The Structure and Development of the Reproductive System in the Coleoptera with notes on its Homologies.

By

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With Plates 7 to 10 and 49 Text-figures.

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PART I. THE MALE.
A. Introduction.

While a great deal of valuable literature upon the morphology and development of the reproductive system in the Insecta is in existence, investigators in the past have made but little attempt to compare their conclusions with those of other workers. There are in existence, therefore, different systems of nomenclature for almost every group studied, often more than one system for the same group, and always a different system for each of the sexes. In consequence, a bewildering number of terms is in use, these being often of popular designation and so of little systematic value.

If the morphological structure of the reproductive organs, and particularly of the external genital appendages, is to be of any phylogenetic significance, it is necessary that the number of terms in use should be reduced to a minimum, and that the selection of terms should be based upon a study of comparative morphology. There is a growing feeling among students of taxonomy and phylogeny that the importance of the reproductive organs has been too long ignored, and attempts to reorganize systems of classification upon this basis have been begun.

In the most recent work upon this subject, such as that of Crampton (7–15), Walker (55 and 56), and Singh Pruthi (42–5), although the conclusions of these authors are not entirely in agreement, much has been done in the reviewing and criticizing of earlier work, towards the establishment of the subject upon a firmer basis.

With regard to the Coleoptera, Verhoeff (49 and 50) has made a survey of the terminal abdominal segments and their appendages in both sexes, while Sharp and Muir (47) have studied the copulatory apparatus in a large number of species. The only authors who have treated the subject from the standpoint of development, however, appear to be Muir (34) and Singh
Pruthi (44 and 45), and the following study is an attempt to supplement their work.

The first and second parts will be devoted to the structure and development of the male and female respectively, the third section to a comparison between the two sexes.

The work was carried out in the Department of Zoology, University College of Wales, Aberystwyth, under the supervision of Professor R. D. Laurie, M.A., to whom the writer is greatly indebted for much valuable advice and criticism. Many thanks are due to Mr. J. R. W. Jenkins, M.Sc., for his unfailing interest and encouragement. The writer also wishes to express her gratitude to the Department of Scientific and Industrial Research for a Grant enabling the research to be carried out.

B. MATERIAL AND TECHNIQUE.

Sitodrepa panicea L. was obtained from samples of cattle-cake which had become infested while stored in the laboratory; Gastroidea polygoni L. was reared from eggs found on weeds of Polygonum spp. during June and July. Larvae were preserved at different stages of development, and when the fully-fed larvae had left the plants prior to pupation, the soil was carefully sieved for the pupae at intervals of seven and fourteen days. Anthonomus pomorum L. was first obtained from ‘capped’ blossoms which were brought into the laboratory for examination towards the end of May. Further specimens were obtained from Cambridgeshire and Devonshire. Rhagium bifasciatum F. was collected from rotten stumps of coniferous trees. Larvae in different stages of development were obtained throughout the year, but the larval period extends over more than one year, and, pupation taking place in late summer and early autumn, the adult emerges almost immediately. Of the pupae obtained and successfully examined all but one proved to be female. The account of the male is, therefore, unavoidably held over.

The adult insects were examined after dissection under the binocular microscope. Larvae and pupae were preserved in Carnoy’s fluid and serial sections prepared in the customary manner.
C. General Structure and Nomenclature.

Before entering into a discussion on the male reproductive system, a brief description of the general structure in the Coleoptera is necessary. The terms used are selected from the systems of nomenclature employed by Sharp and Muir and Singh Pruthi.

A pair of testes occupies a dorso-lateral position, one on each side of the alimentary canal, extending through one or more of the abdominal segments between the first and the seventh. From each testis a fine duct, the vas deferens, leads posteriorly to open with its fellow of the opposite side, into the ejaculatory duct. At the point where vasa deferentia and ejaculatory duct unite, one or more pairs of accessory glands open, either into the vasa deferentia themselves or into the ejaculatory duct. A pair of vesiculae seminales may be present as dilations of the vasa deferentia, or there may be a common vesicula into which they both open.

The copulatory apparatus consists of an invagination of the body-wall known as the ‘aedeagus’ (Sharp and Muir) or the ‘genital pocket’ (Singh Pruthi) (Text-figs. 1 and 2). In structure it consists of a pair of tubes, the one within another, the walls of the inner and outer tubes being continuous at the orifice of the inner tube. The outer tube represents the wall of the

**Text-fig. 1.** Aedeagus extended.

**Text-fig. 2.** Aedeagus retracted.

*cm1*, 1st connecting membrane; *cm2*, 2nd connecting membrane; *ejd*, ejaculatory duct; *g*, gonopore; *ml*, median lobe; *tg*, tegmen.
genital pocket, the inner the ejaculatory duct. This structure readily lends itself to modification. Traction on the ejaculatory duct will withdraw the genital pocket wholly within the body cavity; this is the normal position in repose (Text-fig. 2). The orifice of the genital duct thus becomes proximal, while the orifice of the genital pocket so formed is distal. In the act of copulation pressure exerted within the genital pocket results in its being protruded from the body-cavity as shown in Text-fig. 1.

Having pierced the tip of the genital pocket, the ejaculatory duct enters a median appendage at its base, the gonopore being situated at the apex. This appendage is known as the ‘median lobe’ (Muir, Singh Pruthi), though Verhoeff terms it the ‘penis’.

In some Coleoptera, e.g. Tenebrio molitor, a pair of ‘lateral lobes’ (Singh Pruthi) or ‘parameres’ (Verhoeff) is present, one on each side of the median lobe. The lateral lobes may fuse with each other basally in the mid-dorsal and mid-ventral lines, thus surrounding the proximal region of the median lobe. When all three lobes are present, the copulatory apparatus is said to be of the ‘generalized trilobe type’.

It is usual for a ring-like sclerite to be formed in the wall of the genital pocket by the secretion of chitin. The sclerite is known as the tegmen and may be formed in the outer or the inner wall of the pocket. The remainder of the wall being membranous, this allows of a certain amount of play between the tegmen and the median lobe which enables the latter to be extruded during copulation.

Sharp and Muir distinguish two membranous regions in the genital pocket, namely, the first connecting membrane between the tegmen and the median lobe, and the second connecting membrane between the tegmen and the body-wall. In a subsequent paper Sharp (48) reverses this order, the first connecting membrane becomes the second and vice versa. This, of course, does not alter the relations that exist between the several parts of the copulatory apparatus, and for that reason the earlier system has been retained in this paper.

The value of naming these divisions of the genital pocket as though they were distinct, fixed regions is doubtful, as Sharp
and Muir themselves realize. It tends to foster the idea that the genital pocket is a jointed tube composed of a number of definite sclerites. The tegmen, in point of fact, is not fixed in position at all. In some forms, e.g. various Curculionids, the chitin is deposited in the outer wall of the pocket to form a ring-shaped sclerite, and both first and second connecting membranes can be distinguished. In other forms, e.g. *Tenebrio molitor*, the first connecting membrane, i.e. between the tegmen and median lobe, disappears completely, and the tegmen now appears as the tubular ‘basal piece’; the term tegmen being here applied by Sharp and Muir to the tegmen proper together with the median lobe. In the present paper, the term ‘genital pocket’ will be used to designate the whole of that invagination of the body-wall, while by ‘tegmen’ will be meant either the ring-like sclerite or the ‘basal piece’.

The spiculum gastrale is a Y-shaped or horseshoe-shaped chitinous structure, or simple chitinous rod, lying against the ventral body-wall in the posterior segments of the abdomen. It serves as the basis of attachment for the powerful muscles which control the copulatory apparatus.

The male reproductive system may, therefore, be considered under two headings:

1. **The External Organs or Copulatory Apparatus**, consisting of the genital pocket, with the tegmen, connecting membranes, median and lateral lobes, and spiculum gastrale.

2. **The Efferent System**, comprising the paired testes, vasa deferentia, accessory glands, vesiculae seminales, and ejaculatory duct.

**D. History of the Subject and Homologies.**

1. **The External Organs.**

While the intromittent organ in the Insecta, i.e. the organ in the Coleoptera formed by the median and lateral lobes, has been shown by many authors to arise from originally paired appendages, e.g. Christophers in the Diptera (17) and *Cimex lenticularis* (16), Verson and Bisson in *Bombyx mori*
(54), Haviland (21), Kraepelin (23), Kulagin (30), Michaelis (31) in the Hymenoptera, Zander in the Hymenoptera (59), Trichoptera (60), and Lepidoptera (61), Singh Pruthi (43), George (20) in the Homoptera; Muir and Singh Pruthi are the only authors who have studied its development in the Coleoptera. The latter is of the opinion that the intromittent organ in this order also is paired in origin, but Muir states that it arises as a median, unpaired structure.

If Muir is correct, and the intromittent organ is unpaired in origin, then the Coleoptera form a unique order, the systematic position of which must be carefully revised. But if, as Singh Pruthi states, the intromittent organ originates as a pair of appendages of the ninth sternite, then the question of the homologies of these structures opens up an important line of investigation.

In general, the intromittent organ consists of a median appendage, variously termed the median lobe (Singh Pruthi), penis (Verhoeff, Zander, &c.), phallosome (Christophers), with one or more pairs of appendages on either side. The lateral appendages may be termed inner and outer valves (Zander), parameres (Verhoeff, Muir, Walker, &c.), lateral lobes (Singh Pruthi), androapodite and parameres (Christophers) as well as many other confusing names. In some cases the median appendage is double, i.e. there are two ‘penes’ as in some Dermaptera and the Ephemeroptera.

The difficulties which exist in determining on one system of nomenclature are numerous and formidable. The chief seems to lie in the recognition of an ancestral type of structure to which the parts in the different orders can be referred. Verhoeff (52) in 1903 laid down the foundations for a truer understanding of the relations of the parts. In this study, he gives a detailed account of the structure of the intromittent organ in the primitive Thysanuran Machilis, and attempts to refer Insects of higher orders to the same basic plan. Subsequent research by himself as well as by other authors has shown that Verhoeff was mistaken in many points. The work, however, is important and throws considerable light on the subject. Verhoeff considered that the genital appendages in Machilis are serially
homologous with the appendages found on the preceding abdominal segments and also with the thoracic legs and trophi (mouth parts). The sternites of the eighth and ninth segments are reduced in size, and the appendages, each consisting of a basal joint or coxite (gonocoxtite) which bears an inner appendage, the telopodite, and an outer appendage, the stylus, are situated laterally. The whole appendage has been homologized with the crustacean limb, the coxite representing the basipodite, the telopodite the endopodite, and the stylus the expodite.

According to Verhoeff, there is a tendency for the coxites to become closely united with the sternites, eventually losing their identity and forming with the sternite a 'coxosternum'. Walker shows that such a fusion also occurs in the Orthoptera and that there is a progressive diminution of the styli with their ultimate loss. Verhoeff at first considered that the median appendage is formed by the telopodites of the eighth segment, and he names this organ the 'syntelopodite' or 'penis'. The telopodites of the ninth segment are termed 'parameres'. Later, he stated that the penis does not arise from the eighth segment, but from a segment posterior to the ninth (53). The term paramere then, in its original application, refers to the telopodites or endopodites of the ninth sternite, and in this connexion will be used hereafter.

Verhoeff believed, therefore, that the 'penis' and parameres do not belong to the same segment. Furthermore, that in such cases where a pair of penes exists, e.g. in the Ephemeroptera, and Dermaptera-Diandria, each of these penes is developed from a single telopodite. In the Dermaptera-Monandria, where only one penis is present, this does not represent a syntelopodite, but is the result of the atrophy of one of the pair, and the development of the other, as has been shown by many authors.

More recent workers, with the notable exceptions of Muir and Kershaw (27) and Wheeler (57), whose work will be discussed in Part III of this study, consider that the median and lateral appendages arise from the ninth segment only. To which of the appendages in the primitive insect Machilis, then, can they be compared?

Intromittent organs may be grouped roughly in two classes:
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(a) With a median, and two pairs of lateral appendages.
(b) With a median, and one pair of lateral appendages.
The former group includes the Ephemeroptera, Orthoptera, Homoptera, some Lepidoptera, Trichoptera, some Hymenoptera, and Diptera.

Several possible comparisons may be made:

(i) That the median appendage is a syntelopodite, i.e. it represents the fused parameres, while the inner pair of appendages represents the coxites and the outer pair the styli.

(ii) That the median appendage and the inner lateral appendages are derived from the parameres, while the outer pair represents the coxites and/or their styli.

Walker considers that the penis or median appendage itself is not paired in origin. He says (55, p. 2): ‘The aperture is usually borne upon an outgrowth, the penis or aedeagus, whose walls may be more or less chitinised, or wholly membranous. Where two apertures are present there are likewise two penes (Ephemeroptera) or a more or less deeply bi-partite penis (Dermoptera), but it is more probable that in these orders the penis or penes are not strictly homologous with those of other orders; in fact, it appears as though the penis may have developed independently in several orders.’

He therefore compares the two pairs of appendages present with the parameres and the coxites, with, or without their styli.

Crampton (14) believes that the median appendage is paired in origin and that the double penes in the Ephemeroptera represent the paramer; coxites and their styli also being present.

Zander (59–61), while not expressing an opinion as to the homologies of the various appendages, possibly because he does not consider them to be derived from abdominal ‘limbs’, regards the ‘penis’ and ‘inner and outer valves’ as derived from one pair of primary appendages. Christophers (17) also subscribes to Zander’s account of the development of the appendages, but seems to consider the penis or phallosome as partially derived from a median outgrowth posterior to the ninth sternite.

According to Singh Pruthi (43), there are two pairs of primary
appendages in the Homoptera, the inner pair of which gives rise to both parameres and penis, while the outer pair represents the coxites. He also states that from Zander’s description, he regards the same state of affairs to be present in the Lepidoptera, Trichoptera, and Hymenoptera, where a penis and two pairs of appendages are present. In these orders, where the penis and one pair of appendages only are present, he is of the opinion that the penis represents the parameres, and the lateral appendages the coxites, with or without their styli. The penis in such a case is called by Singh Pruthi an ‘aedeagophore’.

