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THE TERMINAL STRUCTURES OF ORTHOPTEROID INSECTS: A PHYLOGENETIC STUDY

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PART II.

THE TERMINAL ABDOMINAL STRUCTURES OF THE MALE.

The external genitalia of male insects are so variable in structure even within the limits of a single family, that it is a very difficult matter to trace the homologies of their component parts; and much detailed study of many types from all orders must be done before the subject can be placed upon a satisfactory foundation. The difficulties experienced in the present work in comparing the various types of Orthoptera alone have been such that it was found desirable to give a relatively large amount of time and space to this order, and as a result the other orders have necessarily been somewhat sacrificed. Some of them, such as the Plecoptera and Dermaptera, have been but superficially treated, owing to lack of material. It is hoped that these neglected groups will receive their due share of attention at another time.

In addition to the gentlemen to whom acknowledgments were made in the Introduction to this paper, I have to thank Mr. Morgan Hebard and Dr. R. J. Tillyard for the loan or gift of specimens, and Prof. C. R. Crosby for the loan of books from the Library of Cornell University.

My chief regret in connection with the present investigation is that much of the literature on the subject has been inaccessible to me or was received too late to be of use in the preparation of Part I.*

Since this part was published I received copies of two short papers by L. Chopard, entitled "Notes préliminaires sur la conformation de l'extremité abdominale des Orthoptères" and "Note préliminaire sur la conformation de l'organe copulateur des Orthoptères," published in 1917 and 1918, respectively. Still later, when the present work was nearly finished, I received a copy of the same author's fuller treatise entitled "Recherches sur la conformation et le développement des derniers segments abdominaux chez les Orthoptères," published in 1920. In this extensive and valuable work a very large number of forms are discussed and much of my own work has been anticipated. The general conclusions as to the typical structure of the terminal segments in Orthopteroid insects and the male homologies of the parts of the ovipositor are quite in accord with my own, but naturally there are some matters on which our views are not quite in agreement. Some reference has been made to these in the following pages, but unfortunately Mons. Chopard's work was received too late to give it the consideration that it deserves.

GENERAL MORPHOLOGY.

As in the female Pterygote insect, there is also in the male usually a single genital aperture, which, however, has a different position, namely in the membrane between the ninth and tenth abdominal sterna,† though sometimes apparently on the ninth sternum itself. This aperture is typically formed by an invagination of the body wall, into which open the two primitive ejaculatory ducts, the invagination forming a common terminal passage, which itself is usually termed the ejaculatory duct. In the Ephemerida and Dermaptera, however, this invagination does not take place, and although in the latter order the genital aperture is frequently single, it is due either to the abortion of one of the openings or to the fusion of the terminal parts of the two ducts. The aperture is usually borne upon an outgrowth, the penis or aedeagus, whose walls may be more or less

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* Ann. Ent. Soc. Amer., XII, No. 4, Dec., 1919, pp. 267-316. with Pls. XX-XXVIII.

† I. e., the sterna of the 9th and 10th abdominal segments, whether the sternum of segment 1 is present or not.

chitinized or wholly membranous. Where two apertures are present there are likewise two penes (Ephemerida) or a more or less deeply bipartite penis (Dermaptera), but it is probable that in these orders the penis or penes are not strictly homologous with those of other orders; in fact it appears as though the penis may have developed independently in several orders. A slightly bipartite penis has been described as occurring also in certain Plecoptera (Crampton, '18). The bifid termination of the penis in some Acrididæ simulates this condition slightly, but is in no way comparable to it. Among the Apterygota we find double penes in Eosentomon of the Protura (Prell, '13) and a slightly bifid penis in certain genera of Lepismoidea, such as Niçoletia (Escherich, '04), but the former is perhaps not strictly homologous with the other case cited, as it is found upon the eleventh instead of the ninth segment. The occurrence of double penes is probably a very primitive condition, as paired genital apertures are frequent in the more primitive Arthropods, such as the Crustacea and Diplopoda.

The penis is frequently eversible and in the everted condition the chitinized terminal part of the ejaculatory duct may project in the form of a spine, the *virga*. This structure is most typically seen in the Dermaptera, and in such forms as have a bifid penis the virga is likewise duplicated. It also occurs in certain Blattids, and according to Crampton, in some Plecoptera. The membranous eversible wall of the penis is the *glans* or *praeputial sac*.

There is also, primitively, a pair of chitinous processes, the parameres, arising near the base of the penis or from its walls, and having typically a lateral or dorsolateral position. They are well illustrated by the Dermaptera and certain Ephemerida, and it is probable that the titillators of most Orthoptera (although not all the structures so-called) are their homologues. It is uncertain, though in the writer's opinion probable, that the parameres of the Thysanura are morphologically identical with those of the pterygote insects. Crampton ('20) has apparently confused the penes of the Ephemerida with the parameres of other insects under the term "penis valves." Chopard ('18) expresses the view that in the Orthoptera (including the Blattoidea, Mantoidea and Phasmoidea) there are two pairs of processes, which he terms the "valves dorsales" and the "valves ventrales," between which the genital aperture opens, the latter being sometimes borne upon a penis, sometimes not. The structure which he thus designates as dorsal and ventral valves are not always, in my opinion, homologous in these various groups, nor even, in many cases, within the Orthoptera, s. s. The basis for this opinion will be evident after the discussion of the various orders.

The parameres are frequently sunk into invaginations of the body wall, or a common invagination (most Orthoptera), from which they can usually be protruded. The infoldings thus formed may be considerably prolonged into the haemocoele as chitinized apophyses for the insertion of muscles, and sometimes only the invaginations and apophyses are present, the freely projecting part of the parameres having disappeared, or secondary processes may develop from the walls of the invagination. In the Blattoidea, Mantoidea, Grylloblattoidea and Phasmoidea the genital aperture, which may or may not be borne upon a penis, lies between two asymmetrical lateral lobes, which apparently represent the parameres, and I have therefore termed them ***paramere lobes***. They usually bear at least one chitinous process, and where several occur, one appears to be the main process, the others accessory parts. I have, as a general rule, considered the main process to represent the terminal part of the true parameres, but this is to be regarded as merely a tentative hypothesis. Possibly a comparative study of the musculature will throw some light on the homologies of these puzzling structures. In the Blattids there is often but one well-developed process on each side, one of these, right or left, being modified into a strong copulatory hook, which can be completely retracted into a membranous sheath.

Between the base of the penis and the paraprocts (laminæ subanales) there is present in some groups (many Phasmoidea and Orthoptera, some Ephemerida) another sclerite, having the form of a more or less projecting plate. It is by no means evident, however, that the plates situated here in these different groups are homologous structures, and it therefore seems hardly justifiable to designate them by a common term. In the Phasmoidea we have the "vomer sous-anal" of Pantel, which this author regarded as belonging to the 10th sternum, but which, in my opinion, probably arises from the membrane between the ninth and tenth sterna. It projects caudad and appears to form a fourth anal valve. In *Callibaetis ferrugineus* of the Ephemerida there is a somewhat similar plate, but it appears to be exceptional in this order; while in the Orthoptera a somewhat analogous structure, clearly belonging to the same intersternal membrane, is found in a majority of the species. It functions, however, not as an anal valve, but as a part of the genitalia. This is the part I have called the *pseudosternite.* It has been confused by various writers with the "epiphallus" or "titillators" (parameres). Crampton ('18), e. g., identifies this structure in the Acrididæ and Gryllidæ with the "epiphallus" or parameres of the Tettigoniidæ, and Chopard ('18) makes the same error with regard to the Acrididæ, but in the Gryllidæ he considers it a distinct structure, which he terms the "pseudépiphalle." In the latter family it has also been termed the "anchre" by de Saussure and Zehntner ('94) in the genus Gryllotalpa, on account of its anchor-like form in that genus.

Various other structures concerned in copulation are frequently present. Claspers may be developed from the cerci (Dermaptera, Odonata, many Orthoptera); the coxites, or coxites and styli (Grylloblattoidea, Ephemerida); the paraprocts (Odonata Zygoptera, some Orthoptera of the family Tridactylidæ); titillators, copulatory hooks and similar appendages appear upon a great variety of structures, e. g., the 9th sternum (Embiidina, some Blattoidea); the 10th tergum (Embiidina, Grylloblattoidea, some Plecoptera); the supra-anal plate (some Plecoptera); the paraprocts (some Plecoptera and Blattoidea, a few Orthoptera of the family Tridactylidæ); the left cercal basipodite (some Embiidina); and finally from the vicinity of the genital aperture, including the pseudosternite, the parameres and the penis itself (Dermaptera, Ephemerida, Blattoidea, Mantoidea, Orthoptera, etc.)

Other chitinous structures are present in particular groups, the most noteworthy of these being connected with the development of the spermatophore sac in the Orthoptera. These will be considered in the account of this order.

The terga and sterna of the terminal abdominal segments in Orthopteroid insects are also subject to considerable variation apart from that of the more essential genitalic structures, some of these modifications being similar to those found in the females of the same species. Thus we find that in the Orthoptera the supra-anal plate is nearly always well developed in both sexes, while in the Blattoidea, Mantoidea and Isoptera it is vestigial or absent and its place is taken by the 10th tergum. The cerci, when not modified as claspers in the male, are usually similar in the two sexes.

The 8th sternum* is unmodified in the male, as it does not underlie the genital aperture, but the 9th sternum is generally much enlarged and is usually termed the subgenital plate, as it occupies a position in relation to the genitalia analogous to that of the 8th sternum in the female. As this implies a homology that does not exist, the term "hypandrium"† has been recently proposed by Crampton for the male subgenital plate. He does not, however, use it in a strictly morphological sense, but to designate the terminal ventral sclerite, whether this represents the entire sternum or only a part. When the 9th sternum, e. g., is transversely divided, as in the Ephemerida and the Acrididæ, it is the distal part only that is called the hypandrium, but when it is undivided, as in most Orthoptera, Blattoidea, Mantoidea, etc., the entire sternum becomes the hypandrium. As thus used the term is therefore open to objection, as it tends to obscure the homologies of the parts concerned, although it is a convenient one to retain for descriptive purposes.

The 9th sternum is primitively divided into three plates, a basal *sternite* and two disto-lateral *coxites*, each of the latter bearing a terminal stylus. This primitive condition is well exemplified by *Grylloblatta*, especially in the immature stages (Pl. VII, Fig. 66) and certain Ephemerida, such as *Blasturus nebulosus* (Pl. I, Fig. 2), although in the latter the styli (or coxites?) are secondarily segmented. In most Ephemerida, however, the coxites are fused but remain separate from the sternite, so that the former have the appearance of another sternum (*coxale*) and have, in fact, been mistaken for the 10th sternum (Eaton, '88; Morgan, '13). A similar structure is met with in the Phasmoidea and Acridoidea, except that in these groups the styli are wanting. In most groups, however, the sternum is a single large plate, with or without styli, which when present are borne at the distal margin of the plate. Such a sternum thus consists of the united coxites and sternite and has therefore

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* I. e., the sternum of the 8th abdominal segment; in reality it is generally the 7th actual abdominal sternum.

† Incorrectly described as the "ventral portion of the tenth abdominal segment." (Crampton, '18, p. 50).

been termed a *coxosternum* (Verhoeff, '03). Coxosterna bearing styli occur in the Blattoidea, Mantoidea, Isoptera and the Orthopterous family Tettigoniidæ, while coxosterna without styli are present in the Dermaptera, Plecoptera, Embiidina and many other Orthoptera, besides various orders not considered here.

The 10th sternum is generally indistinguishable in the adult state, but in many Plecoptera, Phasmoidea and Odonata it is chitinized, though often not distinctly marked off from the tergum, so that the segment is ring-like. In some cases at least (Phasmoidea, Odonata) this appears to be a secondary chitinization, correlated with the secondary elongation of the segment. Chopard ('17) maintains that the inferior or infero-external surfaces of the paraprocts also belong to the 10th sternum, while the superior or supero-external surfaces represent the 11th sternum, this view being based (1) upon the fact that the tergum of seg. 10 articulates with the lateral margins of the paraprocts, and (2) that these two surfaces of the paraprocts are often separated from one another by a distinct angle and may differ in coloration or degree of chitinisation. It is true that the 10th sternum becomes "absorbed" in the ventral faces of the paraprocts, as has been determined in various species of Orthoptera by one of my students, Miss Norma Ford, who is engaged in a study of the abdominal musculature of Orthopteroid insects, but the 10th sternum does not form the entire ventral surface of the paraprocts and sometimes only a very small part of it.

Chopard ('17) first regarded the supra-anal plate as the tergum of seg. 11, but in his later and more extensive work ('20) he accepts Heymons' view that an eleventh segment is present in the embryo, between the 10th and the supra-anal plate. But, whereas Heymons believes that no part of the 11th segment persists after embryonic life, except the cerci, Chopard considers the sternum of that segment to be represented in the paraprocts, as described above, and considers the supra-anal plate to be a telson, without a sternal counterpart. As my own investigations have been confined to the study of the postembryonic stages I have nothing of value to contribute towards the solution of this problem. I may point out, however, that the paraprocts do not represent the sternum of Heymons' 11th segment, and if this segment is recognized at all it should be recognized in its entirety, including both tergal and sternal regions.

HOMOLOGIES OF THE MALE AND FEMALE ORGANS.

As already pointed out in Part I, the lateral gonapophyses or dorsal valvulæ of the female are prolongations of the coxites of the 9th segment, the styli when present being borne upon their apices; but, except in the Thysanura and many Odonata, sooner or later becoming lost or absorbed during development. The anterior and posterior gonapophyses are homoplastic outgrowths, belonging to the 8th and 9th segments respectively, and, as found in their most primitive condition, in the Thysanura, they are borne upon, or near, the inner margins of the corresponding coxites, close to the bases of the latter.

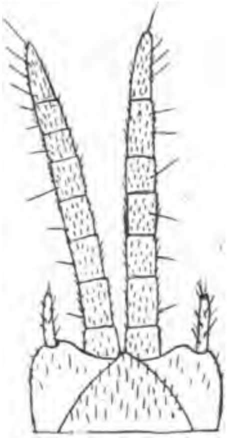

FIG. 1

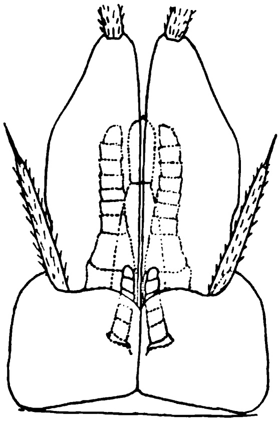

FIG. 2

Fig. 1. *Nicoletia* (*Anelpistina*) *meinerti* Silv., 8th sternum of female. (From Berlese, after Silvestri).

Fig. 2. *Machilis polypoda*, 8th and 9th sterna of male. (From Berlese, after Silvestri).

In the Machiloidea and Lepismoidea the coxites of segment 9 are similar in the two sexes and the sternite has practically disappeared, except in a few Lepismids, such as *Nicoletia*, in which there is a well developed sternite in the female only (Escherich, '05), (Text fig. 1). The posterior gonapophyses are represented by the parameres, which are best developed in the Machiloidea and such Lepismoidea as *Nicoletia* and *Atelura* (Escherich, l. c.) As a rule no structures corresponding to the anterior gonapophyses are present in the male, but Silvestri (nec Berlese, '06) shows clearly in a figure of the male of *Machilis* *polypoda* (Fig. 2), two pairs of parameres, of which the smaller anterior pair arises from the 8th segment in a position corresponding nearly with that of the anterior gonapophyses of the female. Verhoeff ('10) also refers to both pairs of parameres as the male homologues of the two pairs of female gonopods (anterior and posterior gonapophyses), having abandoned his earlier attempt ('03) to show that the anterior pair of parameres are fused in Machilis and Lepisma to form the penis.

Female Gonapophyses.	*Male Homologues.*
Ant. gonapophyses or ventral valves—	true or posterior parameres, or "telopodites" of seg. 9.
Post. gonapophyses or inner valves—	anterior parameres or "telopodites" of seg. 8. (Present only in certain Machiloidea).
Lat. gonapophyses or dorsal valves—	coxites of seg. 9 (gonocoxites), (with styli), or equivalent parts of the 9th coxosternum.

Male gonapophyses are not always of similar origin in the various orders. In the Odonata the two plates covering the genital aperture are homologues of the lateral gonapophyses of the female, as shown by their development (Van der Weele, '06) and are therefore vestigial coxites.

The question as to whether the parameres of the Thysanura and those of Orthopteroid insects* are homologous or not is more difficult to decide. The former are primarily attached to the 9th coxites, having a more or less posterior position, close to the intersegmental membrane. They are thus ventral to the penis. Those of Pterygote insects, in what appears to be their most primitive form, arise from the walls of the penis (Dermaptera), or from the same situation together with parts of the intersegmental membrane (some Ephemerida), having generally a lateral or dorso-lateral position, but sometimes a ventral one. This difference of position throws some doubt on the homologies of these structures with those of the Thysanura, but such a shifting of position is by no means unusual, and as

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* These have been also termed "penis-valves," (Crampton, '20d).

they seem to be characteristic of a very primitive type of genitalia, they are probably structures of ancient origin, whose representatives we should expect to find in the Thysanura. It seems best, therefore, not to distinguish these structures by different terms until further light is thrown upon their origin.

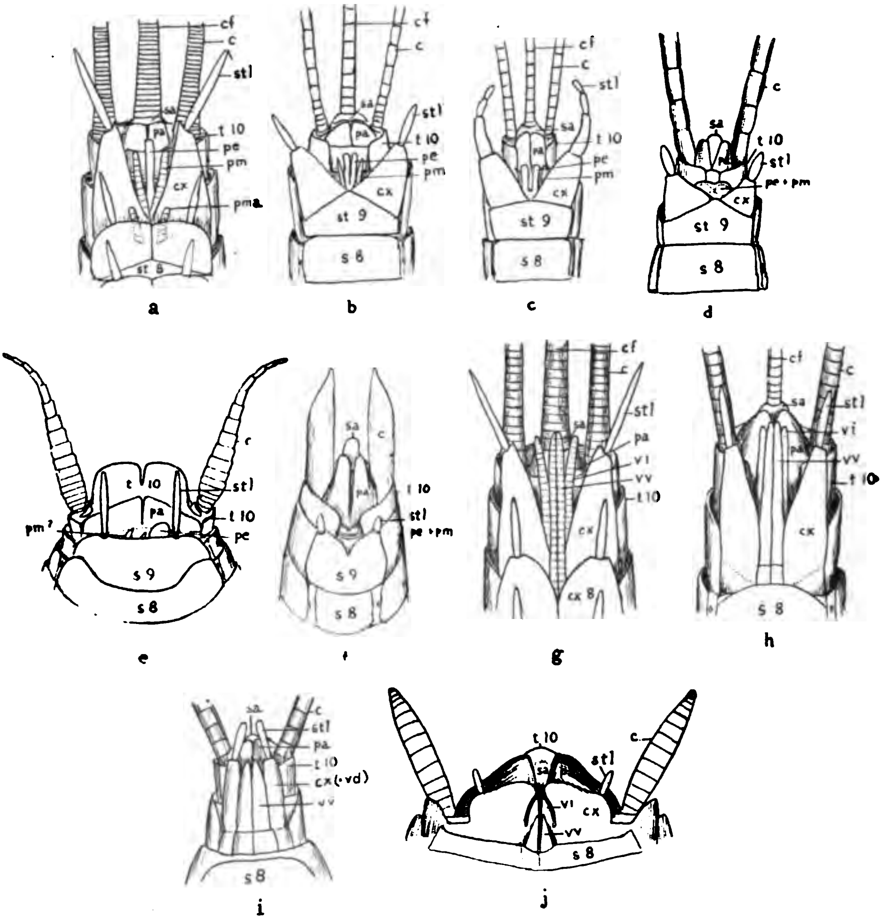

FIG. 3

Fig. 3. Ventral views of terminal abdominal segments, illustrating homologies of male and female structures (semi-diagrammatic). a, *Machilis*, male; b, hypothetical Pterygote type male; c, Ephemerid male; d, *Grylloblatta*, immature male; e, Blattid, male, based on *Periplaneta;* f, Tettigoniid immature male of *Neoconocephalus;* g, *Machilis*, female; h, hypothetical Pterygote type, female; i, *Grylloblatta*, immature female; j, Blattid, immature female of *Parcoblatta*; vd, dorsal valvulæ; vi, inner valvulæ; vv, ventral valvulæ. For other lettering, see page 71.

SPECIAL MORPHOLOGY.

In describing the male genitalia and associated parts in the various orders it will be convenient to take them in a different sequence from that followed in the discussion of the female organs.

Ephemerida.

This group is remarkable for several reasons. The prolongation of the supra-anal plate into a jointed caudal filament or cerciform appendage ("telofilum," Crampton), similar to that of certain Thysanura has been already referred to in Part I. The cerci are longer than in the females, but are otherwise similar. The paraprocts are unchitinized and are covered by the 10th tergum, there being no distinct 10th sternum.

The 9th sternum is very large and is usually divided transversely into two separate plates, of which the distal one is prolonged into a pair of processes, divided into several segments and serving as claspers. These processes are generally considered to be jointed styli, but it is possible that the terminal segments alone represent the styli, the remaining segments belonging to the coxites, which are also represented by the distal of the two sternal plates (the *coxale*), the proximal one being the sternite. The fact that these structures serve as claspers in copulation and that in Grylloblatta the coxites are apparently claspers lends some support to this view. Moreover they contain muscles, which in the Thysanura and Orthopteroid insects only reach the bases of the styli. In some cases the coxites are completely separate, as in *Blasturus nebulosus* Walk. (Pl. I, Fig. 2) or *Callibaetis ferrugineus* Walsh. (Pl. I, Fig. 4), i. e., the distal plate is divided by a median suture. In others (*Heptagenia* spp.) a tripartite division is slightly indicated, the two stylus-bearing parts being indistinctly separated by a median area.

