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Homology of Male Genital Sclerites in Cockroaches (Blattaria) by Means of Analysis of Their Association Patterns[1]

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1. INTRODUCTION

The fundamental arrangement and homology of the male genital structures of the Blattaria proposed by McKittrick (1964) marked a new departure in the morphology and the systematics of the Blattaria (e. g. Roth, 1977, 79). Prior to McKittrick (1964) the male genitalia as such, if elaborately described in a few members, had never been investigated comparatively, since their morphology had been partially dealt with in phylogenetic studies of the orthopteroid insects (e. g. Walker, 1922 ; Snodgrass, 1937 ; Quadri, 1940). In these studies much emphasis was placed on the major features of the structures as compared with those in other orthopteroid insects. Accordingly, the male genitalia of the Blattaria were primarily recognized as a few lobes or clusters of structures, which differ in number among the groups [e. g. two in the Blattellidae or three (bearing additional ventral one) in the Blattidae allies]. The clusters were considered to be essential units of genital structures because they could be traced back in the early stages of ontogeny of the roaches and were commonly designated as "*phallomere*" (Snodgrass, 1935, 37). Since then, this structural unit was, with very few exceptions (Quadri, 1940), uncritically used by researchers. This was true of McKittrick (1964) who determined the homology of the elements packed in each of the units or phallomeres. However, McKittrick's conclusions require further examination, as it was based on the problematical paradigm of Snodgrass (1935, 37) who considered the independence of ventral elements. Naturally because the phallomeres are recognized through the developmental process in the roaches, each phallomere is obviously equivalent to the primary phallic lobe at the early stage of ontogeny. This results in two reasons arguing against the "*phallomere*" as the fundamental units of the genital structure :—

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1) The ventral phallomere did not derived from an independent primary phallic lobe and, when established upon this basis, it was far from a fundamental unit of the genitalia. The genital structures still started from a pair of primary phallic lobes even in species with three phallomeres in the earlier stage of development than observed by Snodgrass (1937) (Quadri, 1940).

2) The phallomeres, if well established upon the primary phallic lobes, still may not be thoroughly homologous throughout the Blattaria. There is no conclusive evidence that homology of the structures in the adult is always distinctive on the basis of homology of sites of the structures during the development. It is probable that, in the groups such as Blattidae and Blattellidae, the structures of adult with similar forms and locations had been constructed by substitution (Matsuda, 1976).

It should be further noted that McKittrick's (1964) conclusions were solely based on comparisons. Marked diversity and asymmetry in the male genitalia make it almost unable to simply identify the structures. This embarrassing case in the Blattaria requires medium for homologization. Our idea is to compare the pattern of *"connection"*, that presently called *"association pattern"*, of the sclerites in order to unfold the homologous elements in the groups. Although the *connection* itself has been known as a criterion of homology (St. Hilaire in Matsuda, 1976), the *association pattern* further involves relative position of the distinct sclerites and membranous regions in the entire genitalia. The pattern is essential to the study since each sclerite as well as attachments of related muscles may frequently undergo reductions, displacements, and shifts in positions. The present study deals with five species representing three distinct types of genitalia. The homologies of all the sclerites were determined using Matsuda's criteira of homology.

2. MATERIAL AND METHOD

(1) Material

Following species are examined.

Periplaneta fuliginosa (Serville)
Blattella germanica (L.)
Blattella karnyi Princis
Blattella subvittuta Hebard
Opisthoplatia orientalis Burmeister

Periplaneta fuliginosa (Serville) is common in the southern warmer areas of the USA and Japan. Japanese populations have usually been reported as three distinct species: *P. picea* Shiraki, 1906, *P. emarginata* Karny, 1908, and *P. filchnerae* Karny, 1908, although all of them were synonymized with *P. fuliginosa* (Furukawa, 1938). Japanese specimens we examined show noteworthy differences in the minor structures of the male genitalia from North American *P. fuliginosa* illustrated by Walker (1922). Material used in the present work was collected from Fukuoka City in Kyushu district of Japan.

Blattella germanica (L.) was from a colony bred in the Research Institute of Agricultural Chemistry of Kyoto University.

Blattella karnyi was obtained from the Kyushu University Collection (specimens from Taiwan collected by T. Esaki in 1937). The population recorded from Taiwan (e. g. Karny, 1915) as *Phyllodromia humbertiana* Saussure (now *Blattella humbertiana)* was recognized to be independent of the latter (Princis, 1964) and determined as *B. karnyi* (Princis, 1969). This species had not been described until the revision done by Asahina (1981).

