

XI. *The comparative anatomy of the male genital tube in Coleoptera.* By D. SHARP, M.A., F.R.S., and F. MUIR, F.E.S.

[Read February 7th, 1912.]

PLATES XLII-LXXVIII.

ARRANGEMENT OF MEMOIR.

- I. INTRODUCTORY.
- II. ORISMOLOGY AND TECHNIQUE.
- III. MORPHOLOGY.
 - A. ANATOMY.
 - B. GENERAL.
- IV. FUNCTION.
- V. TAXONOMY AND PHYLOGENY.
- VI. ALPHABETICAL INDEX TO FAMILIES.
- VII. EXPLANATION OF PLATES.

I. INTRODUCTORY.

THE object of this memoir is to review the structure of the male genital tube throughout the Order Coleoptera. This is not equivalent to a review of the male copulatory organs. The modifications of the abdomen itself are extremely extensive and varied, but we have perforce omitted them, because the time at our disposal was scarcely adequate for the accomplishment of the work, the results of which are here presented.

Mr. F. Muir, having returned to England for a year's vacation in order to recruit his health after a long period of arduous entomological work in the tropics, joined the senior author at Brockenhurst, and the two combined their efforts for the production of this memoir.

A work of the kind is almost indispensable in the present state of Coleopterology, and the authors hope that it will be received as a much needed contribution to a great subject. A subject too as to which, notwithstanding its slight advancement, great misconception is prevalent.

The work has nearly all been carried out in the little laboratory attached to the residence of the senior author at Brockenhurst, and in a period of little more than twelve months. Each of the authors has devoted some independent work to it since Mr. Muir's departure for Honolulu, and it is hoped that this fact will be accepted as some excuse for certain inconsistencies that may be discovered by a severe critic.

The drawings that form so important a part of the work have all been made by the junior author, and consequently on him has fallen the difficult task of deciding as to the ventral and dorsal aspects of the structures. This is far from easy; it is, in fact, beset with sources of deception, as may be seen from the note (as to a discovery made by the junior author) placed in front of our descriptions of the family *Scarabaeidae*.

A primary object of the authors being to make a review extending over all the Order, they could only hope, in the too short time at their disposal, to get together the necessary material by the aid of their friends. Appeals were therefore issued with this object, and met with the most obliging responses; and we naturally desire to tender our warmest thanks to all those who have helped us in this and in other ways. We must mention first of all Mr. G. J. Arrow of the British Museum of Natural History; the only limit to whose kindness has been the reluctance we felt as to taking his attention from more important duties.

Mr. Antwerp E. Pratt made over to us a considerable collection of Coleoptera from New Guinea. This enabled us to examine a number of specimens in the case of certain species, and has been most useful, though, for our purpose, it has been subject to the drawback of several of the forms being new or little-known species.

Mr. J. C. Moulton of Sarawak, Mr. T. Bainbrigge Fletcher of Pusa, Mr. Arthur M. Lea of Tasmania, Mr. W. W. Froggatt of Sydney, sent us useful material. Herr Edmund Reitter of Paskau was so good as to select from his stores and send to us several forms we specially needed. In our own country Commander Walker and Mr. G. A. K. Marshall provided important material. Mr. Geo. Lewis has given us a few interesting forms. Mr. Ford of Bournemouth, and Mr. Janson of London gave themselves considerable trouble in the selection of speci-

mens for us. Mr. Hugh Scott of Cambridge University assisted us in every way that we asked.

Mr. G. C. Champion and Mr. C. J. Gahan have been very good by helping us in the disagreeable task of naming our heterogeneous material.

As regards the taxonomical and phylogenetic portions of the memoir it is desirable that we should say that they are drawn up to display the part that a knowledge of the fertilising structures should have in these two departments of Coleopterology. The senior author has for many years taken an interest in the taxonomy and phylogeny of *Coleoptera*, and it would therefore be absurd to pretend that, apart from consideration as to the sexual organs, he is in complete ignorance as to the bearings of other branches of anatomy, of physiology, of ethology and of ontogeny on the two departments mentioned. But the junior author is comparatively a recent student of these departments; and the senior author, therefore, gave him a free hand in drawing up the tables, and has modified them but little. They represent, therefore, fairly well the results that may be obtained in taxonomy and phylogeny from a preliminary study of the male genital tube. We hope that we have made it clear, in other parts of the paper, that our work is only a very imperfect introduction to this comparatively narrow field of inquiry. But we believe the subject will prove to be of great importance when combined with the results derived through other lines of investigation. There is one point, however, in the memoir that has not been based on study of the aedeagus, viz. the families we have made use of. Though we shall have in the course of this memoir to propose several changes as to the families of Coleoptera, it must not be supposed that the families here dealt with have been decided on from the point of view of the structure of the genital tube. The forms studied were selected in the first instance simply by our desire to study these structures throughout the whole Order. We may, however, say that though certain changes will have to be made, yet our impression is that most of the families at present in use in Coleopterology will have their validity substantiated by a continuance of this study.

The second part of our morphological section deals with the nature of the male organs; and under the heading *Phytophagoidea* in the section phylogeny some more

speculative opinions on the same subject are given; but a brief elementary statement on this point will probably be found useful here. Two simple diagrams (figs. 239 and 239a) have been made with the same object. They are really diagrammatic and do not represent any particular form.

Let a glove be taken, a hole pierced in the tip of one of its fingers, a slender tube attached around this hole, this tube being placed inside the finger and prolonged into the hand-part of the glove: and we have before us a rough model of the genital tube.

This structure lends itself to modification in the readiest manner. By traction on the slender tube the finger of the glove can be entirely drawn into the hand, with the result that the distal orifice becomes proximal. Let the glove finger be restored to its natural position and some hard patches be put on it, and the operation of invagination be again repeated, and it will be noted how protean this simple arrangement can become. Further make some small folds on the finger, and suppose these to grow out (after the fashion of the horns and processes on the heads of Lamellicorn beetles) and the reader will then have a general idea of the structures we are about to consider.

The finger of the glove can be made by some folds to collapse in several layers, like a shut-up nautical telescope, and this telescopic arrangement can be carried to such an extent that Straus-Durckheim (*Melolontha vulgaris*, pl. vi, f. 1) shows in a section of the telescopically collapsed tube no less than eleven superposed layers.

We scarcely need to remark that the retraction and eversion of the genital tube are not brought about by force applied to the duct.

We have had considerable difficulty in arranging our matter in a comprehensible sequence, and the different sections of the memoir are not conformable in this respect. We have endeavoured to diminish the inconvenience resulting from this by means of an alphabetical index of the names of families and groups placed immediately before the explanation of the figures.

In the course of this memoir we have occasion to refer the reader to a passage of the historian Gibbon, relating to the Empress Theodora, the consort of the Emperor who rebuilt the great cathedral of Saint Sophia at Constantinople. We may fittingly close our introductory

remarks by a quotation from the same chapter of this immortal author. He says, "A magnificent temple is a laudable monument of national taste and religion, and the enthusiast who entered the dome of St. Sophia might be tempted to suppose that it was the residence, or even the workmanship of the Deity. Yet how dull is the artifice, how insignificant is the labour, if it be compared with the formation of the vilest insect that crawls upon the surface of the temple!"—Gibbon, "Decline and Fall of the Roman Empire," chap. xl.

II. ORISMOLOGY AND TECHNIQUE.

The following is a list of some of the terms we have applied to parts of the male genital tube, and we add a few synonyms used by other writers. The letters in brackets are those made use of in the plates.

This section is concluded by some critical remarks.

- AEDEAGUS.** The median lobe and tegmen together. It is the Edeagophore of Blaisdell.
- AZYGOS**, or the azygotic portion of the male genital tube. It comprises all the unpaired portion of the tube from the body wall to the divergence of the seminal ducts, where the zygotic portion, or efferent ducts, ends (*b-d* and 5-1, fig. 239).
- BASAL-PIECE** (*bp*). The basal part of the tegmen. It is the "basale" (Blaisdell); external lobes (Packard); basalplatte (Verhoeff); tambour (Straus-Durckheim).
- EJACULATORY DUCT** (*ej*) or stenazygos is the slender portion of the genital tube from the seminal ducts to the internal sac or eurazygos.
- EURAZYGOS** (*e-d* and 5-1, fig. 239). The enlarged portion of the genital tube.
- FIRST CONNECTING MEMBRANE** (*cm1*). The membrane connecting the median lobe to the tegmen.
- INTERNAL SAC** (*is*). The enlarged portion of the azygos which is more or less evaginated during copulation. It is the sac interne (Jeannel); praeputialsack (Verhoeff), and forms part of the ejaculatory duct of most writers.
- LATERAL LOBES** (*ll*). The distal portion of the tegmen. In the generalised trilobe type they form two free processes lateral of the median lobe and often en-

veloping it. They are the "deux branches de la pince" (Straus-Durckheim); mesostili in *Procrustes*, ipofallo in *Lucanus* and perifallo in *Dytiscus* (Berlese); apicale (Blaisdell), lateral lobes (Packard), Parameren (Verhoeff).

MEDIAN FORAMEN (*mf*). The aperture, or lumen, at the base of the median lobe through which the ejaculatory duct passes.

MEDIAN LOBE (*ml*). The central portion of the aedeagus upon which the median orifice is situate. It is the penis of Straus-Durckheim, Verhoeff, Packard and many other writers, Körper (Lindemann), body (Hopkins), ipofallo in *Procrustes* etc., and penis in *Oryctes* (Berlese).

MEDIAN ORIFICE (*mo*). The opening, or area, on the median lobe through which the internal sac is evaginated. It is the "Mundung ductus ejaculatorius" (Verhoeff), fornix edeagi (Blaisdell) and apical opening (Hopkins).

MEDIAN STRUT (*ms*). A single strut, or a pair of struts, proceeding from the basal part of the median lobe. In some cases they are articulated to the median lobe, in other cases they actually form part of the median lobe without articulation or line of demarcation.

POINT OF ARTICULATION (*pa*). The point on the median lobe to which the lateral lobes are attached. In many cases the median lobe and tegmen are connected by intervening membrane and there is no point of articulation.

SECOND CONNECTING MEMBRANE (*cm2*). The membrane connecting the tegmen to the termination of the abdomen. It is the prepuce of Straus-Durckheim (*Melolontha vulgaris*).

SPICULE (*sp* fig. 224a). A sclerite attached by one end to the second connecting membrane. In many cases it is Y- or T-shaped. It is the Stengel (Lindemann), spiculum gastrale (Verhoeff), rod or fork (Hopkins), and is considered by some as being the last sternite. It is not infrequently similar in shape to another sclerite that pertains to another layer of the genital tube.