There are two penes, whose walls may be wholly membranous or accompanied by parameres. In *Callibaetis ferrugineus*, e. g., (Pl. I, Fig. 4) these take the form of slender chitinous bands, extending from the lateral margin of the 10th tergum obliquely mesad and cephalad to the bases of the penes, thence curving along the lateral margins of the penes to their apices. Retraction of the penes is accompanied by the distal part of the parameres.

In this species there is also a sclerite (vo) resembling the "subanal vomer" of the Phasmoidea, consisting of a transverse band of chitin immediately in front of the paraprocts, which is elevated in the middle into a rounded shelf-like projection. On each side the chitin is expanded into a thin plate, which extends to the basal portions of the parameres. In *Blasturus nebulosus* (Pl. I, Fig. 3) and *B. cupidus* each penis bears a single hook arising ventrally near the apex and curved proximad. These have been termed "subappendiculæ" by Crampton, but they appear to represent the distal parts of parameres. Parameres have also been described in *Heptagenia venosa* by Peytoureau ('95) who termed them "aiguillons." In other genera, such as Hexagenia, they are wholly absent.

Dermaptera.

In the Earwigs the large forcipate cerci are associated with modifications of the neighboring sclerites, although the penis retains an apparently primitive structure. The only exception is the aberrant parasitic form *Hemimerus talpoides* Walk., in which the cerci are simple and styliform. Segmented cerci occur in the immature stages of *Dyscritina* and *Diplatys*, (Burr, '11, Zacher, '11), a fact that indicates the more primitive nature of this type of structure.

Correlated with the unusual development of the cerci is the enlargement of the 10th tergum, but there is no marked abbreviation of two preceding terga, such as occurs in the females, and all the terga are free. The 9th sternum is well developed, undivided and without styli. The paraprocts and so-called "opisthomeres" or segments of the supra-anal plate are similar to those of the female. The latter may vary in number from two to four, and as the larger numbers occur only in primative genera, it would appear that they are part of the expression of this primitive condition. They cannot be considered as vestigial metameres, as there is no evidence for the existence of more than eleven true metameres in the abdomen of any insects, but they may possibly represent the vestige of a jointed, caudal filament, like that of the Ephemerida.

In the superfamilies Protodermaptera and Paradermaptera the penis is double or deeply bipartite, the two ejaculatory ducts opening separately, and being thus merely continuations of the vasa deferentia. In the Eudermaptera there is but one penis, apparently due to the complete suppression of the other. In *Forficula auricularia* L. the vasa deferentia unite at the base of the penis with a small sac, from which a single ejaculatory duct leads to the apex of the penis. There is, however, a vestigial second ejaculatory duct, which has no external opening, indicating an originally bipartite penis. In *Hemimerus talpoides* the sole representative of the aberrant suborder Hemimerina, there is a single penis, which when everted possesses two apertures. The vasa deferentia unite to form a single short ejaculatory duct, which near the termination of the penis divides again.

In all the Dermaptera there is a single pair of unsegmented, chitinized parameres, which generally arise from the dorsal and lateral surface of the penis or penes, proximad of the praeputial sacs, although sometimes their position is ventral, as in Hemimerus (Heymons, '12). The parameres exhibit great variation in length, form and details of structure. Apart from the parameres and virga, which is often present in the form of a very slender eversible spine, the penis may be entirely membranous or chitinized in part.

Plecoptera.

In the Stone-flies the general form of the terminal segments and cerci is similar in the two sexes. The ninth sternum of the male is more or less enlarged to form a hypandrium, but is undivided and devoid of styli. The tenth segment is frequently ring-like, owing apparently to the meeting and fusing of the tergal margins in the mid-ventral line rather than to the fusion of terga and sterna, since in some forms the tergal margins are but narrowly separated. The tenth tergum is sometimes produced caudally, or elevated, or mesially divided, in which case the two parts, or "hemitergites," may bear hooks, as in *Arcynopteryx americana* (Klapalek, '12, Fig. 18), or they may be prolonged cephalad over the preceding terga, which are grooved to receive them. I have not found a distinct tenth sternum in any of the forms examined.

The supra-anal plate may be insignificant or almost vestigial, or it may, on the other hand, exhibit remarkable modifications. In *Capnia vernalis* Newp. (Pl. II, Figs. 11–13) it is prolonged into a huge spout-like organ, which is bent upwards and forwards over the terga of the ninth and tenth segments. This structure (spc) consists of a tubular process with a spear-shaped extremity and rests in another more flattened trough-like piece. The two are received into a mid-dorsal groove on segments 9 and 10 and their free extremities are apparently received into a notch under cover of the elevated and slightly produced edge of the 8th tergum. If we examine the ventral surface of this peculiar structure, which is evidently a sperm-conveyor, we see that its base is marked off from the rest of the supra-anal plate by a transverse suture, under the edge of which is the proximal opening into the lumen of the sperm-conveyor. Leading from the opening of the ejaculatory duct is a groove with thickened sides, which passes between the flat paraprocts and along the ventral surface of the supra-anal plate, to the opening of the sperm-conveyor. This is evidently a seminal groove, along which the spermatic fluid is conducted from the ejaculatory duct into the sperm-conveyor through the proximal opening of the latter. There is no true penis in this species.

In the Pteronarcinæ and some, at least, of the Perlinæ (Perlodini) there is a somewhat similar modification of the supra-anal plate, differing from that of *Capnia*, however, in that the median part is deeply invaginated into a pocket, so that there is no prominent, projecting external structure. In some species of *Pteronarcys*, according to Smith ('17), this structure serves as a sperm-conveyor, while in others it is apparently modified for another function, that of a "probe-like organ in opening up the genital passages of the female." In the Perlodini its function is generally, if not always, more of the latter nature, serving apparently as a titillator or copulatory hook. In both groups the structure is similar enough to indicate a common origin.

In *Isogenus frontalis* Newm. (Pl. II, Figs. 14–17), which I have taken as an example of this type, there is a deep, narrow, median invagination of the tenth tergal region, as well as the supra-anal plate. The tenth tergum is thus divided into two "hemi-tergites," each of which is somewhat thickened at its mesocaudal angle, where it bears a few denticles. In other species of this group these angles may be raised into hook-like projections (e. g., *Arcynopteryx americana*, Klapálek, op. cit.) The invaginated part of the tenth tergum forms a large median apodeme (m ap). The supra-anal plate (Fig. 16) consists of a pocket, whose walls are partly membranous, partly differentiated into separate sclerites, which are moved by intrinsic muscles (vide Smith, op. cit.) On each side of the opening of the sac is a somewhat triangular plate, termed by Smith the *para-genital plates* (pg) which seem to be the homologues of the two dorsal basal parts of the supra-anal plate of *Capnia.* In the mouth of the sac can be seen a median chitinous hook (mst) and a pair of lateral rods or styles (lst). These are termed by Smith the median and lateral stylets. They are all connected at base with a strong bar, which bounds the sac in front and joins the base of the median apodeme of the tenth tergum. The copulatory hook, or median stylet, is the "titillator" of other species, of such genera as *Arcynopteryx* and *Skobeleva* (Klapálek, '12), in some members of which it has the form of a long slender spine.

The supra-anal plate is subject to still other modifications, such as, e. g., in *Acroneuria brevipennis* (Crampton, '18), in which it bears a pair of well-developed hooks, while in other forms, such as *Isoperla* sp. (Pl. II, Fig. 18) it is wholly without special modifications, and even imperfectly differentiated.

As it is evident that these modifications have developed within the order, no attempt need be made to homologise them with similar structures found in other orders. Crampton ('18) has compared the appendage of the supra-anal plate (sperm-conveyor) of *Capnia* to the slightly similar horn-like projection of the tenth tergum in certain Odonata (*Ischnura*) and remarks that although not strictly homologous "it is unnecessary to apply different names to the two structures, which are practically the same in their nature and position on the tergal region of the segment bearing them." So far from being "practically the same," they are not only borne by different segments, but are adapted to wholly different functions, that of Capnia being a sperm-conveyor, while that of Ischnura is a brace which fits upon the mesosternal lamina of the female in copulation. Crampton also labels the furcate appendage of the supra-anal plate of *Scudderia furcata* Brunn. with the same abbreviation as he uses for the structures just mentioned, though this is also quite different in nature from either of the others, being a development within the Tettigoniid subfamily Phaneropterinæ.

The paraprocts are generally well developed, chitinized and fused with the bases of the cerci, although in the nymphs of some forms and also the adults of others they may be more distinctly separated. Frequently they bear copulatory appendages in the form of hooks, as in *Isoperla* sp. (Pl. II, Fig. 18), or of long processes which fit together into a spout-like organ (*Dictyopterygella*, teste Klapálek, '12). Crampton's figure of *Acroneuria brevipennis* shows a pair of small hooks on the paraprocts in addition to the larger ones borne by the supra-anal plate.

Owing to lack of material I have been unable to study satisfactorily the penis of the Plecoptera. When present it is usually single, but according to Crampton, the bipartite form occurs in some forms, such as *Nemoura completa* Walk. (l. c., Pl. II, Fig. 16). In this figure processes resembling parameres are represented. In some cases it is membranous and eversible, in others it is partly chitinized, and it may be provided with a virga, as in *Perlesta flavida* (Crampton, l. c., Pl. II, Fig. 14). In *Perla tristis* Hag. it is a large, stout structure of simple rounded form, with a rather large terminal aperture, (Pl. II, Figs. 19, 20). The distal part of the ejaculatory duct has longitudinally folded walls and is darker than the rest of the organ. There are no parameres nor other chitinous parts.

Embiidina.

The only species, males of which I have studied, is the widely distributed *Oligotoma saundersii* Westw., but the numerous figures in Enderlein's monograph of the order (Enderlein, '12) afford a basis for a more general survey of the genitalia of this group.

The most primitive form is undoubtedly the large South American *Clothoda nobilis* Gerst., which is remarkable for the symmetry of the terminal abdominal structures, and for the lack of the various copulatory processes, so strikingly developed in all the other genera. In most of the Embiids there is a shortening of the ninth abdominal tergum and an enlargement of the tenth, somewhat suggestive of the Dermaptera. In *Clothoda* the tenth tergum is short, symmetrical and entire, while in all the other genera it is more or less enlarged and deeply divided into two asymmetrical parts (hemitergites), which are sometimes completely separated. In the great majority of forms each hermitergite bears a more or less hook-like copulatory appendage, but these may differ very greatly in form and position. In *Oligotoma saundersii*, e. g., the dextral hook is much longer and differently shaped from the sinistral one (Pl. I, Figs. 9 and 10).

The ninth sternum is entire and without styli, and, except in Clothoda, is asymmetrical, the apex being well to the left of the median line and bearing another copulatory process. The asymmetry also involves the cerci, which are two-segmented, without including the basipodites. These sclerites are generally inconspicuous, but in *Clothoda* they are well developed, extending mesad in the form of freely projecting plates, somewhat suggestive of the paraprocts of certain Plecoptera, such as *Perla*. One might, in fact, be tempted to interpret the latter as greatly enlarged cercal basipodites rather than as true paraprocts. In Oligotoma the left basipodite bears still another copulatory appendage on its inner side. These various copulatory appendages converge on the left side of the middle line, their position suggesting that in copulation the abdomen of the female is grasped by the male from the right side.

Of the supra-anal plate, paraprocts and penis I have been able to find nothing in *Oligotoma*. They must be extremely vestigial if present at all, although the paraprocts are quite distinct in the females of this order.

It is altogether probable that the special characteristics of the male Embiids, i. e., the asymmetry and the development of the various copulatory appendages, have been evolved within the history of the group itself, since its most primitive living member, *Clothoda*, is lacking in these very features. Accepting this view it is useless to attempt to homologise these processes with those of similar function occurring in other orders.

The male genitalia of the Embiidæ offer little or no evidence as to their relationships with other orders, but there is nothing in their structure to conflict with the view held by MacLachlan, Crampton and others that their nearest affinities are with the Plecoptera. In fact, in the development of copulatory appendages from a great variety of parts, they at least show similar tendencies to the Plecoptera, especially in the division of the tenth tergum into hermitergites, each bearing a hook, a feature which has already been noted in the case of the Plecopteran genus *Arcynopteryx*, and is by no means confined to that genus.

Orthoptera.

In the Orthoptera there is a tendency toward a shortening of the posterior terga, which is most marked in the Acridoidea, while the anal plates are usually well developed but very variable in form. The supra-anal plate is frequently fused with the tenth tergum, but not overlapped nor replaced by the latter as in the Blattoidea, Mantoidea and Isoptera, although in certain Tettigonoidea (Ceuthophilus) the ninth tergum (more rarely the 8th) projects over the tenth and supra-anal plate, thus having the appearance of being the last dorsal segment. The cerci are with rare exceptions unsegmented and short, being frequently modified as claspers. A small cercal basipodite is usually present. The ninth sternum is generally entire, forming a hypandrium, but in the Acridoidea it is divided by a transverse suture, as in the Phasmoidea, the distal plate probably representing the fused coxites. Secondary subdivisions may also occur in some Tettigonoidea. In this superfamily styli are generally present, but they are absent in all the other groups.

Owing to the peculiar and often extremely complex structure of the genitalia it will be convenient to deal with these separately after having discussed the other structures with which we are concerned.

The Terminal Segments, Cerci and Styli.

TETTIGONOIDEA. In most of the long-horned grasshoppers the abdominal segments are not greatly specialized, the terga and sterna being distinct and separate, the latter rather feebly chitinized, and the spiracles occupying the pleural membrane. There is usually relatively little shortening of the 9th and 10th, although sometimes, as in *Ceuthophilus*, the 10th is small, subvertical and concealed by the projecting 9th tergum, which is thus commonly but erroneously termed the supra-anal plate by systematists. The true supra-anal plate is of variable size, but generally inconspicuous, and frequently fused with the tenth tergum in the adult insect. It is not divided transversely, or otherwise, as in many Acrididæ. The paraprocts are commonly lobe-like and but little chitinized. The ninth sternum is typically undivided, though indications of the coxites are sometimes seen in the more or less bifid caudal margin of many forms, this feature being particularly noticeable in young nymphs and sometimes, as in species of *Ceuthophilus*, secondary subdivisions are present. Styli are present in the majority of genera, though frequently absent, as in many of the Rhaphidophorinæ, which in this respect, and also in the more convex and upturned ninth sternum, the unmodified cerci and the structure of the genitalia, approach the Grylloidea. The cerci are generally short, unsegmented and modified to serve as claspers in copulation, but in the Rhaphidophorinæ, with few exceptions, they do not function as such, being like those of the female, comparatively long, flexible and tapering, and covered with sensory hairs. In some species of this family, such as *Pristoceuthophilus cercalis* Caud., the cerci have a few small terminal segments, but this character, though an interesting exception to the general rule in the Orthoptera, is probably an atavistic one. A small cercal basipodite is sometimes, but not always, present. In the large membranous area between the paraprocts and the ninth sternum is the penis, which is described below.

In *Cyphoderris monstrosa* Uhl., (Pl. IV, Figs. 35, 36) an aberrant species, usually placed in the Stenopelmatinæ, a most remarkable modification of the genital structures is present. The ninth sternum is bent vertically upwards and closely applied to the end of the abdomen, which it covers below the paraprocts. Into the narrow pocket thus formed opens the genital passage, whose folded, membranous lips are the only representative of the penis, there being no chitinized parts. There is, however, in place of the titillators or parameres, a large process arising from the 9th sternum. It projects somewhat backward and is then sharply bent downward, terminating below in a pair of divergent spines. The dorsal surface also bears minute spinules. In a nearly full-grown male nymph of this species there is no indication of this structure, and the sternum, though bent up, is less closely applied to the body. In both adult and nymph there is a pair of stout, flattened styli, which, from their position, are at first sight, somewhat suggestive of titillators.

GRYLLOIDEA. In the crickets the abdominal segments are similar to those of the Tettigonoidea, except that the ninth sternum is smaller, more narrowed caudally, and envelopes the genitalia more closely, there being a smaller outlet for the genital cavity; and there is no trace of styli. The inner surface of the sternum is covered by a much folded glandular epithelium. The cerci are not modified as claspers, and are longer, flexible, with long hairs and sensillæ, although unsegmented. There is a small external cercal basipodite. In all these respects they are approached by the Tettigoniid subfamily Rhaphidophorinæ. The anal plates are generally more prominent and heavily chitinized than in the Tettigonoidea. The supra-anal plate is undivided and is sometimes, as in *Gryllus* and *Nemobius*, indistinctly separated from the tenth tergum.

More important characters are found in the genitalia (q. v.)

TRIDACTYLOIDEA. The outstanding characteristics of the males of this group, apart from the penis, are the weakening and infolding of the posterior abdominal terga, particularly those of segments 8, 9 and 10, which are more or less concealed by the overlapping 7th tergum, the dorsal lengths of segments 8 and 9 being greatly reduced by the obliquity of their hind margins; the styliform and sometimes two-jointed cerci, the long moveable processes of the paraprocts and the absence of true styli.*

In *Tridactylus apicalis* Say the terga are mesially grooved with steeply sloping sides, and the 9th is divided and concealed by the 8th, except towards the lateral margins. The 10th is much larger but is likewise divided by the median groove, and the supra-anal plate is also sulcate with only the lateral margins strongly chitinized. The paraprocts are chitinized and bear a pair of slender, styliform processes, like those of the female. The sterna are wider than the terga, the 9th forming a flattened and undivided hypandrium.

In *Ripipteryx* the general characteristics of the terga are similar but with marked variations according to the species.

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* Crampton ('20d) considers these styliform appendages as probably true styli, belonging to seg. 11, the paraprocts representing the coxites of that segment. If these processes were true styli we should expect to find them in some other groups of Orthopteroid insects besides the Tridactylidæ, as well as in the Thysanura, in which styli sometimes occur on nearly all of the abdominal segments. It is noteworthy, however, that even in such Thysanura as *Machilis*, in which the styli are seen in their most primitive and best developed condition. they are absent from the 10th segment and paraprocts. The development of styliform processes in connection with the genitalia is very common in insects and the presence of these processes in this single small group of Orthoptera is an insufficient basis for speculation as to their origin.

In *R. carbonaria* Sauss., the only species I have examined, the 9th tergum, is the only one that is divided. The 10th and supra-anal plate are both of large size, though somewhat sulcate and weakened mesially. The 9th sternum forms a large, somewhat convex hypandrium, and is almost completely fused with the tergum. The cerci are simple and styliform with a distinct basipodite. Just beneath each is a chitinous hook, which apparently belongs to the paraprocts, but is perhaps developed from the cercal basipodite. It is also shown in de Saussure and Zehntner's figure of *R. cyanipennis* (op. cit., Pl. XVII, Fig. 34). The long processes of the paraprocts in *R. carbonaria* Sauss. and *R. forceps* Sauss., are remarkable for their modification as copulatory forceps. They are long and stout, with thickened apices, abruptly bent inwards.

In *R. mexicanus* Sauss., according to the figure of de Saussure and Zehntner (l. c., Pl. XVII, Fig. 30), the cerci are indistinctly divided into nine segments, but it seems probable, on comparison with other species, that this segmentation is not a primitive condition. In this species and others, such as *R. cyanipennis* Sauss., the processes of the paraprocts are not modified to serve as claspers.

ACRIDOIDEA. In the locusts the hind margins of the last two or three abdominal terga are increasingly oblique caudad, this obliquity being associated with a marked shortening of their mid-dorsal lengths, as compared with their lateral margins. These features, together with the large, more or less upcurved ninth sternum, result in a general upturning of the end of the abdomen, the opening of the genital cavity facing dorsad instead of caudad. In respect of the shortening and obliquity of the terga, the group may be compared with the Tridactyloidea, the resemblance to which is greatest in the Acrydiidæ (Tettigidæ), but is even here not very marked.

The segments are all separate in the Acrydiidæ, but in the Acrididæ the 9th and 10th terga are laterally fused, as in the females. A median furcate appendage, the *furcula*, is sometimes borne by the latter, as in *Melanoplus*. The large, usually triangular supra-anal plate is primarily divided by a transverse suture, as in the female (see Part I), but in the adults this division is frequently lost.* The peculiar subdivision of

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* Chopard ('20) has given good reasons for considering this transverse suture to be the true boundary between the 9th and 10th terga, the apparent boundary being a secondary ridge.

this plate in the Acrydiidæ, described in the account of the females, is present also in the males; and the cerci in this family are also similar in the two sexes. In the Acrididæ they are usually larger in the male, serving as claspers in copulation, although often but little modified. In the Acridinæ and Oedipodinæ, e. g., they are small, simple and styliform, while in the Locustinæ they assume a considerable variety of forms, sometimes being forcipate, as in the Old World genus *Calliptamus*, but never, so far as I am aware, armed with teeth or spines, as in the Tettigonoidea. There is a distinct cercal basipodite in all of the forms examined. The paraprocts are broad and flat as in the females.

The structure of the ninth sternum is very peculiar. It is very large, externally convex and upturned, and divided transversely as in the Phasmoidea, the distal plate, commonly known as the subgenital plate, possibly representing the fused coxites. This plate has sometimes been mistermed the tenth sternite. Its margin forms the rim of a deep genital cavity, roofed over by a fold of integument, the *pallium*, which is continuous with the sternal margins, and together with the paraprocts, usually completely conceals the genitalia, although in some species in which the penis is very long the pallium is pushed up into a conical form, the tip of the penis being exposed. In the Acrydiidæ the pallium is more firmly chitinized than in the Acrididæ, its dorsal surface being covered with a pair of plates separated by a median groove. In *Acrydium* (*Tettix*) and *Paratettix* there lie in this groove two slender rods, which terminate near the front margin in a pair of small hooks, resembling titillators and probably serving a similar purpose, the usual titillators (parameres) being absent in this family (Pl. VI, Fig. 60). In *Tettigidea* (*T. lateralis parvipennis* Harr., Pl. VI, Figs. 58, 59) these hooks are absent, but the pallium is still more heavily chitinized than in *Acrydium*, being a decidedly plate-like structure, divided into right and left parts by a median suture. Morphologically the pallium is part of the primitive floor of the genital cavity. Styli are absent in the Acridoidea, although there are some forms, like *Acrydium*, in which two small tubercles on the caudal margin of the ninth sternum are somewhat suggestive of vestigial styli.

