NOTES ON THE DIGESTIVE AND REPRODUCTIVE SYSTEMS OF THE GERMAN COCKROACH*

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The digestive system of the German cockroach (*Blattella germanica* L.) is very simple in structure, presenting the typical insectan parts with little complexity or specialization. The reproductive system is also of a primitive type in the female, but in the adult male it presents a marked specialization of some of the parts, and a reduction of others.

DIGESTIVE SYSTEM

The digestive system (Fig. 1 and 2) is a tube extending the entire length of the insect, beginning at the base of the mouthparts, and ending at the anus, coiled upon itself once in the mid-abdominal region. It consists of an oesophagus, crop, proventriculus, mid-intestine, small and large intestines and rectum. The mid-intestine has an anterior ring of caeca, the enteric caeca, and the small intestine an anterior ring of fine tubules, the malphigian tubules. The salivary glands and their reservoirs lie beside the oesophagus and crop but are not appendages of the digestive tract.

The *oesophagus* and *crop* form a continuous, gradually widening sack, with no division separating them. This sack extends half the length of the body, reaching into the abdominal region. The crop when empty is deeply longitudinally furrowed, less so when gorged with food. The color is white or gray, depending on the food contained. When cleared in xylol the muscles give it a reticulate appearance. The wall of the crop (Fig. 4) consists of three layers, the muscular, epithelial and chitinous layers. The muscular layer comprises two sets of muscle fibres (*m*) running at right angles to each other, and forming a lattice work around the outside of the crop. The epithelium (*ep*) is made up of a single layer of low, cuboidal cells, which have relatively small nuclei. The epithelium secrets a thin chitinous lining (*cl*) which lines the crop. When the crop is empty the epithelium is thrown into small contorted folds, irrespective of the folds of muscle.

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The crop joins bluntly with the *proventriculus,* or gizzard, which is the grinding organ of the digestive tract (Fig. 1, *p*). The gizzard is very short, joining the crop with a broad base and tapering to join the midintestine. It contains six teeth (Fig. 3), which divide the internal surface into six equal areas. The teeth are almost uniform in size and outline, and are dark brown in color. They fit up against the curved upper half of the gizzard, and have a broad, flat base, a thin, pointed tip, and a stout, downcurved beak jutting out two-thirds down the tooth. Between each tooth are eight chitinous lines, light yellow in color, granular in appearance, forming four spatulate loops, the loop being at the top (cephalad). Each tooth rests upon a thick membranous cushion, square from the face view, but with its corners rounded. From the base of each cushion a band of muscle runs down the part of the gizzard which extends into the mid-intestine.

The *mid-intestine* (Figs. 1 and 2, *mi,* and Fig. 5) forms one-half of the intestinal loop. It is almost uniform in thickness, tapering slightly where it joins the small intestine, and its external walls are of a reddish-ochreous color. The caeca (*ec*), which are white, are given off immediately after the junction with the gizzard. These are usually eight in number, forming an eccentric ring, the longer caeca to the inside, the shorter to the outside of the coelome. The two very short pairs point cephalad, but the two longer pairs rest against the mid-intestine, and point caudad. Occasionally a fifth pair of caeca are present, but if so they are merely bud-like protuberances beyond the smallest normal pair. According to Plateau (1874), the caeca excrete a slightly acid substance which emulsifies fats and converts albuminoids into peptones. From near the union of the mid-intestine and the proventriculus a membranous tube, the peritrophic membrane, is continuously secreted, which surrounds the incoming food like a curtain and prevents it coming into direct contact with the delicate epithelial layer (Imms, 1925; Comstock, 1926). This membrane has not been detected in these studies, although it doubtless occurs in this species. The outside muscular layer (*m*) of the mid-intestine is made up of two layers of muscle fibres at right angles to each other, appearing in histological sections as longitudinal, transverse or tangetial, depending upon the angle of the cut. In some slides a third series of muscle fibres appear, running tangentially across the other two. The epithelium (*ep*) consists of a row of slender columnar cells, which line the inner wall of the intestine.

