

On the Post-embryonic Development of the Female Reproductive Organs of *Tribolium castaneum* Herbst

with a Note on the Homology of the Reproductive Organs in the two Sexes

(Coleoptera : Tenebrionidae)

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(With 14 figures)

Introduction

The post-embryonic development of reproductive organs of female beetles differs fundamentally from that of the male and, therefore, the problem of establishing homology between the two involves considerable difficulty. Workers who have attempted this differ among themselves considerably. The author has already described the post-embryonic development of the male reproductive organs of *Tribolium castaneum* Herbst. In the present paper, he deals with the development of the female organs in the same species and attempts to compare the two.

Observations

1. Reproductive organs of the adult

(1) The efferent system. There is a pair of ovaries, each ovary consisting of four acrotrophic ovarioles on the two sides of the alimentary canal in the second to the fourth abdominal segments. Each ovariole opens behind in a rather wide, thin walled chamber, the egg calyx from which it is usually separated by a cellular plug. The egg calyx continues posteriorly into the lateral oviduct which has a slightly different histological structure from the former. The two lateral oviducts of the two sides unite in the median line to form the median oviduct or uterus which opens posteriorly into the highly muscular and wide vagina (Fig. 1).

A large pouch-like outgrowth from the dorsal wall of the vagina near its anterior end marks off the median oviduct from the vagina. This pouch is the bursa copulatrix and it extends anteriorly almost upto the level of the union of the two lateral oviducts. A thin strongly chitinous tube is wound in a few coils over the anterior apex of the bursa. This is the spermatheca and this communicates with the cavity of the bursa by its open end which projects inside the former. A large club-shaped gland, the spermathecal gland, is situated antero-dorsally to the bursa. This gland has no direct communication with the spermatheca; insted it opens into the bursa.

The wall of the gland is composed of two or three layers of cells and the cavity is lined internally by a thin chitinous intima. The opening of the spermathecal gland into the bursa is guarded by a pair of strong, chitinous valves which are controlled by strong bands of muscle fibres. A pair of muscular valves are situated between the oviduct and the bursa.

(2) The ovipositor. Only seven tergites and sternites are externally visible in the adult female, the posterior segments having become inva-

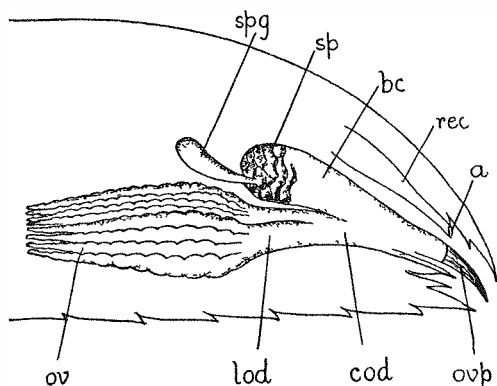


Fig. 1. Female reproductive organs of adult of *Tribolium castaneum* Herbst (diagrammatic representation)

a, anus; bc, bursa copulatrix; cod, common oviduct; lod, lateral oviduct; ov, ovary; ovp, ovipositor; rec, rectum; spg, spermathecal gland

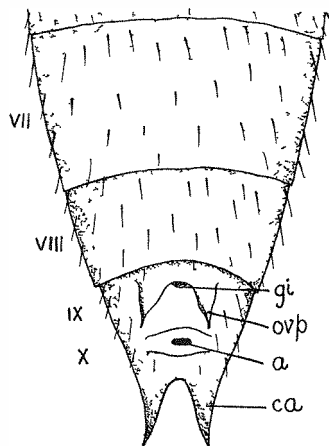


Fig. 2. Posterior part of the abdomen of female larva (ventral view)

a, anus; ca, caudal appendage, gi, primary genital invagination; ovp, ovipositor

ginated. The impushing causes the formation of a genital cavity in which both the ovipositor and the anus are situated. The eighth sternite is larger than the eighth tergite but it is feebly chitinised. The ninth segment is mostly membranous except in its posterior part which is chitinous and split into a pair of thin, broad strips which act as the basal plates for the ovipositor.