The Genitalia.

The male genitalia of the Orthoptera exhibit an even wider range of variation than do those of the females, but, as in the latter, a fundamentally similar plan of structure can be traced in these organs throughout the order, except in a few cases in which they are very degenerate. This plan of structure is characteristic of the Orthoptera *sens. str.*, and is widely different from other orthopteroid groups. Its most distinctive feature is the presence of a pouch or sac into which the ejaculatory duct opens and from the roof or walls of which the parameres arise. The sac has the function in very many forms of a spermatophore sac, and this is probably its primitive purpose.

The penis is commonly large and prominent and its orifice is generally wide with folded walls, there being usually a pair of ventral lobes, or sometimes a single one. The titillators, or parameres, as I believe them to be, are primitively dorso-terminal in position, but their bases are usually more or less retracted, so that they may appear to have no relation to the dorsal surface, being in some cases almost completely concealed from view.

Owing to the shifting of the genital area from a ventral to a posterior position by the elongation of the ninth sternum the penis comes to lie under the paraprocts, and is also typically under cover of a projecting plate, the *pseudosternite*, which forms an arch over its base and serves for the origin of muscles concerned in its movements. This arch is often prolonged on each side into a pair of arms, the *rami*, partly encircling the penis at its base, and more or less produced inwardly into processes, which may be termed *endapophyses*, for the attachment of muscles concerned in the movements of the penis. Sometimes the endapophyses may be separated from the pseudosternite and are present in many forms (Tettigoniidæ), in which the latter has disappeared. In the Acridoidea these structures are further complicated, but their peculiarities need not be considered here.

In addition to the structures just described there may be mentioned also a pair of glandular pouches, lined with chitin, which open separately or by a common duct into the ejaculatory duct, close to its termination in the spermatophore sac. It is sometimes represented by a single sac and is probably connected with the formation of the spermatophore, as it is absent in the Acrididæ and Tridactylidæ, in which apparently no spermatophores are formed.

TETTIGONOIDEA. With the exception of the aberrant Stenopelmatine *Cyphoderris monstrosa* Uhl., and probably other Stenopelmatinæ, in which the penis is degenerate, the male genitalia of the Tettigonoidea, as represented by the forms studied, may be divided into two types, the one represented by the Rhaphidophorinæ, the other by the Decticinæ, Conocephalinæ, Copiphorinæ, Phaneropterinæ, Tettigoniinæ, Meconeminæ and probably by most of the other subfamilies.

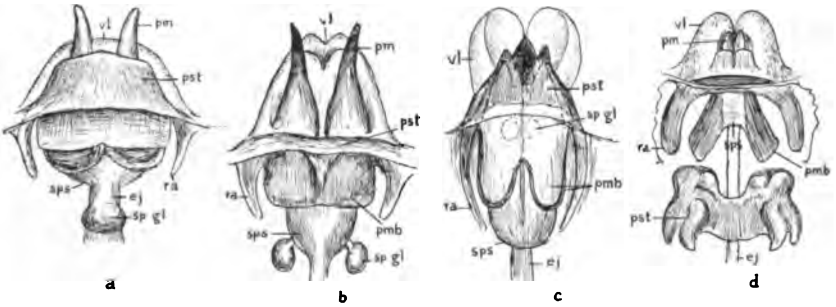

FIG. 4.

Fig. 4. Genitalia of male Orthoptera, dorsal views (diagrammatic); a, Tettigoniid, based on *Ceuthophilus* (parameres partly everted); b, Tettigoniid, based on *Neduba;* c, Gryllid, based on *Gryllus;* d, Acridid, based on *Dissosteira.* For lettering, see page 71.

The first type is the more primitive and may be illustrated by the genus *Ceuthophilus.* Figs. 22–25 show various views of the penis of *C. lapidicola* Burm. In this type the penis is almost entirely membranous, as are also the parameres, which in *C. lapidicola* are only slightly chitinized proximally along their mesial surfaces, the narrow chitinized areas coalescing at base to form a single sclerite. In the resting condition (Fig. 22) the posterior wall of the penis is invaginated, forming the spermatophore sac, into the lower part of which the ejaculatory duct opens (gp). The upper part is marked off from the lower by a slight transverse fold (fps), above which is seen the plate formed by the united bases of the parameres (pmb), which being partly inverted, are otherwise invisible in this position. The fold (fps) corresponds to the floor of the "paramere sac" in Neduba, etc. (see p. 27). In Fig. 25, of Pl. III, which was drawn from a potash preparation, they are shown in a completely inverted position, but this is a position that is prevented in life by the mass of muscles which surround the spermatophore sac.

The mouth of the spermatophore sac is bounded below by a single, large ventral lobe, which is slightly chitinized and densely spinulose. In the retracted condition a deep transverse pocket is formed beneath the ventral lobe.

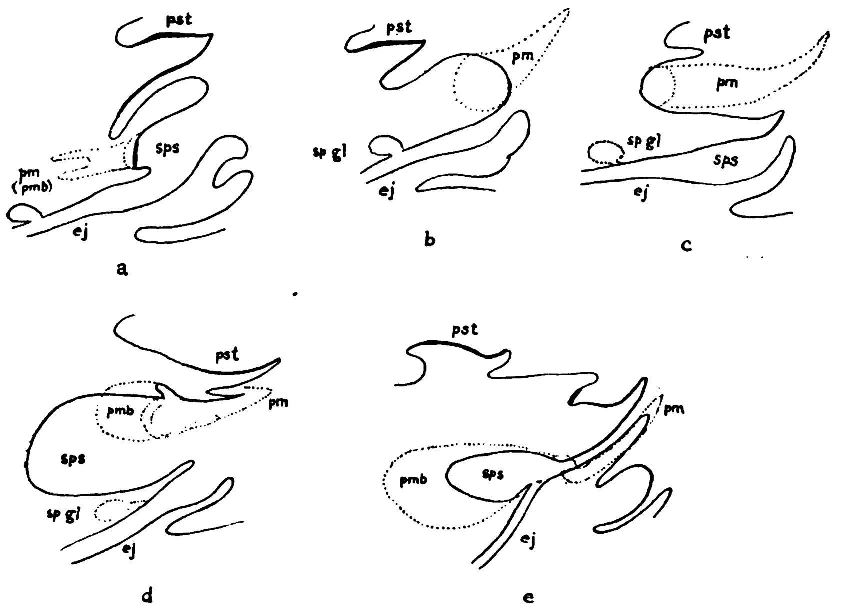

FIG. 5.

Fig. 5. Genitalia of male Orthoptera, diagrammatic median sagittal sections. The dotted lines indicate structures not in the median plane. a, *Ceuthophilus*, retracted; b, same, everted; c, *Neduba;* d, Gryllid, based on *Gryllus;* e, Acridid, based on *Dissosteira* and *Melanoplus*. For lettering, see page 71.

On the roof of the penis there is a pair of small openings with chitinized margins, leading into narrow tubules (Fig. 25), which appear in sections to be partly glandular, but whose lining cuticle is minutely pubescent. In sections of specimens with everted parameres they are drawn backwards into the cavities of the latter. These structures have apparently no homologues in the other types of Orthoptera studied.

Over the base of the penis is the large hood-like pseudosternite, the concavity of which forms a sort of sheath into which the penis is retracted. The rami are not very distinctly developed externally, though connected with one another ventrally by a feebly chitinized arch. Their internal projections or endapophyses, however, are large and prominent.

In the everted position, the penis of this species (Pl. III, Figs. 23, 24), protrudes considerably from beneath the pseudosternite and the pocket beneath the ventral lobe is straightened out. The spermatophore sac is obliterated and the parameres appear as large divergent cornua, which as already stated, are only feebly chitinized proximally along their mesial surfaces.

In this position Ceuthophilus illustrates well what appears to be the primitive, dorso-terminal position of the parameres in the Orthoptera.

Fig. 26 is a posterior view of the end of the abdomen of *C. aridus* Brun., in which the roof of the invaginated penis is strongly retracted and folded ventrad in such a way as to expose the under surface of the pseudosternite. This has been forcibly elevated to show the lower margin, which is bent into a little arch, beneath which the ejaculatory duct passes, covered also, of course, by the thin, collapsed roof of the penis. Although this figure differs greatly in appearance from those of *C. lapidicola* the genitalia are essentially similar in the two species, as far as can be seen in the retracted condition.

Fig. 27 is a similar view of *C. maculatus* Harr., with the genitalia everted. The parameres are very small and there appear to be no openings on the roof of the penis. The pseudosternite is a heavily chitinized gable-like structure, with a median projection, and is prolonged ventrad into distinct rami. It is quite suggestive of certain Gryllidæ such as *Gryllotalpa*.

The second type of genitalia differs from the first in the following features:

1. The absence of the pseudosternite, or its reduction to a very slight membranous fold.*

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* A well developed pseudosternite, together with typical parameres, is figured by Chopard ('20) in *Thyreonotus corsicus* Ramb., a Decticine. Chopard, however, regarded both structures as part of the "epiphallus." The case is important in giving further conclusive evidence that the pseudosternite and parameres are different structures, a view that might otherwise be denied by those who would fail to recognize as parameres the introversible processes of Ceuthophilus.

2. The non-introversible chitinized parameres, whose bases are prolonged cephalad so as to reduce greatly, or even obliterate, the roof of the penis, and to occupy a sac of their own, the *paramere sac*, above the spermatophore sac.

3. The median division of the ventral lobe into two folds, which are membranous and not pubescent.

This type may be illustrated by *Neduba carinata* Walk., a member of the Decticinæ. Posterior, dorsal and lateral views of this species are given in Figs. 29, 30 and 31.

The pseudosternite is practically absent, only a slight, membranous fold being found in its place. The parameres are large cornua with slender, upcurved apices and stout bases, arising from the walls of the paramere sac, the floor of which is also somewhat chitinized. The paramere sac is comparatively large, the spermatophore sac rather small, at least when contracted, and the intervening fold is produced into a pair of short processes which are chitinized ventrally. The ventral lobes are, as usual in this type, wholly membranous. The glandular pouches, opening into the ejaculatory duct at its distal end, are of considerable size.

Of the same general type are the genitalia of *Conocephalus* (*C. brevipennis* Scudd., Figs. 32, 33). They differ from those of Neduba in the form of the parameres, which are represented by a pair of thick, muscular ridges, arising from the floor and sides of the paramere sac. Along the edge of each ridge is a chitinized bar, which meets its fellow in front but diverges caudad, and curving ecto-dorsad around the end of the ridge, terminates in a short spine. These bars are covered with fine spinules. The ventral lobes are of large size and folded inwards to allow considerable expansion of the spermatophore sac. The septum between the paramere sac and the spermatophore sac is simple and unchitinized. The endapophyses are small and concealed beneath the penis, but have distinct inward processes. The glandular pouches opening into the ejaculatory duct are of large size and are lined with chitin.

In the last nymphal instar of *Conocephalus* (Fig. 34) the penis has a simpler tubular form; the parameres, represented merely by the slightly chitinized, dorso-terminal edges of the orifice, being as yet not at all retracted, so that there is no paramere sac at this stage. The ventral lobes are divided into a larger outer and a smaller inner part. The former is distinctly chitinized at the margin, though it is apparently the part which in the adult becomes wholly membranous and bent inwards. The small, inner parts are less chitinized and are readily recognizable also in the adult.

In *Neoconocephalus ensiger* Harr., *Scudderia curvicauda* DeGeer and other species of Scudderia the parameres have no projecting spines. In *S. curvicauda* they are reduced to a pair of rounded tubercles on the floor of the paramere sac, densely beset with spinules. They represent a highly specialized type.

GRYLLOIDEA. The crickets are most remarkable for the complex structure of the spermatophore and its sac. As an example of the family we may first take the common field cricket, *Gryllus assimilis* Fabr. The adult genitalia of this species are shown in Figs. 37–39.

The pseudosternite is readily recognized from its general resemblance to that of *Ceuthophilus.* As in this genus it is a hood-like structure overarching the penis, but it is much more closely connected with the latter than in *Ceuthophilus,* forming what is virtually its chitinized dorsal surface. It terminates in three prongs (pc) which doubtless serve as the titillators and is connected laterally with the slender rami, which pass ventro-cephalad to the floor of the genital cavity. These are not produced into endapophyses. The ventral lobes are large flexible whitish flaps, enclosing a concavity in which the ampulla of the spermatophore rests after it has passed out of the spermatophore sac. The latter is a deep rounded pocket, whose roof and floor are formed of a single strip of thin chitin, bent around the end of the sac and projecting over its mouth in a pair of slender spines (vs), placed closely together. When the spermatophore is in place the filament is curved upwards around the end of the sac, and backwards along the middle of the upper surface, its lateral expansions covering the floor, and serving to anchor it. A narrow median groove in the roof, terminating between the two projecting spines, is the site where the duct is formed.

Upon the roof of the spermatophore sac and beneath the pseudosternite are two arcuate bars, meeting one another in the middle line and continuous laterally with a pair of bars, which appear on the inner surface of the sac near its mouth. These curved bars are formed as evaginations of the roof of the spermatophore sac, as can be seen clearly in transverse sections. From their muscular connections they appear to represent the bases of the parameres, and may be termed endoparameres (Fig. 37, *pmb*). With the parameres may also be associated the lateral bars already mentioned, and perhaps also the two lobes supported by triradiate sclerites, which are situated just beneath the lateral prongs of the pseudosternite, and which are also in close connection with the lateral bars (*ectoparameres*, Figs. 38, 39, pm).

At first sight it would appear as though the spermatophore sac were the homologue of the paramere sac of the Tettigonoidea, but the latter structure is developed merely as a result of the enlargement and inward extension of the paramere bases, in consequence of their function as protrusible titillators, whereas in the Gryllidæ the parameres possess no such modification and have no bases other than the roof of the spermatophore sac itself.

The paired glandular pouches, which open into the ejaculatory duct near its termination, are similar to those of most Tettigonoidea, though somewhat smaller.

The last nymphal stage of *Gryllus* shows some peculiar features. Figs. 40 and 41 are ventral and ventro-posterior views of the genitalia at this stage. The pseudosternite resembles that of the adult, except that its three prongs are very short and blunt. The ventral lobes appear as a flat, bilobed, chitinous flap, covering the site of the genital aperture, which has not yet appeared. Between the pseudosternite and the ventral lobes is the space that later becomes invaginated to form the spermatophore sac. The chitinous layer which lines the latter, and also the median groove and the two terminal points are already indicated, the last-named structures being relatively much larger and stouter and not yet separated into two parts. They are separated from the pseudosternite by a larger space than in the adult. There is at this stage no indication of the parameres.

It may be questioned whether the structures which I have identified as the parameres are the true homologues of these processes in the Tettigonoidea. They are the structures called "titillators" by de Saussure and Zehntner, while Chopard refers to them as the underside of the "pseudépiphalle" (pseudosternite) and recognizes no homologues of the titillators or parameres ("epiphallus"). My reasons for identifying these structures with the parameres are (1) their origin as evaginations of the wall of the spermatophore sac (cf. *Ceuthophilus*), and (2) their muscular connections, which are comparable to those of other groups of Orthoptera.

In *Nemobius fasciatus* DeGeer the male genitalia are surprisingly unlike those of *Gryllus*, considering how nearly related the genera are in other respects (Pl. V, Figs. 42, 43). The pseudosternite is partially retracted and adherent to the overlying integument. It has no median process, but has two pairs of lateral ones, of which the upper may represent the median process of *Gryllus*, the lower ones the lateral processes of that genus. Between the lower pair is another pair of more flexible processes, evidently the homologues of the ectoparameres of *Gryllus*. The pseudosternite extends down on each side at base, but is not narrowed into distinct rami.

The remarkable feature of this form, however, is the spermatophore sac, which is really not a sac at all, as it does not become invaginated, but is merely longitudinally sulcate. At the distal end the plate which lines the "sac" is greatly contracted and has a very narrow channel, but farther proximad it is considerably expanded and much more broadly sulcate. The endoparameres take the form of long slender rods, which are divergent towards their free ends. They have the same origin as in *Gryllus*, viz., as evaginations of the wall of the spermatophore sac. As a result of the form of the spermatophore sac the ventral lobes are far forward and completely hidden, the entire spermatophore sac lying behind them. They are also relatively smaller and less distinctly separated from one another than in *Gryllus assimilis*.

In *Nemobius carolinus* Scudd. the genitalia are very similar to those of *N. fasciatus*, but in the European *N. sylvestris* Fab., according to Lespes ('55 b) there is some approach to *Gryllus* in the longitudinal curvature or slight invagination of the spermatophore sac.

In the tree-cricket *Oecanthus nigricornis* Walk. the genitalia are like those of *Gryllus* in most respects, (Pl. V, Figs. 44–46), differing chiefly in the following features: The pseudosternite has a pair of prominent internal projections just mesad of the bases of the endapophyses. These are only slightly indicated in *Gryllus*. The median prong is represented by a pair of processes close together, while the lateral prongs are almost obsolete. The ectoparameres are broad, rounded and prominent, and are closely connected with the endoparameres, which are long, thin plates, extending forward almost to the end of the spermatophore sac, and are wholly separate from one another. They are lateral rather than dorsal in position, being formed by an infolding of the integument on each side of the spermatophore sac, whereas in *Gryllus* the infolding, though partly lateral, is mainly dorsal, the two endoparameres coalescing in the middle line. In *Oecanthus* the entire endoparamere is a chitinized plate, in *Gryllus* only the arcuate edges are chitinized. The anterior extremities of these plates in *Oecanthus* are free and each bears a slender outwardly projecting spur.

The spermatophore sac of *Oecanthus* is long and compressed, but formed by an invagination similar to that of *Gryllus*. The roof of the sac is, however, much longer than the floor, the mouth being very oblique. The ventral lobes are similar to those of *Gryllus*.

In *Gryllotalpa*, according to de Saussure and Zehntner ('94) the pseudosternite has somewhat the form of an anchor (hence the term "anchre" of these authors), being produced laterally into a pair of long arms which are evidently the rami. The distal prongs are lacking in this genus.

TRIDACTYLOIDEA. *Ripipteryx carbonarius* Sauss. is the only species whose genitalia were studied (Pl. V, Figs. 47–50). On first examination there appear to be no chitinous parts, as these are almost wholly retracted, but in a cleared preparation a structure of some complexity was revealed. This structure is elongate and much depressed and consists of two flattened sacs, dorsal and ventral, connected at their posterior extremities. The ejaculatory duct, which is distally rather wide, with distinctly chitinized walls, opens into the anterior end of the ventral sac, which thus seems to be the homologue of the spermatophore sac. No trace of lateral glandular pouches is present. The dorsal sac is covered with a thin plate, which is little chitinized except along the lateral margins, which are produced cephalad into a pair of long, slender rods, apparently for the insertion of muscles, and at its posterior extremity, where there is a small plate or more heavily chitinized part of the roof of the sac, which barely projects over the genital aperture. The roof of the dorsal sac is evidently the pseudosternite but is so deeply retracted as to be almost wholly an internal structure. As in many Orthoptera, such as *Gryllus*, *Nemobius* and *Ceuthophilus*, the posterior, more exposed part is more heavily chitinized than the anterior, concealed portion. The lateral chitinized margins are also exposed towards their bases and represent the rami (cf. *Nemobius*), while the long, slender, internal processes are the endapophyses. The floor of the dorsal sac represents, of course, the roof of the penis. There appear to be no traces of parameres.

On the whole the gentialia of *Ripipteryx* appear to approach those of *Ceuthophilus* more than any other of the types studied, though the pseudosternite recalls that of *Nemobius* to some extent. The simple dilatation representing the spermatophore sac suggests that of *Ceuthophilus*, or other Tettigoniids, and the deep pocket between the pseudosternite and the penis roof is also suggestive of this genus. Both of these are primitive characters. The long horizontal endapophyses, on the other hand, are more like those of the Acrididæ, though the resemblance may be quite superficial. The striking similarity between the female genitalia of *Ripipteryx* and the Acrididæ is certainly not paralleled by the male genitalia.

ACRIDOIDEA. In the family Acrididæ the genitalia are remarkable for: (1) the great development of the muscles and the chitinous parts which serve for their attachment; (2) the upright or subvertical position of the terminal part of the penis and parameres, correlated with the upcurved, cup-like form of the ninth sternum; (3) the small size of the outlet of the penis; (4) the deeply retracted bases of the parameres (endoparameres), in the form of heavily chitinized wing-like expansions, and the vestigial spermatophore sac, of which they form the lateral walls; (5) the anterior position and complex form of the pseudosternite; (6) the large and strongly chitinized endapophyses, connected dorsally but separated from the pseudosternite; (7) the absence of the glandular pouches of the ejaculatory duct; and (8) the deep pocket between the penis and the floor of the genital cavity.

To illustrate the genitalia of this family we can take the common Black-winged Grasshopper or Carolina Locust (*Dissosteira carolina* L.) (Pl. VI, Figs. 51–54). In order to expose the penis it is necessary to remove the pallium or fold of integument covering the genital cavity behind the paraprocts. The terminal part of the penis is now seen near the posterior end of the genital cavity, and having a subvertical instead of a horizontal position, due to the general upturning of the extremity of the abdomen.

Under the flattened paraprocts lies the pseudosternite, a transverse, heavily chitinized plate of complex form (Fig. 52). It is thus widely separated from the genital aperture, having a position comparable to that of *Ceuthophilus* when the penis of the latter is fully everted.

Immediately in front of the extremity of the penis and partly concealed by a membranous fold a strong transverse arch (ar) may be seen, having a horizontal position. This bar curves forward on each side, passing beneath the surface and continuing far forward beneath the pseudosternite, with which it is connected by strong muscles. The two arms of this arch, from their muscular connections, appear to represent the endapophyses, but have lost their connections with the pseudosternite, the proximal part of the rami being absent. Connected with the arch is a pair of chitinized lobes (ra) flanking the penis and meeting caudad in the median line. From their muscular connections, as determined by Miss Norma Ford, who is now engaged in a comparative study of the abdominal muscles of Orthopterous insects, these lobes appear to represent the distal parts of the rami. There is also a pair of conical elevations arising from the penis roof, where it passes into the rami. These are not structures of morphological importance, however, as they are not of general occurrence in the Acrididæ.

