THE GENITALIA
IN THE
ICHNEUMONIDAE

The Genitalia in the Ichneumonidae

by

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I. INTRODUCTION

In the family Ichneumonidae, the determination of species is often extremely difficult. The keys to the family are based partially upon the characters of the female and cannot always be relied upon for the identification of the males.

Furthermore, it is not at all certain that the present systematic division of the family is a natural one, the situation being summarized by Cushman and Rohwer (1920), who expressed the belief that:-

> "The family Ichneumonidae is a group composed of elements showing remarkable differences but at the same time extreme homogeneity. So true is the latter that the grouping into five universally recognized subfamilies leave the placing of a species in its proper subfamily almost entirely to the imagination or experience of the worker. On the other hand, the strict interpretation of such characters as these keys offer frequently leads even the experienced taxonomist to entirely misplace an insect; and disagreement among workers as to the allegiance of certain genera is very frequent."

This view was supported by Viereck (1916) who keyed out the Ichneumonid species without defining either the traditional subfamilies or the tribes. The difficulty in defining the higher groups is shown by Schmiedeknecht (1933), who recognized thirteen tribes in the Pimplinae, yet keyed out the genera in this subfamily without reference to the tribal grouping.

Under these circumstances, it seems possible that a thorough study of the genitalia of the Ichneumonids may help to solve these difficulties.

The ovipositor in the Pimplinae (Ichneumonidae) has already been shown by Cushman and Rohwer (1920) and Cushman (1922) to possess tribal characters, while the comparative morphology of the female genitalia in the order (including an Ichneumonid and a Braconid) has been adequately studied by Snodgrass (1933). The completion of the systematic evaluation of the Ichneumonid in the female is therefore solely the concern of the taxonomist.

In contrast to this, the male genitalia in the Ichneumonids have been ignored almost completely in classifying the groups and species of the Ichneumonidae, while the morphological significance of these structures in the family and the order has not been satisfactorily determined. An investigation into the structural and systematic aspects of the male genitalia in this family is of greater value to the systematist than one concerned with the female genitalia, for the former would establish a basis for intensive taxonomic study.

That the male genitalia may assist in the classification of the Ichneumonidae is indicated by the occurence of excellent generic and specific characters in other families of the Hymenoptera, while a few of higher taxonomic value have been suggested by Radoszkowski (1891 c). Examples, such as that of the Mesochorini (Ichneumonidae), in which the males can readily be distinguished by the elongate outer claspers, suggest that in this family also, the male genitalia are of real systematic importance. The fact that in many cases the characters of these structures cannot be properly studied until special preparations have been made somewhat decreases their practical value. However, this difficulty is not peculiar to the Ichneumonidae; it is encountered in any group where an examination of the male genitalia has been found necessary.

In their structural characters, the members of the family Ichneumonidae are regarded as being intermediate between the Chalastogastra (Sawflies and Horntails) and the Aculeate Hymenoptera (Ants, Bees and Wasps). A study of the comparative morphology of the male genitalia in these forms should thus be of value since it may (1) allow us to recognise and define the different stages of morphological specialization existing within the Order, (2) provide data which may assist in making a more rational arrangement of the larger groups within the Order and the families and (3) aid in the establishment of a consistent, morphologically sound system of nomenclature within the Order.

The term genitalia is usually applied to the organs of copulation, which are morphologically external, although it is sometimes taken as including the internal reproductive organs. These latter have already been studied in the

Ichneumonidae (Du Buysson 1894; Bordas 1894-1919; Pawlowski 1914) and will not be considered here. However, as the specialization of the Hymenopterous genitalia in the male usually involves modifications in the remainder of the genital segment and these, in turn, affect the tenth and eleventh abdominal segments, the study of the genital region has been extended to include these segments also, when necessary.

II. COMPARATIVE MORPHOLOGY OF THE MALE GENITALIA

A. The Male Genitalia in the Hymenoptera

1. Introduction and Definitions

An extensive but superficial study of the male genitalia of the Hymenoptera was made by Leon Dufour (1841). Supplementary efforts by later workers produced morphological chaos by their failure to give the same names to the same parts. Boulangé (1924), by the publication of tables indicating the terms used by the various workers, introduced a semblance of order; however, this author, like Richards (1934), has preferred to use non-commital terms, having no precise morphological significance outside of the order, this procedure apparently being based upon the belief, expressed by Richards (l.c.), that "it is not possible .... to homologize with certainty the parts of the Hymenopterous genitalia with those of less specialized orders".

Snodgrass asserted (1931, 1933) that the parts of the male genitalia in the Endopterygote insects can be identified by their musculature and articulatory relationships, although later (1935) he described the genitalia "regardless of what may be the morphological relations of the latter". It is certain that in the initial stages of morphological work a non-significant or merely anatomical system of nomenclature is a convenience and, indeed a necessity; nevertheless, the establishment of a uniform system of nomenclature, based upon morphological homologies, throughout the whole range of the group studied, is, as all agree, the ultimate objective of morphological investigation.

It seems evident that, if homologization is possible between the Ichneumonid genitalia and those of other Hymenopterous and Endopterygotous groups, it must be based upon the primitive sub-order Chalastogastra, its parasitic family, the Oryssidae, perhaps being intermediate. Boulangé (l.c.), studied the genitalia and their musculature in the Chalastogastra, in Vespa and in Bombus; he found that the various structures could be arranged in several series, the members of each group being homologous and clearly corresponding in position; however, using myology as the criterion, he found that the inner clasper of Bombus but not Vespa, could be regarded as homologous with the volsella or inner clasper of the Chalastogastra, even though some similarity in form and function existed.

As will be shown later in this paper, the parts of the male genitalia in the Ichneumonidae are clearly homologous with those of the Chalastogastra and therefore, at least, with the Apoidea also.

The male genitalia of the parasitoidal Hymenoptera have, up to the present, received very little attention, though the genitalia of some Chalcids have been described by Embleton (1904), Imms (1916), Grandi (1920-29), James (1926) and Hanna (1934); the development of the appendages in the Braconid Dorycte s by Seurat (1899) and the structure in a few species of Ichneumonids and Braconids by other workers

(Cushman 1913; Pfankuch 1919; Becker 1925; Ceballos 1925; Salt 1931; Glover 1934).

An effort has therefore been made, in the present paper, to identify the parts of the male genitalia of the Ichneumonids with those of the Chalastogastra and with the more generalised forms of insects. Until this has been accomplished, it is obviously impossible to place the terminology upon a sound basis.

As the Hymenopterous genitalia have a series of sclerites peculiar to this order, a system of names must be selected for these parts, the choice being according to the claims of priority or custom, preferably the former.

The nomenclatorial systems of the various workers have been tabulated by Boulangé (1924). The earliest of these were proposed by Audouin (1824), Hartig (1837), Newport (1838), Dufour (1841) and Schenck (1861). Unfortunately, these workers did not confine themselves to the use of similar terms for parts common to the main groups. The application of the law of priority would result in creating a legal monstrosity derived from several systems and thereby losing most of its value; furthermore Audouin's term spatha would have to be applied in a sense that only this author recognised, although the term has been widely used for the dorsal portion of the intromittant organ. Under these circumstances, practicability is the logical criterion.

The next system in order of priority is that of Thomson (1872) and there seems to be little to choose between it and that of Hartig (l.c.). The latter has been sponsored by Rohwer (1919) but has otherwise been ignored. The former is followed by Richards (1927, 1928, 1934), and Mickel (1924, 1928) who are two of the chief workers in this field. Thomson's terms have been more widely used than those of any other author and are applicable throughout the order, exclusive, perhaps of the inner clasper of Vespids; however, modern workers, including Richards (l.c.) employ the term volsella (an older term) for the word lacinia. Therefore, the practical solution of this nomenclatorial problem seems to be for the few workers concerned to have a tacit understanding to use Thomson's method, as modified by Richards.

Thomson's terms were drawn from the supposed homology or analogy between the gnathal and genital appendages,and, to differentiate between them, Crampton (1919) has suggested that the prefix 'gono-' be used for the latter series. To be consistent, it is necessary also to change the term squama to gonosquama to prevent confusion with the Dipterous squama that lies above the halteres.

However, Thomson's terms were originally applied to Bombids, in which the outer clasper is divided transversely into gonostipes and gonosquama. In the Ichneumonids, these are usually fused into a compound structure for which there is no entirely satisfactory term, as the terms gonopod, coxopodite, stylus, harpe and harpago are all morphologically incorrect, while the term stipes-squama of Richards (1934) is clumsy, particularly if the prefix gono- is added. The term forceps was used in 1841 by Dufour but the Dermapterous cerci were called forceps by Burmeister (1839) and perhaps by earlier writers as well; the new term gonoforceps would appear to be both descriptive and applicable.

In dealing thus with the morphological terminology of structures peculiar to the order, one naturally has had to overrule objections of importance but the result has been to form a system that is (1) applicable throughout the order (except, perhaps, to the inner clasper of Vespids) and (2) free from the synonyms so frequent in the literature upon this subject, and (3) used frequently in recent works today, although sometime with minor variations.

The following definitions of terms, used in this paper, are listed below:

Acrosternite
The narrow marginal flange lying anteriorly to the antecosta of the definitive sternal plate.

Aedeagus
The median copulatory organ, formed by the fusion of the parameres with the penis, or with its rudiments, or with the terminal part of the undifferentiated ejaculatory duct.

Antecosta
The anterior, marginal or submarginal ridge on the inner surface of the definitive tergum or sternum; corresponds to the primary, intersegmental fold, on which typically the longitudinal muscles are attached.

Basivolsella
See under Volsella.

Basivolsellar Apodeme
The apodeme at the anterior margin of the volsellar strut.

Chela
See under Volsella.

Coxopodite
The basal segment of a primitive limb.

Distivolsella
See under Volsella.

Distivolsellar Apodeme
The apodeme at the antero-dorsal margin of the distivolsella, supporting the chela.

Dorsal Area of the Volsella
The sclerotic zone lying dorsally to and between the volsellar strut and the anterior apodeme of the volsella.

Epipodite
An exite of the coxopodite.

Ergot
The antero-lateral apophysis of the spathal area in the aedeagus.

Genital Sac
In the male, the ventral invagination of the conjunctival membrane between the ninth and tenth abdominal segments contains the genital organs.

Genital Tergite
In the male Hymenopteron, a lateral half of the ninth abdominal segment.

Genitalia
The external, genital organs.

Gonocardo
The basal, annular or semi-annular sclerite that supports the Hymenopterous gonoforcipes.

Gonocondyle
The medio-ventral apophysis of the gonocardo.

Gonoforceps
One of a pair of the outer, genital claspers in the Hymenopterous male, corresponding in position and function to the harpago of Snodgrass (1935).

Gonopod
One of a pair of primitive appendages at the ventral margin of the ninth sternum in the male (and eighth and ninth in the female) in the Endopterygota; considered as homodynamous with the gnathal appendages and to the thoracic legs.

Gonopore

The external opening of the internal genitalia.

Gonosquama

The differentiated, apical portion of the gonoforcipes; may be either articulated or otherwise.

Gonostipes

The basal portion of the gonoforceps, when the latter bears an apical gonosquama.

Gonostipital Arm

The antero-ventral elongation of the gonostipes.

Harpago

One of a pair of lateral, periphallic processes on the ninth segment, provided with intrinsic muscles and usually having a clasping function; probably homologous with the Hymenopterous gonoforcipes.

Harpe

The apical portion of the claspers in many of the Endopterygota; probably homologous with the Hymenopterous gonosquama.

Hypandrium

The functional, subgenital plate of the male individual;; usually the ninth sternum in the Hymenoptera but, in some specialized forms, the fused eighth and ninth.

Inner Clasper

The processes in the Hymenoptera lying between the outer claspers and the aedeagus and attached to the gonostipes; the term is used without reference to homology.

Orthandria

Chalastogastrous males in which the gonocardo and its appendages do not undergo a lateral torsion; this group appears to include only the Siricids, Pamphiliids and Cephids.

Outer Claspers

In the Hymenoptera, the outer pair of genital claspers, irrespective of their homologies.

Paramere

One of a pair of ventral appendages of the genital segment, originating either at the inner base of the gonopod or between the gonopods (probably the latter); in the Hymenoptera it is fused with other structures, forming an aedeagus.

Parapenes

The secondarily differentiated, postero-dorsal portion of the gonostipes, occurring in the Tenthredinids and in a few Ichneumonids.

Penis

The terminal, evaginated portion of the ejaculatory duct.

Periphallic Organs

The male genital organs, exclusive of those that are phallic.

Phallic Organs

The penis and other male genital organs derived from the area lying between the gonopods.

Pygopod

The lateral appendage lying immediately postero-laterally to the tenth abdominal segment.

Sagitta

One of a pair of elongate, sclerotic rods, supporting internally the lateral portions of the aedeagus; derived from the parameral papilla.

Spatha

The dorsal portion of the aedeagus in the Hymenoptera.

Spathal Rod

The heavily sclerotized rods supporting each antero-ventral corner of the spatha.

Spiculum

The antero-median apophysis of the ninth abdominal sternum in the male Hymenopteron.

Strophandria

Chalastogastrous males in which the gonocardo with its appendages undergo a torsion of 180 degrees; this group appears to include the Cimbicids and the Tenthredinids.

Subcoxa

The proximal part of the coxopodite when this sclerite is differentiated from the coxa.

Syntergite

The lateral sclerite formed by the division of a syntergum into two lateral halves.

Syntergum

The compound sclerite formed by the fusion of the ninth and tenth terga.

Telopodite
That portion of the primitive limb which lies distally to the coxopodite.

Tergite
A part of the definitive tergum.

Volsella
The inner clasper in at least the lower Hymenoptera; it articulates transversely with the ventral margin of the gonostipes and is usually divided, among the Ichneumonids, into (1) the flat, basal basivolsella, (2) the thickened, apical ~~and~~ distivolsella and (3) the articulatory chela borne by the dorsal apodeme of the distivolsella.

Volsellar Strut
The internal ridge between the anterior and the postero-dorsal margins of the basivolsella.

2. The Genital and Postgenital Terga

Among all Endopterygote insects, including the Hymenoptera, Trichoptera, Mecoptera, Lepidoptera, Diptera and Coleoptera, the *male genital segment* is invariably the ninth abdominal. Behind this segment lies the gonopore or genital opening, in the intersegmental membrane and between the two appendages known as the *gonopods* (Snodgrass 1931, pp. 17, 18).

Among the Hymenoptera, it is but seldom that the tergum of the genital segment is not radically modified. Usually this tergum undergoes, in sequence, through the following changes or part of them, viz:- (1) invagination, (2) division into a pair of lateral *genital tergites* (Tg. IX, figs. 16, 17, 20), (3) fusion of these genital tergites with the tergum of the tenth segment to form a *syntergum* (fig. 21) or, alternatively, fusion of the genital tergites with the tergites of the tenth segment, forming a pair of *syntergites* (Sntt., figs. 5, 6, 22) and (4) a reduction in size and functional importance of the syntergites, accompanied often by the loss of the pygopods (figs. 18, 19).

When the tenth tergum is fused with the ninth, the former may be distinguished by (1) the intimate attachment of the rectum by muscles to the posterior portion of the syntergum, (2) the points of attachments of the inter- and intrasegmental muscles in comparison with those of the pregenital segments and (3) the ventro-lateral proximity of the *pygopods* (commonly termed cerci), when these appendages are present. The genital tergites in most Ichneumonids, have a distinct antecosta and this is usually absent in the tenth tergum.

In the Chalastogastra, the most primitive group of Hymenoptera in existence, the ninth tergum is usually divided into two lateral tergites. This is true of most Siricids (Crampton 1919), although in *Sirex juvencus* L. these tergites are joined by a narrow, sclerotized bridge; the same is true of *Xiphidria mellipes* Say (Crampton 1919) and of some species of *Cephus* (Boulangé, l.c.). The incomplete and completed separations of the tergites are shown in *Cephus cinctus* Nort. and *Pteronidea ribesii* Scop. respectively (Tg. IX, figs. 15, 16).

In contrast to the great majority of the Chalastogastra, the parasitic sub-order Idiogastra has the male genitalia completely invaginated (Enslin 1911). In *Oryssus sayi* Westw., as probably in the other members of this sub-order, this invagination has been accompanied by the ninth and tenth terga being reduced in size and in sclerotization, the ninth tergum being divided also into lateral tergites. In this reduction in size, the Oryssids are more specialized than either the Chalastogastra or the Ichneumonidae. Rohwer (1912a) noted that cerci (i.e. pygopods) were absent in the Oryssids but in _O. sayi_, if not the other species also, they are merely concealed by the invagination.

The Ichneumonid genital tergum is always divided medianly and may form (1) a pair of tergites (Tg. IX), as in _Pimpla coelebs_ Walsh (fig. 21); this is rare within the family, (2) a syntergum (Tg. IX), as in _Exeristes roborator_ Fabr. (fig. 20) or (3) a pair of syntergites, as in _Megarhyssa lunator_ L. (fig. 6) and _Banchus falcatorius_ Fabr. (fig. 22). Intermediate forms also occur.

The Chalcids appear to possess a syntergum and a rudimentary eleventh tergum, the syntergum being, in many cases, identifiable by the possession of pygopods (Grandi 1920-29; James 1926; Hanna 1934). It must, however, be noted that in the figures of these authors, the pygopods show that their "ninth tergum" is a syntergum and that Grandi (l.c.) incorrectly identified the gonocardo as the tenth segment. The primitive Chalcid, _Brachymeria intermedia_ Nees is primitive in this respect also, for the ninth and tenth terga are separate, although the former is medianly divided (fig. 17).

In the Aculeate Hymenoptera, the ninth and tenth terga appear to be always fused (Richards 1934) and this fusion is usually accompanied by extensive invagination and the loss of the pygopods. In the Chrysididae only four to six abdominal terga are visible externally (du Buysson 1891). Although both Wheeler (1910) and Donisthorpe (1927) hold that there are ten distinct abdominal segments in the Formicidae, yet the ant *Lasius niger* L. has the sclerotic area of the syntergites almost entirely reduced but their identity is shown by the prominent pygopods (Pyg., fig. 18). Syntergites (Sntt.) are present also in *Vespa maculata* L. (fig. 19), *V. germanica F.* (Boulangé 1924), *Bombus terrestris* L. (Boulangé 1924), *Colletes cunicularius* L. (Morice 1904), *Andrena wilkella* (Kby.) Ill. (fig. 14), *Halictus lerouxii* Latr. (fig. 13) and in *Apis mellifica* L. (Snodgrass 1925). This agrees with the contention of Richards (l.c.) that, in the Aculeate Hymenoptera, the ninth tergum is apparently always reduced to a pair of small syntergites.

While it is evident that the ninth tergum, when fused to the sclerite or sclerites posterior to it, is indubitably in direct contact with the tenth tergum, yet the morphological significance of this latter sclerite is not entirely plain, As noted above, the pygopods are borne upon the tenth segment. According to Boulangé (1924, p. 218), they are appendages of the tergum, although Middleton (1921) rightly claimed that in *Pteronidea ribesii* they lie ventrally to this sclerite. The series of Chalastogastrous and Ichneumonid adults examined during this study suggest, however, that the pygopods lie immediately postero-ventrally to the tergum, arising in the intersegmental membrane. Snodgrass (1931, 1935) holds the view that they are not cerci (i.e. not appendages of the eleventh segment) but may be homologous with the socii of the Lepidoptera. Be their morphological entity what it may, they serve (when present) as admirable landmarks for the postero-lateral margin of the tenth tergum.

The eleventh tergum varies considerably, both in the degree of sclerotization and in its relationship to the tenth tergum. Berlese (1906) claimed that the tenth and eleventh terga were fused together in *Cimbex americanus* L. and separate in *C. axillaris*. This inter-tergal fusion was believed to probably form the Chalastogastrous epiproct (Crampton 1919), while Boulangé (1924) found in *Xeris spectrum* L. (Siricidae) and *Cephus pygmaeus* L. (Cephidae) evidence of fusion through the persistance, in an attenuated state, of the musculature of the two postgenital terga. The same author found that a similar fusion occurred in *Bombus* and *Vespa* also.

However, Snodgrass (1931, p. 97; 1935, pp. 253, 605) considered that the postgenital dorsal sclerite in the Hymenoptera is that of the tenth alone. This is supported by the existence of a broad, membranous area behind the anal sclerite in many Chalastogastrous and Ichneumonid species; in the sawflies *Pteronidea ribesii* and *Dolerus unicolor* Pal. de Beau. respectively this sclerite bears strong setae and setal alveoli, the setae being similar to those of the tenth tergum; in these cases, the setal remains surely must be landmarks of a primarily sclerotic area, which can only be the eleventh tergum. This identification is also supported by the invariable occurrence of the Ichneumonid pygopods in the membrane immediately behind the last functional tergum, suggesting that the eleventh tergum is invariably either fused to the tenth or else de-sclerotized, at least in the Ichneumonids.

The further exploration of this problem is outside the scope of this paper but the morphological value of the pygopods as landmarks makes some reference to it essential, in order to show the significance of the post-genital terga and therefore of the syntergum and the syntergites.

3. The Genital and Postgenital Sterna.

In the Hymenoptera the ninth sternum may be specialized by (1) invagination, the ninth sternum lying dorsally to the eighth, (2) reduction in sclerotization and (3) fusion with the eighth sternum. The Hymenopterous hypandrium is usually formed of the ninth sternum alone, but in a few of the higher groups the eighth sternum is fused with the ninth. The composite character of the hypandrium in the latter case is usually indicated by the presence of (1) the median spiculum; (2) the antecostae of the two sterna and (3) the inter- and intra-segmental muscles.

In the lower Hymenoptera, such as the Chalastogastra (Boulangé, 1924), the Idiogastra and the Ichneumonids, as well as the Chalcids (Grandi, 1920-29; James, 1926, Hanna, 1934), the ninth sternum is well developed. The Aculeate hypandrium is reduced in size and lies dorsally to the eighth (Saunders 1882, 1884a, 1884b; Morice 1899a, 1899b, 1904; Boulangé 1924). Atwood (1934) regarded the eighth and ninth sterna of *Halictus* and *Andrena* as formed by a secondary division of the eighth, the gonocardo being the "base of the ninth ventral segment". In *Halictus lerouxii* and *Andrena wilkella*, a strong muscle, Boulangé's *muscle en sangle*, extends from the anterior part of the syntergite (i.e. from the genital tergite) to the ninth sternum, and short inter-sternal muscles exist between the eighth and ninth sterna. In *Andrena* the acrosternites (Ast.) and antecostae (Ac.) of the two sterna are plain (fig. 14); furthermore, the spiculum (Sp.) has been bent posteriorly, through invagination, forming an internal median ridge in the ninth sternum; in Atwood's figures, the antecosta and spiculum of the ninth sternum are plainly shown as darkly stippled areas. In *Apis mellifica* the ninth sternum is "a well-developed semicircular band, forming the ventral and ventro-lateral parts of the ninth segment. It bears on each side, two conspicuous lobes", the claspers (Snodgrass, 1925).

In the wasps, specialization has been carried further by the fusion of the eighth and ninth sterna (Verhoeff, 1893a; Kluge, 1895; Zander, 1900; Boulangé, 1924) although the hypandrium has been incorrectly interpreted as the eighth sternum and the gonocardo as the ninth by Balfour-Brown (1932).

The hypandrium of *Vespa* is composed of two sterna (Boulangé, 1924), the two antecostae, spiculum, and segmental muscles being prominent. (figs. 36, 37).

In contrast with the development and subsequent degeneration of the ninth sternum, the tenth and eleventh are always retrograde structures, usually being indefinitely demarcated and semi-membranous.. This is plainly due to their early invagination between the terga and the gonopods.

In some Ichneumonids, notably *Pimpla instigator* Fabr. and *Megarhyssa lunator* Fabr., the rigidity of the post-genital sterna is still well preserved. All Ichneumonids have the ventral margin of the anus and the adjoining rectum supported by a sclerotic area that is usually divided medianly and that may vary in shape from hyperbolic to V-shaped or quadrate. In *Ephialtes tuberculatus* Auctt., nec Fourcr., these sclerites bear strong setae with large alveoli, suggesting strongly that these anal structures are not secondarily developed but are remnants of the eleventh sternum, particularly as they lie ventrally to the membranous area that seems to be the eleventh tergum.

In the Chalcid *Brachymeria intermedia*, the post-genital sterna appear to have fused together, forming a long rod that joins the lower lip of the anus to the base of the genitalia (fig. 38); its fusion is not clear and no modification of this kind has been described in other Chalcids by Grandi (1920-1929), James (1926) or Hanna (1934).

As the anal sterna are fragile and minute, as well as being only indirectly concerned with genitalia, they have not been included in this study; however, they must have acquired their present form early in the evolution of the Hymenoptera and may possess group characteristics of interest.

4. The Genital Appendages

Since the basal, annular gonocardo is derived from the gonopods, it is an integral part of the male genitalia in the Hymenoptera, although, in recent years, it has been misinterpreted as the ninth segment by Grandi (1920-1929), Balfour-Browne (1932), Atwood (1934) and Abbott (1935).

(a) The Typical Structure

The male genitalia differ considerably in the various families of the Hymenoptera, yet all exhibit the same fundamental structure, shown in the Chalastogastra (figs. 8-11), as shown by Boulangé (1924). Except in the honey bee, four main parts are distinguishable in the adult, these being (1) the basal, annular gonocardo (Gc.), which bears latero-posteriorly (2) a pair of hollow, hemi-ellipsoidal outer claspers or gonoforcipes, each of which supports by its antero-ventral margin (3) the inner clasper or volsella. The gonoforcipes and volsellae support, by means of muscles and membrane, a median, intromittant organ, that is later shown to be (4) an aedeagus (Aed.).

The gonocardo is attached to the intersegmental membrane lying posteriorly to the ninth segment; it sometimes bears a medio-ventral apophysis, the gonocondyle (Boulangé, 1924). Dorsal to the gonocondyle or gonocondylar area lies the tip of the gonostipital arm, an anterior elongation of the gonostipes, or basal portion of the gonoforceps. The apical part of the gonoforceps is frequently differentiated into a distinct appendage, the gonosquama which may be articulated. Gonosquamae are present in most Chalastogastra (Crampton 1919), in a few Ichneumonids and Vespids, in Bombids and in other Aculeate Hymenoptera; in the Ichneumonids they are not articulated.

The gonostipes bears the volsella, which, among the lower families, normally lies in the vertical plane. The volsella often assumes bizarre shapes. It frequently bears an apical articulatory sclerite, designated in this paper the chela, although termed the pièce en trébuchet by Boulangé (1924); the middle clasper by Peacock (1924) and the squama by Salt (1931) and Glover (1934). The word squama was originally applied by Thomson (1872) to the apical portion of the outer clasper in Bombus (Boulangé 1924; Richards 1934) so that this term is a homonym.

The aedeagus has no close articulation with the remainder of the genital sclerites. In its unspecialized form, the organ consists of a pair of lateral parameres, commonly termed the 'sagittae', joined both dorsally and ventrally by membrane which may become secondarily sclerotized. The aedeagus may assume remarkable modifications in form and size, as in Bombus. The parameres extend anteriorly into the body cavity, far beyond the median membranous area of the aedeagus. The dorsal portion of this membrane may be distinguished as an unusually heavily sclerotized area and then is termed a spatha. Each of its antero-lateral corners forms a lateral apophysis, Boulangé's ergot, which forms a fulcrum about which the aedeagus can pivot in the sagittal plane; the ergot is usually strengthened by accessory spathal rods. The aedeagus is unusually large in the Chalcids (Dufour 1841; Embleton 1904: Imms 1916; Grandi 1920-29; James 1926; Hanna 1934), dwarfing the small outer and inner claspers. In the hive bee, also the aedeagus is abnormally large, but being eversible, is mainly membranous (Snodgrass, 1925).

(b) Ontogenetic Development.

In all Hymenoptera the histoblasts of the male gonopods are situated in the twelfth larval segment behind the head (i.e. the ninth abdominal segment of the adult); this has been demonstrated in the Chalastogastra (Boulangé, 1924), Proctotrupidae (Eastman 1929), Ichneumonidae (Thompson and Parker 1930; Smith 1932), Braconidae (Genieys 1925; Parker 1931; Vance 1932), in the Vespidae, Bombidae and Apidae (Zander 1900) and in other groups.

A study of the ontogenetic development in Sirex (Boulangé 1924), in the Braconid Doryctes (Seurat 1899) and in Vespa and Bombus (Zander 1900) shows that each histoblast develops into a primary papilla that divides longitudinally into the outer and inner claspers. A transverse, basal sclerite is separated from the base of each primary papilla, fusing with its homologue from the other gonopod to form the annular gonocardo.