STENAZYGOS. Is the stenazygotic or slender portion of the azygos (*b-c*, fig. 239).

TEGMEN (*tg*). The term applied to the lateral lobes and

basal-piece together. It is the ring (Hopkins), Gabel (Lindemann).

VENTRAL PLATE (*vp*, fig. 19, etc.). A sclerite on the anterior ventral surface of the basal-piece in some Lamellicorns. In some cases the lateral lobes are consolidated to its anterior edge. The chitinisation of this part varies much.

ZYGOS. Zygotic portion of the male genital tube; and is formed by the two seminal ducts (*a-b*, fig. 239) proceeding from the testes.

METHOD EMPLOYED.

In preparing this memoir it was necessary to make use of a great deal of dried material, some of it fifty and sixty years old, as our time was limited and we could not procure fresher specimens. In such cases we found the following methods acted very well and, if care was used, did not destroy the specimen. The dried specimens were placed in water and allowed to soak for a time according to the size and condition of the specimen, the water being heated if necessary; when thoroughly relaxed the aedeagus was dissected out, either through the opening between the last dorsal and ventral plates, or the last segment was taken off, or the abdomen was taken off at the base, the aedeagus extracted through the basal foramen and, when necessary, the abdomen stuck on to the thorax again. The aedeagus was then placed in weak caustic potash for a time when the muscles would swell up and could then be dissected; in cases where it was necessary to clear off all the muscles the caustic potash was used very strong. To get the internal sac evaginated was a more difficult matter; but with care it was possible to do this by the use of localised pressure, and with the aid of a very finely pointed syringe. By inserting the fine point into the median foramen and gently applying pressure the internal sac can be forced out in a manner, if not quite natural at least near enough to study its shape and structure.

With fresh material it was a much easier matter, especially with bulbous forms such as are found among the Staphylinidae; by placing the aedeagus in water and gently pressing upon the bulb the internal sac can be made to evaginate in a perfectly natural manner.

To study the position taken up by the internal sac

within the uterus during copulation it was necessary to take the beetles in copula, kill them in a strong killing-bottle and then dissect out the whole female organ with the internal sac of the male still in situ.

We may here emphasise the great importance of extracting the structures without injury to the basal parts. It is necessary to give this caution because it too often happens that the dissections of these parts that exist in various collections have been made only with a view to examining the apical portions of the structures. Hence the basal parts are often found to have suffered serious injury.

As there can be no doubt that the nature of the genitalia is destined to play a prominent part in the systematic study of Entomology, the terms to be used in it should be carefully considered. At present great confusion prevails. This is not a matter for surprise when the difficulties that exist are grasped. The male structures form parts and accessories of a genital conduit of which the female genitalia are the continuation and completion. Hence the male parts are really only comprehensible when studied in connection with the female parts; and this, moreover, when the two are functioning. The parts, in fact, have to be restored to the condition they are in during copula.

The terms used in this memoir were of necessity selected soon after the commencement of our work, and we consider it advisable here to state how they appear to us at the conclusion of our undertaking.

AEDEAGUS. This is a most convenient and useful term for the combination of sclerites in the two adjacent layers of the male tube. The term was, we believe, introduced by M. A. C. M. E. Foudras (Altisides, 1859, p. 32). It is probably derived from the Greek *ἄδεια*, signifying the genitals. The use of the Greek word may be seen in the notorious passage of Procopius quoted by Gibbon in footnote 24 of chap. xl of "The Decline and Fall." We doubt whether a better term could be found for this middle complex of male sclerites, and we expect that a word will have to be invented for the corresponding (if not homologous) female sclerites.

MEDIAN LOBE. This term is not free from serious objections, but it is far superior to that of "penis," which applied to Insecta is totally fallacious. The part in

Insecta that most nearly approximates to the Vertebrate penis is the internal sac, the knowledge of which has been almost nothing until its recent inauguration by Jeannel. The median lobe appears to be sometimes a complex or amalgamation of more or less individualised sclerites. (Cf. *Hydrophilus*.)

LATERAL LOBES. Though a very suitable term for the parts in the various trilobe forms, it is inappropriate in cases where the projections (if homologous at all) are medianly situate. Paramere is quite as good as lateral lobes. Cornua (meaning cornua tegminis) is also not free from objection, and accessory process is rather cumbersome. Tegminal lobes might do if the term tegmen be itself accepted.

BASAL-PIECE. Perhaps this term may stand till more is known about the cases in which it is two pieces, and those in which it appears to be absent.

INTERNAL SAC. Probably the term Vesica might be preferable. But this part of the conduit is so protean in form and development that it might be better to invent a term indicating a structure that is predominantly membranous.

TEGMEN. This term seems convenient and adequate for the layer of sclerites external to the median lobe. The elytra of grasshoppers are frequently called tegmina, but we do not think this objection to our use of the term a serious one.

CONNECTING MEMBRANES. This term cannot be commended. It gives the idea that the sclerites are the important structures. But the tube may exist without sclerites and is it then a connecting membrane?

Other terms (such as Prepuce) that have been used for various parts are totally unsuitable. We consider that it is premature to endeavour to establish permanent terms for the parts of the complex genitalia of Insects till the various Orders have been more thoroughly examined and compared.

chitinous on the outer edges (*ms*) and membranous down the middle (*m*). Tegmen forming a ring, with a large dorsal cap-piece slightly emarginate at tip, and a keel-like strut on the ventral aspect.

Internal sac long with two small pads (*a*) of chitinous short spines.

Caryoborus nucleorum (Pl. LXXII fig. 197).

Median lobe large, the distal two-sevenths forming a flattened tube, with the ventral edge of the median orifice pointed and projecting beyond the dorsal edge, the basal five-sevenths forming a large sclerite on the dorsal aspect. Tegmen forming a ring, with lateral lobes consolidated together forming a cap-piece, slightly emarginate at tip; at the base of the lateral lobes and consolidated to them there is a large, inflated semi-chitinated membrane (*a*) which is consolidated to the median lobe; this may represent a chitination of the first connecting membrane. On the ventral side is a Y with a long strut (*b*). Internal sac long, without complex armature.

This family comes within the Chrysomelid group.

Family CHRYSOMELIDAE.

Forms examined: As this is one of the most extensive divisions of Coleoptera, we arrange the species specially studied in thirteen groups.

1. ORSODACNINAE. *Orsodacne nigriceps* Latr., England.
2. DONACIINAE. *Donacia (Plateumaris) sericea* L., and *comari* Suffr., *D. bidens* Ol., *semicuprea* Panz., and *lemnæ* Fabr., England.
3. SAGRINAE. *Mecynodera balyi* Clark, Australia. *Carpophagus banksiae* Macl., Australia. *Diaphanops westermanni* Schönh., Fremantle, Australia. *Polyoptilus* sp. aff. *erichsonii* (not in Brit. Mus. Coll.), Australia. *Sagra amethystina* Guér. var., W. Africa. *Sagra nigra* Ol., Assam.
4. TIMARCHINAE. *Timarcha geniculata* Germ., Asturias. *T. tenebricosa* Fabr., England.
5. CRIOCERINAE. *Crioceris asparagi* L., England.
6. CLYTHRINAE. *Labidostomis longimana* L., Istria. *Clythra laeviuscula* Ratz., Pyrenees. *Lachnaea palmata* Lac. ? Pyrenees. *Saxinis saucia* Lec., California.
7. CRYPTOCEPHALINAE. *Cryptocephalus aureolus* Suffr. England. *C. asturiensis* Heyd. ? Asturias.

8. EUMOLPINAE. *Eumolpus surinamensis* F., S. America. *Chrysochus pretiosus* Fabr., Bohemia. *Glyptoscelis cuprascens* Lec., California.

9. CHRYSOMELINAE. *Orina elongata* Suffr., and *O. speciosa* L., Piedmont. *Chrysomela sharpi* Fowl., Scotland. *Gastrophysa raphani* Herbst., Scotland. *Paropsis variolosa* Marsh.?, Sydney. *Phytodecta 5-punctata* L., Piedmont. *Phyllodecta vitellinae* L., and *P. vulgatissima* L., England and Scotland.

10. GALERUCINAE. *Diabrotica soror* Lec., California. *Galerucella* spp., England.

11. HALTICINAE. *Haltica coryli* All., England.

12. HISPINAE. *Spilisma imperialis* Baly ?, Australia. *Cephaloleia* sp. aff. *nigropictae* Baly ?, S. America.

13. CASSIDINAE. *Mesomphalia pascoei* Baly, Ecuador. *Aspidomorpha 4-maculata* Ol., Nyasaland.

Figs. 198 to 216 Pls. LXXII, LXXIII, and LXXIV, relate to these forms.

Orsodacne nigriceps (Pl. LXXII fig. 198).

Distal half of the median lobe forming a flattened tube, with the ventral edge of median orifice slightly cleft at tip, and projecting beyond the dorsal edge, the basal half formed of two long struts on dorsal aspect. Tegmen forming a ring-piece with cap divided at tip. Internal sac long, projecting much beyond the median foramen. A slightly chitinated cone at the apex carries the opening of the ejaculatory duct.

The two struts of the median lobe and the long sac place this nearer to the Longicorn type than to other Chrysomelidae.

Donacia sericea (Pl. LXXII figs. 199, 199a, 199b).

Median lobe large, chitinous, tubular and curved, with the median orifice at apex and the median foramen large, occupying the ventral face of the basal half (*mf*). Tegmen forming a ring-piece; on the dorsal side the cap forms a slender lobe with hairs at the tip on the ventral face. The strut forms a large keel. Internal sac large with complex armature at its apex. This armature consists of a pair of lateral curved plates (*c*) and a median process (*b*) through which the ejaculatory duct passes and opens on its tip, a chitinous block (*d*) supports the structure at its junction with the membrane.

D. comari.

Is very like *D. sericea* but the cap is divided at the tip. The arma-

ture on the apex of the internal sac differs in details (Pl. LXXII figs. 200, 200a).

D. bidens and *D. semicuprea*.

Aedeagus very like *D. comari*, but the armature on the sac is totally different (Pl. LXXIII, figs. 201 and 202).

D. lemnae.

Has the cap long and thin. The armature on sac is distinct from those described above (Pl. LXXIII fig. 203).

Carpophagus banksiae (Pl. LXXIII figs. 204, 204a).

