tubules of the accessory glands and the outer coat by the larger glands (Snodgrass, 1940). The larger peripheral tubules of orientalis are white and opaque when freshly dissected. Most of the smaller tubules contain each a dark inner portion compressed into irregular folds. (Snodgrass, 1940).

Spermatophore formation in Blattidae differs from that of other families in that it is formed only during copulation. This is due to the fact that a spermatophore mould is absent in the blattids, its place being taken by a lateral pouch borne on the ductus ejaculatorius. In the families of Tettigoniidae, Gryllidae and Acrididae the phallic organs are developed into a mechanism of spermatophoric insemination. The spermatophore mould of Acrididae, Tettigoniidae and others is an intricate structure consisting of various cavities formed by the ecto- and endophallus. The spermatophore is formed before copulation and kept in the mould. In the blattids this mould is absent, its place being taken by a small ejaculatory pouch, in which the spermatophore is formed during copulation.

Khalifa (1950) gives the following data on the spermatophores of Blattidae:—

"In germanica the spermatophore adheres to the eighth sternum of the female. It is an oval, flattened mass, milky in general appearance and tough in consistency. The tip is inserted into the widened spermathecal groove in such a way that the two spermathecal openings come in direct contact with the two openings of the sperm sacs of the spermatophore. Three distinguishable secretions go to make up the body of the spermatophore. A clear transparent mass covering the
ventral surface of the spermatophore, a milky white mass that contains the two sperm sacs, and a translucent lamellated mass which forms the dorsal wall of the spermatophore and is in close contact with the female sclerites after copulation.”

In each sperm sac of the spermatophore of *germanica* the spermatozoa are arranged with their heads in a layer applied to the walls (Khalifa, 1950). The spermatophore remains attached to the sclerites in the genital chamber of the female for twelve hours during which time the spermatozoa migrate to the spermathecae. The spermatophore shrinks and eventually releases itself from the sclerites. The spermatozoa have to be chemically activated before they leave the spermatophore and this activation is achieved by the secretion from the spermathecal glands of female roaches. (Khalifa, 1950). The male accessory glands of *germanica* are of three different lengths (Khalifa, 1950).

The spermatophore consists of three layers formed by the three groups of accessory glands. Firstly an amount of the milky substance secreted by the long tubules, moves into the ejaculatory pouch. This is surrounded by the secretions of the other two sets of tubules. A certain number of spermatozoa then moves from each vesicula seminalis into the milky middle layer. According to Khalifa (1950), the spermatophore then moves along the ductus ejaculatorius and during copulation its tip is inserted into the spermora of the female.

In *maderae* there are three groups of accessory glands, and as the spermatophore consists of three layers, it is assumed that each group of glands is responsible for one layer. The first group of accessory glands occupies a central position in the mass of tubules. It is formed by a few short tubules, that have the appearance in fresh dissections of being translucent with a folded opaque structure running along the centre. (Fig. 5, I). This group does not differ much from the second group which has slightly longer tubules. (Fig. 5, II). These tubules are translucent and glistening in fresh dissections. The tubules of the third group are longer and thicker than those of the other two groups and are white and opaque (Fig. 5, III). The writer did not determine which layers of the spermatophore were formed by each of the three groups of accessory gland tubules.

The spermatophore of *maderae* is a tough, white structure with two sperm capsules or sacs and a duct through which the spermatozoa enter the spermathecae (Fig. 6). In *germanica* there are two ducts but in *maderae* only one although this point is not quite certain because sections could not be made through the spermatophore. It is placed in the genital chamber of the female during copulation and the tip is inserted in or placed near the spermora. The spermatophore remains in the genital chamber of the female for approximately one day and then dries up and drops from the genital chamber.

**Vesiculae seminalis**: These vesicles are found amongst the accessory gland tubules at the anterior end of the ductus ejaculatorius. (Fig. 5). The
spermatozoa are stored in them until the time of copulation, when they are enclosed in the spermatophore.

In orientalis, americana and germanica vesiculae seminales are present (Snodgrass, 1940) although Miall and Denny (1886) mentioned that in many cases vesiculae seminales are absent and spermatozoa are found in the accessory glands.

The seminal vesicles of germanica are two small oval sacs arising from the end of the right terminal branch of the ductus ejaculatorius (Snodgrass, 1940). They are partly concealed by the accessory glands. In orientalis and americana there are two groups of small pyriform sacs arising from the ventral surface of the ductus ejaculatorius.

In maderae the vesiculae seminales are two pyriform, white sacs. Before copulation they are large and noticeable. The two vesicles are situated amongst the accessory glands and open into the anterodorsal surface of the ductus ejaculatorius.

Ductus ejaculatorius: Primarily the gonads possessed two primitive outlet ducts that had their external openings at the base of the appendages of the tenth abdominal segment, (Snodgrass, 1940). These primitive ducts are represented in the embryos of insects by the mesodermal coelomic ampullae. The vasa deferentia therefore retain their original mesodermal origin, but the ductus ejaculatorius is a secondary invagination.

"As the development of the male exit system of the Orthoptera progresses the mesodermal ampullae leave the appendages of the tenth segment and independently migrate forward and medially into the posterior part of the ninth abdominal segment. Here the ampullae unite to form a bilobed mesodermal vesicle into which open the two vasa deferentia. At the same time a median, tubular ingrowth of the ectoderm has formed between the ninth and tenth abdominal segments ventrally, which forms the ejaculatory duct. The ectodermal duct unites with the mesodermal vesicle and the lumina become continuous. The ejaculatory duct is therefore a composite structure.” (Snodgrass, 1940).

In maderae the ductus ejaculatorius is a thick white tube. Posteriorly the duct opens in the endophallus of the external genitalia. Laterally the duct forms a diverticulum in which the spermatophore is formed during copulation. This ejaculatory pouch is replaced by an intricate ecto-end endophallus in the higher developed families of the Orthoptera, namely the Tettigoniidae and Acrididae.

Fig. 6. — maderae. Spermatophore.
Fig. 7. — maderae male. Sagittal, dorsoventral section through the terminal segments of the abdomen. Diagrammatic.
Fig. 8. — Structure of a gonopod. Diagrammatic. (From Snodgrass, 1931.)
Fig. 9. — maderae male. Phallic organs. Ventral view. Semi-schematic.
Fig. 10. — maderae female. T.S. young oocyte. Semi-schematic.
Fig. 11. — maderae female. T.S. nearly mature oocyte. Semi-schematic.
Phallic gland: There is a small gland near the posterior end of the ductus ejaculatorius which opens at the base of the left phallomere of the external genitalia. The function of this phallic gland is unknown, but it may be associated with the "prostate gland" of the Tettigoniidae (Snodgrass, 1940).

The phallic gland of orientalis is an elongated sac tapering posteriorly into the base of the left phallomere where it terminates in a duct that opens on a membranous area between two median distal lobes of the appendage (Snodgrass, 1940). In americana the phallic gland is subdivided into several branches. In germanica the gland consists of a mass of coiled tubules, its long slender duct opens on the phallic integument mesad of the mouth of the sac containing the left phallomere (Snodgrass, t.c.).

In maderae the phallic gland consists of two or three branched tubules opening on the anterior end of a slender duct which opens in a membranous area at the base of the left phallomere. The structure of the external genitalia is described below.

Khalifa (1950) mentions a "conglobate gland" which is defined as "a glandular appendage of the male sexual organs, opening upon one of the external structures." One can therefore assume that this is a homologue of the phallic gland. It is claimed by Gupta (in Khalifa, 1950) that the conglobate gland plays a part in building up the spermatophore. He states that the conglobate gland secretes the outer layer of the spermatophore as it is laid onto the female sclerites. Sections through the conglobate gland before and after copulation show that the lumen of the duct always contains a small amount of secretion (Khalifa, t.c.). It is therefore difficult to determine whether this gland secretes more actively during copulation.

2. External genitalia

i. FEMALE: The external genital structures of female Blattidae consist of the ovipositor which is closely associated with the genital chamber and the vestibulum. Although in blattids the ovipositor and its related structures are located internally as a result of the invagination of the eighth and ninth sternites, this organ is in reality an external structure, as can be seen in the case of related families such as the Acrididae and Tettigoniidae.

The external genitalia are situated on the seventh, eighth and ninth abdominal sterna. They are entirely concealed in a large invagination above the seventh sternum which is prolonged posteriorly beneath the ventral parts of the succeeding segments. The area behind the ovipositor includes the sternite of the tenth segment and the under surfaces of the paraprocts, belonging to the eleventh segment. In americana and orientalis the eighth and ninth tergites are usually reduced in size and the tenth often considerably produced backward between the cerci, substituting the supra-anal plate. This plate is wanting in adult
female cockroaches. In adult females of *americana* the proctiger lies caudad of the seventh tergum and above the large terminal lobes of the seventh sternum. It is a small papilla, namely the reduced tenth segment and bears the anus. Closely associated with it are the remnants of the eleventh segment, consisting of the dorsal epiproct and the ventral paraprocts. It projects from the concealed ninth segment and carries the cerci laterally. The dorsal plate of the proctiger is the tenth tergum. In *madera* females the caudal margin of the tenth tergum is deeply notched mesially, so as to appear almost forked. It carries the cerci. A proctiger was not discernible, although an epiproct is present.

The openings of the internal organs, namely the gonopore, spermorae, and the openings of the spermathecal glands and accessory glands, are situated in the dorsal wall of the genital chamber on the eighth and ninth sternites respectively. There has been some uncertainty in the past as to the definite positions these openings occupy and it is important to determine their exact position in relation to the external genitalia. In primitive insects the opening of the gonopore is meant to have been on the seventh sternite, but in most insects is found on the eighth or ninth sternites. In *madera* the gonopore is found situated in the genital chamber in the region of the reduced eighth sternite. Posterior to this opening, also on the eighth sternite, are the openings of the spermathecal ducts. The opening of the accessory glands is on the ninth sternite, at the base of the dorsal valves of the ovipositor. In *orientalis* and *americana* the median oviduct opens on the dorsal surface of a fold of the eighth sternite. According to Nel (1929) the gonopore in *germanica* is on the invaginated inner surface of the seventh sternum, namely the eighth intersternal membrane. Nel (t.c.) also concludes that the sperm receptacles of Blattidae, since they open on the eighth intersternal membrane, are not homologous with the spermatheca of other Orthoptera. These conclusions are incorrect however, since it was found by Snodgrass (1933) and other authors that the fold bearing the gonopore is a part of the eighth sternum. There is therefore no discrepancy between the Blattidae and other Orthoptera as regards the situation of the gonopore and the spermathecal opening. It is, however, possible that the female gonopore originated in the Blattidae on the posterior part of the seventh sternite as it is known to do in various other insects, and that the position of the definitive opening is secondary.

The openings of the spermathecal ducts in *madera* are situated in the dorsal wall of the genital chamber, immediately posterior to the gonopore. In *orientalis* and *americana* the spermathecal aperture is situated on a small sclerite which is a part of the eighth sternite, but in *madera* the whole of the eighth sternum is more or less membranous.