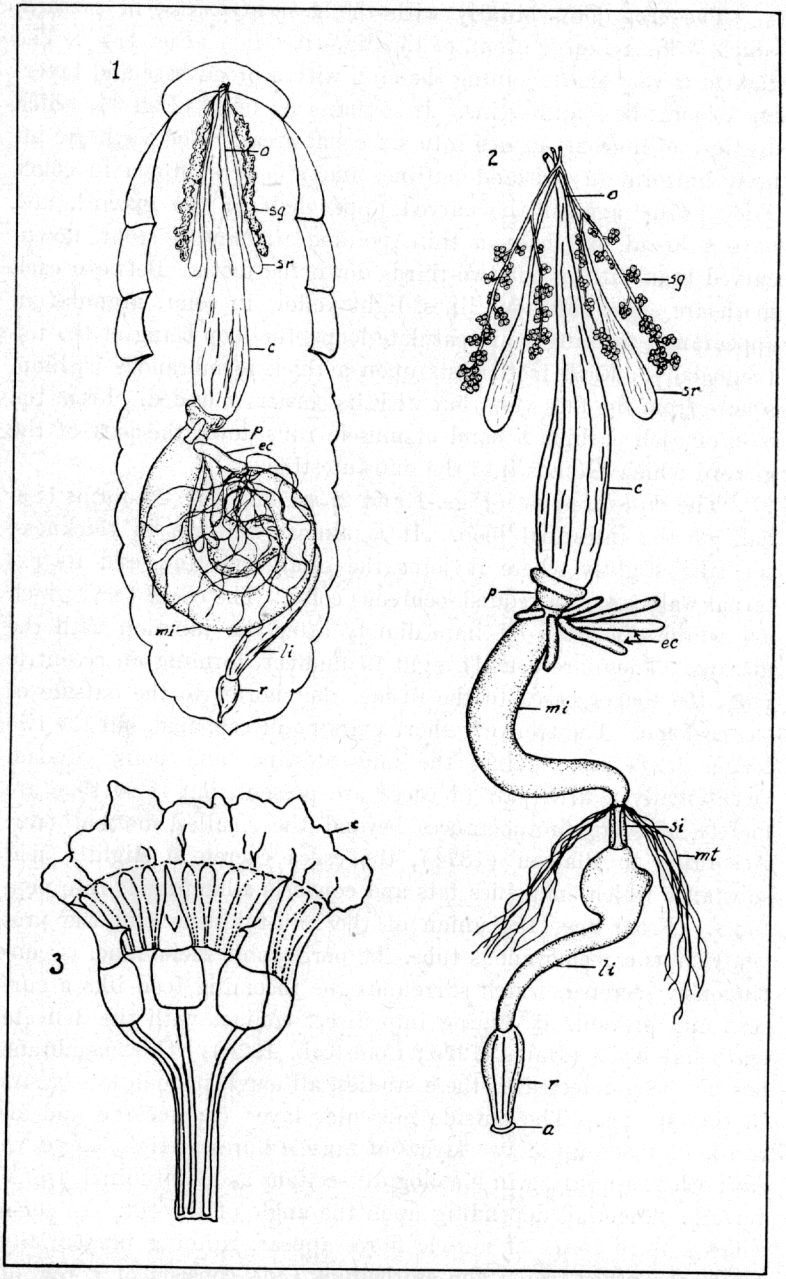

FIG. 1. Dorsal view of digestive tract and salivary glands, *in situ*.
FIG. 2. Dorsal view of digestive tract and salivary glands, extended.
FIG. 3. Inner wall of proventriculus.

These cells do not excrete a chitinous lining, so that it is in this region that most active digestion and absorption of food takes place. In secreting the digestive agencies, the cell forms a clear substance (ep^1) which forms like a drop in the swollen apex of the cell, then apparently bursts and discharges its contents into the interior of the stomach, nothing but a shrivelled cell-wall and nucleus remaining (ep^2). At their apices the epithelial cells bear a "striated hem" (*sh*) (Imms, 1925), which is thought by different authors either to be a series of minute canals or to consist of fine plasmic processes. The spent cells are continually replaced by new cells formed in the epithelial buds (*epb*), which are groups of regenerative cells scattered throughout the epithelium at the base of the cells.