George (20), working on the Homoptera homologizes the subgenital plates with the coxites, and states that the aedeagus and ‘so-called parameres’ are derived from the endopodites. He regards the parameres as organs of no morphological significance which arise as outgrowths from the aedeagus.

The second group includes the Dermaptera, Odonata, and Coleoptera. Here there are a median appendage and but one pair of lateral appendages, or, as in some Coleoptera, a median appendage only. These may have been derived in either of the following ways:

(i) The median appendage from the parameres, the lateral appendages from the coxites,
(ii) The median and lateral appendages together from the parameres.

On account of the position of the median and lateral appendages, it is considered unlikely that both should have been derived from the coxites.

In the Odonata, parameres are absent, and the lateral appendages, which bear styli in the nymphal instars, are thought to represent the coxites (George). This reduction of the genitalia associated with the ninth segment is correlated with the development of secondary structures having a copulatory function and situated in the anterior region of the abdomen. The lateral appendages in the Dermaptera represent the parameres (Crampton, Walker, Singh Pruthi).

The lateral appendages in the Coleoptera were at first declared by Muir (34) to be merely outgrowths from the aedeagus. Later, however (38), he suggested that they might be the
homologues of the coxites. To lend weight to this suggestion he writes: ‘In some Coleoptera, a distinct pair of lobes is found arising from the base of the median lobe, quite independent of the lateral lobes (coxites) on the tegmen.’

From this quotation one might infer that this ‘distinct pair of lobes’ is the homologue of the pair of parameres in the Trilobe forms. There is, however, a distinct similarity between the above account and Zander’s description of the Trichoptera-Limnophilidae, where the gonopore is situated on the median of three ‘endäste’, and a pair of lateral ‘valvae’ is also present.

Singh Pruthi is of the opinion, however, that coxites are not present in the Coleoptera, but that the median and lateral appendages together are homologous with the parameres. Where only the median appendage is present, the structure is termed an aedeagophore and represents the fused parameres. The discussion of this interesting problem will be returned to later.

Owing to absence of chitinization, the abdominal segments posterior to the eighth are often indistinguishable in adult Coleoptera. As a result, there arises the question as to whether a tergite or sternite takes part in the formation of the external genitalia. Muir and Singh Pruthi are agreed as to the improbability of this view and the results of other workers (e.g. Crampton, Christophers, Walker) are in accordance. Hopkins (24), however, considers that the spiculum gastrale represents the modified ninth sternite.

(2) The Efferent System.

According to Nussbaum (40, Pediculus, Goniocotes, and Blatta), the current impression that the efferent ducts of the larva unite to form the whole system of sexual ducts is incorrect; they form only the vasa deferentia, all other parts of the efferent system, viz. ejaculatory ducts and accessory glands, developing from the ectoderm. Christophers (Diptera and Cimex) regards the vasa deferentia as mesodermal structures and compares their mode of origin with that described by Zander in the Hymenoptera. Here he is at fault, since Zander evidently considers that the vasa deferentia arise
from the ectoderm. Verson and Bisson (Bombyx mori, 54) ascribe a mesodermal origin to the vasa deferentia and glands, while the ejaculatory duct develops as an ectodermal outgrowth. Wheeler (Xiphidium) states that except for a very short terminal posterior region which is ectodermal in origin, the whole of the efferent system is derived from the mesoderm. George is of the same opinion. Muir (Coleoptera) and Singh Pruthi (Homoptera and Coleoptera) find that the whole of the efferent system, even to the terminal portions of the vasa deferentia, is ectodermal in origin. Michaelis (Honey-bee), Seurat (Doryctes gallicus), and Kulagin (Platy-gaster sp.) also agree that all parts of the reproductive system, with the exception of the testes, are ectodermal in origin.

Again, Nussbaum, Verson and Bisson, and Michaelis are of the opinion that the ejaculatory duct arises from paired rudiments which subsequently fuse to form a median duct. Wheeler believes that all except the posterior terminal region is paired in origin, while Muir, Singh Pruthi, Christophers, Zander, Seurat, Kulagin, and George all state that the ejaculatory duct is unpaired in origin.

With reference to the accessory glands, the most generally accepted view is that of Escherich (19), viz. that one pair of glands is of mesodermal origin (the mesadenia), the other of ectodermal origin (the ectadenia). Escherich's work refers mainly to the Coleoptera and is confirmed by Blatter (3), while Bordas (4-6) is of the opinion that where one or more pairs of glands exist, they are of mesodermal origin. Recent work by George shows the same conclusion. Singh Pruthi, Nussbaum, and others regard all glands as having been derived from the ectoderm.

E. Development.

(1) Sitodrepa panicea L.

(a) Adult Structure.

Posterior to the eighth segment, the sternites are indistinguishable, a membranous area intervening between the eighth sternite and the anus. In repose, this area is folded into the body and forms the genital pocket within which the intromittent
organ lies. The intromittent organ consists of a median lobe and two lateral lobes, which are asymmetrically placed, the median lobe piercing the left lateral lobe at its base (Text-fig. 3).

The first connecting membrane is not present, the tegmen forming a ring at the base of the median and lateral lobes.

A heavily chitinized, horseshoe-shaped spiculum is present, lying against the ventral body-wall with its arms directed posteriorly: it gives attachment to powerful muscles.

The testes occupy a dorso-lateral position extending from the

second to fourth abdominal segments. Each testis is composed of six testicular follicles. The vasa deferentia are short and in the fifth segment open into the lateral or paired branches of the ejaculatory duct. At the junction of the paired ejaculatory ducts are situated the openings of two pairs of accessory glands, the larger pair being internal, the smaller pair external. The median ejaculatory duct formed by the union of the paired ejaculatory ducts is short and straight. Posteriorly it pierces the genital pocket, traverses the tegmen, and opens at the apex of the median lobe.

(b) Structure of the Immature Insect.

(i) The External Organs. The Larva. In the larva, nine distinct tergites and sternites are present. The sternites
are much shorter than the tergites, with the result that normally the body is curled up with the head almost touching the tip of the abdomen. The ninth tergite is broad, and curves downwards and outwards so that from the ventral surface it appears somewhat horseshoe-shaped. Posterior to the ninth sternite, but not separated from it by a distinct suture, is a sclerite which fits into the concavity of the tergite. This sclerite may represent the whole, or a part of the tenth segment. Distally, it bears a papilla which protects the anus (Text-fig. 4).

Immediately anterior to the anus is a longitudinal depression which represents the primary invagination of the genital system. No genital plates or appendages are present in any of the larval instars, and it is, therefore, difficult to distinguish between the sexes.

The Pre-pupa. When the pre-pupal stage has been reached the male may be recognized by its smaller size.

During this instar, besides the numerous changes involving the eversion of the appendages of the head and thorax, a certain amount of development of the external genitalia takes place. The depression posterior to the ninth sternite deepens, and in sections is seen to be an invagination of the ectodermal layer; this is the rudiment of the ejaculatory duct. On each side of the invagination, an appendage arises as an evagination of the ectodermal layer. Thus the gonopore is primarily bordered by a pair of appendages (Text-fig. 5).

This pair of primary appendages becomes doubled by the appearance of a vertical cleft (Text-fig. 6), and almost immediately the inner pair of appendages so formed fuses along its dorsal and ventral margins so that a tubular organ is formed which is pierced basally by the ejaculatory duct. The gonopore hence comes to lie at the apex of this organ which is the median lobe. At its base, the median lobe is not completely separated from the left lateral lobe, so that a certain amount of asymmetry occurs.

The Pupa. When pupation takes place, there is no reduction in the number of body segments; nine tergites and sternites can still be recognized. With the straightening of the abdomen, the anus moves caudad. Anterior to it are the three genital
appendages, the median lobe being the most prominent, and the left lateral lobe the smallest (Text-fig. 7).

With the maturation of the pupa a second invagination occurs immediately anterior and ventral to the first; this is the genital pocket. As the process of invagination proceeds, the genital appendages become drawn in with the dorsal wall of the pocket. At the point of origin of the genital appendages, the ectodermal layer of the appendage is continuous with that of the pocket (Text-fig. 8).

In transverse sections, therefore, the lobes appear as diverti-
cula of the dorsal wall of the genital pocket, projecting downwards into its cavity (fig. 3, Pl. 7).

At a later stage of development the evagination of the apex of the pocket commences, carrying with it the genital appendages (Text-fig. 9).

Thus is formed a double-walled structure, the genital pocket,

![Text-fig. 8](image1)

**TEXT-FIG. 8.**
Longitudinal section showing invagination of genital pocket of *Sitodrepa panicea* L. *ejd*, ejaculatory duct; *gp*, genital pocket; *ll*, lateral lobe; *ml*, median lobe.

![Text-fig. 9](image2)

**TEXT-FIG. 9.**
Longitudinal section showing evagination of genital pocket of *S. panicea* L. *ejd*, ejaculatory duct; *gp*, genital pocket; *ll*, lateral lobe; *ml*, median lobe.

pierced by the ejaculatory duct. The evagination proceeds until the genital lobes lie immediately within the mouth of the original invagination of the pocket as shown in Text-fig. 9. A transverse section through this region is illustrated in fig. 4, Pl. 7, which shows the outer wall of the genital pocket, the lateral lobes, and the median lobe pierced by the ejaculatory duct.

The spiculum gastrale arises in the following manner. During the early pupal stadium, before the process of evagination has taken place, a pair of lateral grooves is formed in the wall of the genital pocket. These grooves first make their appearance in the distal region of the pocket. Anteriorly they become very deeply sunken and a ventral blind pouch is wholly separated from the pocket (Text-fig. 10).

As the pupa matures the latero-ventral pouches formed by
the in-sinking of the grooves in the posterior region become completely constricted away from the wall of the pocket to form the two distally directed arms of the spiculum. These arms are connected anteriorly by the ventral pouch separated early in development. By the heavy deposition of chitin the spiculum eventually assumes the horseshoe formation familiar in the adult (Text-fig. 11).

(ii) The Efferent System. The Larva. In the larva, the only portions of the efferent system which are developed are the testes. These occupy a dorso-lateral position in the
second and third abdominal segments. Each is composed of six testicular follicles, the epithelial cells of which are rounded and closely packed, with dense contents and well-marked nuclei. Each follicle is invested by a sheath of connective tissue.

The Pupa. After pupation the testes are seen to extend from the second to fourth segments, growth having taken place in such a manner that the posterior region of each testis curves downwards to occupy a ventro-lateral position. The epithelial mass appears to have been subjected to a process analogous to segmentation, for, instead of forming a dense central core in each follicle, six or seven masses can be seen within the sheath of connective tissue (figs. 1 and 5, Pl. 7).

Towards its posterior distal region each follicle narrows considerably and passes into a short duct, the vas efferens, which is of smaller diameter than the follicle. Histologically these ducts consist of a solid core of epithelial cells invested by connective tissue, both layers of cells being continuous with the corresponding layers in the follicle (figs. 6 and 7, Pl. 7).

The six vasa efferentia of each side unite to form the vasa deferentia, which extend into the fifth abdominal segment, where they end blindly. As yet they have very small lumina (fig. 7, Pl. 7, Text-fig. 12).

As the pupa matures, the vasa deferentia elongate and extend as far as, but not beyond, the posterior border of the fifth sternite (Text-fig. 13). They now possess distinct lumina. Near the testes, the vasa efferentia are still solid, but distally, before opening into the vasa deferentia, the cells of the epithelial layer become arranged around a central cavity. The vasa deferentia are of a similar structure to the vasa efferentia, but are of a greater diameter.

The ejaculatory duct, as already noted, arises from an ectodermal invagination situated posterior to the ninth sternite (Text-fig. 5). This invagination extends into the fifth segment, at the anterior border of which it divides into two short lateral branches. At its origin, each of these branches gives rise to an anteriorly directed blunt outgrowth, the rudiment of the median accessory gland.

The lateral divisions of the ejaculatory duct early become
constricted longitudinally and give rise to two pairs of structures, the more posterior and ventral being the rudiments of the paired or lateral ejaculatory ducts, the more anterior and dorsal, the rudiments of the lateral accessory glands (fig. 2, Pl. 7). In Text-fig. 12, for the sake of clearness, the lateral accessory glands are shown as originating wholly anterior to the paired ejaculatory ducts; fig. 2, Pl. 7, shows more precisely the dorso-ventral arrangement.

As growth proceeds, the median ejaculatory duct elongates, with the result that the point of origin of the paired ejaculatory ducts and the accessory glands is carried forwards into the fourth segment. The median accessory glands extend as far as the anterior border of the third segment. The paired ejaculatory ducts have also elongated, and now extend almost to the posterior border of the fifth segment, where they receive the openings of the mesodermal vasa deferentia (Text-fig. 13).

Histologically, the ejaculatory duct is composed of a layer of epithelial cells bounded by a basement membrane and a thick coat of muscular fibres. In a young pupa, the chitinous lining which is secreted by the epithelial cells and is characteristic of the mature pupa and adult has not yet been laid down (fig. 9,
Pl. 7). The glands are of a similar structure to the ejaculatory duct, but the muscular layer is poorly developed, while the epithelial cells are larger. The inner pair of glands is of a greater diameter than the ejaculatory duct and has a conspicuous lining of chitin (fig. 8, Pl. 7). The outer pair of glands is of a much smaller calibre.

(2) Gastroidea polygoni L.

(a) Adult Structure.

The testes lie one on either side of the alimentary canal, in the dorsal region, extending from the first to the fifth abdominal segments. Each testis is bilobed, the one lobe being slightly more anterior and dorsal, the other more posterior and lateral. A slender vas efferens arises from each lobe of the testis, the two ducts uniting in the third abdominal segment to form the vas deferens.