Median lobe large, chitinous, tubular and curved; the median orifice at apex, the median foramen occupying the ventral basal half. Tegmen forming a ring-piece, with a very long lobe as cap. Internal sac large with complex armature at apex (204a) consisting of a pair of complex side lobes (c) and a slender median process (b) through which the ejaculatory duct passes and opens on its apex.

Mecynodera balyi.

Median lobe well chitinised, curved and fairly short, forming a flattish tube; the ventral edge of the median orifice projecting beyond the dorsal edge: median foramen large, occupying the ventral portion of the basal half. Tegmen forming a ring-piece, with large cap apically deeply divided and furcate; the median strut or keel on the ventral aspect, of median size. Internal sac not extending through the median foramen. Armature at apex of sac consisting of a slender median process on which the ejaculatory duct opens, two chitinous plates embedded in the membrane below the median process, and a Y-piece above also embedded in the membrane.

Polyoptilus sp.

This is very like *Mecynodera* but the cap is less furcate at the tip.

Diaphanops westermanni.

This is very like *Polyoptilus* sp. ?; the cap is differently shaped, being broader distally and bearing there a small emargination; the armature at the apex of the internal sac (Pl. LXXIII fig. 205) consists of a slender process on which the ejaculatory duct opens (a) protected by a stronger and broader process above it (b), a broad plate (c) grooved along the centre supports the membrane below and another and smaller plate (d) supports the membrane above. N.B.—In the figure, (d) and its pointing line are imperfect.

Sagra amethystina (Pl. LXXIII figs. 206, 206a).

Median lobe well developed, chitinised, tubular and curved; the ventral edge of the median orifice projecting beyond the dorsal edge, pointed but not cleft. There is a very long prolongation of the tegmen dorsally, and this is grooved along the middle, and has a short, narrow division at tip. Internal sac not projecting beyond the median foramen, which is large and occupies the ventral portion of the basal half of the median lobe. Sac complex in shape, with two sclerites on each side of the base (a—a) to support it; armature at apex consisting of a slender median process on which the ejaculatory duct opens, with another brush-like process above it and chitinous sclerites supporting its base.

Sagra nigrata.

Of the same type as *Sagra amethystina*; the armature at apex of sac consisting of a slender process on which the ejaculatory duct opens, protected by a wider and curved process above, broadened at the base where it is attached to the sac; on each side is a patch of stiff hairs.

Crioceris asparagi.

Median lobe well developed and chitinised, with the ventral lip of the median orifice projecting slightly beyond the dorsal edge; the median foramen occupying the greater part of the ventral surface of the basal half. Tegmen consisting of a small Y-piece and a moderate-sized strut, or keel, on ventral aspect, dorsal part entirely membranous and without any trace of prolongation as cap. Internal sac short with a strong chitin-piece at apex on which the ejaculatory duct opens.

Labidostomis longimanus.

Median lobe forming a well chitinised, short, nearly straight tube, slightly flattened on dorsal side of distal half, with the ventral edge of the median orifice projecting beyond the dorsal edge; median foramen large, occupying the ventral aspect of the basal half; a slight constriction divides the basal and distal halves. Tegmen consisting of a small shield-shaped-piece, keeled along the middle on the inner side, on the ventral aspect of median lobe, without traces of lateral lobes. Internal sac short, with complex chitinous armature which closes the median orifice. Stenazygos excessively elongate, many times longer than the whole insect.

Clythra laeviuscula (Pl. LXXIII fig. 208).

Median lobe well developed and chitinised, forming a tube, the

distal half flattened on the dorsal aspect and bearing three keels, a median and a pair of lateral; the ventral edge of the median orifice coming to a small point but not projecting far beyond the dorsal edge; slightly constricted about middle; median foramen occupying the ventral aspect of the basal half. Tegmen in form of a shield-shaped sclerite, with the corners not meeting on the dorsal face, and no trace of prolonged cap. Internal sac small with complex armature consisting of a long chitinous flagellum (*a*) and a pair of strong, curved, chitinous spines (*b*). Stenazygos not investigated.

Lachnaea palmata.

In this species the median lobe is well developed, curved near the apex, but straight beyond. The armature on sac consists of a small spine-like flagellum and a pair of large spines, with a complex process closing the median orifice consisting of a plate bearing a median curved tongue and a pair of lateral, rounded plates. The tegmen is Y-shaped, the strut being slender and bifurcate at end.

Saxinis saucia.

Median lobe very slightly curved, with the ventral edge of median orifice pointed and extending slightly beyond dorsal edge; the median orifice closed by the armature on the sac. Median foramen occupying the ventral portion of basal half. Tegmen V-shaped.

Cryptocephalus aureolus.

Median lobe well developed and chitinised, the distal half being considerably flattened; the ventral edge of median orifice drawn out to a fine, flattened point, with the tip curved downward, projecting much beyond the dorsal edge; median foramen occupying the whole of the ventral side of the basal half. Tegmen shield-shaped, with a keel along the middle of the inner side. Armature on sac not examined.

Cryptocephalus asturiensis?

Of the same type as *C. aureolus*, but the ventral edge of the median orifice drawn out into a blunt point and not turned downward. Armature on sac complex, that at the base closing the median foramen; at the apex there are two broad, bifurcated spines and a flattened median sclerite, but no flagellum.

Eumolpus surinamensis (Pl. LXXIII figs. 207, 207*a*).

The apical third of the median lobe strongly curved and slightly flattened, the ventral edge of the median orifice pointed and projecting far beyond the dorsal edge, the basal two-thirds consisting

of a broad curved piece on the dorsal side, the ventral part being occupied by the median foramen; between the distal third and the basal two-thirds there is a strong constriction. The tegmen consists of a Y-piece, with a long strut on the ventral aspect and only membrane on the dorsal, and without trace of cap-piece. Internal sac long, with apical armature consisting of a twisted chitin plate (*a*) through which the ejaculatory duct runs, and opens on its apical edge (207*a*). Beyond (basally) the sac the duct forms a long chitinous tube, four times the length of the aedeagus, and then enlarges somewhat so as to become a slender chitinous chamber.

This is very remarkable on account of the extreme elongation of the stenazygos. Apparently this part, which is at least four or five times as long as the eurazygos, is also made as slender as possible. It is difficult to say whether it is not rather an altered part of the eurazygos than a specialisation of the duct.

It may possibly function as a flagellum, invaginated during inactivity. A thorough examination of this structure and its function in Eumolpidae would be very interesting. In *Chrysochus pretiosus* this stenazygos (or pseudostenazygos) is quite as slender as in *Eumolpus*.

Glyptoscelis cuprascens.

Median lobe well developed and chitinous, bent at right angles about middle, the distal half forming a flattened tube, with the ventral edge of the median orifice drawn out beyond the dorsal edge and pointed; the median foramen placed on the ventral aspect of the basal half. The dorsal face of the basal half cleft down the centre making it into two struts. Tegmen forming a broad shield-shaped sclerite, the apex of the shield being attached to the median lobe and the wide part extending ventrally, not meeting on dorsal side of median lobe and having no trace of cap-piece. Sac and stenazygos not examined.

Orina elongata (Pl. LXXIII fig. 209).

Median lobe well developed and chitinised, curved, tubular, with the ventral edge of the median orifice drawn out to a point greatly beyond the dorsal edge, thus placing the median orifice on the dorsal aspect; median foramen smaller than in Eumolpinae, etc., occupying only the basal sixth of the ventral aspect. Tegmen consisting of a small V-shaped sclerite, not meeting on dorsal aspect and showing no trace of cap-piece. Internal sac of moderate size, with a strongly chitinised flagellum on which the ejaculatory duct opens.

Orina speciosa.

Median lobe forming a long, fairly slender tube, slightly curved; ventral edge of median orifice bluntly pointed, turned downward and projecting slightly beyond the dorsal edge, which is rounded and turned upward; median foramen occupying the ventral face of the basal sixth. Tegmen forming a V-piece, not meeting on dorsal aspect and without any trace of cap-piece. Internal sac nearly as long as the median lobe with a fairly thick flagellum arising from the apex, and through which the ejaculatory duct passes, nearly as long as the sac.

Gastrophysa raphani.

Median lobe very short and broad; the ventral edge of median orifice pointed and projecting beyond the dorsal edge; the dorsal edge forming a flat fold, or lid, over the orifice, thus giving it a horse-shoe shape. Tegmen forming a V-shaped piece on ventral aspect of the median lobe. Sac not examined.

Chrysomela sharpi.

Median lobe well developed and chitinised, with the ventral edge produced somewhat beyond the dorsal edge and rounded, the median foramen occupying about one-sixth of the ventral basal portion. Tegmen forming a semi-ring without trace of cap-piece. Internal sac large, with a curved, slender flagellum on which the ejaculatory duct opens.

Paropsis variolosa? (from Sydney) (Pl. LXXIV figs. 210, 210a).

Median lobe well developed and chitinised and flattened horizontally; the ventral margin of the median orifice bluntly pointed and produced far beyond the dorsal edge, thus placing the orifice in a dorsal position; median foramen occupying one-sixth of the basal ventral portion, which is slightly constricted off from the distal five-sixths. The chitinisation of the dorsal edge of the median orifice is continued on to the base of the internal sac as two short broad strips (a). Tegmen forming a slender semi-ring-piece, with only a minute strut (s) and not meeting on the dorsal aspect. Internal sac large, bearing a strong, curved flagellum on which the ejaculatory duct opens. This form comes near to *Orina*.

Phytodecta 5-punctata.

Median lobe tubular and slightly curved; the lateral edges of the median orifice produced into two flattened, curved spines which curve over the orifice; median foramen occupying the ventral basal

third. Tegmen V-shape. Internal sac nearly as long as the median lobe, bearing at its apex a curved flagellum slightly longer than the sac.

Phytodecta olivacea.

Is near to *P. 5-punctata*, but the lateral spines at the edge of the median orifice are greatly flattened, meet on the median ventral line, and curve downward, and are asymmetrical, the right one being produced into a short point on the outer side and the left rounded. Internal sac bearing a flagellum.

Phyllodecta vitellinae (Pl. LXXIV figs. 212, 212a, 212b).

Median lobe stout, tubular, constricted one-fourth from the base; the ventral edge of median orifice produced beyond the dorsal edge and bluntly pointed; median foramen occupying the ventral aspect of the basal fourth, on the dorsal aspect of the base is a deep emargination. Tegmen forming nearly a complete ring, but not quite complete on the dorsal face, no trace of cap-piece. Internal sac short, bearing armature in the shape of a flat, curved spine on each side (a) and a median complex plate (b).