The small intestine (Fig. 1 and 2, *sm*) is a short section of the digestive tract of small bore. It has a thick wall, and gives out at its junction with the mid-intestine the malphigian tubules. These arise in six clusters. They are long and thread-like, and twine throughout the abdominal visceral mass. According to Imms the histological structure of the small intestine of this species is quite similar to that of the rectum. The small intestine, together with the following length of the digestive tract, possesses an inner chitinous lining. The malphigian tubules (Fig. 9) are very simple in structure, consisting of flat, cuboidal epithelial cells surrounding the lumen.

The *large intestine,* or colon, is nearly as long as the crop. Where it joins with the small intestine, the colon is large and bulb like, posteriorly constricting to a regular tube about the thickness of the mid-intestine, and tapering to a small passage where it enters the rectum. The wall of the large intestine (Fig. 6) is composed of the typical three layers, muscular (*m*), epithelial (*ep*) and chitinous (*cl*). The inner muscular band is very thick, the outer one somewhat scattered and sparse. In the bulb-like upper portion of the colon the epithelium is thrown up into declevitous folds (Fig. 6), the cells of the folds being large and irregular, those between them being small and cuboidal, many of the latter giving rise to thread-like processes (*epp*). In the lower portion of the colon the ridges are lower, and the epithelium appears more evenly wave-like. The chitinous layer is thin and regular.

The rectum (Figs. 1 and 2, r) is small and urn-like in appearance, large at the top and small at the bottom. Six longitudinal