In the fourth segment, the vasa deferentia open into the lateral ejaculatory ducts. At their junction are situated a vesicula seminalis and a slender tubular accessory gland. The paired ejaculatory ducts unite in the fifth segment to form a common duct which runs forward to the anterior border of the fourth segment, here turning upon itself to pass into a much wider and dilated portion which extends to the anterior border of the seventh segment. The duct then narrows suddenly and bends forward again, running as far as the fifth segment almost to the point of union of the vasa deferentia. Here the duct makes another and final loop, and enters the copulatory apparatus at its anterior extremity as the ejaculatory duct proper. The gonopore is situated at the apex of a single median appendage.

The tegmen is ring-shaped, and situated in the outer wall of the genital pocket; both first and second connecting membranes are therefore present (Text-fig. 14).

The spiculum is V-shaped and is closely attached to the genital pocket.

(b) Structure of the Immature Insect.

(i) The External Organs. The Larva. In the larva, nine abdominal tergites and sternites are visible. The anus is
borne by a sclerite situated between the ninth tergite and sternite and hence representing some portion of the tenth segment. No genital appendages are present, and the invagination of the genital pocket has not yet been commenced.

The Pre-pupa. During the pre-pupal instar various changes involving the development of the reproductive system occur. Posterior to the ninth segment, the genital pocket makes its appearance as a wide-mouthed invagination of the ectodermis. This invagination extends anteriorly to the middle of the sixth segment, where it becomes considerably constricted and so continued within the body as the short and wide ejaculatory duct (Text-fig. 15).

As development proceeds, the proximal region of the genital pocket is evaginated, carrying with it the ejaculatory duct, the opening of which lies at the apex of the evagination. Thus the genital pocket forms a double-walled tube which is traversed by the ejaculatory duct, with the gonopore situated at its posterior extremity (Text-fig. 16).

The genital appendages develop in the following manner. In the ectodermal layer at the apex of the genital pocket, four clefts make their appearance (fig. 11, Pl. 7). These clefts extend until the ejaculatory duct is completely separated from the wall of the genital pocket. At the same time, the cavity of
the ejaculatory duct is enlarged until it meets the dorsal and ventral clefts, aiding in the formation of a pair of plates bordering the gonopore (fig. 12, Pl. 7). The ectodermal layer of the inner margins of these plates is thus continuous with the epidermis lining the ejaculatory duct. The plates are simple appendages devoid of apical styli. At this stage of development, all the structures derived from the epidermis are thick-walled with greatly reduced lumina. The cavity of the genital pocket is reduced to a very small space surrounding the ejaculatory duct and genital appendages. No secretion of chitin has yet taken place within the genital pocket.

The Pupa. After pupation has taken place, nine tergites and sternites can still be identified. The sclerite representing the tenth segment bears, anterior to the anus, the longitudinal depression marking the opening of the genital pocket. No appendages are visible externally (Text-fig. 17).

Further evagination of the genital pocket takes place, the apex now lying in the middle of the seventh segment. At the same time the ejaculatory duct elongates considerably, growth taking place in the posterior region.

The genital plates now become fused at their bases, the distal borders remaining free.

The spiculum gastrale is formed in a manner similar to that
already described for *Sitodrepa panicea* L., and Text-figs. 10 and 11 will again serve as illustrations. Posteriorly, between the seventh and eighth segments, a pair of latero-ventral folds arises in the genital pocket formed by the ingrowth of the wall. Anteriorly these folds converge, finally meeting and cutting off a ventral pouch. This pouch represents the anterior concavity of the spiculum, the posterior folds, its forks.

The maturation of the pupa and its transformation into the adult now consist of the elongation of the ejaculatory duct and its acquisition of a muscular layer; and in the considerable shrinkage of the walls of all organs of ectodermal origin, consequent upon the deposition of a thick layer of chitin by their cells.

(ii) The Efferent System. The Pre-pupa. No signs of the efferent system can be detected until the pre-pupal instar has been reached. In the pre-pupa, the testes occupy a dorsal position in the abdomen, extending from the middle of the second to the fourth segment. A vas efferens leaves each testicular lobe, uniting with its fellow of the same side to form the vas deferens. The vasa deferentia are slender ducts extending from the posterior border to the third segment to the middle of the fifth segment (fig. 10, Pl. 7, Text-fig. 18).

At this stage of development the ejaculatory duct is a short wide tube diverging in the middle of the fifth segment into two lateral or paired ejaculatory ducts, which form a loop to the
posterior border of the segment before bending forwards to unite with the vasa deferentia (Text-fig. 18). Arising at the point of division of the ejaculatory duct, and internal to the paired ducts, are two short glands (fig. 18, Pl. 8; Text-fig. 18).

The Pupa. As growth proceeds, the testes enlarge considerably and extend, in the young pupa, to the anterior border of the first abdominal segment. In old pupae they extend posteriorly into the fifth segment. The ejaculatory ducts are also subjected to elongation, and four growth-centres are involved, one posterior, one primary anterior, and a pair of secondary anterior centres.

The posterior growth-centre is a ring of tissue situated in the ejaculatory duct immediately anterior to, and surrounding, the
gonopore. The cells of the ectodermal layer at this point multiply rapidly, so that the original wide, thick-walled ejaculatory duct is gradually pushed anteriorly, and eventually out of the copulatory apparatus. The portion of the ejaculatory duct intercalated between the original invagination and the gonopore is a long tube, slender and with a very fine calibre (figs. 16 and 21, Pl. 8). When growth in this region is complete, this slender duct emerges from the copulatory apparatus in the fifth segment and here makes a loop backward (fig. 15, Pl. 8) to the anterior border of the seventh segment. The duct now bends forwards again (fig. 16, Pl. 8) and passes into the original wide tube.
This condition is found towards the end of the pupal instar (Text-fig. 22).

At the same time growth is taking place in the anterior region. The primary anterior growth-centre is situated immediately posterior to the division of the ejaculatory duct. Growth in this region results in the intercalation of a second slender duct between the bases of the paired ejaculatory ducts and the proximal extremity of the original invagination. It proceeds in such a manner that the point of union between the paired ejaculatory ducts and the vasa deferentia remains in the fifth segment. The intercalated section is thrust forwards in a loop, reaching to the posterior border of the third segment, where it passes into the original tube (fig. 18, Pl. 7; Text-figs. 19–23).

In the mature pupa, then, the unpaired portion of the ejaculatory duct is divisible into three regions (Text-figs. 22 and 23).

1. The slender ejaculatory duct proper which traverses the copulatory apparatus and opens at the gonopore (fig. 16, Pl. 8), leaving the copulatory apparatus in the fifth segment and thence running posteriorly again into the sixth to pass into

2. the original wide invagination which has the form of a sac extending from the middle of the sixth to the posterior border of the third segment (fig. 13, Pl. 7; figs. 14 and 15, Pl. 8). Here it passes into

3. the anterior slender duct (fig. 13, Pl. 7) which now runs posteriorly to the fifth segment, where it divides to form the paired ejaculatory ducts.

The two secondary anterior growth-centres are to be found, one at the base of each lateral ejaculatory duct (Text-fig. 21).

Growth here results in the lateral extension of the ducts in the fifth segment, so that their points of union with the vasa deferentia are removed farther from the mid-ventral line (figs. 14 and 15, Pl. 8; Text-fig. 22). At the growth points, each ejaculatory duct becomes swollen considerably to form the vesicula seminalis at the base of the gland. The latter is seen in sections to be slightly sunken into the cavity of the swelling (fig. 14, Pl. 8; Text-figs. 22 and 23).
Histologically the vasa deferentia are seen to be of mesodermal origin. They are slender ducts composed of a single layer of small cells directly continuous with the epithelial layer of the testis. They are invested by a delicate sheath of connective tissue (fig. 17, Pl. 8). The ejaculatory duct, glands, and vesiculae seminales are ectodermal in origin. During the pre-pupal instar their walls are composed of a single layer of large cells, bounded externally by a basement membrane. No secretion lines the lumina. In the mature pupa the terminal portion of
the ejaculatory duct is extremely slender. The cells lining it are very small, the muscular layer is poorly developed, and the cavity of the duct is very small indeed (fig. 21, Pl. 8). The middle, wide portion of the duct is lined with large cells and has a prominent muscular coat (fig. 20, Pl. 8). Its lumen is conspicuous and is lined with chitin. The anterior regions of the ejaculatory duct, glands, and vesiculae seminales are of a similar structure. The glands, vesiculae seminales, and posterior region of the ejaculatory duct have no muscular investments (Glands, figs. 18 and 19, Pl. 8).

It is possible to distinguish the vas deferens from the lateral branches of the ejaculatory duct at any stage of development owing to the differences in size and histology. The disparity in calibre is most noticeable in the pre-pupal instar, while the presence or absence of the chitinous lining is a criterion in the more mature insect.

(3) *Anthonomus pomorum* L.

(a) Adult Structure.

The testes are bi-lobed, the one lobe lying posterior to the other. From the testes the vasa deferentia lead posteriorly to open into the paired ejaculatory ducts. Posterior to their junction with the vasa deferentia, the paired ejaculatory ducts are dilated to form vesiculae seminales, the openings of a pair of accessory glands being situated immediately anterior to the latter. The median ejaculatory duct is formed by the union of the paired ejaculatory ducts and is a fine tube piercing the copulatory apparatus.

Both connecting membranes are present, the tegmen is ring-shaped with an anteriorly directed strut, while the median lobe is slender and curved, forking anteriorly. The spiculum gastrale is a simple, straight rod (Text-fig. 24).

(b) Structure of the Immature Insect.

(i) External Organs. The Larva. Nine tergites and sternites are present, the anus being situated on a sclerite posterior to the ninth sternite. No genital appendages are visible externally. Transverse sections of a fully grown larva,
about to enter the quiescent pre-pupal instar, show that the genital pocket has already developed as a shallow ectodermal invagination immediately posterior to the ninth sternite. The cells lining the invagination are large and closely packed, and the ventral wall gives rise to a pair of thickenings which are

the rudimentary genital appendages. Between the appendages the genital pocket is prolonged into the body-cavity as a very short blind tube, the rudiment of the ejaculatory duct (Text-fig. 25).

The Pupa. After pupation has taken place the abdomen is still seen to consist of nine tergites and sternites, the ninth tergite bearing a pair of stout caudal spines. Immediately posterior to the ninth sternite is situated the mouth of the genital pocket (Text-fig. 26).

In transverse sections it can be seen that further invagination of the genital pocket has taken place and that this now extends as far as the posterior border of the sixth segment. A certain amount of evagination of its proximal region has already taken place, and the gonopore, bordered by the basally fused appendages, lies at the posterior border of the seventh segment (fig. 23, Pl. 8). As the pupa matures, growth of the genital pocket is continued until it reaches the middle of the fifth segment. At the same time further evagination takes place and eventually the gonopore lies at the apex of the genital pocket.

The spiculum gastrale originates during the pupal instar as a ventral fold of the genital pocket extending from the fifth to the seventh segments. The fold becomes entirely constricted
from the pocket and lies below it as an ectodermal tube (fig. 26, Pl. 8). The deposition of chitin gives it the familiar rod-like appearance. Text-fig. 27, A, B, and c, illustrate stages in its development.

Before the process of chitinization is complete, the abdominal segments posterior to the seventh become withdrawn into the body-cavity, so that in the adult beetle only seven abdominal segments can be recognized.

The deposition of chitin in the walls of the genital pocket now takes place, differentiating connecting membranes, tegmen, median lobe, and spiculum gastrale. With the secretion of chitin the cells of the ectodermal layer decrease noticeably in size.

(ii) The Efferent System. In the young pupa the testes are very little developed. The anterior lobe is situated in the fourth, the posterior lobe in the fifth segment. A fine duct leaves each lobe at its hinder border, that of the anterior extending to the posterior border of the fourth segment, that of the posterior being very short. The ducts are very fine indeed and

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**Text-fig. 25.** Longitudinal section through posterior border of ninth sternite of *Anthonomus pomorum* L. *ga*, genital appendage; *gp*, genital pocket; *rejd*, rudiment of ejaculatory duct.

**Text-fig. 26.** Terminal abdominal segments of pupa of *A. pomorum* L. Ventral view. × 60. *an*, anus; *csp*, caudal spine; *mgp*, mouth of genital pocket; *IX T*, ninth tergite; *IX S*, ninth sternite; *VIII T*, eighth tergite; *VIII S*, eighth sternite.
at this stage of development have no communication with each other (Text-fig. 28).

The ejaculatory duct is now a thick-walled, wide tube extending to the posterior border of the sixth segment. Here it divides into two lateral branches. Each of the latter shortly

![Text-fig. 27, A, B, C.](image)

Stereogram of development of spiculum gastrale in *Anthonomus pomorum* L. *ejd*, ejaculatory duct; *spg*, spiculum gastrale; *wgp*, wall of genital pocket.

re-divides in the dorso-ventral plane, the dorsal division being the rudiment of the pair of accessory glands, the ventral of the lateral or paired ejaculatory ducts (fig. 22, Pl. 8; Text-fig. 28). The glands and ducts are thick-walled blind structures with wide cavities.

As the pupa matures and the genital pocket lengthens, the point of divergence of the ejaculatory ducts becomes carried forwards into the fifth segment. The ducts themselves lengthen and extend into the fourth segment. The rudiment of the gland becomes longitudinally divided into two and immediately
TEXT-FIG. 28.
Schematic representation of efferent system in young pupa of *Anthonomus pomorum* L. *ag*, accessory gland; *A* 4–A 7, fourth to seventh abdominal segments; *gp*, genital pocket; *lejd*, lateral ejaculatory duct; *mejd*, median ejaculatory duct; *te*, testis; *vd*, vas deferens.

TEXT-FIG. 29.
Schematic representation of efferent system in maturing pupa of *Anthonomus pomorum* L. *ag*, accessory gland; *A* 3–A 6, third to sixth abdominal segments; *gp*, genital pocket; *lejd*, lateral ejaculatory duct; *mejd*, median ejaculatory duct; *te*, testis; *vd*, vas deferens; *vs*, vesicula seminalis.