Continuous with the upper (morphologically posterior) edges of the rami are the ventral lobes (vl), two slender, suberect, valve-like processes, beset with minute spinules. They are straight, close together, and bound the genital aperture behind. They are covered in front by the *dorsal lobes*, (dl), a bilobed flap, which is an extension of the penis roof.

The inner surface of the ventral lobes is continuous, in this species, with the apices of the parameres (ectoparameres, pm). These pass ventrad a short distance, then bend sharply dorsad and again ventro-cephalad, expanding into a pair of divergent, wing-like plates (the endoparameres, pmb), which lie beneath and between the endapophyses, with which they have powerful muscular connections.

Lying between the endoparameres, where they most closely approach one another, is a small sac, formed, like the paramere sac of the Tettigonoidea, by the inward prolongation of the endoparameres, but having also a strong resemblance to the spermatophore sac of the Gryllidæ. It opens into the ejaculatory duct, which is also dilated ventrally at the junction. The sac and ventral dilatation appear to represent a vestigial spermatophore sac (sps) and are here considered as such. The wing-like expansions of the endoparameres have essentially the same relation to the spermatophore sac as in the Gryllidæ, especially in such genera as *Nemobius* and *Oecanthus*. They extend far beyond the end of the sac, however, the latter being of comparatively small size and doubtless quite functionless.

The distal parts of the penis, including the rami, rest in the concavity of a single large lobe, which may be called the *subventral lobe*. It is separated from the floor of the genital cavity by a flattened space, the *subgenital sac*, which extends far forward beneath the penis.

The plan of structure just described for Dissosteira was found to be essentially the same in various species of Acridinæ, Oedipodinæ and Locustinæ and is doubtless general throughout the family.*

The variations in details of form, however, particularly of the pseudosternite and the parts surrounding the outlet of the penis, are numerous and often striking, even within the limits of a genus, and in certain genera, such as *Melanoplus*, they would afford useful taxonomic characters if they could be more readily seen in dried specimens.

The pseudosternite bears two pairs of ventral apophyses, to which muscles from the ninth tergum and sternum are attached and is elevated into a variety of prominences, cristate, spinous or tuberculate (ppst), according to the species. In *Melanoplus* there is a pair of anterior dorsal crests, which vary in size in different species, being, e. g., moderately high in *M. bivittatus* Say (Figs. 55, 56) and extremely high in *M. femur-rubrum* DeGeer.

In this genus the ectoparameres are free (Fig. 57) and are enclosed by the ventral lobes, which are not valve-like as in Dissosteira, but broad and collar-like, surrounding the outlet of the penis. They are flexible, but little chitinized, and are

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* This excludes the Acrydiinæ, which are here considered as a distinct family, Acrydiidæ.

covered with minute, regularly arranged spinules. They are continuous with the dorsal lobes, which are black and more heavily chitinized, with sharp, excavated margins, apparently serving as titillators. In *M. femur-rubrum* the dorsal and ventral lobes are comparatively free from one another and the former project dorsad in the form of slender, sharp-pointed processes of irregular form, while in *M. bivittatus* (Figs. 55, 56), the dorsal lobes are much shorter and are folded within the ventral lobes in a complex, scroll-like fashion. There is a strongly chitinized bridge connecting the dorsal lobes with the arch of the endapophyses. In place of the subventral lobe there is only a pair of soft, irregular folds of integument. The expanded bases of the endoparameres are much more strongly divergent than in *Dissosteira.*

The genitalia of the Acrydiidæ are astonishingly unlike those of the Acrididæ, though occupying a similar position, the outlet of the penis having a suberect position and the poststernite lying far forward under the paraprocts. It is evident that the genitalia of this family have undergone a marked degeneration of structure. Three genera were examined: *Tettigidea* (*T. lateralis parvipennis* Harr.), *Acrydium* (*A. ornatum* Say and *A. granulatum* Kirby) and *Paratettix* (*P. cucullatus* Burm.)

In *Tettigidea* the pseudosternite is V-shaped, recalling that of *Ceuthophilus maculatus* Harr., except that, instead of the upright position of the latter, the arch is tilted forward so as to be almost horizontal. It becomes evident on seeing the pseudosternite in this form, that the forward tilting of this sclerite has taken place in all the Acridoidea and is an expression of the same process of shifting that has brought about the upright position of the genital outlet. The recurved apex of the pseudosternite in *Tettigidea* is armed with a group of spines.

Behind and between the arms of the pseudosternite are two narrow plates, which curve inward and terminate behind in a pair of lobes on each side of the genital aperture. These plates appear to be the rami, but the endapophyses, so strongly developed in the Acrididæ are entirely absent. The genital aperture is wide with folded membranous walls, and near the termination of the ejaculatory duct is a dilatation which represents the spermatophore sac. There are no traces of the parameres. In contrast to the loss of the chitinous parts in the genitalia proper the pallium is strengthened by two distinct plates, separated by a median groove.

In *Acrydium* and *Paratettix* the rami are absent and the pseudosternite is more slender with a much smaller median process, but the pallial structures are more complex than in *Tettigidea*, there being between the pallial plates a pair of slender bars, each terminating in front in an upcurved hook, which probably has some function in copulation.

Phasmoidea.

In the stick-insects and their allies the terminal abdominal terga of the males are all well developed and the 10th tends to replace the supra-anal plate, which is often vestigial or obsolete. In *Timema californicum* Scudd. (teste Crampton, 1, c., Pl. 5, Figs. 53, 65) the latter is distinct and only partly overlapped by the 10th tergum; in *Diapheromera femorata* Say it is a small and membranous lobe, while in *Anisomorpha buprestoides* Stoll. (Pl. VIII, Fig. 71), it is wholly absent. The paraprocts are well developed in *Timema*, of fair size in *Anisomorpha*, rather small in *Diapheromera*. In these genera they are little, if at all, chitinized, but, according to Chopard ('20), who examined a large number of forms, they are commonly chitinized except on their mesal surfaces. The cerci are short, unsegmented and often modified as claspers (*Diapheromera*). The sternal region of the terminal segments preserves its primitive horizontal position, that of the 9th and 10th being in about the same plane, so that the genitalia are ventral in position, as in the Dermaptera, not terminal as in the Orthoptera, Blattoidea, etc. The 9th sternum is commonly divided into two parts, a proximal plate, usually short, and a distal plate, which is a more or less free flap, or "hypandrium," covering the genitalia. As in the Acridoidea and Ephemerida the proximal plate is probably the true sternite, the distal plate the united coxites. There are no true styli. In *Timema* and *Anisomorpha* the 9th sternum shows its more primitive form, in that it is broadly connected with the tergum, both basally and laterally, but in *Diapheromera* and many other genera the sternite forms a short stalk, bearing the perfectly free hypandrium, which forms a cup-like receptacle for the genitalia. In such forms the posterior and greater part of the sternal area is uncovered by any part of the true sternum.

On this part we find the genitalia, so that it must be considered as belonging properly to the intersternal membrane between segments 9 and 10, although it underlies the 9th tergum.

This area in its distal part may be more or less chitinized (the "post-sternite" of Crampton) or may bear a projecting plate, the *subanal vomer* ("vomer sous-anal" of Pantel), (Fig. 71, vo). Pantel considered the vomer to belong to the 10th sternum, but it appears to me to arise from the membrane just in front of this segment.

The elongation of the 9th tergum without a corresponding development of the true sternum has a parallel in the Odonata, in which the genitalia likewise have the appearance of belonging to the sternum itself, rather than the intersternal membrane.

The large size of the 10th sternum is likewise probably due to secondary elongation of the segment, and the primitive 10th sternum may be almost entirely absorbed in the bases of the paraprocts (vide p). Sometimes the cleft between the paraprocts is continued cephalad as a more or less distinct groove almost or quite to the base of the 10th sternal region.

The male genitalia of the Phasmoidea form an irregular, asymmetrical mass, suggestive in a general way of the Blattoidea, Mantoidea and Grylloblattoidea. I have studied the male genitalia of only two species, *Diapheromera femorata* Say and *Anisomorpha buprestoides* (Stoll.).

In the former (Figs. 74, 75) the genitalia form a prominent, asymmetrical structure slightly divided, especially on the ventral face, by an oblique groove, on the left side of which the ejaculatory duct opens. This duct is directed slightly dextrad, and opens directly on the ventral surface, there being no invaginated pouch as in the Orthoptera, and no virga. The dorsal surface of the genitalia is covered by a chitinous plate (dpl) from which a blunt cornu (possibly the paramere) arises on the left side (pm?). There is no such process on the right side, but on the postero-ventral surface, next to the median groove, there is a pair of plates, which apparently form a sort of clasper (cl), and from which an apophysis (ap) for the attachment of muscles projects inwards. The presence of this clasper on the left side is suggestive of the Mantids, certain Blattids and *Grylloblatta*. The left lobe is ventrally thin-walled, a feature which is also somewhat suggestive of *Grylloblatta*.

In *Anisomorpha buprestoides* (Figs. 72, 73) the genitalia form a shorter mass, which is sunk into a pocket formed by the enclosing hypandrium. There is practically no fissure dividing it into right and left halves, the two parts of which it is composed being evidently primarily dorsal and ventral (dpl, vpl), though actually placed so obliquely that the dorsal part is dorso-dextral, the ventral part ventro-sinistral. The greater part of the genitalia is flexible with unchitinized walls, but the dorsal surface is considerably chitinized and this sclerite plainly corresponds to the dorsal plate of *Diapheromera*. It has a prominent sinistral angle which represents the sinistral cornu of *Diapheromera*, and there is a somewhat thickened longitudinal part which seems to represent the primitively median dorsal region. The opening of the ejaculatory duct is well to the right, but lies in a wholly membranous area, there being no clasper like that of *Diapheromera*.

Since the present study was made Chopard ('20) has published descriptions and figures of the genitalia of a number of Phasmids, many of which are much more complex and more suggestive of the Blattids than the forms described above. He recognizes in their typical composition four genital valves, of which the two superior sometimes (e. g., *Anisomorpha*) unite to form a single dorsal plate, while the two inferior valves may unite to form a single ventral plate. The genitalia are extremely variable, being in some cases wholly membranous, in other cases very strongly sclerified, while in still others they are partly membranous with many separate plates and processes, very suggestive of the Blattids.

The genitalia of the Phasmoidea thus resemble those of the Grylloblattoidea, Mantoidea and Blattoidea (with exceptions in certain details) in that they appear to consist primarily of right and left lobes (or pairs of lobes), asymmetrical in size, form and position, partly membranous and partly chitinized, with the opening of the ejaculatory duct lying between them and not borne upon a conspicuous penis. In the two forms described here the opening of the ejaculatory duct is directed somewhat dextrad, as in the other groups mentioned, and in *Diapheromera* there is a dextral clasper with an internal apophysis, a feature also somewhat common in the Blattoidea and Mantoidea.

Grylloblattoidea.

The sole member of this order is *Grylloblatta campodeiformis* Walk., the male genitalia of which have been described in detail by the writer ('19).

In the adult male the ninth segment, particularly the sternum, is large, while the tenth is small, though prominent. The intersternal area on which the genitalia are situated is thus vertical, as in the Orthoptera, Blattoidea and Mantoidea.

Viewed from above (Fig. 62) the terminal segments appear symmetrical or nearly so, but from below (Fig. 63) or behind (Fig. 64) a pronounced degree of asymmetry is apparent. This asymmetry involves the ninth sternum, the tenth tergite and the genitalia.

The ninth sternum is remarkable for the retention of the primitive division into sternite and coxites. The sternite is of about the same size and form as the tergite, from which it is separated only by a suture. It is nearly symmetrical, although the left side is slightly shorter than the right. The coxites, although of equal length, are very different in size and form. The left coxite is broadly triangular and strongly convex. Its base extends from the tergo-sternal suture to a point well to the left of the middle line. The right coxite is confined to the right side, having a much narrower base. It is also triangular, but bears a strong spur from its upper margin, directed meso-caudo-dorsad. Both coxites are moveably articulated with the sternite and bear well-developed styli upon their apices.

The tenth tergum is narrowed beyond the bases of the cerci to a truncated apex, but does not form a freely projecting plate. It is continued ventrad around the bases of the cerci, terminating below in a pair of free, unequal arms, which nearly meet one another in the middle line. The left arm is the longer and is wholly chitinized, except at the apex, which is slightly expanded into a little disc or pad. The right arm is chitinized only at the base and is without the terminal pad. It has the appearance of a functionless structure. The tenth sternum is obsolete in the adult.

The cerci are exactly like those of the female, being long and cylindrical and divided into eight distinct segments. There is a small, ventro-mesial, cercal basipodite. The supra-anal plate is extremely vestigial, distinctly more so than in the female, though prominent enough in the nymph. The paraprocts are also rather small and membranous.

The genitalia are bulky and very irregular. As in certain Phasmoidea, Blattoidea and Mantoidea there are two large lobes, (paramere lobes, rl, ll) separated by an oblique fissure, extending from about the mid-ventral line to the middle of the left side at the base of the tenth tergum. Both lobes project somewhat beyond the margins of the coxites, the exposed parts of their ventral surfaces being somewhat chitinized. There is no chitinized dorsal surface as in the Phasmids, but just below the paraprocts there is a narrow transverse chitinous plate, divided lengthwise into two parts, each of which is elevated at the right extremity into a rounded backward projection. This may represent the dorsal plate of the Phasmids, the projections being perhaps homologous with the right cornu or paramere, but it might not unreasonably be also compared with the pseudosternite.

The right lobe bears upon its dorso-caudal surface a heavily chitinized prominence (cl), divided into two parts, which are irregularly folded and bear several blunt tooth-like processes. This prominence, together with the processes mentioned in the preceding paragraph, and the spur of the right coxite, with which they are closely associated, appear to form a clasping apparatus, in which the left arm of the tenth tergum may perhaps be included.

The left lobe is wholly membranous, except a small ventral chitinized area, but it is produced into a long, thin-walled, tubular sac, which is doubtless normally invaginated, when not in use.

The presence of the chitinous prominence on the right side, but not on the left, is suggestive of the Phasmid, *Diapheromera* (q. v.), and the eversible sac of the left lobe much resembles that of many Blattids, such as *Blattella* and *Parcoblatta*, except that in the latter the sac forms a sheath for a protrusible hook, while in *Grylloblatta* no such hook is present, and it is therefore difficult to conjecture as to what its function may be.

The opening of the ejaculatory duct could not be found in the single adult male of *Grylloblatta* available for study. It will almost certainly be found in the fissure between the two lobes. The mesoventral angle of the left lobe is produced into a process, which lies in a fold of the right lobe. This process is slightly grooved mesially, the groove being continued along the interlobar fissure. Possibly this is a seminal groove, the process bearing it being a sort of rudimentary ædeagus, similar to many blattids, such as *Periplaneta*. In this genus, and in other Blattids, Mantids and Phasmids, the ejaculatory duct is more closely associated with the left lobe than the right.

NYMPH. In the immature male of *Grylloblatta* the coxites are more nearly alike in size and form, although the asymmetry is evident in the specimens studied. These evidently belong to two successive instars, the later of which appears to belong to about the penultimate stage.

In the younger nymph (Fig. 66) the tenth segment is relatively large, its sternal surface being nearly in the same plane with that of the ninth. The supra-anal plate and paraprocts are much larger and more prominent than in the adult. The left coxite is distinctly larger than the right and the latter shows no trace of the spur present in the adult. The tenth tergum is symmetrical and without free prolongations of the ventrolateral margins. Between these margins is a distinct, though small and membranous, tenth sternal area. In the intersternal membrane are two oval, slightly elevated areas, which are the rudiments of the two genital lobes.

In the older nymph (Figs. 67, 68) the tenth segment is relatively somewhat smaller and the tenth sternal area almost obliterated by the closer approximation of the ventro-lateral margins of the tergum. The supra-anal plate and paraprocts have decreased in size. The genital area is no longer horizontal but subvertical in position, and the genital lobes are much larger and separated by an oblique fissure, as in the adult, but there are as yet no chitinous processes nor eversible sac. The ninth sternum, coxites and styli have not changed appreciably, though there is a slight increase in their asymmetry.

Blattoidea.

In the male cockroach the abdominal terga, cerci and cercal basipodites are essentially like those of the female. The eighth and ninth terga are abbreviated, while the tenth replaces the aborted supra-anal plate and is often considerably prolonged caudad. It is however, narrowed on the sides, terminating beneath the bases of the cerci. The ninth sternum forms a large hypandrium, much like that of many Tettigonoidea, and usually bears styli upon its hind margin. It is a coxosternum, sternite and coxites being completely fused. It is often very asymmetrical, sometimes bearing a lobe or process on one side but not on the other, and the styli are often unequally developed and asymetrically placed. The paraprocts are broad and depressed and are usually chitinized beneath, at least in part; the chitinized portions meeting the margin of the tenth tergum and thus appearing to represent the tenth sternum, with which they have been identified by Chopard ('17).* They are frequently strongly asymmetrical and may bear a hook on one or both sides. The upper surface and sometimes a pair of mesial lobes are membranous.

The genitalia are strongly asymmetrical and show a wide range of variation. They consist, essentially, of an ædeagus or penis, upon which the ejaculatory duct opens, sometimes at the base, sometimes upon a retractile spine (virga); and two outgrowths or processes, primitively dorso-lateral to the penis, each of which bears one or more chitinous parts. These are usually very differently developed on the right and left sides, and their relative positions seem to be primarily similar to that of the two lobes in *Grylloblatta*, *i. e.*, they are obliquely shifted, so that the right process overlaps the left. In what appears to be the most primitive form met with in the types studied (dextral process of *Blattella*), their structure consists of a freely projecting shaft, whose base has been deeply sunk into the hæmocoele, to serve as an apophysis for the attachment of protractor and retractor muscles, while from the folds surrounding the pocket thus formed secondary chitinizations for the attachment of muscles may also develop. Such a form of process is protrusible and retractile to a certain extent, but apparently cannot be completely ensheathed. In the left process of *Blattella*, however, we have a modification of this form, in which the shaft has the form of a hook and can be completely withdrawn into a deep membranous pocket or sheath whose walls are without secondary chitinizations, and which is not prolonged into an apophysis, the muscles being attached directly to its base.

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* See p. 7.

The opposite extreme is seen in *Blatta* or *Periplaneta*, in which there are two lobes, separated by an oblique fissure, each bearing several chitinous plates, prolonged into a variety of peculiarly shaped processes, none of which are capable of being invaginated. In such cases it is exceedingly difficult to determine which of these processes are homologous with those of *Blattella*, or even the homologies of the right and left lobes of the same species; but the complex folding of the lobes suggests that the various plates and processes have arisen secondarily as chitinizations of the folds surrounding the sheath of the primary process. As these two processes arise primitively dorso-lateral to the aedeagus, as can be seen in the nymph, it seems reasonable to consider them tentatively as the parameres of which some representative would be expected to occur in so generalized a group as the Blattoidea.

The following species were studied in detail: *Blattella germanica* L, *Parcoblatta pensylvanica* DeGeer, *Blaberus atropos* Serv., *Periplaneta brunnea* Burm., *P. fuliginosa* Brunn. and *P. americana* (L.).

Blattella germanica L. (Pl. IX, Figs. 80–83). In this species the tenth tergum is produced into a large flexible flap, the ninth sternum is very asymmetrical and the styli are unequal in size, close together and both to the left of the middle line. The paraprocts are asymmetrical and divided into two parts, a small membranous, pubescent lobe, next to the anus, and below this a transverse chitinous strip, which meets the edge of the tenth tergite and bears a prominent hook. The dextral hook curves upward and is simple, the sinistral hook curves downward and is bifid. The penis is large and somewhat conical and the ejaculatory duct opens upon a long, straight, retractile spine or virga.

The dextral paramere consists of the following structures: An irregular pocket with folded walls, which is produced internally into a long slender apophysis, whose outer extremity is bifurcated. Articulating with its outer branch and forming a prolongation of the ectodorsal edge of the pocket is a projecting blade or shaft, and connected with the inner branch is a chitinous strip, forming the ventro-mesial edge of the pocket. A rounded lobe with a chitinous margin is folded into the pocket on its inner side and serves for the origin of protractor muscles, which are inserted into the inner side of the apophysis. The projecting blade appears to be the primary part of the paramere, whose base has been invaginated for the insertion of muscles, while the folded edges of the invagination have become chitinized for muscular attachment.

The sinistral paramere* is a large hook, which, when not in use, is completely retracted into a membranous sheath. Muscles are inserted directly into the inner end of the hook. When protruded this is a very conspicuous structure, extending beyond the edge of the ninth sternum.

Parcoblatta pensylvanica DeGeer (Figs. 84-88). The genitalia of this species are essentially smiliar to those of *Blattella germanica*. The ninth sternum is but slightly asymmetrical, but the paraprocts are strongly so. Each is divided into an outer hook and an inner lobe. The dextral hook is a large, heavily chitinized structure, whose base meets the edge of the tenth tergite. The sinistral hook is much feebler and is scarcely chitinized. The relative sizes of the lobes is reversed, the sinistral being much the larger. The penis is similar to that of Blattella, the ejaculatory duct very slender and opening near the apex of the slender, slightly curved virga.

The sinistral paramere resembles that of *Blattella* except in the lack of a prominent shaft, which is reduced to a mere angular flap, overhanging the opening of the pocket. The sinistral paramere is a retractile hook, like that of *Blattella*, but much shorter and stouter. When retracted the curved end of the hook is generally slightly exposed, as in Fig. 84.