According to Zander (1900, 1901, 1903) the parameral papilla in Lepidoptera, Trichoptera and Hymenoptera is formed from the base of each primary papilla, soon to fuse with its fellow and with the ejaculatory duct to form an aedeagus. This mode of the formation of the parameres was generally accepted as true until recently, when Mehta (1933) claimed that the parameres in Lepidoptera develop earlier than the lobes of the gonopod and independently of the primary papilla. Moreover, Mehta was able to support his ideas by citing evidence from the Hymenoptera (Michaelis 1900) and from the other main orders in the Endopterygota. The significance of this is discussed in the next section.

Among the Hymenoptera, the formation of the genitalia is always along somewhat similar lines but variations occur both in the number of adult appendages and in the order of their differentiation. Unfortunately, most workers upon this aspect studied the genitalia of the honey bee, in which these structures are aberrant; only two pairs of secondary papillae have been found, either the parameres being absent (Zander 1900, 1922; Snodgrass 1925) or else the outer and inner claspers remain undifferentiated from each other (Michaelis 1900; Boulangé 1924).

Of greater interest is the disagreement between the developmental and myological evidence. The chronological development in Sirex, Vespa and Bombus is shown diagramatically (fig. 1); unfortunately, the description of the Braconid Doryctes by Seurat (1899) is inadequate for this purpose. The differentiation of the parameres (Pr.) occurs later than the separation of the individual outer and inner claspers (O.C. and I.C.), both in Sirex (Boulangé 1924) and Vespa (Zander 1900), although their volsellar muscles are not homologous (Boulangé 1924). Yet the reverse is true of Bombus, for the parameres are differentiated before the appearance of the two pairs of claspers (Zander l.c.), although the genital muscles are homologous with those of Sirex (Boulangé l.c.).

The discrepancies between these data suggest that the ontogenetic evidence should be interpreted cautiously but perhaps assist in showing the independence of the parameres from the gonopod and thereby provide support for the contention of Mehta (l.c.) that the claspers, but not the parameres, are gonopodal in origin.

Before our available ontogenetic data can demand much respect in studies of the Hymenopterous genitalia, it is evident that they must be adequately verified and supplemented. At present, they appear to be probably of little value in comparing the genitalia of adults, unless supported by other evidence.

(c) The Morphological Significance.

According to Snodgrass (1931, 1933), the typical male gonopod of an adult insect consists fundamentally of a basal <u>coxopodite</u>, an apical stylus or <u>telopodite</u> and a meso-basal, unsegmented <u>paramere</u>. The coxopodite may be free, fused to its fellow or joined to other parts of the genital segment. The parameres of the higher insects are fused to the terminal portion of the ejaculatory duct, forming the median, intromittant aedeagus, while the stylus is represented by the clasper; each of the latter may be divided into a pair of claspers also (Snodgrass 1931, p. 192). Accessory structures may be present but almost invariably have no muscles and therefore are distinguishable from the paramere and stylus, which are attached by muscles to the coxopodite.

These conclusions may have to be modified in regard to the gonopodal origin of the paramere, for these are radically altered by the above-mentioned, ontogenetic findings of Mehta (1933), should these prove valid,

The term paramere was proposed by Verhoeff (1893 b) for a paired appendage lying laterally at the base of the Coleopterous penis. Since this time, these terms have frequently been applied loosely, especially when the parameres are already united as an aedeagus. The location of the Coleopterous parameres upon the penis shows that these structures are phallic, not gonopodal, and with this Snodgrass (1935) concurs. Yet the parameres of the Endopterygote orders are widely believed to be gonopodal in origin, as stated by Snodgrass (1931, 1933).

Substantiated by the data of workers in other orders, Mehta's work indicated the probability that the basic data, as outlined by Snodgrass (1931, 1933) are partially incorrect, the parameres never being gonopodal. Should this be so, Mehta has clarified considerably the current concepts, not only upon parameres, but also upon the fundamental structure of the male genitalia in the Endopterygota, a group in which a common, basic form is to be expected.

Recently Snodgrass (1935) has reviewed the male genitalia of insects and his conclusions are quite at variance with his previous ones (Snodgrass 1931, 1933). The term paramere is accepted in the Coleopterous sense but in this work, he has adopted a terminology "that can be applied consistently to the major structural elements regardless of what may be the morphological relations of the latter". The genital structures are divided into two classes, phallic and periphallic. The phallic organs are "immediately concerned with the function of coition; they include the phallus and various accessory or supporting structures associated with the latter. The periphallic organs are movable or immovable lobes or processes that have for the most part a grasping or clasping role in the function of copulation". The phallic organs, including the parameres, are evolved from the conjunctival membrane posterior to the ninth sternum or in the genital chamber anterior to the membrane. The "periphallic structures arise peripherally, generally from the annulus of the ninth abdominal segment but also from the other segments often closely associated with the latter in the genital complex". They may include a pair of lateral movable claspers .... and various immovable lobes or processes arising from the tergum or sternum; the movable claspers or harpagones. To the writer, these concepts seem inadequate for the positive identification of some of the genital appendages.

Applying these concepts to the Hymenoptera, Snodgrass suggests that their genitalia are entirely phallic, the gonocardo and gonostipites being formed from the phallobase and the median appendage being an aedeagus; the gonosquamae "may be termed parameres since they are at least analogous with the parameres of Coleoptera", even though he states that the apices of the parapenes are "structures of the same nature" as the gonosquamae. How little is realized of the morphology of these Hymenopterous structures is shown by these suggestions that the parameres may be either the gonosquamae or parapenes, or, if the word aedeagus is to be construed rigidly, even a part of this median organ also.

These surmises of Snodgrass were reached through the assumption that function is the logical basis for the differentiation between genital parts. Even if this were so, the peripheral position of the gonocardo and gonostipites, together with the clasping role of the latter, show that these are periphallic according to Snodgrass' latest concepts. The evolution of appendages, either inside or outside of the genital chamber, or in the adjacent membrane, is not a valid criterion of homology in this case, for the harpagones of Lepidoptera (i.e. the harpes) arise within the genital cavity (Zander 1903; Mehta 1933), yet these structures are declared peripheral by Snodgrass (1935). Furthermore, in the Lepidoptera and Trichoptera, the basic evolution of the claspers and the median organ is similar to that in the Hymenoptera (Zander 1900, 1901, 1903); yet the claspers in the first two groups are dubbed periphallic but those of the Hymenoptera phallic! The claspers of the Mecoptera were found to agree in musculature with those of the sawflies (Boulangé 1924), yet the Mecopterous claspers are termed periphallic and those of the Tenthredinids phallic. As the morphological data cannot permit the Hymenopterous claspers to be classified as phallic when those of related orders are not so, it is evident that some means of separation, other than function alone, must be used to recognise the parameres.

The parameres and other genital appendages in the adult have been identified more satisfactorily by Pruthi (1929), who considers the parameres as derived from the median papillae, while the gonopods are in the same general planes as the ninth sternum, lying under the penis and parameres. Thus Pruthi agrees with Mehta (1933) that the parameres are attached laterally to the base of the penis (it should be noted that Pruthi's aedeagus is the penis, as interpreted in this paper.

It must be remembered that the origin and position of appendages are not the sole guides to their homologies, for the direction of articulation of limbs is an unusually stable landmark (Snodgrass 1931). Since the gonopods are believed to be homodynamous with the thoracic limbs, a comparison of the genital claspers with the primitive, thoracic limb may be of value in determining the homologies of the genitalia.

The primitive, thoracic limb consists of the basal coxopodite (Cxp.) and the distal telopodite (Tlp.), their muscles extending from the base of the coxopodite to the base of the telopodite, as in fig. 2 (Snodgrass 1927, 1935). The coxopodite moves in a horizontal plane upon the body, the secondarily differentiated coxa moving in the same plane also, while the telopodite articulates vertically upon the coxopodite (Snodgrass l.c.), as shown in fig. 4. Since both the primary papillae of the thoracic limbs and the genital histoblasts are formed upon the ventral surface of the body, the initial, inherent movement of the undifferentiated coxopodite is sagittal. The subsequent development of the insect causes the thoracic papillae to migrate laterally, while the genital appendages move posteriorly; the coxopodite of the latter therefore secondarily articulate in a vertical plane, while the telopodite is horizontally movable. The significance of this is shown later.

From the ontogenetic data, it is plain that the Hymenopterous gonopod is basally fused to its fellow, forming the gonocardo (Zander 1922). This fusion is indicated in the adult by a medio-ventral or medio-dorsal suture or else a corresponding internal ridge; among the Ichneumonids, the ventral fusion is shown in many species, while the dorsal fusion is plainly shown in Nototrachys foliator Fabr. and Trogus lutorius Fabr. The gonocardo, therefore, must represent either the two coxopodites or else their bases.

As the median, intromittant organ is derived from the fusion of the ejaculatory duct with paired rudiments, this composite organ is evidently an aedeagus. The Chalastogastra, a primitive group in the order, has a primitive aedeagus also, for it often consists almost entirely of the duct, of the two elongate sagittae and of connective membrane; it seems evident that the parameres are represented by the sagittae, especially since the latter are found throughout the members of the order (except perhaps Apis mellifica) and form the inflexible, lateral parts of the compound organ.

The outer and inner claspers are provided with well-developed muscles, so that, according to Snodgrass (1931), neither can be purely accessory structures, Crampton (1920, 1931) suggested that the gonosquama is the stylus and Richards (1934) supported him by indicating that the gonostipes and gonosquama probably form the apical portion of the coxopodite with its stylus. The latter author suggested also that the volsella is a two-segmented paramere and the median organ an aedeagus; his basic definitions evidently differ radically from those of Snodgrass (1931, 1933). Becker (1925) concluded that the volsella of the Tenthredinidae and Ichneumonidae represents the trochanter and femur, and the Bombid volsella the femur! The gonosquama then presumably would be an epipodite. As Becker appears to have compared the Hymenopterous genitalia directly with those of the Apterygota, the lack of intermediate forms seems to entirely invalidate his conclusions.

A homology between the volsella and the telopodite is suggested by the constant presence of the articulating chela in the lower families of the Hymenoptera. Moreover, the volsella in the Chalastogastra and Ichneumonoidea has a constant, diagonal, internal thickening, the *volsellar strut* (V.Str.) (figs. 9, 117-127), suggesting the remnant of the arthrodial thickening in a flattened limb joint, the adjacent limbs being joined by Boulangé's muscle *Q* (fig. 8); however, this strut appears to be secondary, for its function is to prevent buckling of the volsella during the contraction of Boulangé's muscle *Q*. Furthermore, there are no condyles in the gonostipito-volsellar joint, although they should be present in an articulatory limb that is derived from a primitive leg.

The lack of homology between the volsella and the telopodite is further shown by the base of the volsella being almost flat in the primitive Hymenoptera, so that, if this homology is correct, the telopodite (or, possibly, the apex of the coxopodite) must have changed basally from the normal, tubular form to one that has been either very strongly compressed or else split along the main axis of the limb, spread outwards and flattened.

The first method of evolution is impossible, for there is no sign of fusion between the opposite sides of the limb (except possibly the volsellar strut), the basivolsella being thin and almost diaphanous. Furthermore, the intrinsic muscles of the tubular limb must have been gradually replaced by (or developed into) an efficient, complex extrinsic system. It is absurd to postulate the occurrence of both of these two radical, changes, each of which is highly improbable.

The second method of formation seems to be equally impossible. The longitudinal fission, unfolding and flattening of the basal part of the telopodite, accompanied by extensive internal changes, could only have evolved slowly, yet intermediate forms appear to be absent. Furthermore, this change from the tubular form to that of a plate would weaken the telopodite at the very time that it was being adapted as a clasper, a structure that is essentially strong. This theory can be accepted only if accompanied by further proof and in the absence of a more logical explanation.

The absence of homology between the telopodite and the volsella is shown by the origin of the latter. This structure is formed from the lateral papilla by an apical or medio-apical fission, the volsellar region being the smaller. This suggests that neither an endite or exite is present but also that, if one is present, then the volsella is an endite of the telopodite.

Moreover, the base of the paramere is joined to the base of the chela by Boulangé's muscle N in both the Chalastogastra (fig. 8) and the Ichneumonidae (fig. 7). Even if it is conceded that the paramere is gonopodal in origin, yet one cannot recognize the existance of a primary muscle that extends between a basal appendage of the coxopodite and the apical telopodite. Either this muscle is secondary, which is improbable, or else the identification of the telopodite is incorrect.

The morphological relationship between the gonopod and the volsella is emphasized by the detailed, adult structure of the latter.

The separation of the volsella and gonostipes is anteriorly incomplete in some Siricids, as in Sirex sp. (Enslin 1912, fig. 15) and in both Sirex juvencus and Xeris spectrum (Boulangé 1924, p. 228); the same phenomenon also occurs in widely separated species of Ichneumonids (fig. 97) and is discussed later. While this is indicative of a similar morphological relationship between the inner claspers of these groups, yet, coupled with the primitive nature of the family Siricidae, it further suggests that the volsella originated from the gonoforceps.

The view that these two structures are primitively one is supported by the appearance of the Ichneumonid basivolsella, in which (1) the setae and alveoli are facing the aedeagus, (2) the muscles lie laterally to the basivolsella and (3) the curvature of this sclerite is mesal. Together, these factors strongly suggest the rounded shape and musculature of the mesal portion of the gonopod. The setae are evidently primary, because they are small in comparison with the alveoli; furthermore, the setae and alveoli only occur postero-ventrally, as in *Ichneumon grotei* Cress. (fig. 121), this being a position favoured by the basivolsellar curvature for the survival of setae from the attritional effects of invagination, yet an unsuitable place for the development of tactile organs to be used during coition. The curvature of the basivolsella is, in itself, insignificant for the shape may be due to a coincidence or to the tension exerted by Boulangé's muscle *Q* (fig. 8), although this muscle probably is not used except during coition and this would be seldom. Individually these three factors are not of much weight, yet, when correlated with each other and with the ontogenetic development of the volsella, one can only conclude that the volsella and gonoforceps in the Ichneumonidae are primitively one structure.

These reasons, incidentally, serve also to show the falsity of the idea that the volsella may have originated directly from membrane, instead of from sclerotic structures; the form and musculature of the volsella is far too specialized to be associated with such an extensive change, one that is already so complete that there are no intermediate forms, even in the most primitive of the Hymenoptera.

Since the volsella and gonostipes primitively form either a part or all of a single appendage, it is necessary, before their identity is established, to determine the significance of the gonocardo and of the remainder of the gonoforceps.

Since the parameres are appendages derived either from the coxopodite or from the area meso-basally adjacent to it, and since the aedeagal muscles extend to the gonostipes and volsella rather than to the gonocardo (muscles *H*-*L*, *M*, *N*; figs. 7, 8, 10), the gonostipes and volsella must be derived from the coxopodite, agreeing with the conclusions of Crampton (1931, nec 1920) in so far as the gonostipes are concerned, Neither the articulation of the gonocardo upon the genital segment nor the movement of the gonostipes upon the gonocardo is sufficiently in one plane, the vertical, to identify the subcoxae or the coxae, should these have been differentiated in the Hymenopterous gonopods. The gonocardo appears to have been secondarily differentiated from the bases of the coxopodites, this being at least analogous to the formation of the trochantins from the thoracic limbs, for both structures allow additional articulation.

Since the gonocardo is the basal portion of the coxopodite, then the primary muscles, extending from its base to the base of the telopodite (fig. 2), should be attached beyond the base of the gonostipes; nevertheless, the contrary is the case in both the Chalastogastra (figs. 8, 10) and the Ichneumonidae (fig. 7), for the only muscles extending posteriorly from the gonocardo are D, E, F, and G and these are attached to the anterior margin of the gonostipes. However, if the paramere is considered as gonopodal, then muscle J extends to the apex of the parapenial area and muscle M to the chela (figs. 9, 10); in this case, the gonosquama must be a secondarily divided portion of the telopodite.

As an alternative, one can conclude that the primary muscles of the gonopod have degenerated owing to the extensive torsion of structural modifications that this appendage has undergone. The primary muscles extending between the bases of the coxopodite and of those of the telopodite would move the gonopod laterally and, as pointed out by Abbott (1935), there is no genital muscle able to do this. The genitalia then must be spread apart laterally by blood pressure; blood pressure has already been noted as a factor in the functioning of the male genitalia in the honey bee (Snodgrass 1925), in which however there are no functional claspers and the aedeagus is mainly membranous. In the Ichneumonids this factor would also account for the rotation of the volsella from the subvertical resting position to the horizontal copulatory attitude, the gonoforceps being closed during copulation by the contraction of muscle J, exserting the aedeagus and causing muscle L to draw the gonopods towards the ergots of the aedeagus and therefore to each other. Should this be the case, then the primary muscles of the gonopod (fig. 4) would fall into disuse so that the gonopodal muscles of today would be short for they would be formed secondarily for the articulation of secondary sclerites (fig. 4). To the writer, this seems to be the most logical reason for the absence of primary muscles.

One could also conclude that the primary muscles of the thoracic limbs have no homologues in the gonopod. However, both the thoracic limbs and the gonopods are believed to have primitively formed parts of a series of similar appendages, adapted for either walking or swimming. The primitive musculature in these structures would then be identical, those of the gonopod apparently being the intrinsic muscles used by Snodgrass (1931) to identify these structures.

If the parameres eventually prove to be gonopodal, then the gonosquama is a part of the telopodite, since muscle _J_. shows that the parapenial area is part of the telopodite. If, on the contrary, the parameres and the gonopods are entirely separate structures, then the origin of the gonosquama is still an open question. The weight of evidence seems to be in favour of the latter.

The gonosquama articulates in many of the Chalastogastrous males and is present, but rigid, in some Ichneumonids, Vespids, Bombids and other Hymenopterons. As its presence in these groups appears to be sometimes only of generic or specific value, it may be argued that they are purely secondary and that the telopodite is indistinguishably fused with the gonostipes in all the groups; on the other hand, the gonosquama articulates laterally, as should the telopodite. The available evidence, therefore, seems inconclusive in establishing the true morphological nature of the gonosquama.

Upon these grounds it is felt reasonable to suggest that the Hymenopterous genitalia in the males are derived in the following manner:-

Primitive Structure		Genital Structure
Gonopod	Coxopodite	Gonocardo (the lateral half) Gonostipes Volsella
	Telopodite (?)	Gonosquama
Parameres Penis		Aedeagus

It should also be noted that (1) the parameres may be gonopodal in origin and (2) the inner clasper in the Vespidae is still a morphological problem, although apparently gonostipital.

5. Functional Adaptations

The trend of development in the genital segment and its appendages is remarkable, consisting of a series of changes, the one usually initiated by the next but frequently both proceeding simultaneously. To understand the causes of these modifications, it is necessary to study the growth of the gonopods.

While, according to Snodgrass (1931), the insect gonopods usually develop in the intersegmental membrane behind the ninth sternum, yet the ontogenetic data cited above suggest that the Hymenopterous appendages originate in the sternum itself. This disagreement must be due to the gonopods being attached to the intersegmental membrane which is invaginated above the ninth sternum. In either case, the gonopods are formed within an invagination and are closely linked to the ninth sternum, for, while functionally external, they are when at rest at least partially invaginated into the body cavity and their weight is supported directly by the hypandrium.

As the immature gonopods grew posteriorly, they extruded beyond the ninth sternum and gradually subjected the latter, not merely to a greater weight, but to a torsion. The latter appears to have been resisted to some extent by developing the muscles between the eighth and ninth sterna and by increasing their leverage through the elongation of the spiculum, to which they are attached. The torsion was met also by the further invagination of the appendages into the abdomen, the appendiculo-segmental connective tissue thus forming Boulangé's genital sac. While this occurred in both the Chalastogastra and Ichneumonidae, yet the sagittal growth of the gonopods in the bees and wasps was much greater, causing the invagination, not of the genitalia alone, but of the segments to which they are attached.

This migration created a difficulty in the exsertion of the genital organs. Since these appendages are either sternal or intersternal in origin, they are not joined to the genital tergum by muscles; as a result, muscular extrusion of the genitalia would be difficult, if not impossible, unless it were aided by an increase in the blood pressure in this region.

The gonoforcipes were enlarged in the transverse plane also and this caused a difficulty in the passing of the invaginated claspers posteriorly through the genital segment for coition. The elasticity of the genital segment was increased at first by the median fission of the gontergum into gonotergites, this process being complete in the Ichneumonids and in most of the Chalastogastra. These tergites fused with the tenth tergum or its tergites and, in response to the continued demand for a larger passage for the gonopods, the syntergum or the syntergites were reduced in size among the Aculeate groups. The final, extreme stage was reached with the Bombidae, in which the gonopods are enormous and entirely invaginated, while the syntergites are functionless, vestigial structures.

However, the need for elasticity in the genital segment accounts only for the formation of the tergites and their reduction, not for the inter-tergal fusion. After the gonotergites were formed, if not before, the genital tergum should have migrated anteriorly in response to the pull exerted by the invaginated genitalia through the membrane of the genital sac. Instead, these tergites migrated postero-ventrally to fuse with the tenth tergum. As mentioned above, the weight of the copulatory organs are borne primarily by the hypandrium so that the enlargement of these structures would pull the gonotergites ventrally. As both the hypandrium and the genitalia developed posteriorly, they formed a lever about the posterior margin of the eighth sternum, pulling posterio-ventrally upon the gonotergites. The existence of such a torsion is suggested by the spiculum being segmentally unique and an excellent lever to neutralize this force.

The strain of bearing the enlarged hypandrium and gonopods was borne chiefly by the eighth sternum and the ninth tergum, but, as the latter was already weakened by the need for flexibility of the genital segment, the increased burden hastened the disintegration of the gonotergum. The strain then was passed along to the eighth and tenth terga. The eighth was a large normal segment but the opposite was true of the tenth. Consequently, the tenth was frequently affected by the growth of the genital appendages. However, the tenth tergum would be held together to some degree by the attachment of the proctodaeal muscles, since the tenth is the last functional segment. The presence of the proctodaeum and its tergal muscles must have prevented the tenth from moving posteriorly in sympathy with the ninth; otherwise, the ninth tergites could not have been brought into contact with the tenth in order to fuse with it.

Thus, the modifications occurring in the genital and postgenital terga and the genital sternum are correlated with the growth of the genital appendages, due to physical strains.

The origin of the gonocardo is also of interest. It is plain that the posterior growth of the ninth sternum and the invagination of the gonopods would create tension upon the conjunctival membrane between the hypandrium and the gonopods. Such tension, if sufficiently powerful, could split from the gonopods the two basal gonopodites that later unite to form the gonocardo. This theory of causation is supported by the occurrence, in all the main Endopterygote orders, of an enlarged ninth sternum and by their possession of small, genital sclerites basal to the functional claspers; these may be gonopodites, as suggested by Pruthi (1925). Furthermore, such basal sclerites and enlarged hypandria are common to all Rhynchotous families, except the Coccidae, and in this family the former are absent and the latter small (Pruthi, l.c.). Therefore from these data, there seems to be a perfect correlation between these two factors, although this is only circumstantial evidence in regard to the cause of this phenomenon, particularly since the gonocardo is differentiated early in the development of the insect.

The volsella was divided from the gonopod by a secondary division of the gonostipito-volsellar sclerite, the fission beginning meso-apically, developing more extensively upon the dorsal surface, and eventually detaching the volsella entirely from the remainder of the gonopod, excepting sometimes antero-basally. Dorsally the fissure was broadened, allowing (1) the volsella to move transversely upon the ventral margin of the gonostipes and (2) the parameres and the adjoining membrane to move posteriorly.

These deductions upon the causes of the genital modifications are necessarily somewhat speculative in character, even though they are drawn from series with many intermediate forms, for they are based solely upon the physical mechanism of the genitalia and upon forces that cannot be accurately measured. Nevertheless, the data appear to show that the increase in the size of the genitalia has initiated a series of essential, supplementary modifications and therefore support the theory of orthogenesis. However, as efficient coition is essential to the survival of bisexual species, some students of evolution may regard the genitalia as being peculiarly susceptible to changes that superficially support the orthogenetic concept.

B. The Ichneumonid Male Genitalia

1. The Structure and Musculature

The Ichneumonid genitalia resemble those of the Chalastogastra, a closely related but less specialized group, in which, however, the genitalia vary greatly in form. The Ichneumonids differ from the Chalastogastra in (1) the frequent formation of a syntergum or of a pair of syntergites, (2) the invariable absence of the parapenes, (3) the absence of a distinct gonosquama in most species,

(4) the greater refinement or specialization of the volsella and its greater uniformity of shape and (5) the greater degree of sclerotization in the aedeagus. Upon these points, the Ichneumonids are nearer to the parasitic sub-order Idiogastra, as represented by <u>Oryssus sayi</u> although this species has a non-articulated gonosquama and its aedeagus is only weakly sclerotized.

The main homologies between the Chalastogastrous genitalia and those of the Ichneumonids are quite evident, if shape, position and articulation are sufficient criteria; this, however, does not apply to the inner claspers and, to show this relationship, it is necessary to describe in detail the structure of the Ichneumonid inner clasper. This appendage is assumed to be a volsella and the proof shown subsequently.

The volsella of <u>Neotypus americanus</u> Cush. is typical of this structure as it occurs in the Ichneumonids so that both the external (or mesal) and internal views of this organ in the vertical position have been shown (figs. 119, 120). It should be noted that all drawings of this appendage show a large basal piece that is shaded by broken lines; these lines do not represent complete de-sclerotization, but, instead, a sclerotic plate that is extremely thin compared with the remainder of the volsella, being amost comparable to membrane in appearance. This plate is termed the <u>basivolsella</u> (Bv.) and is braced by the internal <u>volsellar strut</u> (V. Str.) which divides the basivolsella by passing from the anteroventral margin to the postero-dorsal corner of the basivolsella. The anterior apex of the strut is developed into the *basivolsellar apodeme*, which may be curved ventrally, laterally or dorsally. The postero-ventral margin of the basivolsella bears the strongly sclerotized *distivolsella* (Dv.) in which the apical margins are usually incurved and fused, forming a hood. The antero-dorsal margin of the distivolsella is prolonged into the *distivolsellar apodeme* (Dv. A.) to which is attached dorsally the chela (Ch.) which almost invariably is articulated.

The volsellae in most sawflies bear but little resemblance to the inner claspers of the Ichneumonids, except that they have in common two distinct sclerites, the anterior *pièce complémentaire* of Boulangé (1924) (which corresponds to the basivolsella and distivolsella) and the dorso-apical *pièce en trébuchet* (which is identified with the chela).

The position and articulation of the Ichneumonid inner clasper is quite similar to that of the Chalastogastra. The same variation in articulation occurs in both, since the Siricid volsella moves either feebly or not at all upon the gonostipes, although freely in the Tenthredinids (Boulangé l.c., p. 228); while the former is true at least of some species of Ichneumonids, although the latter is far more common.

The volsellar strut is a constant feature of the Ichneumonid inner clasper and is plainly identical in position with the diagonal nervure of Boulangé (l.c., pp. 62, 97), as shown in the Siricids and in the Tenthredinid, *Tenthredella mesomelas* L. (fig. 117). It occurs also in the

Tenthredinid, Dolerus similis Nort., (fig. 118) in which the anterior end is developed into an apophysis, corresponding to the anterior apodeme of the Ichneumonids.

The apex of the pièce complémentaire in both T. mesomelas (fig. 117) and in D. similis (fig. 118) shows a striking similarity to the Ichneumonid distivolsella in having the apical hood and the antero-dorsal apodeme. Furthermore, this apodeme is present in Oryssus sayi (fig. 113*) a member of the intermediate, parasitic Idiogastra.

Nevertheless, the diversification of form in the Chalastogastra suggests that there is a possibility that these similarities are due only to convergent evolution and then are insignificant; this is supported by the view held by Boulangé that the inner clasper of the Vespids is not homologous with the volsella of the Chalastogastra. On this account, the muscles of the Chalastogastrous and Ichneumonid genitalia (and the adjacent sclerites) have been compared. Unfortunately, the males of the family Oryssidae are too rare to have included a representative of this intermediate group for dissection.

The Pimpline Megarhyssa lunator was selected for this work since its great size allowed the use of the binoculars instead of the microtome the lack of appreciable amounts of melanin permitting the satisfactory transmission

*This figure supports the tentative conclusions held by Crampton (1919) in regard to the volsellar structures in the Oryssidae.

of light through the sclerites; the elongation of the abdomen and of the genitalia tends to isolate many of the muscles so that they can easily be recognized but sometimes it also tends to change their axes. The muscles of _M. lunator_ are compared with the morphological type of the Chalastogastra, as established by Boulangé (1924), whose system of myological nomenclature is therefore followed (figs. 8-11). Muscles _D_, _E_, _F_ and _L_ are not shown in the illustrations of _M. lunator_ (fig. 7) but their positions are described. The muscles and their possible functions in _M. lunator_ have already been briefly described by Abbott (1935).