TEXT-FIG. 30.
Schematic representation of efferent system in an old pupa of *A. pomorum* L. *ag*, accessory gland; *A* 3–A 6, third to sixth abdominal segments; *gp*, genital pocket; *lejd*, lateral ejaculatory duct; *mejd*, median ejaculatory duct; *te*, testis; *vd*, vas deferens; *vs*, vesicula seminalis.

Posterior to the openings of the glands the lateral ejaculatory ducts are dilated to form the vesiculae seminales (figs. 24 and 25, Pl. 8).

The testes undergo a forward migration and now lie in the third abdominal segment. The ducts from the two lobes unite at the anterior border of the fourth segment, and the vas
deferens so formed is a slender tube provided with a distinct lumen. It is of very much smaller diameter than the derivatives of the ejaculatory duct and is easily distinguishable therefrom. Posteriorly the vas deferens becomes rather swollen and its lumen is obliterated (fig. 24, Pl. 8). The swollen ampulla thus formed is applied to the blind end of the ejaculatory duct (Text-fig. 29).

Eventually the intervening walls break down. The hitherto solid ampulla acquires a lumen and communication between the cavities of the vas deferens and ejaculatory duct is established (Text-fig. 30).

The ejaculatory duct and its derivatives, viz. vesiculae seminales and glands, have the thick-walled, chitin-lined structure characteristic of organs of ectodermal origin (figs. 29 and 30, Pl. 8), while the vasa deferentia are lined by much smaller cells and have no secreted intima (figs. 27 and 28, Pl. 8).

F. Conclusions.

From the foregoing studies the following conclusions may be reached.

(1) The External Organs.

(a) The Intromittent Organ.

The mode of development of the intromittent organ in the Coleoptera is similar to that in other orders of the Insects, viz. it develops from a pair of appendages of the ninth segment. In Sitodrepa panicea L. these appendages actually develop as diverticula of the posterior border of the ninth sternite and are externally visible throughout the pupal instar. In Tenebrio molitor L., Gastroidea polygoni L., and Anthonomus pomorum L. the appendages develop within the genital pocket from the ectodermal layer bordering the gonopore. Since the latter is situated immediately posterior to the ninth sternite, the appendages arise in this case also from the posterior border of that segment.

The intromittent organ in the adult may be either of the tri-lobe types, when a median lobe and a pair of lateral lobes are present as in Sitodrepa panicea and Tenebrio
molitor, or there may be a median lobe only as in Gastroidea polygoni and Anthonomus pomorum.

In the former case, the median lobe arises by the fusion of a second pair of appendages which is cut off from the primary appendages; in the latter, the primary pair of appendages fuses to form the median lobe without any preliminary division.

From their median position, one on each side of the gonopore, their unsegmented nature and late appearance in development, it appears that the genital appendages in the Coleoptera are homologous with the parameres in other Insecta and hence correspond with the endopodites of the Crustacean limb.

The genital papillae which, according to Singh Pruthi, are present in the larvae of Tenebrio molitor and represent the coxites, were not observed in the types studied in the present paper or in the larvae of Ceuthorrhynchus pleurostigma and Rhagium bifasciatum which were examined.

In other orders of the Insecta where coxites are present, e.g. in the Homoptera, these appear at an early stage in development and are either separate from the parameres from the commencement as in the Homoptera, or become divided off from them at an early stage of development as in the Trichoptera and Hymenoptera. The parameres are differentiated at a much later stage of development.

George's insistence that the parameres in the Homoptera are nothing more than outgrowths of the aedeagus (20), emphasizes a very real need for the adoption of a system of nomenclature that shall be universally applicable. In the example cited, the distinction is of little significance as both parameres and aedeagus are known to have been derived from a pair of primary appendages corresponding with the endopodites or telopodites of the ninth segment. Hitherto, too much stress has been laid on the secondary division of the endopodites. The term 'paramere' in its original application refers to the endopodites of the ninth segment, and if a satisfactory name for the parameres and their derivatives can be adopted, an important step will have been made towards the simplification of the subject. It is therefore suggested that the term paramere be completely
rejected and that the following terms be applied to the derivatives of the endopodites of the ninth segment. (1) The aedeagus when only a median appendage or a single pair of appendages is present. (2) The median and lateral lobes of the aedeagus when a median and a pair of lateral appendages are present.

The terms selected are not new, but their adoption would serve to introduce order into the chaos which at present exists.

With regard to the question as to whether the tri-lobe form is more primitive than the single lobe form, Sharp and Muir consider the former the more primitive, the latter being derived therefrom.

There seems to be a close connexion between the loss of the first connecting membrane and the presence of the tri-lobe intromittent organ, while in the single lobed type both connecting membranes are present. Which of these represents the primitive condition, however, is still an unsettled question and cannot be satisfactorily decided as yet.

(b) The Spiculum gastrale.

In Sitodrepa panicea and Gastroidea polygoni the spiculum gastrale was seen to arise as a pair of lateral folds in the wall of the genital pocket which later became completely constricted therefrom; in Anthonomus pomorum it was derived from a ventral pouch cut off from the genital pocket. In Tenebrio molitor the spiculum was stated to have arisen as a pair of ectodermal invaginations of the body-wall, just posterior to the ninth segment. While the mode of origin in the three cases differs slightly, viz. in the first two being derived from an invagination of the body-wall, in the third directly from the body-wall, they may still be termed homologous structures.

A similar difference in mode of origin occurs in the genital appendages, which in Sitodrepa panicea arise from the body-wall and in Tenebrio molitor, Gastroidea polygoni, and Anthonomus pomorum are derived from the wall of the genital pocket.
(c) The Body Segments.

Since the spiculum gastrale and the genital pocket are already in existence at a time when the full complement of tergites and sternites is visible, it is impossible that a tergite or a sternite should form the whole, or a part of, the structures in question.

(2) The Efferent System.

(a) The vasa deferentia are derived from the original efferent passages and are hence mesodermal in origin, not extending beyond the posterior border of the seventh segment as is usual in the Insecta.

There are, however, conflicting accounts of the development of these ducts. Wheeler, for example, describes the embryonic rudiments of the vasa deferentia in *Xiphidium*, as extending into the ninth segment, as do Christophers in the Diptera and George in the Homoptera. The majority of other authors, e.g. Packard (41), Korschelt and Heider (29), Singh Pruthi, state definitely that the original efferent passage terminates in the seventh segment. Moreover, these rudiments, according to Wheeler, Christophers, Verson and Bisson, and George, are wholly mesodermal in origin, while Muir, Singh Pruthi, Packard, and Zander are of the opinion that at least the terminal portions of the vasa deferentia are derived otherwise than from the original mesodermal rudiments. The following extract from Packard, ex Korschelt and Heider, illustrates the latter view: 'In the male . . . it (i.e. the original efferent passage) is not along its whole length transformed into the vas deferens, but its terminal distal portion degenerates and is replaced by a newly formed terminal portion of the vas deferens, which unites with the ectodermal ductus ejaculatoris.'

From his study of the efferent ducts in *Tenebrio molitor* Singh Pruthi fails to find any trace of the vasa deferentia as mesodermal structures, and hence concludes that the degeneration of the original efferent duct has taken place to such an extent that the vasa deferentia are confined wholly to the region of the testes. He concludes, further, that the ducts which function as vasa deferentia in *Tenebrio molitor* are secondary structures of ectodermal origin, extending beyond
the posterior limit of the mesodermal vasa deferentia, viz. the posterior border of the seventh segment. In support of this statement, he refers to his own work on the Homoptera, in which the vasa deferentia or paired ejaculatory ducts, as he subsequently names them, are derived from ectodermal structures, terminating near, though not actually opening on, the eighth abdominal segment. He also quotes from Muir to the effect that: 'The zygos (vasa deferentia) are supposed to be of mesodermal origin, but they seem to develop continuously from the stenazygos (ejaculatory duct).'

In all the three species examined the vasa deferentia are present as slender ducts of mesodermal origin. In Sitodrepa panicea they extend to the posterior border of the fifth segment, in Gastroidea polygoni to the posterior border of the fourth, and in Anthonomus pomorum only to the middle of the fourth segment. A varying degree of degeneration of the terminal region of the original efferent passages has therefore taken place. This degeneration has been compensated for by the development of secondary structures, the lateral or paired ejaculatory ducts, which arise early in the prepupal instar as outgrowths of the median ejaculatory duct. They are hence ectodermal in origin and as a rule do not extend farther than the fifth abdominal segment. A statement to the effect that the paired ducts of the efferent system are wholly mesodermal, or wholly ectodermal in origin, must, therefore, be modified. The ducts appear to be partly mesodermal and derived from the original efferent passages, partly ectodermal in origin, the extent of each region varying with the species.

(b) With the exception of the vasa deferentia, the efferent system is ectodermal in origin. So far as the ejaculatory duct is concerned, this statement is now generally accepted as correct. With reference to the accessory glands, however, there is some difference of opinion.

According to Escherich, whose work refers mainly to the Coleoptera, the accessory glands in the male may be divided into two categories—those which arise as diverticula of the vas deferens and are hence mesodermal in origin (mesadenia), and those which arise as diverticula of the ejaculatory duct and
are hence ectodermal in origin (ectadenia). Blatter confirms this view, while Bordas states that the glands, whether one or more pairs are in existence, are of mesodermal origin. Christophers, Verson and Bisson, and George are also of the opinion that the glands are of mesodermal origin. Singh Pruthi notes that the views of Escherich and Blatter need modification, himself describing both pairs of glands as arising from diverticula of the (functional) vas deferens, and hence probably of ectodermal origin.

It would appear that the glands in Sitodrepa panicea, Gastroidea polygoni, and Anthonomus pomorum all arise as diverticula of the lateral ejaculatory ducts. Histologically the glands closely resemble the ejaculatory duct. Furthermore, they are frequently so much larger in calibre that it is unlikely that they should have originated as outgrowths of the slender vasa deferentia.

In Anthonomus pomorum and Gastroidea polygoni the vesiculae seminales are obviously dilations of the paired ejaculatory ducts, and, like them, of ectodermal origin.

(c) That the efferent system, other than the vasa deferentia, is unpaired in origin.

Nussbaum, Michaelis, and Verson and Bisson seem to be the last advocates of the theory of the paired origin of the ejaculatory duct, Wheeler regarding the terminal ectodermal region as unpaired in origin.

In Sitodrepa panicea, Gastroidea polygoni, and Anthonomus pomorum, there is no doubt that the ejaculatory duct is unpaired from the very beginning, hence its derivatives also, viz. the paired glands and vesiculae seminales, must also be regarded as fundamentally unpaired in origin.

PART II. THE FEMALE.

A. General Structure and Nomenclature.

In general plan and arrangement, the reproductive organs of the adult Coleopteran female resemble those of the male. A pair of ovaries occupies a dorso-lateral position, extending through one or more of the abdominal segments between the
first and the seventh. Each ovary is subdivided into two or more ovarioles, a slender duct leading from each into the oviduct. The oviducts are paired and of varying length and calibre. They unite with the lateral branches of the uterus. These unite together to form a median duct which may be termed the uterus or the vagina. Opening into the mid-dorsal region of the uterus, a little posterior to the junction of the paired branches, is a blind sac. This sac receives the duct of the accessory gland and the opening of the tubular spermatheca.

The uterus opens posteriorly to the ninth segment. The gonopore is usually borne at the apex of a median tubular appendage and is bordered by a pair of palpi.

Posterior to the eighth segment the body-wall remains membranous, as in the male, and the segments are withdrawn into the body-cavity.

Ventral to the uterus is a Y-shaped rod which serves as the basis of attachment for the muscles which control the uterus and the associated structures. As in the male, therefore, the reproductive system may be considered under two headings:

1. The External Organs or Ovipositor.
2. The Efferent System, comprising ovaries and oviducts, uterus, spermatheca, and accessory glands.

B. History of the Subject and Homologies.

1. The Ovipositor.

The ovipositor in the Insecta generally is derived from three pairs of lobes which arise in the larval instar, one pair on the eighth and two pairs on the ninth sternite. This mode of development has been described by Zander in the Hymenoptera (58), Haviland in Lygoceros sp. (21), and Kraepelin in the Honey-bee (28). Seurat (46) describes the development of the first pair of lobes in Doryctes gallicus from the seventh segment, and of the other two pairs from the eighth. If, as seems likely, he has included the first abdominal segment with the thorax, these segments being normally fused together in the Hymenoptera-Apocrita, then the seventh and eighth segments here will correspond to the eighth and ninth segments in
other Insecta. Wheeler, in *Xiphidium* (57), states that the ovipositor lobes are developed from outgrowths of the eighth, ninth, and tenth segments, those of the tenth having migrated anteriorly to lie between those of the ninth during development. This view has received little support from the investigations of other workers.

As in the male, so in the female, Verhoeff (52) compares the three pairs of ovipositor lobes with the primitive genital appendages in *Machilis*. He gives the following table of comparison for the females of Pterygote insects:

- Eighth abdominal segment. Two Gonocoxites or a Coxosternum. Two Telopodites (Anterior Ovipositors) or absent.
- Ninth abdominal segment. Two Gonocoxites, or absent, but never a coxosternum. Two Telopodites (Posterior Ovipositors) or absent.

That is to say, that the anterior or ventral ovipositor lobes represent the telopodites or endopodites of the eighth segment; the dorsal ovipositor lobes, the telopodites or endopodites of the ninth segment; the posterior or lateral ovipositor lobes, the coxites of the ninth segment.

The most recent work on the subject of the homologies of these appendages, viz. that of Crampton (7–15), Walker (55), and Singh Pruthi (43 and 45), is entirely in agreement with this basic plan laid down by Verhoeff. Nel (39) considers that the anterior ovipositor lobes are homologous with the coxites and not the telopodites of the eighth segment.