We have examined several of two varieties that go under this name, a blue variety from Forbes sand-hills and a southern one, with a bronzy green form; in these we find a constant difference in the shape of the emargination on the dorsal edge of the base of the median lobe, the northern variety has a round emargination (fig. 212a) and the southern a nearly parallel-sided emargination (fig. 212b). More extended observations on this species are greatly to be desired. We think it possible that there may be two.

Phyllodecta vulgatissima.

This is near to *P. vitellinae*, but the distal end of the median lobe is more flattened horizontally, and the constriction near base is not so deep. The armature on sac is on the same plan, but more complex and lies inside the median orifice, and when the sac is slightly evaginated entirely alters the appearance of the orifice.

Timarcha geniculata (Pl. LXXIV fig. 211).

Median lobe well developed and chitinised, the ventral edge pointed and produced a little beyond the dorsal edge, the dorsal edge forming a pointed strip over the orifice; median foramen occupying the ventral aspect of the basal third, the dorsal face being cleft, thus making it into a pair of struts (ms). Tegmen forming a ring-piece with a curved plate, or cap, on dorsal aspect, shallowly

emarginate at tip, on the ventral aspect the ring-piece projects as a long strut (b). Sac large, with a slender flagellum (fg) rising from the apex.

The basal part of the median lobe being divided into two pieces, and the complete ring-piece with a cap on the dorsal side separate this genus from the Chrysomelinae. *C. tenebricosa* is of the same type, but the cap-piece is smaller in proportion. Hence we propose Timarchinae as a distinct subfamily. As Donaciinae and Sagrinae approximate this structure, the Timarchinae should be placed between them and Chrysomelinae.

Diabrotica soror.

In this Galerucid the median lobe forms a long, curved tube: the basal foramen extends ventrally for one-third of the length of the tube: at the distal extremity there is a short acumen, and the dorsal face of the tube is membranous for nearly one-third of the length. The tegmen consists of a pair of slender, nearly parallel and nearly contiguous rods, these diverge very abruptly, and then converge again a little so as to partially embrace the median lobe, but they are unconnected by chitin on the dorsal aspect.

Galerucella spp.

Agree with the above in respect of the tegmen; but the basal part of the median lobe is very different, the tube being more complete at the base, and provided there with a pair of hooks. These hooks also exist in *Galeruca tanaceti* and in *Lochmaea*. In the last-mentioned genus the median lobe is of highly irregular form, and instead of forming a single curve, the two extremities of the organ are curved in opposite directions (as occurs less markedly in *Haltica*).

So far as we can form an opinion as to the Galerucinae from the few forms examined, it would appear that their chief characteristics are (1) the indefinite delimitation of the median orifice, entirely dorsally placed and unprotected; and (2) the small tegmen, forming only delicate rods.

Haltica coryli.

Median lobe straight, tubular, somewhat flattened, ventral edge of median orifice produced into a point, projecting beyond the

dorsal edge; chitinisation of the dorsal edge forming three strips which close the orifice; median foramen occupying the ventral portion of the basal fourth. Tegmen Y-shape without traces of cap-piece. Internal sac fair size with armature that appears to be comparatively simple.

Although the aedeagus in Halticinae is much used for discriminating the species, we have not met with any satisfactory account of it; the sac, with its armature, the base of the median lobe, and the foramen, as well as the condition of the tegmen, being in fact almost entirely neglected.

Spilispa imperialis (Pl. LXXIV fig. 213).

Median lobe well developed and chitinised, strongly bent at about two-thirds from apex, bent up at right angles at the curve, with the median foramen occupying the ventral portion; median orifice with ventral edge rounded and produced beyond dorsal edge. Tegmen T-shaped, with the forks of the T embracing the median lobe.

Cephaloleia sp. ? (Pl. LXXIV fig. 214).

Median lobe tubular, strongly curved, with ventral edge of median orifice pointed and projecting far beyond the dorsal edge; median foramen occupying the ventral portion of the basal third. Tegmen Y-shape. Internal sac long, passing through the median foramen; nature of armature not observed.

Mesomphalia pascoei (Pl. LXXIV figs. 215, 215a).

Median lobe long, thin, tubular and flattened slightly, curved nearly at right angles about one-fourth from base and deeply constricted; median foramen occupying the ventral portion of the basal fifth; ventral edge of median orifice pointed and projecting well beyond dorsal edge. Tegmen Y-shaped. Internal sac not large, bearing at apex a flattened tube like flagellum (fg), on which the ejaculatory duct opens, and a plate embedded in the sac below (a). The ejaculatory duct in this species is semi-chitinous, and forty-eight millimetres long.

Aspidomorpha 4-maculata (Pl. LXXIV fig. 216).

Median lobe stout, tubular and bent at forty-five degrees two-fifths from base; median orifice with ventral edge bluntly pointed and only produced a little beyond dorsal edge; median foramen occupying ventral part of basal fifth. Tegmen Y-shape. Internal sac without armature.

The Chrysomelidae form an interesting series of groups which further research will perhaps separate into distinct families. The most primitive type is *Orsodacne*, which approaches *Parandra*. We find forms wherein the tegmen is not divided, though it has a comparatively large cap (*Timarcha*), and others in which the median lobe becomes tubular, *Orina*, etc. Apparently a still more modified form is that in which the tegmen is reduced to a delicate Y or V-shaped piece. An overwhelming majority of the existing species belong to the divisions in which the tegmen is thus reduced (*Chrysomelinae*, *Galerucinae*, *Halticinae*). The modifications of the tegmen will probably be found of considerable assistance in the classification of this enormous group of Coleoptera.

Family CERAMBYCIDAE

Forms specially examined: *Parandra* sp. n.? New Guinea. *Mallaspis xanthaspis* Guér.?, ? Colombia. *Aromia moschata* L., England. *Chloridolum dorycum* Boisd., New Guinea. *Gnoma stenostomoides* Th., New Guinea. *Monohammus longicornis* Th., New Guinea. *Macrochenus guerini* White, ? N. India. And various others not calling for special remark.

Figs. 217 to 221 Pls. LXXV and LXXVI.

Parandra sp.? (probably undescribed) (Pl. LXXV fig. 219).

Median lobe somewhat flattened horizontally with dorsal and ventral edges of median orifice pointed, the orifice extending back some distance on each side; from the dorso-lateral edges of the base two flat, narrow struts are given off. Tegmen forming a ring with a pair of pointed processes, separate to near their base, on the dorsal aspect, and a median strut (*cs*) on the ventral aspect. Internal sac large, without armature.

Aromia moschata.

In this well-known insect (Pl. LXXV fig. 217), the sac is largely developed, and bears a complex armature near the apex (*a*).

Chloridolum dorycum.

This is similar to *A. moschata*, but the armature of the sac is even more complex, and is shown in some detail in figs. 218 and 218a Pl. LXXV. There is a deeply cleft chitinous plate (*ab*) bearing hair at the two extremities (*ac*); a large chitinous plate

(*d*) with the sides curved up, and another plate (*e*) below it, and this is produced into a blunt median keel (*f*); there is a large diverticulum (*g*) as in *Aromia*. A considerable part of the sac is beset with small, chitinous teeth.

Among the forms of this large family that we have examined there is a great uniformity of type, the median lobe having the orifice at the tip and extending along the side, the sclerites on the dorsal and ventral aspects being separated by a membrane running along each side, from orifice to foramen; the base of median lobe prolonged into two struts; tegmen ring-shaped, with a divided projecting process, the division generally very deep; internal sac long, projecting into the body forwards beyond the median foramen in the state of repose.

It is in the great development of the sac, and the diversities in its armature that we must seek the peculiarities of the family. *Parandra*, so far as the genital tube is concerned, appears to be the lowest form; in it we have found no specialisation of importance. A general resemblance between the tube of *Parandra* and that of Cucujoidea is evident at first sight (compare *Parandra*, fig. 219 with *Cucujus*, fig. 97, or *Passandra*, fig. 96). In the section phylogeny we have shown reasons for supposing that this general resemblance may be deceptive.

We have examined various other Cerambycidae without finding anything to make it necessary to increase the length of this memoir by including them. But there is one point we must mention briefly. Bordas has pointed out that in certain Cerambycidae there appear to be present two ejaculatory ducts. In other words that the stenazygos is wanting. We also have observed this fact in *Gnoma* (Pl. LXXV fig. 220) and in some species of *Monohammus* (Pl. LXXVI figs. 221 and 221a).

That this fact is of much morphological importance is not clear to us. It may perhaps be due to the great extension of the sac (or eurazygos). And in fact in another closely allied species of *Monohammus* we have found a distinct stenazygos. The structure as it has appeared to us in *Monohammus longicornis* is shown in Pl. LXXV fig. 221, and in 221a where the sac is everted. It is then seen to be studded with small spines, and bears two diverticula, thus acquiring a singular resemblance to the head of a dog; and it will be seen that there is a short

base on dorsal and ventral side. Basal-piece slightly shorter than lateral lobes.

The specimen at our disposal is greatly destroyed by *Anthrenus*. The elongation of the lateral lobes is remarkable. Burmeister considered this form to be related to *Euchirus*, and there appears to be a great similarity in the aedeagus of the two, but we cannot say to what extent this is true of anything but the hard sclerites. The general shape of the aedeagus is one that is frequent in the Melolonthine series of genera.

Obs.—The aedeagus of Scarabaeidae is readily recognised (if Trogidae, Lucanidae and Passalidae are excluded) by the following definitions:—

Tegmen greatly developed, the basal-piece enormous, consisting of an anterior part unchitinised beneath, and a more distal tubular part to which are attached apically the varied lateral lobes (frequently called forceps or parameres); the median lobe drawn within the basal-piece, and thus concealed, membranous except at the extreme base where there are, more or less well developed, elastic chitinous supports; sac large, frequently provided with remarkable, varied chitinous structures.

The perfection attained varies greatly. There are higher and lower forms in each of the great divisions. The number of forms examined is not sufficient to enable us to follow up this remark profitably.

MORPHOLOGY.