The accessory glands open into the dorsal wall of the vestibular chamber at the posterior end of the genital chamber, in the region of the ninth sternite. (Fig. 2.). The opening is situated between the basal parts of the ovipositor.
The vestibulum lies above the seventh sternum and is a large triangular fold. The short ovipositor therefore serves as an egg guide. It directs the oocytes and the secretions of the accessory glands into the vestibulum. These secretions are the components of the ootheca.

The eggs of Blattidae are fertilized in the genital chamber by the spermatozoa, which have previously been stored in the spermathecae. After fertilization the eggs are pushed into the vestibulum by the ovipositor and are enclosed in the ootheca. In *madera* the ootheca is largely absent despite the presence of well developed accessory glands. It is represented merely by a thin transparent membrane encasing the eggs. It can be considered as a rudiment of the strongly developed ootheca as it is found in *americana*.

The external genital organs of female Blattidae consist mainly of the ovipositor, which is relatively simple and reduced in comparison with the intricate structures found in most other Orthoptera. An ovipositor formed from appendicular processes of the abdomen is in general present only in insects having the female genital opening on the eighth abdominal sternite, or between the eighth and ninth sterna (Snodgrass, 1933). In cases where the gonopore has been transposed to the ninth segment, the ovipositor has been suppressed in all cases.

The invagination above the seventh sternite is the genital chamber. The vestibulum is a secondary invagination and is only the anterior portion of the cavity. The ovipositor is enclosed in the genital chamber. The ovipositor consists of three pairs of appendages, namely the valvulae. In addition a number of accessory plates are often found.

The first pair, or ventral valvulae are formed by the gonapophyses of the gonopods of the eighth segment. They are mostly simple lobelike structures arising from the first valvifer which is a modification of the limb base of the original segmental appendage. (Fig. 3). From the second valvifer two appendages are formed, namely the true segmental appendages or second valvulae, also called the inner valvulae. In addition however, there are secondary outgrowths of the second valvifer, which have no relation to the gonapophysis of the ninth segment. These outgrowths form the third or dorsal valves. In the Blattidae these valves form a pair of blades of the ovipositor, together with the first and second valvulae. The origin of the third valves is unknown, but it has been proved by Snodgrass (1933) that they are not styli as has been supposed. They are therefore considered to be accessory outgrowths of the second valvifers. (Fig. 3). In the adult roach each limb base of the ninth segment is clearly differentiated into a basal second valvifer and a large free distal third valvula.

In the past there has been some uncertainty as to the origin of the valvulae. Snodgrass (1933) and Nel (1929) supposed that the gonapophyses represented modified ventral abdominal appendages homodynamous with the legs. Heymons (in Nel, 1929) considered that the gonapophyses represented specially developed structures which
could not be referred to as probably having been limbs before. Newell (1918) quotes the following authors and their opinions:

“Lacaze-Duthiers regarded the genital appendages as modified ventral sclerites of their respective somites. Haase said they are integumental structures of a somewhat higher order than styles. Weismann, Kraepelin, Cholodkovsky and Wheeler have regarded these extremities as homologous with the segmental extremities.”

According to Nel (1929) Verhoeff in 1902 developed an interpretation of the genital segments and the gonapophyses which has been accepted more or less universally, namely that the ovipositor lobes, borne mesially on the eighth and ninth sternites, represent modified distal leg segments or telopodites.

The writer gives a diagrammatic sketch taken from Snodgrass (1933) to illustrate the origin of the three pairs of valvulae. (Fig. 3). The explanations given by Snodgrass for the origin of the valvulae seem to the writer to be the most probable.

In *germanica* the three pairs of ovipositor lobes are reduced and almost entirely membranous (Nel, 1929). The eighth sternum is reduced and largely desclerotized while its appendages, the ventral valves, are connected with the two pairs of valvulae of the ninth segment by a tongue and groove arrangement.

In the Blattidae the ovipositor does not serve as an organ with which to deposit the eggs in the soil as is the case in the Acrididae. In the Acrididae the valves are also closely associated with one another by means of interlocking grooves and ridges (Snodgrass, 1935). This feature was also mentioned by Nel (t.c.) in the case of *germanica*. In *maderae*, however, there is no close connection between the valvulae beyond the base. Styli mostly disappear ultimately or become indistinguishable from the apices of the dorsal valvulae, although they are to be seen in the nymphal stages. The development of the genitalia in the nymphal stages will be discussed below.

Walker (1919) studied the cockroach *Cryptocercus punctulatus* (Scudd.) and found that the ovipositor is degenerate and the valvulae and valvifers very feebly sclerotized. This he considers is due to an arrested development rather than a primitive condition.

At the bases of the first valvulae there sometimes occur a number of small sclerites called the basivalvulae. In some insects the basal structure of the ovipositor includes median sclerites lying between the second valvifers, known as the intervalvulae. The intervalvular sclerites are remnants of the ninth abdominal sternum. In *maderae* very few sclerotized areas are present in the genital chamber and no signs of basivalvulae or intervalvulae were seen. These sclerotized areas, such as the basivalvulae, are found in the termite species of *Mastotermes darwiniensis* Froggatt, *Kalotermes hubbardi* Banks, *Macrotermes natalensis* (Hav.), *Hodotermes mossambicus* (Hagen) and others (Browman, 1935 and Geyer, 1951).
The external female genitalia of *maderae* are comparatively simple and might be considered as of a primitive condition. It may also be due to arrested development as was determined by Walker (1919) in *punctulatus*. The ventral valves of the ovipositor arise from small sclerotized first valvifers and each consists of a semimembranous lobe, slightly sclerotized at its base and along its mesal surface (Fig. 4). These valves are much smaller and more simple than the corresponding ones found in *americana*. When the valvulae are viewed from underneath, the dorsal valves can be seen protruding dorso-caudad of the ventral valves. They are slightly more slender than the ventral valves and have larger sclerotized areas, including a slightly sclerotized area along their outer margins. The spermora is situated on a membranous area of the eighth sternum anterior to a transverse sclerotic ridge of the ninth sternum which probably represents the second valvifers and parts of the ninth sternite. The dorsal valves possess sclerotized ridges, but on the whole they are membranous. The aperture of the accessory glands is visible at their bases.

No evidence of a tongue and groove relationship between the ventral valves and the dorsal and inner valves, such as was found by Nel (1929) in *germanica*, was observed in *maderae*. The valvulae seem to function totally independent of one another. In the case of *germanica* two small sclerotized areas are seen laterad of the valvulae just posterior to the first valvifers. They are two of the few remaining sclerotized areas of the ninth sternum, which has lost its sclerotization to a large extent. In *maderae* these areas are absent. The sclerotic parts of the eighth sternum are represented by two large, corrugated, semisclerotized areas between which the gonopore is situated (Fig. 4). Laterad of the basis of the ovipositor, on the membrane supporting it, two sclerites of the eighth sternum are present. They articulate with the long, ventral arms of the ninth sternite. These arms extend inward into the genital chamber and are remainders of the ninth sternite. Comparable sclerotized areas are found on the eighth sternum (Fig. 4).

Nel (1929) found in *germanica* a spermatic groove between the spermathecal aperture and the gonopore, by means of which the sperms are able to locate the eggs. In *maderae* there is no sign of such a special groove as the whole area is membranous and contains various folds and grooves. The eggs are fertilized as they pass the spermathecal aperture and are then guided by the ovipositor into the vestibulum where they are enclosed in the thin, membranous ootheca.

Chopard (1950) calls the vestibulum the "incubatory pouch." He considered it to be present in every viviparous species of cockroach, such as *javanica* and *laevigata*. In addition to these viviparous species, however, the vestibulum is present in oviparous species such as *americana* and *orientalis*. It seems to be of common occurrence among the Blattidae.

The external female genitalia of different species of cockroaches are much more alike than their external male genitalia. In the females, on the whole, the different structures and organs can easily be identified. Of the species studied, the external genitalia of *maderae* very closely resemble those of *germanica*, although there are many noticeable differences, such as the
presence of a membranous oötheca in *maderae* and more sclerotized areas in the genital chamber of *germanica*. This relationship between *maderae* and *germanica* is also noticeable in the case of the males, as will be seen in the discussion on their external genitalia.

**ii. MALE.** The external genital organs of male cockroaches occur ventrally on the eighth and ninth abdominal segments. These segments usually undergo adaptive structural modifications that mark them as the genital segments. The remainder of the abdomen can then be divided into a pregenital and a postgenital region.

As in the case of the female, the appendages of the eighth and ninth abdominal segments of the male cockroach can be termed gonopods, because of the association of the openings of the genital ducts with these segments. They are, however, not necessarily modified for reproductive purposes in the male.

"Typically a gonopod is distinguished from the pregenital and postgenital appendages by the development of a median process from the proximal part of its base." (Snodgrass, 1931) (Fig. 8). The complete gonopod consists of a basal lobe, a distal stylus and a gonapophysis. In the female cockroach these structures are easily discernible, such as the gonapophyses that form the valvulae. In the males, however, these structures are much more intricate. In all male pterygote insects the gonapophyses of the eighth segment are lacking (Snodgrass, 1931). In male Blattidae there is a further reduction, namely in the gonapophyses of the ninth segment. They are present only as a pair of small, nonmusculated styli borne on the posterior margin of the ninth sternal plate. The true phallic organs are secondary outgrowths of the anterior wall of the genital chamber. The copulatory organs of the males can therefore not be homologized with the segmental appendages of the abdomen as is the case in the females. The genital chamber of the male cockroach is formed by an inflection of the tenth intersternal membrane and is situated dorsad of the ninth sternal plate (Snodgrass, 1931). The ninth sternite is extended posteriorly to form the subgenital plate or hypandrium.

Posterior to the ninth segment are the postgenital segments. In the male cockroach including *maderae* the tenth tergum is short with an entire caudal margin in comparison with the female, where it is forked (Newell, 1918). The tenth sternum is small and retracted. The eleventh somite consists of the tergum or epiproct, which carries the cerci, and the sternum, which has the form of two membranous paraprocts. Actually the cerci are borne on a membranous area between the paraprocts and the epiproct. In other insects they are often borne by the tenth tergum. In *germanica* there is no differentiation into an epiproct and paraprocts, but the whole of the eleventh segment forms a membranous proctiger. (Snodgrass, 1940.)

According to Newell (t.c.) the cerci should also be included under the genitalia. Snodgrass (t.c.) however, considers them as telopodites of the terminal segment. In most cases the cerci are functionally sensory organs, though they are frequently modified for mechanical purposes, such as true limbs. In the Blattidae, however, the cerci never form a part of the copulatory
organs. In *americana* the cerci of the adult insect “arise from between the lateral angles of the last tergal plate and the upper angles of the paraprocts, but the terminal plate of the dorsum is here clearly a composite sclerite formed of the united tenth tergum and the eleventh tergum or epiproct” (Snodgrass, 1931).

In approximately all Pterygota the male genital aperture lies between the ninth and tenth segments. Apparent exceptions occur where some of the terminal segments are fused or one or more of the pregenital segments have been obliterated (Snodgrass, 1931). The male copulatory organ of blattids also arises from the tenth intersternal membrane, which is invaginated to form the genital chamber.

The phallic organs of Orthoptera are modified to a larger or lesser extent, for the production of spermatophores and the transfer of the latter to the genital chamber of the female. The number of phallic lobes in the different families of the Orthoptera varies. In the Blattidae and Mantidae the external genitalia consist of three phallic lobes, but in the Tettigoniidae the intricate intromittent organ is formed by six outgrowths of the anterior wall of the genital chamber (Snodgrass, 1940).