Zander does not agree that the ovipositor lobes are the homologues of segmental appendages. The following quotations make clear his attitude to the subject: 'The earliest rudiments of the thoracic legs are found in *Apis* in the embryo, while the rudiments of the sexual appendages do not appear until the larva is four days old.'

Also: 'All these facts show clearly that the rudiments of the embryonic abdominal appendages and the gonapophyses in the *Hymenoptera* belong to two different periods of development; the former are of a true embryonic nature and are only present in the embryo; the latter first appear in the larval instar. And so long as the change of the one into the other has not been
observed, no author can prove that the gonapophyses and the embryonic abdominal appendages are the same structures.'

Nevertheless, it is generally accepted by the most recent investigators, that the ventral ovipositor lobes represent the endopodites of the eighth segment, the dorsal lobes the endopodites, the lateral lobes the coxites of the ninth. Furthermore, Zander's reasoning is faulty: the larva of Apis is apodous, yet it is not doubted that the embryonic thoracic appendages are the forerunners of those legs which are present in the pupa and adult, although wanting in the larva.

In the Coleoptera the gonopore is bordered by a pair of plates bearing palps at their apices. These plates have been variously described as the divided seventh, eighth, or ninth sternite. Verhoeff (50) originally believed that ten tergites and sternites were present in the female Coleoptera, and that the ovipositor was formed from the posterior segments of the body which are retractile. The plates bordering the gonopore represented the divided tenth sternite, and the palpi at their apices the modified cerci. Moreover, he asserted that the form of the ovipositor was modified by function, and that three main types of modification occurred, namely:

(a) When the eggs were deposited in the ground, the ovipositor was provided with 'Grabinstrumenten'.

(b) When in splits and cracks in wood, with a 'Legerohre'.

(c) When in the tissues of young plants with a 'Legesabel'.

If the eggs were merely deposited broadcast, then no ovipositor was developed.

Although Verhoeff modified this view considerably, and in later years considered the ovipositor to be of a true appendicular nature (52), there seems to linger a general belief, based on this former paper of his, that the distal abdominal segments in the Coleoptera have become telescoped one into another, to form a retractile tube which functions as an ovipositor (25).

The most recent work on the subject is by Singh Pruthi, who has studied the development of the genital plates in the larva and pupa, and considers them to be homologous with the lateral ovipositor lobes in other Insecta. Hence they represent the coxites of the ninth segment.
(2) The Efferent System.

While the gonopore in the male is constantly located posterior to the ninth sternite, there is considerable variation in position of the female aperture in the different orders.

In the Ephemeroptera (33) there is a pair of apertures, the oviducts opening separately posterior to the seventh sternite; in the Orthoptera, the gonopore is posterior to the seventh sternite according to Wheeler, to the eighth according to Walker and Crampton, to the seventh in such forms as Blatella and Forficula, and on the eighth in Locustana and Colemania, according to Nel (39); in the Hemiptera-Homoptera (Singh Pruthi and George, 20) and Heteroptera (Christophers and Cragg, 16) posterior to the eighth sternite; in the Diptera (Awati, 1; Christophers, 18) posterior to the eighth segment; in the Macrolepidoptera (Jackson, 26) there are two apertures, one posterior to the eighth sternite, the other posterior to the ninth; in Bombyx mori (Verson and Bisson, 54) one aperture posterior to the ninth; in the Hymenoptera (Kraepelin, 28; Haviland, 21; Kulagin, 30; and Zander, 58) and Coleoptera (Singh Pruthi) the gonopore is located posterior to the ninth sternite.

This variability raises the important question as to whether the gonopore in the different orders is strictly homologous. Singh Pruthi suggests that this is not so, but that three conditions are represented:

(a) Where there is a pair of apertures posterior to the seventh sternite, these represent the openings of the oviducts;

(b) Where there is a single aperture or gonopore posterior to the eighth sternite, this corresponds to the opening of the uterus;

(c) Where there is a single aperture or gonopore posterior to the ninth sternite, this is the opening of the spermatheca.

George and Nel also suggest that the evolutionary tendency lies in the posterior shifting of the gonopore.

An interesting problem arises here which will be more fully discussed in Part III, namely, whether the uterus in the female is homologous with the ejaculatory duct in the male, and to
which, if any, of the three apertures in the female does the male gonopore correspond?

Much confusion is also associated with reference to the mode of development of the uterus and its appendages. Herold (22) and Balbiani (2) state that the uterus is formed by the fusion of the posterior regions of the paired oviducts and is hence mesodermal in origin; Verson and Bisson, that the uterus and vagina are derived from paired ectodermal vesicles in the eighth and ninth segments which subsequently fuse to form a median duct; Nussbaum (40), that the efferent ducts arise as paired rudiments of ectodermal origin, the azygos condition being secondary and consequent upon the fusion of the zygos rudiments; Jackson, Seurat, Kulagin, Heymons (23), Christophers, Singh Pruthi, George and Nel, that the uterus is unpaired and ectodermal in origin.

Opinions being so much at variance, the development of the genital system in Sitodrepa panicea L., Gastroidea polygoni L., Anthonomus pomorum L., and Rha-gium bifasciatum F. is of interest.

C. Development.

(1) Sitodrepa panicea L.

(a) Adult Structure (Text-figs. 31 and 32).

The ovaries form large compact masses extending from the second to the fourth abdominal segments. The oviducts are short and run transversely towards the middle line where they unite to form the uterus. A short distance posterior to the junction of the two oviducts a dorsal pouch opens into the uterus. This dorsal pouch receives the common duct of a tubular spermatheca and the bi-lobed accessory gland. In the seventh segment, together with the rectum, the uterus enters a double-walled chitinous cylinder formed by the telescoping of the posterior abdominal segments into the body. The eversion of this cylinder causes the ovipositor to be extruded some distance during oviposition. The gonopore opens posterior to the ninth sternite at the tip of the tubular ovipositor. Its opening is
bordered by a single palp, that of the right side being absent. Ventral to the cylinder formed by the invagination of the body-wall, and extending through the sixth and seventh segments is a Y-shaped chitinous rod, the fork of the Y being directed posteriorly. Powerful muscles serving to extend the posterior segments of the body during oviposition are attached to the rod.
(b) The Immature Insect.

(1) The Ovipositor. The Larva. In the larva nine distinct tergites and sternites are present. The anus is situated on a sclerite posterior to the ninth sternite, with a linear depression marking the position of the future genital aperture, immediately anterior to it. No genital appendages are present.

The Pupa. When pupation takes place, the body undergoes a certain amount of shortening, especially in the terminal abdominal segments. Nine tergites and sternites can still be recognized, and with the straightening of the abdomen the anus moves caudad. The genital depression is now seen to lie between the bases of a pair of appendages of the ninth sternite which takes the form of a pair of two-jointed plates. The plate on the left side is provided with an apical palp; on the right side the latter is absent (Text-fig. 33). This asymmetry is a constant condition in the female.

Transverse sections through the posterior border of the ninth segment show that the appendages are outgrowths of the ectodermal layer bordering the genital depression. The latter takes the form of an invagination of the body-wall, at first shallow, but deepening as the pupa matures, its external opening forming the gonopore (fig. 34, Pl. 9). The genital appendages subsequently become fused together so that the
gonopore, at first situated between their bases, now moves posteriorly and comes to lie at the apex of the median appendage formed by their fusion (fig. 35, Pl. 9).

(c) The Efferent System.

The Larva. In the larva the only parts of the efferent system which can be recognized are the ovaries. These occupy a dorso-lateral position, one on each side of the alimentary tract in the fourth and fifth abdominal segments. Each ovary is composed of six ovarioles which consist of a central mass of epithelial cells bounded by a basement membrane and an external coat of connective tissue. The epithelial cells are closely packed with well-marked nuclei.

During the pre-pupal instar the ovaries elongate to some extent and now reach from the middle of the third to the middle of the fifth segments (Text-fig. 34). At this stage it is impossible to detect any trace of the oviduct.

The genital depression, as previously noted, is an invagination of the ectoderm, situated posterior to the ninth sternite. At first shallow, this invagination later sinks more deeply into the body-cavity and extends anteriorly to the middle of the eighth segment as a blind tube. This is the rudiment of the spermatheca, and its external opening, the future gonopore, is bordered

**Text-fig. 33.**

Terminal abdominal segments of pupa of *Sitodrepa panicea* L. Ventral view. × 90. *an*, anus; *g*, gonopore; *ga*, genital appendage; *gl*, genital palp; *VIII S*, eighth sternite; *IX S*, ninth sternite.
by the genital appendages (figs. 32, 33, and 34, Pl. 9; Text-fig. 34).

The uterus originates as an unpaired invagination of the ectodermal layer between the eighth and ninth sternites and extends below the spermathecal rudiment to the anterior border of the seventh sternite, where it ends blindly (Text-fig. 34).

In the pre-pupa, therefore, the terminal unpaired region of the efferent system is represented by two separate and distinct invaginations of the ectoderm, originating independently and having separate external openings.

The Pupa. In a young pupa the ducts from the ovarioles are seen to develop from the epithelial layer continuous with the distal posterior region of each ovariole. As development proceeds, the short ducts on either side unite to form the paired oviducts (figs. 36 and 37, Pl. 9). By the time the pupa is mature, communication between the blind ends of the paired oviducts and the paired uteri (vide infra) has been established.

Several changes may also be noted in the terminal region of the genital ducts. The spermathecal rudiment has widened and now extends to the anterior border of the seventh sternite, where it bends over, its free distal extremity being directed posteriorly and being divided longitudinally into two, the rudiments of the dorsal sac in the adult and of the functional
spermatheca and the accessory gland. The uterus has lost its external opening, the latter being completely closed over, its cavity has widened, and it now extends to the anterior border of the sixth sternite, where it bifurcates, the paired uteri thus formed ending blindly (fig. 31, Pl. 9). During the early stages of pupation, the rudiments of spermatheca and uterus approach one another near the anterior border of the eighth sternite, the ventral wall of the spermatheca being closely applied to the dorsal wall of the uterus. A little later, the intervening walls break down, and communication between the cavities of the two ducts is freely established throughout their whole length, except for a very short region posterior to where the dorsal sac, accessory gland, and spermatheca end freely in the seventh segment (fig. 39, Pl. 9; Text-fig. 35).

The single sexual duct thus formed has, therefore, three regions:

1. An anterior region derived wholly from the rudiment of the uterus.
2. A posterior region derived wholly from the rudiment of the spermatheca.
3. A median region whose dorsal wall is derived from the...
The dorsal wall of the spermathecal rudiment, whose ventral wall is derived from the ventral wall of the uterine rudiment.

The gonopore is not therefore the primary aperture of the uterus, this having been closed over during development, but the opening of the spermatheca.

As the pupa matures, growth in the posterior unpaired region of the uterus results in the spermatheca and gland being carried anteriorly. The point of divergence of the paired uteri is also carried forward so as to cause the formation of a loop in these latter which extend into the fifth segment.

Communication between the blind ends of the paired uteri and the end of the mesodermal oviducts is not established until a later stage in the adult. The so-called oviducts of the adult are thus partly derived (in their anterior region) from the ducts developed from the posterior region of the ovaries, partly (in their posterior region) from the anterior branches of the uterus.

The chitinous rod arises late in the pupal instar as an invagination of the intersegmental membrane between the seventh and eighth sternites. It extends below the uterus as far as the sixth sternite. The ectodermal cells which line the invagination secrete a chitinous deposit which eventually forms the rod in the adult (fig. 42, Pl. 9; Text-fig. 36). The cavity of the invagination is at first open, but by progressive chitinization the mouth becomes closed over.

Histology. In the young pupa the spermathecal rudiment is of small diameter and is lined by a layer of large epithelial cells bounded by a basement membrane. No chitinous intima has yet been secreted (figs. 32 and 33, Pl. 9). The uterus is of a similar structure, but is smaller in diameter (figs. 31 and 32, Pl. 9).

In the mature pupa the three regions of the uterus are clearly defined. The anterior region and the paired uteri are of a large diameter, the epithelial cells are large and have well-marked nuclei. A well-developed muscular layer and a heavy deposit of chitin which almost obliterates the lumen of the duct are also present (fig. 38, Pl. 9). The median region has a characteristically pear-shaped outline and the dorsal and ventral regions are clearly defined. It closely resembles the anterior
region, but the cells of the epithelial layer are smaller, the chitinous deposit is less heavy, and the muscular layer is very well developed (fig. 39, Pl. 9). The dorsal sac is lined by a layer of small flattened epithelial cells. No muscular layer is developed and the cavity is filled with the chitinous secretion. The spermatheca proper is of a similar structure (fig. 41, Pl. 9). The accessory gland is lined by a layer of large irregular cells, the very dense contents of which obscure their outline. No muscular layer is present and the lumen is small (fig. 40, Pl. 9). The common duct of the spermatheca and accessory gland is provided with a muscular coat.

The posterior region of the uterus is much reduced in diameter. Its muscular layer is poorly developed (fig. 43, Pl. 9).

Maturation. Concurrent with the processes of development described above, the body segments are subjected to a process of chitinization. This however does not take place uniformly all over the body; the abdominal segments posterior to the eighth remain for a while membranous and flexible. While in this state the posterior region is subjected to a gradual telescoping process with the result indicated in Text-fig. 37.