B. GENERAL.

A BRIEF statement of the anatomical terms we have used will be found in the early portion of the Memoir (*Orismology*, p. 481). The term genital tube is used because it conveys the idea of the chief characteristic of the parts. Whatever else they may be, however different they may appear, their combination to form a perfect tube without orifices, is remarkable: the one "orifice" that exists is not a real one. It arises from the invagination of the tube into itself. The genital tube is therefore a doubled tube, one end of which is a continuation of the body wall, while the other divides into a fork, of which one

branch proceeds to each testis. In a peculiar structure of this kind it is evident that the homologisation of the parts is attended with some special difficulties. Extensibility and retractibility of the tube are carried to an extraordinary perfection, and the length of the tube is in some cases enormous compared with the size of the creature, and yet the "orifice" may in one position of the organ be placed near the distal, in another position near the proximal extremity. The same "orifice" is in fact at one moment of the creature's existence placed inside and quite near to the centre of the body, while at another moment it may be placed far away, at the extremity of the extended tube. The walls of this protean structure become in some places hard, and form sclerites. The study of these sclerites is one of the chief aids in our endeavour to understand the changes the tube may have undergone during its evolution.

The homologies of the various parts of the male genital tube are, within certain limits, very easy to follow, and even in some of the most extreme forms can be made out by anatomical comparison. But beyond the limits we have alluded to, the questions become very difficult, and will really only be settled by studies of the ontogeny that at present are not forthcoming. As misconception has been, and still is prevalent to a considerable extent, there are a few general points to which we must allude. According to our view the genital tube commences where the body wall ends. Anatomically it is not easy to decide where that spot is, because body wall and genital tube are continuous.

Embryologists consider with good reason that the stomodaeum and proctodaeum are the poles of the body wall, therefore all parts that have their origin on the dorsal aspect of these openings are tergal, and all parts on the ventral aspect are sternal. The genital tube, being ventral of the anus, can therefore contain no tergal parts; though one or more sternites may enter into its composition.

Hopkins* considers our tegmen in *Pissodes* as "representing the apodeme of the ninth tergite." Bugnion† considers that in *Cissites testaceus* the median lobe ("gouttière interne") is derived from the ninth segment, and the tegmen ("gouttière externe") from the tenth segment.

* U. S. Dept. Agr. Technical Series, No. 20, Part I, 1911.

† Bull. Soc. Ent. d'Egypte, 4^{me} Fascicule, 1910.

We cannot agree with these interpretations without proof from studies of the development.

The question as to a sternite, or part of a sternite, being included in the male genital tube leads to the consideration of the number of abdominal segments, a subject beyond the scope of this memoir. The following points, however, bear upon it. In the majority of beetles the first tergite is often entirely membranous, and the first, second, and, sometimes, the third sternites are also membranous; beyond these the segments are distinct, and, in many cases, there appears to be one sternite missing.

In *Enarsus bakewelli* (fig. 92b) there is a distinct ventral plate between the anus and the aedeagus, and in *Cupes clathratus* (fig. 104-104b) there is a pair of sub-anal appendages. These facts seem to indicate that there exists in some cases a sternite between the anus and aedeagus although it is only represented by membrane in so many forms.

We have not been able to find the eleventh (Berlese) sternite in *Lucanus cervus*. In this species, as in a great number of others, the rectum is capable of being evaginated. In some cases the rectum has chitinous supports to facilitate this process. In the larvae of many of the Cassidae the rectum is quite telescopic, and is thrust out and turned up to enable the larva to fasten filaments of excrement to its back. If any part of the aedeagus is of chroötic (pertaining to the body wall*) origin it is the tegmen, which in that case is derived from one of the sternites. When a sclerite of the genital tube exterior to (or anterior to) the tegmen exists it may probably be of chroötic nature.

The only observation as to development that we can at present contribute to this discussion is a slight one on a Cistelid. In the larva of *Cistela (Eryx) atra* there are nine distinct tergites and sternites, the ninth sternite bearing a pair of small papilla-like processes; in the pupa there are also nine distinct tergites and sternites, and the ninth sternite bears the pair of papillae; in the female imago the genital styles are direct continuations of these papillae on the ninth sternite, and they lie within them at the end of the pupal stage.

* We have introduced this term because the more correct word, somatic, has already a wider meaning, as opposed to the germinal tissue or plasma.

Our limited material did not show us the development of the male parts; but in the imago there are nine distinct tergites and eight distinct sternites, the ninth sternite appearing to be represented by a Y-shaped sclerite (fig. 234). A large amount of dechitinisation has apparently taken place at the apex of the abdomen, as well as at the base, and it is possible that some part of the large membranes at the apex (*i.e.* at the base of the genital tube) may represent sternites.

We divide the genital tube into the following parts. A pair of seminal ducts leading from the testes forms the zygotic portion (fig. 239 *a-b*), and the long, single, highly irregular tube, folded back and joined to the body wall, forms the azygotic portion (fig. 239 *b-d*, 5-1). The paired, or zygotic portion (*a-b*), along with certain glands opening into it, is considered to be of mesodermic origin,* and the azygotic, along with certain glands, of ectodermic origin. Bordas† points out that very little is known as to the origin of these glands, and consequently objects to the terms ectadenia and mesodenia applied to them by Escherich, and calls them accessory, or annexed glands. We are not concerned with them here.

The first part of the azygotic portion of the genital tube (fig. 239 *b-c*) consists of a long, more or less slender, tube (the stenazygotic portion); beyond this the tube enlarges and forms the eurazygotic portion (*c-d* and 5-1). In many cases this enlargement of the azygotic portion of the tube takes place before it is reflected outwards to continue its course to join the body wall. We call that portion of the eurazygos that is usually not external (*c-d*), the "internal sac" ("sac interne" of Jeannel).

In all cases that we have observed the internal sac is evaginated during copulation, and forms a continuation of the external parts of the genital tube. In a great number of forms there is no demarcation between the stenazygotic and the eurazygotic portions of the tube before the outward reflection above mentioned; in such cases we say that the internal sac is undifferentiated. That portion of the tube that is reflected and thus forms the external portion of the organ we call phallic. But we

* On this subject see Escherich, Zeitschr. wiss. Zool. lvii, 1893, p. 620.

† Bordas, Ann. Soc. Ent. France, lxxviii, 1899, p. 510.

must admit that the term is not a good one. The part in question is highly complex. It is in fact the layer, or layers, of the tube of which sclerites of the aedeagus form a large, or the larger, part.

The sclerites on the phallic portion of the genital tube form two groups. (1) Those situate on the distal portion of the tube (furthest from the body wall), which we call the median lobe (fig. 239, 5-4), and (2) those situate nearer the base, which we call the tegmen (3-2). The membrane between these two groups of sclerites we term the first connecting membrane (4-3), and the membrane at the base, joining on to the body wall, we term the second connecting membrane (2-1). The median lobe, together with the tegmen, we term the aedeagus.

The point where the genital tube is reversed (5-d) we call the median orifice, and the lumen at the base of the median lobe (4-to corresponding spot below) we call the median foramen. Similar terms could be applied to the tegmen, but we have not found them necessary for our descriptions.

Having thus given a description of the four parts of the tube, we now give remarks as to the structures of each of the four divisions.

The second connecting membrane (or prephallic portion of the tube) varies in extent according to the size and shape of the aedeagus. In certain cases (i. e. *Laccobius* and *Sphenophorus*) it is chitinised in part, and forms a covering round the aedeagus. At, or near, the base there is in many forms a chitinous rod with one or two prongs at the end, embedded in the membrane. This is the "Stengel" of Lindemann, "Rod" or "fork" of Hopkins, and "Spiculum gastrale" of Verhoeff. Hopkins considers it as representing the ninth sternite. A comparison of this in the various families would be of great interest, but would entail a study of the body segments, a task beyond the scope of this memoir. We have therefore left it out of consideration.

The phallic portion of the tube is the one that has chiefly attracted the attention of coleopterists. It consists partly of membrane, partly of sclerites, and there may be most extreme differences in the chitinisation of its different parts, excessively hard chitin being continuous with delicate membrane. We have already explained that we call the sclerites in question the aedeagus, and that this consists of two parts, viz. median lobe and tegmen.

In the vast majority of cases the median lobe is well developed and quite distinct from the tegmen. In the more generalised (or trilobe) form it is well developed, and more or less tubular, with the median orifice situate on the distal extremity, and the median foramen at the basal extremity. In many trilobe forms it is articulated to the lateral lobes by a more or less distinct condyle on the dorsal side of the median foramen; in such cases the first connecting membrane (*cm* 1) is short, and the median lobe can only turn upon its point of articulation (*pa*). A pair of median struts are often attached to the base of the median lobe to give support to the muscles that actuate it. In the Scarabaeidae the median lobe is comparatively reduced in chitinisation, and often in size, and in the more highly evolved forms the tegmen entirely envelopes and conceals it. In the Tenebrionid type the reduction of the median lobe reaches its maximum; in some of their forms it is only represented by a small membrane on which the median orifice is placed. The line of evolution of the median lobe in the Staphylinidae is from a tubular form, with a basally placed median foramen, to a bulbous form, with the median foramen placed nearer to the median orifice. This reaches its maximum development in *Xantholinus*. In the Cucujoidea group and in the Phytophagoidea the median lobe is generally tubular (at any rate on the distal portion), and the first connecting membrane long, so as to allow the median lobe a large amount of play through the more or less ring-like tegmen.

The tegmen, in the more generalised groups, consists of two parts, the basal-piece, and a pair of lateral lobes. The chitinisation of the basal-piece then often forms a shield-shaped plate on the ventral aspect, the dorsal aspect being membranous. Unless the chitinisation forms a complete tube the membranous dorsal part and the second connecting membrane are indistinguishable. The lateral lobes in their generalised form consist of a pair of more or less pointed lateral organs, their outer surface being continuous with the basal-piece, their inner surface connecting to the base of the median lobe, and their position being that they lie one on each side of the median lobe.

In position, size and form the lateral lobes differ so much in various families that their true homology in the different groups will probably be only settled after tracing their modifications through long series of forms, and by studying

their ontogeny. It will be noticed that they are paired, or longitudinal, in arrangement, whereas the other structures of the phallic part of the tube are single and transversely separated. This paired condition of the lateral lobes tempts one strongly to identify any paired processes on the phallic division of the tube (even when median) as being lateral lobes. And it is probable that we and others have too readily succumbed to this temptation.

It is in connection with this point that the term tegmen becomes very useful, for we can homologise the combination more certainly than we can the lateral lobes alone.

The difference in position of the lateral lobes may be accompanied by their partial (or complete?) consolidation. If the chitinisation of the basal parts of the lobes extend towards the longitudinal middle line of the tube at the expense of the membranous creases that exist, the two lateral lobes can become joined, and it is possible that the conjunction may go so far as to obliterate their primitive duality. This consolidation can occur either dorsally or ventrally, and we must look on a distinction so established (as has been pointed out by Verhoeff) as of great importance. It creates a difficulty in adjusting the position of various forms of "Heteromera," Cioidae, etc.