The ovipositor is a paired structure and it encloses the female genital opening between its two valves. Each half consists of three important parts — the coxite, the stylus and the paraproct. The coxite is a somewhat triangular plate attached to the valvifer (the basal plate being furnished by the ninth segment) by a narrow membrane. Its posterior conical part bears a posteriorly directed, rod-like process, the stylus at its posterior, outer margin. Both the coxite and the stylus bear many chitinous hairs at their posterior margin. On the inner side of the coxite, there is a membranous structure, the paraproct, whose posterior part is highly chitinised. The entire ovipositor can be everted out of the genital cavity.

On the ventral side of the vagina, there is a Y-shaped chitinous rod, the spiculum gastrale, whose bifurcated end lies towards the posterior side in contact with the seventh sternite.

2. Development of reproductive organs

(1) The efferent system. Larva. The efferent system in the female develops considerably late. The only structure visible in the larva in this connection is a small invagination of the body wall of the posterior border

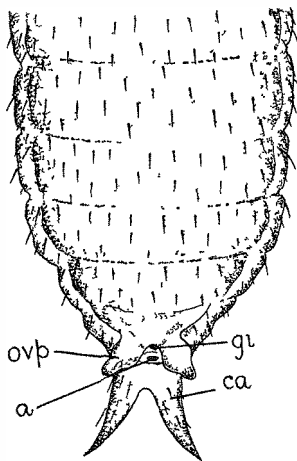


Fig. 3. Posterior part of the abdomen of female pupa (ventral view). Lettering as in fig. 2

of the ninth sternite between the bases of the two genital appendages (Fig. 2). This invagination, often called the primary genital invagination, runs forward upto the eighth segment where it ends blindly and is, in fact, the rudiment of the genital pouch. It may, therefore, be preferably called the spermathecal rudiment and its opening is the future gonopore.

Pupa. In the pupa, the invagination on the ninth sternite, i. e., the spermathecal rudiment, deepens further and extends upto about the sixth abdominal segment. Meanwhile, there also appears a narrow groove near the posterior border of the eighth sternite which elongates and finally gives rise to a tube which also runs anteriorly upto about the sixth segment (Figs. 4 to 9). This tube is the rudiment of the median oviduct or the uterine rudiment. Both

the invaginations run almost parallel to each other in the abdomen, the narrow uterine rudiment lying ventrally to the older and broader spermathecal rudiment.

During their growth, the two tubes come close in their median part and finally get applied to each other respectively by their adjacent dorsal and ventral walls. The lateral walls of the wider posterior invagination (spermathecal rudiment) now grow a little downwards so as to enclose the narrower uterine rudiment. Finally, the intervening tubes become confluent (Figs. 10 to 13).

While these changes occur in the median part of the two tubes, their anterior ends continue their forward growth separately. The anterior end of the uterine rudiment in the fifth segment swells up to form an ampulla-like structure which widens and finally bifurcates longitudinally into two tubes, the lateral oviducts. The spermathecal rudiment, on the other hand, divides by a horizontal division giving rise to a narrow dorsal part — the rudiment of the spermathecal gland and a broader ventral part which