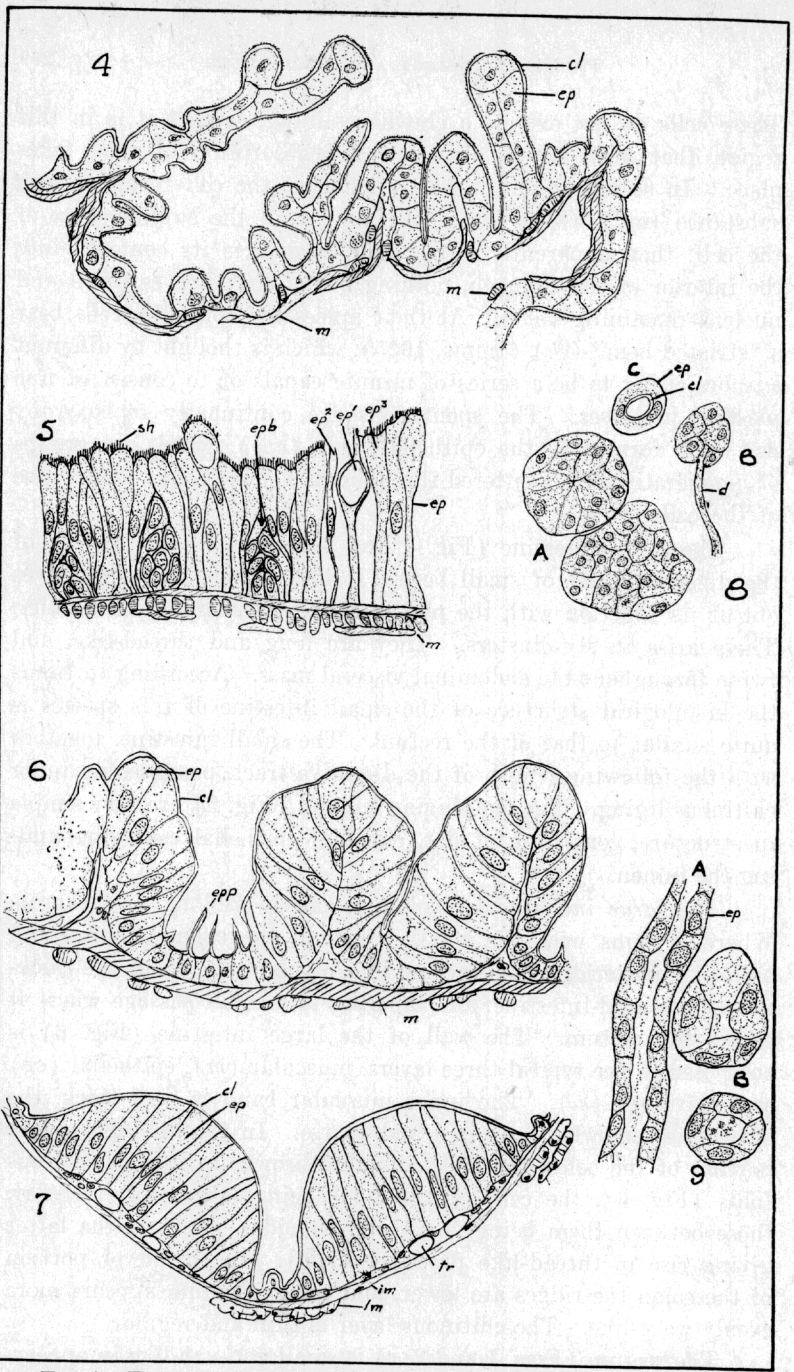

FIG. 4. Transverse section of wall of crop. FIG. 5. Longitudinal section of wall of mid-intestine. FIG. 6. Transverse section of wall of large intestine. FIG. 7. Transverse section of rectum. FIG. 8. Salivary glands: A, section of acini; B, section of acinus showing duct; C, transverse section of large duct. FIG. 9. Malphigian tubules: A, longitudinal section; B, transverse section.

dark bands, running its whole length, are visible on the exterior, the external indications of the internal epithelial bands. The wall of the rectum (Fig. 7) is composed of the same layers as the colon. The circular (inner) muscular band (*im*) forms a regular sheet around the tract. The longitudinal muscle fibres (*lm*) are congregated into six thick bands placed at the intervals between the epithelial folds. The epithelium (*ep*) is molded into six longitudinal, equal major folds. Between each of the large folds there is a minor fold one cell in width. The chitinous layer (*cl*) almost touches the basement membrane between each of the twelve folds. In the large folds the epithelial cells are slender and columnar, tallest in the middle, decreasing in height towards the edges. The nuclei are usually situated at about one-half the height of the cell, but occasionally occur at the base. The chitinous lining is thin and even, similar to that in other parts of the digestive tract.

SALIVARY GLANDS

The salivary glands are not appendages of the digestive tract, but so intimate are they with the latter that no description is complete without their consideration.

The salivary glands and their reservoirs (Fig. 1, *sr* and *sg*) lie longitudinally appressed to the crop, reaching half its length. The main duct of both the glands and reservoirs are separate in the thoracic region, uniting in the head near the outlet of the salivary glands on the hypopharynx. The glands are in two halves, one on each side of the crop, each half again dividing, the inner branch being slightly the smaller. The acini, or groups of actively secreting cells, are clustered at the end of small branches from the main ducts, and when extended (Fig. 2, *sg*) resemble long bunches of grapes. The two main ducts of each half of the gland unite below the last acini, and the main ducts thus formed unite above the oesophagus just within the thorax. The two reservoirs (*sr*) lie one on each side of the oesophagus, are slightly longer than the salivary glands, and are partly hidden by them in their natural position.

The acini of the salivary gland (Fig. 8) have no lumen. The duct of each acinus (*d*) is composed of revolute, thin epithelial cells, similar to those lining tracheae. The larger ducts are composed of thick, spongy-looking cells, which secrete the chitinous lining of the duct. The cells of the acini are typically cone-shaped, the apices of the cells meeting in the centre, with the nucleus