The abdomen of _M. lunator_ is both narrow and elongate, the sterna being so strongly invaginated that the ventral margins of the terga touch in places. No muscles appear to join the tergum of one abdominal segment to the sternum of the immediately anterior or posterior segment (fig. 5); the absence of this type of oblique muscle identifies the lateral parts of the syntergites as the genital tergites (fig. 6), their fusion to the tenth tergites being incomplete posteriorly. The posterior boundary of the latter segment is indefinite, since the Tenthredinid pygopods are borne upon the tenth tergum (Snodgrass 1935), although the Ichneumonid pygopods are invariably separated from the tenth tergum by some membrane, this space being accentuated in _Megarhyssa_ so that it resembles the eleventh tergum.

The syntergites are joined to the ninth sternum by a well-developed muscle, Boulangé's _muscle en sangle_.

The hypandrium is joined to the gonocardo by muscles *A*, *B* and *C*; the first two extend from the spiculum to the gonocondyle and to the antero-lateral margin of the gonocardo respectively, lying closely together, as in *Sirex juvencus*. Muscle *C* is weak but distinct in *M. lunator*, extending between the latero-posterior portion of the hypandrium and the gonocondyle. The Ichneumonid gonocondyle resembles that of Orthandria in being either minute or absent; the development of the gonocondyle is associated with the lateral torsion of the genitalia in the Strophandria (Crampton 1919).

The gonocardo is joined to the basal margin of each gonostipes by muscles *D*, *E*, *F*, and *G*; *D* and *E* cross each other ventrally, while *F* and *G* are dorsal. Muscle *D* is attached medianly to the gonocondyle and *E* similarly to the gonostipital arm; as *M. lunator* has long gonostipital arms, *D* and *E* lie dorsally to the gonocardo, *E* being short. Muscle *F* extends laterally from the antero-median portion of the gonocardo and is rudimentary, for this part of the gonocardo in *M. lunator* is membranous. Muscle *G* joins the antero-lateral margin of the gonocardo to the antero-median margin of the gonostipes and its direction has been changed from being almost transverse to nearly longitudinal, due to the sagittal elongation of the gonocardo; *G* has therefore assumed a part of the function of *F*.

Five muscles, H-L, join the gonostipes to the aedeagus. Muscle H is narrowly attached to the base of the paramere and broadly to the base of the gonostipital arm; it is well developed in Megarhyssa; its function is that of raising the apex of the aedeagus, which is balanced about the ergots by membrane and muscles. Muscle I, connecting the gonostipital arm to the ergot, is strong in M. lunator and serves to retract the aedeagus, sharing this function with the slender muscle K, which extends antero-dorsally from between the ergots to the gonostipes. Muscle J causes the exsertion of the aedeagus and connects the base of the paramere to the postero-dorsal part of the gonostipes; J is long and strong in Megarhyssa and in the Tenthredinids, although short in Sirex, Bombus and Vespa (Boulangé 1924); the length of J in M. lunator may be due to the elongation of the gonostipes but then the same should be true of Vespa, unless only the apical part of the Vespid gonostipital area has been developed posteriorly. Muscle L extends laterally from the ergot to the gonostipes and is both short and weak in Megarhyssa.

In Megarhyssa the gonosquama appears to be incompletely fused; muscle T is present, extending from the baso-lateral portion of the gonostipes to the gonosquama; the short gonosquamo-gonostipital muscle U and the intrinsic gonosquama muscle V were not identified in Megarhyssa, perhaps due to the gonosquama not articulating in this species.

The volsella articulates only weakly in the Siricids but strongly in the Tenthredinids (Boulangé 1924) so that the muscles of the Ichneumonid volsella should resemble those of the latter group. Muscles O and P unite the volsellae to the gonostipites. Muscle O is absent in the Orthandria and in *M. lunator* but joins the base of the Tenthredinid basivolsella to the apico-lateral part of the gonostipes. Muscle P, joining the antero-lateral margin of the gonostipes to the distivolsella, is present in all of these groups; it is well developed in *Megarhyssa* and is attached broadly at the base (this is not shown in fig. 7).

Two muscles, M and N, join the volsella to the aedeagus. The former extends from the apex of the chela to the extreme base of the paramere and is absent both in the Tenthredinidae and in *M. lunator*, although present in Siricids. Muscle N joins the Chalastogastrous chela basally to the base of the paramere. A moderately weak muscle is attached to the base of the chela in *Megarhyssa* but its basal attachment was not definitely established.

The volsella has three intrinsic muscles, Q, R and S, each attached to the base of the basivolsella and extending respectively to the apex of the distivolsella, the apex of the chela and the base of the chela. Muscle Q is present in the Siricids and is large in *M. lunator*; in the Tenthredinids it appears to be attached to the chela but Boulangé (1924, p. 71) is not definite upon this point. In *M. lunator* the attachment is definitely at the basal apodeme of the distivolsella, although this was plain in only one slide. Muscle R is absent in *Megarhyssa*, as there are no muscular fibres visible within the chela, while S seems to be reduced to some weak fibres.

The muscles of *M. lunator* disagree in detail with those of either the Orthandria or Strophandria alone, but, when these are considered together, there can be no doubt that the gonocardo, gonostipes, gonosquama, basivolsella, distivolsella, chela and aedeagus are homologous in the three groups, the basi- and distivolsella together corresponding to Boulangé's *pièce complémentaire*.

2. Function

While much has been written upon courtship among the Hymenoptera, including some Ichneumonids, yet only a few inadequate references have been made to the function of the genital parts of the male Ichneumonid during coition or, indeed, even to the coital attitude of the male.

As early as 1799, De Geer described the seizure of the female subgenital plate (i.e. the eighth sternum) by the outer claspers of a male Ichneumon, while Rohwer (1915) noted that the inner claspers and aedeagus in the sawfly *Euura macgillrayi* Roh. were inserted into the genital cavity at the base of the subgenital plate. Neither Boulangé's own work nor his review of the literature adds anything further in regard to the functioning of the inner claspers and aedeagus.

The usual Ichneumonid position of copulation seems to be that of *Pimpla instigator*, in which the male is dorsal to the female with his abdomen curved below the tip of the female's and somewhat to one side in order to avoid the ovipositor. In *Megarhyssa lunator* the male lies above the female with the apex of his abdomen below that of the female and the aedeagus is inserted from the anterior direction, since the female gonopore opens anteriorly. (Abbott 1934, 1935). In *Paniscus*, the male finally assumes a pendent position (Vance 1927); this may be true of *Angitia fenestralis* Hlmgr. also, for specimens taken *in copulo* were only loosely held together after being killed in alcohol and this may be due, not to chemical reactions upon the muscles, but to the adults having died before the pendent attitude was reached. This variation in copulatory position suggests that there may be a correlation between the coital attitude and structure, as suggested by Abbott (1935).

In this regard, it is interesting to note that in *Xiphidria* (Chalastogastra: Orthandria) the copulation is dorsal (Rohwer 1915), there being no transverse rotation of the appendages in this group (Boulangé 1924), although in at least some of the Strophandria, the males and females mate while facing in opposite directions (Rohwer 1915; Boulangé 1924; Hopping and Leach 1936).

Specimens of the Ichneumonid *Angitia fenestralis*, taken *in copulo*, were examined. In this species, the distal parts of the outer claspers grip the lateral portions of the subgenital plate of the female (fig. 12), who no doubt extrudes her gonopore at the same time. The volsellae are rotated into the horizontal plane, due to the muscular, ventro-posterior exsertion of the aedeagus and the increase in the blood pressure. The distivolsellae are bent upright through the contraction of muscle *Q* and the chelo-distivolsellar pincers are directed dorsally in respect to the male (but ventrally and slightly anteriorly with reference to the female). In this position, the pincers of the volsella are closed upon the intersegmental membrane of the female, due either to the action of the chelar muscles or to the exserted aedeagus pulling the base of the chela posteriorly. The function of the volsellae is apparently to seize the conjunctival membrane, keeping it taut so that the aedeagus can be inserted into the female gonopore and be retained there. The aedeagus is exserted with its apex directed ventrally and, as it is strongly curved ventrally in this species, both its shape and its position at right angles to the main axis of the genitalia assist to retain the aedeagus in position during copulation. It should be noted that the function of the volsella was not definitely shown by dissections, due to the relaxations of the claspers but these conclusions were strongly indicated.

III. TAXONOMY OF THE HYMENOPTEROUS AND ICHNEUMONID GENITALIA

A. Introduction

During the last twenty five years, there has been considerable disagreement upon the identity of the type species of some of the early Ichneumonid genera and, therefore, upon their correct generic names (Morice and Durrant 1914; Viereck 1914, 1921; Cushman and Rohwer 1918; Cushman 1921; Roman 1932, 1933). The merits of many of these proposed names are at present under the consideration of the International Commission upon Zoological Nomenclature (Stiles 1936); the names used in this study are therefore those consecrated by time and employed by Schmiedeknecht (1930, 1932, 1933, 1935). This is of advantage also in that the majority of the species studied in this paper are European.

The classification of the Ichneumonidae is also still unsettled. The most recent, complete classification is that of Schmiedeknecht (1930). This has been brought further into line with recent thought by his unfinished series of fascicles, supplementing his Opuscula Ichneumonologica; in these he has adopted some of the concepts of Cushman and Rohwer (1920), dividing the tribe Pimplini (s.l.) (Schmiedeknecht 1933).

The generic limits of many Ichneumonid genera are very indefinite at the present time and this condition is clearly shown in this study, where both holarctic and nearctic species are used. As an example, the nearctic species of the genus Ichneumon L. (i.e. Amblyteles Cush. et al.) frequently cannot be placed with certainty within any of the genera or subgenera recognized by European workers (Cushman 1928; Peck 1933), although Cresson (1877) attempted to do this. Cushman's concept of the genus Ichneumon has been retained. The genus Hemiteles of Schmiedeknecht (1930, 1932) was considered by him as a single unit for the sake of convenience; it is a very large group, susceptible to subdivision, as shown by Roman (1910) and Cushman (1928). Similarly the genus Pimpla, as recognized by Schmiedeknecht (1930), is now divided into a number of subgenera or genera (Cushman 1928; Schmiedeknecht 1933).

When possible, the type genus of each tribe was selected for study. While, from the systematic viewpoint, the type genus should be studied whenever possible, yet, when material is scarce, the substitution of another genus may not be always detrimental and, in some cases, even advantageous. The type genus was arbitrarily created the nomenclatorial representative of a higher group, although possibly atypical. The type species is the systematic representative of a group but that is no criterion of its possession of the morphological attributes primitively common to the majority of that group. While, in theory, the characteristics of a group should be shown by a graduated series, yet, in practice, such thoroughness is often limited by time, material and expense in publication.

These limitations have prevented any close study of specific differences so that variations termed specific may prove to be only intra-specific. The practical restraints of material also preclude the thorough testing of any taxonomic inferences so that suggestions of this nature must be regarded as _purely tentative_, requiring the evaluation of the intensive systematist.

In order to aid the latter to evaluate the data presented in this paper, the names of the Ichneumonid species studied are listed below, the genera and species being grouped alphabetically in their respective tribes and subfamilies as recognized by Schmiedeknecht (1930), subject to his revision of the Pimplinae (1932). Cushman's division of the Pimplini (1922) has also been indicated. Since the name _Ephialtes_ L. is here used in the traditional sense for certain members of the Pimplini, all species of _Ephialtes_ Cush. are referred to by his subgeneric name _Itoplectis_, here used with generic status merely to avoid a confusion in names.

ICHNEUMONIDAE

1. ICHNEUMONINAE

A. Joppini
    Trogus lutorius Fabr.

B. Ichneumonini
    Ichneumon animosus Cress.
    Ichneumon grotei Cress.

Ichneumon longulus Cress.
Ichneumon perscrutator Wsm.
Ichneumon variegatus Cress.
Neotypus americanus Cush.

C. Phaeogenini
Phaeogenes gaspesensis Prov.
Phaeogenes hariolus Cress.

D. Alomyini
Alomyia debellator Fabr.

2. CRYPTINAE

A. Stilpnini
Atractodes sp.

B. Phygadeuonini
Glyphicnemis crassipes Prov.
Microcryptus basizonius Grav.
Neostricklandia sericata Cush.
Stylocryptus subclavatus Say

C. Hemitelini
Cecidonomus inimicus Grav.
Hemiteles (*Astomaspis*) *fulvipes* Grav.
Hemiteles (*Astomaspis*) *submarginatus* Bridgm.
Hemiteles (*Hemiteles*) *hemipterus* Fabr.
Hemiteles (*Hemiteles* *subzonatus* Grav.

D. Pezomachini
No representative.

E. Cryptini (including Mesostenini)
Acrornicus junceus Cress.
Cryptus sexannulatus Gr.

3. PIMPLINAE

A. Lissonotini
Cylloceria sexlineata Say
Lissonota varia Cress.

B. Glyptini
Glypta fumiferanae Vier.
Glypta rufiscutellaris Cress.

C. Lycorini
No representative.

D. Phytodietini
Phytodietus annulatus Prov.

E. Theroniini
Theronia fulvescens Cress.
Theronia melanocephala Cress.

F. Polysphinctini
Polysphincta sp. (P. venator De Gant?)
Zatypota percontatoria Grav.

G. Labenini
No representative.

H. Rhyssini
Megarhyssa citraria Ol.
Megarhyssa greenei Vier.
Megarhyssa lunator Fabr.
Rhyssa persuasoria L.

I. Acoenitini
Phaenolobus arator Rossi

J., Xoridini
Deuteroxoides vittifrons Cress.

K. Odontomerini
Odontomerus canadensis Prov.
Odontomerus pinetorum Thoms.

L. Pimplini

(a. Pimplini Cush.)
Ephialtes (Calliephialtes) grapholithae Cress.
Ephialtes tuberculatus Auctt. Angl. nec Fouer.
Exeristes roborator Fabr.
Pimpla brevicornis Grav.
Pimpla (Iseropus) coelebs Walsh
Pimpla detrita Holmgr.
Pimpla examinator Fabr.
Pimpla instigator Fabr.

(b. Ephialtini Cush. and Roh., nec Auctt.)
Apechthis ontario Say
Itoplectis (Ephialtes Cush.) pedalis Cress.
Itoplectis (Itoplectis) conquisitor Say
Itoplectis (Itoplectis) obesus Cush.

4. TRYPHONINAE

A. Mesoleptini
- Hadrodactylus typhae Geoffr.
- Lagarotus insolens Grav.
- Lophyroplectus luteator Thunb.
- Mesoleius multicolor Grav.
- Mesoleius tenthredinidis Morl.
- Perilissus (Spanotecnus) filicornis Grav.

B. Tryphonini
- Erromenus crassus Cress.
- Tryphon incestus Holmgr.

C. Cteniscini
- Exenterus canadensis Prov.
- Exenterus claripennis Thoms.
- Exenterus lepidus Holmgr.
- Exenterus marginatorius Fabr.

D. Paniscini
- No representative.

E. Bassini
- Bassus tricinctus Grav.
- Homotropus pectoratorius Grav.

F. Orthocentrini
- Orthocentrus sp.

G. Exochini
- Exochus sp.
- Triclistus curvator Fabr.

H. Metopiini
- Metopius sp.

5. OPHIONINAE

A. Ophionini
- Enicospilus ramidulus Grav.
- Ophion obscurus Fabr.

B. Nototrachini
- Nototrachys foliator Fabr.

C. Ophionellini
- Hymenopharsalia foutsi Cush.

D. Anomalonini
    - *Agrypon flaveolatum* Grav.
    - *Anomalon flavifrons* Grav.
    - *Exochilum circumflexum* L.

E. Campoplegini
    - *Dioctes obliteratus* Cress.
    - *Inareolata punctoria* Rom.
    - *Omorgus borealis* Zett.
    - *Omorgus ensator* Grav.
    - *Omorgus mutabilis* Holmgr.

F. Cremastini
    - *Cremastus* (*Cremastus*) *flavo-orbitalis* Cam.
    - *Cremastus* (*Cremastus*) *geminus* Grav.
    - *Cremastus* (*Cremastus*) *interruptor* Grav.
    - *Cremastus* (*Cremastus*) *minor* Cush.
    - *Cremastus* (*Zaleptopygus*) *incompletus* Prov.
    - *Demophorus robustus* Brischke
    - *Pristomerus vulnerator* Panz.
    - *Pristomerus appalachianus* Vier.

G. Porizonini
    - *Orthopelma luteator* Grav.

H. Plectiscini
    - No representative.

I. Banchini
    - *Banchus falcatorius* Fabr.
    - *Exetastes fascipennis* Cress.
    - *Exetastes fornicator* Fabr.
    - *Exetastes matricus* Prov.

J. Mesochorini
    - *Mesochorus pectoralis* Ratz.
    - *Cidaphus occidentalis* Cush.

B. The Value of the Genitalia in the Order Hymenoptera

The male genitalia have been widely used for taxonomic purposes in the principal Pterygote orders, including the Hymenoptera. Among the latter group, these appendages have been invaluable in some Aculeate families, although they have not been used extensively in the Chalastogastra and Ichneumonoidea.

The ignoring of the male genitalia in these lower groups does not seem to be due to a lack of suitable characters, for the diversity of form has been shown by both Crampton (1919) and Boulangé (1924). Crampton, however, drew no systematic conclusions and did not include any specific studies so that his work cannot be evaluated until combined with that of Boulangé; then it is evident that good specific characters occur in *Cimbex*, *Xiphidria*, *Tenthredella*, *Dolerus* and *Cephus*, a wide representation of the Chalastogastra. Boulangé (l.c.) considered the aedeagus to be the best source of specific characteristics and Benson (1931) found the shape of the ninth sternum in the Tenthredinid genus *Athalia* to be specific in value, while the gonosquamae and parapenes were used by Rohwer (1912b) to separate the Tenthredinid genera, *Lagium* and *Zalagium*.

The separation of the Oryssidae from the Chalastogastra is supported by the radical difference in the resting position of the genitalia, those of the former always being concealed (Enslin 1911, Rohwer 1912a), while those of the latter are infrequently so.

Differences have been observed among the Ichneumonids, more especially the elongate gonosquama of *Banchus*, *Hemiteles nanus* Grav., *Lathrolestes* Foerst., and *Parabates* Foerst. (Pfankuch 1919), as well as those of the Mesochorini (Pfankuch 1919; Ceballos 1925, Schmiedeknecht 1930). The genitalia of *Amblyteles* sp., *Cryptus* sp. *Ichneumon lineator* Fabr., *Pimpla roborator* Fabr., *Psilosage ephippium* Holmgr. (Tryphoninae) and Metopius dissectorius Panz, are dissimilar (Ceballos 1925), as are those of Hemiteles hemipterus Fabr., Collyria calcitrator Grav. and Pimpla detrita Holmgr. (Salt 1931), while those of Calliephialtes sp. (Cushman 1913) and of Mesostenus sp. and Tryphon sp. (Becker 1925) differ again from each other. These drawing are valueless in forming any taxonomic opinions except to show that there are radical differences occurring within the family.

The workers upon the Aculeate groups have used the male genitalia extensively, especially the Apoidea (Radoszkowski 1885a), Colletidae (Radoszkowski 1891a; Morice 1904), Andrenidae (Hagens 1874, 1882; Saunders 1884b; Radoszkowski 1891b; Atwood 1934), Megachilidae (Mitchell 1935a, b; 1936), Bombidae (Radoszkowski 1884; Kruger 1919; Richards 1927, 1928), Pompilidae (Radoszkowski 1888), Chrysididae (Radoszkowski 1889), Vespidae (Kluge 1895, Bequaert 1931), Tiphiidae (Malloch 1926; Allen and Jaynes 1929), Mutillidae (Radoszkowski 1885b; Mickel 1924, 1928) and in the Sphecoidea (Radoszkowski 1891c; Parker 1917, 1929; Porter 1927). Most of these workers confined themselves to a study of the hypandrium and of the undissected genital parts and found the hypandrium, the apices of the outer claspers, of the inner claspers and of the aedeagus were extremely valuable in the identification of species. The situation seems to be adequately summed up by Mickel (1928), who states, in reference to the Mutillidae, that:-

"the genitalia of the male have proved of inest-

> imable value in settling certain points, especially in groups of males that are superficially alike. It has been possible to determine that certain external characters were of specific value by using the genitalia as a criterion. On the other hand, certain groups of males quite different in superficial appearance possess genitalia that are practically identical, so that these structures have been of assistance not only in the distinguishing of species, but also in determining the relationships of species, which is exceedingly important from the viewpoint of phylogeny."

As a consequence of the extensive, specific differentiation, the occurrence of generic and supra-generic characters seems to be rare. Hagens (1874) suggested some for groups among the Apoidea but they do not appear to be well substantiated by his data. The posterior spines of the hypandrium in some Bemicini were considered as generic, while the shape of the spatha served to distinguish all but two of the twelve American genera (Parker 1917, 1929). The presence of the pygopods has been used by both Saunders (1884b) and Radoszkowski (1891c) as the first step in separating the Sphecoids, although in the Lasiini (Formicidae) it is of generic interest (Emery 1925). A marked similarity of the genitalia was noted among the Pseninae (Sphecidae) and among the Tiphiidae, although the apical portions are subject to specific variation (Malloch 1933). This similarity is true also of many other groups; for example, the gonoforcipes of <u>Andrena</u> and <u>Halictus</u> (Apoidea), as illustrated by Atwood (1933), seem to form two very distinct groups, although they are closely related. There, then, appears to be reasonable grounds for suspecting that generic and possibly super-generic characters are present in the Ichneumonid genitalia. Such an occurrence may be true in the Sphecoidea, for a key to the group was made by Radoszkowski (1891c), using chiefly the form of the inner clasper, the parapenial area and the gonosquama. While few species were used in support of this key, yet the great experience of this worker may entirely offset this objection.

The existence of these higher characters is suggested also by the work of Boulangé (1924), who stated that the basal portions of the Chalastogastrous genital sclerites were of greater value in determining the larger groups that were the apices, due to the restraint placed upon differentiation by the muscular attachments. Should this be so, it is not surprising that few characters of the higher denominations have been found, since most of the workers cited appear to have studied the genitalia as an undissected unit.

In contrast to these views, Richards (1927, 1934) holds that (1) almost any sclerites are liable to differentiation in the genus Bombus and (2) in each of the main divisions of the Aculeate groups, specialization takes place through fusion and, as this may occur within a family or even within a genus, it is not possible at present to use the male genitalia to any great extent in classification. While these views are not diametrically opposed to those of Radoszkowski, yet they do suggest that Radoszkowski's may need considerable modification and possibly even rejection.

Considering the evaluation of the genitalia in other Hymenopterous groups, it seems probable among the Ichneumonidae, that (1) there are numerous specific differences, occurring chiefly among the apical portions of the sclerites, (2) generic and suprageneric characters are rare, to be found probably in the basal parts of the sclerites and (3) if the differences involve fusion, then they must be regarded as probably abnormally variable. The work of Ceballos (1925) and Salt (1931) shows that Berthoumieu (1894) was incorrect in believing that there are no significant differences in the Ichneumonid genitalia but the former workers make no suggestion as to the possible taxonomic value of these structures.

The purpose of the taxonomic portion of this paper is to estimate the amount of variation that occurs in the genitalia of the Ichneumonid males. The differences may be of real, practical value, the quoted findings of Mickel (1928) upon these structures in the Mutillids then being perhaps equally applicable to the Ichneumonids. On the other hand, the Ichneumonid genitalia may be merely concealed structures, their differences only separating groups or species that are already readily recognized. This practical evaluation of the genital structures, however, must be left to the intensive systematist, only the type of variation being shown in this paper.

C. The Genital and Postgenital Terga among the Ichneumonids

As shown above, the Hymenopterous gonotergum slowly evolved from the form of the pregenital tergum, first as gonotergites and subsequently as either a syntergum or a pair of syntergites, the syntergites later degenerating. This series of modifications occurring gradually in the Hymenoptera suggests that these structures should possess characters of value in identifying large groups within the Ichneumonids, although the conclusions of Richards (1934) in regard to the fusion of sclerites in the Aculeates suggest otherwise.

Within the Ichneumonidae, the gonotergum is apparently always divided and it may be fused to the tenth tergum which may be split into a pair of lateral tergites, although there is no significant reduction in the size of the syntergites. Unfortunately, these changes are not linked to the larger groups, for the inherent tergal characters (if present) appear to be concealed or partially masked by other influences, these being probably either the depressed, cylindrical or compressed shape of the abdomen or else the variations in the proportions of the hypandrium and of the gonopods.

When compared with the specific variation of the hypandrium and the genital appendages, the compression or depression of the abdomen may be considered as distinctly inherent and, if so, there should be a correlation between the gonotergal form and the extreme knife-edge type of compressed abdomen. Among the ten most suitable species (taken without regard for taxonomic considerations), *Ophion obscurus*, *Enicospilus ramidulus* and *Anomalon flavifrons* (all closely related), as well as *Hymenopharsalia foutsi* have synterga, while *Acrornicus junceus*, *Banchus falcatorius* and *Lophyroplectus luteator* have syntergites; *Cremastus* spp., *Agrypon flaveolatum* and *Exochilum circumflexum* have a syntergum that is partially separated medianly. Evidently, if abdominal shape is an inherent factor in the modification of the genital tergum, it is completely dominated by more superficial characters and can be ignored.

The specific characteristics of the ninth and tenth terga are found in (1) the general proportions, (2) in the degree of inter-tergal fusion and (3) in the degree of the division in the tenth tergum,

Proportional variations appear to be common, some being shown in the lateral views of species belonging to the genera *Glypta*, *Theronia*, *Exetastes* and *Exenterus* (figs. 23-30).

The degree of fusion between the terga may vary specifically, as shown in the complete fusion in *Glypta fumiferanae* and anastomosis in the anterior portion of *G. rufiscutellaris* (figs. 23,24). The latter condition is found also in *Cecidonomus inimicus*, while the closely related *Hemiteles* species have the inter-tergal fusion completed.

The division of the tenth tergum is not always uniform within a genus. *Cremastus* has a series of species that includes synterga, almost completely separated syntergites and intermediate forms (figs. 31-34). In *Itoplectis conquisitor* the syntergum is completely fused medianly but incompletely so in *I. obesus*, while *I. pedalis* has syntergites with complete intersegmental fusion. Similarly, a wide variation occurs in *Pimpla*, since *P. examinator* and *P. instigator* possess synterga and *P. brevicornis* syntergites with incomplete intersegmental fusion, while *P. detrita* and *P. coelebs* have separate tergites in both terga (fig. 21); the former species, however, has been placed in *Epiurus* by Roman (Salt 1931). It should be noted *Pimpla* is a large, heterogenous genus, containing both external and internal parasites (Thorpe 1930).

Apart from *Hemiteles*, *Cremastus*, *Pimpla* and *Pristomerus*, the terga of each genus are of one type only. It is possible to take the view that all these exceptional genera are heterogenous, *Cremastus* and *Pristomerus* already being divided into subgenera (Cushman 1920). Even so, it is shown that great tergal variation can occur within a tribe, as in Phygadeuonini, Hemitelini, Pimplini, Cremastini, Pristomerini and Mesoleptini. Yet in certain groups the tergal structures appear to be fairly uniform. Among the twenty-two species of the Ichneumoninae and Cryptinae (including fourteen genera), nineteen possess complete syntergites; however, two others, *Cecidonomus inimicus* and *Glyphicnemis crassipes* have the intertergal fusion incomplete, while the ninth and tenth terga of *Stylocryptus subclavatus* are divided into separate tergites. The terga of the other three subfamilies are remarkably varied, although tribally they show a uniformity of structure, apart from the exceptions already mentioned. The data are insufficient to show distinctly that the terga may be inherently constant within a tribe but, if this is so, then such uniformity of structure is usually either partially or entirely masked by specific differences.

While studying the gonotergum, variations in the antecosta were seen, the anterior process in some Pimplinae being especially conspicuous. Since the antecosta is an internal ridge, serving as a place of attachment for muscles, it is unlikely that this structure would be greatly modified by the minor changes in the genitalia. The antecosta may, therefore, be a guide to the higher relationships of the Ichneumonids. This, together with the unusual opportunity of observation, is sufficient excuse for the inclusion of a study of the antecosta, even though it may not be closely connected with the topic of genitalia.

No deliberate comparisons were made between the pretergal and gonotergal antecostae, yet they appeared to be similar, as is to be expected.

The genital antecosta may be (1) *linear* in form, as in *Exenterus marginatorius* (fig. 30) (2) *ovate* towards the ventral margin, as in *Glypta rufiscutellaris* (fig. 24), or (3) *pendant*, a somewhat quadrate process projecting anteriorly from near the ventral margin of the antecosta, as in Exeristes roborator (fig. 20) and Itoplectis conquisitor (fig. 35). Since these terms are arbitrarily chosen, intermediate forms occur so that occasionally a compound term has to be used. Sometimes the antecosta appears to be absent and, in this case, it was assumed to be linear in form.