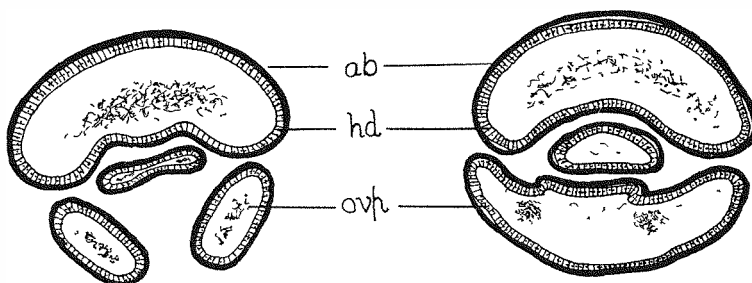


Fig. 4

Fig. 5

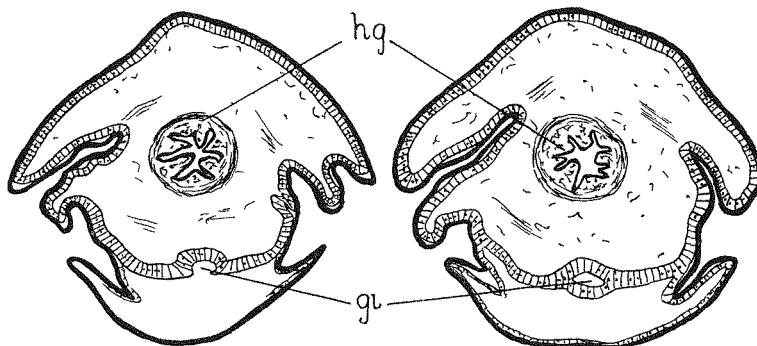


Fig. 6

Fig. 7

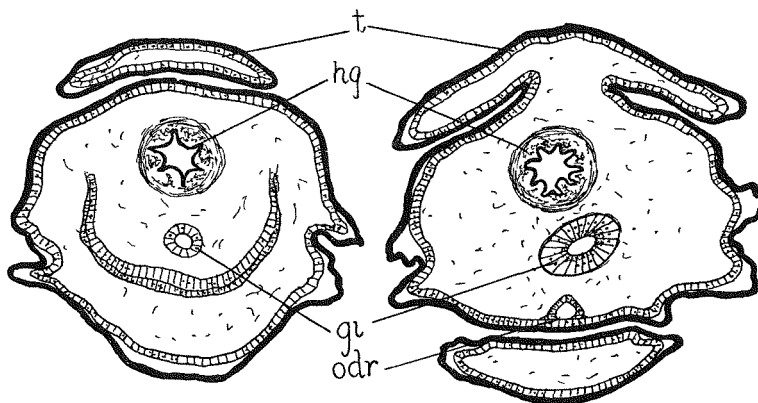


Fig. 8

Fig. 9

Fig. 4—9. T. S. through different regions of the abdomen of the pupa. Fig. 4. T. S. through ninth segment showing the two genital appendages. Fig. 5. T. S. through a little anterior region of the ninth segment. The appendages have united at the base. Figs. 6 and 7. T. S. through further anterior regions showing the formation of the spermathecal rudiment. Fig. 8. T. S. through the posterior region of the eighth segment showing the spermathecal rudiment but not the uterine rudiment. Fig. 9. T. S. through a little anterior region of the eighth segment showing the formation of the uterine rudiment. ab, abdomen; gi, primary genital invagination; hd, hypoderm; hg, hind gut; odr, uterine (oviducal) rudiment; ovp, ovipositor, t, tergum

elongates further and gets differentiated into an anterior part, the spermatheca and a posterior part, the bursa copulatrix.

It has been mentioned that the two invaginations communicate with each other in their median part, i. e., in the sixth and seventh abdominal