Blattella subvittata from Taiwan in the collection of Kyushu University was examined. *B. subvittata* Hebard, 1929 that had been synonymized with *B. sauteri* (Karny, 1915) was distinguished and placed under the subspecies of the latter (Asahina, 1981). However, Roth (1985) concluded that *subvittata* and *sauteri* are distinct species.

The senior author collected *Opisthoplatia orientalis* in 1977 on Amakusa Island of Kumamoto Prefecture (Kyushu). This is a large wild cockroach belonging to the Epilamprinae (Blaberidae) and, in Japan, distributed only in the southernmost area. This cockroach is characterized by an apterous oval body and extreme dimorphism in the body size (male is much smaller than female).

(2) Method for genital preparation

Before observation of skeletal elements, the male terminalia were detached from body, deposited in 5 % KOH at 100°C for 5 minutes, washed with water, and stained with Mayer's haematoxylin for easy observation. For orientation and dissection a pair of forceps with pointed apices were used. The material thus prepared was observed under a binocular.

The musculature of *P. fuliginosa, B. germanica,* and 0. *orientalis* was studied using freshly killed specimens or those preserved in 60 % alcohol. Dissection of muscles was made under a binocular using a pair of acutely pointed forceps. During the dissection, newly exposed surfaces of the tissues were stained with Mayer's haematoxylin. The detached terminalia of the dried specimens in *B. karnyi* and *B. subvittata* were boiled more than 10 minutes in water. In order to reduce adhesion between the tissues under dissection, further, the terminalia were often treated with 5 % KOH solution at 20°C for 20 seconds, washed with water, and if necessary stained with Mayer's haematoxylin.

All drawings of the sclerites and muscles were reconstructed from partial sketches made during the dissection and are more or less schematic.

3. PROCEDURE OF TREATMENT

(1) Procedure of homologization

The male genitalia of Blattaria has been regarded as a secondary outgrowth in the membrane between the ninth and tenth abdominal sternites (Crampton, 1925 ; Snodgrass, 1935, 37), and with this view, we are apt to assume their recent derivation and independence of origin of the different forms of the structures. In fact, the common explicit features that suggest the ancient condition of the structure are very rarely observed at a casual glance because of the great discontinuity of shapes and arrangement of structural elements in the existing forms. Despite the discontinuity, there still exist in the forms some correspondences of sclerites that imply the descent of initially specialized structures (proto-types) of the stem ancestors. The proto-type, if appropriately established, may favor the study of homology between the various types of genital structure by comparing it with the latter. McKittrick (1964) designated the male genitalia of *Cryptocercus punctulatus* (Cryptocercidae) as the reference type for comparison assuming that it represented the most primitive condition in the Blattaria, but her assumption lacked conclusive evidences as discussed later. We cannot detect proto-types of the genitalia directly on information from fossil cockroaches or indirectly on evidence obtained from other insect groups. Accordingly, common features of the structures must be exclusively inferred from the vestiges that have been left in existing species of the Blattaria.

Any composite structure requires a constant rule to arrange the elements of the structure (now called constitution), besides its concrete shape. When the genitalia are compared between families (sensu McKittrick, 1964) considerable gaps exist in the number of sclerites. Accordingly, when one considers only the sclerotic elements, the constitution of the structure is only inadequately expressed. However, in the prevailing view that genital structures are derived from the sternal intersegmental membrane, and that sclerites and membrane are common but strictly different phases in the epidermis, membranous elements should be taken into account when the sclerites themselves are identified. Accordingly, the entire region of the epidermis between the ninth and tenth sternites (=genital cavity) where the genital structures occur was studied.

In order to study the constitution of the structures we found it helpful to use the Matsuda's (1976) first subsidiary criterion of homology :

> "the position of a structure relative to neighboring structure, called '*connections*"'.

This criterion (=first major criterion of homology of Remane (1956, 61)) is simply applied in the identification of sclerites in the wing base or basal structures of segmental appendages (Matsuda, 1976), where the compared structures are arranged in a relatively plane surface or epidermis.

In the present case, the genitalia assume a complex three-dimensional form so that *connecitons* in the given two sclerites or membranous regions are clearly understood only after the structures are unfolded and converted into a two-dimensional plane. The unfolded genitalia in a plane showing the schematic map in which the sea (=membranous background) and islands (sclerotic parts) are expressed maintaining ordinary relative positions of the sclerites (see Figs. 6, 7, 8, 9). Both the sea and islands are here commonly called the "*subregions*" (of the entire genital epidermis). However, when such subregions are considered, two difficulties occur :

1) Regions of epidermis mostly cannot be distinctly demarcated : when the two neighboring subregions are in common membranous, or however sclerotic when they fuse into a common plate, we can not draw the border between them.
2) For the same reason stated above, size and proportion of a subregion is not shown specifically.