The tergal antecosta is linear throughout the Ichneumoninae, Cryptinae and Ophioninae, exclusive of a small process in Hemiteles submarginatus and an oval thickening in both Mesochorus pectoratorius and Cidaphus occidentalis (Mesochorini); the two latter exceptions stress the remoteness of the Mesochorini from the other tribes of the Ophioninae. Exetastes was also an exception, for in E. matricus and E. fascipennis the antecosta is lineo-ovate, although in E. fornicator it is linear; however, the genus is aberrant, being placed midway between the Ophioninae and the Pimplinae by Schmiedeknecht (1935) and in the Lissonotini by Cushman (1928).

The great uniformity of the antecosta among the Ichneumoninae, Cryptinae and Ophioninae is in strong contrast to the variation that occurs among the Pimplinae and Tryphoninae and emphasizes the heterogeneity occurring in the latter two.

Among the Pimplinae this diversity is indicated also by the primitive or linear antecosta being characteristic of the Lissonotini, Odontomerini, Acoenitini and Pimpla (Iseropus) coelebs, groups that are widely separated from each other. This suggests that they may be the primitive members of four different natural groups, more especially since these represent respectively the four original tribes of the Pimplinae, i.e. the Lissonotini, Xoridini, Acoenitini and Pimplini as recognized by Gravenhorst (1829), Holmgren (1859), Ashmead (1901) and Schmiedeknecht (1930).

The ovate antecosta occurs in Glyptini and Phytodietini, while the pendant form is found in the Pimplini (s.s), except Pimpla (Iseropus) coelebs. The intermediate, ovato-pendant type occurs throughout the Theroniini, Polysphinctini, Rhyssini and Xoridini. The ovate forms suggest that the Glyptini and Phytodietini are moderately primitive, particularly since (1) strong Lissonotine affinities have been noted in the Glyptini (Cushman and Rohwer 1920) and (2) the Phytodietini have been grouped with the Lissonotini by Foerster (1868), Ashmead (1901) and Schmiedeknecht (1930), although lately given tribal rank by Cushman and Rohwer (1920)and Schmiedeknecht (1930). Cushman and Rohwer (l.c.), however, regard the Lissonotini and Glyptini as forming a group that is not at all closely related to the Phytodietini or to the rest of ths subfamily, although akin to the Banchine Exetastes.

Cushman and Rohwer (l.c.) also separate the Odontomerini from the Xoridini. Odontomerus spp. possess linear antecostae, while this structure is ovato-pendant in Deuteroxoides vittifrons; this may mean that either the tribe Odontomerini is more primitive than the Xoridini or else the two groups are unrelated.

However, while the shape of the antecosta may assist in determining the tribal relationships within the Pimplinae, yet more data must be obtained before this structure is accurately evaluated in this group. The possibility of the antecosta being tribal in value is enhanced by its uniformity in the Ichneumoninae, Cryptinae and Ophioninae, while the antecosta in the Tryphoninae shows marked agreement with the taxonomic groupings.

Among the Tryphoninae, the pendant antecosta occurs in the members of the Bassini, Metopiini and the Orthocentrini, although it was not seen in the Exochini; the first two tribes from the Tryphonides schizodonti and T. aspidopi respectively, while the latter two form the Tryphonides prosopi, these being supertribes recognized from early times by Holmgren (1855), Morley (1913) and Schmiedeknecht (1930). The occurrence of a linear antecosta in Exochus sp. and an ovate one in Triclistus curvator (Exochini) perhaps indicates (1) that the Exochini are related to the Orthocentrini, being the more primitive portion of the supertribe and (2) that the antecosta may be of tribal value, rather than supertribal.

The majority of the Tryphoninae, however, occur in the Tryphonides homalopi, in which the antecosta varies from linear to lineo-ovate with the ovate form rarely occurring. Specific differences may occur, for, in the four species of Exenterus studied, E. canadensis and E. marginatorius have an ovate antecosta, while E. claripennis and E. lepidus have lineo-ovate ones; it is difficult to know what weight to place upon these variations. However, it should be noted that the small number of Tryphoninae examined, together with the large number of subtribes recognized in this group, may easily invalidate conclusions that may seem probable.

The same is perhaps true of all of the subfamilies, yet the shape of the antecosta in some groups is remarkably constant and does suggest that these basal structures may prove, upon closer study, to possess super-generic characteristics that are very seldom subject to masking by generic or specific variations. This possibility is augmented by the deplorable state of the taxonomy in this group, for, in view of this, it would indeed be surprising if the correlation between the antecostal form and the taxonomic opinions was higher, particularly since one cannot expect to be able to group the major divisions of any taxonomic group by employing merely one structure.

D. The Ichneumonid Hypandrium

As in most of the Hymenoptera, the posterior and lateral margins of the Ichneumonid hypandrium is specific in value, this being shown in *Ichneumon*, *Phaeogenes*, *Hemiteles*, *Exetastes*, *Glypta*, *Theronia*, *Omorgus*, *Cremastus*, *Pimpla*, and *Exenterus* (figs. 39-67). De-sclerotization in the median line sometimes occurs, as in *Exetastes* spp., *Cremastus* spp. and in *Tryphon incestus* (fig. 68). However, caution is advisable in the use of the shape of the hypandrium since intra-specific variations occur in Exeristes roborator and probably in other groups also; moreover, the curvature and outline of the ninth sternum can be altered by differences in the preparation of mounts. In Megarhyssa, there appeared to be no differences between the species, although the form in the genus is distinctive (fig. 69).

While the greater portion of the hypandrium is specific in value, yet the antecosta with its median spiculum appears to be as significant as the tergal antecosta in revealing higher group characteristics, for there is a high negative correlation between the maximum width of the gonotergal antecosta and the length of the spiculum - if the gonotergal antecosta is linear, the spiculum is long and vice-versa. This correlation is almost perfect in the Ichneumoninae, Cryptinae and Ophioninae and is high in the other two subfamilies. Since the antecostae and spicula are only roughly classified, it is surprising that the correlation should be as high. In no case was a positive correlation found.

As a source of specific differences, the hypandrium appears to be the most promising of the sclerites of the genitalia and the genital segment, not only because it varies in form,but because many of its characteristics may be seen without dissection and because its large size usually permits a reasonably easy dissection to the novice.

E. The Ichneumonid Gonocardo

As noted above, the annular gonocardo is formed by the fusion of two lateral, semicircular sclerites, each differentiated from the base of a gonopod. Among the Ichneumonids, these gonopodites are broadest ventro-laterally or laterally, their apices tapering towards the median line of the abdomen.

The ventral tips of these sclerites are almost invariably fused together as a narrow bridge; this area of juncture is always narrow, even when the gonocardo is unusually broad ventro-laterally, as in Megarhyssa lunator (figs. 70, 71, 112) and Banchus falcatorius (fig. 72). Medio-ventrally there is sometimes a small internal ridge or apophysis, presumably the remnant of a suture existing before the fusion was completed; these structures are noticeable in the more heavily sclerotized gonocardines.

The dorsal portion of these gonopodites vary greatly in shape. A complete annulus is typical of the Ichneumoninae and of the less specialized tribes among the Ophioninae, while in the other families the meso-dorsal apices are usually joined by membrane alone. Unfortunately, these generalizations are not entirely true of all groups, for both Neotypus americanus (Ichneumoninae) and Stylocryptus subclavatus (Cryptinae) are exceptional; furthermore, as these genera are typical of their respective subfamilies, it is likely that many exceptions will occur in groups intermediate to these larger groups.

An intergradation of these types also occurs in the Ophioninae. The gonocardo is completely annular in the less specialized tribes, including the Ophionini, Nototrachini, Ophionellini, Anomalonini, Campoplegini, Cremastini and Pristomerini. The species *Ophion obscurus*, *Agrypon flaveolatum* and *Exochilum circumflexum* (figs. 73-75) may suggest a tendency for the primitive gonocardo to be medio-dorsally broad in the longitudinal direction, although this is not true of all, *Enicospilus ramidulus* (fig. 85) having a fairly narrow dorsal bridge. The same region appears to be consistently very narrow in the intermediate tribes Cremastini and Pristomerini (figs. 76-80) and to have degenerated into membrane among the highly specialized tribes, Banchini, Porizonini and Mesochorini (figs. 72, 81,82). It is of passing interest to note that the completely annulate gonocardo of Ophionellini agrees with the position assigned to it by Cushman (1922).

It should be noted, however, that the Porizonini are represented only by *Orthopelma luteator*, the genus being aberrent and related to the Pimplinae (Schmiedeknecht 1930), although placed in the Porizonini by both Schmiedeknecht (l.c.) and Cushman (1928). The remaining two specialized tribes, Mesochorini and Banchini, are also perhaps only placed provisionally in the Ophioninae. The Banchini may be related to the Lissonotini through the genus *Exetastes*, which is placed with the Banchini by Schmiedeknecht (l.c.)

and in the Lissonotini by Cushman (1928); the remoteness of the genus has been emphasized by earlier taxonomists including Handlirsch (1925), who created a subfamily for the genus; this attitude is supported by the occurrence of Braconid characteristics in the respiration of the Banchine larvae (Thorpe 1932). The Mesochorini, too, have been regarded as remote, for Foerster (1868) and Viereck (1916) raised the group to family rank, and Schmiedeknecht (1910) to subfamily rank. The group is differentiated from almost all other Ichneumonidae by the extremely elongate outer claspers in the males (fig. 82); the peculiarly flattened head and enlarged areolet are also highly characteristic. When the apparently consistent habit of hyperparasitism is also considered, it appears that the Mesochorini may merit elevation to the rank of supertribe.

Upon these grounds, it is evident that the more specialized tribes of the Ophioninae may possibly not be true members of the subfamily and, if so, the Ophioninae are characterized by a completely annulated gonocardo. However, there were not enough species available in these tribes for this to be determined.

While the gonocardo undoubtedly possesses characteristics common to large groups within the Ichneumonidae, yet this structure also shows definite specific differences. Viewed in cross-section, the ventral portion may be straight, as in *Ichneumon longulus* (fig. 114) or incurved as in *I.*

variegatus (fig. 115). The gonocardo, when seen from below, frequently exhibits variation, the medio-ventral portion being either straight, curved anteriorly or curved posteriorly. The anterior curve is present in *Cremastus* spp., (figs. 76-78) although the form of this portion of the gonocardo may vary specifically. Within *Ichneumon*, *Phaeogenes* and *Hemiteles* (*Astomaspis*) both the straight and the posteriorly curved forms occur, the former in *I. grotei* (barely curved), *P. hariolus* and *H. fulvipes* (fig. 83) and the latter in the other *Ichneumon* spp. examined, in *P. gaspesensis* and in *H. submarginatus* (fig. 84). In the examined species of *Omorgus* and *Exenterus* this area was invariably straight.

Among the Pimplinae also, the ventro-median portion of the gonocardo is of specific interest. *Megarhyssa citraria* is readily distinguished from the American species, *M. lunator* and *M. greenei*, by the antero-ventral notch in the former being but half the length and V-shaped without parallel sides (figs. 70, 116). Within the genus *Pimpla*, too, this area possesses diagnostic characters. A prominent antero-median lobe distinguishes *P. brevicornis* from the other species that were examined. Some *Pimpla* species, including *P. examinator*, *P. instigator* and *P. detrita* are exceptional among the Ichneumonids for the two lateral halves (i.e. the basal gonopodites) have not fused ventrally; unfortunately, this has weakened the gonocardo, making it difficult for the unwarned to extract the genitalia without separating the two halves of the gonocardo. *Apechthis* ontario (fig. 86) Itoplectis conquisitor and I. obesus are distinguished by the median portion being bent posteriorly as a broad 'V' but this is not true of I. Pedalis

Yet, while the gonocardo may vary within a genus, the similarity of this structure in some genera, notably Ichneumon, Megarhyssa, Glypta, Cremastus and Exenterus suggest that these specific differences have not entirely concealed some characters of higher value.

F. The Ichneumonid Gonoforceps

The tribe Mesochorini is usually distinguished from other Ichneumonids by its singular, extremely elongate gonosquamae, although this character is possessed also by Ctenopelma sanguineum Prov. (Tryphoninae) and by some or all of the Ophionellini. It is then to be expected that the gonoforcipes may be of use in identifying some of the larger groups. This, however, seems highly improbable for, while individual groups sometimes possess a common facies, yet only rarely, as in Megarhyssa and the Mesochorini, does one find that such facies are peculiar to one group.

This infrequence is due, at least in part, to the fact that each part of the gonoforceps may be differentiated specifically. Basally, the form of the gonostipital arm may vary within a genus, as in Cremastus, Hemiteles (Astomaspis), Theronia, Glypta, Ephialtes and Exenterus (figs. 76-78, 83-84, 87-96), as well as in Ichneumon and Phaeogenes. The main portion of the gonoforceps may vary in shape within a genus but seldom as radically as in Ephialtes, Theronia and Exenterus. The apex of the outer claspers often varies greatly within genera such as Hemiteles, Glypta, Ephialtes, Cremastus and Exenterus (figs. 98-111).

G. The Ichneumonid Volsella

The Ichneumonid volsella is a very flexible structure, this being necessitated by its function of finding, clasping and stretching the membrane that is adjacent to the female gonopore. Due to this versatility of form in the individual, there seems to be no ideal method of mounting these structures without subjecting some part to possible distortion.

By drawing the ventral view of the entire genitalia with the gonoforcipes widely gaping, Salt (1931) has been able to show in a single drawing the gonocardo, gonoforcipes, volsella and the apical portion of the aedeagus. However, this method certainly distorts the gonoforcipes, while the basivolsella may lie in any position from the horizontal plane to an almost vertical one and, even if a uniform position is maintained for the basivolsella, the attitude of the chela and the distivolsella may still vary greatly within the individual. For these reasons, the portrayal of the volsella in this matter is not satisfactory for the study of the volsella, although it does convey some idea of the general structure of the genitalia.

The lack of control over the attitude of the apical portions is sufficient reason for discarding any method of mounting in which the volsella is shown either attached to the gonoforcipes or else grouped with the aedeagus and the other volsella (even though in the latter case the volsella and aedeagus are easily extracted together by passing a fine dissecting needle between the gonoforcipes and the volsellae).

The least objectionable method appears to be to dissect out the volsella and to mount it with a cover slip that is unsupported by any of the plastercine pillars described in the discussion upon technique. In this way, the chela and distivolsella are brought into the same plane as the basivolsella. This method, however, does result in the volsella occasionally being torn during dissection, partly because of its smallness but, indeed, sometimes of necessity, since the basivolsella of a few species is fused to the gonostipes. In addition, if the anterior apodeme is well developed laterally, it may be flattened and then appear to be either slightly dorsal or slightly ventral; on the other hand, if this apodeme is not flattened, it may permit the basivolsella to slightly rotate upon it. However, to the author, these objections appear to be minor when compared with those of the other methods, particularly as the apical portions of the volsella seem to be the most valuable.

The Ichneumonid volsella has been illustrated in several planes by Cushman (1913), Becker (1924), Ceballos

(1925) and Salt (1931) but their works collectively do appear, nevertheless, to show that this structure does vary considerably. However, as they dealt with thirteen species, representing eleven genera and all five of the traditional subfamilies, no taxonomic conclusions can be made from their work.

The typical Ichneumonid volsella is similar to that of *Neotypus americanus* (figs. 119, 120), the names of the parts being indicated in these figures. The area dorsal to the volsellar strut is termed, when present, the *dorsal area* of the volsella (D.A.), its margin almost invariably being supported anteriorly by the basivolsellar apodeme (Bv.A.).

While the volsella usually is completely separated by membrane from the gonoforceps, yet eleven exceptions were found, these representing four tribes in the Tryphoninae and one each in the Ichneumoninae, Cryptinae and Ophioninae. This character, therefore, appears to be widely spread, yet intermittant, among the Ichneumonidae. This peculiarity is evidently specific, at least in some groups, for a sclerotic tongue connects the antero-ventral part of the basivolsella to the gonostipes in *Ichneumon longulus* (fig. 97), *I. grotei* and *I. variegatus*, although the volsella is free in *I. animosus* and in *I. perscrutator*. In the genus *Cremastus* also, *C. incompletus* and *C. geminus* have the volsella joined broadly to the gonostipes, although the other species examined in this genus have the volsella entirely separated.

This latter condition is true also of *Neostricklandia sericata*, *Lagarotus insolens*, *Homotropus pectoratorius*, *Bassus tricinctus*, *Triclistus curvator* and *Metopius* sp. The fusion in the last species occurs for more than half of the total length of the volsella.

Among the Ichneumoninae except *Neotypus americanus*, the basivolsellar apodeme is large, curving ventrally (figs. 121, 122), and this is true also of the single examined species of the Stilpnine *Atractodes*. Among the Phygadeuonini, the apodeme is small but among the more specialized Cryptinae, as *Hemiteles hemipterus* (fig. 123), the apodeme is large and extended dorsally. To this *Hemiteles subzonatus* is an exception, for the apodeme is small and appears to be ventro-lateral.

The size of the dorsal area is closely correlated with the dorsal growth of the basivolsellar apodeme, for it is absent in the five *Ichneumon* species, scarcely present in *Alomyia debellator* and narrow in the other Ichneumoninae, as well as in *Atractodes*. Among the Phygadeuonini, the dorsal area is moderate in size, while it is well developed in the more specialized Cryptinae, such as *Cryptus sexannulatus* (fig. 125). In the Phygadeuonine, *Glyphicnemis crassipes*, however, the apodeme is small and does not support the large dorsal area. The two other exceptions to this graduated series are those which do not concur with the agreement between the apodeme and the taxonomic arrangement, *Neotypus americanus* having a large dorsal area, while this is absent in Hemiteles subzonatus. This suggests that there is a closer correlation between the form of the apodeme and that of the dorsal area than between the shape of these structures and the taxonomic grouping within the Ichneumoninae and Cryptinae.

This also appears to be true of the other subfamilies, although, again, each subfamily has a strong tendency towards a particular type of apodeme with its corresponding form of the dorsal area.

Among the Tryphoninae, the basivolsellar apodeme is usually weakly developed, although it is strongly curved laterally in Triclistus curvator and ventrally in Erromenus crassus.

In the Ophioninae the apodeme is invariably ventral, the dorsal area being absent, exceptions occurring in Orthopelma luteator, Exetastes spp., and Enicospilus ramidulus. The first species has the apodeme developed dorsally, while the dorsal area is large; however, as the genus Orthopelma is aberrant (Schmiedeknecht 1930), this case may be disregarded. In Exetastes spp. the dorsal area is present, although the apodeme is ventral and lateral; this genus is also aberrant (Cushman 1928; Schmiedeknecht 1930). In Enicospilus ramidulus (fig. 124) the genitalia are unusually elongate so that this variation in volsellar form may be due to the need for reinforcement, for the apodeme is not of the normal dorsal type.

The form of the basivolsella divides the Pimplinae into two main groups, the Phytodietini being intermediate. The more specialized tribes are separated from the Lissonotini and Glyptini by the apodeme being well developed dorsally and by the great growth of the dorsal area. This agrees with the data upon the antecosta, which grouped together the Lissonotini and the Glyptini, as well as possibly the Phytodietini.

While the basivolsella is essentially a basal structure in which one may expect to find subfamily or tribal characters, yet it is also subject to generic or specific changes, not only in its fusion with the gonostipes (as already mentioned), but also in its proportions. The outline within some of the examined genera is similar, although specific differences may occur, as in _Ichneumon_. In this genus the narrowness of the basivolsella in _I. grotei_ (fig. 121) and _I. longulus_ separates these species from _I. animosus_ (fig. 122), _I. variegatus_ and _I. perscrutator_.

Among most of the Ichneumonidae, the apical portions of the volsella vary little from the type of _Neotypus americanus_ (figs. 119-120) although characters of perhaps generic value are to be found in the shape of the chelar apex, for this may vary from being bluntly rounded, as in _Neotypus americanus_ and _Glypta_ spp. to being sharply pointed, as in _Ichneumon_ spp. Within the genus, _Ichneumon_ the length and shape of the chela varies, as shown in _I. grotei_ (fig. 121) and _I. animosus_ (fig. 122). A remarkable difference occurs in *Cremastus*, the chela being normal in both *C. minor* (fig. 126) and *C. flavo-orbitalis*, although it is fused to the basivolsella in *C. incompletus* (fig. 127) and *C. geminus*. This is of special interest as it emphasizes the fact that a character may appear to be extremely stable within the entire family and be masked at times by a specific variation, perhaps more particularly when the variation involves either a fusion or fission of sclerites.

H. The Ichneumonid Aedeagus

The shape of the typical Ichneumonid aedeagus is a weakly depressed cylinder, having the posterior apex curved somewhat ventrally and an elongate paramere extending anteriorly from each side. However, bizarre forms may occur within the family, as in *Agrypon flaveolatum* (figs. 129, 141) and *Exochilum circumflexum* (fig. 140).

The parameres are primitively joined to each other by membrane but the latter is often partially sclerotized, more particularly the dorsal or spathal area; this process is completed in some of the higher members of the Pimplinae (figs. 70, 128, 134, 146-154), a medio-ventral fold (V.R.) being formed just in front of the apex. In most Ichneumonids, however, this fold is membranous and allows the ventral portions of the valves to separate laterally. On this account, the valves must be closed before comparisons are made in either the ventral or dorsal views.

The free anterior portion of the parameres are also subject to distortion, due to the softening action of the potassium hydroxide, their shape therefore being of little taxonomic value. However, the anterior apex in *Hemiteles fulvipes* is dilated vertically, both upwards and downwards, in the form of a fishtail; in the other studied species of *Hemiteles* the paramere is rod-shaped, this being the almost invariable form in the Ichneumonidae. The length of the free portion may also vary specifically, as it is proportionately much less in *Ichneumon perscrutator* (fig. 135) than in the other species studied in this genus (figs. 136, 137).

These five species are readily divisible into three groups by their aedeagal shape. In both *I. grotei* (fig. 136) and *I. longulus* the aedeagus has small ergots and a dentate medio-ventral ridge, the ergots being long and the ridge without teeth in *I. variegatus* (fig. 137), *I. animosus* and *I. perscrutator* (fig. 135). The latter is readily distinguished from the others by the less falcate appearance and the shortness of the parameres.

All parts of the aedeagus seem to be differentiated specifically at times, as can be readily seen in *Hemiteles*, *Ichneumon*, *Phaeogenes*, *Glypta*, *Theronia*, *Ephialtes*, *Pimpla*, *Itoplectis*, and *Exenterus* (figs. 83-84, 135-139, 142-158). The diverseness in form between species must conceal and offset to a very great extent any intrinsic character of higher value, although some of the species within a genus do appear to have a facies common to the aedeagus.

IV TECHNIQUE

Since the terminalia of the Ichneumonids are nearly always small, both care and practice are needed in the dissection of the genital sclerites. As the genitalia averaged between one and two millimetres in length and perhaps half a millimetre in width, they needed special treatment; A short description of the technique may therefore be of value.

When the genitalia were unusually small, the tip of the abdomen was cut off, treated chemically and then dissected in glycerine upon a slide. Usually, however, the insect was relaxed and dissected under the binocular, being held between the left thumb and the index finger so that the apex of the abdomen protruded upwards between them. The ninth abdominal segment was extracted from its invaginated position within the eighth by inserting a coarse, hooked minuten pin between the two segments and gently tearing the terminalia away from the abdomen. The apex of the abdomen was moistened with water so that the terminalia would adhere to the adjacent part of the thumb or to the dissecting hook, instead of falling to the stage of the binocular or elsewhere and perhaps being lost. Special care had to be taken in extracting the genitalia because the gonocardo in many species is easily broken.

The finer dissection was carried out in glycerine. The volsellae and aedeagus were separated from the gonostipites by placing the genitalia ventrally and passing a fine dissecting needle anteriorly between each gonostipes and its volsella; the gonostipes was held upon the slide by the dissecting needle placed between the genitalia from in front, the rounded portion of the needle preventing fractures of the gonoforceps. The volsellae then were easily separated from the aedeagus. With small specimens, however, it is risky to hold the genitalia in this manner so that a 'holder' was made, consisting of a glass slide on which two square cover slips were mounted so that two of their corners touched each other and two of their adjacent sides were almost parallel. A small amount of glycerine was placed between the two slips, the genitalia then being submerged in it and passed up the narrowing fissure until the glass sides held the sclerites sufficiently firmly to allow dissection.

In studying the musculature, specimens were used that had been preserved in a dry condition for from one to ten years. These were relaxed, soaked in water for several days until the muscles had assumed their former size, dissected to show the desired muscles and then mounted in De Faure's solution. In the dried specimens, the waste products and the other internal tissues did not conceal the arrangement of the muscles, which were plainly visible, although fresh material or material kept in liquid would have been difficult to study myologically.

After the removal of the terminalia from the abdomen, these sclerites were immersed for eight hours in a 10% solution of cold potassium hydroxide. As this alkali is able to modify the appearance of sclerites, particularly perhaps apodemes, either a hot solution or a longer period may be injurious.

After the potash treatment the genitalia were left overnight in distilled water and then placed either in glycerine for immediate dissection or else preserved in a third of the standard strength of De Faure's solution. With either treatment, the alkaline residue, if present, would be neutralized by glycerine, De Faure's containing a large amount of this liquid.

The diluted De Faure's solution is advantageous as a storage medium because (1) its glycerine content prevents evaporation to dryness (2) the sclerites, already softened by the potash, are kept in that condition, (3) the solution has a clearing reaction upon the sclerites, (4) the sclerites can be transferred directly to either water or to glycerine for immediate examination or dissection and (5) the structures are ready for immediate mounting in De Faure's solution.

The genitalia were stored in small vials measuring approximately 1.0 by 0.3 inches. These vials were sorted into groups according to the taxonomic affinities of the specimen and then these placed in larger vials. Only one third of each small vial was filled with the solution and the vials were always kept upright; this prevented the sluggish liquid from ever reaching the corks and the sclerites perhaps being lost. The sclerites invariably sank to the bottom of the containers so that the smaller vials could be handled with considerable freedom. Care, however, had to be observed in removing and restoring sclerites with dissecting needles, for sclerites could adhere to the needles and then either be lost or else contaminate another vial. The smallest of the sclerites needed to be mounted after dissection, either upon cardboard or else upon slides, as they were difficult to find within the vials.

Temporary mounts were made with glycerine, while De Faure's solution, as recommended by Imms (1929), was found to be a rapid, satisfactory method for permanent amounts. In either case, a simple method of making cells, adopted from Farnham House, was found very useful. Square cover slips were used, each corner being supported by a small pillar of plastercine so that the slip lightly rested upon the sclerite to be mounted; the sclerite could be moved about below the slip by moving the slip horizontally until the object was in the right position.

When temporary mounts of the collective genitalia were needed and the gonoforcipes were widely spread apart, the glass holder already described was used to move the appendages into the desired position and then covering them with a slip; care had to be taken to prevent physical and optical distortion. As the genitalia vary in size, several holders had to be made to suit the varying depth of the gonoforceps. Only a small amount of glycerine could be used, else convection currents would be formed, particularly if a lamp were used.

All drawings of mounts were made with an eyepiece micrometer, marked with squares so that the proportions should be reasonably accurate. The use of the camera lucida was abandoned because of the difficulty in discerning between the layers of external and internal sclerites in the unseparated genitalia.

It is regrettable that illustrations of form cannot be used more fully in this study, because of the cost of reproduction, particularly since a small drawing can present in a compact form numerous data; many of these have either to be eliminated in a written description or else interpreted by words of comparison that are frequently vague, even when aided by measurements.

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VI. SUMMARY

(1) The male genitalia and the adjacent sclerites in the Ichneumonid, Megarhyssa lunator Fabr., are shown by myological comparison to be homologous with structures occurring in other Hymenopterous groups, especially in the Chalastogastra.

(2) To aid in the establishment of a uniform terminology, the male Hymenopterous genitalia have been compared with the primitive form. The basal gonocardo, the gonostipes or base of the outer clasper, and the volsella or inner claspers are derived from the coxopodite, while the gonosquama or apex of the outer clasper may represent the telopodite.

(3) The primary muscles, if originally present, have atrophied, their role then being assumed by short secondary muscles supplemented by fluctuations in the blood pressure of the genital region.

(4) The ninth tergum of the male Ichneumonids appears to be invariably divided into a pair of lateral tergites; these are usually fused to the tenth tergum, which may also be divided medianly. The ninth and tenth terga are not greatly reduced in size. These characters are of value in showing that the Ichneumonidae are more closely related to the Chalastogastra than to the Aculeate Hymenoptera.

(5) The degeneration of the ninth and tenth terga, among the higher Hymenoptera, is correlated with the increase

in both size and weight of the genital appendages. This appears to be due to the physical stresses involved, as well as the need for greater elasticity in the genital segment so that the invaginated genital organs may be extruded for copulation.