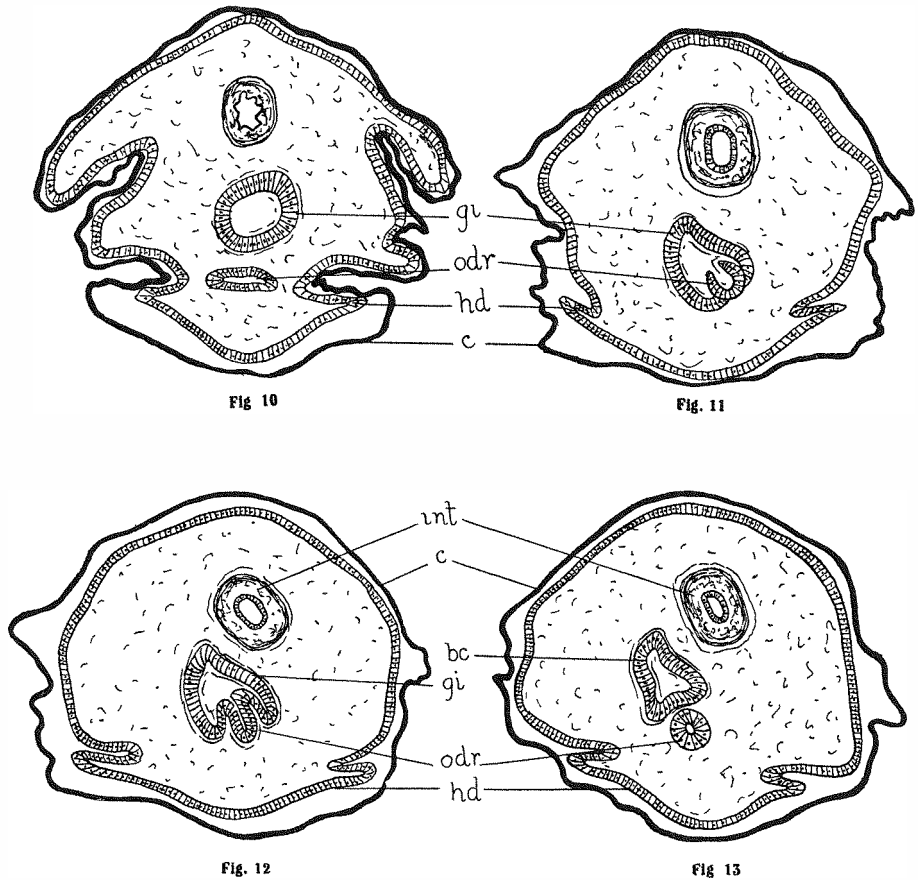


Fig. 10—13. T. S. through the abdomen of pupa in the 8th and anterior segments

Fig. 10. T. S. through eighth segment showing the uterine and spermathecal rudiments separate. Figs. 11 and 12. T. S. through anterior segments showing the establishment of communication between the two. Fig. 13. T. S. through further anterior region where the two rudiments are again separate

bc, bursa copulatrix; c, chitin; gi, primary genital invagination; hd, hypoderm; int, intestine; odr, uterine rudiment

segments. The free posterior part of the uterine rudiment now disappears along with its opening on the eighth sternite so that both the passages now open to outside by a single opening on the ninth sternite which is the

original opening of the spermathecal rudiment and not that of the uterine rudiment (Fig. 14, i, ii and iii).

Each ovary, meanwhile, gets differentiated into four ovarioles, covered by the germinal epithelium which extends posteriorly as the true lateral oviduct (the egg calyx) uniting with one of the two bifurcated ends of the median uterine rudiment, that is the ectodermal paired oviduct of its

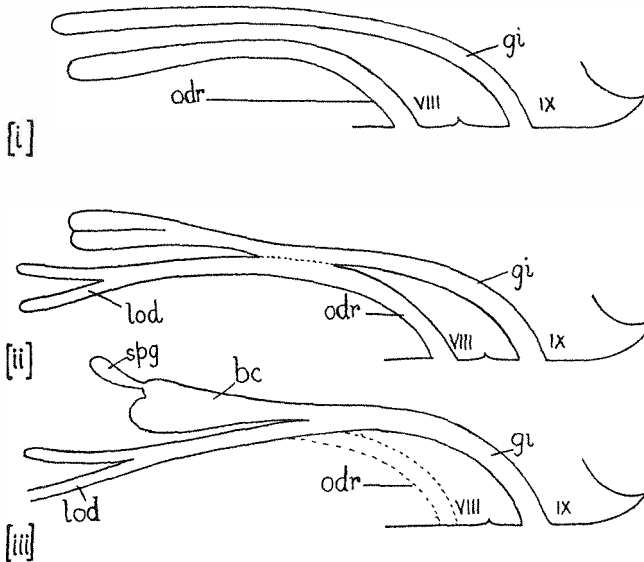


Fig. 14 (i, ii & iii). Diagrammatic representation of the development of the efferent ducts bc, bursa copulatrix; gi, primary genital invagination; lod, lateral oviduct; odr, uterine rudiment; spg, spermathecal gland

own side. Thus the complete ducts have a mixed origin and its posterior ectodermal part arises from the originally unpaired invagination on the eighth segment.