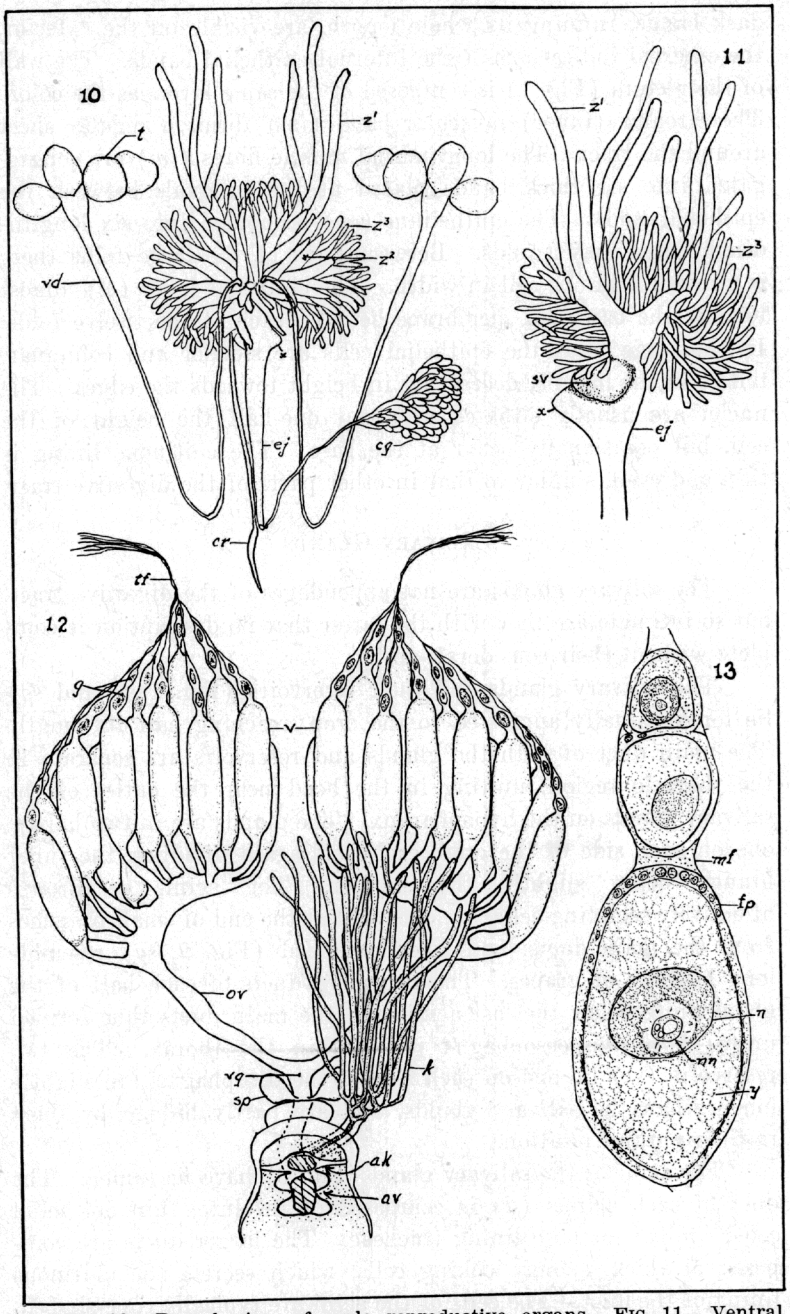

FIG. 10. Dorsal view of male reproductive organs. FIG. 11. Ventral view of accessory gland of male. FIG. 12. Dorsal view of female reproductive organs. FIG. 13. Longitudinal section through a young ovarian follicle.

situated towards the circumference of the acinus. These cells stain readily with haematoxylin and appear purple and constitute the large majority of the cells. A small number of cells situated on the circumference of the acinus are flatter than these and do not appear to have any contact with the centre of the acinus or the duct. They do not stain with haematoxylin, but stain readily with eosin, so they appear red in the ordinary counterstained sections. Thus there appears to be a striking similarity between these purple and red staining cells, both in staining quality and in position, to the chief and parietal cells, respectively, of the human gastric glands (Lewis and Stohr, 1913).

REPRODUCTIVE SYSTEM IN THE FEMALE

The female reproductive organs (Fig. 12) consist of the typical paired ovaries and oviducts, a vagina, two spermathecae, a colleterial gland, and the genital armature. Each *ovary* consists of numerous ovarian follicles attached to the oviduct by a stalk. The follicles each contain a large pre-natal egg forming the vitellarium (*v*), which is long, cylindrical and rounded at the ends, surmounted by two small paranatal eggs, one very small, the two forming the germarium (*g*), the follicle then tapering into a thin terminal (*tf*). The filaments of each ovary unite and are securely anchored by numerous small tracheal threads (*tr*) proceeding from the third abdominal spiracle. One tracheole follows each filament and descends to the egg. The number of follicles making up each ovary varies very greatly, but judging from several individuals examined just before egg laying, the usual number is about twenty-four. The two ovaries of the same individual have not always the same number, sometimes with a difference as great as five. In each ovary near maturity, there are usually three to six follicles which appear under-developed.