Blaberus atropos Serv. In this large roach the ninth sternum is somewhat asymmetrical, the styli of similar size and widely separated. The paraprocts are less sharply divided into outer chitinized and inner flexible parts, and only the dextral hook is present, this being short, blunt and strongly curved. The penis is very different from that of the two preceding types, being a large, fleshy outgrowth, deeply channeled above and bearing numerous spinules on the inner surface of the channel near its extremity. Lying in the channel is an irregularly chitinized process, probably a modification of the virga, but the ejaculatory duct does not open upon it, but at the base of the aedeagus and is a much wider passage than in *Blattella* and *Parcoblatta*. The dextral paramere is much like the sinistral

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* Chopard ('20) identifies this process incorrectly with the penis (p. 98, Fig. 15).

one of these genera, consisting of an eversible hook, whose sheath forms an irregular membranous prominence which is continued sinistrad with a long membranous fold under the paraprocts to the corresponding dextral prominence. The latter is much smaller and bears an irregularly folded structure with chitinous edges, which in general appearance is suggestive of the dextral paramere of *Parcoblatta*, but which is probably more nearly comparable to the sinistral structure of *Periplaneta* in a very aborted condition.

In this species is seen something of the tendency met with in *Blatta*, *Periplaneta*, the Mantidæ and *Grylloblatta* of the dextral paramere (or paramere-bearing outgrowth) to overlap the sinistral one.

PERIPLANETA. In this genus the paraprocts are symmetrical but the genitalia are strongly asymmetrical and exceedingly complicated. The paraprocts are dorsally but little chitinized, but are covered ventrally by large plates, which are separated only by the anal fissure, and simulate closely a divided sternum. They are without the hooks met with in the other forms described.

The paramere lobes are both large and prominent, particularly the sinistral, and are separated by a very oblique fissure, from which a large fleshy lobe representing the penis (the "lame mediane" of Peytoureau, '95)* emerges below and is directed obliquely dextrad. The wide ejaculatory duct opens upon its membranous dorsal surface, near the apex. The ventral surface is somewhat chitinized.

The three species of *Periplaneta* examined differ greatly in the details of the genitalia, but agree in general structure.

The dextral paramere is fundamentally similar to that of *Blattella*, but is much more complex and its parts more heavily chitinized. In *P. fuliginosa* Serv. the basal apophysis is short and broad, and concave on its inner face. The shaft is an irregular, curved sclerite, divided into proximal and distal parts, the former strongly folded and articulating with the apophysis with which it is connected by muscles. The distal part is bifurcate, the upper branch short and terminating in several irregular teeth, the lower long and slender and tapering to a point. The chitinized inner fold of *Blattella* and *Parcoblatta* is

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* The process termed the penis by Peytoureau is a part of the sinistral lobe. Peytoureau, however, observed correctly the position of the genital aperture.

developed into a large bivalved prominence (Pl. X, Figs. 91–93), which perhaps serves as a clasper* (cf. *Stagmomantis*). Strong muscles connect the upper valve with the apophysis, as in Blattella, though their action is probably quite different, appearing in the case of *P. fuliginosa* to elevate the valve.

In *Periplaneta brunnea* Burm. the two processes representing the distal part of the shaft are modified into a pair of hooks, as shown in Fig. 96, and the clasper is also of different form. In *P. americana* L. the upper of the processes (the short one in *P. fuliginosa*) is the well-known "bird's head" process, termed by Crampton "fimbrilobus." It is a broad, flat structure, clearly belonging to the dorsal surface of the paramere lobe, and has the form shown in Fig. 99. The other process, so strongly developed in *P. fuliginosa* and *P. brunnea*, is reduced to an insignificant hook. The parts representing the clasper are of simpler structure and more easily recognized as the chitinized walls of the pocket from which the apophysis is formed.

The sinistral paramere lobe (Figs. 94, 95) is apparently not comparable in detail with the dextral. In *P. fuliginosa* it is divided into three principal processes, a dorsal, a ventro-lateral and a ventro-mesial. As seen from the left side (Fig. 95) the dorsal and ventro-lateral processes appear separated by a deep distal cleft. The dorsal process is chitinized along the side, terminating in a sharp point, but is membranous above and on the oblique inner surface. The ventro-lateral process is well chitinized and is the long, slender titillator (pm) which curves dextrad and dorsad, tapering to a pointed apex. The ventro-mesial part is free from the dorsal process only distally, where it terminates in a rounded lobe and a slender spur or hook. The dorso-mesial surface also bears two smaller, sharp-pointed processes and above these two membranous lobes.

In *Periplaneta brunnea* Burm. the same parts are recognizable but differ more or less in form, particularly the ventro-mesial process, which terminates in a long, straight spine, and the dorso-mesial sclerites, which, instead of bearing straight spines, are low tubercles covered with minute spinules.

In *P. americana* L. the ventro-lateral process is stouter and tipped with a hook, the ventro-mesial process is somewhat

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* The "tuberculum" of Berlese.

similar and also resembles that of *P. fuliginosa.* The part which represents the dorsal process is bent up sharply distad and terminates in a large chitinous knob. The dorso-mesial surface is marked by two longitudinal furrows and bears another large chitinous tubercle.

Although it is impossible to determine with certainty from the few types studied which of the various processes borne by the sinistral lobe in *Periplaneta* is the homologue of the eversible hook of *Blattella* and *Parcoblatta,* it appears probable that it is the long ventro-lateral process, this being the longest, most independent, and apparently the most constantly present of these parts. It is also lodged within a furrow formed by the other two parts, which may therefore be possibly looked upon as secondary outgrowths from the paramere sheath.

By reason of the resemblance of the sinistral lobe of *Periplaneta* to that of the Mantids, and the non-retractile character of all its processes, it is probably a more primitive type than that of *Blattella* and *Parcoblatta,* in spite of its complexity of structure. The symmetrical paraprocts and hypandrium, and possibly the more elongate joints of the cerci may also be marks of primitive organization.

Mantoidea.

The male Mantids are very similar to the Blattids with respect to their genitalia and other abdominal structures.

Only three species were studied: *Stagmomantis carolina* L., *S. floridensis* Davis and *Mantis religiosa* L.; and these are all essentially similar in the parts with which we are concerned, so that, unless stated otherwise, the following remarks will apply in particular to one species, *S. carolina.*

The terga, cerci and anal valves are similar to those of the female, the tenth tergum, as in the Blattids, replacing the supra-anal plate, which, however, remains as a membranous vestige. In some newly hatched Mantids of an unknown species from Japan it is quite distinct and only partly overlapped by the tenth tergite (Pl. XI, Fig. 109), a fact which has been pointed out recently by Chopard ('17).

The ninth sternum is a somewhat elongate plate, symmetrical and bearing large styli upon its hind margin. This margin is but little excavated in the adults of any of the species seen, but in the young nymphs referred to in the preceding paragraph a deep V-shaped notch separates the two coxites, though these are at all stages fused with the sternite. In all these respects the Mantid nymphs resemble those of the Tettigonoidea.

The genitalia (Pl. XI, Figs. 105–107) are strongly asymmetrical and consist of two paramere lobes, whose relative positions are similar to those of Periplaneta.

The dextral lobe is very much smaller than the sinistral, which it overlaps slightly, being little developed except dorsally. It may be compared in some measure with that of such Blattids as *Blatella* and *Parcoblatta.* A slender basal ventral piece (pmb) evidently represents the basal apophysis of the Blattids, although not actually internal; and as in Blattella and Parcoblatta, though less distinctly so, it is bifurcated at base, the lower branch curving sharply around and terminating in the small, heavily chitinized ventral prominence, while the other branch ends in a similar process just above it. These two structures serve as a clasper in copulation, as I have ascertained in the case of a female specimen, whose genitalia are still connected with those of a male, although all but the end of the abdomen of the latter is missing, having doubtless been eaten by the female, as is the habit of many Mantids. The clasper is possibly homologous with that which appears as such in some Blattids, such as *Periplaneta.*

The upper jaw of the clasper is continuous above with the large, dorsal, shelf-like flap (df) which is readily compared with the dorsal plate (base of shaft) in the dextral paramere of Blattidæ (cf. *Periplaneta fuliginosa*, Fig. 100).

The sinistral paramere lobe bears a distinct resemblance to that of Periplaneta, especially as seen from the left side (cf. Figs. 95, 108), in which position parts representing the dorsal and ventro-lateral processes of *Periplaneta* are seen, though in the case of the Mantid the latter would be more appropriately termed the ventral process, as its broad chitinized base forms the entire ventral surface of the lobe and extends far over upon the right side, where it meets the narrow ventral portion (apophysis) of the dextral lobe. The process itself is bent dorsad in *Stagmomantis*, but in *Mantis religiosa*, in which it is much longer and more slender, it is directed dextrad. The dorsal process curves strongly to the left and in *S. carolina* is bifurcate. It appears to arise from beneath the dorsal plate, but it is closely connected with the latter and in other species seems to form a part of it.

This dorsal plate bears some resemblance to that of the right side and is probably its homologue, though not a free flap as in the latter case.

The inner surface of the lobe is for the most part membranous, but there are two small, though heavily chitinized, plates, which lie close to the mouth of the ejaculatory duct. In *S. floridensis* one of these is prolonged into a flagellum, while in *Mantis religiosa* they are both short and spinulose. These parts appear to represent the small sclerite which occupy a similar position in Periplaneta. There is no evident representative of the ventro-mesial process, unless it be one of these. The ejaculatory duct is a large tube passing between the two lobes, which are virtually wrapped around it. It opens upon the inner, membranous surface of the sinistral lobe, immediately beneath the two small, dark, inner sclerites. There is only the feeblest indication of an ædeagus.

Isoptera.

The same two species of "termites" were studied as in the case of the females, viz., *Termopsis angusticollis* Hagen and *Leucotermes flavipes* Kollar. The results of this study supplement those obtained from the females in showing that the Isoptera are most nearly related to the Blattoidea and Mantoidea, and form with these groups a distinctly natural assemblage.

The general appearance of the end of the male abdomen in *Termopsis angusticollis* (Figs. 76, 77), is similar to that of the female, but, as in the Blattids and Mantids, differs in the presence of styli. The character of the segmentation agrees closely with these groups. The last three tergites are, like those of the female, curved slightly ventro-caudad, all being much shortened laterally. The tenth is considerably enlarged and takes the place of the supra-anal plate, which is not present as a distinct structure. Close to the ventro-caudal margins of the tergites are the spiracles. The cerci are similar to those of the female.

The sternal region is quite blattoid in structure. The sternum of the ninth segment forms a large, undivided, subgenital plate, bearing a symmetrical pair of styli on the caudal margin. The genital cavity is much smaller than in the Blattidæ and contains no chitinized parts. In neither of the forms could I find a penis of any sort, merely a median genital aperture with membranous walls. The absence of external genitalia is without doubt a secondary condition. The points of resemblance to the Blattids and Mantids are so numerous as to leave no doubt that the Isoptera are closely related to them, and this belief carries with it the assumption that external genitalia were present in the common ancestor of these groups. The genitalia of this ancestral form were probably asymmetrical, since they are of this type in *Grylloblatta*, a form that is somewhat more primitive than the members of the other three groups.

Zoraptera.

An interesting paper by Crampton on the external anatomy of *Zorotypus hubbardi* Caudell has recently appeared (Crampton, '20), in which some details of the terminal segments of both sexes are given. The general appearance of these segments recalls the Isoptera, to which order Crampton regards the Zoraptera as nearly related, and it is stated by this writer that "the terminal segments in general and of the winged females in particular are quite Isopteroid." He does not specify in what respects they are Isopteroid, and a study of his figures does not confirm the statement. The ninth tergum in both sexes is much reduced and bears a horn-like projection in the male; the tenth appears to form with the supra-anal plate and paraprocts a continuous sclerite. The cerci are short and unsegmented.

More important than these, however, are the sternal characteristics. The ninth sternum of the male, so conspicuous in the Isoptera, is seemingly absent or represented only by a membranous lobe, while the eighth, according to Crampton's figure, takes the place of it as a subgenital plate. In the female the eighth sternum is well developed, not reduced and concealed by the seventh as in the Isoptera, Blattids and Mantids, while there is an additional sclerite below the anus, not represented in these groups.

The male genitalia (Figs. 78–79) resemble those of the Mantids, as pointed out by Crampton. The sinistral process appears to be the same as that which I have considered to be probably the sinistral paramere in the Blattid *Periplaneta*, or the Mantid *Stagmomantis*, but the large dextral lobe is not certainly its fellow of the opposite side, but may belong to the same lobe, since in the Mantids the sinistral lobe is greatly developed and bears two processes or more, while the dextral is greatly reduced. It may, therefore, be possible that both hooks shown in the figure belong to the left side and that the dextral lobe does not show or may be absent.

Odonata.

In the dragonflies the general elongation of the abdominal segments includes the terminal ones, although the tenth is small as compared with the others, except the first.

The ninth sternum covers much less than the entire sternal region of the ninth segment, there being a considerable area posterior to the genitalia, which is morphologically part of the membrane between the ninth and tenth sterna, though it may be more or less chitinized and appears to be part of the sternum itself. The genitalia thus appear to be situated upon the ninth sternum rather than upon the succeeding intersternal area. In other words the ninth sternum has not kept pace with the elongation of the tergum and the genitalia thus appear to be shifted cephalad.

The ninth sternum is not modified as a subgenital plate, but there are two small, flat plates on each side of the genital aperture and partly overlapping it. In the nymphs of the suborder Zygoptera and in those of certain Anisoptera such as the Aeshninæ these plates are readily seen to be homologous with the lateral gonapophyses (dorsal valves) of the female, as pointed out by Van der Weele ('06), and are therefore coxites. In the young nymphs of some Zygoptera vestigial styli are borne at their apices, though these disappear later.

In the ninth sternum is thus preserved the primitive division into sternite and coxites.

The genital aperture is surrounded by a chitinous ring and may be slightly elevated upon a small papilla, but there is no functional penis morphologically comparable to that of other insects, the copulatory organs being situated upon the sterna of the second and third segments and having no homology with the genitalia of other orders. The problem of the origin of these accessory genitalia is an exceedingly difficult one but is outside the scope of the present paper. Their structure has been ably dealt with by Schmidt ('15).

The 10th segment has a remarkably well developed sternum, which, however, often shows a tendency to fuse with the tergum, although its boundaries may be clearly defined.

Behind the 10th segment are two paired processes and an unpaired one, which upon anatomical grounds alone would be unhesitatingly interpreted as the cerci, paraprocts and supra-anal plate. In the Anisoptera what appear to be the cerci and supra-anal plate are the structures termed by systematists the superior and inferior appendages, these structures serving as claspers in copulation. In the Zygoptera the homologue of the inferior appendage is rudimentary in the adult, but bears the median caudal gill in the nymph, while the structures called the inferior appendages in the adults and which bear the lateral caudal gills in the nymph are apparently the paraprocts. In the adults of Anisoptera they are inconspicuous and do not function as claspers as they do in the Zygoptera.

This interpretation of these parts, which seems obvious to the comparative anatomist, is denied by Heymons and others on embryological grounds, the apparent paraprocts being interpreted as the true cerci, while the apparent cerci are regarded as secondary structures, termed "cercoids." Three small papillæ, a dorsal and two ventral, which surround the anus in the nymphs of some dragonflies, are considered to be the true supra-anal plate (telson) and subanal plates (paraprocts); the apparent supra-anal plate being the 11th tergite. I believe that further investigations will show that the former, more obvious interpretation is the correct one. It has full support from the standpoint of comparative myology, as determined by Miss Norma Ford, whose results, however, are not yet published. Moreover, if we adopt Heymons' view we are forced the improbable conclusion that the 11th segment is an embryonic structure in all insects except the Odonata, while in this order it is highly developed and morphologically exactly replaces the 12th segment of other insects.

SUMMARY OF THE CHARACTERISTICS OF THE ORDERS.

BASED ON THE TERMINAL ABDOMINAL STRUCTURES OF THE MALES.

EPHEMERIDA. Terminal segments (9–10) well developed; ninth sternum consisting of sternite and coxites, which may be separate or united, and bear long jointed styli; supra-anal plate feebly developed, but a telofilum present, generally long and multi-articulate like the cerci; paraprocts but little developed and largely or wholly membranous; genitalia consisting of double symmetrical penes, with or without parameres; virga absent in the forms studied; post-sternum present or absent.

DERMAPTERA. Terminal segments all distinct, none reduced; the tenth tergum greatly enlarged; ninth sternum forming a large, undivided hypandrium without styli; cerci very large, forcipate, unsegmented (except in immature stages of some genera); supra-anal plate divided into two or three segments, the second and third perhaps representing a vestigial telofilum; paraprocts in the form of thin, flat, free plates, occupying the sternal region of segment 10, there being no true tenth sternum in the types studied; penis elongate, bifid or double, with paired apertures, or single with one aperture; a virga or virgæ present; also a pair of parameres, usually lateral or dorsolateral arising from the walls of the penis.

EMBIIDINA. Terminal segments distinct, the ninth tergum shortened, the tenth large, somewhat asymmetrical and divided more or less completely into hemitergites bearing dissimilar copulatory processes; ninth sternum forming an asymmetrically triangular hypandrium, terminating in a copulatory process, without separate coxites or styli; cerci two-jointed, slightly asymmetrical, with rather large basipodites, of which the left may bear a copulatory process; the various copulatory processes converging toward the left side; supra-anal plate and paraprocts undeveloped (or vestigial); penis absent.

In the primitive genus *Clothoda* the parts are symmetrical, the tenth tergum undivided, the basipodites very large and projecting inward and the copulatory processes all absent.

PLECOPTERA. Terminal segments well developed, but not elongated, the ninth and tenth often more or less annular;

ninth sternum undivided and without styli, usually but little modified as a hypandrium; cerci typically elongate and multi-articulate; supra-anal plate extremely variable, sometimes simple and indistinctly separated from the tenth tergite, sometimes modified to form complex copulatory organs, which may be freely projecting and bent forwards to occupy a groove on the dorsum of the terminal segments, or concealed in a pocket which divides mesially the 10th tergum; paraprocts usually large and often fused with bases of cerci, frequently bearing copulatory hooks; penis, when present single (rarely bifid?), eversible, with or without a virga; sometimes with parameres.

ORTHOPTERA. Terminal segments more or less shortened; ninth sternum enlarged to form a hypandrium, sometimes divided by a transverse suture, with or without styli; cerci moderate or short, unsegmented (with rare exceptions, v. *Tridactylus*), often modified as claspers; with a small basipodite; supra-anal plate generally well developed, sometimes divided into a separate 11th tergite and telson (Acrididæ), not concealed by the tenth tergum; paraprocts variable, rarely (Tridactylidæ) bearing cercus-like processes; penis generally large, the ejaculatory duct emptying through a spermatophore sac, into which (typically) the bases of the parameres are retracted; a pseudosternite typically present, forming a collar over dorsum of penis and prolonged ventrad into a pair of rami, from which arise inward projections or apophyses for muscular attachment. Numerous modifications of this plan occur.

PHASMOIDEA. Terminal segments elongated, the genitalia being ventral instead of posterior in position; ninth sternum transversely divided, a small sternite being separated from a large, more or less-flap-like hypandrium (united coxites), without styli; cerci short, generally modified as claspers; supra-anal plate usually vestigial or absent, paraprocts moderate or prominent; penis apparently situated on the ninth sternal region, in reality on the elongated and secondarily chitinized interval between the ninth and tenth sterna, stout, asymmetrical, more or less distinctly divided into right and left lobes, the right overlapping the left, the ventrally placed genital aperture thus directed somewhat dextrad; dorsal surface somewhat chitinized and bearing in some forms a pair of cornua (parameres?).

GRYLLOBLATTOIDEA. Terminal segments not elongated, the tenth small but prominent; its lateral lobes prolonged ventro-mesad into a pair of asymmetrical copulatory arms; ninth sternum very large and asymmetrically divided into sternite and coxites bearing styli, the coxites probably serving as claspers; cerci segmented as in the female, with small basipodite; penis large, divided into two asymmetrical lobes, the right overlapping the left, the genital aperture probably in the intervening fissure; dextral lobe bearing an irregular, chitinous process; sinistral lobe with no chitinous process, but with an eversible membranous sac; a pair of plates bearing dextral copulatory processes near the dextral coxite, which bears an additional process; the processes together forming a clasping apparatus on the right side.

BLATTOIDEA. Terminal segments slightly abbreviated, but the tenth tergum prolonged into a flap which serves as a supra-anal plate; ninth sternum forming a large, undivided, but styligerous hypandrium; cerci of moderate length, flattened, multi-articulate; supra-anal plate disappearing in early nymphal life; paraprocts flattened, generally more or less chitinized beneath and often bearing asymmetrical copulatory hooks, or a single dextral hook; penis asymmetrical, consisting of a median lobe or process, directed more or less dextrad, bearing the genital opening, which is sometimes situated on a retractile virga, and two dissimilar lateral lobes, of which the dextral tends to overlap the sinistral, these lobes bearing the parameres (?) and frequently other accessory chitinous processes. One of the parameres may be modified into a retractile copulatory hook; the dextral lobe may bear a clasper.

MANTOIDEA. Terminal segments but little abbreviated, the tenth tergum forming a flap which serves as a supra-anal plate; ninth sternum forming a very large, but undivided hypandrium, bearing styli; cerci of moderate length, less flattened than in the Blattoidea, multi-articulate; supra-anal plate vestigial and membranous; paraprocts broad, somewhat flattened, unchitinized in the types studied; penis strongly asymmetrical, consisting of two dissimilar paramere lobes, the sinistral very large, the dextral small and overlapping the sinistral; ejaculatory duct wide, opening on the mesial surface of the sinistral lobe, with which the vestigial penis-lobe is fused. Sinistral lobe with a dorsal plate and two copulatory processes or titillators, of which the ventral represents the paramere (?), and one or two accessory processes; dextral lobe with a dorsal plate and a small ventral clasper.

ISOPTERA. Terminal segments scarcely abbreviated; the tenth tergum prolonged, serving as a supra-anal plate; ninth sternum forming a large undivided hypandrium, bearing styli; cerci short, of two to several segments; true supra-anal plate absent as a distinct structure; paraprocts broad and somewhat flattened, but little chitinized; penis absent or reduced to a small membranous lobe, the genital aperture single and median; no copulatory processes present.