During imago formation, the walls of the spermatheca, the bursa copulatrix and the vagina secrete chitin internally and muscle fibres surround these from outside.

(ii) The ovipositor. Larva. The abdomen of the female larva resembles that of the male and distinctly shows nine tergites and sternites. Between the ninth sternite and the ventral part of the ninth tergite, on the ventral side, there is a small slightly chitinised piece, the anal segment, representing the rudiment of the tenth segment. The ninth tergite also bears a pair of straight caudal appendages posteriorly.

A pair of somewhat triangular ectodermal genital appendages arise from the posterior border of the ninth sternite (Fig. 2). These are fairly large and when fully developed, broader at the base and conical poste-

riorly with a slight constriction in the middle. There are a few hairs on its posterior part. Thus, these appendages differ clearly from the uniformly broad primary genital appendages of the male larva.

Soon after, a small invagination, the primary genital invagination, appears between the bases of the two appendages. The appendages and the invagination persist throughout the larval period. Temporary appendages and impushings do not appear at any stage in the larva.

Pupa. During pupation, there is no change in the number of body segments but the segments become slightly larger than those of the male. The body straightens out and consequently the anal plate is shifted to the posterior end of the body while the caudal appendages become slightly dorsal.

The genital appendages increase in size and become differentiated into a broad anterior part and a narrow somewhat cylindrical posterior part (Fig. 3).

During imago formation, these two parts undergo further differentiation and chitination. Thus the broad anterior part transforms into the coxite, while the narrow posterior part into the stylus. The posterior part of the ninth sternite gives rise to the valvifers, and the rest of the ninth sternite remains membranous.

Discussion

(4) The efferent system. While there is considerable difference of opinion regarding the origin of the paired efferent ducts in other orders of insects, it is clear that in the Coleoptera they are not purely mesodermal as hitherto considered, but partly mesodermal and partly ectodermal. The author's observation in *Tribolium castaneum* in this respect are entirely in agreement with those of SINGH PRUTHI (1924), METCALFE (1932) and RAKSHPAL (1946). The point of union of the two parts is, however, difficult to determine and has not been mentioned by earlier workers either. In the Ephemera, the paired openings on the seventh sternite are regarded to represent the primitive gonopores (HEYMONS, 1890; WHEELER, 1893). We may, therefore, reasonably assume that the mesodermal part of the ducts, wherever these exist, do not extend beyond this segment. In the pupa of *T. castaneum*, the paired ectodermal ducts have been observed upto the anterior border of the sixth segment and, therefore, it appears likely that in this animal the union occurs somewhere in the fifth segment; and if the histological nature of the egg calyces and the oviducts in the adult has any relation with their origin we may regard the former to be mesodermal parts of the paired ducts.

WHEELER (1893) and GEORGE (1929) have described the median oviduct to be wholly or partly mesodermal in origin and NUSBAUM (1882) regards that it arises by the confluence of the originally paired ducts. Workers on beetles, however, observe that it arises from a single unpaired invagination of the hypoderm on the seventh or eighth segment. In

Tenebrio, SINGH PRUTHI derived it from the posterior border of eighth segment and found that it gets into communication with the spermathecal rudiment arising from the ninth sternite and bifurcates at its anterior end into two branches. The spermathecal rudiment finally closes and only one opening remains. RAKSHPAL (1946) also observed the development of the median oviduct (vagina) from the eighth segment but described the origin of the spermatheca from a horizontal division of the former and not independently. The vaginal opening later shifts to the ninth segment. HEBERDEY (1931) noted the two unpaired invaginations in *Hydroporous ferrugineus* on the seventh and eighth sternites respectively. METCALFE's observations are essentially in agreement with those of SINGH PRUTHI. The observations in *Tribolium* are similar to those made by SINGH PRUTHI and METCALFE, since in this insect also the median oviducts and parts of the lateral oviducts arise from an invagination on the eighth sternite. But it differs from that of RAKSHPAL since it shows two distinct invaginations and the final genital opening and the vagina are derived from the invagination on the ninth sternite and not by the shifting of the invagination of the eighth segment. It is also clear from the previous accounts and the author's own observations that, so far as the *Coleoptera* is concerned, there is no indication of a paired origin of the oviducts. SINGH PRUTHI's contention, therefore, that the primitive nature of the oviducts is paired is not supported from work in this order and is obviously due to his attempt to homologise the median oviduct with the ectodermal paired ejaculatory ducts.

