NOTES ON THE ONTOGENY OF THE GENITAL TUBES IN COLEOPTERA.

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In 1912 Dr. Sharp and I, after an extensive anatomical study of the male genital tube of Coleoptera, published ¹ the conclusions we arrived at, along with details of this organ in most of the families of Coleoptera. Upon my return to Honolulu I started a series of observations on the development of this organ to see if the conclusions we had arrived at by anatomical studies could be sustained. Field work in the Orient took me away from Honolulu before I could finish this work and my notes remained unpublished; similar reasons prevent me from completing the work now, but as my observations may throw some light upon this subject I publish the following résumé.

My observations were made upon Rhabdocnemis obscurus, Carpophilus humeralis and Ccelophora inaequalis, and a few on Opatrum seriatum. Unfortunately the first three all have "ring-shape" tegmina and are highly specialized forms, and the observations on Opatrum were not extensive enough to demonstrate the development of the tegmen. It is to be hoped that a detailed study of the ontogeny of a more generalized "trilobe" form will be made.

In the early stages of the male pupa of these species the testes are attached, each by a fine testicular thread to a small mass of cells between the ninth and tenth sternites (1a). This cellular mass forms an invagination (genital invagination) of the hypoderm of the developing imago; it increases in size and the bottom grows

¹ Trans. Ent. Soc., Lond., 1912; III, 477-642; figs. 1-239.
into the cavity, forming the pregenital tube (tg. + mt. + is.); at the apex of this tube, where the testicular threads are attached, another invagination takes place forming the ejaculatory duct (1b, 2). At the base of the pregenital tube of *R. obscurus* a fold arises which develops into the tegmen (1c); the tube lengthens by the apex growing into the cavity of the invagination and the base through the tegminal fold, into the body cavity (1d). A constriction round the middle of the pregenital tube divides it into two portions, the apical portion forming the internal sac and the basal the median lobe (3). As the internal sac increases in length it lies crumpled up within the invagination and is not withdrawn into the median lobe until after the imago is fully developed (4). In Lamellicorns and Staphylinids I have also observed that the internal sac is not withdrawn into the median lobe until the imago is fully developed.

From each side of the base of the median lobe a long invagination of the ectoderm takes place, these become highly chitinized and form the median struts: at first broad, more like those in *Cerambycidae*, they afterwards become slender. From a medio-ventral point on the tegminal fold arises a larger invagination which also becomes highly chitinized (along with the tegminal fold) and forms the tegminal strut (1e). From a point on the anterior wall of the genital invagination a slender invagination takes place, grows round to the right side, becomes chitinized and forms the spiculum (3, 4, sp.). The basal portion of the walls of the genital invagination becomes chitinized (4a) and, together with the membranous apical portion (4b) attached to the tegmen, form the second connecting membrane. If the cædeagus be dissected out of a half or three fourths developed pupa and placed in acetic acid, so as to cause the cells to swell up, the true nature of the folds and invaginations forming the tegmen, tegminal and median struts and spiculum will be observable.

Lateral lobes are outgrowths from the tegminal fold. In *Carpophilus humeralis* they at first form two large rounded lobes, eventually growing to the pointed processes found in the adult (5). In the same insect the internal sac, which is exceedingly long, first grows to the mouth of the genital invagination and then grows into the body cavity; the flagellum at first is a short thick process (5 fg) and lengthens with the internal sac.
In Calophora inaequalis the lateral lobes are at first flat, broad processes (6); the median dorsal "cap piece" (7 tg) appears to arise by an outgrowth from the tegminal fold beneath the lateral lobes, the latter eventually attaining a more dorsal position and become long and slender. As the median lobe lengthens it grows into the body cavity, but as its base is attached to the median strut it assumes the curved shape common to this family (7).

The armatures on the internal sac arise as folds and chitinizations, and sometimes are continued on to the median lobe; this is not strange as the median lobe and sac are all one at first.

These observations of the ontogeny of the genitalia support the conclusions Dr. Sharp and I came to after extensive anatomical studies, that this organ is a median tube with folds and chitinizations, and lend no support to the theory that one or more sternites go to its composition.

In the more generalized forms of Coleoptera (8) there are nine distinct tergites and nine distinct sternites. Below the last tergite lies the anal tube (9 an) which in some forms is well developed and chitinized, and is considered by some to represent the tenth tergite and sternite. Berlese even makes out another beyond this in Lucanus cervinus and calls it the eleventh tergite. In Enarsus bakewelli there is a distinct plate between the anus and the cœdeagus and in Cupes clathratus there is a large pair of appendages which would indicate segmental appendages; but in the vast majority the anal tube is membranous and not differentiated from the second connecting membrane. In more specialized forms the ninth sternite is reduced and sometimes forms a T-, Y- or V-shaped sclerite. In R. obscurus nothing is left of it, unless it be the spicule.