ZORAPTERA. Ninth tergum abbreviated; tenth fused with supra-anal plate and paraprocts; cerci short and unsegmented; ninth sternum absent or membranous, the eighth apparently taking its place as a hypandrium; penis consisting chiefly of two asymmetrical processes, the sinistral a slender titillator, the dextral a large lobe bearing a subapical dorsal hook; position of genital aperture unknown.

ODONATA. Terminal segments elongated, the genitalia ventral in position; ninth sternum consisting of sternite and two separate, rudimentary coxites, without styli; the membrane between the ninth and tenth sterna somewhat chitinized so as to appear to belong to the ninth sternum; tenth sternum distinct; true or primitive penis very small and simple, without parameres (replaced by secondary penis on sternum of segment 2); cerci short and unsegmented; supra-anal plate elongate and projecting (Anisoptera) or small and inconspicuous, (Zygoptera); paraprocts rather large, without appendages (Anisoptera), or with copulatory processes (Zygoptera). In nymphs of many genera indications of a possible twelfth segment are present.

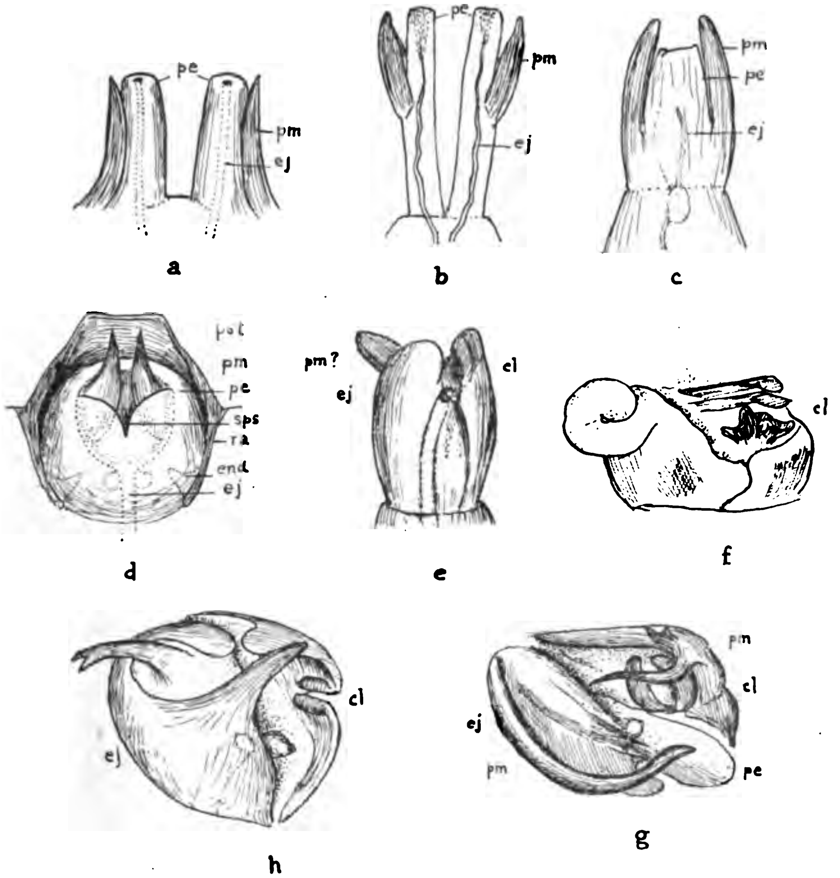

FIG. 6.

Fig. 6. Diagrams of male genitalia of Orthopteroid types of insects. a, Ephemerida, based on *Callibaetis;* b, Dermaptera, based on *Anisolabis;* c, Dermaptera, based on *Forficula;* d, Orthoptera, generalized type, based mainly on *Ceuthophilus;* e, Phasmoidea, *Diapheromera;* f, Grylloblattoidea, *Grylloblatta;* g, Blattoidea, based on *Periplaneta;* h, Mantoidea, based on *Stagmomantis.* For lettering, see page 71.

CONCLUDING REMARKS ON THE PHYLOGENY OF ORTHOPTEROID INSECTS.

In any attempt to unravel the relationships of a group of organisms it is obvious that the entire structure of the body should be taken into account. It would be beyond the scope of this paper, however, to do this for the Orthopteroid orders of insects, but it may be useful to examine the results of our studies of the terminal abdominal structures from this point of view, taking into consideration, at the same time, results obtained and opinions held by other workers on various regions of the body.

Few will deny, I think, that the Pterygota are descendants of either a single species of winged ancestor, or a group of nearly related forms in which the wings were evolved under similar conditions from homologous parts. The evolution of wings is a unique and anomalous development in the Arthropoda, and their invariable presence on the same two body segments with the same fundamental structure and plan of venation makes it exceedingly improbable that they have arisen independently in more than one group of nearly allied forms. Accepting this view, we must assume that there was a single species of common ancestor of winged insects possessing either wings or the appendages from which wings were evolved.

It is also generally agreed upon that the Thysanura is a primitively wingless group, as their general structure reveals a number of features that are more primitive than those of existing Pterygote insects.

If these premises are correct it follows that where structures or characters are found in both Thysanura and Pterygota, that are undoubtedly homologous, these structures or characters were present in the common ancestral Pterygote form, as also in the common ancestor of the Thysanura and Pterygota.

Thus, from what has been learned regarding the terminal segments and genitalia of the Orthopteroid insects, we should expect to find in the common Pterygote ancestor the following characters:

In both sexes:

(1). 10th sternum small, simple, distinct from paraprocts, without styli.

(2). A distinct supra-anal plate, bearing a segmented cerciform appendage.

(3). Well developed paraprocts, without additional appendages.

(4). Multi-articulate cerci.

In the male:

(5). Ninth sternum divided into sternite and styligerous coxites.

(6). Genitalia arising from the membrane between the sterna of segments 9 and 10, including a pair of parameres.

In the female:

(7). Eighth sternum with a median pair of appendages, the anterior gonapophyses.

(8). Ninth sternum represented mainly by the two elongate styligerous coxites, the lateral gonapophyses, and a median pair of appendages, the posterior gonapophyses.

(9). Genital apertures in the membrane between the sterna of segments 8 and 9.

There were probably two male genital apertures, each on a separate penis, as in the Ephemerida. The single penis of the Thysanura has probably been independently acquired, apparently by the union of the two primary penes, with no invagination to form a common ejaculatory duct. Otherwise we have to assume that the double or bipartite penis in the Ephemerida and Dermaptera as a secondary condition.

The double genital apertures of female Ephemerida are likewise to be considered as probably a primitive character, although their position between the 7th and 8th sterna is secondary. The occurrence of a single aperture in both the Thysanura and the majority of the Pterygota must be regarded as a parallelism, and not a surprising one, as a tendency towards a distal union of the genital ducts is very common in the Arthropoda.

The retention of this primitive character together with others, such as the median cerciform appendage, jointed coxites, the numerous moults, occurrence of a subimago stage, etc., stamp the Ephemerida as far removed from other orders and indicate that their line of descent had separated off before those of the other orders had become differentiated.

Next to the Ephemerida the Odonata are the most clearly circumscribed group, having no near allies among recent insects. The 9th sternum of the male preserves clear traces of the original division into sternite and coxites, and the lateral gonapophyses of the female are unique among Pterygote insects in retaining the styli in the adult stage. They also resemble the Thysanura (Machiloidea and Lepismoidea) somewhat in the form of these structures and their relation to the other two pairs of gonapophyses. In their venation and general structure of the body they show no near relationship to the other groups here considered and may be regarded as having probably separated off next in order after the Ephemerida.

In the remaining orders we may recognize two general trends of evolution. In the one the tarsi became 3-jointed (or remained thus), the ovipositor was reduced and subsequently in most cases wholly lost, the coxites of the male were fused with the 9th sternite, and the styli disappeared in both sexes.

One of the branches from this stock gave rise to the Plecoptera and probably from the same branch arose the Embiidina. From another branch the Dermaptera were evolved. The cerci were originally segmented in all of these groups, but lost this primitive character in the Dermaptera. The ovipositor was probably reduced in the common ancestor of all these orders and completely disappeared in all but a few of the Dermaptera.

The terminal abdominal structures, however, throw little light on the relationships of these groups and the views expressed here are based largely on the work of Crampton.

The other trend of evolution among Orthopteroid insects shows itself in the presence of 5-jointed tarsi, a well developed ovipositor, the retention of separate styligerous coxites in the male and the loss of the double penis. In most of the modern descendants of this branch, however, the coxites of the male have fused with the 9th sternite, or with one another, in many the number of tarsal joints has been secondarily reduced, while in some the ovipositor has become vestigial or absent.

In this assemblage of groups there are two types of genitalia so distinct as to indicate with some probability two main lines of divergence. In one of these we have the true Orthoptera, in which the primitive bilateral symmetry of the penis has been retained, but the organ has acquired a peculiarly complex structure very distinct from that of any other group. In the earliest representatives of this line (Protorthoptera?) there was undoubtedly a well-developed ovipositor without styli; a subgenital plate was formed in the female from the 8th sternum and in the male from the fused coxites, which in all but the branch leading to the Acridoidea, united also with the 9th sternite. Styli were present in the males of primitive forms. The cerci were probably short and unsegmented or had few segments (as indicated by Tridactylus, in which the two-jointed cerci may be a secondary feature). The tarsi may have been 5-jointed in the earliest forms, as suggested by many Tettigoniidæ, but in all modern species the actual number of joints is 4 or less. The primitive plecopteroid form of body was apparently lost at an early stage, correlated with the development of saltatorial hind legs.

The second type of male genitalia is seen in the Phasmoidea, Grylloblattoidea, Blattoidea, Mantoidea and Zoraptera (?), and was doubtless present in the forbears of the Isoptera. This type of genitalia is asymmetrical and consists of the ejaculatory duct, sometimes borne upon a penis, between two unequally developed lobes or processes, right and left, which probably represent the parameres. The sagittal plane is usually so shifted that the right lobe overlies the left. Associated with this type of genitalia is a distinct tendency towards the reduction of the supra-anal plate.

These peculiarities are least marked in the Phasmoidea, which probably separated first. In this group many of the primitive Plecopteroid characters have been retained, particularly in the cervical sclerites, propleura, small and widely separated coxæ, and in the presence in such primitive forms as Timema, of well developed intersegmental sclerites in front of the meso- and metaterga (Crampton, '19). The cerci became short and lost their segmentation, while the male coxites fused as in the Orthoptera and lost their styli. The development in the female of a large subgenital plate from the 8th sternum also recalls the Orthoptera. These last features together with the rather strongly Orthopteroid wing-venation make the position of the order doubtful. It is perhaps equally well placed at the base of the Orthopteran stem, in which case the resemblance of the penis to that of the other orders in which it is asymmetrical must be looked upon as a case of convergence.*

In the Grylloblattoidea the ovipositor is retained in its primitive exposed form, there being no distinct subgenital plate. The coxites in the male remain separate from the 9th sternite, and the supra-anal plate, though small, is distinct in the adult. The Plecopteroid form of body is retained, with many primitive features, e. g., in the cervical sclerites, the propleura, and separate latero-sternites of the meso- and metasterna. The legs, however, are Blattoid and the coxæ large and close together like all of the Blattoid groups.

In the Blattoidea, Mantoidea and Isoptera so many common features are present that we need have no hesitation in considering them as belonging to one common stock. The ovipositor is concealed by a large subgenital plate, the modified sternum of the 7th abdominal segment. It is reduced in the Blattoidea and is vestigial or absent in the Isoptera. The coxites of the male have fused with the ninth sternite, but the styli are retained. The penis, except in the Isoptera, in which it has disappeared, is remarkable for its extreme asymmetry of structure, which as in *Grylloblatta*, may be shared by neighboring parts. The cerci tend to shorten, being generally reduced in the Isoptera to two segments. The supra-anal plate is replaced by the 10th tergum. Among other peculiarities is the form of the cervical sclerites, the ventral pair of which meet in the middle line. The tarsi are primitively 5-jointed, even in the Isoptera, in which the number of segments is commonly reduced.

The exact relationship of the Isoptera to the other two orders is very uncertain. The form of the body and position of the head is more "plecopteroid" and hence apparently more

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* The abdominal musculature, according to Miss Ford, shows a nearer relationship to the Blattoid-Mantoid type than to the Orthopteran type.

primitive than in these orders, but this may be due to adaptation to a life in passages or galleries, in which the flattened form of the Blattids would be a disadvantage. The thoracic sclerites are simpler and in some respects apparently more primitive than those of the Blattids, as shown by Crampton, but these more primitive features may have been present in extinct cockroaches. The similarity of the two pairs of wings is evidently secondary, due to reduction of the anal area of the hind wings. This is indicated by the distinctly expanded anal area of the hind wings in the primitive genus Mastotermes, in which the venation also approaches more closely the Blattid type. On the whole, however, it is perhaps best to consider the Isoptera as springing from the Protoblattoidea, a palaeozoic order from which probably all three orders of the Blattoid group were developed. As far as the terminal abdominal structures are concerned the Blattoidea and Mantoidea are more like one another than are the various families of Orthoptera.

The Zoraptera appear to have affinities with the Grylloblattoidea and the three orders just discussed. Like the former they are plecopteroid in the structure of the cervical sclerites, even more so, on account of the presence of a dorsal sclerite in this region (Crampton, '20). The thoracic sclerites show points of resemblance to *Grylloblatta* and the Isoptera, while the coxæ are large and much like those of Grylloblatta. The asymmetrical penis also apparently belongs to the type characteristic of the group of orders we have been discussing. On the other hand there is a loss in the male not only of the styli but of the 9th sternum itself (unless it be represented by the membranous lobe shown in Crampton's figure) (l. c., Pl. VII, Fig. 2), a structure otherwise so conspicuous in this assemblage of groups. The lack of modification of the 7th abdominal sternum as a subgenital plate places it nearer *Grylloblatta* than the other three orders, but Crampton finds important points of resemblance with the Isoptera. The reduction of the tarsal joints to two and the cerci to a short unsegmented structure, and the modification of the anal plates are peculiarities which set this order somewhat apart from the others, but I should place it tentatively as a branch arising near the point of divergence of the Grylloblattoidea from the Protoblattoidea.

This position is consistent with Crampton's views as to its relationships with the Plecoptera and Isoptera and probably also the Psocida.

These relationships are expressed in the accompanying table (Fig. 7).

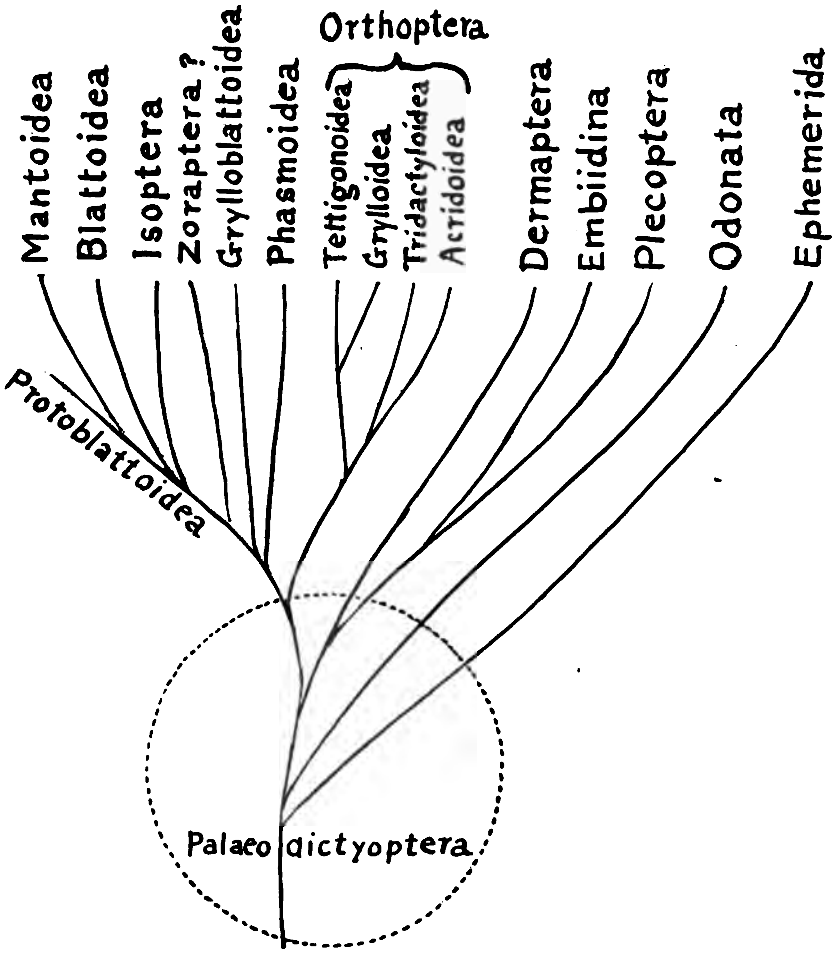

Fig. 7. Phylogeny of Orthopteroid Insects.

APPENDIX TO PART I.

There are a few matters discussed by Chopard ('20) in his excellent treatment of the female genitalia of the Orthoptera, on which my views do not quite coincide with his. The most important of these are the following:

Origin of the "pileolus" and subgenital plate in the Tettigonoidea and Grylloidea. Chopard contends that the subgenital plate in these groups develops, not from the 8th sternum (sternite) but from the membrane between the 8th and 9th sterna. His observations on ***Pholidoptera femorata*** Fieber agree closely with mine on *Ceuthophilus* and *Conocephalus* and his conclusions are reasonable, but it appears to me unnecessary to give up the view that the subgenital plate is formed from the 8th sternum. According to Chopard the 8th sternum is already, at the 2nd nymphal stage, reduced to two lateral pads, one at the base of each ventral valve. During subsequent growth these become shifted more and more laterad and finally form the small triangular plate, which is termed by Chopard the "pileolus" (valvifer). The subgenital plate appears at the third nymphal stage in the form of a pad, or fold, arising from the membrane, which separates the base of the ovipositor from the 7th sternum. This view seems to imply that the "genital pocket," under the subgenital plate, is an infolding of the membrane, but it appears to me to be formed rather by an infolding of the 8th sternum itself, which is quite flexible in the young nymph; so that, according to the latter view, the subgenital plate may be interpreted as an outgrowth from the basal part of the 8th sternum. The greater part of the sternal area is thus represented by the lining membrane of the genital cavity. This view is sustained by Miss Ford's findings in her study of the musculature of the parts in question, which are as yet unpublished. The two parts considered by Chopard to be the vestiges of the 8th sternum are the structures for which I have employed Crampton's term "basivalvula" and are, of course, quite properly assigned to this segment. But, although they do become shifted laterad, as Chopard states, they clearly do not become the pileolus or valvifer. This is derived from that part of the 9th sternal area which lies laterad of the bases of the dorsal valvulæ. Even in the adult the intersegmental groove can be traced along the front margin of the valvifer, and the apodeme which runs along this boundary line is frequently continued along the front margin of the valvifer. Chopard's "pièce laterale" in the Blattoidea and Mantoidea is the same structure and is likewise ascribed by him to the 8th sternum. The "pièce laterale en baguette" is the valvifer together with the intersegmental apodeme which in the Blattids crosses a wide membranous area between the valvifer and the tergal margins.

Position of the genital aperture in the Blattoidea and Mantoidea. Chopard maintains that the genital aperture in these groups lies between the 7th and 8th sterna, instead of occupying its usual position between the 8th and 9th. This is a subject upon which I did not lay sufficient stress in Part I of this paper. The aperture in question has certainly experienced a forward shifting, as it lies distinctly cephalad of the bases of the ventral valves of the ovipositor, and is overhung by the "epigynum," which I agree with Chopard in considering as the homologue of the subgenital plate of the Orthoptera. But, as I consider this plate to belong to the 8th sternum rather than the membrane between the 8th and 9th sterna, I should describe the genital aperture as occupying the 8th sternal area, although the sternum itself has virtually disappeared as an individual sclerite. The position of the genital aperture in the Orthoptera and Grylloblattoidea is not really fundamentally different from this.

Ovipositor of the Isoptera. Since Part I of the present paper was published an interesting article by Crampton appeared entitled "The Terminal Abdominal Structures of the Primitive Australian Termite, *Mastotermes darwinensis* Froggatt (Crampton, '20). The important fact brought out is the presence in females of the solider caste in this species of three pairs of gonapophyses of distinctly primitive form, the lateral pair (dorsal valvulæ) terminating in well developed styli. As shown in Crampton's figure the resemblance to the immature Blattid or Mantid is unmistakable, much closer than to *Grylloblatta*, although all of these four types are much alike in essentials. The short, broad lateral gonapophyses, clearly forming part of the 9th sternum, and the reduced 8th sternum, overlapped by the large 7th sternum, are strongly Blattoid features.

The presence of these gonapophyses in Mastotermes is a clear proof of their having been present in the ancestral termites, and confirms my interpretation of the extremely rudimentary structures in Termopsis, which I took to represent a vestigial ovipositor.

ERRATA—PART I.

P. 286, 11th line from bottom; *R. forcipata* is an error for *R. forceps* Sauss. The species figured, however, is *R. carbonaria* Sauss.

P. 315, 13th line from bottom; for "*Ripipteryx forcipata* Sauss." read "*Ripipteryx carbonaria* Sauss."

P. 316. The explanation of Fig. 34, as given, applies to Fig. 35, that of Fig. 35 to Fig. 36, and so on to the end, the last figure being No. 75, instead of 76. The correct explanation of Fig. 34, which was omitted, is as follows:

34. Same; ventral view of dorsal and inner valvulæ.

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REFERENCE LETTERING.