(6) Among the Ichneumonidae, any part of the genitalia or of the adjacent sclerites may vary specifically. Differences that appear of value in identifying groups almost invariably have exceptions; while some of the latter may be due to misplacements of groups, yet the number of exceptions, particularly those concerned with fusion or fission, show that specific variations mask characters of a higher value to such an extent as to make the latter, in most cases, at least unreliable.

(7) While dissecting the genital segments, the form of the antecostae in the ninth tergum and sternum were observed. These structures appear to be of value in grouping tribes.

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VIII. ABBREVIATIONS USED IN THE PLATES

The abdominal segments are numbered with Roman numerals. The muscles of the male genitalia are lettered from A to V in accordance with the system of Boulangé (1924) for the Chalastogastra. Abbreviations, other than those listed below, are explained on the page opposite each plate.

Ac.....antecosta
Aed....aedeagus
Ast....acrosternite
Bv.....basivolsella
Bv.A...basivolsellar apodeme
Ch.....chela
Cx.....coxa
Cxp....coxopodite
D.A....dorsal area of the
basivolsella
D.M....depressor muscle of
telopodite
Dv.....distivolsella
Ejac.D.ejaculatory duct
Erg....ergot
Fm.....femur
Gc.....gonocardo
Gf.....gonoforceps
Gsq....gonosquama
Gst....gonostipes
Gst.A..gonostipital arm
Gtt....gonotergite
I.C....inner clasper
L.M....levator muscle of the
telopodite
M......muscle
Mb.....membrane
O.C....outer clasper

Ov.....ovipositor
Ov.S...ovipositor sheathe
Pn.....penis
P.P....primary papilla
Pp.....parapenes
Pr.....paramere
Ptar...pretarsus
Pyg....pygopod
Scx....subcoxa
Snt....syntergum
Sntt...syntergite
Sp.....spiculum
S.Pl...sensory plate
Spt....spatha
S-s....intersternal
St.....sternum
Tar....tarsus
Tb.....tibia
Tg.....tergum
Tlp....telopodite
T-s....tergo-sternal
T-t....inter-tergal
V.A....ventral area of the
basivolsella
V.R....ventral ridge of
the aedeagus
V.Str..basivolsellar strut

Plate I

Fig. 1. Diagrams showing the Developmental Stages of the Male Genitalia in:-

- (a) *Sirex* (according to Boulangé 1924) and *Vespa* (Boulangé after Zander 1900)
- (b) *Apis mellifica* (according to Snodgrass 1925 after Zander 1900)
- (c) *Apis mellifica* (according to Michaelis 1900)
- (d) *Bombus* (according to Boulangé after Michaelis 1900)

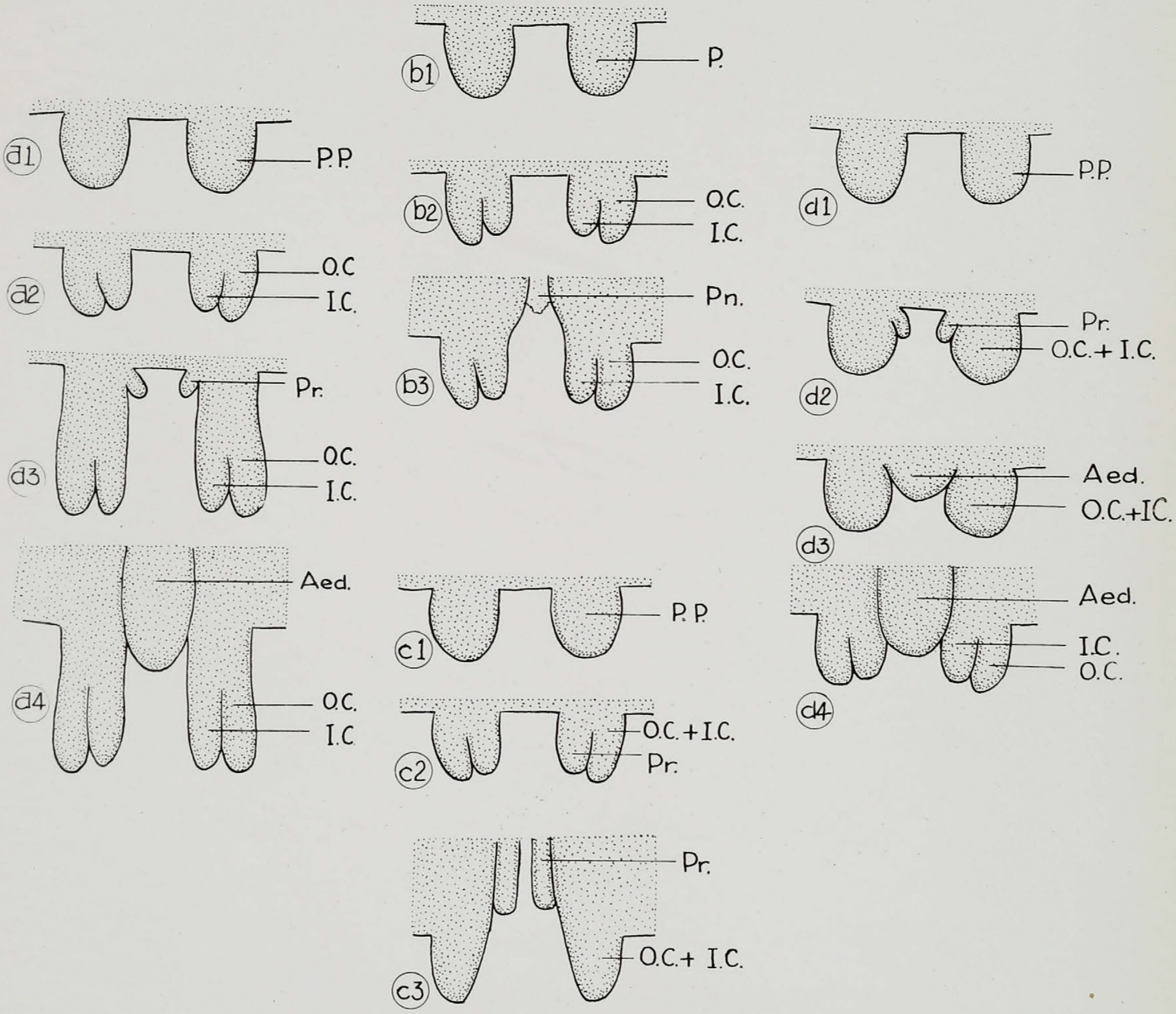

b1
P.
a1
P.P.
b2
O.C.
I.C.
d1
P.P.
a2
O.C
I.C.
b3
Pn.
O.C.
I.C.
d2
Pr.
O.C.+ I.C.
a3
Pr.
O.C.
I.C.
d3
Aed.
O.C.+IC.
a4
Aed.
O.C.
I.C
c1
P. P.
d4
Aed.
I.C.
O.C.
c2
O.C.+I.C.
Pr.
c3
Pr.
O.C.+ I.C.

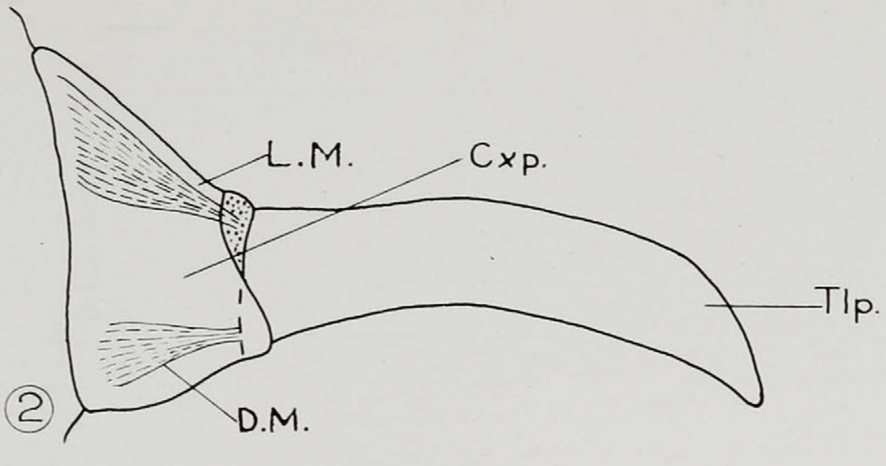
PLATE I

Plate II

Fig. 2. Diagram of the Coxopodite and Telopodite of a Primitive Limb, showing the Levator and Depressor Muscles of the Telopodite (after Snodgrass 1935)

Fig. 3. Diagram of a Secondarily Divided Limb, showing the Development of the Secondary Muscles (after Snodgrass 1927, 1935)

Fig. 4. Diagram of a Thoracic Limb, illustrating the Subcoxa, Coxa and Telopodite, together with their Basal Axes (a-a, b-b and c-c respectively) about which they move (modified after Snodgrass 1931)



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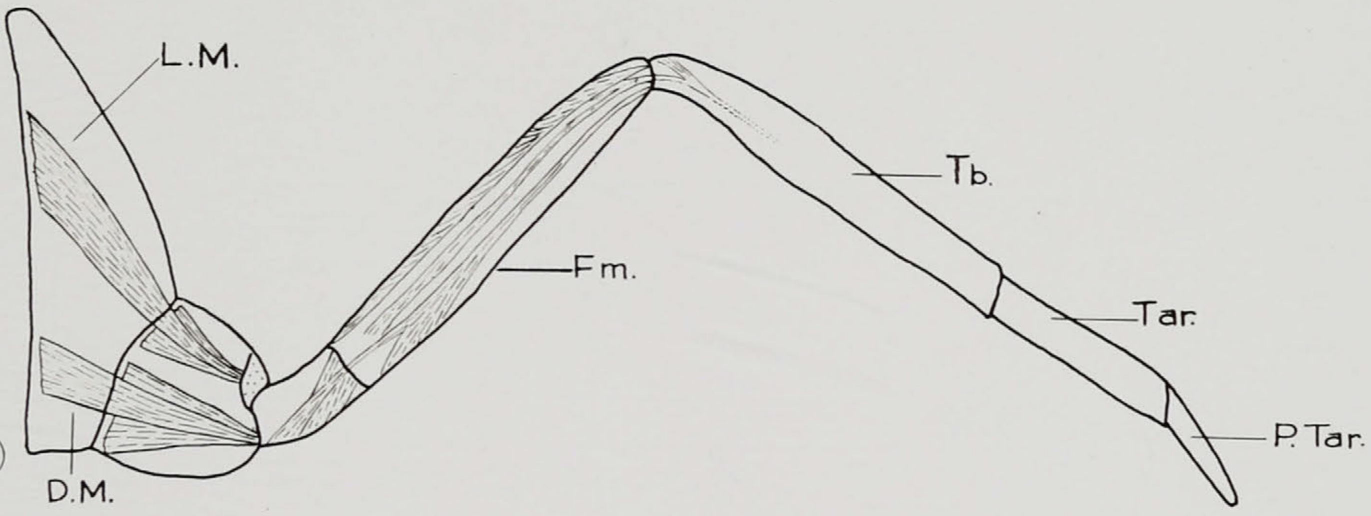

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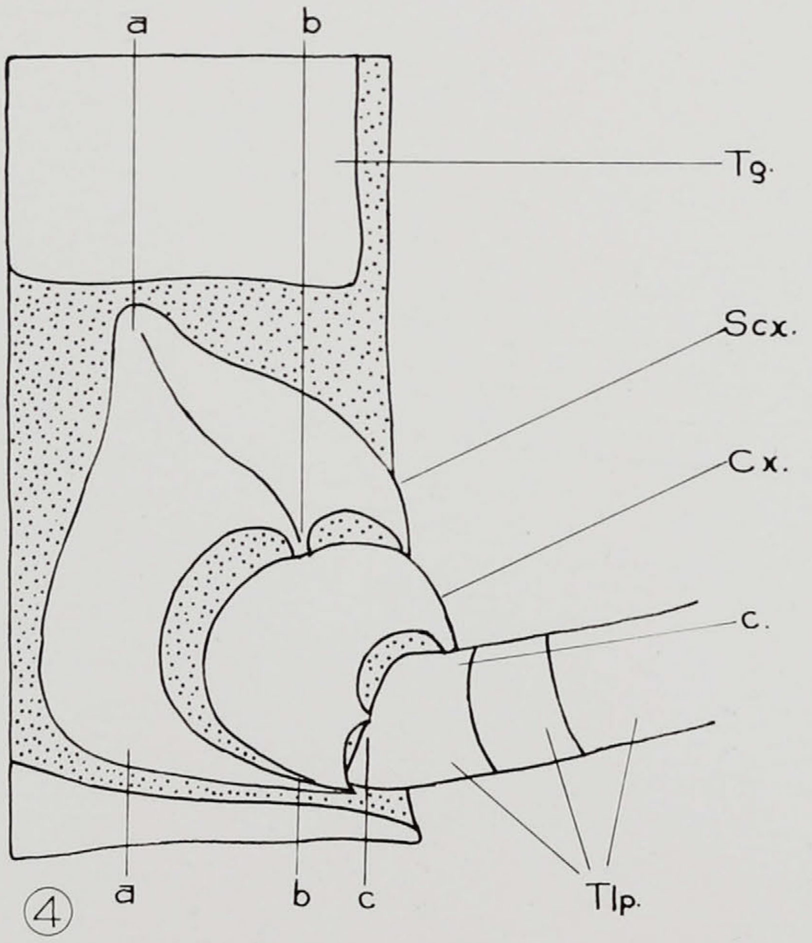

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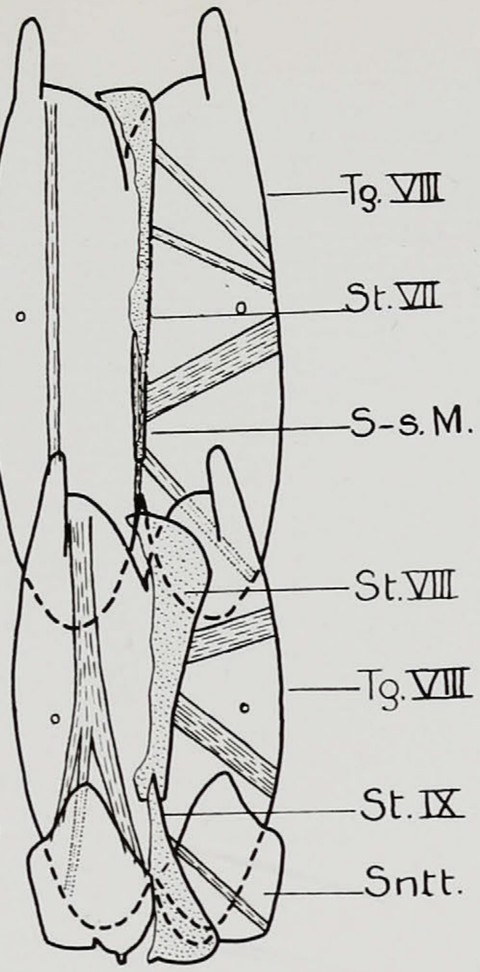
PLATE II

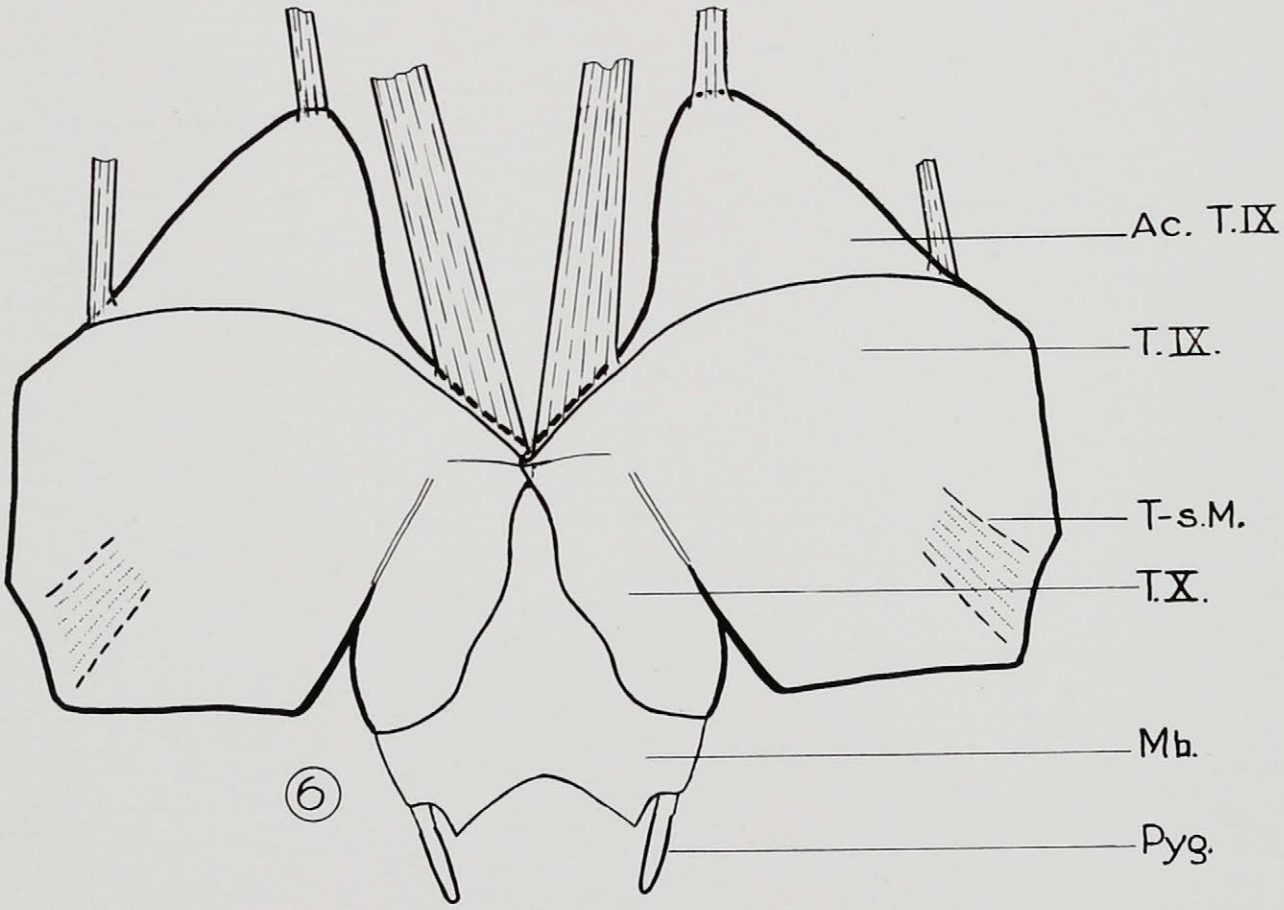
Plate III

Fig. 5. *Megarhyssa lunator*. Ventral View of Abdominal Segments VII-X, the Terga spread horizontally and the Left Side of each Sternum removed; Sternal Muscles placed to the Left of the Stippled Sterna, the Tergal and Tergo-sternal Muscles to the Right

Fig. 6. *Megarhyssa lunator*. Dorsal View of the Syntergites and their Muscles, the Syntergites placed in the Horizontal Plane


Tg. VIII
St. VII
S-s. M.
St. VIII
Tg. VIII
St. IX
Sntt.

⑤

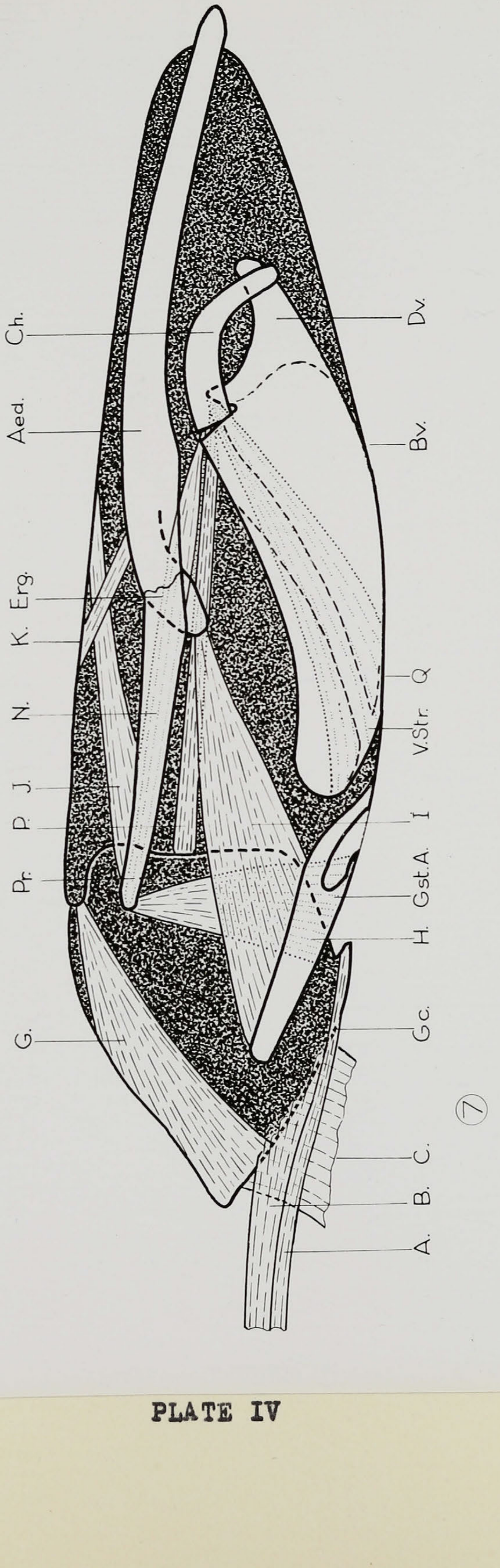

Ac. T. IX
T. IX.
T-s. M.
T. X.
Mb.
Pyg.

⑥

PLATE III

Plate IV

Fig. 7. *Megarhyssa lunator*. Inner Aspect of the Right Half of the Genital Appendages, showing the Muscles (exclusive of Muscles D, E, F and L)



⑦

PLATE IV

Plate V

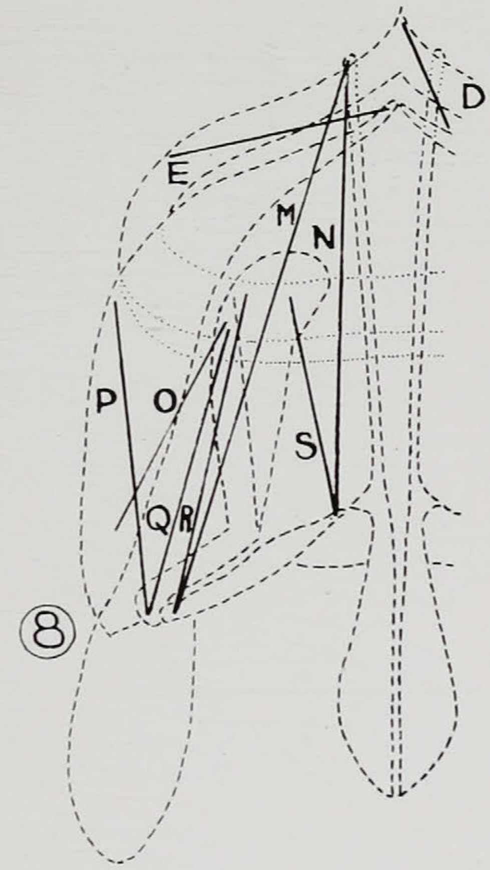
Diagrams of the Genitalia and Genital Muscles in the Chalastogastra

Fig. 8. Ventral View of the Genital Muscles, the Volsella placed in the Horizontal Plane; Sclerites shown by Broken Lines and Muscles by Solid Lines (redrawn after Boulangé 1924)

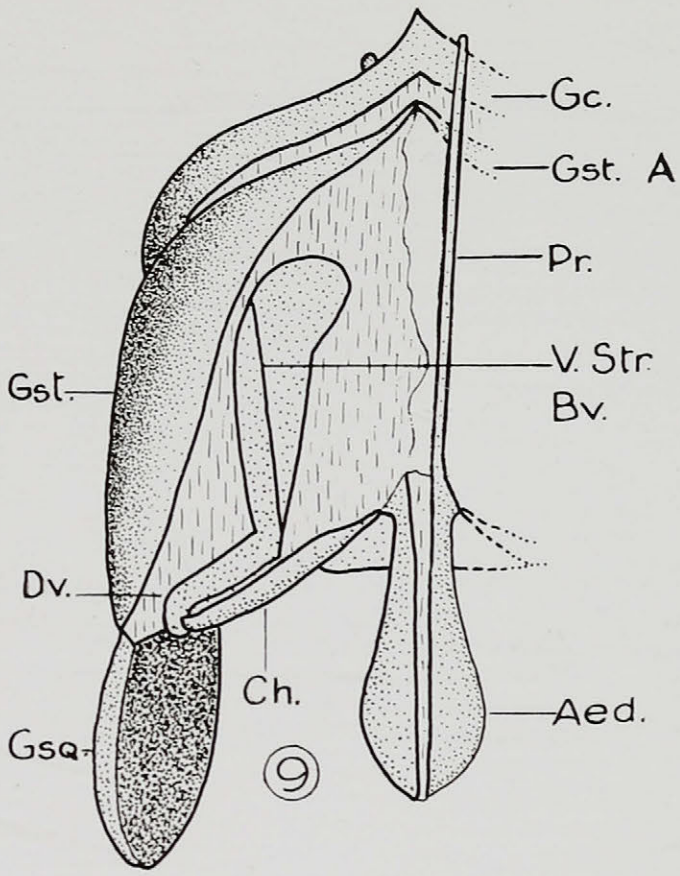
Fig. 9. Sclerites in Figure 8 shown in Relief

Fig. 10. As in Figure 8 but Dorsal; Membranous Areas shown by Broken Lines

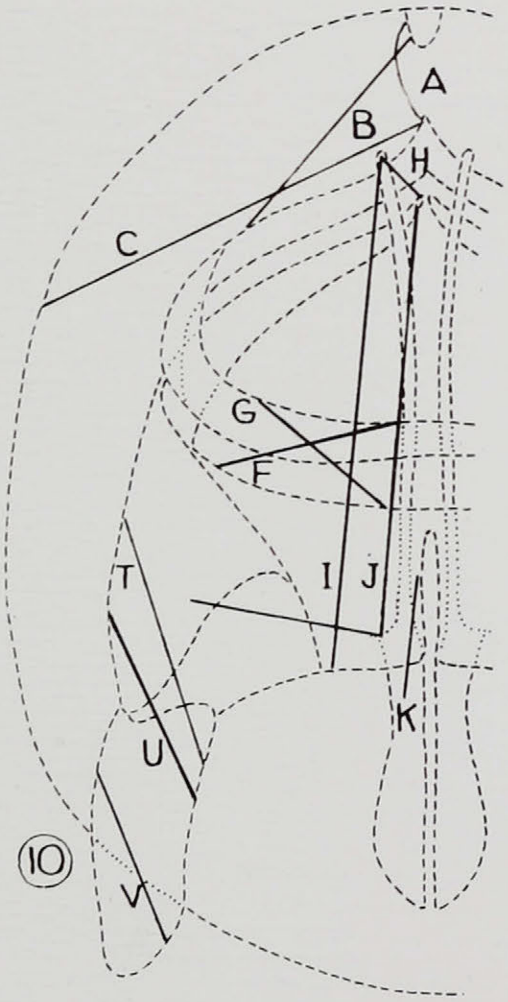
Fig. 11. As in Figure 9 but Dorsal


D
E
M
N
P
O
S
Q
R

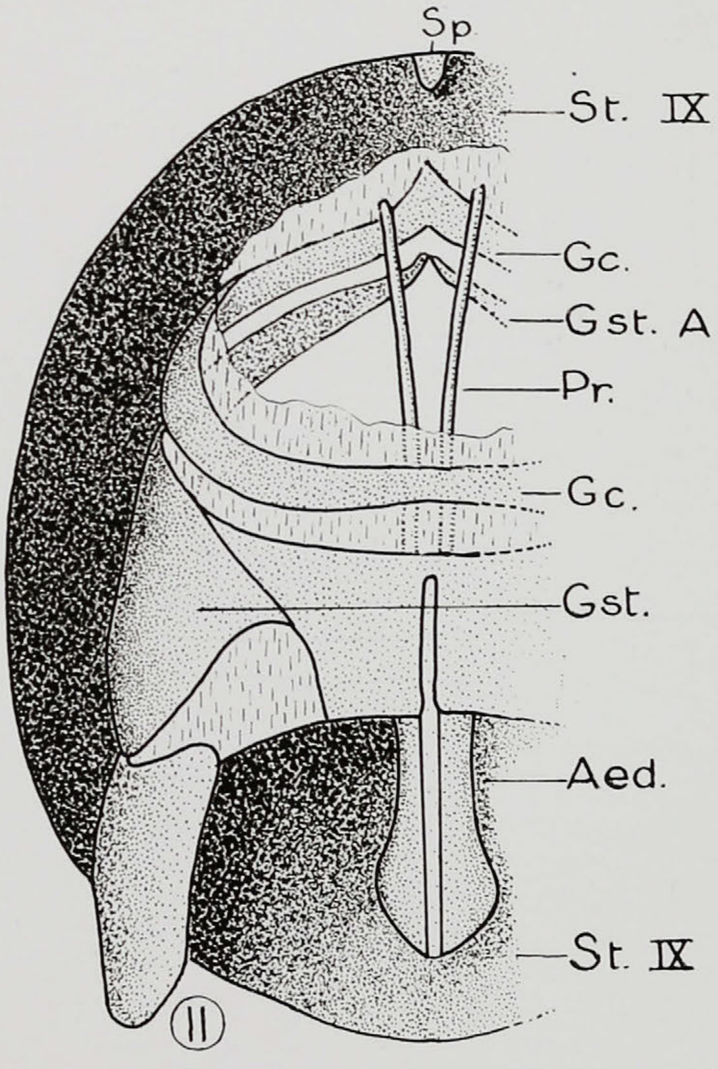
⑧


Gc.
Gst. A
Pr.
V. Str
Bv.
Gst.
Dv.
Ch.
Aed.
Gsq.