Despite these difficulties, or due to their very nature, it is possible to restrict the subregions (=*SRs*) to a constant number so that, whenever sclerotized or membranous, they agree throughout the groups.

The subregion (= *SR*), as the morphological concept used here, is then defined as :

> the smallest and indivisible unit which is a part of the bordered region in a plane and, in this entire region, possesses its own relative position determined by its relations with other surrounding SRs.

SR serves as the basic unit in this study and is based on the assumption that throughout the Blattaria an equal number of genes corresponds with and regulates the structure of each SR.

The rules of correspondence between SRs and observed sclerites or membrane are formulated as follows :

1) Principally a single sclerite corresponds with a single SR.
2) A single sclerite can spread over two or more SRs, or two or more SRs can participate in a single sclerite.
3) A membranous region around a free sclerite often corresponds with a single SR together with the sclerite, or a single SR often includes a sclerite and surrounding membranous region.
4) On the other hand, occasionally a membrane can correspond with one or more SRs by itself. Large expanded membranous areas, in the types of genitalia that are membranous, may correspond with one or more SRs which are sclerotic in certain types of strongly sclerotized genitalia.

Here, any neighboring structures (SRs) are not always closely adjacent, but in most cases are free from one another, but unstable in form and position. In this situation *connection,* which seems to imply a relatively tight relationship between neighboring structures, is not adequately descriptive. Therefore, we proposed the term "*association*" for special cases of *connection* where the subject (sclerite or SR) which should be identified by other structures (SRs) must in turn serve as an objective for the latter in the relationship of the SRs or sclerites. Even in this situation, we can still recognize the loose relationship or *association* between the given two SRs, unless they are intervened by a third SR.

When SRs are symbolized by points and associations of every two SRs are replaced by lines, the map of unfolded genitalia produces an "*association graph*" (Plate 1, Fig. 1). In the graphs, thus obtained, regardless of forms or position of the sclerites, the relationship between SRs or the genital constitution is expressed as an "*association pattern*". Thereby the sclerites or SRs in the different types of the genitalia can be related and homologized through the comparison of the graphs omitting superficial differences.

Another criterion used here is the third major criterion of Remane (1956, 61) :

> "When the connection of a structure is obliterated, the structure can still be identified (homologized) by the presence of intermediate conditions of the structure" (after Matsuda, 1976).

In the Blattellidae and Blaberidae, male genital structures are largely replaced by membrane and thereby fewer sclerites are observed. If the blanks in the membranous region are properly made out assuming the ordinary occupation of SRs, association graphs obtained from such families are also relatable one to the other. When indistinguishable, vestigial SRs present as sclerites in relatively close allies, it is possible to recognize the SRs in the specialized forms that have considerably reduced sclerites. The five species we examined in the present study were not sufficient to determine complete information about number and arrangement of SRs so that, we referred to drawings of four species of the Blattidae by Walker (1922), Crampton (1925), and Snodgrass (1935, 37). They allowed us to determine the positions of generally unrecognizable SRs in the association graphs of the three distinct types of the genitalia because certain species possessed intermediate types of SRs.

Finally, we must mention the use of the attachments of other independent systems structures like musculature and innervation as landmarks to identify the sclerites. Matsuda (1. c.) maintained that "essentially the two systems (exoskeleton and musculature) develop independently. Because of -this tendency, homologous muscle often come to be attached to different parts of exoskeleton in different adult insect." He also gave three special cases and a general case in which the muscles could hardly be used as landmarks in determining sclerites to which the muscles were attached (p. 35-36).

There is much discontinuity in the genital structure among the families. According to Matsuda's three special cases this is interpreted as: 1) reduction or obliteration of the exoskeleton (in the Blaberidae and Blattellidae) ; 2) development of new structure by means of the secondary fusion of two adjacent structures ; 3) occurrence of unique displacement of exoskeleton in each family. Accordingly, attachments of the muscles were used supplementally in order to identify (or homologize) the sclerites. And some constantly observed muscles were used in order to reinforce the homology of the sclerites (SRs) which were exclusively determined through the analyses of association patterns.

(2) **Historical review and problem**

Early morphologists had already distinguished two quite different types of genitalia in the Blattaria (e. g. Walker). The genitalia consisting of three lobes (e. g. Blattidae) have been considered more primitive than those comprising two lobes (e. g. Blattellidae) because of their structural complexity. In the morphological works dealing with the family Blattidae, there were two opposite views regarding the fundamental plan of the male genitalia. The first considered that the genitalia consisted of two lateral lobes or clusters of structures. The second stated that the genitalia comprising three distinct lobes.