(For additional lettering, see explanation of figures).

ar—Arch of endapophysis.
bc—basipodite of cercus.
c—cercus.
cf—caudal filament or telofilum.
ch—copulatory hook.
cl—clasper.
cx, cx 9—coxite, coxite of 9th segment.
cxx—coxale or united coxites.
cxl, cxr—left and right coxites.
dl—dorsal lobes of penis.
ej—ejaculatory duct.
end—endapophysis.
fps—floor of paramere sac.
gl p—glans of penis or penis lobe.
int s m—intersternal membrane.
int t m—intertergal membrane.
ll—left paramere lobe.
lst—lateral stylet.
m st—median stylet.
pa—paraproct.
pal—pallium.
pal pl—pallial plate.
pc—postcornua or processes of pseudosternite.
pe—penis.
pg—paragenital plate.
pm—paramere, or its main process; ectoparamere.
pmb—base of paramere, endoparamere.
pmo—opening into paramere.
pms—paramere sac.
pst—pseudosternite.
ra—ramus of pseudosternite.
rl—right paramere lobe.
s 7, s 8, etc.—sternum of 7th, of 8th segment, etc.
sa—supra-anal plate.
sp—spiracle.
sp gl—lateral glandular pouches.
spc—sperm conveyor.
sps—spermatophore sac.
st, st 7, etc.—sternite, sternite of segment 7, etc.
stl, stl 7, etc.—stylus, stylus of 7th segment, etc.
svl—subventral lobe.
t 7, t 8, etc.—tergum of 7th segment, of 8th segment, etc.
v—virga.
vl—ventral lobe of penis.
vs—dorso-median spines of spermatophore sac.

EXPLANATION OF PLATES.

PLATE I.

1. *Machilis* sp. (Machiloidea). Ventral view of terminal segments.
2. *Blasturus nebulosus* Walk. (Ephemerida). Ventral view of terminal segments.
3. Same, ventral view of penis.
4. *Callibaetis ferrugineus* Walsh. (Ephemerida). Ventral view of terminal segments.
5. *Forficula auricularia* L. (Dermaptera). Lateral view of terminal segments.
6. Same, ventral view of penis.
7. *Anisolabis maritima* (Gene). (Dermaptera). Ventral view of end of abdomen.
8. Same, ventral view of penis.
9. *Oligotoma saundersii* Westw. (Embiidina). Dorsal view of end segments. r ap 10, 1 ap 10, right and left copulatory appendages of 10th tergum.
10. Same, ventral view of end segments. Lettering as in Fig. 9.

PLATE II.

11. *Capnia vernalis* Newp. (Plecoptera). Dorsal view of end segments.
12. Same, ventral view of end segments.
13. Same, lateral view of end segments.
14. *Isogenus frontalis* Newm. (Plecoptera). Dorso-caudal view of end segments, the 10th and anal segments being somewhat upturned. sc, sac containing stylets, formed by invagination of the supra-anal plate. The 10th tergum is also divided into hemitergites by a median invagination, which forms a ventral apodeme.
15. Same; dorsal view of separated 10th and anal segments. The hemitergites of segment 10 are somewhat spread apart to expose the supra-anal plate. m ap, apodeme formed by invagination of 10th tergum.
16. Same, ventral view of isolated supra-anal plate. sc, sac containing the stylets and supported laterally by the paragenital plates.
17. Same, lateral view of isolated supra-anal plate, together with ventral apodeme (m ap), formed by median invagination of 10th tergum. sc as in Fig. 16; bb, basal bar connecting stylets with apodeme.
18. *Isoperla* sp. (Plecoptera). Ventral view of end segments. The copulatory hooks are processes of the paraprocts. Segments 8 to 10 are annular, the terga and sterna being fused.
19. *Perla tristis* Hag. (Plecoptera). Ventral view of end segments, the 9th sternum partly cut away to show the penis. Copulatory hooks as in Fig. 18. The 10th sternum is not separable from the intersternal membrane.
20. Same, ventral view of penis.
21. *Aeshna canadensis* Walk. (Odonata). Ventral view of terminal segments.

PLATE III.

(Orthoptera—Tettigonoidea).

22. *Ceuthophilus lapidicola* Burm. Posterior view of penis with parameres retracted; fps, a temporary fold, formed by the retraction of the parameres and dividing the shallow spermatophore sac into an upper and lower part, the upper part corresponding to the paramere sac of most Tettigonoidea (Figs. 30 and 32), and the spermatophore sac in the Gryllidæ; pmo, opening into the invaginated parameres.

23. Same, posterior view of penis with parameres everted. The spermatophore sac is obliterated and the genital aperture concealed by the ventral lobe.
24. Same, lateral view of penis with parameres almost completely everted. Potash preparation.
25. Same, dorsal view of penis, with parameres retracted and inner parts exposed. Potash preparation. The parameres are unnaturally retracted owing to removal of enveloping muscles.
26. *Ceuthophilus aridus* Bruner? Posterior view of end of abdomen with penis very strongly retracted. The roof of the penis is drawn below the level of the ventral lobe, the walls thus forming a pair of lateral ridges. The pseudosternite is forcibly elevated to show the small arched passage (ar ej), which bridges over the ejaculatory duct in the retracted condition.
27. *Ceuthophilus maculatus* (Harr.). Posterior view of end of abdomen, the penis everted, but the parameres probably only partly so.
28. *Ceuthophilus lapidicola* (Burm.). Late nymphal stage. Dorsal view of penis with internal parts exposed. Potash preparation.

PLATE IV.

(Orthoptera—Tettigonoidea).

29. *Neduba carinata* Walk. Posterior view of end of abdomen. vs,* the valve-like plates on the under side of the fold (fps) that separates the spermatophore sac proper from the paramere sac.
30. Same, dorsal view of separated penis; potash preparation. The pseudosternite (pst) is represented only by a membranous fold (cut away on the right side). pmo, opening into paramere, occupied by muscles in the natural condition.
31. Same, lateral view of separated penis; potash preparation.
32. *Conocephalus brevipennis* (Scudd.). Posterior view of penis.
33. Same, dorsal view of penis.
34. *Conocephalus fasciatus* (DeGeer). Last stage of nymph; posterior view of end of abdomen. The parameres are represented only by a slight chitinization of the roof of the penis, just inside the wide genital aperture.
35. *Cyphoderris monstrosa* Uhl. Posterior view of end of abdomen. cps, a large, hook-like copulatory process, arising from the vertically placed sternum of segment 9.
36. Same, lateral view of the 9th sternum, showing the large copulatory process (cps).

PLATE V.

(Grylloidea and Tridactyloidea).

37. *Gryllus assimilis* (Fabr.). (Grylloidea). Dorsal view of separated penis, ventral lobes omitted. The integument is cut through just in front of the pseudosternite.
38. Same, ventral view of penis, the free parts of the ventral lobes cut off in order to show the spermatophore sac and structures underlying the pseudosternite.
39. Same, lateral view of separated penis; potash preparation.
40. Same, postero-ventral view of genitalia of last nymphal stage.
41. Same, ventral view of genitalia of last nymphal stage.
42. *Nemobius fasciatus* (DeGeer). (Grylloidea). Dorsal view of separated genitalia. The anterior, lighter part of the pseudosternite lies beneath the outer integument. The ventral lobes are represented as showing through from above.
43. Same, ventral view of genitalia.

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*sv, in Figs. 30 and 31.

44. *Oecanthus nigricornis* Walk. Dorsal view of separated genitalia; potash preparation.
45. Same, posterior view of genitalia.
46. Same, lateral view of genitalia; potash preparation.
47. *Ripipteryx carbonaria* Sauss. (Tridactyloidea). Dorsal view of terminal segments. ch, copulatory hooks, apparently arising from the paraprocts.
48. Same, lateral view of terminal segments. Lettering as in Fig 47.
49. Same, dorsal view of penis; potash preparation. In front of the reflected integument (int) the organ lies beneath the outer surface.
50. Same, right lateral view of penis; potash preparation.

PLATE VI.

(Orthoptera—Acridoidea).

51. *Dissosteira carolina* L. Dorsal view of terminal segments.
52. Same, dorsal view of genitalia; potash preparation.
53. Same, ventral view of genitalia; potash preparation.
54. Same, lateral view of genitalia; potash preparation.
55. *Melanoplus bivittatus* (Say). Dorsal view of genitalia; parts in their natural position.
56. Same, dorsal view of genitalia with the pseudosternite omitted; potash preparation. The dorsal and ventral lobes are spread apart so as to show their relations to the parameres and to one another.
57. Same, ventral view of genitalia; potash preparation. The ventral lobes are spread apart to show the entire parameres. The ejaculatory duct is cut off at its junction with the spermatophore sac.
58. *Tettigidea lateralis parvipennis* (Harr.). Left lateral view of terminal segments. The pallial plates are elevated, exposing the proximal part of the rami.
59. Same, antero-dorsal view of genitalia. Only the anterior edges of the pallial plates are seen, these plates being elevated to expose the genital cavity.
60. *Acrydium granulatum* Kirby. Antero-dorso-lateral view of terminal segments. gc, opening into the genital cavity; pal h, pallial hooks.
61. *Melanoplus bivittatus* (Say). Median sagittal section through genitalia.

PLATE VII.

(Grylloblattoidea).

62. *Grylloblatta campodeiformis* E. Walk. Dorsal view of terminal segments.
63. Same, ventral view of terminal segments.
64. Same, posterior view of end of abdomen. cxp, process borne by right coxite, and forming with cl and lm a copulatory clasping apparatus; es, eversible sac, arising from left paramere lobe; at 10, arm of 10th tergum, with terminal sucker-like disc.
65. Same, ventro-posterior view.
66. Same, half-grown nymph. Ventral view of terminal segments.
67. Same, full-grown (?) nymph. Ventral view of terminal segments.
68. Same, full-grown nymph. Posterior view of end of abdomen.

PLATE VIII.

(Grylloblattoidea, Phasmoidea, Isoptera, Zoraptera).

69. *Grylloblatta campodeiformis* E. Walk. Right lateral view of terminal segments. cxp, spur-like process of right coxite; es, eversible sac arising from left paramere lobe.
70. Same, left lateral view of terminal segments.
71. *Anisomorpha buprestoides* (Stoll). (Phasmoidea). Ventral view of terminal segments. dpl, dorsal plate; vpl, ventral plate.
72. Same, dorsal view of penis.
73. Same, ventral view of penis.
74. *Diapheromera femorata* (Say). (Phasmoidea). Dorsal view of penis. ap, apodeme arising from base of cl; dpl, dorsal plate; pm (?) cornu, possibly representing the left paramere.
75. Same, ventral view of penis. Lettering as in Fig. 74.
76. *Termopsis angusticollis* Hagen (Isoptera). Ventral view of terminal segments.
77. Same, left lateral view of terminal segments.
78. *Zorotypus hubbardi* Caudell. (Zoraptera). Left lateral view of terminal segments. (After Crampton).
79. Same, dorsal view of genitalia. (After Crampton).

PLATE IX.

(Blattoidea).

80. *Blattella germanica* (L.). Posterior view of end of abdomen. The thin flap of the tenth tergum is elevated and the ninth sternum depressed to show the genitalia.
81. Same, dorsal view of genitalia and underlying parts, after removal of terga. The paraprocts are spread apart. The hooked left paramere is retracted into its sheath (sh). ap s 9, apophysis of 9th sternum.
82. Same, dorsal view of right paramere. The "clasper" (cl) probably serves here only for the attachment of muscles.
83. Same, ventral view of right paramere.
84. *Parcoblatta pensylvanica* (Burm.). Posterior view of end of abdomen, the 9th sternum cut away to show the genitalia. The left paramere is retracted, only the end of the hook being exposed. Each paraproct bears a copulatory hook, of which the right is large and heavily chitinized.
85. Same. dorsal view of right paramere. The "clasper" (cl) probably only serves for the attachment of muscles.
86. Same, ventral view of right paramere.
87. Same, dorsal view of left paramere, partly everted from its sheath.
88. Same, posterior view of abdomen of young nymph, showing the vestigial supra-anal plate.
89. *Periplaneta* sp., last stage of nymph. Ventral view of genitalia.
90. Same, ventral view of genitalia, with penis lobe (gl p) depressed.

PLATE X.

(Blattoidea).

91. *Periplaneta fuliginosa* Brunn. Dorsal view of right paramere. dcl, dorsal valve of clasper; pml, shaft of paramere, terminating in the processes pm^1, pm^2, etc.
92. Same, ventral view of right paramere. vcl, ventral valve of clasper. For other lettering see Fig. 91.

93. Same, ventro-lateral view of right paramere, the two valves of the clasper, dorsal (dcl) and ventral (vcl) forced open.

94. Same, dorsal view of left paramere or paramere lobe. pm, shaft of paramere; ll^1, ll^2, etc., secondary processes from paramere lobe.

95. Same, lateral view of left paramere. Lettering as in Fig. 94.

96. *Periplaneta brunnea* Burm. Ventral view of right paramere. For lettering see Figs. 91 and 92.

97. Same, dorsal view of left paramere. Lettering as in Fig. 94.

98. *Periplaneta americana* L. Ventral view of right paramere. For lettering see Figs. 91 and 92.

99. Same, dorsal view of left paramere. Lettering as in Fig. 94.

PLATE XI.

(Blattoidea, Mantoidea).

100. *Periplaneta fuliginosa* Brunn. (Blattoidea). Dorso-posterior view of genitalia, the 9th sternum strongly depressed. pm, main shaft of left paramere; the secondary processes borne by ll lying to the right; pm^1, basal part of shaft of right paramere; pm^2, the principal terminal process.

101. *Blaberus atropos* Serv. (Blattoidea). Posterior view of end of abdomen, the 9th sternum, which is asymmetrical, somewhat depressed to show the genitalia. The 10th tergum is foreshortened. The right paramere, a long copulatory hook, is completely retracted within its sheath. The right paramere lobe extends far to the left in the form of a horizontal flap.

102. Same, left paramere.

102. Same, dorsal view of left paramere. df, dorsal flap.

103. Same, postero-dorsal view of left paramere, with the dorsal flap (df) reflected.

104. *Stagmomantis carolina* (L.) (Mantoidea). Posterior view of end of abdomen, the 9th sternum strongly depressed. lpm, the main process of the left paramere lobe, probably homologous with pm in Fig. 100; ll^1, ll^2, processes from left paramere lobe; df, dorsal flap of right paramere (cf. Figs. 100 and 101).

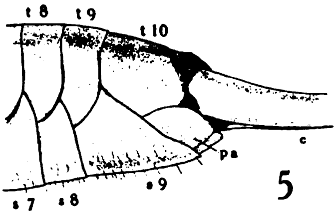
105. Same, dorsal view of genitalia in natural position. The clasper (cl) is represented as showing through, as in a cleared preparation. r pmb, base of right paramere. Other lettering as in Fig. 104.

106. Same, ventral view of genitalia. r pm, l pm, right and left paramere bases. Other lettering as in Fig. 104.

107. Same, ventral view of isolated right paramere.

108. Same, lateral view of left paramere. Lettering as in Fig. 104.

109. Newly hatched nymph of undetermined Japanese Mantid. Ventral view of terminal segments, showing well-marked supra-anal plate and processes of the 9th sternum, representing coxites and styli.



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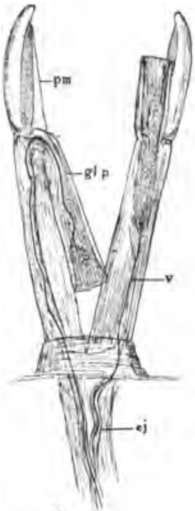

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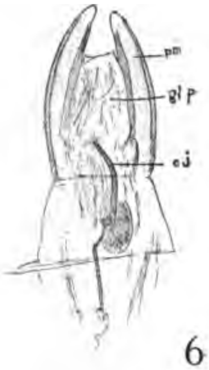

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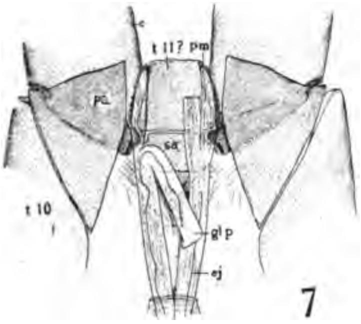

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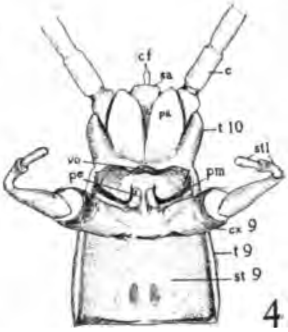

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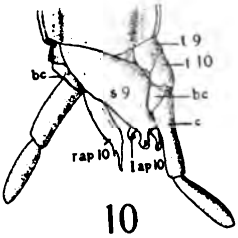

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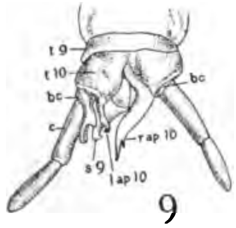

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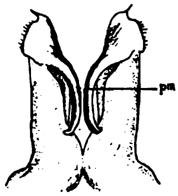

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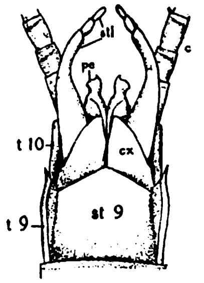

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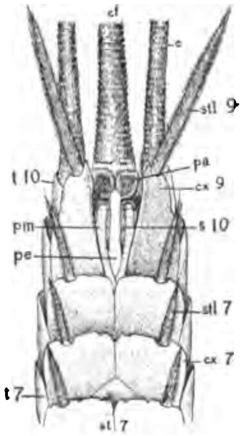

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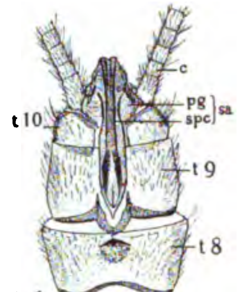

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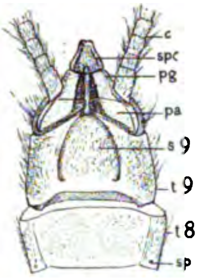

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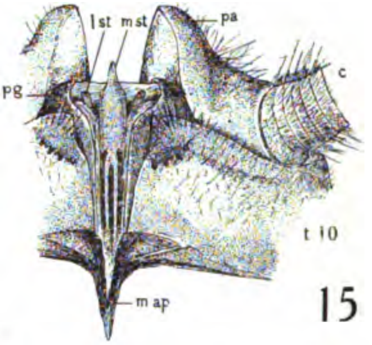

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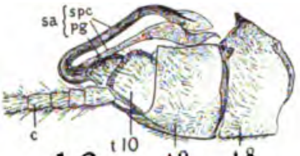

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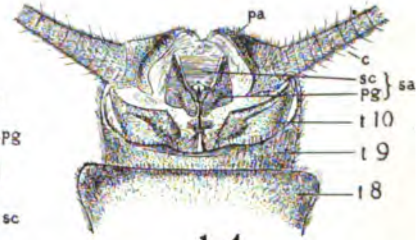

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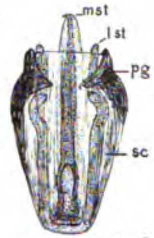

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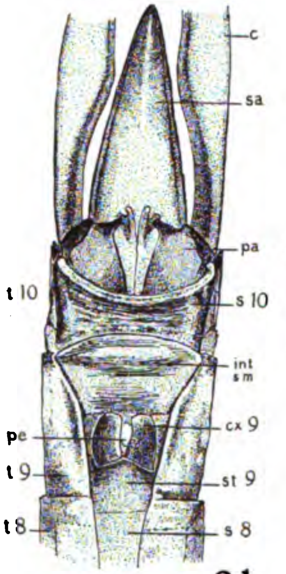

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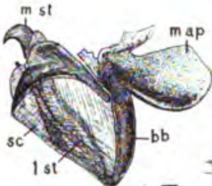

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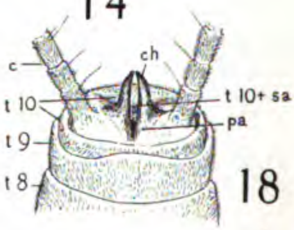

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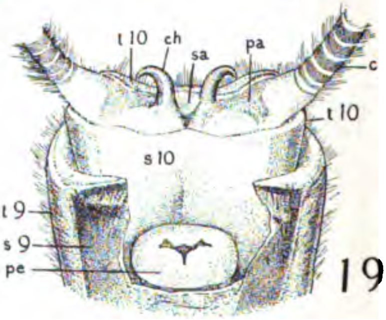

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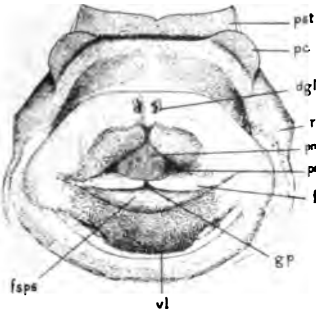
E. M. Walker.