⑨


A
B
H
C
G
F
I
J
T
U
K
V

⑩


Sp.
St. IX
Gc.
Gst. A
Pr.
Gc.
Gst.
Aed.
St. IX

⑪

PLATE V

Plate VI

Fig. 12 *Angitia fenestralis*. Lateral View of the Terminal Abdominal Segments during Copulation

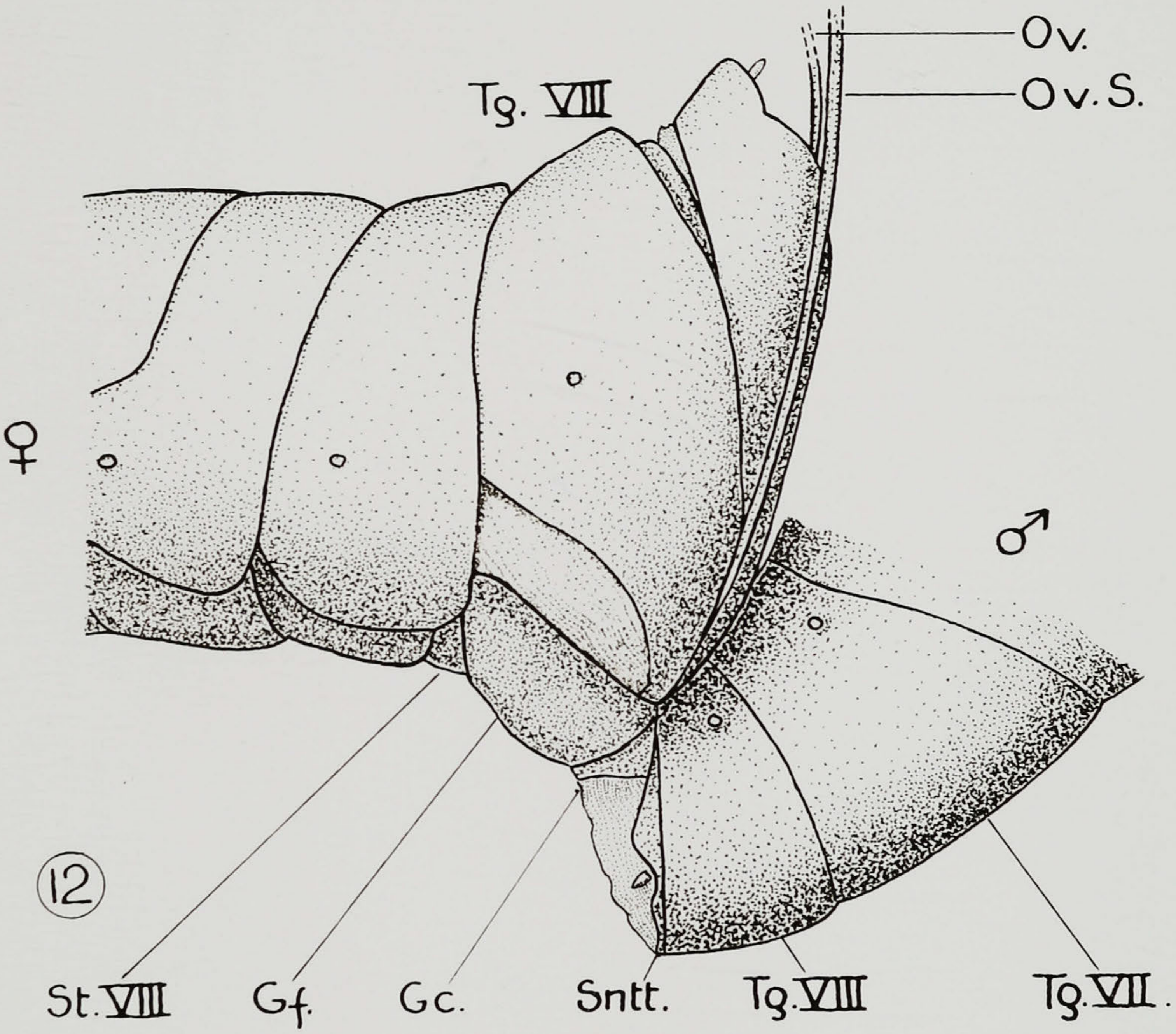


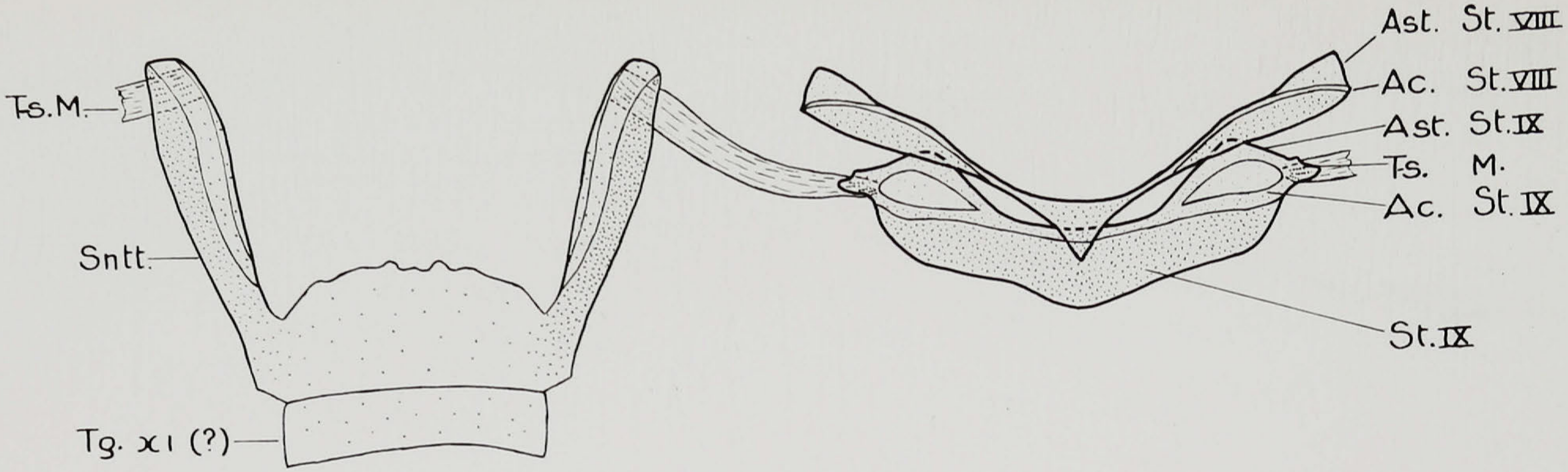
PLATE VI

Plate VII

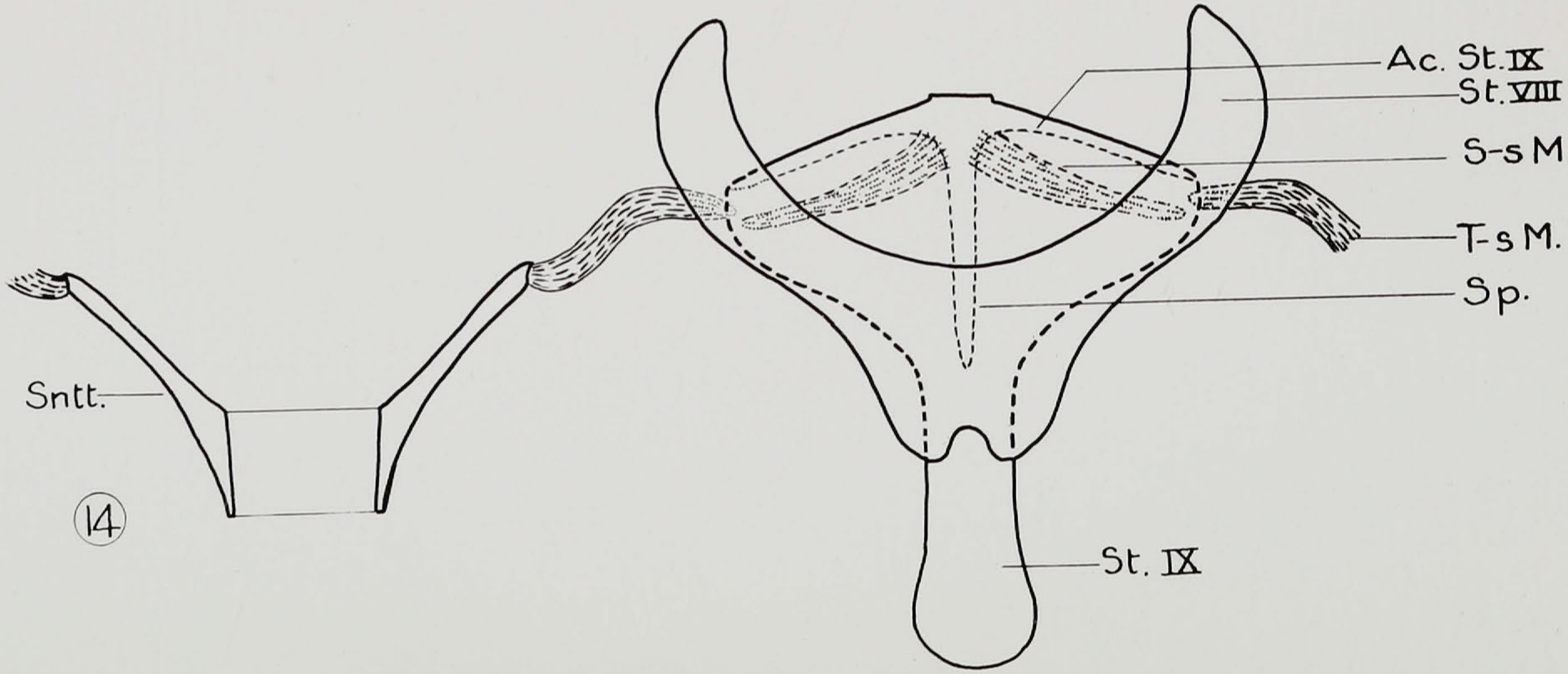
External View of the Syntergites, the Eighth and Ninth Sterna, and the Connecting Muscles; Stippled to show the Degree of Sclerotization.

Fig. 13 *Halictus lerouxii* (Apoidea)

Fig. 14 *Andrena wilkella*. (Apoidea)


Ts.M.
Sntt.
Tg. x1 (?)
Ast. St. VIII
Ac. St. VIII
Ast. St. IX
Ts. M.
Ac. St. IX
St. IX

⑬


Sntt.
Ac. St. IX
St. VIII
S-s M.
T-s M.
Sp.
St. IX

⑭

PLATE VII

Plate VIII

Fig. 15. Cephus cinctus (Cephidae). Dorsal View of the Terminal Abdominal Segments

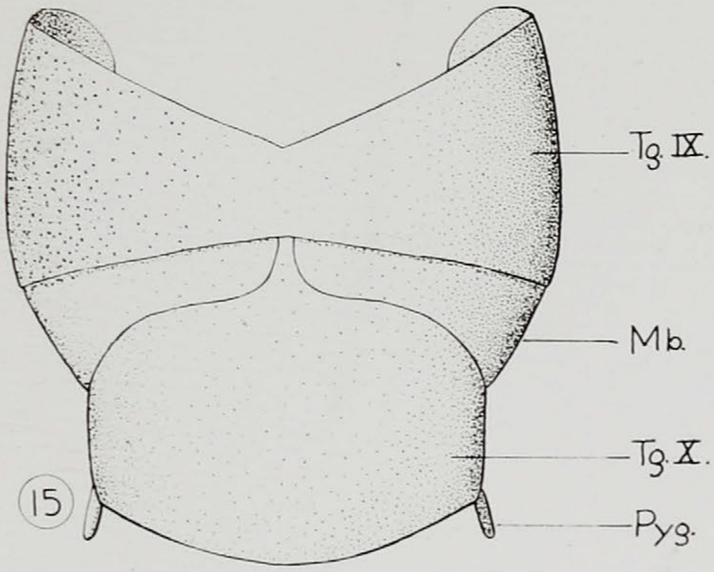
Fig. 16. Pteronidea ribesii (Tenthredinidae). As above

Fig. 17. Brachymeria intermedia (Chalcididae). As above

Fig. 18. Lasius niger (Formicidae). As above

Fig. 19. Vespa maculata (Vespidae). As above

Fig. 20. Exeristes roborator (Ichneumonidae). Dorsal View of the Syntergum, showing the Line of Median Fission in the Tenth Tergum (a-a) and the Line of Inter-tergal Fusion (b-b)



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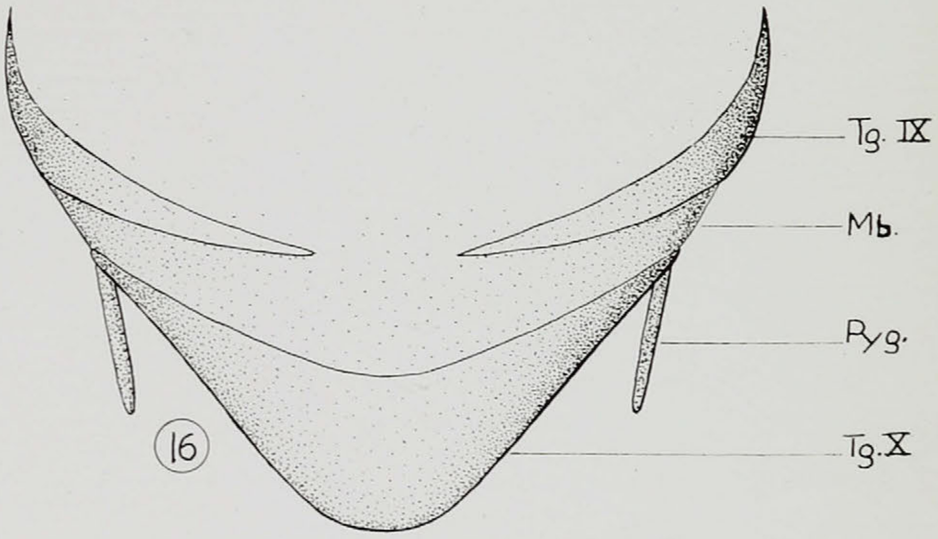

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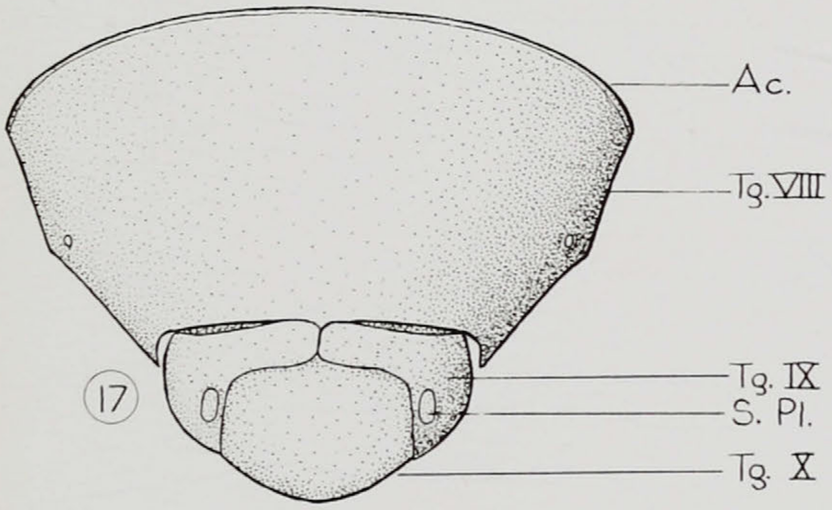

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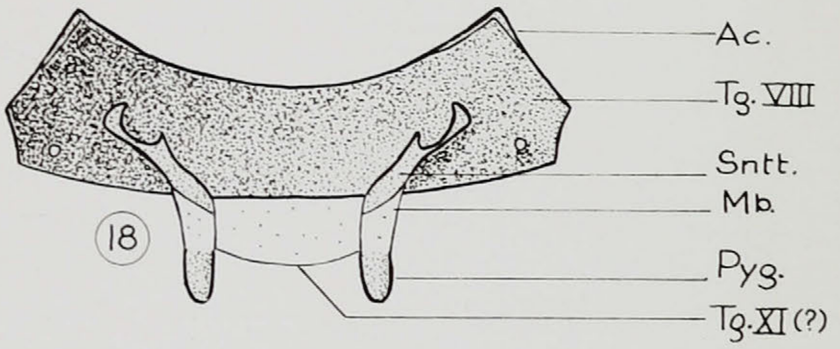

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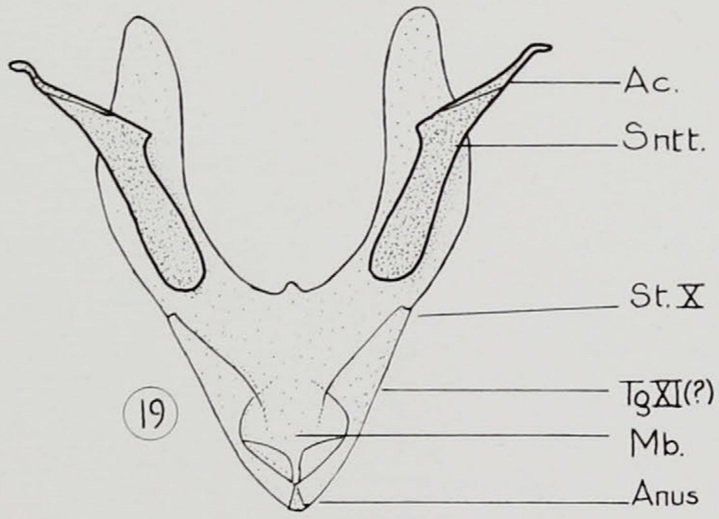

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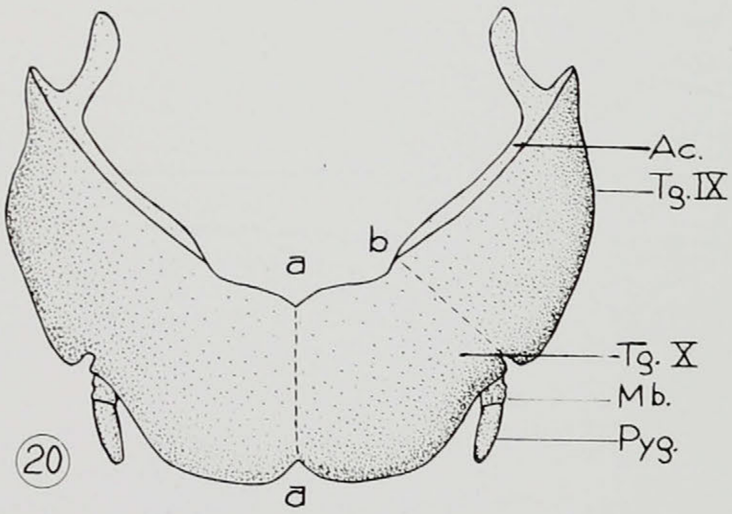

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PLATE VIII

Plate IX

The Ninth and Tenth Terga; the Antecosta (Ac.) shown by a Dotted Line

Fig. 21. *Pimpla (Iseropus) coelebs*. Dorsal View of the Tergites of the Ninth and Tenth Terga

Fig. 22. *Banchus falcatorius*. Dorsal View of the Syntergites

Fig. 23. *Glypta fumiferanae*. Lateral View of the Ninth and Tenth Terga

Fig. 24. *Glypta rufiscutellaris*. As above

Fig. 25. *Theronia fulvescens*. As above

Fig. 26. *Theronia melanocephala*. As above

Fig. 27. *Exetastes fascipennis*. As above

Fig. 28. *Exetastes matricus*. As above

Fig. 29. *Exenterus claripennis*. As above

Fig. 30. *Exenterus marginatorius*. As above

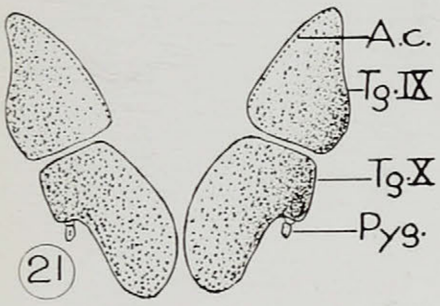
Fig. 31. *Cremastus flavo-orbitalis*. Dorsal View

Fig. 32. *Cremastus geminus*. As above

Fig. 33. *Cremastus minor*. As above

Fig. 34. *Cremastus incompletus*. As above

Fig. 35. *Itoplectis conquisitor*. Lateral View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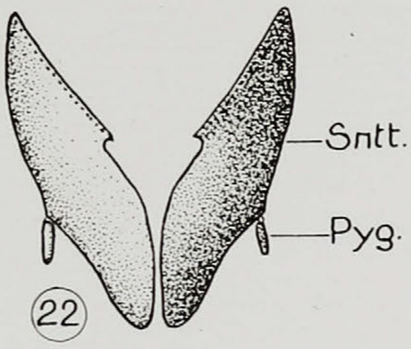
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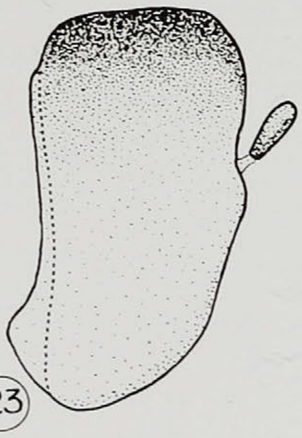
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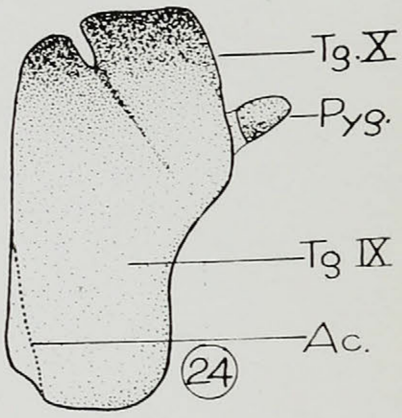
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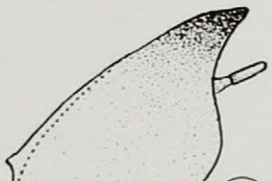
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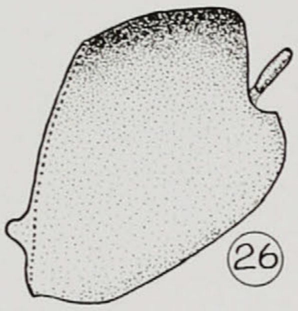
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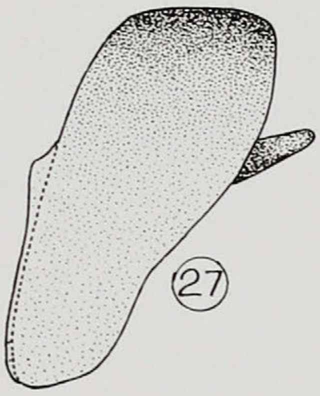
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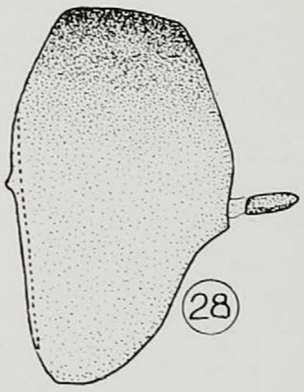
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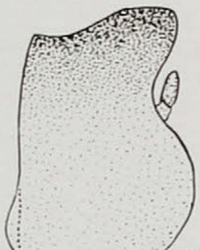
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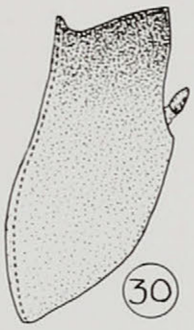
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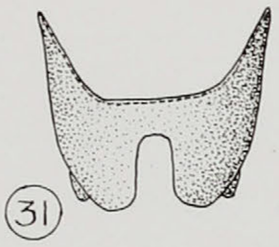
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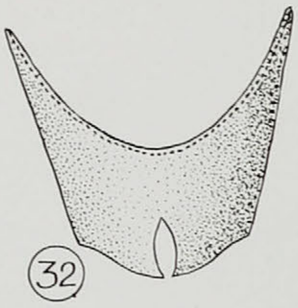
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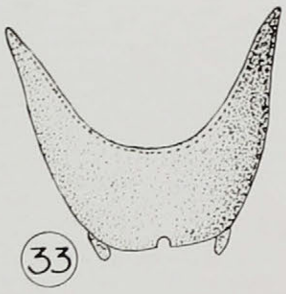
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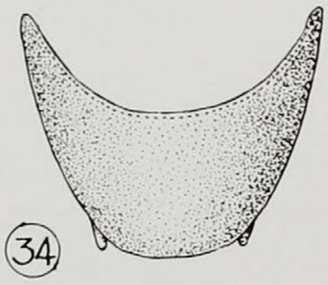
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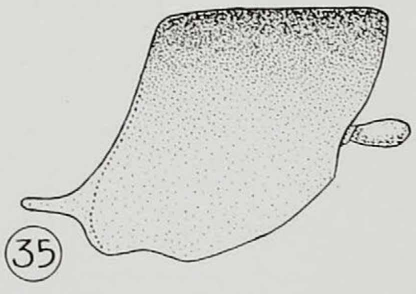
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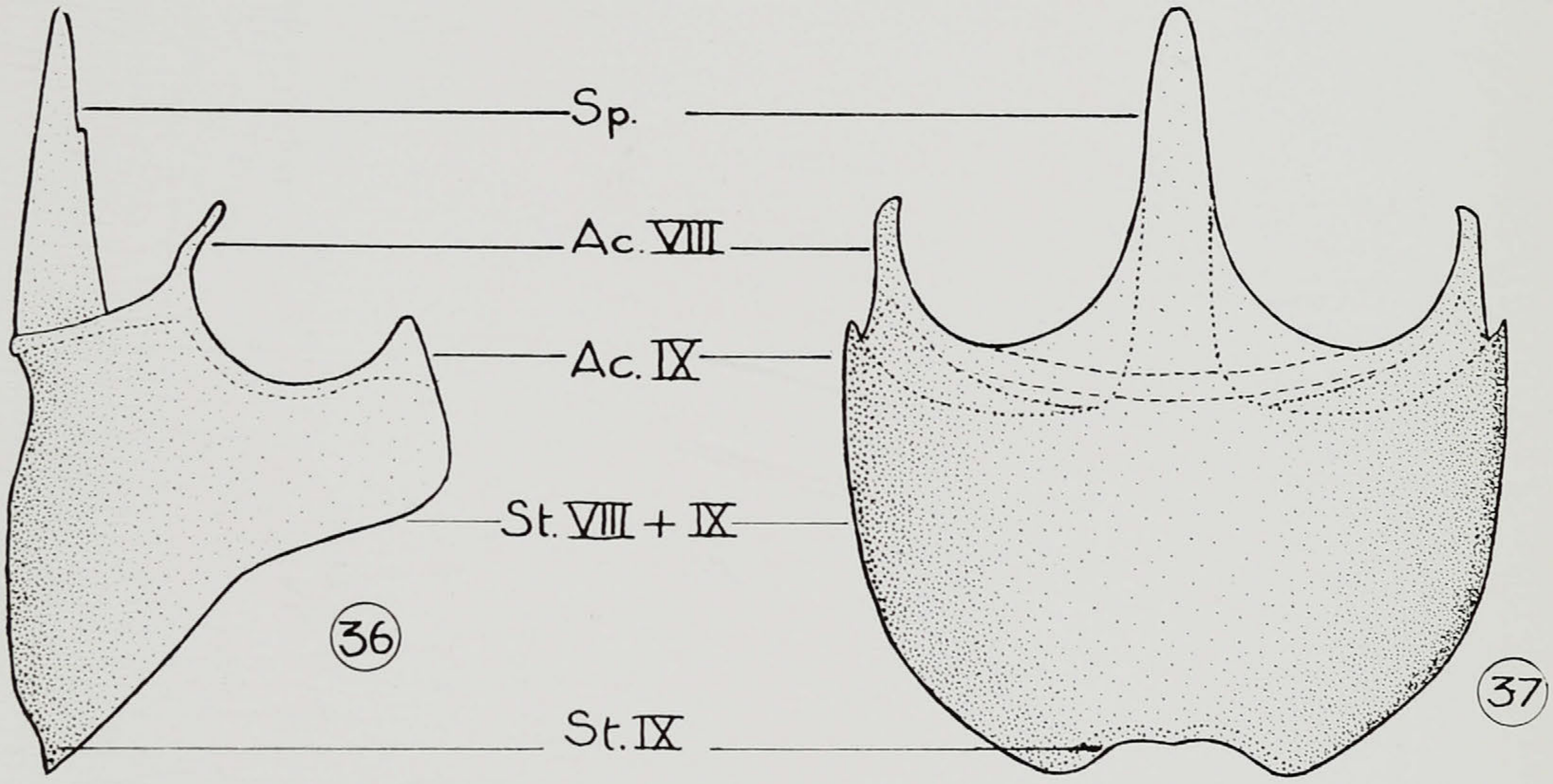
PLATE IX

Plate X

Fig. 36. *Vespa maculata* (Vespidae). Lateral View of Hypandrium.