The anus and gonopore thus come to lie very close together,
while the point of origin of the chitinous rod is again brought closer to the gonopore (Text-fig. 37). Owing to the fact that the gonopore is situated anterior to the anus, the body-wall appears to be more deeply sunken ventrally and reaches anteriorly further than dorsally. Transverse sections through a newly emerged adult in which the telescoping process is complete show this very clearly. The telescoped body-wall first makes its appearance at the posterior border of the seventh segment as a pair of blind tubes a little to each side of, and ventral to, the uterus. Each tube extends towards the middle line, where the two meet, their intervening walls breaking down to form a single crescent-shaped tube with a common, very narrow cavity (Text-fig. 38). More posteriorly, the horns of the crescent arch upwards, and finally unite dorsally in the eighth segment, above the rectum which now lies close to the uterus (fig. 43. Pl. 9; Text-fig. 39). Between the seventh and eighth
segments, the rectum and uterus are comparatively free, being only partially enclosed by the crescent; from the eighth segment to the tip of the abdomen, they are wholly enclosed within the double-walled tube formed by its closure. Posteriorly, a secondary in-sinking of the body-wall between the anus and the gonopore separates the rectum from the uterus and in transverse sections each appears to be enclosed within an epithelial tube of its own (Text-figs. 40 and 41). Distally the gonopore opens between the genital appendages posterior to the ninth sternite, with the anus posterior to the gonopore.

Histologically the tube is obviously of ectodermal origin and presents the following structure passing from within outwards (fig. 48, Pl. 9).

1. An epithelial layer of large irregular cells with cell-marked nuclei.
2. A cavity.
3. An epithelial layer, the cells of which are regular and not so large as in (1).
4. A poorly developed layer of circular muscles.

Secretion of chitin by the two epithelial layers takes place and a thin layer bounds the cavity (2) externally and internally.

By various stages of increased chitinization the adult form is now reached. The inner wall of the telescoped posterior region becomes hard and rigid with a heavy deposit of chitin, the outer wall remaining membranous to a large extent.

(2) Gastroidea polygoni L.

(a) Adult Structure.

In the mature female the abdomen is so very greatly distended by the large number of eggs that the sternites and tergites appear as isolated sclerites with much enlarged intersegmental membranes. The gonopore is a large, transverse slit posterior to the ninth sternite, and its aperture is bordered by a pair of widely separated appendages (Text-fig. 42).

The ovaries extend from the first to the third abdominal segments. The oviducts are short and very wide. They unite in the fifth segment to form the uterus which receives dorsally the common duct of the spermatheca and the accessory gland.
As a result of the distension of the abdomen, the telescoping of the posterior segments does not take place to any great extent; neither is the chitinized rod formed ventral to the uterus.
Owing to the large number of eggs present in the abdomen, the wide and thin-walled nature of the uterus, and the absence of highly chitinized parts, it is an extremely difficult matter to make a satisfactory dissection of the adult. The above description has, therefore, been compiled with the aid of serial sections taken through a mature pupa in which the eyes and mouth parts had acquired the colour and form of the adult.

(b) The Immature Insect.

(1) The Ovipositor. The Larva. In the female larva, as in the male, nine tergites and sternites and the reduced tenth segment can be recognized. Externally, there is no sign of genital appendages and the female larva is hence indistinguishable from the male.

The Pupa. After pupation has taken place, the female is easily recognized by its larger size, attaining to a length of 5 mm., while the male only measures 4-4½ mm.

The sexes may also be distinguished by the presence of genital appendages in the female.

Nine tergites and sternites can still be recognized and posterior to the ninth sternite is the wide-mouthed invagination of the genital duct. This is bordered by a pair of jointed appendages bearing palpi at their apices (Text-fig. 43). The
plates arise as diverticula of the ectodermal layer at the posterior border of the ninth sternite, and in the young pupa are massive and thick-walled (fig. 47, Pl. 9). In older pupae they become much reduced in size and remain distinct from each other with the palpi widely separated (fig. 49, Pl. 10).

(c) The Efferent System.

In the young pupa the ovaries occupy a dorso-lateral position extending from the third to the fifth abdominal segments. Each ovary is composed of numerous ovarioles. The oviducts are as yet undeveloped, but the terminal region of each ovariole assumes a duct-like structure, the cells of the epithelial layer being arranged around a central cavity.

The unpaired region of the genital duct arises quite early in the pupal instar as two separate invaginations of the ectoderm. The first invagination is formed immediately posterior to the eighth sternite and is the rudiment of the uterus. It extends as far as the anterior border of the seventh segment, where it divides to form two wide lateral ducts, the paired uteri. The uterine pore is very wide (figs. 44, 45, and 46, Pl. 9).

Posterior to the ninth sternite and at a slightly later stage of development a second invagination is formed. This extends only to the posterior border of the eighth segment and is the rudiment of the spermatheca. It is entirely separate from the uterine rudiment throughout its whole length (figs. 45, 46, and 47, Pl. 9).

As the pupa matures the ovaries undergo a forward migration, and eventually occupy a position extending from the middle of the first to the middle of the third abdominal segments. The ducts from the ovarioles unite to form a pair of oviducts, one on each side of the body. These extend at first from the middle of the second to the middle of the fourth segment. Here they diminish greatly in size, losing their lumina and having the appearance of solid cords of cells (fig. 51, Pl. 10).

Meanwhile, the rudiment of the uterus has elongated considerably and now extends to the middle of the sixth segment. Here it bifurcates and the paired uteri so formed meet the oviducts in the fourth segment. Although the blind ends of the
uteri and oviducts are apposed to one another (fig. 52, Pl. 10), communication between their cavities is deferred for a considerable period and does not take place until the end of the pupal instar.

The rudiment of the spermatheca now extends to the middle of the seventh segment, it becomes divided into two by a longitudinal furrow, the dorsal half going to form the accessory gland and the ventral half the tubular spermatheca. The rudiment of the gland soon becomes differentiated into a bag-like gland and a long and narrow duct.

In the eighth segment the spermathecal and uterine rudiments lie close together, and towards the posterior border of the segment their intervening walls break down and their cavities merge into one (fig. 48, Pl. 9). The uterus now loses all trace of its former opening posterior to the eighth sternite, the uterine pore being completely closed over during growth. The opening of the spermatheca posterior to the ninth sternite becomes the functional gonopore of the adult (fig. 49, Pl. 10).

Thus, as in *Sitodrepa panicea*, the unpaired portion of the sexual duct in the female has three primary divisions:

1. The anterior region derived wholly from the rudiment of the uterus;
2. The posterior region derived wholly from the rudiment of the spermatheca;
3. The median region, of which the dorsal wall is derived from the spermathecal rudiment, the ventral wall from the uterine rudiment.

At maturity the uterus and spermatheca have grown forwards to such an extent that the posterior unpaired region now extends as far as the anterior border of the seventh segment. The spermatheca and gland lie in the fifth segment. The paired uteri diverge at the anterior border of the fifth segment and their union with the paired oviducts takes place at the posterior border of the third segment. The oviduct is correspondingly shortened in length and the adjacent walls of uterus and oviduct have broken down, communication thus being established between the cavities of the two ducts.

**Histology.** Each ovariole is composed of a mass of epithelial
cells bounded by a delicate basement membrane. The oviducts are mesodermal in origin and are formed by the union of the short ducts from the ovarioles. They are lined by a layer of epithelium invested by a basement membrane (figs. 55, 56, and 57, Pl. 10).

In the young pupa the ectodermal layer of the spermatheca and uterus is composed of large regular cells, and the cavities of the invaginations are small (figs. 44–7, Pl. 9).

As the pupa matures the cavities of uterus and spermatheca widen considerably, the cells forming their walls secrete a chitinous lining and shrink noticeably (fig. 48, Pl. 9; fig. 52, Pl. 10).

The accessory gland has a wall composed of larger regular epithelial cells which have very dense contents. The cavity of the gland is small and is lined with the secretion of the epithelial layer (fig. 53, Pl. 10). Its duct is of a smaller diameter and its cells are small and regular. The wall of the tubular spermatheca is very similar to the duct of the gland (fig. 54, Pl. 10).

The absence of a well-developed muscular system in connexion with the uterus is noticeable, the latter remaining a very wide, thin-walled duct. The genital appendages do not become fused together. No telescoping of the posterior segments of the abdomen takes place here, and the elaborate double-walled cylinder, so conspicuous in sections and dissections of the females of Sitodrepa panicea, is entirely absent.

(3) Anthonomus pomorum L.

(a) Adult Structure (after Miles, 32).

'The female reproductive organs consist of two ovaries, one on each side of the body. Each ovary is composed of two ovarian tubes opening into a common oviduct which leads into the uterus.

'At the anterior end of each egg-tube a terminal filament is located; this serves to suspend, or connect, the ovaries with the strands of the fat-body.

'The oviducts at their posterior extremities lead into a common chamber, the uterus, and its lower portion, the vagina. The
bursa copulatrix runs into the uterus; it is connected with the receptaculum seminis and the accessory gland.

'At the posterior extremity of the vagina are two heart-shaped chitinous plates, produced posteriorly into two small rounded papillae. A chitinous rod runs from the median region of the uterus to the posterior extremity of the vagina. The function of the chitinous plates is suggested to be the guidance of the ovum at oviposition.'

In the above description by Miles the 'bursa copulatrix' corresponds to the 'dorsal sac' opening into the uterus in *Sitodrepa panicea* and *Gastroidea polygoni*. Whether this structure actually functions as a bursa copulatrix is as yet undecided, and, therefore, the use of this term has not been adopted in the present study. The 'receptaculum seminis' corresponds similarly to the 'spermatheca'. The 'heart-shaped chitinous plates' with their 'apical papillae' represent the genital appendages which in this species do not become fused together.

(b) The Immature Insect.

(i) The Ovipositor. Nine abdominal tergites and sternites are present in the larva. A sclerite representing the tenth segment intervenes between the tergite and sternite of the ninth segment and bears the anus. No genital appendages are present.

After pupation has taken place nine tergites and sternites are still recognizable. As in the male, the ninth tergite is prolonged into a pair of caudal spines.

Posterior to the ninth sternite is a depression bordered by a pair of appendages. The depression marks the opening of the spermathecal invagination. The appendages are small plates bearing palpi at their apices (Text-fig. 44).

In transverse sections the genital appendages are seen to be diverticula of the ectodermal layer of the ninth sternite.

(ii) The Efferent System. Until the last stages of the pupal stadium the ovaries and oviducts are very little developed. Miles observes that in young adults soon after emergence the egg-tubes are quite undeveloped, and remain so until the following spring.
The rudiment of the ovary consists of a pair of ovarioles which at this stage of development take the form of delicate cords of epithelial cells. Each ovariole is invested by a sheath of connective tissue and extends from the middle of the first to the middle of the second abdominal segment. In its posterior region the epithelial cells of the ovariole become arranged around a small cavity to form a very slender duct (fig. 60, Pl. 10).

The rudiment of the uterus may first be observed during the pre-pupal instar. Enlarged ectodermal cells form a thickened plate extending for half the length of the eighth sternite. A groove is formed, commencing posteriorly, and gradually extending the length of the plate (fig. 55, Pl. 10). Eventually the groove becomes converted into a tube opening posterior to the eighth segment.

A similar plate of cells in the ninth segment gives rise to the rudiment of the spermatheca, its aperture being bordered by the genital appendages (fig. 56, Pl. 10). The mode of development of the uterus and spermatheca is thus essentially similar to that noted in the previously described species.

During the pupal stadium the uterine rudiment grows forward into the fourth abdominal segment, where it divides to form the paired uteri. The union of the paired uteri and oviducts was not observed in any of the sections obtained, and is evidently deferred for a longer period than in other species.

The spermathecal rudiment also grows forward, and its blind anterior end becomes divided into two tubes which are destined to form the functional spermatheca and accessory gland of the adult.

In the course of development the rudiments of uterus and spermatheca approach one another, and finally their intervening walls break down, so that a common cavity and one composite duct are formed. The original opening of the uterus becomes closed over and lost, and in the adult the contents of the uterus are discharged into the spermatheca, the original opening of which functions as the gonopore (fig. 57, Pl. 10).

The chitinous rod which acts as a support to the uterus and to which powerful muscles are attached, originates as a ventral invagination of the ectodermis between the seventh and eighth
sternites. This invagination extends anteriorly into the fifth segment, and the rod is formed within it by the secretion of chitin (fig. 57, Pl. 10).

**Histology.** The ducts from the ovarioles are mesodermal structures, being lined by epithelium and invested by a sheath of connective tissue (fig. 60, Pl. 10).

The paired uteri and other structures of ectodermal origin are composed of a layer of regular cells and their cavities are lined by a chitinous secretion. In the paired uteri this secretion almost fills the cavity of the duct; in the other ducts it is present as a thin layer. The median uterus and spermatheca are provided with outer coats of circular muscles which are not present in the paired uteri and the accessory gland.

Towards the posterior region of the abdomen and the body-wall becomes sunken in around the uterus as shown in Text-fig. 45. This telescoping does not affect the rectum, and in transverse sections the uterus appears to be surrounded by a double-walled tube of ectodermal origin (fig. 58, Pl. 10).

*Anthonomus pomorum*, therefore, appears to be a type intermediate between *Sitodrepa panicea* and *Gas-
troidea polygoni; the telescoping of the posterior abdominal segments having taken place to a less extent than in the former, to a greater extent than in the latter.

**Text-fig. 46.**

Adult structure of *Rhagium bifasciatum* F. × 8. *ag*, accessory gland; *c*, chitinous cylinder; *chr*, chitinous rod; *cov*, connective tissue of ovary; *dsp*, dorsal sac (spermatheca); *g*, gonopore; *m*, muscle; *od*, oviduct; *op*, ovipositor; *r*, rectum.

(4) *Rhagium bifasciatum* F.

(a) Adult Structure (Text-figs. 46 and 47).

Two large ovaries are present, each being provided with a short and wide oviduct. The oviducts open into the paired uteri which by their union form the median uterus. In the posterior region of the abdomen the latter enters, in company with the rectum, a strongly chitinized double-walled cylinder.
formed by the telescoping of the abdominal segments posterior to the seventh. A dorsal sac which receives the duct of an unpaired gland opens into the uterus.

The ovipositor is a short and stout chitinized tube, its origin from a pair of appendages being indicated by a longitudinal dorso-ventral suture. The gonopore is situated between a pair of small, club-shaped palpi.