Walker (1922) regarded the genitalia of the Blattaria commonly as a two lobed-composite structure based on the examination of seven species (four *Periplaneta* spp., a *Parcoblatta* sp., a *Blaberus* sp., and a *Blattella* sp.). The lateral lobes of the Blattaria were tentatively labeled *"parameres"* in relation to similar structure of the other orthopteroid insects. The *parameres* in the orthopteroids were further suggested to be homologues of the genital structures of the Thysanura, which in present morphological terminology, is called *gonapophyses* or *endites*. The third ventral lobe under the gonopore in the Blattidae was regarded as the *penis*, which in present terminology corresponds to *aedeagus*, a structure in some Pterygote insects arising around the gonopore independently of the primary phallic lobes.

Crampton (1925) examined *Periplaneta americana* (Blattidae) and claimed that the term *paramere* does not adequately express the structure since the term was applied to "entirely different structures in the Apterygota and Pterygota, and different investigators apply the term to so many different structures in different insects". He did not regard the lateral lobes as homologous with the gonapophyses but considered them as secondarily formed outgrowths around the intromittent organ. However, regardless of origin, he shared the same view with Walker concerning on the general plan of the entire structure, since he labeled the third ventral lobe (*penis* of Walker) as "*penislobus*[3]" which was considered to be partially homologous with aedeagus of some other Pterygote insects.

Modern insect morphologists understand the general plan of the genitalia as originating from the unpaired structure after the view of Snodgrass (1935, 1937). Snodgrass (1935) considered the genital structure as a secondary outgrowth after Crampton (1925) and proposed a new term "*phallomere*" as substitute for the *paramere*. The third ventral lobe in the Blattidae was considered to be of equal morphological weight to the lateral lobes, hence it was termed "*ventral* **phallomere".** Snodgrass (1937) studied four species of Blattaria ; a Blattidae sp., two Blattellidae spp., and a Blaberidae sp. His fundamental units of the structure were mostly obtained from the developmental stages of the Blattidae, where the three rudiments of the phallomere are constantly recognized around the gonopore. For this reason, he did not accept the *penis* of Walker (1. c.) and Crampton[3], since he believed that the region above the base of the ventral phallomere in *Blatta orientalis* (Blattidae) is a *phallotreme*.

Besides *Blatta orientalis,* Snodgrass (1937) studied the genital rudiments in the nymphs of *Blattella germanica,* and found three rudiments of the genital lobes, although the middle one was dorsal to the phallotreme. Because of its position above the phallotreme, he called the median rudiment *virga*. The homologue of the ventral phallomere that should lie below the phallotreme was not found in *Blattella germanica*. Consequently, he had to present two different plans in the genitalia of Blattaria. The origin of the ventral phallomere in the Blattidae was not interpreted but merely stated that three lobes are shown typically in *Blatta* and *Periplaneta*, suggesting the priority of the three lobed genitalia over two lobed one in the phylogeny of Blattaria.

Quadri (1940) disagreed with Snodgrass (1937) and insisted that in the Blattidae, the genitalia consisted of paired lobes. The genital rudiment of *Blatta orientalis* in the first and second nymphal instars that appeared earlier than observed by Snodgrass (1. c.) were "clearly present as a pair of outgrowths……and not as three outgrowths of phallomeres as described by Snodgrass." In the third instar, he observed, these paired lobes were divided respectively into dorsal and ventral parts so that there were four valves which surround the opening of the ejaculatory duct. In his work, the term "*penis valve*" was applied to the genitalia of the Blattaria "after the works done by Crampton, Chopard, George, Metcalfe, Else, Sharif, and others" (Quadri, 1940).

Today, both conclusions of Snodgrass (1937) and Quadri (1940) concerning the general plan of the genitalia are questionable because of too much weight given to the events during ontogeny. It is noteworthy that the ontogenetical sequences of a life do not always repeat its phylogenetical sequences. Accordingly, "homology of structures should be based primarily on the end result of ontogeny (of adult structure) upon which natural selection works" (Matsuda, 1976).

McKittrick (1964) placed the Blattaria at the suborder rank of the order

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[3] The real penis of the Crampton (1. c.) is, according to Snodgrass (1937), a "small lobe on the base of the ventral phallomere, which is evidently a part of the interphallic fold containing phallotreme".