Extension transversely of conjoined lateral lobes might lead to the formation of a tubular chitinous sheath such as we find in Trogositidae, Cleridae, Byturidae. Or such a sheath might be formed by unconjoined lobes extending both above and below, and if a sheath be formed, by abbreviation it may become a "ring." Or a ring may be formed by extension of the angles, or margins of the basal-piece. We can only briefly indicate some of the numerous modifications that are possible of these phallic sclerites.

In Staphylinidae the part of the tube wall that is in so many families chitinised to form the basal-piece, remains membranous, and in other families of the Staphylinodea the basal-piece is small. In Tenebrionoidea the basal-piece is long, and usually forms the chief part of the aedeagus.

Some morphologists have supposed (as we have already said) that the lateral lobes are modified abdominal appendages; on the other hand it may be suggested that some Coleoptera have never possessed lateral lobes. This point is briefly discussed in the section of phylogeny.

The internal sac varies in size, shape and armature in

the different groups, and even in allied species. In the Scarabaeidae it is nearly always excessively large, and is often produced into long diverticula (i. e. *Hexodon*, fig. 25a). In Lucanidae it is found in every stage, from a simple form, in which it is scarcely distinguishable from the stenazygos, to a form such as *Lucanus cervus* (fig. 8). In this species the internal sac is not drawn into the median lobe, but when at rest it is folded down on to the broad median lobe. The sac is produced into a long flagellum, supported on each side by a thin strip of chitin; the stenazygos* continues through the flagellum to its tip. To obtain a similar position of the orifice in Cerambycidae the great sac must be completely everted.

The phenomenon of the internal sac being permanently everted is not confined to the Lucanidae, but appears among the Scarabeidae, Heteroceridae and Lycidae. In *Spilota regina* (fig. 20) the armature of the sac consists of two strong chitinous projections from the apex, and a strong chitinous plate beset with stout spines, the basal part of the sac being membranous. A comparison with allied forms demonstrates that these structures are part of the internal sac, and that the median lobe is normal in shape and size. In *Metriorrhynchus* (fig. 186) there is no doubt as to the everted condition of the internal sac, and it may be doubted whether its invagination is possible in some of these cases.

The flagellum appears in various conditions, as to size, etc., in different families or portions of families. In the Brentidae it reaches an enormous length and fineness, and at the base the stenazygos can be seen running into the flagellum, but further on they appear to amalgamate, as we cannot separate them. Among the Staphylinidae *Pinophilus rectus* has an enormous flagellum coiled up within the median lobe. The other forms of armature situated on the internal sac are very various, and have been described in many species in the special anatomical part of this memoir; cf. various species of *Donacia* (fig. 199), and *Carpophagus* (fig. 204a).

In another portion of this memoir we show that in many

* In the special anatomical portion of this memoir we have always spoken of this stenazygotic portion of the tube as the "ejaculatory duct," but this is a functional term, and by other writers is often applied to the internal sac; it would probably be well to abandon it.

of the types the internal sac is everted during copulation, and it is probable that this method is the usual one; though the Cerambycidae may be peculiar in their mode of eversion.

In a great many forms the line of demarcation between the internal sac and the median lobe is obscured, for in some cases the chitinisation of the median lobe is continued on to the internal sac, and in others the distal end of the median lobe is membranous. The fact that in many cases the basal portion of the sac, and in other cases the whole sac, is permanently evaginated prevents us from distinguishing the two portions by their positions when at rest.*

Of the zygotic portion of the genital tube we do not speak, as it is beyond the scope of this memoir. And the stenazygos only concerns us because in many forms it is impossible to sharply define it from the eurazygos, before the latter is reflected to form the phallic portion of the tube. In such forms we speak of the internal sac being undifferentiated (i. e. *Hydrophilus*). In cases where the internal sac is differentiated it is sharply defined from the stenazygos by its size, and often by chitinisations situate on the sac at the point of juncture of the two parts.

In *Eumolpus* and *Chrysochus* the stenazygos forms a very long slender structure like a flagellum.

Bordas† has pointed out the existence of two completely separated ejaculatory ducts in certain Longicorns (*Lamia*, *Batocera*, etc.). We have also observed this fact in some *Monohammus*, *Gnoma*, etc. Bordas considers that this furnishes an argument in favour of the theory that the terminal parts of the canal were primitively of paired origin. It is possible, however, that this feature is of secondary origin, brought about by the abbreviation and suppression of the stenazygos and the lengthening of the zygotic portions, thus causing the zygotic portions to open into the eurazygos; in some *Monohammus* there is a short stenazygos (fig. 221a).

* Since this was written one of the writers, F. Muir, has observed the development of the aedeagus in *Sphenophorus obscurus*. The median lobe and internal sac arise as a single tube which eventually differentiates into these two portions, the internal sac not being invaginated into the median lobe until the pupa is fully developed and ready to emerge. In many forms, as we have remarked, no distinct line of demarcation ever appears.

† C.R. Ass. franc. av. Sci., 1899, p. 540.

IV. FUNCTION.

Although a knowledge of the functions of the different parts of the male genitalia is essential to a comprehension of our subject, yet knowledge is at present so little advanced that we can here offer to the student only a general statement and a few suggestions.

The matter for the starting of a new generation is prepared in the centres of the bodies of two separate individuals, and it is necessary that the two essences should be brought together. This of course is effected in the Insecta by copula. During the copula an unobstructed road must exist. This is the genital conduit, and is formed in part by the genital tube of the male and in part by the genital tube of the female. These structures of two different individuals form functionally a single organ. The sex structures are unique in this respect. And they are not correlative with the life of the individuals, but with the life of the generations.

The importance of a correlative knowledge of the genital tube of the female is absolute, but from the point of view we take there is but little information.

The female Coleopteron is usually (possibly always) provided with a spermatheca—a special vessel for the reception of the matter transmitted along the male genital tube. It would appear that this spermatheca is generally placed near the base of the azygotic portion of the female genital tube.

The male structures are therefore directed to the object of placing the sperm in the spermatheca. The first question that arises is as to whether this is accomplished directly or indirectly. Must the sperm be deposited directly in the spermatheca? Or is it sufficient that it be placed in some other part of the female tube?

No positive answer can be given to this question at present. It appears from the vague remarks that one finds in literature that the general idea is that the placing of the sperm in any portion of the female tube is adequate. The opinion we ourselves entertain is, however, the reverse of this. We incline to the view that in a large number of cases, the male structures actually place the sperm in the spermatheca, however remote that structure may be from the orifice of the genital tube of the female. The flagellum

appears to be an organ admirably adapted for this purpose, and its occurrence and reoccurrence in so many isolated forms is, to say the least, highly suggestive. Even in cases where there is no true flagellum, it may well be the case that the functional orifice of the male (not to be confounded with our "median orifice") is applied to the orifice of the spermatheca. See on this point our figures 58 and 63.

Certainty as to this point can only be obtained by repeated observations of the genital tube during its functional activity, and as to this we have been able to make but few observations.

In *Rhagonycha fulva* ♂ the sac is large and rounded, with three pairs of diverticula along the posterior surface, and a large patch of strong spines on the ventral side (fig. 237a, a); the duct opens between the most dorsal pair of diverticula. During copulation this sac distends the uterus to its own size, and the patch of spines covers the entrance to the oviducts. The abundance of this species would make it a convenient form to work out all the details of copulation on.

Unfortunately the process of killing the insects causes the muscles that actuate the internal sac to relax or contract, and so the exact relations of the sac and the female parts are never fully revealed. The shape of the female parts does not exactly correspond to the shape of the male sac and all its diverticula, etc., but there is a co-relationship between them, and apparently they always take up the same position in any one species. Besides the direct evidence as to the importance of the internal sac and its evagination during coition there is the great mass of indirect evidence afforded by the complex armatures that are developed upon them, especially at the apex. In *Pissodes* Hopkins* calls this armature the "seminal valve," but in the various examples of the different families that we have examined the armature does not function as a valve. In cases where there is no differentiated internal sac it is difficult to state how much of the duct is evaginated, but judging by observations made on certain Hydrophilidae a large amount is turned out. The evagination is done, at any rate in part, by blood pressure, and the invagination by the contraction of muscles attached to certain points on the internal sac and to the median lobe.

* U.S. Dept. Agr. Technical Series, No. 20, part I, 1911.

In certain forms the median lobe is specially contrived to effect this blood pressure. In *Xantholinus* the median lobe forms a chitinous egg-shaped chamber, having a membranous band round the middle; muscles pass from the dorsal chitinous portion to the ventral chitinous portion. The contraction of these muscles causes the chitinous portions to approach one another, and thus exert pressure on the fluid in the bulb which forces out the long internal sac. In the case of *Pinophilus* where the sac is exceedingly long, and lies coiled up, with a chitinous flagellum running right through it like a spring, it is not likely that the sac is evaginated; in fact, the chitinisations on its base prevent such a thing. In this case muscular contraction round the coiled sac causes the distal end of the flagellum to be thrust out through the median orifice, the chitinisations on the base of the sac acting as a guide; upon the relaxation of the muscles the flagellum acts as a spring, the coils distend, and the distal end of the flagellum is retracted.

The action of the flagellum is obscure, but the fact that it appears in such diverse families denotes its great functional importance. It would be of great interest if some one would take any form in which this structure is greatly developed (e.g. *Lucanidae*, *Brenthidae*) and kill while in copula and dissect the female, to see if any part of the internal sac is evaginated, and to what part of the female genital tube the flagellum penetrates.*

In the Longicorns the capacious sac is very long, and it seems improbable that it is entirely evaginated, but only direct observation will decide this point.

The various spines and hairs that are found on the sac are generally pointed basally; this prevents the sac being withdrawn from the uterus of the female while the sac is distended. The various diverticula found on the sac do not appear to correspond to diverticula in the female, but they take up constant positions, and may serve as pads to

* Since writing the above one of the writers, F. Muir, has observed the copulation of *Cryptomorpha desjardinsi*. This is a Cucujus-type with a ring-shaped tegmen with a pair of lateral lobes, a long internal sac with a very long and slender flagellum. In this species the whole of the long internal sac is evaginated and enters the long female tube, the flagellum proceeding still further into the female genital tube. The spermatheca is small and attached to the uterus by a long slender duct. Whether the flagellum actually traverses this duct and penetrates the receptaculum he was not able to observe.

keep open certain spaces between the sac and the wall of the female tubes. Observations on the positions taken up by the sacs within the vagina during copulation are greatly to be desired.