Ventral to the uterus is a strongly chitinized Y-shaped rod attached to the body-wall and to the chitinized cylinder by powerful muscles. The whole structure closely resembles that of the reproductive system in *Sitodrepa panicea*.

(b) The Immature Insect.

(i) The Ovipositor. In the larva nine tergites and sternites are present. Posterior to the ninth segment is a sclerite which is produced dorsally into a short spine. This sclerite bears the anus which is bordered by a pair of fleshy papillae. No genital appendages are visible externally, even in the largest of larvae examined; neither can any invagination indicating the position of either the spermatheca or the uterus be detected (Text-fig. 48).
In the pupa the same number of tergites and sternites can still be recognized. The ninth segment bears posteriorly a pair of large appendages, each of which is provided with an apical palp. Immediately anterior to the bases of the appendages the ninth sternite is marked by a longitudinal depression which forms the opening of the uterine invagination (Text-fig. 49).

On the emergence of the imago the number of visible abdominal segments is seen to have been reduced to seven. The ovipositor protrudes between the seventh sternite and tergite and is seen to have been formed by the fusion of the appendages of the ninth segment, their apical palps remaining free. The fate of the segments posterior to the seventh is evident as soon as a dissection of the female has been made. These segments have been retracted into the body to form the double-walled cylinder which encloses the rectum and uterus. This cylinder does not form the ovipositor, the latter being of a true appendicular nature, but merely serves as a mechanism whereby it may be withdrawn into the body or extruded therefrom (fig. 62, Pl. 10).

(ii) The Internal Ducts. In the larva there is little development of the ovaries or the oviducts.
In the pupa, while lack of material rendered it impossible to trace the development step by step, several interesting points could be noted in sections.

The ovaries and the oviducts leading therefrom are mesodermal in origin. Each ovary is composed of several ovarioles lined by a layer of epithelium and invested by a sheath of connective tissue (fig. 63, Pl. 10). In the young pupa the oviducts are quite solid (fig. 64, Pl. 10).

As in the females of the other species examined, the functional uterus of the adult is derived from two primary invaginations of ectodermal origin which subsequently fuse to form a single duct. The uterine pore is easily observed in young pupae, being situated posterior to the eighth segment. In older pupae this primary aperture is closed over and the opening of the spermatheca may be observed between the bases of the genital appendages immediately posterior to the ninth segment. Later, by the fusion of the latter, the gonopore moves posteriorly to become situated between the palpi at their apices.

Sections through a mature pupa show clearly that the posterior region of the uterus arises as a single tube of ectodermal origin. It has a conspicuous lining of chitin and is invested by a well-developed coat of circular muscles. This region of the uterus is derived wholly from the original spermathecal invagination arising posterior to the ninth segment. In this posterior region also, the uterus is, with the rectum, enclosed in a double-walled cylinder of ectodermal origin. The manner of appearance of this cylinder, and its structure, are very similar to those of the cylinder present in *Sitodrepa panicea*. It is evidently formed by the telescoping of the body segments posterior to the seventh (fig. 62, Pl. 10).

Anterior to its enclosure in the chitinous cylinder the uterus becomes clearly divisible into two regions, both of ectodermal origin and of similar structure (fig. 61, Pl. 10). The dorsal region represents the spermatheca of the adult, and is derived from the anterior extremity of the original spermathecal rudiment. Anteriorly, it becomes divided, the one division forming the duct of the accessory gland, the other the functional spermatheca.

The ventral region represents the uterus of the adult, and is
derived from the primary uterine invagination which is formed immediately posterior to segment eight. Some little distance anterior to its separation from the spermatheca, the uterus divides into two lateral branches. These extend to the posterior region of the oviducts, becoming applied to the blind ends of the latter. Communication between the cavities of the oviduct and uterus is not established until a later stage in development (fig. 64, Pl. 10).

The chitinous rod is formed, as in other species, as an invagination posterior to the seventh sternite (fig. 61, Pl. 10).

D. Conclusions.

From the foregoing account of the structure and development of the female reproductive system in Sitodrepa panicea, Gastroidea polygoni, Anthonomus pomorum, and Rhagium bifasciatum, the following conclusions may be drawn:

(1) The Ovipositor and Associated Structures.

The ovipositor in the Coleoptera is derived from a pair of palp-bearing plates, which may or may not fuse to form a median tubular organ bearing the gonopore. From their position, mode of origin and structure, these plates appear to be homologous with the lateral ovipositor lobes in other Insecta, and hence represent the coxites of the ninth segment with their styli.

There appears, however, to be some foundation for Verhoeff's statement in 1893 (50), that the posterior abdominal segments are modified in relation to oviposition. The ovipositor itself has been shown to be of an appendicular nature, but in some species of Coleoptera, e.g. Sitodrepa panicea, Rhagium bifasciatum, the intersegmental membranes between the posterior abdominal segments eight to ten undergo an increase in length. While still membranous and flexible, this region becomes telescoped into the body-cavity and is subjected to a process of chitinization, the outer wall remaining membranous, the inner wall forming a stiff chitinous cylinder. Powerful muscles are developed for the eversion and retraction of these segments. When the structure is retracted, the uterus
and rectum appear to be enclosed within a double-walled cylinder. By the eversion of this cylinder the ovipositor becomes thrust well outside the body at the tip of the long and tapering tube formed by the posterior segments. This is well illustrated in Text-fig. 32.

Moreover, there seems to be some correlation between the extent to which this telescoping takes place, the degree of fusion between the genital appendages, and the mode of oviposition. For example, in *Gastroidea polygoni*, where the eggs are deposited in rows on the surfaces of leaves, and the abdomen is very much distended with eggs at the time of oviposition, little or no withdrawal of the posterior segments takes place; the uterus and rectum are free to the tip of the abdomen, and the genital appendages have the appearance of reduced plates bordering the gonopore. Here there seems no need for the extrusion of the body to facilitate the deposition of the eggs, and, to quote Verhoeff: 'Where the eggs are scattered broadcast, no ovipositor (i.e. no telescoping of the body segments) is present.'

In *Sitodrepa panicea* and *Rhagium bifasciatum*, on the contrary, the double-walled cylinder enclosing rectum and uterus is most noticeable in sections through the abdomen of the pupa and in dissections of the mature adult. In the former species the eggs are deposited in cracks and grooves in the substratum, in the latter in the wood of coniferous trees. The prolongation of the abdomen into a narrow retractile tube, together with the fusion of the appendages to form a tubular ovipositor, is apparently advantageous.

The case of *Anthonomus pomorum*, however, presents a difficulty. According to Miles, the female weevil eats a hole in one anther lobe of a blossom, and then extends her ovipositor, thrusting it down into the prepared aperture. In the females of *Anthonomus* which were examined it was found that the prolongation of the body was very slight, and that when retraction had taken place, there was no close connexion between the body-wall and the uterus and rectum. Moreover, the genital appendages remain free and do not fuse to form a tubular ovipositor.
While no hard and fast rule can be laid down, therefore, that the act of oviposition is facilitated in the manner suggested, or that the modifications noted are correlated with function, yet in the four species studied, three at least of the types suggested by Verhoeff appear to be present, namely:

(a) The 'Legerohre' for the deposition of the eggs in the bark or the wood of trees, e.g. *Rhagium bifasciatum*.

(b) The 'Legesabel' for the deposition of eggs in the soft tissues of young shoots, e.g. *Anthonomus pomorum*.

(c) The absence of any special modification when the eggs are to be scattered broadcast, e.g. *Gastroidea polygoni*. The case of *Sitodrepa panicella* seems to approximate most nearly to that of *Rhagium*, viz. to the 'Legerohre'.

Finally, the mode of oviposition in connexion with the structure of the ovipositor and the terminal abdominal segments must be studied in a great many species before a definite statement on the subject can be pronounced or the possible value in taxonomy estimated.

The chitinized rod ventral to the uterus originates as an invagination of the body-wall posterior to the seventh sternite. As this rod is already in existence when the full complement of body segments can still be recognized, it cannot represent the part or the whole of a converted body segment. Whether the homologue of this rod is present in other Insecta is an open question. A similar ectodermal invagination posterior to the seventh segment is described by George (20) in *Philaenus spumarius*. This goes to form the anterior region of the common oviduct (i.e. uterus), the posterior portion being derived from the ectoderm of the eighth segment. George also describes an invagination of the ninth segment which goes to form the accessory gland. It is possible that the line of evolution in the Coleoptera has been such that the anterior region of the common oviduct has been derived from the duct originating posterior to the eighth segment, its posterior region from the duct originating posterior to the ninth. The duct originating
posterior to the seventh segment thus loses all connexion with the efferent system and is converted into the chitinous rod.

(2) The Efferent System.

(a) There appears to be a shortening of the original efferent passage noted by Korschelt and Heider so that the oviducts are partly derived from the mesoderm, partly from the ectoderm. The extent of the ectodermal portion, which consists of a pair of outgrowths from the uterus, is indicated by the conspicuous lining of chitin which is present.

(b) All other parts of the efferent system, viz. uterus, spermatheca, and accessory gland, are ectodermal in origin. This point may be confirmed by direct observation of their development as well as by the study of their histological structure. Singh Pruthi, Nussbaum, Jackson, and others are in agreement as to this point, while the views of Herold and Balbiani are in opposition.

(c) All parts of the efferent system, with the exception of ovaries and oviducts, are unpaired in origin.

No paired rudiments of uterus, spermatheca, or gland were observed, the azygos condition being primary and not secondary as Nussbaum concluded.

In this matter Wheeler states that the vagina in the Orthoptera is derived from an unpaired invagination originating between the seventh and eighth sternites. Singh Pruthi, Nel, and George also find that the uterus is unpaired in origin.

Jackson appears to effect a compromise, for, while the uterus according to him is unpaired throughout its length, the accessory or sebaceous gland is paired in origin, while the spermatheca and receptaculum seminis are derived from a pair of vesicles situated posterior to the eighth segment. These vesicles fuse, losing all trace of their original paired nature, and subsequently give rise to the spermatheca and receptaculum seminis, one behind the other in the median line.

Verson and Bisson regard all parts of the efferent system as derived from the fusion and secondary modification of two pairs of ectodermal vesicles, one pair situated posterior to the eighth,
the other to the ninth, segment. Their work seems to have been influenced greatly by the conclusions of Jackson.

(d) The spermatheca and uterus arise independently, the one behind the ninth, the other behind the eighth segment. Communication between the two is established secondarily.

This is in accordance with the views of Jackson and Singh Pruthi, but in contradiction to those of Balbiani, who describes the spermatheca as arising from an outgrowth of the uterus.

In discussing Jackson's work, Singh Pruthi makes the mistake of referring to him as an author who regards the spermatheca as an outgrowth of the uterus itself. According to the original text Jackson describes the paired vesicles which subsequently give rise to the spermatheca and vesicula seminalis as being already in existence when the uterus first makes its appearance. It is true that the rudiments of the spermatheca and uterus are from the first in connexion with each other, as Singh Pruthi states, but Jackson describes very definitely the mode of development of both structures, and it is clear that he regards each as derived separately from the ectodermis.

(e) The rudiment of the uterus, which arises posterior to the eighth sternite, is homologous with the genital duct in those of the Insecta in which the gonopore is located posterior to the eighth sternite, and the primary opening of the uterus which subsequently becomes closed over and lost, is the homologue of that gonopore.

The functional gonopore of the Coleoptera, viz. the original aperture of the spermathecal rudiment, posterior to the ninth sternite, cannot be considered homologous with the gonopore in such Insecta where the latter is derived from the primary uterine pore.

There thus appears to be a progressive migration of the gonopore in the Insecta from posterior to the seventh, to the eighth, and finally to the ninth, segments. Singh Pruthi suggests that in the first case the gonopore represents the aperture of the true mesodermal oviduct. George, however, describes an ectodermal invagination arising posterior to the seventh sternite, the aperture of which becomes closed over in growth. Nel also suggests that the primary location of the aperture of the
unpaired oviduct (ectodermal) is posterior to the seventh sternite. There seems to be some confirmation for this suggestion in the study of the development of the chitinous rod in the Coleoptera.

Where the gonopore is located posterior to the eighth sternite it represents the aperture of the uterus, where posterior to the ninth, of the spermatheca. Christophers (Diptera) describes the origin of the uterus posterior to the eighth segment, with the invagination of the spermatheca in close connexion. The 'caecus' arises as an invagination posterior to the ninth segment. At a later stage of development these three structures all open into a common atrium. Now, if it be supposed that the invagination posterior to the ninth segment in the Diptera represents the spermathecal invagination, that in the course of development communication between the 'caecus', 'spermatheca', and uterus be established, the caecal opening being closed over and the uterine pore functioning as the gonopore; then the similarity between the mode of development and the homologies of the female reproductive system in the Diptera and the Coleoptera are at once clear.

With reference to the same point Jackson seems to have been in possession of the facts, but to have misinterpreted their significance. The 'posterior pair of vesicles' situated in the ninth segment and giving rise to the sebaceous glands is evidently the spermathecal rudiment, the 'anterior pair of vesicles' in the eighth segment corresponding to the uterine rudiment. The process which he describes as the 'backward migration of the gonopore' is thus seen to be the establishment of communication between the rudiments of uterus and spermatheca.

PART III. THE HOMOLOGIES OF THE MALE AND FEMALE REPRODUCTIVE SYSTEMS IN THE COLEOPTERA.

Parts I and II of the foregoing study would be incomplete without some attempt to analyse the homologies that exist between the male and female reproductive systems. Each sex has been considered separately and its homologies discussed, it
now remains to make a comparison between the two sexes. Various difficulties attend this task, since mode of origin, growth and development, as well as adult morphology, must be taken into consideration. The following conclusions, however, seem justifiable.

A. THE GENITAL APPENDAGES, viz. COPULATORY APPARATUS AND OVIPOSITOR.

Since the intromittent organ (median and lateral lobes of the aedeagus) represents the endopodites of the ninth segment, while the ovipositor is derived from the coxites and styli of that segment, the male and female genital appendages in the Coleoptera cannot be regarded as homologous.