The external genitalia of all blattid males consist of genital lobes or phallicmeres, associated with the mouth of the ductus ejaculatorius. In Tettigoniidae and Acrididae the genital lobes unite to form a single phallus (Snodgrass, t.c.), but in the Blattidae they remain separate.

Snodgrass (t.c.) divides the males of Blattidae into two groups according to the structure of their phallic organs, namely: a. The type found in the subfamily Blattinae, and b. as found in the other subfamilies, such as the Ectobiinae, Pseudomopinae, Nyctiborinae, Epilamprinae, Panchlorinae and Perisphaerinae.

a. **The Blattinae-type**: This form of genital structure occurs in *orientalis* and *americana*. The three genital lobes are called the left, right and ventral phallicmeres.

The left phallomere arises on the left side of the anterior genital chamber wall and its base is sunken into a shallow pocket of the wall. It consists of a number of strongly sclerotized hooks and processes and is more elaborately sub-divided than the right phallomere.

The right phallomere is situated in a median position above the genital opening. Its base is sunken into a pocket of the genital chamber wall, which is deeper than that of the left phallomere. This phallomere also consists of a number of horny processes.

The ventral phallomere is a simple lobe projecting from beneath the right phallomere. The genital opening or phallotreme is situated on its dorsal surface. “Since the terminal part of the genital exit passage contains a sclerotization in its wall, it is probably a phallic invagination or endophallic sac rather than the end of the true ductus ejaculatorius which is continuous with it.” (Snodgrass, 1940.)

b. **The type found in subfamilies other than Blattinae**: This type of blattid phallic structure is characterized by the absence of the ventral phallop-
mere, a simplification of the other two phallomeres and by the development of an eversible median lobe containing the phallogtreme. (Snodgrass, 1940.)

The left phallomere of maderae, which falls in this group, is a strongly sclerotized rod with a terminal hook which is contained in a deep pouch of the anterior wall of the genital chamber. This phallic pouch is thrown into a large number of folds and the whole structure is strongly protractile. During copulation the left phallomere is extended from the posterior end of the abdomen to play a part in clasping a sclerite in the genital chamber of the female (Fig. 9).

In the case of germanica the left phallomere clasps the crescentic sclerite anterior to the ovipositor. As the external male and female genitalia of maderae are approximately similar to those of germanica, it may be assumed that copulation takes place in a similar manner in the two species.

The right phallomere of maderae is very much smaller than the left one and it consists of two small sclerotized lamellae with a short apodeme projecting between them. This phallomere is also contained in a small pouch of the genital chamber wall (Fig. 9).

The ventral phallomere of orientalis and americana is replaced in maderae by a conical membranous lobe projecting from between the phallomere pouches. It is called the penis and from it arises an endophallic apodeme that reaches into the body cavity. The penis of germanica carries at its apex a small sclerotized spine or virga (Snodgrass, 1940). In maderae this spine is absent.

The phallogtreme is on the ventral side of the penis and it leads into an endophallic sac which receives the ductus ejaculatorius at its anterior end. The fact that the phallogtreme is found on the ventral side of the penis in germanica and maderae, and on the dorsal side of the ventral phallomere in americana and orientalis, suggests that the penis of germanica and maderae and the ventral phallomere of americana and orientalis cannot be associated with one another. The median lobe forming the penis in germanica and maderae appears to be a secondary evagination at the mouth of the endophallic sac (Snodgrass, 1940).

Snodgrass (1936) states that the exact use of the phallic organs of Blattidae during mating has not been observed. Khalifa (1950), however, gives the following description of mating in germanica:

"The male carries the female on his back at the beginning of copulation, but they soon assume an end to end position. As the male slips under the body of the female the hooked left phallomere is fully extended. It is directed upwards and inserted into the female genital chamber, clasping at the large crescentic sclerite situated in front of the ovipositor. When it securing a hold, the couple take up the end to end position. The male then acquires a hold on the ovipositor. When the end to end position is obtained the two lateral hooks lying on both sides of the male anus move backwards to hold the ovipositor from both sides at a point near its base. The male then starts to build up a spermatophore in the pouch of the ejaculatory duct and when it is fully developed the large endophallus is evaginated and directed
towards the spermathecal groove, presumably with the help of the medial virga."

In *maderae* mating was only observed on one occasion. The writer was unable to ascertain the exact movements of the phallic structures and only observed that the male carries the female on his back at the beginning of copulation with their heads in the same direction and the venter of the female resting on the dorsum of the male and that they later assume an end to end position. Owing to the fact that the structure of the phallic organs of *germanica* and *maderae* closely resemble one another, however, one may assume that the process of copulation occurs in approximately the same fashion in the two insects.

B. Histological studies

i. FEMALE. Histological studies were made on the female internal genital organs of *maderae*. The following organs were studied: the ovaries; the lateral oviducts; the oviductus communis; the genital chamber; the vestibulum; the spermathecae; the spermathecal glands and the accessory glands.

*The ovaries:* Each ovary of *maderae* consists of fifteen to twenty ovarioles opening separately at the anterior enlarged end of the lateral oviduct which is termed the calyx. Each ovariole can be divided into three portions, namely the terminal filament, the germarium and the vitellarium. A short pedicel connects the ovariole with the lateral oviduct. The terminal filament is a solid strand of cells, enclosed by a tunica propria. In adults, however, the cells may have degenerated (Deegener, 1911) so that the terminal filament consists of plasma with a few scattered nuclei.

The middle section of an ovariole, which consists of the germarium and the vitellarium, represents the intermediate part of the embryonic gonad, which contains the germ cells. (Snodgrass, 1935). The walls of the ovariole consist of a layer of follicular epithelium. The thin tunica propria is situated on the outside of the follicular epithelium and it envelopes each ovariole. In the case of *maderae* the ovarioles are held together by a thin sheath of connective tissue.

The follicular epithelium, which forms the wall of each ovariole, also divides the ovariole into a series of chambers in which the oocytes develop. Each oocyte is therefore completely enclosed by a layer of follicle cells (Figs. 10, 11).

According to Snodgrass (1935) the anterior portion of the ovariole, the germarium, contains "the germ cells in an active state of division and incipient differentiation." The vitellarium is "the region where the cells grow and attain their mature size."

The ovarioles of *maderae* are of a panoistic type and true trophocytes are wanting. The oocytes are nourished by the follicular
epithelium, which plays an active physiological rôle. On the one hand
the epithelium absorbs food material from the blood and elaborates
it in the cytoplasm of the cells while, on the other hand, it discharges
the elaborated food products into the egg tubes. (Snodgrass, 1935).
The nutrient material for the oöcytes is supplied either from the daily
food of the insect absorbed into the blood or from the food reserves
stored in the fat body.

The oögonia in the germarium are enclosed in a thin tunica propria
and each cell consists of a large nucleus surrounded by a small amount
of cytoplasm. The chromatin appears in the form of granules and stains
darkly. The oögonia develop into oöcytes. It is difficult to discriminate
between oögonia and primary oöcytes.

According to Carpenter (1928) the nucleus of the primary oöcyte
undergoes a reduction division (meiosis) by which the nuclear material
and the number of chromosomes are reduced by one half. In the cell
division that takes place after the meiotic division the chromosomes
merely split (mitosis). This maturation division may take place after
fertilization. When the sperm nucleus enters the ovum during fertili­
zation the zygote nucleus becomes quantitatively double that of either
gamete and the number of chromosomes is restored to normal.

In young oöcytes of maderae the cytoplasm is clear and transparent
and vacuoles and granules are absent. As the oöcyte develops, granules
make their appearance in the cytoplasm (Fig. 10) and the "alveolar
spheres" of yolk also develop. The nucleus and nucleolus in young
oöcytes are spherical. In later stages the nucleolus takes on an irregular
shape and divides (Geyer 1951, Nath and Mohan 1929). Apparently
these newly formed bodies of the nucleolus move out of the karyoplasm
into the deutoplasm and disappear.

Young oöcytes do not occupy the entire egg-chamber formed by
the follicle cells. The unoccupied space is filled with a transparent
hyaline plasma. As the oöcytes develop, they gradually fill the chamber
and displace this hyaloplasm. At the periphery of each oöcyte a thin
membrane is visible, which probably is the remnant of the cell wall of
the oögonium.

As the oöcytes grow older the yolk develops. It becomes visible
in the form of alveolar bodies that are found at the periphery of the
oöcyte. Later these alveolar spheres are distributed throughout the
oöplasm and form the characteristic yolk of the mature oöcyte.

Yolk formation in americana was described in detail by Nath and
Mohan (1929). According to them "the nucleolus loses its opacity and
develops vacuoles inside it, which bore through the nuclear membrane
and migrate to the periphery of the egg. Ultimately the nucleolar
extrusions break up into several homogeneous globules which are the
yolk spheres sensu stricto". Nath and Mohan (t.c.) also mention fatty yolk,
which represents the enlarged Golgi vesicles containing free fat.
In _maderae_ the yolk spheres at first lie just entad of the follicular epithelium, probably because of the fact that the nutritive fluid flows to the oöcyte from the outside through the follicular epithelial cells and the periphery of the oöcyte is therefore the most favourable place for the growth of the yolk. Later on yolk is also found in the region of the nucleus.

When the oöcytes approach maturity, they fill approximately the whole egg-chamber. Along the periphery of the oöcytes protoplasmic strands are found that apparently connect the oöcytes with the surrounding follicular epithelium.

In mature oöcytes of _maderae_ the yolk is fully developed and consists of globular spheres scattered in the oöplasm. The cells of the follicular epithelium are well defined, with large nuclei, apparently in an active state of secretion (Fig. 11). It is difficult to cut sections of mature oöcytes imbedded in wax and owing to this the vitelline membrane and the chorion could not be studied in _maderae_. According to Snodgrass (1935) the chorion is secreted by the follicular epithelium of the egg-chamber and is non chitinous.

Beyond the last egg-chamber in _maderae_ the follicle cells form a plug, which prevents the mature oöcytes from escaping into the lateral oviduct. The lumen of each pedicel is closed at the anterior end by the epithelial plug (Snodgrass, 1935). The walls of the pedicel consist of a single layer of elastic epithelium.

When the oöcytes are fully mature the epithelial plug disintegrates and the oöcytes move into the lateral oviduct. As the oöcyte leaves the follicle chamber, the walls of the chamber collapse, the epithelial walls degenerate and form the corpus luteum (Snodgrass, 1935). The oöcyte moves along the lateral oviduct into the median oviduct. It is inseminated as it emerges from the median oviduct and passes the spermathecal orifice into the genital chamber.

The lateral oviducts: The walls of each lateral oviduct consist of a layer of epithelial cells resting upon a basement membrane, surrounded by a sheath of internal circular and external longitudinal muscles. The anterior portion of each duct is enlarged to form a calyx into which the ovarioles discharge mature oöcytes. In this area the epithelium is strongly folded and the muscularis at this point is thicker than that of the remaining portion of the duct (Fig. 12). This fact is more noticeable in the case of older females where the ovaries contain fully developed oöcytes.
Each lateral oviduct opens separately into the common oviduct. In the posterior portion of each duct the epithelium is again thrown into numerous folds. The middle portion of each duct differs from the anterior and posterior parts in that the epithelial layer is not so strongly folded. The nuclei of the epithelial cells are prominent and there are signs of a secretion in the lumen of the duct (Fig. 13). This secretion probably lubricates the duct and enables the oocytes to pass freely along it.