Fig. 37. *Vespa maculata* (Vespidae). Ventral View of Hypandrium

Fig. 38. *Brachymeria intermedia* (Chalcididae). Lateral View of the Male Genitalia and the Tenth Sternum



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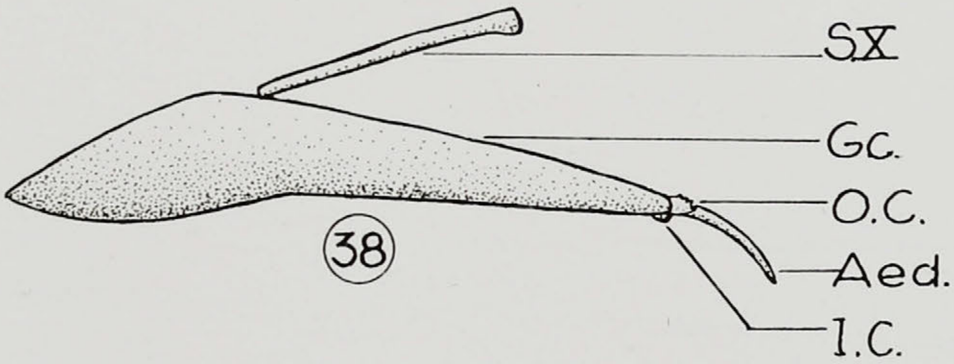

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PLATE X

Plate XI

Ventral View of the Ninth Sternum; Membranous Areas shown by Broken Lines

Fig. 39. *Ichneumon variegatus*

Fig. 40. *Ichneumon animosus*

Fig. 41. *Ichneumon perscrutator*

Fig. 42. *Ichneumon grotei*

Fig. 43. *Phaeogenes gaspesensis*

Fig. 44. *Phaeogenes hariolus*

Fig. 45. *Hemiteles hemipterus*

Fig. 46. *Hemiteles subzonatus*

Fig. 47. *Hemiteles fulvipes*

Fig. 48. *Exetastes fascipennis*

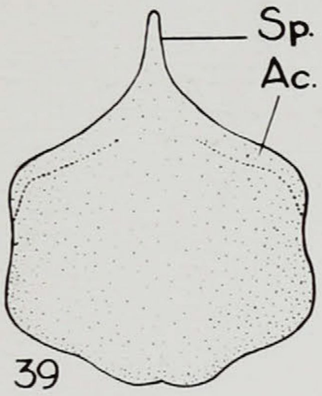
Fig. 49. *Exetastes matricus*

Fig. 50. *Glypta rufuscutellaris*

Fig. 51. *Glypta fumiferanae*

Fig. 52. *Theronia fulvescens*

Fig. 53. *Theronia melanocephala*



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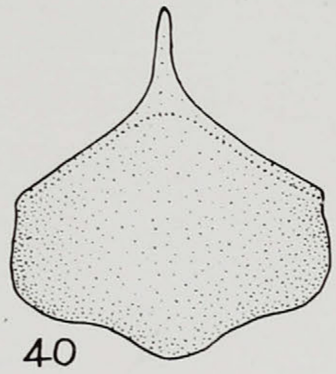

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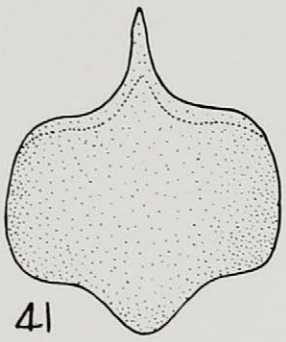

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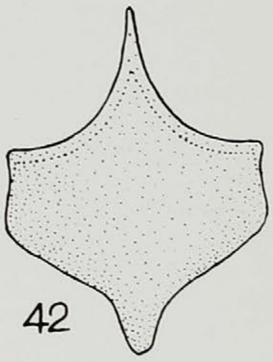

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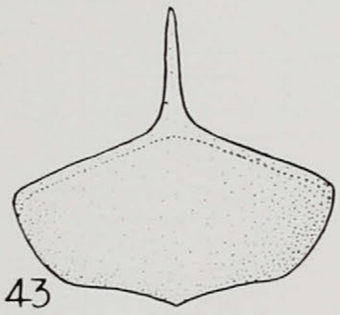

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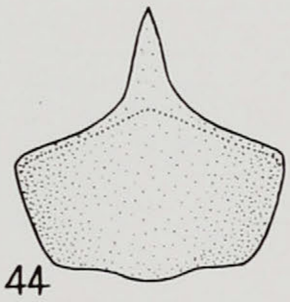

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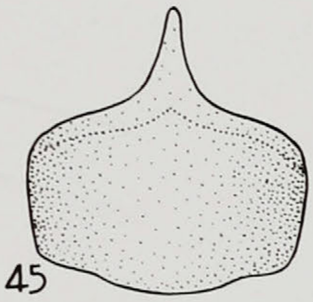

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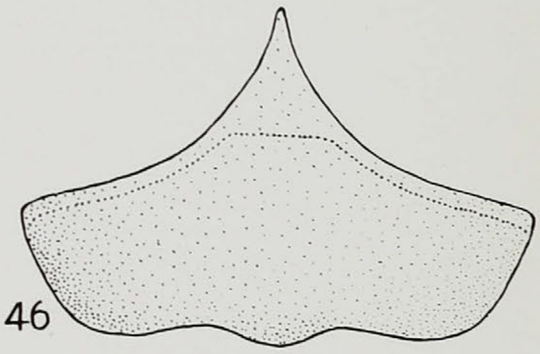

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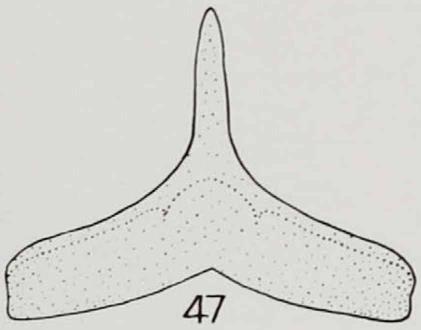

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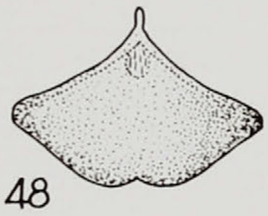

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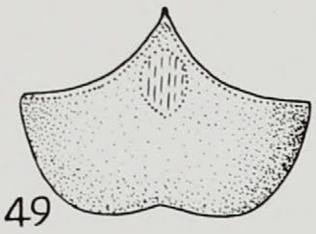

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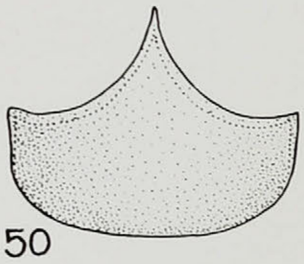

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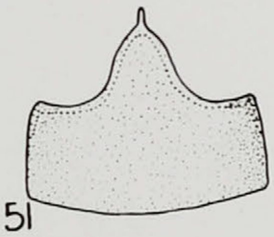

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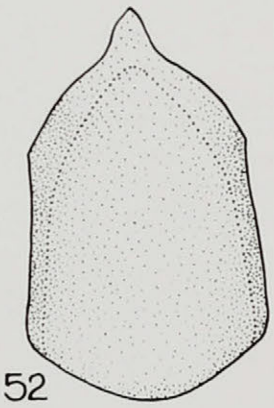

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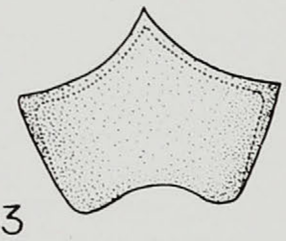

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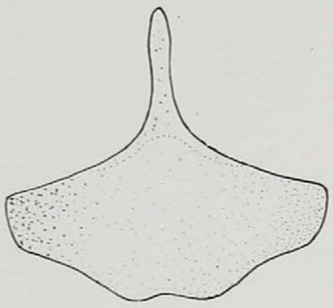
PLATE XI

Plate XII

Ventral View of the Ninth Sternum; Membranous Areas shown by Broken Lines

Fig. 54.	Omorgus borealis
Fig. 55.	Omorgus ensator
Fig. 56.	Omorgus mutabilis
Fig. 57.	Cremastus incompletus
Fig. 58.	Cremastus flavo-orbitalis
Fig. 59.	Cremastus minor
Fig. 60.	Cremastus geminus
Fig. 61.	Cremastus interruptor
Fig. 62.	Pimpla coelebs
Fig. 63.	Pimpla instigator
Fig. 64.	Exenterus claripennis
Fig. 65.	Exenterus canadensis
Fig. 66.	Exenterus marginatorius
Fig. 67.	Exenterus lepidus
Fig. 68.	Tryphon incestus
Fig. 69.	Megarhyssa lunator



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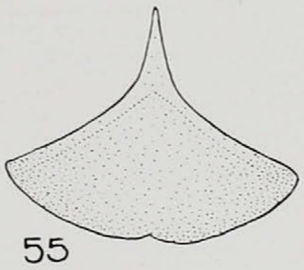

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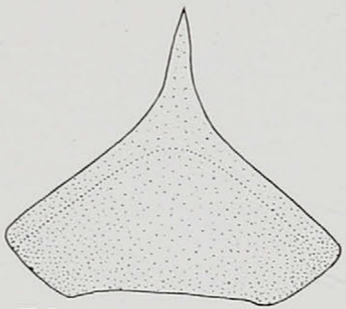

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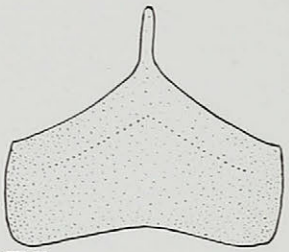

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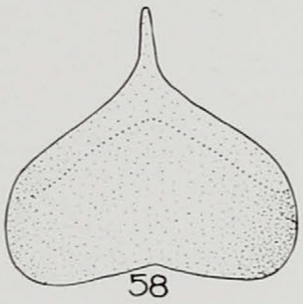

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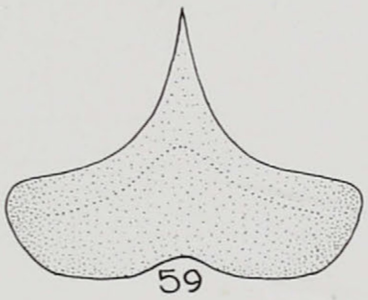

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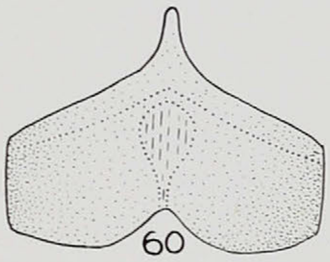

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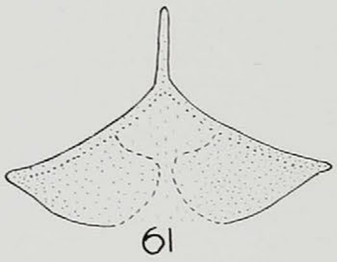

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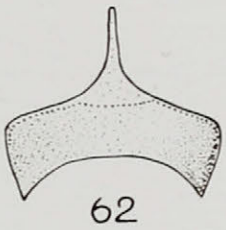

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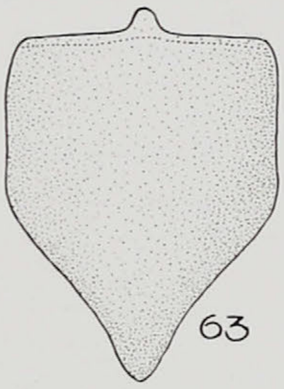

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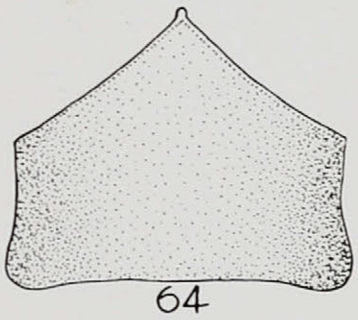

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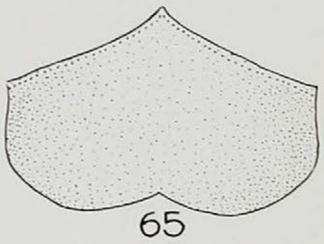

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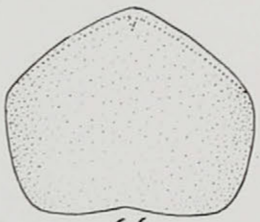

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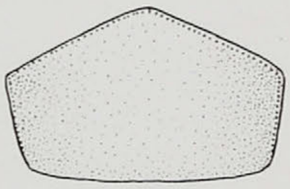

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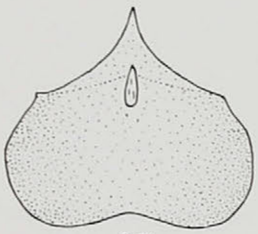

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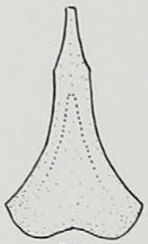

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PLATE XII

Plate XIII

The Genitalia

Fig. 70. Megarhyssa lunator. Ventral View

Fig. 71. Megarhyssa lunator. Dorsal View

Fig. 72. Banchus falcatorius. As above

Fig. 73. Ophion obscurus. As above

Fig. 74. Agrypon flaveolatum. As Above

Fig. 75. Exochilum circumflexum. As above

Fig. 76. Cremastus minor. As above

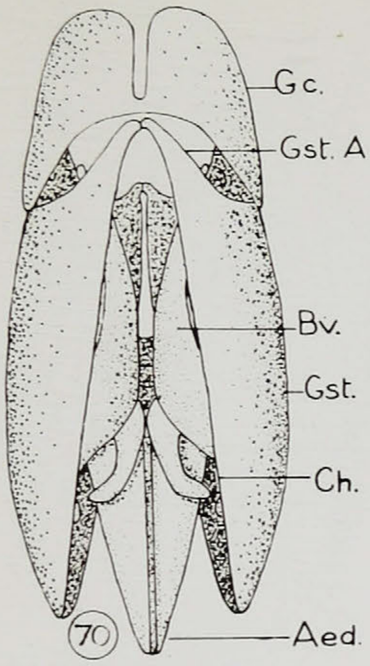
Fig. 77. Cremastus geminus. As above

Fig. 78. Cremastus flavo-orbitalis. As above

Fig. 79. Pristomerus vulnerator. As above

Fig. 80. Demophorus robustus. As above

Fig. 81. Orthopelma luteator. As above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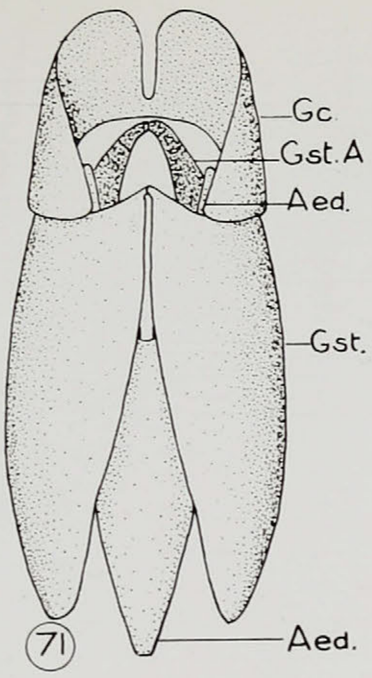
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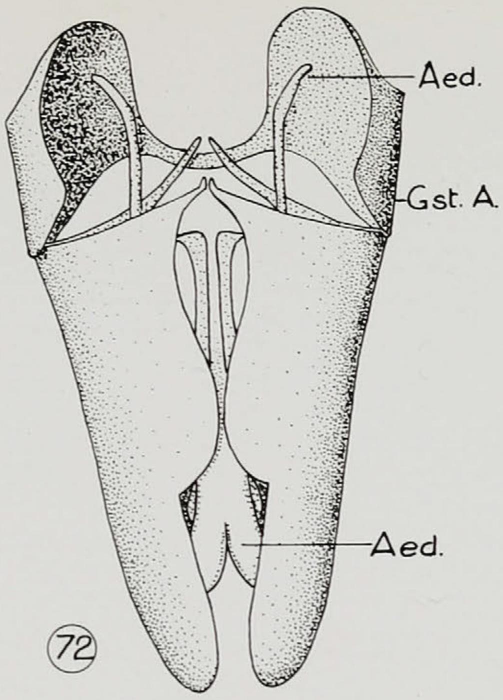
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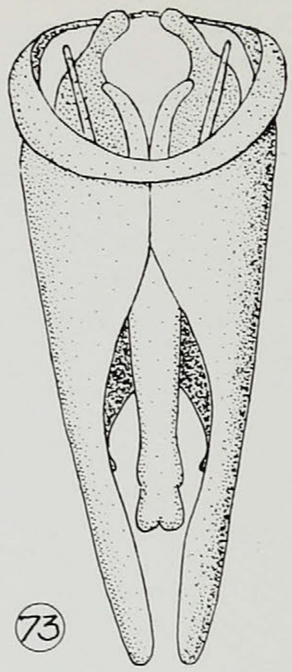
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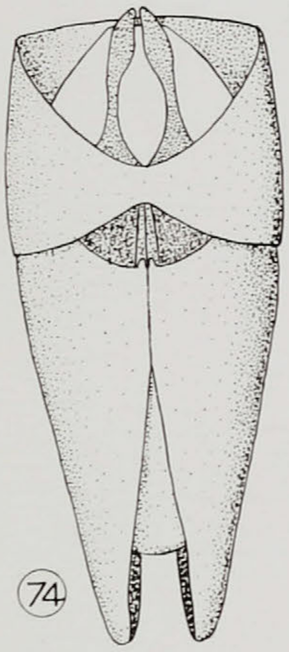
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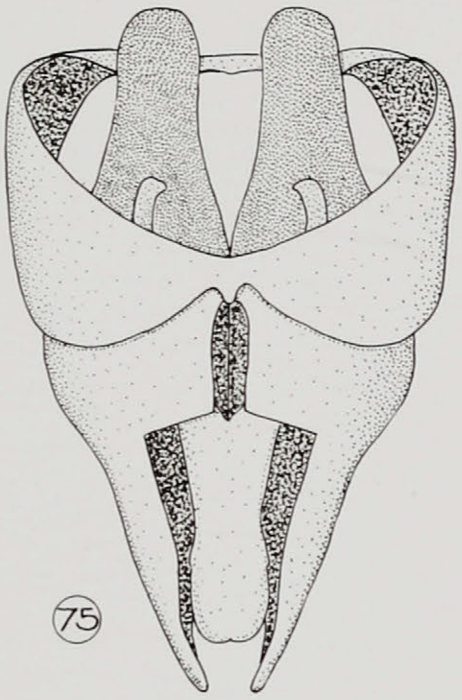
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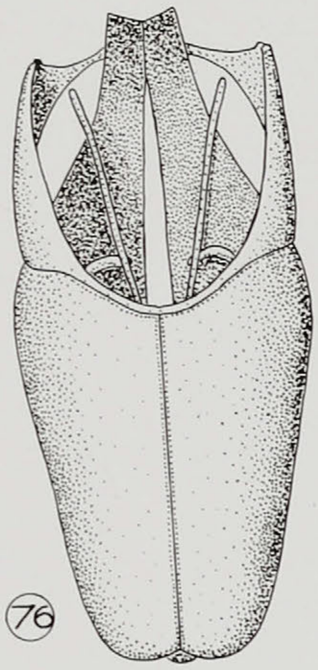
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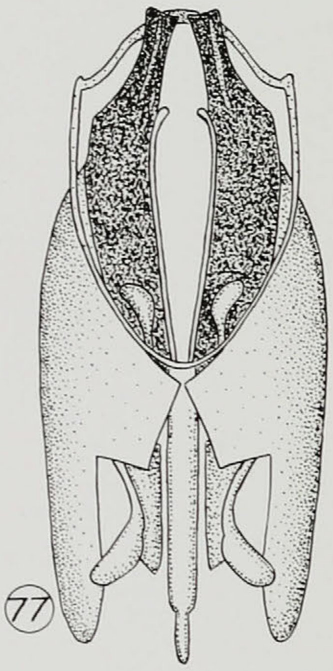
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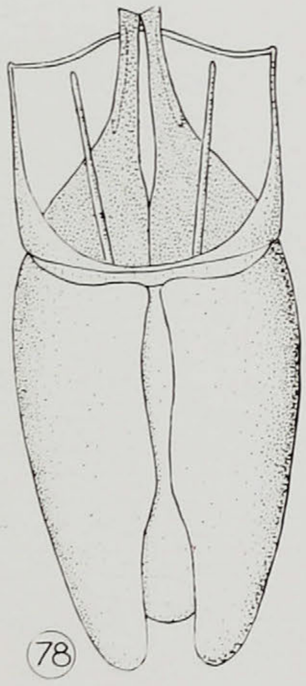
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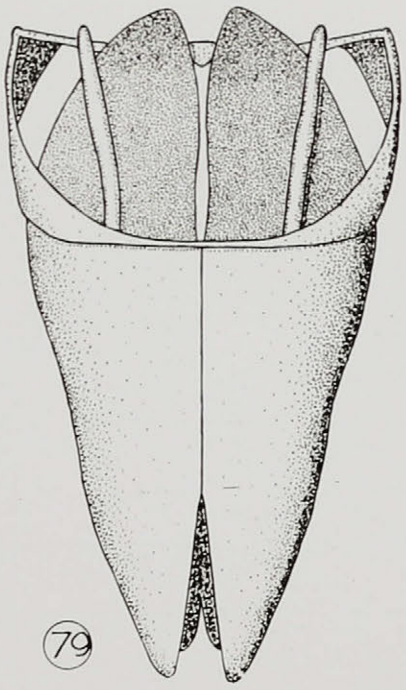
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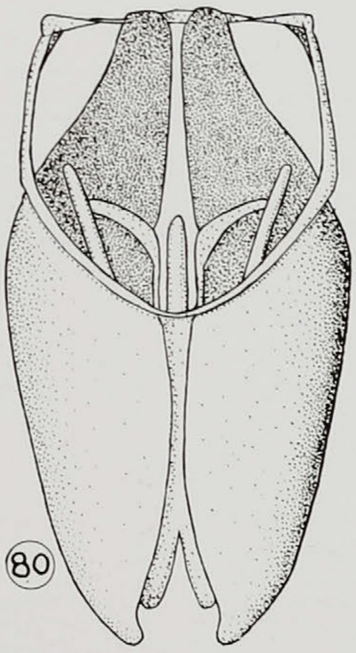
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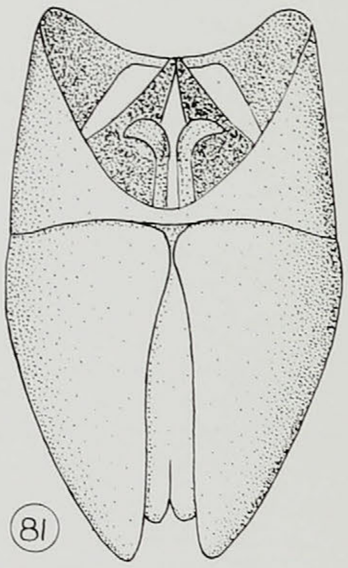
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PLATE XIII

Plate XIV

The Genitalia

Fig. 82. *Mesochorus pectoralis*. Dorsal View

Fig. 83. *Hemiteles fulvipes*. As above

Fig. 84. *Hemiteles submarginatus*. As above

Fig. 85. *Enicospilus ramidulus*. As above

Fig. 86. *Apechthis ontario*. As above

Fig. 87. *Theronia fulvescens*. As above

Fig. 88. *Theronia melanocephala*. As above

Fig. 89. *Glypta rufiscutellaris*. As above

Fig. 90. *Glypta fumiferanae*. As above

Fig. 91. *Ephialtes tuberculatus*. As above

Fig. 92. *Ephialtes grapholithae*. As above

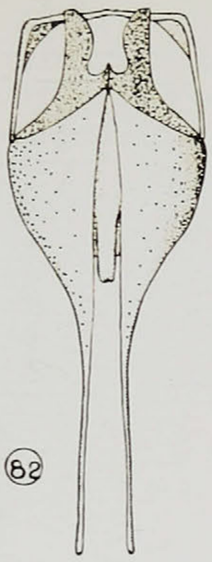
Fig. 93. *Exenterus canadensis*. As above

Fig. 94. *Exenterus claripennis*. As above

Fig. 95. *Exenterus lepidus*. As above

Fig. 96. *Exenterus marginatorius*. As above

Fig. 97. *Ichneumon longulus*. Ventral View, showing the Basal Fusion of the Volsella to the Gonostipes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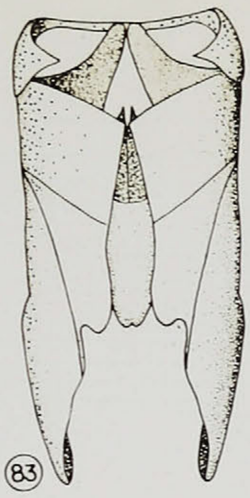
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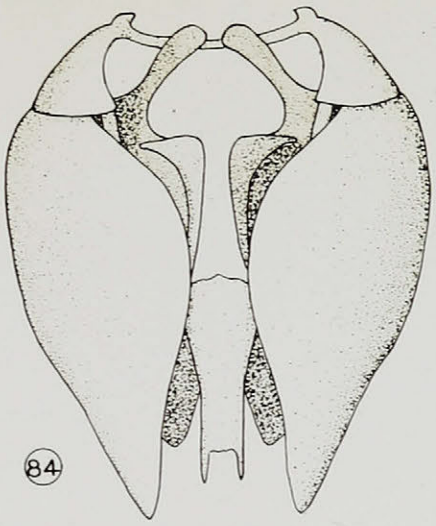
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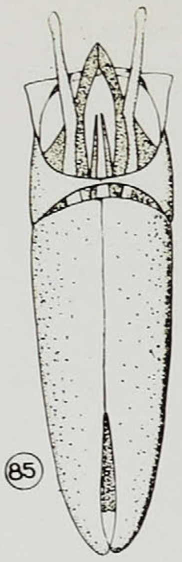
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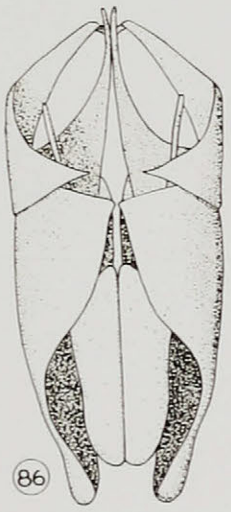
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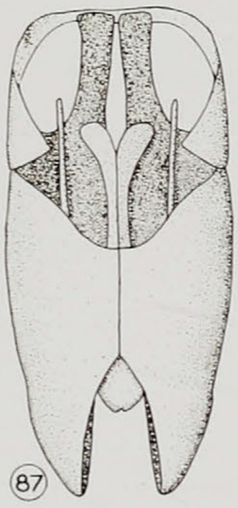
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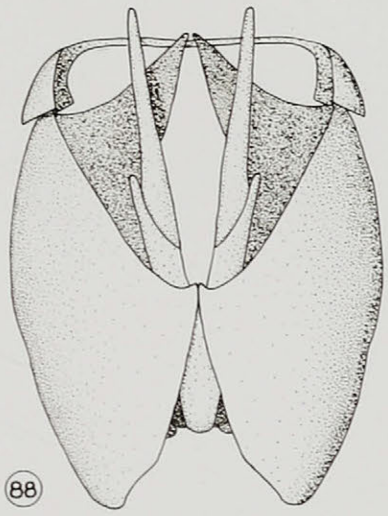
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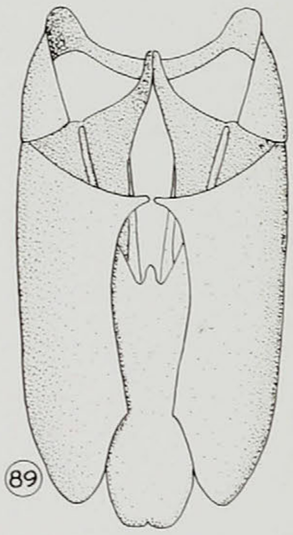
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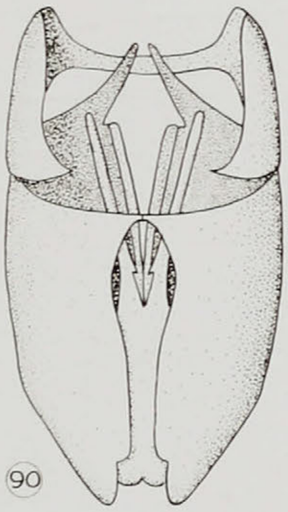
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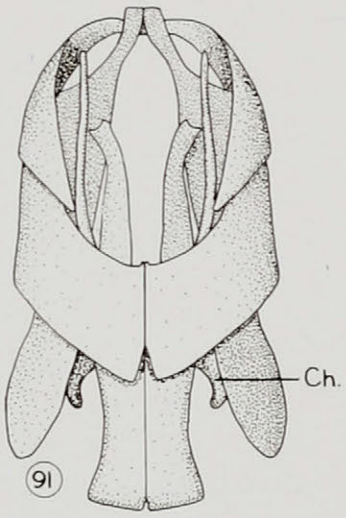