In Anomala orientalis and allied species the large tambour tegmen is ventral during development, and so has the appearance of being a sternite; in this case it would have to be the tenth sternite and the median orifice would be posterior to it, but we see by the ontogeny that this lies between the ninth and tenth. The tegmen in Ædemeridae is the most sternite-like one of all that I have examined and a knowledge of its development would be of interest.

The probability of a tergite taking any part in the formation of the cœdeagus appears to me to be so remote that, if it were not for the fact that such a theory is widely maintained, I would not confute it.
In insects the anus is the direct development of the proctodæum, and how a tergite can take part in the formation of a tube on the ventral surface, without the position of the anus shifting during ontogeny, I cannot understand. The onus of evidence lies with those who claim such a development.

Dr. Hopkins in a recent work remarks:

"It is quite evident that element a [median lobe] represents the tenth sternite, b [armature on internal sac] the tenth tergite, c [tegmen] the ninth tergite, and d [spicule] the ninth sternite, while b1 and b2 [apical armature on internal sac] appear to represent elements of either the tenth tergites or of both the tenth tergite and tenth sternite. It might also be well to consider in future investigations the possibility of their representing the tenth pleurites or even an additional eleventh segment."

To me none of these statements are at all evident, and some are quite illogical; all available evidence is against them. The most important part of the organ, the internal sac, is not accounted for, perhaps because it is membranous. Chitinization is often looked upon as the important thing whilst the membrane is disregarded, whereas the latter is the important part. This is certainly so in the òedeagus of the vast majority of Coleoptera, the internal sac being the chief organ and the armature (end plates) but secondary.

As before remarked the stenazygos is formed by the invagination of the spot to which the threads from the testes are attached. The zygos is supposed to be of mesodermic origin, but it appears to develop continuously from the stenazygos.

In the female pupa of *R. obscura* the genital invagination takes place down the middle of the ninth sternite. The "ovipositor" is composed of modified body segments or of sternites, the genital styles being developed directly from the appendages of the ninth segment of the larva and pupa. The ovary is at first composed of two small cells which lengthen out and meet together at one end; these are in touch with one another and the end of the oviduct for some time before the walls break down and communication between the two ovaries and the duct is established. The oviduct appears to be a continuous development of the azygos or uterus and there-

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2 Explanatory remarks in brackets are by the present writer.
fore of ectodermic origin. The spermatheca arises from the azygos or uterus.

**Conclusions.**

My studies of the ontogeny and anatomy of the male genital tube in Coleoptera lead me to the following conclusions: those relating to the internal sac naturally do not apply to those forms where it is not differentiated.

The Óœdeagus arises as a tubular organ at the base of an intersegmental invagination between the ninth and tenth sternites. By transverse folds it differentiates into three sections: a basal or outer section (tegmen), a median segment (median lobe) more or less surrounded by the tegmen, and a distal segment (internal sac), which is generally invaginated within the median lobe. Cases occur in different families in which each of these segments is reduced or absent.

There is no evidence that one or more sternites take part in the composition of the Óœdeagus; the only sternite that could do so is the tenth, but it is more likely that this becomes dechitinized (except in Enarsus) and incorporated into the anal tube or the second connecting membrane.

No tergite takes part in the composition of the Óœdeagus.

Where the ninth sternite is well developed there is no spicule, but it often has a pair of projections, or a single projection, from its base, and the latter may be represented by the spicule in such forms that have no ninth sternite.

Figures 1a–e are diagrammatic, figures 2–9 are all drawn from specimens with the aid of a camera lucida.

**EXPLANATIONS OF FIGURES.**

Fig. 1a to e. Diagrammatic representation of the development of the male Óœdeagus.

Fig. 2. Early stage of genitalia of $\sigma^+$ pupa of *R. obscura*.

Fig. 3. Later stage of same.

Fig. 4. Nearly mature stage of same.

Fig. 5. Early stage of genitalia of $\Phi^+$ pupa of *Carpophilus humeralis*.

Fig. 6. Early stage of genitalia of $\sigma^+$ pupa of *Ccelophora inaequalis*.

Fig. 7. Later stage of same.

Fig. 8. Lateral view of abdomen of *Dermestes vulpinus*.

Fig. 9. Ninth segment of same.