The lateral oviducts are well provided with tracheae. The muscularis probably plays an important rôle in the backward movement of the ova along the ducts. "By means of peristaltic movements these muscles push the ova caudad from the ovaries to the oviductus communis" (Geyer, 1951). The two lateral oviducts open separately into the common oviduct and retain their separate lumina for a considerable distance into the common oviduct.

Oviductus communis: "The median oviduct belongs to the secondary exit apparatus formed as a series of invaginations of the body wall" (Snodgrass, 1935).

The wall of the median oviduct of maderae females consists of a layer of epithelial cells with large, prominent nuclei. The epithelial layer is thrown into a large number of folds, so that it has the appearance of a large number of cells arranged in an irregular pattern (Fig. 14). The basement membrane is therefore also folded irregularly. The median oviduct differs from the lateral ducts in that it has a cuticular intima, which is continuous with the cuticula of the body wall. The entire duct is surrounded by a thick muscularis, consisting of circular and longitudinal fibres; the former predominating; the inner layer of muscles comprise mostly the circular and the outer the longitudinal fibres.

The lumen of the oviductus communis at its anterior portion is roughly divided into two halves by backward prolongations of the epithelium of the lateral oviducts (Fig. 14). These two halves probably represent the lumina of the two lateral oviducts and lie next to one another. In sections through the furthermost anterior portion of the duct, it seems as though the partition forms a complete septum, entirely separating the lumina of the two lateral oviducts.

The oviductus communis opens into the genital chamber in the thickened anterodorsal area of the genital chamber wall. In this portion of the duct, the lumina of the two lateral ducts have united to form a single lumen, surrounded by the folded chitinous intima and epithelium (Fig. 15).

The genital chamber: The genital chamber is an inflection of the body wall caudad of the seventh sternum. Histologically the genital chamber wall consists mainly of longitudinal and circular muscles (Fig. 15). It is a sac-like structure and, apart from the muscular sheath, the walls con-
Van Wyk: Genital Organs of Blattids

sist of the same elements as the body wall. There are, however, noticeable differences in the structure of its dorsal, ventral and lateral walls.

In the lateral walls and in the posterior portion of the dorsal wall the following structures are found: (1) The thick muscular layer consisting of circular and longitudinal fibres; (2) the basement membrane which has a folded appearance; (3) the small epithelial cells and (4) the cuticular intima which is very thick and characteristically bears long spines or “setae” which project into the lumen of the genital chamber (Fig. 16).

In the cephalic portion the anterodorsal wall of the chamber is thickened considerably and protrudes into the lumen. In this thickened area the openings of the oviductus communis and the spermathecae are found (Fig. 15), the muscles are well developed and the epithelium is also strongly folded. The epithelium apparently secretes affluenty, because there is a thick layer of granular secretion between the epithelium and the cuticular intima and in the lumen. The epithelial cells are different from those of the remainder of the wall of the genital chamber. They are long cells, narrower at their apices than at their bases and are much more prominent than those of the remainder of the wall. The intima of this area is devoid of spines, although it is thick and noticeable. (Fig. 17). Owing to the thick muscular layer in this area, it appears as though the genital chamber is more muscular in the cephalic than in the caudal portion.

In the ventral portion of the genital chamber the epithelial folds are more pronounced and more regular, resembling the vestibular papillae. In this region of the genital chamber wall there is also a very thick muscular layer and a basement membrane with well defined cells which form a folded epithelium. The intima is very thick and is intensely folded, but without spines. In the lumen of the genital chamber a secretion is found which probably has the function of aiding the movement of the ova and spermatophores in the genital chamber. The openings of the spermathecal glands are in the dorsolateral walls of the genital chamber. The two glands open separately into the lumen of the latter.

Vestibulum: The roof of the vestibular chamber is continuous with the lateral and ventral walls of the genital chamber. (Figs. 2 and 15). There is a narrow opening between the two chambers through which the eggs pass. In the vestibulum the epithelium is modified to form a large number of glandular papillae projecting into its lumen (Fig. 18). Each papilla consists of a number of epithelial cells which have lengthened considerably. The nuclei of these cells are situated apically. In the apical portion of the papilla there is also a large amount of granular secretion. According to Brunet (1951) in the “vestibular organ” of americana there is also an apical portion in which a large amount of secretion is found. This he called the “storage layer”. “Overlying the epidermal layer is a thin layer of laminated endocuticle,
exterior to which is the storage layer, followed by an outer layer of endocuticle and the epicuticle." (Brunet, t.c.). In maderae there is apparently also a "storage layer" at the apex of each epithelial papilla, but no signs of an endocuticle was observed at its inner surface. The cuticular intima is found surrounding each papilla (Fig. 18).

In the papillae small intercellular canaliculi can be observed which are continued through the thick cuticular intima surrounding each papilla. No intracellular canaliculi were observed. The epithelial cells are situated on a basement membrane, which is surrounded by a strong muscular sheath consisting of circular an dlongitudinal fibres arranged in an irregular pattern.

The function of these epithelial papillae has not been exactly determined, but Brunet (t.c.) states: "The specialized cells of the vestibular wall in americana are in a position to coat the egg as it passes through the vestibulum, with their secretion, and may well contribute to the substance which binds the eggs together within the outer casing of the ootheca" (Brunet, t.c.).

The writer made a few chemical tests on the secretion of the maderae vestibulum. It was found that the secretion is a protein containing tyrosine and arginine in the molecule. Free tyrosine which may play a part in the hardening of the ootheca may also be present. No carbohydrates are present in the secretion. The function of the vestibular secretion is not at all clear and leaves scope for further study.

Spermathecae: The spermatheca is an invagination of the integument at the posterior end of the ventral part of the eighth abdominal segment (Snodgrass, 1935).

In maderae the two spermathecae open separately into the genital chamber (Fig. 15). Each spermora is a small oblong dorso-ventral opening. The lumen is lined with a thick cuticular intima ectad of which is a layer of epithelial cells situated on a basement membrane (Fig. 19). Surrounding the bases of the spermathecae are layers of circular and longitudinal muscular fibres. These muscular sheaths are thick and strong, consisting mainly of circular fibres. These strong muscular structures have the function of opening and closing the spermorae.

---

Fig. 17. — maderae female. T.S. antero-dorsal thickened wall of genital chamber. Semi-schematic.
Fig. 18. — maderae female. T.S. vestibular wall. Semi-schematic.
Fig. 19. — maderae female. T.S. proximal portion of spermatheca. Semi-schematic.
Fig. 20. — maderae female. T.S. wall of distal portion of spermatheca. Semi-schematic.
Fig. 21. — maderae female. T.S. spermathecal gland.
Fig. 22. — maderae female. T.S. basal portion of accessory gland.
The structure of the apical portion of each spermatheca is approximately the same as that of the basal portion, except that the muscularis is relatively undeveloped (Fig. 20). The epithelium, situated on a basement membrane, consists of a single layer of elongated cells, sometimes somewhat irregularly arranged with large nuclei. There is a thick layer of secretion at the apex of the epithelial cells and in the lumen of the spermatheca. This layer of secretion forms a “storage layer”. When this secretion moves into the lumen it probably serves as sustenance for the spermatozoa. Apically, abutting on the chitinous intima, a few scattered nuclei are visible. These were described by Brunet (1951) in the accessory glands of females of *america* as “chitinogenic cells”. These cells are small and conical and are characterized by their scarcity of cytoplasm. The nuclei seen in the spermathecal epithelium resemble those found in the accessory glands (Fig. 22) and therefore this term can also be applied in this case.

Intercellular canaliculi can be observed in the epithelial layer, leading from it, through the secretion, and opening in the chitinous intima. No intra-cellular canaliculi were observed.

A thick cuticular intima forms the lining of the spermatheca. It bears the openings of the numerous canaliculi from the epithelial layer along its inner surface. There is a storage layer of secretion between the intima and the epithelial cells (Fig. 20). According to Geyer (1951), the muscular layer in the spermatheca of *Macrotermes natalensis* (Haviland) has a double function, “first, to move the nonflagellate sperms in the first instance from the spermora to the distal end of the spermatheca and vice versa when the sperms are required for impregnation of the oocytes. Its second function is probably to close the lumen of the organ and to prevent the flowing out of the sperms and the secretion produced by the epithelial layer. The peristaltic movements of the spermatheca also serve to squeeze the epithelial secretions through the inter-cellular canals into the lumen of the spermatheca.”

Although the spermathecae of *maderae* are not clearly divided into a proximal duct and a distal spermatheca proper, the spermatozoa are apparently chiefly stored in the distal portion. The proximal portion is filled with a granular secretion, which may serve as food for the spermatozoa. The spermatozoa of *maderae* are provided with long flagellae and can therefore move of their own accord. The function of the muscular layer in this connection will therefore not be as important as in the case of *natalensis*. Each spermatheca is well provided with tracheae.

The spermathecae open into the genital chamber dorsad of the opening of the common oviduct (Figs. 1 and 2). In a transverse section through the genital chamber at this point the openings of the spermathecae and the common oviduct are clearly visible (Fig. 15).

*The spermathecal glands*: The spermathecal glands are long, thin and branched tubules opening into the genital chamber posterior to the opening of the spermathecae. (Figs. 1 & 2). Their walls consist of long, cylindrical epithelial cells arranged in a thick layer and situated
upon the basement membrane (Fig. 21). The nuclei of the epithelial cells are large and spherical. Apparently chitinogenic cells are present at the apices of these epithelial cells. They are characterized by their scarcity of cytoplasm (Brunet, 1951). A large number of canaliculi are visible, which traverse the cuticular intima and open into the lumen upon its inner surface. The intima is thick and sometimes slightly folded. Probably intra-cellular canaliculi are also present, but they were not observed. A very thin muscular sheath consisting mainly of a few longitudinal fibres surrounds each tubule of the spermathecal glands.

The lumen of each tubule contains a large amount of secretion. The rôle of this secretion is unknown. In the case of orientalis and americana the spermathecal gland is an apical branch of each spermatheca. In these cases the secretion of the gland activates the spermatozoa and has a direct influence on the reproduction of the blattids (Snodgrass, 1933). In the case of maderae, the spermathecal gland and the spermathecae are separated, and the secretion of the gland probably has not such a direct influence on the spermatozoa. The function of the secretion of these glands is therefore probably that of lubrication or something else as yet undetermined.

**The accessory glands:** The accessory glands and their common duct are the only ectodermal parts of the female reproductive system that may possibly be homologous with similar parts of the male system (Snodgrass, 1935).

In orientalis the left accessory gland is larger than the right and its tubules surround those of the right gland. The two glands differ in histological structure and in the nature of their secretions (Pryor, 1940).

Morphologically the left gland of maderae is slightly larger than the right and the tubules are thicker and more opaque. The histological structure of the two glands is however identical, although a slight difference can be seen in the nature of the secretion.