In a young ovary (Fig. 13) the three eggs do not show such a great difference in size as in an older one (Fig. 12). They all have, near the centre, a very large nucleus (*n*), which possesses a distinct nucler membrane. Within it is a clear area in the middle of which is a large, deeply-staining nucleolus (*nn*) containing several pellucid droplets. Around the nucleus, and occupying the greater part of the egg, is the yolk (*y*), and surrounding the egg is the developing follicular epithelium (*fp*). At this early stage the follicular epithelium is a more or less primitive plasmic body with nuclei only in the apical portion. The follicular mem-

brane (*m*) is very fine, and continuous throughout the entire length of the follicle. In ovaries which are almost mature the two paranatal eggs are relatively minute and the basal egg very large. The yolk in the latter (Fig. 14, *y*) is distinctly cellular and very greatly increased in proportion to the size of the nucleus. The follicular epithelium (*fp*) is a distinct cellular envelope around the egg, the cells flattened, each cell with a distinct nucleus. At the apex of the egg there is a cap of columnar epithelial cells (*gc*) whose shape and position, together with the fact that in the younger ovaries the nuclei in the epithelium are only at the apex, strongly suggest that this is the generative centre for the follicular epithelium.

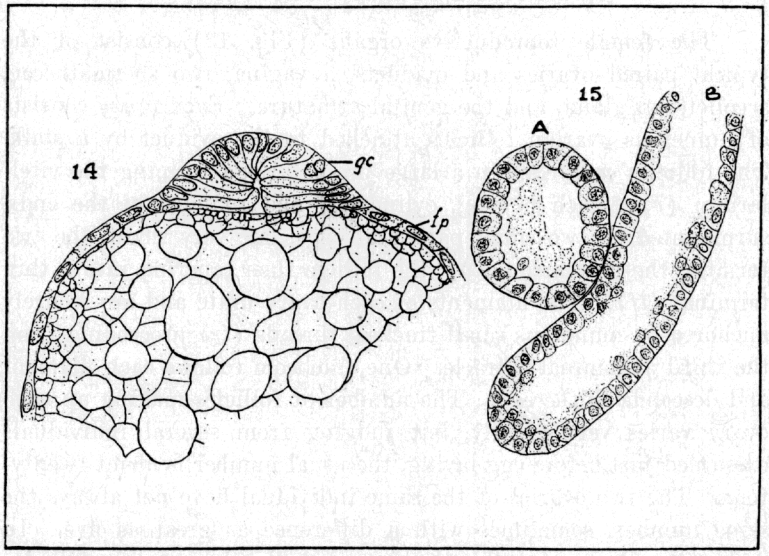

FIG. 14. Longitudinal section through apex of almost mature vitellarium.
FIG. 15. Colleterial gland: A, transverse section; B, longitudinal section.

From the cluster-like ovaries the two *oviducts* (*ov*) pass back and unite in a broad Y to form the *vagina* (*vg*). The oviducts are long and sinuate, the vagina is short and straight. No egg-calyxes have been found even in mature specimens. The vagina passes through a hard, cushion-like structure (*q*) which is attached to the genital plate (*w*), and opens through a valve (*av*) situated in the middle of the latter. Just before it enters the genital armature the vagina bears two ovoids sacs (*sp*) which are con-

sidered to be *spermathecae.* They are situated on the dorsum of the vagina one on each side of the meson. Miall and Denny (1886) record only one spermatheca in *Blatta orientalis* L.

The *colleterial gland* (*k*) is composed of a large number of long, thin tubes resulting from frequent abrupt dichotomous divisions of the base or duct. The duct opens through an aperture immediately above that of the vagina. The tubes (Fig. 15) consist of a wall of cuboidal epithelial cells resting upon a thin outside membrane, which is thick and gelatinous around the duct. This large gland secretes the substance which forms the wall of the ootheca.