In certain orders, e. g., *Odonata*, certain *Hymenoptera*, *Lepidoptera*, etc., the spermatheca originates from the median oviduct or vagina (NEL, 1929). In the *Coleoptera*, most workers (SINGH PRUTHI, HEBERDEY and METCALFE) have shown that the two arise separately. RAKSHPAL alone states that the spermatheca arises from the original invagination of the median oviduct by the division of the latter into two tubes by the appearance of a horizontal shelf. The observations in *Tribolium* confirm those of the previous workers showing clearly that the spermatheca and oviduct have separate origin, although the two get connected later on. It is also evident from the observations that the vagina of the adult is derived from the posterior part of the spermathecal rudiment.

It was BERLESE (1909) who contended that the spermatheca in the different groups of insects is not homologous and may arise from any of the seventh, eighth, ninth or tenth segments. SINGH PRUTHI considered that it primitively arises from the ninth segment. GEORGE (1929) and NEL (1929) supported BERLESE and regarded it an organ of greater functional than fundamental significance. It is true that the spermatheca arises from the ninth segment in a variety of insects including some *Orthoptera*, *Lepidoptera*, *Homoptera*, etc. Nevertheless, it has also been shown to originate from the eighth segment in *Heteroptera*, *Diptera*, certain *Orthop-*

tera, *Dermaptera*, *Isoptera*, etc. Evidently, while the origin in these forms shows a variation, it is characterised by a degree of constancy within the groups themselves. How could this be explained? It appears that the invagination on the ninth segment does not really represent the primary spermathecal invagination but a secondary development which may be called 'the invagination of the genital pouch' and which leads to the formation of structures like the vagina, bursa, etc., the original spermathecal opening having shifted from its original position on the eighth segment to this secondary position. The morphological distinction often clearly observed between the spermatheca, on the one hand, and the remaining parts of the genital pouch on the other, as well as the presence of similar invaginations giving rise to the vagina and the associated structures in various insects lend confirmation to this possibility.

2. The ovipositor. VERHOEFF (1893) was the first worker to suggest that the ovipositor consists of modified abdominal appendages. Of the three pairs of ovipositor lobes found in the majority of insects, he derived the ventral lobes from the telopodites or endopodites of the eighth segment, the dorsal lobes from the telopodites of the ninth segment and the lateral or posterior lobes from the coxites of the ninth segment. Although differing from him regarding the precise morphological nature, the view of appendicular origin has been generally accepted by all subsequent workers except ZANDER (1903). In the *Coleoptera*, the single pair of appendages found in the adult develop from a pair of rudiments in the larva. In *Tenebrio molitor*, SINGH PRUTHI (1924) showed that a pair of appendages which appeared on the ninth sternum in the larva give rise to the ovipositors. Likewise, METCALFE (1932) also showed that a single pair of appendages arises which later transforms into the ovipositor. Raksphal (1946) described a pair of groove like impushings on the ninth sternum which fuse in the median line to form the chitinous pouch in which the genital palps are produced as a pair of buds. In *Tribolium*, such impushing have not been observed and the ovipositors develop from a pair of simple appendages on the ninth sternum as described by SINGH PRUTHI or METCALFE. Thus, despite some differences in all these cases, it has been shown that the ovipositors develop from a single pair of ectodermal rudiments on the ninth sternum.