In the basal portion of the accessory glands the epithelium consists of large cylindrical cells with prominent nuclei situated in the basal portions of the cells (Fig. 22). The basement membrane is clearly defined and is surrounded by a thin layer of circular muscles. The epithelial cells secrete affluently and a thin chitinous intima is present. Canaliculi are absent, although protoplasmic strands connect the secretion in the lumen with the epithelium. In the lumen an amount of granular secretion can be observed. This secretion has a vacuolar appearance.

In the distal portions of the glands the epithelial cells are more flattened and the epithelium apparently thinner than in the proximal part (Fig. 23). The basement membrane and the cuticular intima are easily visible and few muscular fibres are present. The canaliculi of the epithelial layer are small and therefore difficult to discern. At the apex of the epithelial cells chitinogenic nuclei are visible (Fig. 22).
In the right gland the histological structure is apparently similar to that of the left gland, although the secretion appears to be more granular and the epithelial cells somewhat longer. The chitinogenic cells are clearly visible and the lumen is filled with secretion.

At the point where the accessory glands open into the genital chamber, the epithelium and intima are strongly folded. The lumen of the duct is therefore small. The duct is enclosed by a strong muscularis, consisting of longitudinal and circular fibres. The canaliculi in the epithelium and the intima can not be seen, owing to the folds. These folds probably make the duct capable of much stretching.

In the female accessory glands of *americana* there are four types of glandular epithelial cells, according to their length and structure. (Brunet, 1951). In *maderae* the epithelial cells are uniform.

The secretions of the accessory glands of blattids have the function of forming the ootheca in which the eggs are enclosed during the development of the embryos in the vestibulum. (Pryor, 1940). In *maderae* the ootheca is thin and of a transparent yellowish colour. According to Pryor (1940) the bulk of the ootheca is formed by the left accessory gland, while the secretion of the right gland serves to stick the eggs together at the time they enter the ootheca. The secretion of the right gland also functions as a hardener and stabilizer (Brunet, 1951, Pryor, t.c.). In species such as *americana* where the ootheca is well developed, the left gland is larger and more prominent than in *maderae*.

ii. **MALE.** The following internal organs of the male were studied histologically: The testes; the vasa deferentia; the accessory glands; the vesiculae seminales; the ductus ejaculatorius and the phallic gland. **The testes**: Each testis of *maderae* consists of approximately ten to fifteen sperm tubes of follicles compactly grouped together. They run parallel to one another and open into the anterior portion of the vas deferens, which is slightly prolonged into the centre of the testis. The tubes of each testis are contained in a peritoneal sheath and the wall of each testicular tube consists of a cellular epithelial sheath (Fig. 24). The walls of the tubules probably serve as trophic intermediaries between the blood surrounding the gonads and the germ cells within them, as the walls of the ovarioles. (Snodgrass, 1935). The testicular tubes possess...
no terminal filaments and are held in position by connective tissue strands, the peritoneum and tracheae.

As in the case of the ovarioles of the female, the testicular tubes can be divided into several zones, according to the stage of development of the germ-cells. The apical part is the gerarium, which contains the primary spermatogonia. Following this is the zone of growth in which the spermatogonia begin to divide and multiply. Next is the maturation zone in which the meiotic and mitotic divisions take place. Lastly comes the zone of transformation where the spermatocytes develop into spermatids and finally into mature spermatozoa (Snodgrass, t.c.).

In the apical portions of the sperm tubes of Acrididae, Gryllidae, Blattidae and other Orthoptera there is a characteristic large cell termed the apical or Versonian cell, which is regarded mostly as a spermatogonium specialized as a trophocyte. (Snodgrass, t.c.).

According to Carson (1945) the apical cell is centrally located in the distal end of each testicular follicle. "It is surrounded by a number of primary spermatogonia, the nuclei of which are peripherally located with respect to the apical cell, which sends out long cytoplasmic processes between them. The cytoplasm of the apical cell is densely packed with mitochondria. The fuchsinophil mitochondria in the spermatogonia are strikingly polarized towards the processes of the apical cell and can be seen as distinct masses, lying opposite one another on either side of an apical cell process. This relationship is again highly suggestive that a transfer occurs or that materials in solution are resynthesized in the cytoplasmic process of the spermatogonium" (Carson, t.c.). Apart from its nutritive function, the apical cell may also function as "a supporting structure adapted to the optimal production of the spermatogonia as it forms the architectural basis for the stroma in which the spermatogonia are proliferated." (Carson, t.c.) It also has been believed that the apical cell is a primary spermatogonium from which all the other spermatogonia are produced. (Snodgrass, 1935).

According to Snodgrass (1940) the gonads of males of Orthoptera in general are present at the time of hatching in the form of two cords lying immediately below the heart, extending from the rear half of the third abdominal segment into the anterior half of the sixth. "Now an indifferent mesoderm cell leaves the periphery of the gonad and pushes into the centre of each germ cell group, where it sends out cytoplasmic processes that fill the spaces between the germ cells. This becomes the apical cell. The growth of the apical complexes causes a series of lobes to appear on the dorsal surface of the gonad, which are the beginnings of the definitive sperm tubes." (Snodgrass, 1940). One would therefore expect an apical cell to be present also in the testicular follicles of maderae.

Sections were made of the testes of eight roaches, but no clear indication was found of the presence of an apical cell. In one instance,
Van Wyk: Genital Organs of Blattids

however, a large nucleus was observed with a mass of surrounding plasma in which numerous spermatogonia were suspended. This might be the apical cell with its surrounding primary spermatogonia (Fig. 24).

The primary spermatogonia undergo a number of divisions. Eventually they become the secondary spermatogonia (Fig. 24). According to Snodgrass (1940) they take with them some of the capsular cells investing the apical complex, which, attaching themselves to the secondary spermatogonia, become the cyst cells that give rise to the sperm cysts. In *maderae* no cyst cells were observed, and there was also no indication that the secondary spermatogonia lie together in groups or cysts. The spermatogonia undergo a prolonged period of intense proliferation, growth and differentiation.

In *maderae* the spermatogonia are closely packed in the apical portion of the tube. The chromatin can be clearly seen in the form of granular structures suspended in the karyoplasm (Fig. 24).

The secondary spermatogonia develop into primary spermatocytes as a result of an ordinary division with the chromatic granules still clearly visible. Lower down in the testicular tube the chromatin loses its granular structure and takes on the form of long threads of chromatin, i.e. the chromosomes, lying in a tangled mass. When a primary spermatocyte is preparing to divide into two secondary spermatocytes, its chromosomes become grouped together in pairs and the members of each couple separate again (Fig. 25). In this way a reduction division takes place and the number of chromosomes in each secondary spermatocyte is half the original. (Carpenter, 1928). After division, the chromosomes slowly lose their identity and again take on the shape of granular chromatic structures.

In the zone of transformation further divisions take place. Each secondary spermatocyte divides to form two spermatids, the chromosomes splitting, so that their number is maintained. Four spermatids are therefore formed from each primary spermatocyte (Carpenter, t.c.) The spermatids of *maderae* are small, with large nuclei in which the granular chromatin is clearly visible. (Fig. 25).

The spermatids are then transformed into the spermatozoa. At first the spermatozoa are broad, with large heads (Fig. 24) but later the heads become smaller, the flagella longer and they assume the characteristic shape of mature spermatozoa. Towards the end of spermiogenesis, much mitochondrial material is discarded by each transforming spermatid (Carpenter, 1945). “After the formation of the spermatozoa of *Macrotermes natalensis* the residual portions of the spermatids not included in the spermatozoa disintegrate, flow into the testicular cavity and are eventually emitted together with the sperms.” (Geyer, 1951.)

In the posterior portion of the testicular follicle the spermatozoa are present in large numbers. They lie in rows with the heads of the spermatozoa in each row in the same direction. The flagella give the impression of a waved structure (Fig. 24). The vas deferens penetrates
a short distance into the testis and the follicles open into it intra-
testicularly. The follicles open directly into the vas deferens and vasa
efferentia are absent. The spermatozoa move into the vas deferens
and along it by means of their flagella and the peristaltic movements
of the vas deferens. They are stored in the vesiculae seminales until copulation
occurs, when they are enclosed in a spermatophore.

The vasa deferentia: The vasa deferentia are of mesodermal origin and a
chitinous intima is therefore absent along their entire length. (Fig. 26).
These ducts open separately to the exterior in Protura, Ephemerida and
some Dermaptera, but in other insects they unite with the anterior end
of a median, ectodermal ejaculatory duct (Snodgrass, 1935).

In the intra testicular portion the wall of the vas deferens consists
of a single layer of epithelial cells with prominent nuclei, situated on a
clearly defined basement membrane. Apparently there is little secretion
from the epithelial cells in this portion. The cells are somewhat flatter
than those of the remaining portion of the duct. Along the entire length
of the vasa deferentia few muscular fibres are present, but in the anterior
portion a few longitudinal muscles can clearly be discerned. (Fig. 26).

In the posterior portion of the vas deferens the structure of the
wall is very similar to that of the anterior portion. The walls consist
of columnar epithelial cells with large, prominent nuclei and a small
amount of secretion is found in the lumen of the duct. At the apices of
the epithelial cells irregular strands and granules of secretion are visible.
The basement membrane is folded. Towards the posterior portion of
the duct the muscularis is totally absent, except where the vasa
deferentia open into the ductus ejaculatorius. The lumina of the vasa
deferentia at the point where they open into the ejaculatory duct con-
tain a secretion in which the spermatozoa are suspended.

In madera each spermatozoön has a long flagellum which enables
it to move along the vasa deferens. This probably explains the fact that
a muscularis is practically undeveloped. The secretion of the epithelial
cells of the duct may also assist the spermatozoa in their backward
movement towards the ductus ejaculatorius.

The accessory glands: Three groups of accessory glands open into the
anterior portion of the ductus ejaculatorius. Since they are of meso-

Fig. 30. — madera male. L.S. wall of vesicula seminalis. Semi-schematic.
Fig. 31. — madera male. T.S. posterior portion of ductus ejaculatorius.
Fig. 32. — madera male. L.S. wall of ejaculatory pouch. Semi-schematic.
Fig. 33. — madera male. L.S. wall of phallic gland. Semi-schematic.
Fig. 34. — madera female. Posterior sternites of first instar nymph.
Fig. 35. — madera female. Posterior sternites of second instar nymph.
Fig. 36. — madera female. Posterior sternites of third instar nymph.
Fig. 37. — madera female. Posterior sternites of fourth instar nymph.
dermal origin, as indicated above a chitinous intima is therefore wanting.

In maderae there are approximately thirty to forty tubules. Morphologically the difference between the three groups is clearly observed, as indicated above, but histologically the groups appear to differ only in the nature of their secretions, and even then it is not possible to distinguish clearly each group from the other.

The first group consists of a few tubules that have the appearance morphologically of consisting of an inner opaque tube surrounded by an outer transparent layer. Histologically it is not possible to notice the difference between these tubules (Fig. 5, I) and those of the second and third groups (Fig. 5, II & III).

The secretion of this first group of glands was found to consist of a protein containing arginine and tyrosine residues and the Biuret reaction proved the presence of at least two peptide linkages. No carbohydrates were found to be present. The tubules belonging to each group of glands were dissected out for special histological studies but they are very small and got lost during the processes of dehydration and imbedding.