REPRODUCTIVE SYSTEM IN THE MALE

The male adult reproductive system (Figs. 10 and 11) exhibits a very marked reduction of the testes and specialization of the accessory glands.

The *testis* (*t*) is composed of four or five round follicles arranged in a flat cluster. In this species they appear quite fully developed although small in the adult, but Miall and Denny (1886) state that in *Blatta orientalis* they are fully formed only in the large nymphs and are degenerate and small in the adults. The *vas deferens* (*vd*) is a long, thin tube running from the testis to the ejaculatory duct, making in its journey a long narrow loop into the posterior part of the body. It is almost bulbous at the testis, narrowing to a fairly wide tube, then narrowing again to form a much thinner one, and entering the ejaculatory duct at the base of the tubules of the accessory glands. The *ejaculatory duct* (*ej*) is a stout tube tapering towards the posterior end and at its anterior end giving rise to or serving as the seat of various structures. The most conspicuous of these is a large ball of tubules (z, z^2, z^3), comprising the *accessory gland,* the function of which is unknown. Seen from the dorsal aspect (Fig. 10) this mass shows three distinct kinds of tubules: (1) a small number (eight to twelve) of long, thick tubules (z) which are much larger than the others and extend forward much beyond them, (2) a large number of shorter, yet fairly thick tubules (z^2) occupying most of the dorsal aspect, and (3) a greater number of thin tubules (z^3) arising behind those of (2) and extending slightly beyond them in an almost even circle. From the ventral aspect (Fig. 11) the long tubules are seen to be prolongations of the ejaculatory duct, and to these the term "ectadenia" of Escherich (Imms) fits

well. The two series of short tubules evidently arise from the dorsal surface of the ejaculatory duct at the point where the vasa deferentia enter it, and to these the term "mesadenia," also of Escherich, is applied. On the right side of the ejaculatory duct is a conical evagination (*x*), and on the ventral side, adjacent to it but at a slightly higher level is an irregular bulb-like process (*sv*). This may represent the *seminal vesicle.* Just before the ejaculatory duct enters the mass of genital armature it is joined by the duct of another gland (*cg*) made up of closely appressed but distinct tubules. Miall and Denny (1886) consider it under the name "conglobate gland." The function of this gland, also, is unknown. Attached to the ejaculatory duct by transparent muscle is a long, thin, chitinous rod (*r*), a little longer than the duct, and surmounted at the posterior end by a sickle-like head. This rod is, no doubt, a part of the genital armature.

REFERENCES CITED

IMMS, A. D.

1925. A General Textbook of Entomology. London. 689 pp.

LEWIS, F. T., and STOHR, P.

1913. A Textbook of Histology. Philadelphia. xi + 539 pp.

MIALL, L. C., and DENNY, A.

1886. The Structure and Life-history of the Cockroach. London.

PLATEAU, F.

1874. Recherches sur les Phenomenes de la Digestion chez les Insectes. Mem. Acad. Belg., Vol. XLI.

LIST OF ABBREVIATIONS USED IN PLATES

a — anus
ak — opening of colleterial gland
av — opening of vagina
c — crop
cg — conglobate gland
cl — chitinous lining
cr — chitinous rod
d — duct
ec — enteric caeca
ej — ejaculatory duct
ep — epithelium
ep^1 — discharging epithelial cell
ep^2 — burst epithelial cell
ep^3 — normally shaped epithelial cell
epb — epithelial bud
epp — epithelial process
fp — follicular epithelium
gc — generative cap
im — inner muscle
k — colleterial gland
li — large intestine
lm — longitudinal muscle
m — muscle
mi — mid intestine
mf — follicular membrane
mt — malphigian tubules
n — nucleus
nn — nucleolus
o — oesophagus
ov — oviduct
p — proventriculus
q — "cushion" of female genitalia
r — rectum
sg — salivary glands
sh — striated hem
si — small intestine
sp — spermatheca
sr — salivary reservoir
sv — seminal vesicle (?)
t — testis
tf — terminal filaments
tr — tracheoles
v — vitellarium
vd — vas deferens
vg — vagina
w — genital plate
x — conical evagination of ejaculatory duct
y — yolk
z^1 — ectadenia
z^2 — mesadenia
z^3 — mesdaenia