The pressure necessary to drive the viscid fluid from the testes through the long slender ducts must be very great, and the thick coating of muscles surrounding the ducts serves to this end. The pressure behind such a flagellum as is found in *Baryrhynchus miles*, where it is 12 mm. long, and .006 mm. in outside diameter toward the tips, must be well directed and considerable.

It is worthy of note that the armature of the sac of *Donacia sericea*, etc., recalls the parts of the aedeagus, there being a median lobe, through which the ejaculatory duct passes, and opens on its apex, and a pair of lateral lobes. There is, as it were, a secondary aedeagus within the aedeagus. To find out the action of these pieces during copulation would be of interest.

Whether the lateral lobes in such a trilobe form as *Ceratognathus* pass into the vagina and then diverge and thus hold the female, we are unable to say. In *Stenus speculator* (fig. 232) the lateral lobes are placed along the outside and hold the female. In Coccinellidae they are placed on the outside of the female venter, and appear to have no hold. In some of the Cistelidae the hind body-segment is developed into claspers to retain the female. In *Malthodes* (fig. 233) and *Malthinus* (fig. 235) the last abdominal segment is used as a clasper, and the last segments of the females have depressions into which the ends of the claspers fit to give them a firmer hold. In *Telephorus* and *Rhagonycha* the edge of the vagina is held between the tongue of the tegmen (fig. 236a) and the median lobe. In these species the aedeagus takes nearly a half turn during copulation (fig. 238). The twisting of the aedeagus during copulation is common to many forms, and in some it makes a complete half turn. This is the case in the Caraboid type. In such an one as *Dytiscus punctulatus* the aedeagus, when at rest and drawn into the abdomen, lies on its side, and when thrust out the median lobe curves downwards, but its true orientation is with the median lobe curved upward as we figure it (fig. 37).

It is probable that in many forms the female does not play an entirely passive part in the act of copulation; as to which see the remark made under *Cyphon*.

We may conclude these very fragmentary observations by pointing out that the diversity of the structures indicates a considerable variety of functional detail.

V. TAXONOMY AND PHYLOGENY.

TAXONOMY.

It has been supposed that the copulatory structures are bad guides in classification, although they are generally admitted to be of the first importance for the discrimination of species. If, however, the extreme importance of the genital conduit be seized, it will appear that its structure must certainly be of very great assistance in taxonomy.

We have in this memoir considered the male portion only of the genital conduit, and that in a very imperfect manner. It seems possible that if the female part of the conduit were studied important distinctions would be found therein. The only considerable contribution to this subject we are acquainted with is the work of Stein (Mon. Geschl., Organe, etc.). This was published sixty years ago, and was not specially directed to the consideration of the conduit, but so far as we can form an opinion from it, and from our own limited observations and a few other memoirs, the probability of important differences in the female structures is confirmed.

Under these circumstances it will be suggested that we are not justified in making taxonomical generalisations on the subject of the genital conduit at present. With that suggestion we entirely concur. Nevertheless, as taxonomy has been carried on with little or no consideration of this important branch of anatomy, we think it important to introduce this subject, notwithstanding the very incomplete state of our knowledge.

The generalisations that follow are, it will be seen, imperfect and unsatisfactory. Possibly wider inquiry may bring to light important distinctions we have failed to appreciate, and it is also probable—we may say certain—that such inquiry would reveal the existence of annectant forms we are unacquainted with. As a further apology for the following generalisations we may ask that it shall be remembered that the other data of Coleopterous taxonomy are also very incomplete.

	PAGE		PAGE
Derodontidae	532	Othniidae	551
Discolomidae	524	Parnidae	531
Dryopidae	531	Passalidae	579
Dytiscidae	492	Paussidae	490
Ectrephidae	535	Pelobiidae	491
Elateridae	545	Phalacridae	514
Endomychidae	525	<i>Phytophagoidea</i>	620 & 634
Erotylidae	523	Platypidae	572
Euenemidae	546	Platypsyllidae	506
Georyssidae	531	Proterhinidae	528
Gyrinidae	493	Pselaphidae	509
Haliplidae	491	Ptinidae	534
Helotidae	521	Pyrochroidae	553
Heteroceridae	531	Pythidae	553
Histeridae	512	Rhipiceridae	545
Hydrophilidae	494	Rhipiphoridae	556
Ipidae	572	Rhysodidae	490
Lagriidae	551	Rhysopaussidae	550
Lamprimidae	576	Scaphidiidae	506
Lathridiidae	527	Scarabaeidae	580
Leptinidae	506	<i>Scarabaeoidea</i>	627 & 634
Lioidae	502	Scolytidae	572
Lucanidae	573	Scydmaenidae	508
Lycidae	533	Silphidae	502
Lymexylonidae	542	Sinodendronidae	576
Malacodermidae	535	Sphaeritidae	511
<i>Malacodermoidea</i>	623 & 634	Sphindidae	533
Melandryidae	552	Staphylinidae	496
Meloidae	556	<i>Staphylinidea</i>	626 & 633
Monommidae	552	Synteliidae	511
Monotomidae	514	Temnochilidae	516
Mordellidae	555	Tenebrionidae	548
Mycetaeidae	526	<i>Tenebrionioidea</i>	624 & 634
Mycetophagidae	529	Throscidae	546
Niponiidae	512	Trichopterygidae	507
Nitidulidae	515	Trictenotomidae	557
Oedemeridae	554	Trogidae	577
Ommadidae	521	Trogositidae	516
Ostomidae	516		

EXPLANATION OF FIGURES.

The figures are all original, and have been drawn with the aid of a camera lucida from our own dissections. The scale of magnifica-

tion is varied. Although this point is not of great importance for our purposes, the scale is in most cases indicated by a line placed near the figure. When no number accompanies the line then the length of the line is 1 mm. and the magnification of the figure is indicated by that of the line. When a number accompanies the line, the number indicates the length of the line in millimetres or a fraction of one.

The connecting membranes between certain parts are only partially shown in the figures. To have invariably introduced them would have involved the use of shading; and much artistic ability would even then be required to distinguish the scleritic from the membranous parts. The student will recollect that these membranes always exist connecting the median lobe to the tegmen, and the tegmen to the body wall. Sometimes a part of one of the membranes is shown, and it is then indicated as such by the torn edge.

The position shown is very frequently not a true profile, but a partial one, thus allowing more of the parts to be seen and inferred. The drawings have all been made from specimens in a wet, or relaxed, state; and the student must not expect to find exactly the same appearances in dried and collapsed preparations.

The figures are as a rule uniform as regards their longitudinal position, the distal end being to the right so that a side-view shows the left side. In a few cases, in order to show certain structures, the right (not the left) side is figured; and in that case in order to make comparison more easy the figure is orientated so as to make the right side look as if it were the left one, and it is stated to be "reversed."

Broken lines indicate parts that are lying below the structures represented by unbroken lines. They are introduced to show the continuity of portions that are not actually seen in such a dissection as that figured. Where these concealed parts are the sac and the duct the broken lines are reduced to dots.

We use both single and double letters to indicate special parts. The double letters are used uniformly throughout the figures, and are explained below this, and more fully on pp. 481-483. The meaning of a single letter will be found by reference to that descriptive portion of the memoir to which the figure pertains.

EXPLANATION OF DOUBLE LETTERS.

aed = aedeagus.

an = anus.

bp = basal-piece.

cm 1 = first connecting membrane.

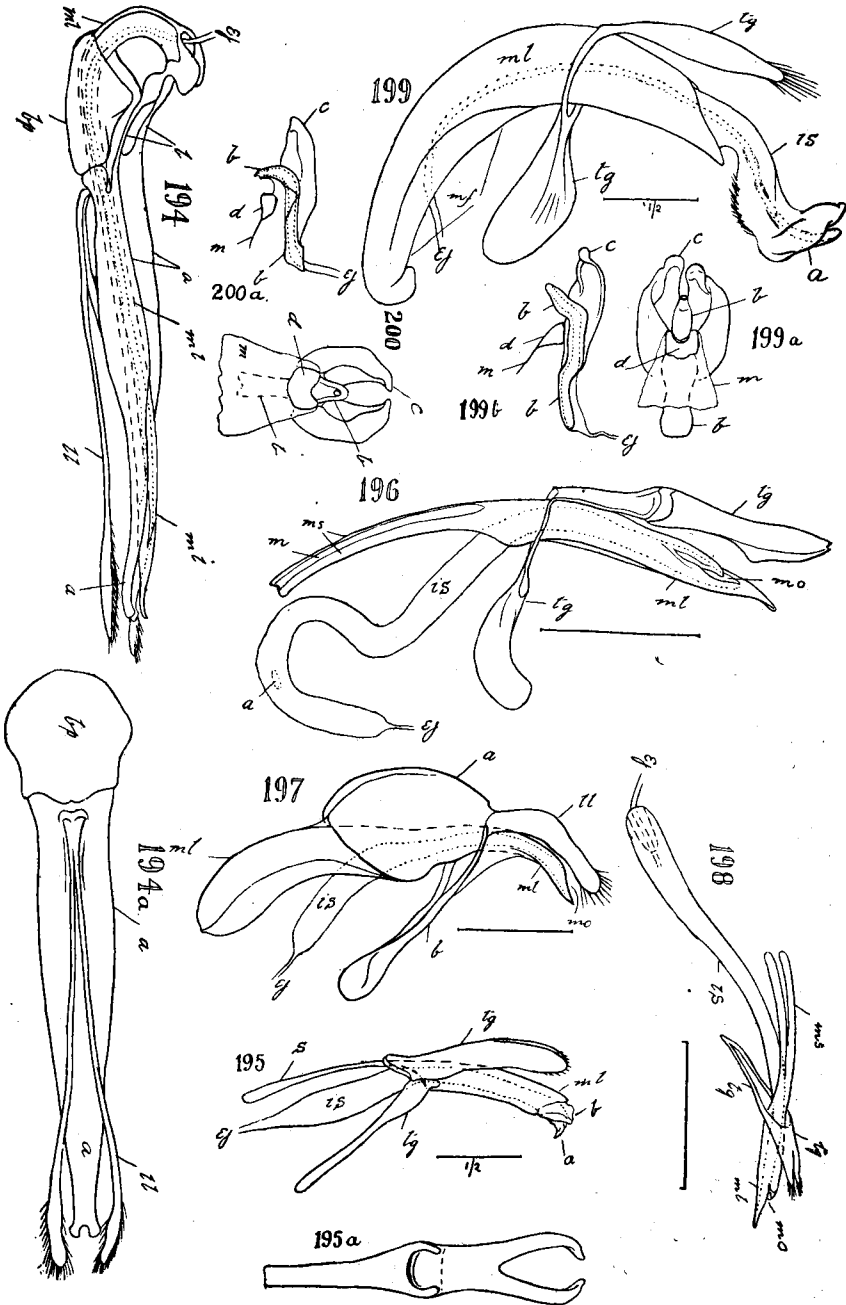
- cm 2* = second connecting membrane.
ej = ejaculatory duct.
fg = flagellum.
is = internal sac.
ld = last dorsal plate.
ll = lateral lobes.
lv = last ventral plate.
mf = median foramen.
ml = median lobe.
mo = median orifice.
ms = median strut.
pa = point of articulation.
pd = penultimate dorsal plate.
pv = penultimate ventral plate.
rt = rectum.
sp = spiculum.
tg = tegmen (lateral lobes + basal-piece ; or basal-piece
without lateral lobes.
ts = tegminal strut.
vp = ventral-piece.