The tubules of the second group are easily distinguished histologically. Morphologically they are translucent. Their walls are formed by a very thin epithelium, consisting of flat cells resting upon a basement membrane (Fig. 27). A muscularis is apparently totally absent. The lumen of the tube is filled with a vacuolar secretion consisting of a plasma with an amount of suspended granules. In many cases the vacuoles are smaller in the outer region, i.e. near the epithelium, than in the centre of the lumen.

Morphologically the tubules of the third group are much longer and thicker than those of the other two groups. They are opaque and white. In this case the epithelium is thicker than that of the second group, the nuclei are larger and the secretion has a more uniform texture. The basement membrane is clearly visible, but a muscularis is absent (Fig. 28). In many cases the secretions of some of these glands stain a darker colour than others. On the whole it seems that the glands of the third group stain a darker shade than those of the second group. The secretion of the glands of the second group stains pink, while that of the third group appears to be more purple. In some instances the secretion is drawn away from the epithelium so that the glands do not all look similar. It is therefore very difficult to determine precisely the number of tubules belonging to each of the three groups, owing to the fact that there are so many variations in the structure of the tubules and their secretions.

At the bases of the accessory glands the epithelium is apparently thicker than at their apices. In this portion the tubules are also surrounded by a muscularis, consisting of circular and longitudinal muscles, which is continuous with that of the ductus ejaculatorius (Fig. 29). The accessory glands and the vesiculae seminales all open into the
ductus ejaculatorius at its anterior end (Fig 29). The accessory glands discharge their secretions which form the spermatophore into the ductus ejaculatorius and these secretions probably eventually congregate in the ejaculatory pouch.

The vesiculae seminales: The vesiculae seminales are outgrowths of the anterior mesodermal portion of the ductus ejaculatorius, together with the accessory glands (Snodgrass, 1940). The spermatozoa are stored in them in a tangled mass, until copulation occurs, when they are included in the spermatophore.

In maderae the seminal vesicles are two large pyriform sacs situated slightly on the right hand side of the anterior end of the ductus ejaculatorius and are somewhat hidden, in the mass of accessory glands (Fig. 5). The walls consist of large cylindrical epithelial cells with more or less round nuclei (Fig. 30). A thin muscularis consisting of ental longitudinal fibres and ectal circular fibres surrounds each vesicula seminalis. The longitudinal fibres predominate. The seminal vesicles are well provided with tracheae. In orientalis the spermatozoa are generally found in the vesiculae seminales with their heads imbedded in the epithelial wall and their vibratile flagella projecting like cilia into the lumen. (Snodgrass, 1940). In maderae the spermatozoa lie in a tangled mass in the vesiculae seminales, sometimes retaining the wave-like appearance they assumed in the testes, but apparently never with their heads imbedded in the epithelium.

The epithelium secretes a substance, the nature of which was determined to be of a proteinaceous character. In this substance the spermatozoa are imbedded during their stay in the seminal vesicle.

When copulation takes place, they move along the ductus ejaculatorius and are enclosed in the spermatophore which is formed in the ejaculatory pouch.

The ductus ejaculatorius: The ductus ejaculatorius is an independent structure mainly of ectodermal origin, although the anterior portion, into which the vasa deferentia, accessory glands and vesiculae seminales open, is of mesodermal origin.

In the anterior portion of the duct the structure is as follows:—

The epithelium and basement membrane are strongly folded (Fig. 29). They are enclosed by a well developed and thick muscularis consisting chiefly of an inner layer of longitudinal muscles and an outer layer of circular fibres, although this pattern is not very consistent.

Towards the posterior end, the ductus ejaculatorius becomes narrower, but the epithelium is still folded and the well developed muscularis is retained (Fig. 31). In the posterior portion of the duct the muscularis also consists of inner longitudinal muscles and outer circular fibres, arranged in a somewhat irregular pattern.

Owing to the fact that this part of the ductus is of ectodermal origin
a well developed cuticular intima is present. This forms a layer lining the lumen and is also folded. In the anterior portion, the lumen of the duct may contain the spermatozoa or secretions of the accessory glands or both.

In the Blattidae no spermatophore mould is present as in the Acrididae and Tettigoniidae and the spermatophore is formed during copulation in the ejaculatory pouch. This pouch is a semi-diverticulum of the ductus ejaculatorius and is situated posterior to the openings of the accessory glands and vesiculae seminales.

In the pouch the epithelial cells are considerably lengthened and they give the impression of being capable of secreting affluenty (Fig. 32). Nuclei are prominent, forming a layer in the centres of the cells. Chitinogenic cells are also present, situated between the epithelium and the chitinous intima. A large number of inter- and intracellular canaliculi are visible, which often traverse the whole length of the epithelial cell. The cuticular intima is comparatively thin and contains the openings of the canaliculi. The muscularis in this portion of the ductus ejaculatorius is well developed, probably assisting the pouch to expand when a spermatophore is being formed and also assisting in its ejection during copulation.

The nature of the secretion was found to be that of a protein, containing arginine.

Specimens were not found with a spermatophore present in the pouch, owing to the fact that the spermatophore is only formed during copulation (Khalifa, 1950). It therefore only remains in the pouch for a comparatively short period of time.

The phallic gland: This gland is found at the posterior end of the ductus ejaculatorius and opens to the exterior at the base of the left phallomere. Its function has not been determined although Khalifa (1950) attributes to it the function of secreting a substance which forms an additional layer of the spermatophore.

The wall of the gland is built up of long cylindrical epithelial cells with prominent round nuclei (Fig 33). The cuticular intima is comparatively well developed and it is perforated by the openings of numerous inter- and intracellular canaliculi. The outer layer of the gland is formed by the basement membrane and the muscularis is absent.

The nuclei of the epithelial cells are situated near their bases. At
Van Wyk: Genital Organs of Blattids
the apices of the epithelial cells chitinogenic cells are also present, with prominent nuclei and very little cytoplasm. In the lumen of the gland traces of a secretion are seen, but whether these are always present, or only at certain times, is not known. This secretion is a protein, containing arginine. Owing to the fact that the gland opens at the base of the left phallemere, it may have a stimulating or lubricating effect on this organ.

IV. DEVELOPMENT OF GENITALIA AND STERNA IN NYMPHAL STAGES OF MADERAE

A. Development of sterna

i. FEMALE. There are six nymphal instars in maderae. During the development of female nymphs the abdominal sternites undergo a series of changes. These changes take place from the first to the last nymphal ecdysis. Of these the most important is the invagination of the eighth, ninth and tenth sternites above the seventh sternite. The last named sternite forms the subgenital plate or hypogynium. Of further importance is the fact that styli are present on the posterior margin of the ninth sternum in the younger nymphs, but they disappear in the penultimate nymphal moult.

In first instar nymphs the sterna of the genital segments namely the seventh, eighth and ninth are clearly discernible. The seventh sternum is longer and more noticeable than the eighth. The ninth sternum carries postero-laterally the two styli.

Male and female nymphs can be differentiated by means of the presence of a medio-posterior fissure in the ninth sternum in female nymphs. This fissure is already clearly discernible in the first instar. (Fig. 34).

In the first four instars this is the only method by which it is possible to differentiate between the two sexes. In the second and third instar female nymphs the sternites retain their shape and serial arrangement as in the first instar, but in the fourth instar the first signs are seen of the invagination of the eighth, ninth and tenth sternites.

The eighth sternite is obscured from view to a large extent by the seventh sternite and when viewing the insect from its ventral side, two small sclerotized lobes are seen projecting laterally from the posterior margin of the seventh sternite. These are the remnants of the eighth sternite. (Fig. 37).

During the second, third and fourth nymphal instars the fissure on the medio-posterior margin of the ninth sternite progressively extends forward.

When viewing the insects ventrally, two additional appendages are seen projecting from above the ninth sternite. These are, however, situated dorsad of the ninth sternite and are attached to the coria between the tergite and sternite. It seems, however, as though they
are borne by the tenth tergite. They are the cerci. These cerci, are actually the segmental appendages of the eleventh abdominal segment, but owing to the reduction of this somite, are now carried by the tenth tergum (Figs. 34 to 47).

In female nymphs of the fifth instar the eighth sternite is almost entirely concealed by the seventh sternite and a considerable portion of the ninth sternite has also been invaginated, owing to the formation of the genital cavity dorsal to the seventh sternite. The fissure on the posterior margin seems to divide the ninth sternite in fifth instar nymphs into two lobes (Fig. 38). In the case of the fifth instar male the posterior margin of the ninth sternite is entire (Fig. 45).

In the sixth, or final nymphal instar the eighth and ninth sternites are invisible, having been completely drawn into the body as a result of the formation of the genital cavity. The seventh, or subgenital sternite is very large and pronounced. Furthermore, the styli have been lost during the penultimate moult. The posterior end of the abdomen of a sixth instar female nymph therefore shows ventrally a large subgenital plate, dorsal of which are visible the two cerci. (Fig. 39). The same arrangement of structures is found in the case of the adult female (Figs. 39 & 40).

The tergites do not undergo important modifications during the development of the female. The hindmost tergite is the tenth.

It is very small and retracted in all the instars and is fused with the atrophied eleventh.

In the adult female the eighth and ninth sternites have become dechitinized to a large extent and it is often difficult to establish their identity.

The external genitalia of the adult female develop from the eighth and ninth sterna in the later nymphal stages. The ovipositor comprises the external genitalia, and it is composed of three pairs of valvulae: one pair belonging to the eighth sternum and two pairs to the ninth.

The development of the external genital appendages in the different nymphal stages is discussed below.

ii. MALE. In the first four nymphal stages of madcrae the male and female insects are approximately identical.

In the fourth nymphal instar the eighth sternite is drawn into the body above the seventh sternite in both the male and female but to a lesser extent in the former. In fourth, fifth and sixth nymphal instars and in the adult male the eighth sternite is still clearly visible, although to a lesser extent than in the first instar. The ninth sternite retains its normal form and is not invaginated (Figs. 44, 45, 46 & 47). In the case of the males the genital chamber is found dorsal of the ninth sternite and not dorsal of the seventh as is the case in the females. The ninth sternite of the last two nymphal stages and of the adult male is therefore larger than in the female, and forms the male subgenital plate or hypandrium.
The styli are retained in the adult males and they are situated in membranous areas on the postero-lateral margins of the ninth sternite. (Fig. 47).

The caudal portion of the abdomen of adult males consists ventrally of the long ninth sternite carrying the styli. Anterior to this are the short eighth and seventh sternites. Dorsally this portion of the abdomen consists of the tenth tergum carrying the cerci, and the ninth, eighth and seventh tergites. The tenth sternite is small and is drawn into the genital cavity as a result of the formation of the genital chamber dorsad of the ninth sternite. (Fig. 7). In the later nymphal stages and in the adult, the external genitalia are formed as independent evaginations of the anterior wall of the genital chamber.