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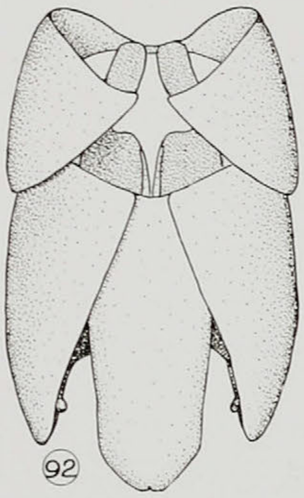
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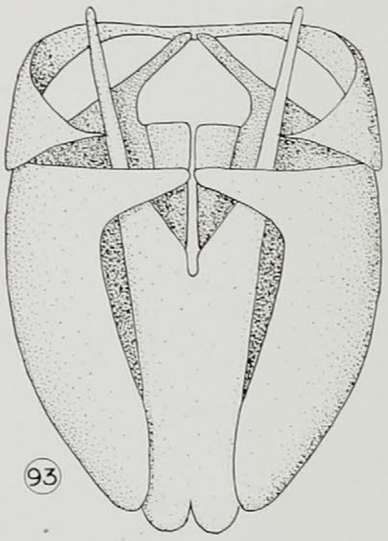
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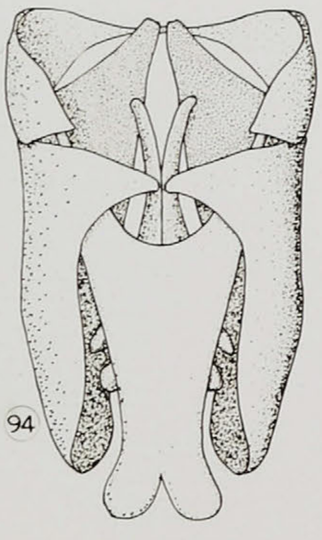
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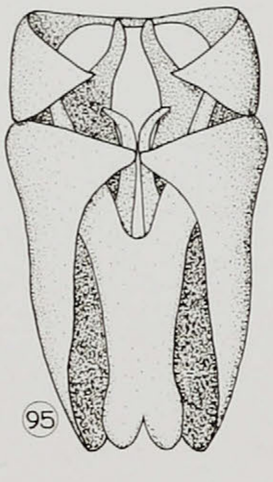
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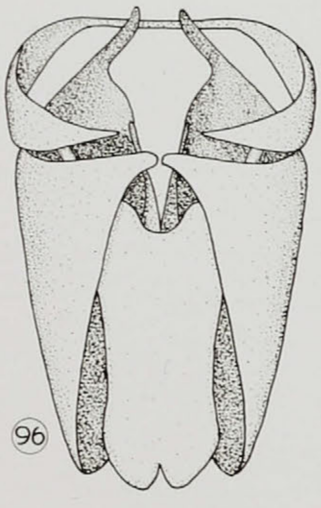
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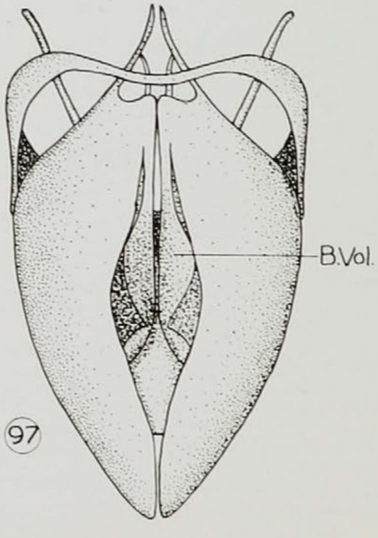

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PLATE XIV

Plate XV

Fig. 98. Hemiteles fulvipes. Lateral View of the Genitalia

Fig. 99. Hemiteles submarginatus. As above

Fig. 100. Glypta rufiscutellaris. As above

Fig. 101. Glypta fumiferanae. As above

Fig. 102. Ephialtes tuberculatus. As above

Fig. 103. Ephialtes grapholithae. As above

Fig. 104. Cremastus interruptor. As above

Fig. 105. Cremastus geminus. As above

Fig. 106. Cremastus minor. As above

Fig. 107. Cremastus incompletus. As above

Fig. 108. Exenterus canadensis. As above

Fig. 109. Exenterus claripennis. As above

Fig. 110. Exenterus lepidus. As above

Fig. 111. Exenterus marginatorius. As above

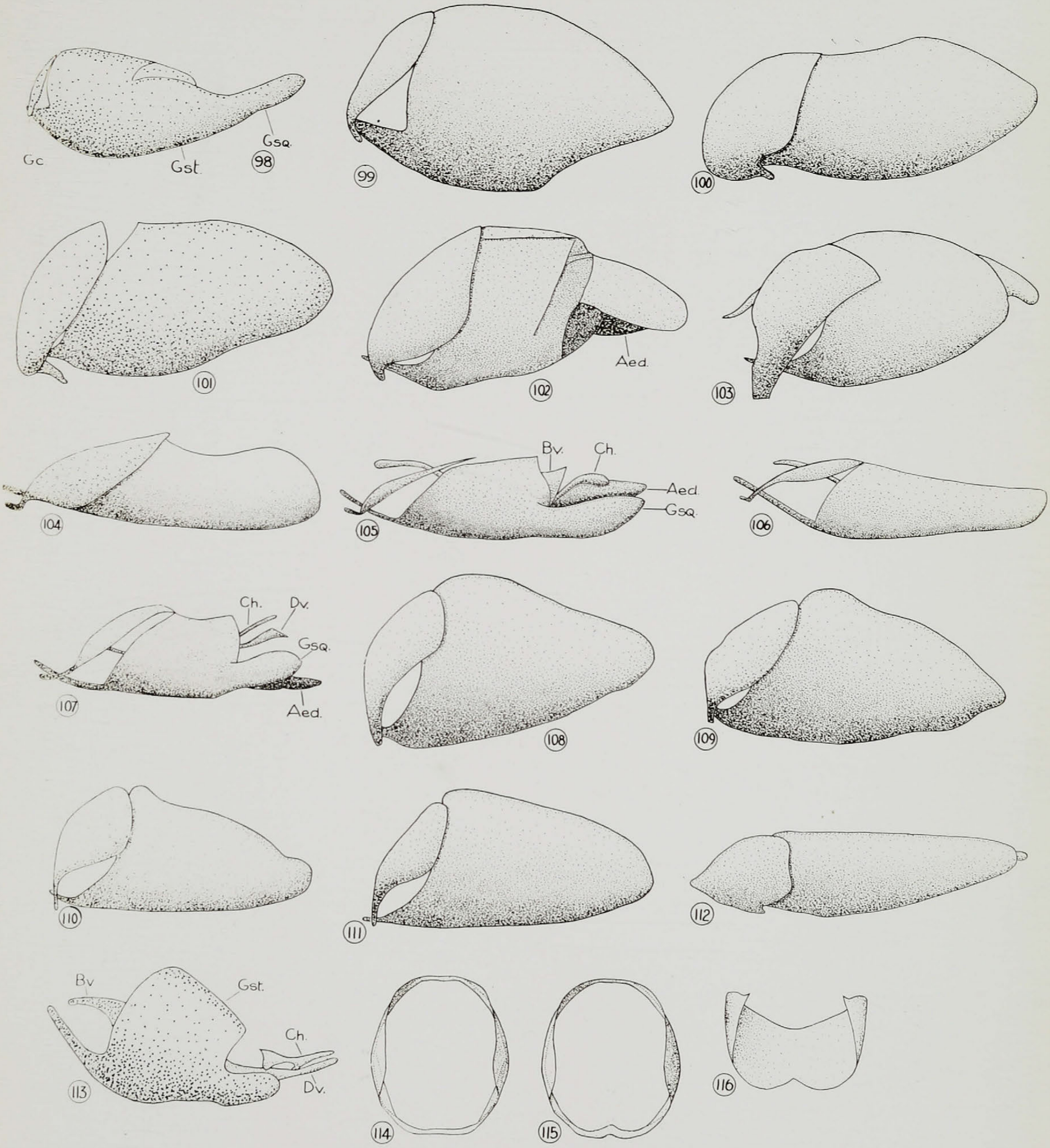
Fig. 112. Megarhyssa lunator. As above

Fig. 113. Oryssus sayi (Oryssidae). As above, but the Gonocardo absent

Fig. 114. Ichneumon longulus. Posterior View of Gonocardo

Fig. 115. Ichneumon variegatus. As above

Fig. 116. Megarhyssa citraria. Dorsal View of Gonocardo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Dv.
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Bv
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PLATE XV

Plate XVI

The Volsella

Fig. 117. *Tenthredella mesomelas* (Tenthredinidae). Ventral View of the Volsella in the Horizontal Plane and the Adjacent Sclerites (redrawn and shaded after Boulangé 1924)

Fig. 118. *Dolerus similis*. Internal View of the widely separated Volsella and Gonoforceps

Fig. 119. *Neotypus americanus*. Lateral or Internal View

Fig. 120. *Neotypus americanus*. Mesal or External View

Fig. 121. *Ichneumon grotei*. As above but showing Portion 'a' of the Basivolsella, fused to the Gonostipes

Fig. 122. *Ichneumon animosus*. External View

Fig. 123. *Hemiteles hemipterus*. As above

Fig. 124. *Enicospilus ramidulus*. As above

Fig. 125. *Cryptus annulatus*. As above

Fig. 126. *Cremastus minor*. As above

Fig. 127. *Cremastus incompletus*. As above but showing the Adjacent Parts of the Gonoforceps

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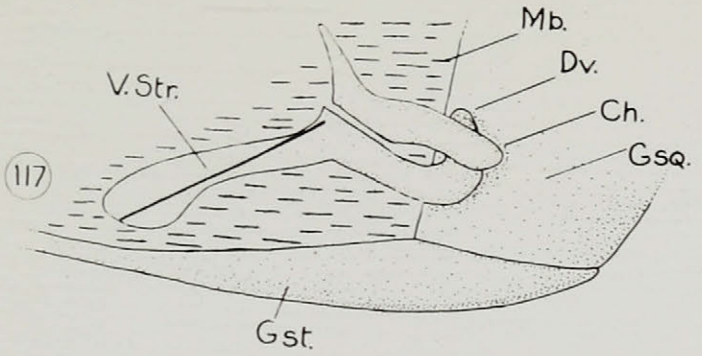

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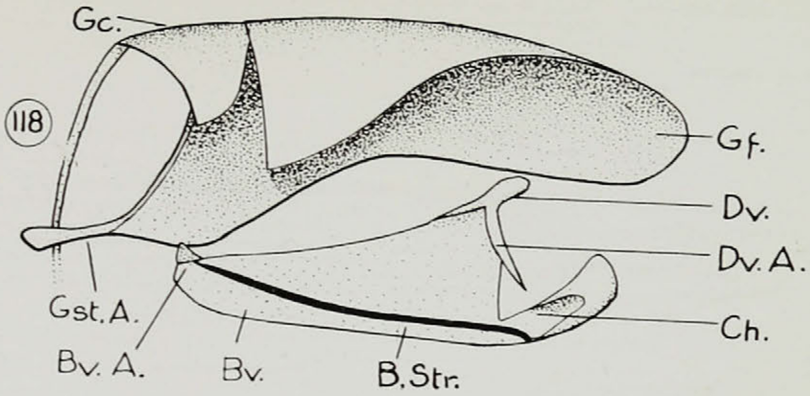

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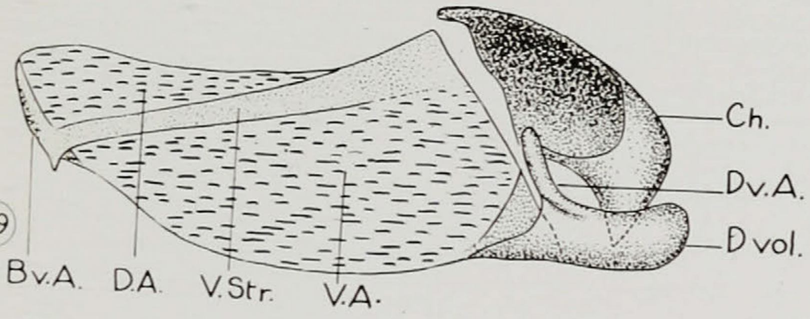

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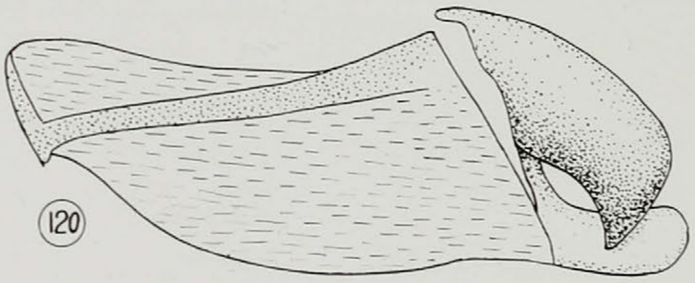

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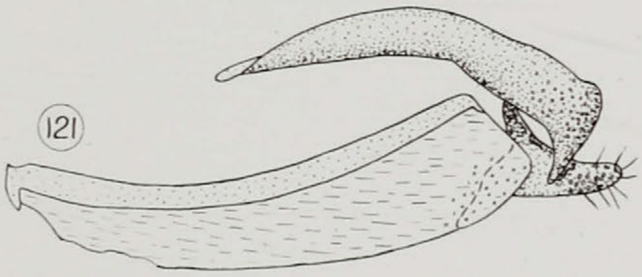

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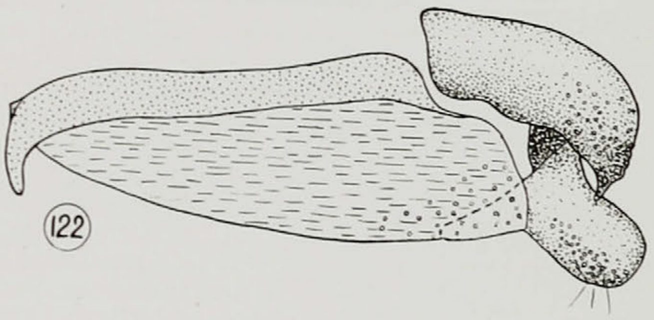

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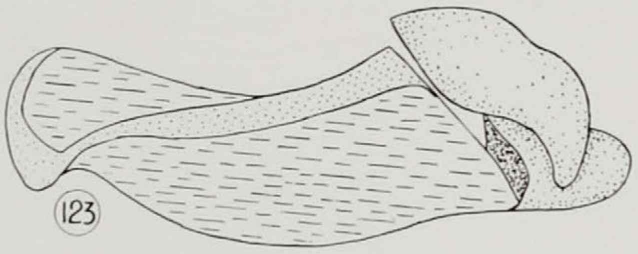

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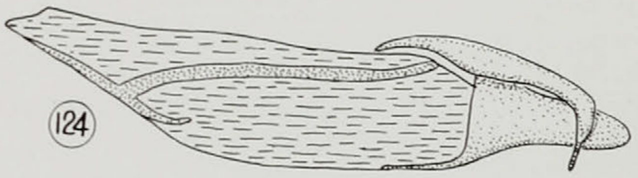
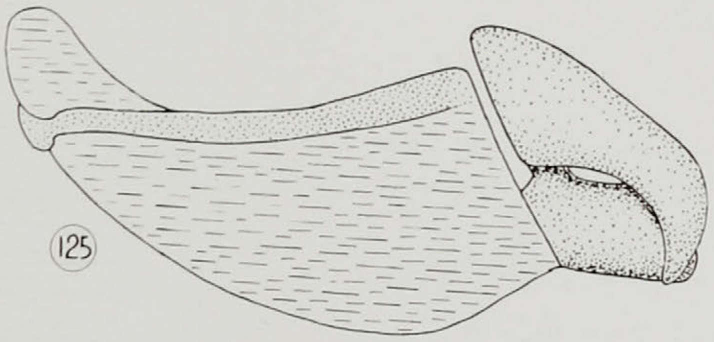
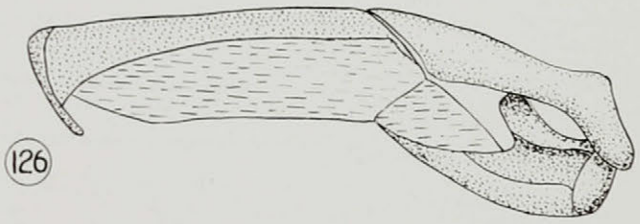


125



126



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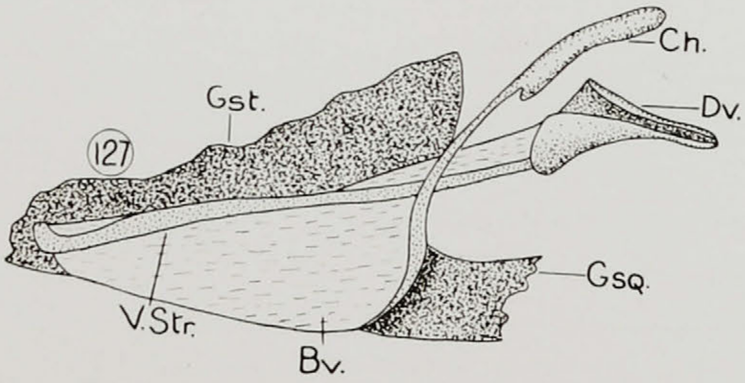
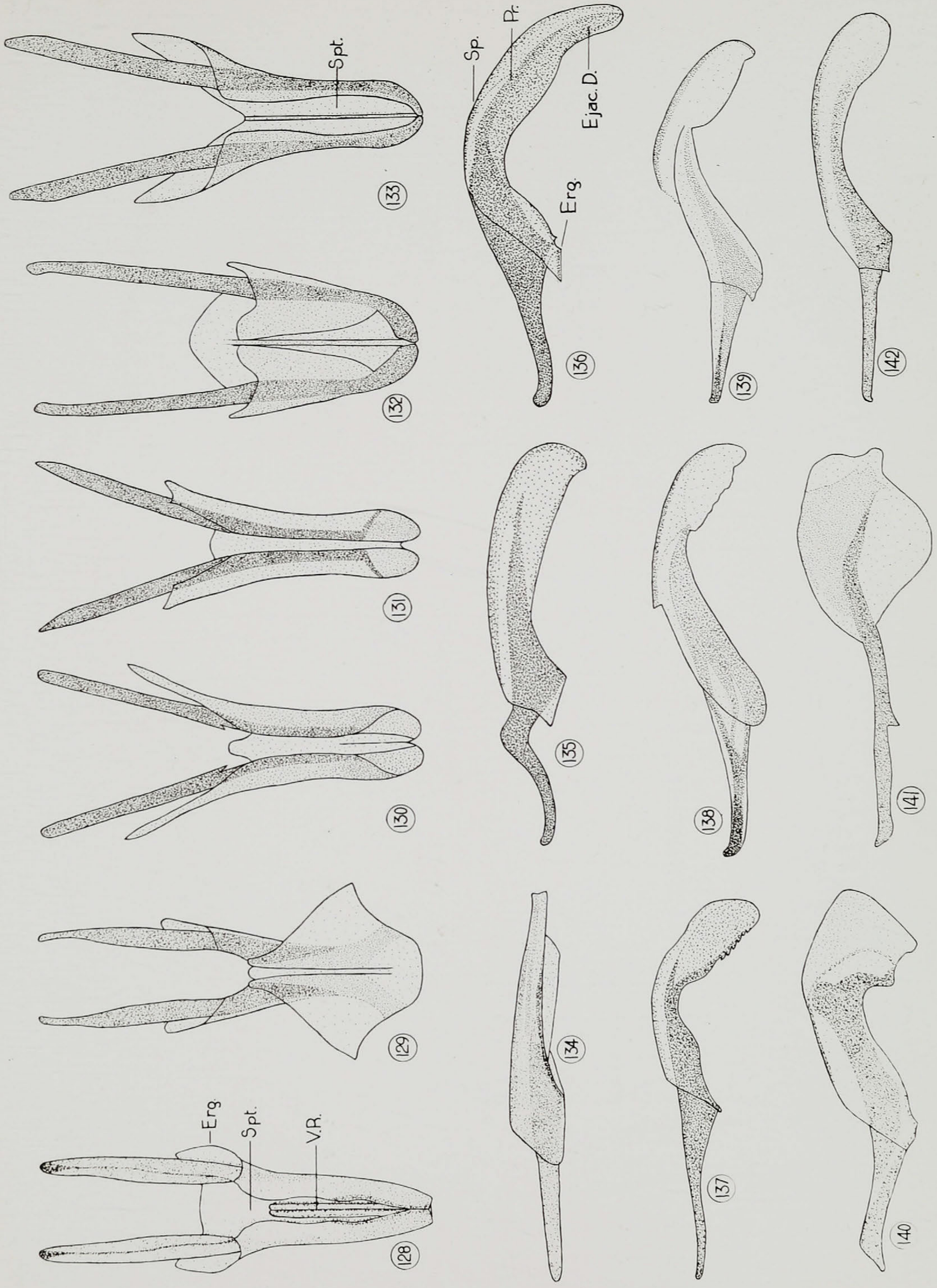


PLATE XVI

Plate XVII

The Aedeagus

Fig. 128. *Megarhyssa lunator*. Ventral View
Fig. 129. *Agrypon flaveolatum*. As above
Fig. 130. *Glypta fumiferanae*. As above
Fig. 131. *Glypta rufiscutellaris*. As above
Fig. 132. *Theronia fulvescens*. As above
Fig. 133. *Theronia melanocephala*. As above
Fig. 134. *Megarhyssa lunator*. Lateral View
Fig. 135. *Ichneumon perscrutator*. As above
Fig. 136. *Ichneumon grotei*. As above
Fig. 137. *Ichneumon variegatus*. As above
Fig. 138. *Phaeogenes gaspesensis*. As above
Fig. 139. *Phaeogenes hariolus*. As above
Fig. 140. *Exochilum circumflexum*. As above
Fig. 141. *Agrypon flaveolatum*. As above
Fig. 142. *Glypta fumiferanae*. As above



128
Erg.
Spt.
V.R.
129
130
131
132
133
Spt.
134
135
136
Sp.
Pr.
Ejac. D.
Erg.
137
138
139
140
141
142

PLATE XVII

Plate XVIII

Ventral View of the Aedeagus

Fig. 143. *Glypta rufiscutellaris*
Fig. 144. *Theronia fulvescens*
Fig. 145. *Theronia melanocephala*
Fig. 146. *Ephialtes grapholithae*
Fig. 147. *Ephialtes tuberculatus*
Fig. 148. *Pimpla brevicornis*
Fig. 149. *Pimpla coelebs*
Fig. 150. *Pimpla detrita*
Fig. 151. *Pimpla instigator*
Fig. 152. *Itoplectis conquisitor*
Fig. 153. *Itoplectis obesus*
Fig. 154. *Itoplectis pedalis*
Fig. 155. *Exenterus canadensis*
Fig. 156. *Exenterus claripennis*
Fig. 157. *Exenterus lepidus*
Fig. 158. *Exenterus marginatorius*

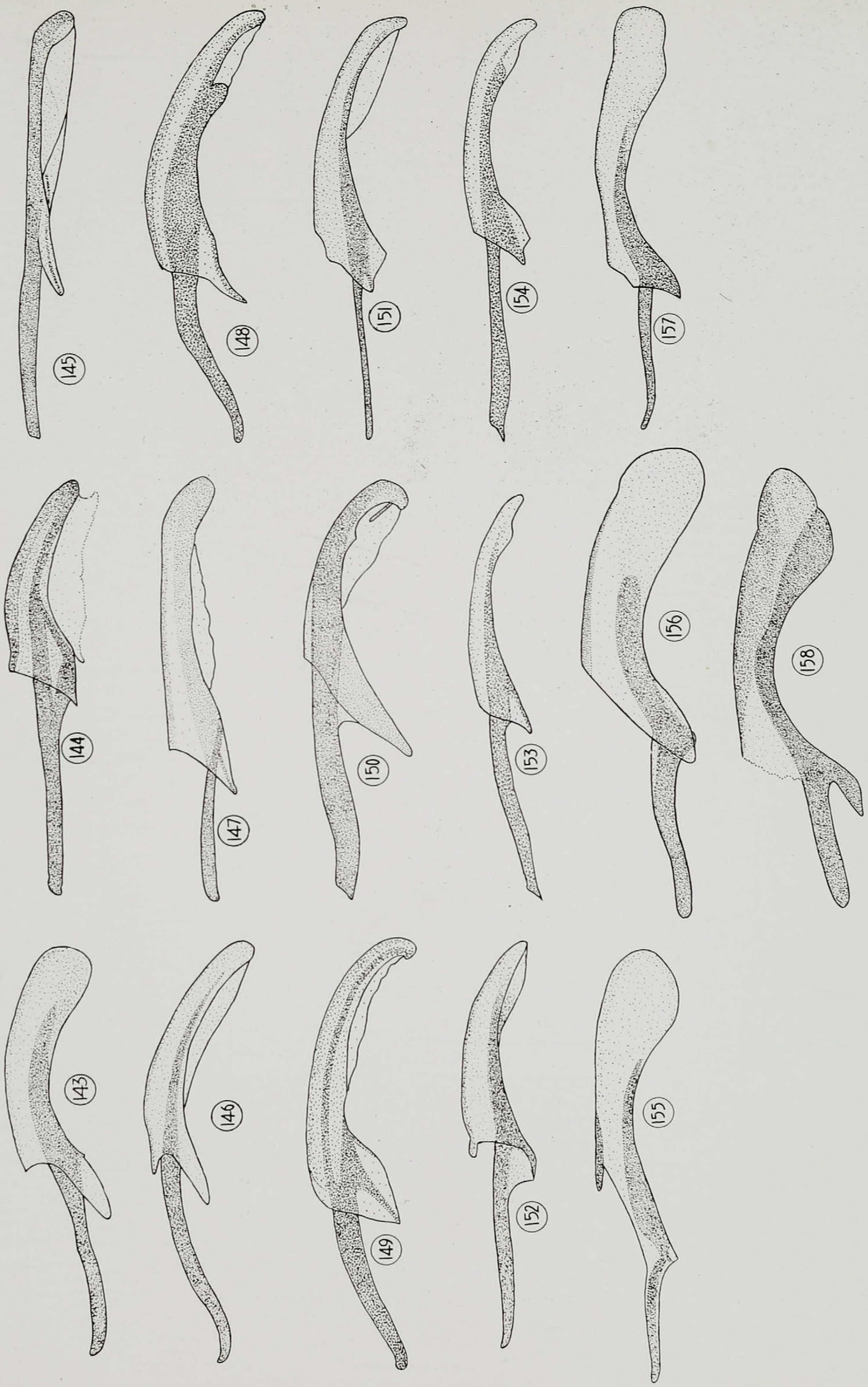


PLATE XVIII