Homology of the Male and Female Reproductive Organs

The efferent system. In insects other than *Coleoptera*, most workers regard the vasa deferentia and lateral oviducts as mesodermal and hence consider them homologous. In *Coleoptera*, SINGH PRUTHI regarded that the entire vas deferens of the adult is ectodermal while a part of the lateral oviduct remains mesodermal so that the vas deferens is not homologous with the lateral oviduct. METCALFE (1932), however, has shown that the anterior part of the vas deferens upto the third, fourth or fifth

segment, is mesodermal. In *Tribolium* also, the present worker has shown that a part of the vas deferens is definitely mesodermal. It seems likely that the part of the vas deferens lying anteriorly to the seminal vesicle and the egg calyx are homologous structures.

Regarding the posterior part of the paired efferent passages, SINGH PRUTHI has contended that since the original position of the opening of the paired ejaculatory duct is on the eighth sternum, the vasa deferentia are homologous to the lateral oviducts on the eighth sternum as these arise as lateral outgrowths of the 'uterine invagination' of the eighth segment which is also originally paired. There is no observation except that of NUSBAUM (1882) showing paired origin of the uterus. In *Coleoptera*, all workers agree that the ectodermal ejaculatory duct arises from the ninth sternum and the median oviduct from the eighth segment. Therefore, there does not appear any reason for regarding these structures homologous, nor their forward derivatives, that is, the ectodermal vasa deferentia and the lateral oviducts respectively.

On the basis of his observations in *Carpophilus*, that in the early stages the gonopore is situated on the eighth segment from where it later shifts to the ninth segment, RAKSHPAL (1946) does not consider the gonopores in the two sexes as homologous. All other workers, however, are of the opinion that the invagination of the spermatheca or the genital pouch is situated on the ninth segment and hence I consider the male and female gonopores as homologous. This may not be equally true of other groups, as for example, the *Lepidoptera* in which the openings for copulation and oviposition remain separate.

While hardly any generalization can be made regarding the accessory glands in the two sexes, the investigations so far carried out in *Coleoptera* go to show that in the male, these arise, as a rule, from the primary genital invagination on the ninth sternite and in the female, from the invagination of the genital pouch or spermatheca, also arising from the ninth sternum. The belief, that certain accessory glands in male beetles are mesodermal, has already been disproved. It can, therefore, be stated generally that these glands in the two sexes of beetles are also homologous.

The external genitalia. SINGH PRUTHI is the only worker in *Coleoptera* who has described temporary "genital papillae" in the male. He regarded these as homologous to the coxites and the subsequently appearing permanent appendages to the telopodites. Since he also considered the ovipositors to represent the coxites, he could not homologise the median lobe or aedeagus with the ovipositors. Nevertheless, it has been shown by WALKER (1922) that the coxites have a tendency to fuse with the sternum. It seems, therefore, that in the majority of beetles, the coxites do not appear at all and the male copulatory apparatus consisting of the median and one pair of lateral lobes represents the telopodites. Again, since the nature of early development of the ovipositor greatly resembles that of the male genitalia

and the coxites tend to become absorbed in the female also, our only inference could be that the ovipositors are also homologous with the telopodites. The conclusion is, therefore, that such a male copulatory apparatus is homologous with the ovipositor of the female.

SUMMARY

The entire efferent system of *Tribolium* originally develops from two invaginations — the primary genital invagination or spermathecal rudiment formed on the posterior border of the ninth sternite in the larval stage and the uterine rudiment formed on the eighth sternite in the pupal stage. As the two invaginations develop, they form two tubes running one upon the other. Later, their median parts come in close contact with each other, the walls of the spermathecal rudiment go down to embrace the uterine rudiment and finally, the two become confluent, their anterior and posterior parts remaining distinct. Meanwhile, the anterior part of the spermathecal rudiment divides by a horizontal cleft into a dorsal part which gives rise to the spermathecal gland and a ventral part which gives rise to the spermatheca and the bursa; the anterior end of the uterine rudiment divides to form the lateral oviducts which joins with the mesodermal lateral oviducts. The posterior part of the uterine rudiment now disappears so that a single pore on the ninth segment is left.

The ovipositor arises from a pair of rudiments on the sides of the primary genital invagination. Later these differentiate into the coxites and styli.

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