B. Development of genitalia

1. Internal organs

i. FEMALE. The author did not study the internal genital organs of *maderae* in the different nymphal stages but Nel (1929) and Snodgrass (1933) studied their development in *germanica* and a short summary is given here of their results:

In *germanica* the mesodermal oviducts arise from a pair of ampullae originally situated in the tenth segment. In the first nymphal instar they have migrated to a position beneath the epidermis of the posterior part of the seventh sternum. The mesodermal oviducts are continued from the ampullae anteriorly and dorsally to the ovaries as solid cords of cells (Nel, 1929). In the second instar the first signs were observed of the ectodermal invagination which ultimately becomes the oviductus communis. In the succeeding instars the common oviduct increases in size and length. In the fifth instar it is provided with a clear lumen into which the ampullar ends of the paired oviducts open. Additional invaginations are now formed, which develop into the spermathecae and the accessory glands. It is generally believed that the common oviduct is of unpaired origin, but Nusbaum, quoted by Nel (1929) believes it is formed by a coalescence of paired rudiments.

The gonads are mesodermal structures developed in the dorsal parts of the splanchnopleure as ridges of the latter extending continuously through several abdominal segments to enclose the germ cells (Snodgrass, 1933).

ii. MALE. The internal genital organs of male cockroaches develop in
approximately the same fashion as those of the female. This development was not studied in the case of *moderae* but was studied by Snodgrass (1940) for Orthoptera in general. He made the following conclusions:—

At the time of hatching the gonads have the form of two cords lying immediately below the heart, extending from the rear half of the third abdominal segment into the anterior half of the sixth. Each gonad is continuous with a number of cells arranged in a long strand and termed by Snodgrass the “cell strand”. This proceeds posteriorly to become the free part of the genital duct, namely the vasa deferentia. The embryonic vasa deferentia end posteriorly with the hollow terminal ampullae, as in the female. These ampullae are inserted into the appendage rudiments of the tenth abdominal somite. The ampullae are ventral remnants of the coelomic sacs of the tenth somite and similar, though transient ampullae, may occur in the preceding abdominal somites. The ampullae persist, first as terminal parts of the lateral ducts and later united as an anterior part of the definitive median ejaculatory duct. As the development continues, the rudiments of the appendages of the tenth abdominal segment shift towards the median line, but the ampullae leave the appendages and independently migrate forward and medially into the posterior part of the ninth abdominal segment. Here the ampullae unite with each other to form a bilobed mesodermal vesicle into which open the two vasa deferentia. At the same time a median tubular ingrowth of the ectoderm has formed between the ninth and tenth segments, which is the ejaculatory duct. This duct unites with the mesodermal ducts and their lumina become continuous. Snodgrass (1936) also states: “Hexapods are always opisthogonate in that the genital ducts extend posterior from the gonads and open near the end of the body”.

2. External organs

i. FEMALE. In order to define the structure of the female external genital organs it is necessary to determine the origin of the different parts of which they are composed. The ovipositor of female cockroaches is formed by the segmental appendages of the eighth and ninth abdominal segments, namely the gonopods (Snodgrass, 1933). The gonopods of the eighth segment form simple lobes which in the adult female, assume the shape of simple lobe-like valves of the ovipositor. The gonopods of the ninth abdominal segment undergo a further differentiation. Originally each gonopod, that of the eighth as well as that of the ninth segment, consisted of a limb base containing a gonapophysis and a stylus (Fig. 8). The gonapophyses of the eighth gonopod develop into the valvulae of the eighth segment, i.e. the first or ventral valves. The ninth gonopod gives rise to two pairs of valvulae, namely the inner or second valves formed from the gonapophyses, and the secondary dorsal or third valves (Snodgrass, 1933). The third valves
are formed by an additional enlargement of the limb base (Fig. 3a). A structure, resembling the styli on the posterior margin of the ninth sternite is situated at the apex of this enlargement. This structure is also called a “stylus” by Snodgrass (1933). Since the author is accepting Snodgrass' theory on the origin of the external genitalia this term is retained throughout this discussion.

There is no doubt about the similarity of origin of the anterior lobes or ventral valves of the eighth segment and the inner or second valves of the ninth. No outgrowths homologous with the lateral lobes or dorsal valves of the ninth segment are found on the eighth.

The styli of the ninth gonopods can be seen situated on the dorsal valves of maderae nymphs in the sixth instar. (Fig. 50). They disappear during the final moult.

The appendicular morphology of the female roach of maderae appears to be somewhat different from that described by Snodgrass (t.c.) and this deviation is not easily explained. In the first five female nymphal stages of maderae two styli are also present on the posterior margin of the ninth sternum. (Figs. 34 to 38). It is unlikely that two pairs of styli are present on the ninth segment and the problem arises whether the styli found on the dorsal valves are true styli or not, and if they are, what then is the origin of the styli found on the posterior margin of the ninth sternite? The presence of styli on the dorsal valves of roaches in general is mentioned by Snodgrass (1933) in americana. This was verified by the author. Snodgrass, however, gives no explanation for the structures occurring on the posterior margin of the sternite. In termites styli are found on the ninth sternite in final nymphal instars, (Geyer, 1951, Browman, 1935), but are absent in adult females.

It was assumed that the gonapophyses of the gonopods represent the telopodites of the original segmental appendages (Snodgrass, 1931). It is, however, clear that the telopodites are represented in the genital appendages by the styli, which may be provided with muscles and can be divided into segments or not. The cerci of the eleventh segment represent the telopodites and are therefore homologous with the styli of the ninth. The appendages of the tenth abdominal segment are the pygopods. In some cases these appendages are retained in adult insects, as in Locusta viridissima (Berlese in Snodgrass, 1931). Generally, however, the tenth somite is fused with the eleventh and loses the status of an independent body segment. Its segmental appendages are then also absent.

In the first, second and third instars of maderae the genital valves can not be recognized externally. In the fourth instar the ventral valves are visible in the form of two simple, membranous lobes projecting from the posterior portion of the eighth sternum, which is also more or less membranous (Fig. 48). In the fifth instar the ventral valves have enlarged considerably and the inner valves have started their development. They are small and membranous and are situated on the ninth sternum (Fig. 49). In the sixth nymphal instar the ventral and inner
Valves are enlarged and the dorsal valves are visible on the ninth sternum, posterior to the inner valves. A stylus is attached to the distal end of each dorsal valve. Each stylus is joined by a stalk to a dorsal valve (Fig. 50). During the final moult these styli are discarded. In the adult female the three pairs of valvulae have attained their full development and consist of membranous lobes with small sclerotised basal areas. The limb bases of the gonopods of each segment are reduced and form the valvifer at the base of the valvulae. The female ovipositor of *maderae* is relatively simple and reduced in size in comparison with that of other orthopteroid families such as the Acrididae (Fig. 4).

ii. **MALE.** The phallic organs of male cockroaches are not formed by the segmental appendages of the genital segments as is the case in the external genitalia of the female. The gonopods of the eighth segment are entirely absent and those of the ninth are present only in the form of small nonmusculated styli on the posterior margin of the ninth sternite. The phallic organs are independent outgrowths of the genital integument around the mouth of the ductus ejaculatorius (Snodgrass, 1940).

In the first three nymphal stages no external signs of the genitalia are visible. In fourth instar male nymphs of *maderae* a lobe-like outgrowth of the genital chamber wall above the ninth sternite becomes visible. This lobe undoubtedly represents the left phallomere of the adult because in the later nymphal stages a hooked structure is found within it. This lobe is clearly the beginning of the mature form of the organ (Fig. 51). In *germanica* a smaller lobe is also present in the young nymph which is the structure from which the right phallomere will develop. (Snodgrass, 1940). In *maderae* however, the right phallomere of the adult insect is much smaller than that of *germanica*, and in the first five nymphal stages this lobe is absent (Figs. 51 & 52). In the sixth or final nymphal stage the left phallomere has approximately attained the structure it assumes in the mature male. It is contained in a deep, wrinkled sac evaginated from the genital chamber wall and its apex has acquired the characteristic hooked structure (Fig. 53). The right phallomere is represented by a small lobe, which is also an outgrowth of the anterior genital chamber wall. A short sclerotized rod is found between the two phallomere lobes. It is the structure from which the mature endophallic apodeme develops. In the adult insect these phallo­meres have reached their maximum development (Fig 9).
In male cockroaches there are two types of phallic structures. In species such as *americana* and *orientalis* there are three phallic lobes, which are visible in the nymphs as three independent structures. In *maderae* there are only two phallic lobes, the third or ventral lobe being absent. Its place is taken by an evagination of the genital chamber wall around the mouth of the ductus ejaculatorius which is termed the penis. The penis is a membranous lobe which could not be identified in the nymphal stages.

In blattids the phallic lobes retain their independent structure after the insect has completed its development. In the case of other Orthoptera such as the Tettigoniidae and Acrididae the phallic lobes unite with one another to form a composite structure, the phallus. In the nymphal stages of insects belonging to these families, however, the phallic lobes are also separate and independent of one another.

**V. SUMMARY AND CONCLUSIONS**

Studies were made on the morphology and histology of the internal and external genital organs of adults of *Leucophaea maderae* (Fabr.). In addition, observations were made on the development of the external genitalia and their corresponding sterna in the nymphal stages.

**Morphological studies**

1. **Female internal:** Fifteen to twenty ovarioles are found in each ovary. They open separately into the anterior end of the lateral oviduct. The genital chamber is a muscular sac, formed by the invagination of the eighth and ninth abdominal sternites above the seventh sternite. The oviductus communis, spermathecae and spermathecal glands open into the genital chamber, while the openings of the accessory glands are situated at its posterior end. A well developed vestibulum is present, owing to the fact that the eggs are stored in it for a comparatively long period. It is a membranous structure and is expansible to a large extent. The secretion of the vestibulum is a protein containing tyrosine and arginine in the molecule.

Two strongly-divided glands open into the genital chamber posterior to the openings of the spermathecae. They are termed the spermathecal glands and can possibly be homologized with the glandular branches of the spermathecae of *Blatta orientalis* L. and *Periplaneta americana* L. The two accessory glands are comparatively small. They secrete the substances that form the thin, yellowish, membranous oötheca in which the eggs are enclosed. The secretion of the left gland is a protein and that of the right stabilizes the protein of the oötheca and also serves to stick the eggs together. The presence of a thin, membranous oötheca may be considered as an adaptation to this insect's viviparous habit of reproduction.
2. Male internal: Each testis is a globular body formed by a mass of sperm tubes united in a common peritoneal sheath, which converge upon the anterior end of the vas deferens. The accessory glands are of mesodermal origin. There are three groups, the first group has tubules which are translucent with an opaque tube running along the centre. The second group has a larger number of long, translucent tubules, while those of the third group are still longer and more opaque. The secretions of these three groups of accessory gland tubules build up the spermatophore in the ejaculatory pouch. The spermatophore consists of three layers, probably corresponding to the secretions of the three groups of glands. The vesiculae seminales are found among the accessory glands and are also of mesodermal origin. They consist of two white, pyriform sacs in which the spermatozoa are stored until copulation takes place. The ductus ejaculatorius is a composite structure. The anterior portion is of mesodermal origin and the posterior portion is an ectodermal invagination. A diverticulum of the ductus ejaculatorius forms the ejaculatory pouch, in which the spermatophore is formed. The phallic gland opens at the base of the left phallomere. It consists of two branched tubules opening on the anterior end of a slender duct.