For a fuller explanation of these letters see pp. 481-483.

Correction.

P. 491. If the position of Fig. 39 (*Haliphus*) be considered correct as regards upper and lower aspects, then it is the right lateral lobe. That is the broad one, not the left as stated in the text.

DEC. 24, 1912.



EXPLANATION OF PLATE LXXII.

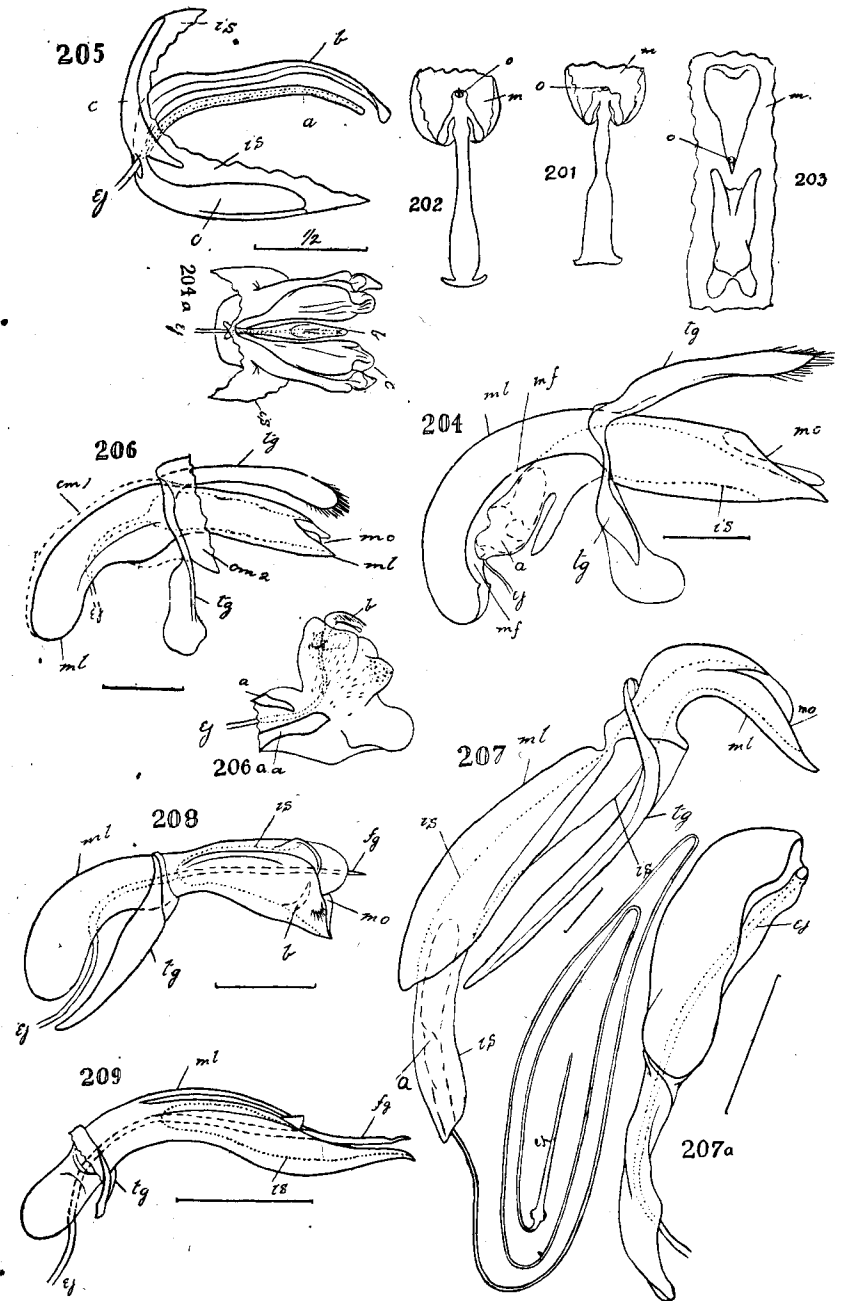
- FIG. 194. *Trictenotoma thomsoni*, lateral view.
 194a. " " , ventral view.
 195. *Bruchus rufimanus*, lateral view.
 195a. " " , dorsal view of tegmen.
 196. *Caryoborus*, sp. n. ?, lateral view.
 197. " *nucleorum*, lateral view.
 198. *Orsodacne nigriceps*, dorso-lateral view.
 199. *Donacia sericea*, lateral view with sac evaginated.
 199a. " " , armature on apex of sac.
 199b. " " , lateral view of median piece and right lateral piece of armature on apex of sac.
 200. *Donacia comari*, armature on apex of sac.
 200a. " " , lateral view of median and lateral pieces of armature.

Descriptions on pp. 557-560. Explanation of the letters used uniformly on pp. 481-483.

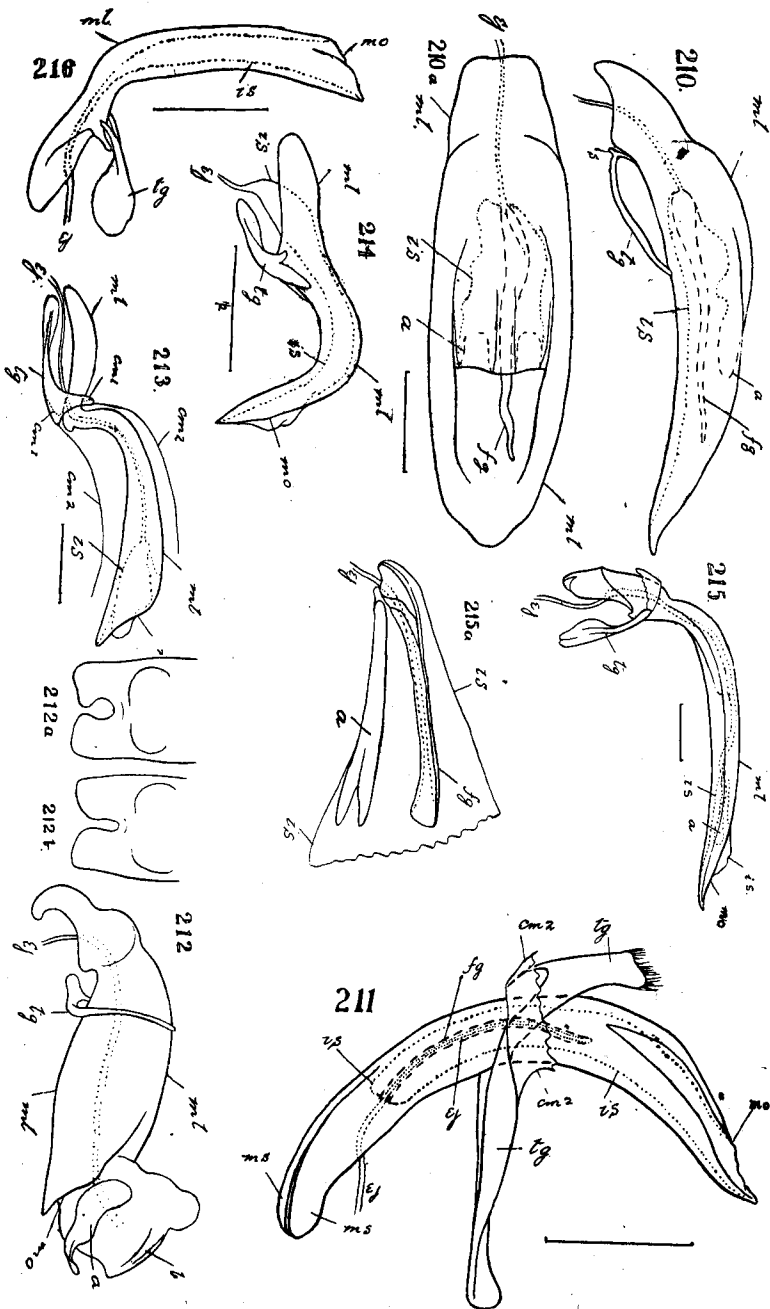
EXPLANATION OF PLATE LXXIII.

- FIG. 201. *Donacia bidens*, armature at apex of sac.
 202. " *semicuprea*, " " "
 203. " *lemnae*, " " "
 204. *Carpophagus banksiae*, lateral view.
 204a. " " , armature at apex of sac.
 205. *Diaphanops westermanni*, " " "
 206. *Sagra amethystina*, lateral view.
 206a. " " , evaginated sac.
 207. *Eumolpus surinamensis*, lateral view.
 207a. " " , armature on apex of sac.
 208. *Clythra laeviuscula*, lateral view.
 209. *Orina elongata*, lateral view.

Descriptions on pp. 560-563. Explanation of the letters used uniformly on pp. 481-483.



GENITAL ARMATURE OF COLEOPTERA.



EXPLANATION OF PLATE LXXIV.

- FIG. 210. *Paropsis variolosa*?, lateral view.
 210a. " " , dorsal view.
 211. *Timarcha geniculata*, lateral view.
 212. *Phyllodecta vitellinae*, lateral view, with sac evaginated.
 212a. " " (sandhill variety), base of median lobe.
 212b. " " , base of median lobe.
 213. *Spilispa imperialis*, lateral view.
 214. *Cephaloleia*, aff. *nigropictae*, lateral view.
 215. *Mesomphalia pascoei*, lateral view.
 215a. " " , armature at apex of sac.
 216. *Aspidomorpha 4-maculata*, lateral view.

Descriptions on pp. 564-567. Explanation of the letters used uniformly on pp. 481-483.