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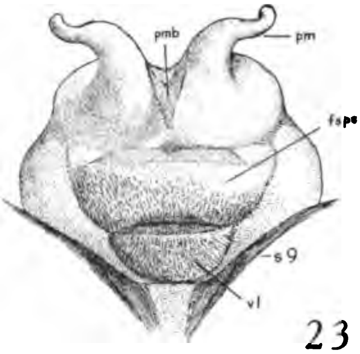

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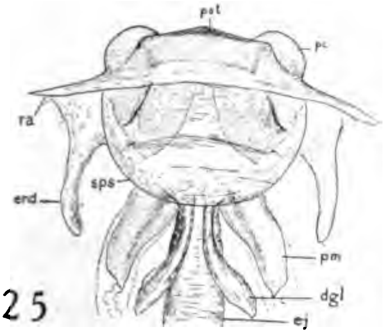

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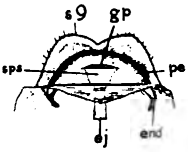

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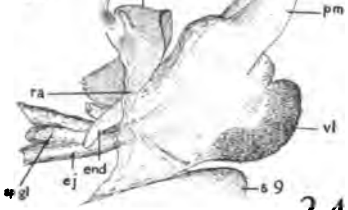

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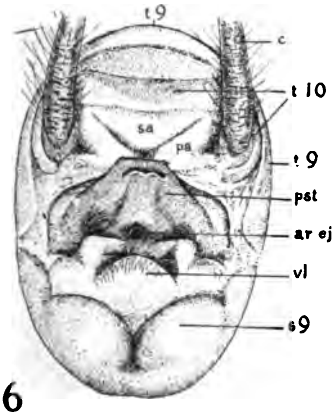

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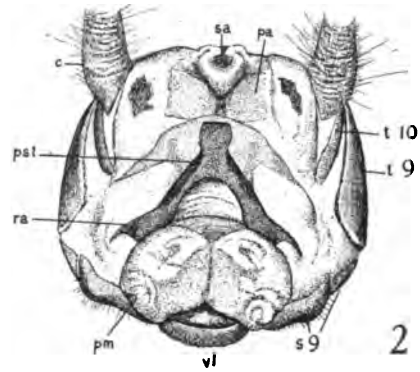

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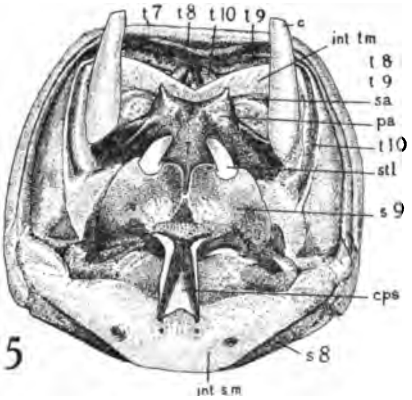

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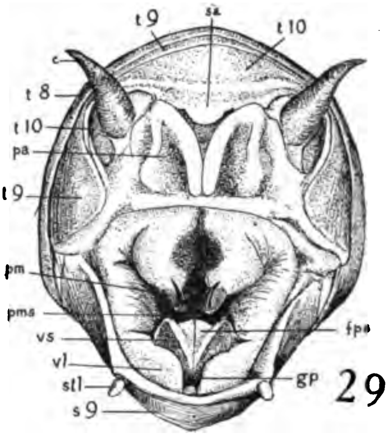

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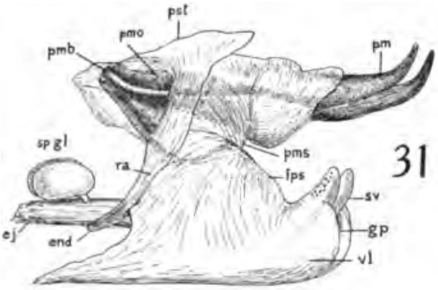

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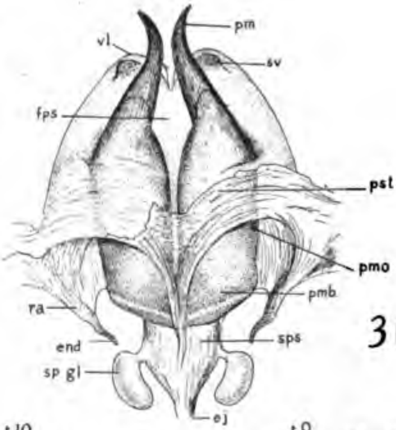

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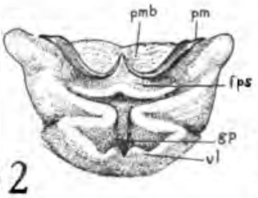

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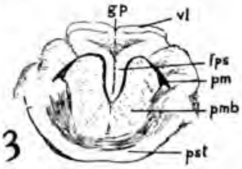

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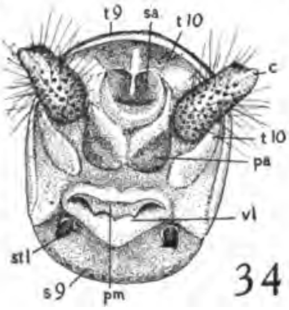

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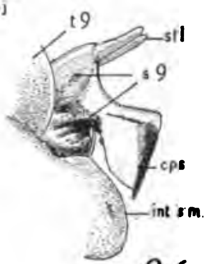

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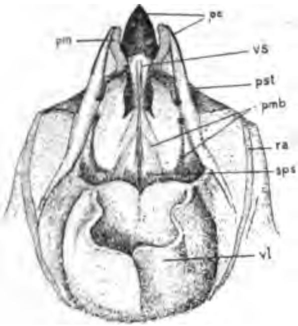

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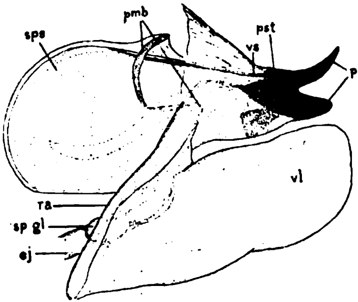

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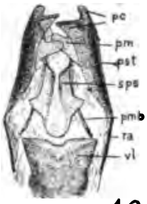

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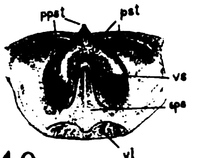

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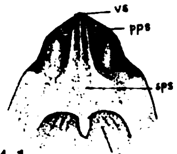

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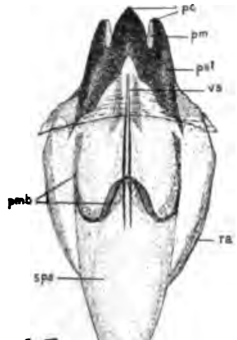

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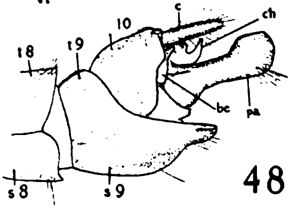

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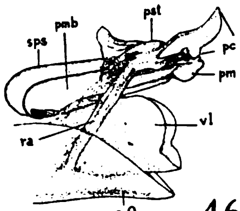

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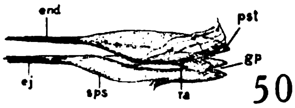

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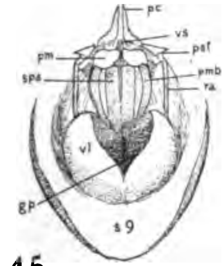

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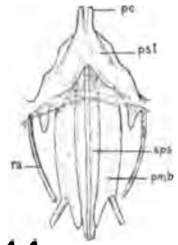

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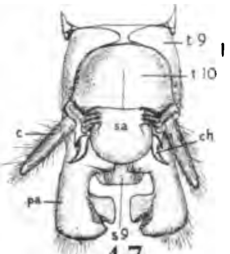

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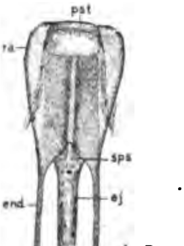

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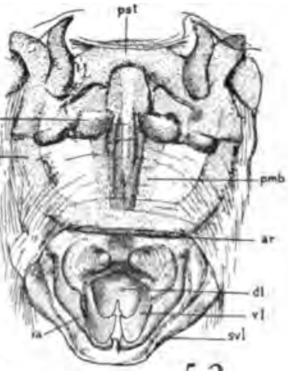

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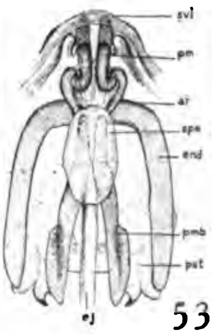

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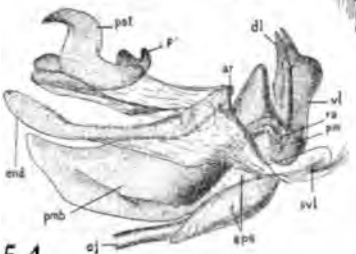

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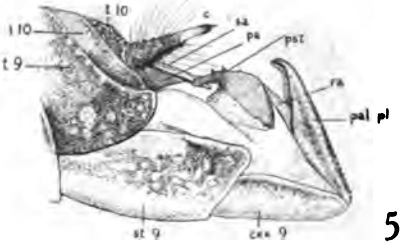

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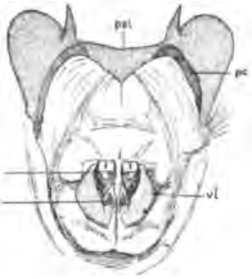

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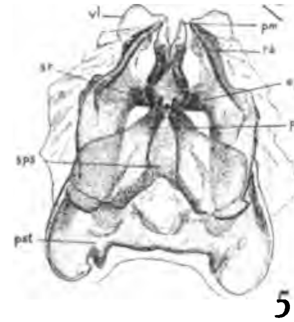

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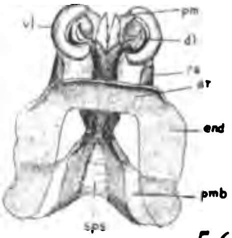

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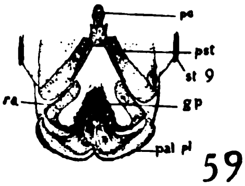

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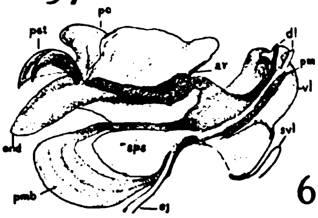

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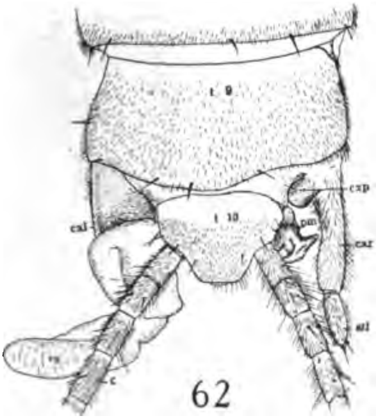

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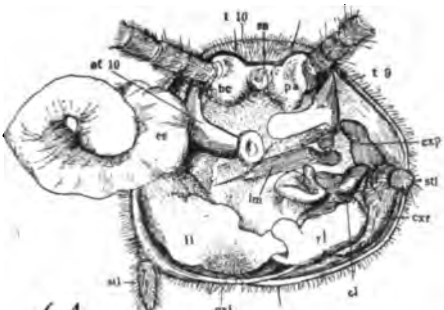

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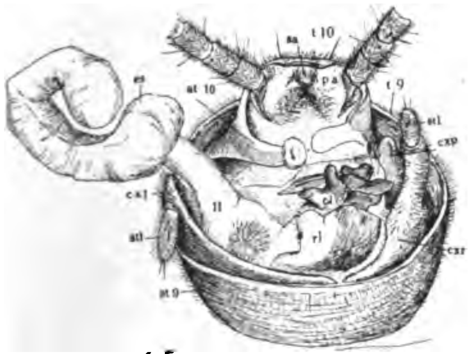

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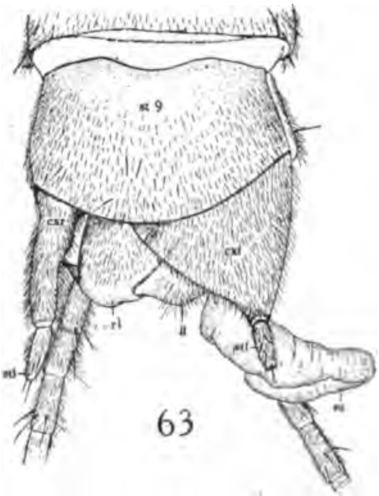

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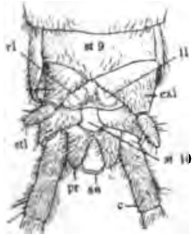

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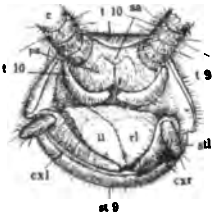

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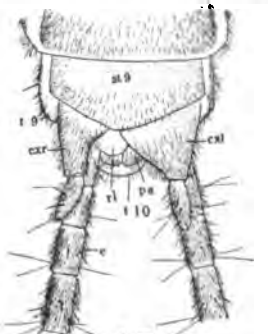

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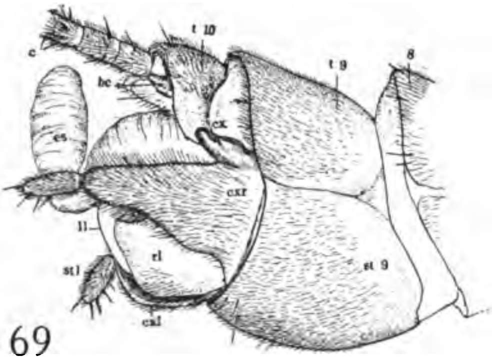

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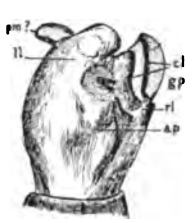

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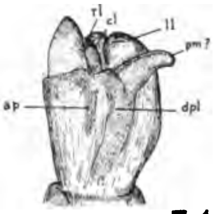

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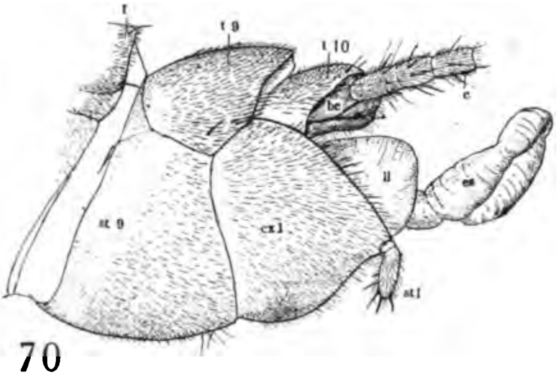

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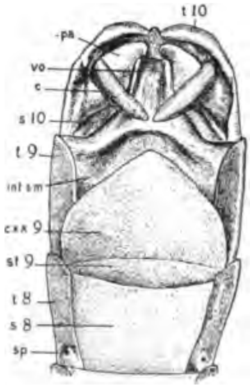

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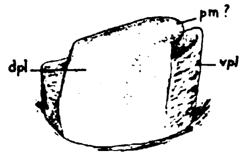

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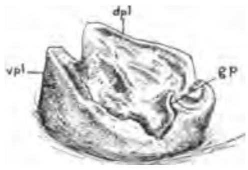

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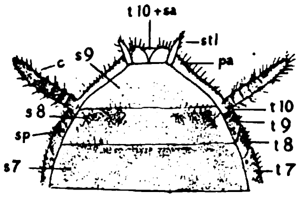

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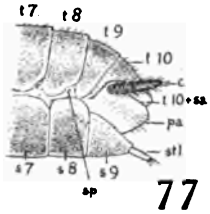

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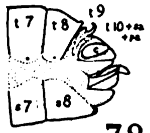

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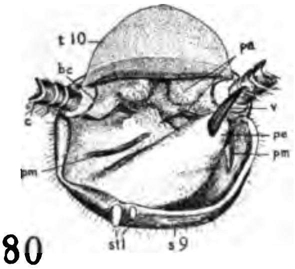

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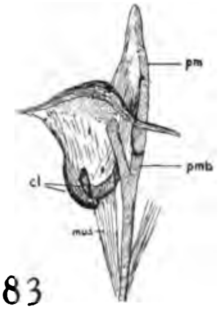

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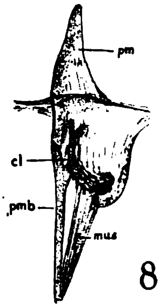

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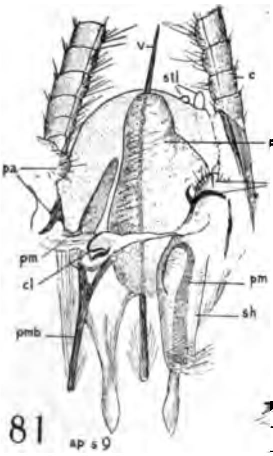

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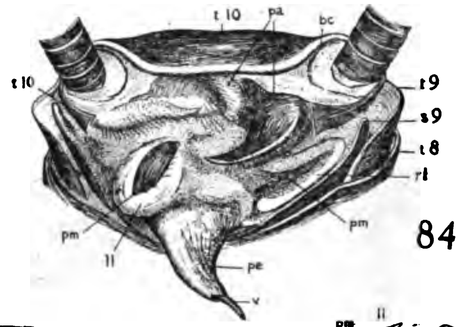

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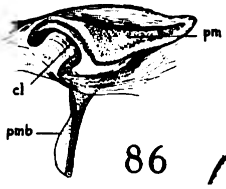

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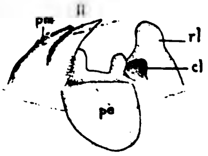

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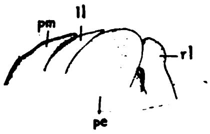

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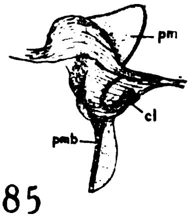

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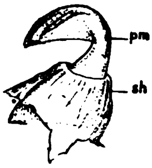

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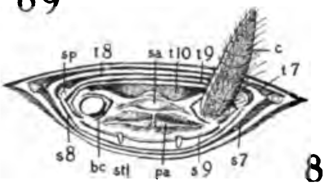

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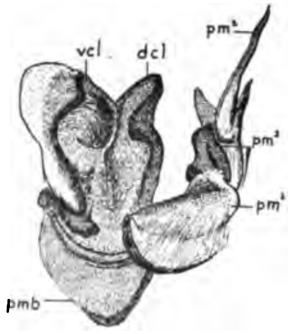

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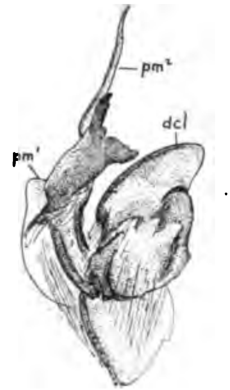

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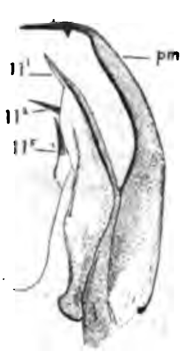

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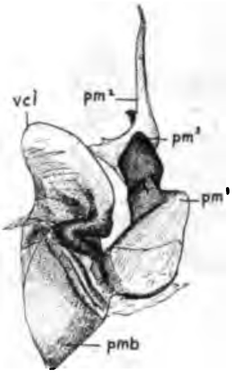

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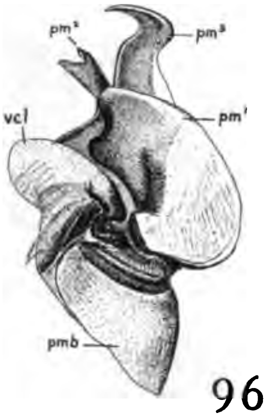

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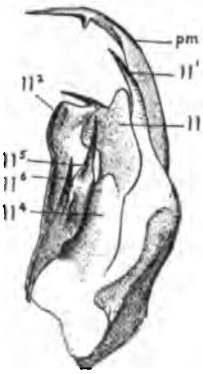

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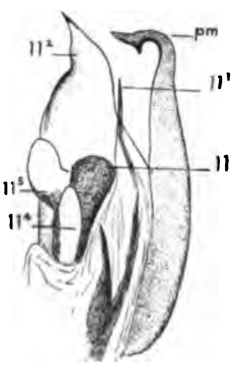

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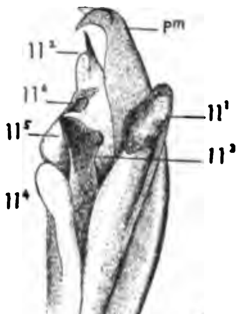

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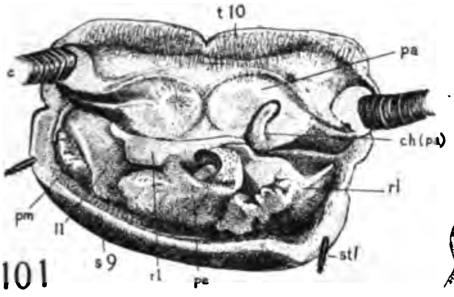

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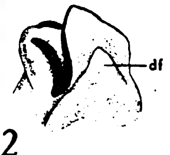

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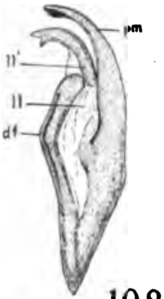

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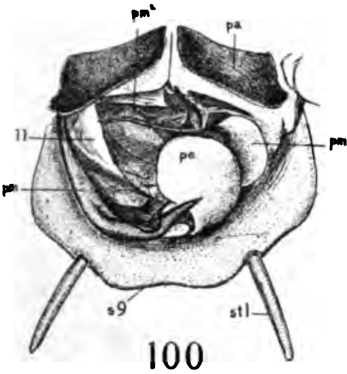

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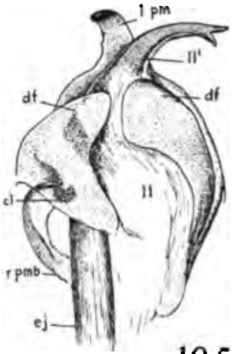

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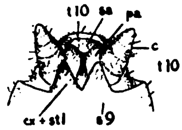

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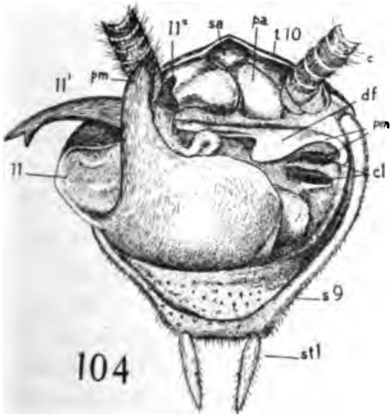

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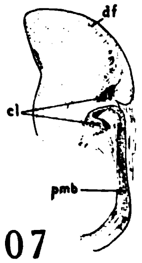

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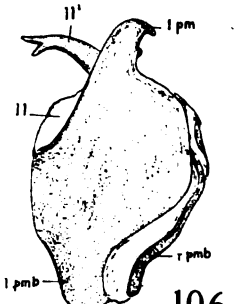

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E. M. Walker.