This conclusion has already been arrived at by Singh Pruthi (42–5).

In other orders of the Insecta where the three pairs of primary appendages are present in the female, and two pairs in the male, the appendages of the ninth segment, viz. the ‘telopodites’ and ‘coxites’ in both sexes are homologous. The homologues of the anterior pair of ovipositor lobes in the female, viz. the telopodites or endopodites of the eighth segment, are never present in the male.

While some authors such as Zander (58–61) will admit no relationship between the appendages of the two sexes, even of those borne by the ninth segment, others, such as Wheeler (57), Kershaw and Muir (27), make an attempt to show that in the male as well as in the female three pairs of primary appendages are present.

Zander states emphatically: ‘dass die Stachelapparat und die männlichen Geschlechtsanhänge weder in toto noch in ihren Theilen irgend welche morphologische Übereinstimmung erkennen lassen. Beide sind total differente Bildungen.’

This seems unnecessarily sweeping, and Singh Pruthi considers that Zander’s results indicate that the appendages in male Hymenoptera represent the endopodites and coxites of the ninth segments, and are hence homologous with the dorsal and lateral ovipositor lobes. It must be borne in mind, however, that Zander does not consider the genital appendages to be
serially homologous with segmental appendages, and hence sees no reason why any relation between the appendages of the two sexes should be considered to exist.

Wheeler, at the other extreme, homologizes the male and female appendages with the styli of the eighth, ninth, and tenth segments, the last pair having undergone a forward migration in the course of development. More recently, Kershaw and Muir describe three pairs of appendages in the Homoptera which ‘arise in exactly the same place as in the female’, viz. one pair on the eighth sternite and two pairs from an area which appears to be the enlarged eighth–ninth intersegmental membrane. They also consider the first pair of appendages to represent the coxites of the eighth segment—‘while there is no evidence to show that $g_3$ (i.e. the homologues of the lateral ovipositor lobes) are the coxites of the ninth’.

Their zeal for an exact comparison between the male and female leads them to locate the male gonopore in the Homoptera between the eighth and ninth sternites, whereas all other investigators place it posterior to the ninth sternite. Apart from the fact that Singh Pruthi, working on the same group, found but two pairs of appendages on the ninth segment of the male, the above quotation shows that in their conclusions Kershaw and Muir differ essentially from other investigators; the anterior pair of ovipositor lobes is not considered homologous with the coxites of the eighth segment, but with the endopodites thereof (Verhoeff (49-53), Walker (55 and 56), Crampton (7-15), Singh Pruthi).

For these reasons the conclusions of Kershaw and Muir are not considered to shed any new light on the subject.

It is considered rather that with regard to the genitalia of the Insecta no general statement can be made, but that the condition prevailing in any particular group must be decided on after careful consideration. In this way only can the significance of the structures be realized and harmony be restored.

B. The Efferent System.

While the ovaries and testes are strictly homologous structures, the oviducts and vasa deferentia cannot be entirely
considered as such. The original efferent passages derived from the posterior region of the ovarian and testicular rudiments have, in the Coleoptera, undergone a greater or less amount of shrinkage, e.g. in the males of *Sitodrepa panicea*, *Gastroidea polygoni*, and *Anthonomus pomorum* the mesodermal *vasa deferentia* are reduced considerably in length and their terminal regions are supplemented by outgrowths from the ejaculatory duct. A similar process seems to have taken place in the females of all species examined, the terminal regions of the mesodermal oviducts being replaced by outgrowths from the uterus. Those portions of the *vasa deferentia* and *oviducts* which are derived wholly from the mesodermal rudiments are homologous structures; the ectodermal portions of the paired ducts must, however, be considered separately.

In the female the ectodermal regions of the oviducts are derived from outgrowths of the uterus; in the male the corresponding regions of the *vasa deferentia* from ectodermal structures, the origin of which is disputed.

According to Singh Pruthi, in his account of the development of *Tenebrio molitor*, the *vasa deferentia*, or paired ejaculatory ducts as he calls them, are wholly ectodermal in origin and are homologous with the paired ejaculatory ducts in the Homoptera. These latter develop from ectodermal ducts originating near, though not actually opening at, the posterior margin of the eighth sternite. From these facts Singh Pruthi concludes that the paired ejaculatory ducts are homologous with the uterine rudiment which arises in the female posterior to the eighth sternite. Since the uterus is unpaired in origin this seems to be a doubtful comparison.

If the gonopores in the Coleoptera are homologous, as seems likely, since both are located posterior to the ninth sternite, then the primary ducts, of which the gonopores are the apertures, namely, the ejaculatory duct and the spermathecal rudiment, are homologous structures. So much is admitted by Singh Pruthi. But, in *Sitodrepa panicea*, *Gastroidea polygoni*, and *Anthonomus pomorum*, it was found that the paired ejaculatory ducts arise as outgrowths from the
median ejaculatory duct as was suggested by Muir (34), and therefore can have no relation to the uterus which is derived from posterior to the eighth sternite and hence to the paired uteri which arise as outgrowths from the latter.

It appears, therefore, that in the Insecta, when the gonopore in the female is located posterior to the ninth segment, it may be considered to be the homologue of the male gonopore, each being derived from the aperture of a primary invagination located posterior to the ninth segment. Where the primary uterine pore functions as the gonopore of the adult, it cannot be regarded as strictly homologous with the opening of the ejaculatory duct.

In some cases, e.g. the Diptera, the homologue of the male gonopore is at first present as the aperture of the ‘caecus’, but this later becomes closed over, or moves forwards, the uterine pore functioning as the gonopore.

Some Lepidoptera retain both uterine and spermathecal apertures in the adult, while in the Coleoptera a third type of specialization is met with, the uterine pore being closed over and lost, while the spermathecal opening is the functioning gonopore of the adult.

LITERATURE.


15. —— “Correction of a Statement concerning the Terminal Abdominal Structures of Male Insects”, ibid., vol. 53, 1921, p. 72.


59. —— “Beiträge zur Morphologie des männlichen Geschlechtsanhänge der Hymenopteren”, ibid., 1900, pp. 461–89.
EXPLANATION OF PLATES 7-10.

LETTERING.

ag, accessory gland; b, bend in posterior region of ejaculatory duct; bm, basement membrane; c, chitinous cylinder; ca, outer wall of chitinous cylinder; ch, chitinous intima; chr, chitinous rod; conn, connective tissue; dsp, dorsal sac (spermatheca); ep, epithelial layer; g, gonopore; ga, genital appendage; ge, clefts separating off genital appendage from genital pocket; gl, genital palp; gp, genital pocket; hit, lateral or paired uterus; l, lumen; Lejd, lateral ejaculatory duct; ll, lateral lobe; lut, lateral or paired uterus; m, muscle; mejd, median ejaculatory duct; mejda, anterior region of mejd; mejdb, median region of mejd; mejdc, posterior region of mejd; ml, median lobe; nu, nucleus; od, oviduct; put, uterine pore; r, rectum; rsp, spermathecal rudiment; rut, uterine rudiment; s, space between inner and outer walls of chitinous cylinder; sec, secretion of epithelial layer; sp, spermatheca; sp.g, rudiment of spiculum gastrale; t, transition between anterior and median regions of ejaculatory duct; t', transition between median and posterior regions of ejaculatory duct; te, testis; tf, testicular follicle; vd, vas deferens; ve, vas efferens; vs, vesicula seminalis.

PLATE 7.

Figs. 1-9.—Sitodrepa panicea L. The Male.
Figs. 1-4.—Transverse Sections through the Pupa from Anterior to Posterior.

Fig. 1.—The testes and accessory glands. X 80.
Fig. 2.—Origin of the lateral ejaculatory ducts and accessory glands. X 200.
Fig. 3.—Anterior border of the genital pocket at the base of the genital appendages. X 200.
Fig. 4.—The genital appendages. X 200.

Figs. 5-9.—Histology of the Efferent System.

Fig. 5.—Testicular follicle. X 440.
Fig. 6.—Vas efferens. X 440.
Fig. 7.—Junction of vas efferens and vas deferens. X 440.
Fig. 8.—Portion of wall of accessory gland. X 580.
Fig. 9.—Median ejaculatory duct. X 580.

Figs. 10-13.—Gastroidea polygoni L. The Male.
Figs. 10-12.—Transverse Sections through Pre-pupa from Anterior to Posterior.

Fig. 10.—Origin of lateral ejaculatory ducts and accessory glands. X 130.
Fig. 11.—Apex of genital pocket showing clefts separating off the genital appendages. $\times$ 130.

Fig. 12.—The genital appendages. $\times$ 130.

Fig. 13.—Young Pupa. Transverse Section showing Growth in the Anterior Region of the Ejaculatory Duct. $\times$ 130.

**PLATE 8.**

Figs. 14-21.—Gastroidea polygoni L. The Male.

Figs. 14-16.—Transverse Sections through the Mature Pupa from Anterior to Posterior.

Fig. 14.—Median and lateral ejaculatory ducts, glands, vesicula seminalis, and vas deferens. Section indicated by arrow A in Text-fig. 22. $\times$ 130.

Fig. 15.—Loop in posterior region of ejaculatory duct. Section indicated by arrow B in Text-fig. 22. $\times$ 130.

Fig. 16.—Junction of median and posterior regions of ejaculatory duct. Section indicated by arrow C in Text-fig. 22. $\times$ 130.

Figs. 17-21.—Histology of the Efferent System.

Fig. 17.—Testis and vas deferens. $\times$ 800.

Fig. 18.—Vesicula seminalis. $\times$ 600.

Fig. 19.—Accessory gland. $\times$ 900.

Fig. 20.—Median region of ejaculatory duct. $\times$ 580.

Fig. 21.—Posterior region of ejaculatory duct. $\times$ 1100.

Figs. 22-30.—Anthonomus pomorum L. The Male.

Figs. 22 and 23.—Transverse Sections through the Pre-pupa from Anterior to Posterior.

Fig. 22.—Origin of lateral ejaculatory ducts and accessory glands. $\times$ 200.

Fig. 23.—Gonopore and genital appendages. $\times$ 200.

Figs. 24, 25, and 26.—Transverse Sections through the Pupa from Anterior to Posterior.

Fig. 24.—Testes, vas deferens, glands, ejaculatory duct, and vesicula seminalis. $\times$ 170.

Fig. 25.—Origin of lateral ejaculatory ducts. $\times$ 190.

Fig. 26.—Genital pocket and spicule. $\times$ 200.

Figs. 27-30.—Histology of the Efferent System.

Fig. 27.—Testes and vas efferens. $\times$ 440.

Fig. 28.—Vas deferens. $\times$ 440.

Fig. 29.—Accessory gland. $\times$ 770.

Fig. 30.—Median ejaculatory duct. $\times$ 730.

**PLATE 9.**

Figs. 31-43.—Sitodrepa panicea L. The Female.

Figs. 31-4.—Transverse Sections through a Young Pupa. Anterior to Posterior.

Fig. 31.—The anterior forking of the uterine rudiment. $\times$ 200.
Fig. 32.—The uterine and spermathecal rudiments. × 200.
Fig. 33.—The uterine pore. × 200.
Fig. 34.—The spermathecal pore or gonopore and the genital appendages. × 200.
Fig. 35.—The Ovipositor in an Older Pupa. × 200.

Figs. 36-43.—Histology.
Fig. 36.—Ovariole. × 250.
Fig. 37.—Oviduct. × 250.
Fig. 38.—Uterus. × 300.
Fig. 39.—Uterus and dorsal sac (Spermatheca). × 200.
Fig. 40.—Accessory gland. × 290.
Fig. 41.—Spermatheca proper. × 380.
Fig. 42.—Chitinous rod. × 280.
Fig. 43.—Chitinized cylinder enclosing rectum and uterus. × 330.

Figs. 44-8.—Gastroidea polygoni L. The Female.
Figs. 44-7.—Transverse Sections through a Young Pupa. Anterior to Posterior.
Fig. 44.—Anterior forking of uterine rudiment. × 200.
Fig. 45.—Uterine and spermathecal rudiments. × 200.
Fig. 46.—Uterine pore. × 200.
Fig. 47.—Spermathecal pore or gonopore and genital appendages. × 200.
Fig. 48.—Transverse Sections through a Mature Pupa.
Fig. 48.—Uterus and dorsal sac (Spermatheca). × 200.

Plate 10.

Figs. 49-54.—Gastroidea polygoni L. The Female.
Fig. 49.—Transverse section through a mature pupa: gonopore and genital appendages. × 260.
Figs. 50-4.—Histology.
Fig. 50.—Ovariole and oviduct. × 280.
Fig. 51.—End of oviduct in young pupa. × 330.
Fig. 52.—End of oviduct and lateral uterus in an old pupa. × 350.
Fig. 53.—Accessory gland. × 550.
Fig. 54.—Spermatheca proper. × 550.

Figs. 55-60.—Anthonomus pomorum L. The Female.
Figs. 55-6.—Transverse Sections through the Eighth and Ninth Segments in the Pre-pupa.
Fig. 55.—Eighth sternite and uterine rudiment. × 160.
Fig. 56.—Ninth sternite, spermathecal rudiment, and genital appendages. × 160.
Figs. 57–9.—Transverse Sections through a Mature Pupa. Anterior to Posterior.
Fig. 57.—Uterus and dorsal sac (Spermatheca). × 170.
Fig. 58.—Uterus and chitinous cylinder. × 170.
Fig. 59.—Gonopore and genital appendages. × 170.
Fig. 60.—Ovarian Tubes. × 400.

Figs. 61–4.—Rhagium bifasciatum F. The Female.
Fig. 61.—Uterus and dorsal sac (Spermatheca) in a mature pupa. × 130.
Fig. 62.—Uterus, rectum, and chitinous cylinder. × 130.
Fig. 63.—Ovariole. × 150.
Fig. 64.—Oviduct and lateral uterus. × 150.