3. Female external: The ovipositor is much reduced in size and membranous to a large extent. It has lost the function of a true ovipositor and serves only as an egg-guide between the genital chamber and the vestibulum. The openings of the internal genital organs are closely related to the ovipositor, especially those of the accessory glands. The ovipositor consists of three pairs of appendages, namely the valvulae. The ventral valvulae are simple lobelike structures arising from the first valvifer, which is the modified limb base of the eighth abdominal segment. Two appendages are attached to the second valvifer, namely that of the ninth segment. These are the dorsal valves, which are more slender, but have larger chitinized areas than the ventral valves, and the inner valves, which are shorter and more membranous than the dorsal valves. Very few sclerotized areas are present in the genital chamber. The simple structure of the ovipositor may be considered as a primitive condition. It may, however, also be due to heterogonic growth.

4. Male external: Cockroaches can be classified into two groups according to the structure of the male external genitalia. The external genitalia of maderae belong to the second group. The ventral phallomere found in roaches belonging to the first group is replaced by the penis with the phallostreme on its ventral surface. The left phallomere of maderae is contained in a deep pouch of the genital chamber wall and is a simple retractile structure with a hooked extremity. The right phallomere is smaller than the left, but it is also sclerotized and contained in a shallow pouch. The true segmental appendages of the ninth abdominal segment are represented by two small unsegmented styli on the posterior margin of the ninth sternum.
Histological studies

1. Female.

The wall of each ovariole consists of follicular epithelial cells, and each ovariole is surrounded by a tunica propria. The ovarioles are held together by a thin sheath of connective tissue. The oocytes are nourished by the follicular epithelium; the ovarioles being of a panoistic type. The oögonia are visible in the germarium of each ovariole. They change into oöcytes in the vitellarium. Gradually yolk-spheres become visible, at first just entad of the follicular epithelium. When the epithelial plug situated beyond the last egg-chamber disintegrates the oöcytes move into the lateral oviduct. The walls of the lateral and median oviducts consist of an epithelial layer, a basement membrane and a surrounding muscularis. In the median oviduct, however, a cuticular intima is present. In the anterior portion of this duct, the lumen is divided into two lateral portions, representing the backwardly extended lumina of the two lateral oviducts. The genital chamber wall consists mainly of longitudinal and circular muscles. The dorsal, ventral and lateral walls differ in histological structure from one another. The epithelium of the vestibulum is modified to form a large number of glandular papillae, with inter- and intracellular canaliculi leading into the lumen.

The muscularis at the base of each spermatheca is considerably thicker than that at its apex. Chitinogenic cells are present in the apices of the epithelial cells. The spermatozoa are stored chiefly in the distal portion of each spermatheca. The epithelial cells of the spermathecal glands are long. Apparently chitinogenic cells are present and a large number of intercellular canaliculi open into the lumen. The histological structure of the right and left accessory glands is approximately identical. Canaliculi and chitinogenic cells were observed in the epithelium.

2. Male.

The follicles of the testes are formed from epithelial cells, and an apical cell is probably present in each follicle, but was not observed. Primary and secondary spermatogonia, primary and secondary spermatocytes, spermatids and long flagellate spermatozoa were seen in the follicles. Morphologically three groups of accessory glands were determined. Histologically, however, only two groups were identified. In the vesiculae seminales an epithelium and a muscularis were observed. The spermatozoa lie in a tangled mass in the lumina of the vesicles, imbedded in the secretion of the epithelium. The anterior portion of the median oviduct is of mesodermal origin, while in the posterior ectodermal portion a well developed cuticular intima is present.

In the ejaculatory pouch the epithelial cells are very long, containing a large number of inter- and intracellular canaliculi. Chitino-
Van Wyk: Genital Organs of Blattids

genic cells are present between the epithelium and the intima. In the phallic gland the inter- and intracellular canaliculi are also very numerous. The function of the phallic gland has not been definitely determined, although its secretion may stimulate or lubricate the left phallomere.

Development of genitalia and sterna in nymphal stages

A. Development of female sterna: Male and female nymphs can be differentiated by means of a medio-posterior fissure in the ninth sternum in female nymphs, which is already discernible in the first instar. In the fourth instar the eighth, ninth and tenth sternites gradually become invaginated above the seventh. In the sixth instar the eighth and ninth sterna become quite invisible. In the first five instars a pair of styli is present on the posterior margin of the ninth sternite. They are lost in the final moult.

B. Development of male sterna: In the fourth instar the eighth sternum is drawn into the body above the seventh sternite to a lesser extent than in the case of the female. The ninth sternite remains clearly visible throughout, forming the subgenital plate or hypandrium. The styli on the posterior margin of the ninth sternite are retained throughout the nymphal instars and are present in the adult male.

C. Development of female genitalia: The ovipositor is formed by the segmental appendages of the eighth and ninth abdominal segments. The ventral valvulae are formed from the eighth and the dorsal and inner valvulae from the ninth segment. In the first, second and third instars the valves can not be recognized externally. In the fourth instar the ventral valves appear, in the fifth the inner valves and in the sixth the dorsal valves. A stylus is attached to each dorsal valve in the sixth instar nymphs, but is lost during the final moult.

D. Development of male genitalia: The external phallic organs of male cockroaches differ from the ovipositor in females in that they are not formed from the true segmental appendages, these being represented only by the styli on the posterior margin of the ninth sternite. In the fourth instar the left phallomere begins to develop. In the sixth instar the left phallomere has approximately attained the structure it assumes in the mature insect, while the right phallomere is represented by a small lobe. A short sclerotized rod is found between the two phallomere lobes. It is the structure from which the endophallic apodeme develops. The penis could not be identified in the nymphal stages.
VI. ACKNOWLEDGMENTS

The writer wishes to thank Prof. J. W. C. Geyer for suggesting this subject and for his help and guidance in connection with this investigation. Further thanks are also due to Dr. J. C. Faure, formerly Professor of Entomology at this University, for his interest, to Dr. J. J. Matthee for his help in connection with the chemical tests, and Prof. C. Brink of the Department of Physiology for advice on the histological procedure.

The writer also wishes to acknowledge the financial aid given by the Council for Scientific and Industrial Research for the publication of this paper.

VII. LIST OF ABBREVIATIONS USED IN FIGURES

ac.gl. — accessory glands.
an. — anus.
ap.IX.S. — apodemal arm of ninth sternum.
b.m. — basement membrane.
can. — canalicul.
cer. — cercus.
ch.c. — chitinogenic cell.
chr. — chromatin.
c.i. — chitinous intima.
c.mcl. — circular muscle.
d.ej. — ductus ejaculatorius.
d.val. — dorsal (third) valvula.
ej.p. — ejaculatory pouch.
en.ap. — endophallic apodeme.
end. — endophallus.
epth. — epithelium.
epth.ac.gl. — epithelium of accessory gland.
epth.d.ej. — epithelium of ductus ejaculatorius.
epth.p. — epithelial papillae.
epth.s. — epithelial sheath.
ex.g. — external genitalia.
f.cls. — follicle cells.
g.ch. — genital chamber.
gon. — gonopore.
gonap. — gonapophysis.
i.val. — inner (second) valvula.
kplm. — karyoplasm.
l.b. — limb base.
l.g.ch. — lateral wall of genital chamber.
l.m. — lumen.
lm.d.ej. — lumen of ductus ejaculatorius.
l.mcl. — longitudinal muscle.
l.nu. — large nucleus.
l.phm. — left phallomere.
opr. — oviporus.
ov. — ovary.
par. — paraproct.
pen. — penis.
ph.gl. — phallic gland.
ph.o. — phallic organs.
p.sh. — peritoneal sheath.
p.spg. — primary spermatogonium.
rec. — rectum.
r.phm. — right phallomere.
r.phm.l. — lobe of right phallomere in nymphal stages.
r.phm. s. — sac of right phallomere.
S. — sternite.
sc.VIII.S. — sclerotized area of eighth sternum.
secr. — secretion.
secr. a.d. — secretion of antero-dorsal wall of genital chamber.
s.l. — storage layer.
sp. — spermatheca.
spd. — spermatid.
spd. — spermatids changing into spermatozoa.
sp.gl. — spermathecal gland.
spr. — spiracle.
spm. — spermatocyte.
spmz. — spermatozoön.
spr.c. — sperm capsule.
spr.d. — sperm duct.
s.spg. — secondary spermatogonium.
s.spm. — secondary spermatocytes.
st. — seta.
sty. — stylus.
t. — tergite.
tes. — testis.
t.f. — terminal filament.
t.fol. — testicular follicle.
t.p. — tunioa propria.
LIST OF ABBREVIATIONS (Continued)

I.phm.h. — hook of left phallomere.
I.phm.l. — lobe of left phallomere in nymphal stages.
I.phm.s. — sac of left phallomere.
musc. — muscularis.
nu. — nucleus.
nucl. — nucleolus.
od.c. — oviductus communis.
od.l. — oviductus lateralis.
oöc. — oöcyte.
oöp. — oöplasm.
oöth. — oötheca.
tr. — trachea.
v.a.IX.S. — ventral arm of ninth sternum.
vac. — vacuole.
val. — valvifer.
1.valv. — First valvifer.
2.valv. — Second valvifer.
v.d. — vas deferens.
v.es. — vestibulum.
v.sem. — vesicula seminalis.
v.val. — ventral (first) valvula.
y.sph. — yolk sphere.

VIII. GLOSSARY OF TERMS

"Deutoplasm" — The yolk or food plasm of an ovum.
"Genitalia" — The genital organs collectively, but usually applied only to the external genitalia.
"Gonad" — The ovary or testis, or the embryonic rudiment of either, formed of splanchnic mesoderm cells enveloping the germ cells.
"Gonapophysis" — Any part of a segmental appendage closely associated with the genital segments and having some function intimately related to introduction or the deposition of eggs.
"Gonopod" — Appendage of a genital segment or an associated segment modified for some purpose in connection with copulation, intromission or oviposition.
"Gonopore" — The external opening of a genital duct, whether exposed or concealed in a secondary invagination of the integument.
"Hypandrium" — The subgenital plate of the male, usually the ninth abdominal sternite.
"Hypogynium" — The subgenital plate of the female, usually the seventh abdominal sternite.
"Karyoplasm" — The nuclear substance in contra-distinction to the cytoplasmic material.
"Muscularis" — A muscular sheath investing all parts of the insect alimentary canal, accessory glands, tubular spermatheca, etc.
"Oviporus" — The posterior opening of the genital chamber.
"Phallomeres" — Phallic organs having the form of lobes produced from the genital chamber wall in the neighbourhood of the gonopore.
"Phalotreme" — The distal opening of the endophallus, the functional exit aperture of the genital tract when the true gonopore is contained in an endophallic chamber.
"Spermorna" — The mouth of the duct of the spermatheca.
"Stylus" — A small unsegmented process borne on the posterior margin of the ninth abdominal sternite of nymphal and adult males and nymphal females, and on the dorsal valvulae of nymphal females.
"Valvifers" — The basal plates of the ovipositor, carrying the valvulae.
"Valvula" — The three pairs of processes forming the blades of the ovipositor.
"Vestibulum" — An external genital cavity formed above the seventh abdominal sternum when the latter extends beyond the eighth.

IX. BIBLIOGRAPHY

Papers marked with an asterisk have not been consulted in the original.