Dictyoptera. In her systematics, the male genitalia were of much importance in distinguishing the two superfamilies, Blattoidea and Blaberoidea, under the suborder. In the former (including Blattidae and Cryptocercidae) the genitalia exclusively consist of three main lobes or phallomeres, while in the latter (including Blaberidae, Blattellidae, and Polyphagidae) it contains two main lobes although the third ventral lobes are obsoletely recognized in the Polyphagidae. Homology of the sclerotic components of the phallomeres was determined through the examination of 24 species. In relating the sclerites among the different subfamilies, she first chose *Cryptocercus punctulatus* (Blattoidea : Cryptocercidae) as a reference type for comparison. This selection was made on two bases : 1) "the corresponding female genitalia were the most primitive examined" ; 2) "various sclerites of the phallomeres appear to be in their simplest form" in the species examined and "without evidence of reduction". She adopted Snodgrass' general plan that the genitalia consists of three main phallomeres of equal morphological weight. In the *Cryptocercus*, she found three simple sclerites in both the right and left phallomeres but no more division in the ventral phallomere. Sclerites in the lateral lobes (phallomeres) were briefly numbered as *R1*, *R2*, R3 on the right and

Table 1. Historical review of terminology (1). Blattinae right phallomere.

Present work	Walker (1922)		Crampton (1925)	Snodgrass (1937)	Quadri (1940)	McKittrick (1964)	Guthrie & Tindall (1968)
Dld	ecto-paramere	2	serrate lobe (serrata)	dorsal plate of dorsal lobe	right dorsal penis valve	R1	dikella
Dlm				sinistral prongs			
Dlv		1	basiserrata	ventral plate of dorsal lobe			sclerite 1
Dlvm			falx	left arm of ventral plate			–
Dll		3		distal arm of ventral plate			falx
D2d	dorsal clasper		opponentes	capsular sclerite		R2	sclerite 2
D2v	ventral clasper			ventral valvular sclerite			sclerite 3
D2l			basarcus	basal plate of apodeme			sclerite 4
D3	base of paramere or endoparamere		basilarnina	apodeme		R3	right phallobase
Vd	–		penis	sclerite of endophallic wall			phallotoreme
vv	penis		penislobus (sublamina)	ventral phallomere	right ventral penis valve	V	ventral gonapophysis

L1, L2, L3 on the left for ease of reference. Then they were applied to the sclerites of other species of the different subfamilies.

Guthrie & Tindall(1968) described the male genitalia of *P. americana*. Considering three main lobes in the structure, their concept on the fundamental framework of the genitalia is essentially agree with that of Snodgrass (1935, 37), although they called the lobes *gonapophyses* for phallomeres. They completely disrdegared McKittrick's (1964) terminology and described the detailed structures with new terms or after Crampton's (1925) terminology.

More elaborate terminology of male genitalia were proposed in the Blaberidae (Roth & Gurney, 1969 ; Roth, 1969, *70, 73)* partially amending the system of terminology of McKittrick (1. c.). Although the male genitalia of the Blaberidae are quite simple and uniform, they are specifically provided with a conspicuous plate at the postero-ventral position of median rod. According to McKittrick's (1. c.) indication, Roth & Gurney (1969) identified this structure in the species of *Epilampra* with *L2d* and termed another rod-like structure (real *L2d*) just dorsal to it "*L2bp*" (*basal plate of L2*). Later Roth (1970) corrected the confusion on *L2d* of McKittrick (1. c.) and identified the former structure in the genus as "prepuce" (*P* as abbreviation) and recognized the latter as *L2d* as he had already indicated in *Blaberus* spp. (Roth 1969).

Table 2. Historical review of terminology (2). Blattinae left phallomere.

Present work	Walker (1922)		Crampton (1925)	Snodgrass (1937)	Quadri (1940)	McKittrick (1964)	Guthrie & Tindall (1968)
D1d	left paramere lobe	3	asperate lobe (acutolobus)	s	left ventral penis valve	L1	asperate lobes
D1l		4		v			
D1m		5	–	u			acantholobus
D1v		2	pointed process (acutolobus)	t		L2-v	acutolobus
D1vm		6	endoprocessus	–			
D2d	ectoparmere		titillator	q, q′	left dorsal penis valve	L3	grumolobus basal sclerite of grumolobus
D2v	–		basuncus	–	–		
D2l	left paramere lobe	1	pseudopenis	r	left dorsal penis valve	L2-d	pseudopenis
D3			basal arch (andrarcus)				left phallobase
Vd	–		penis	sclerite of endophallic wall			phallotreme
Vv	–		–	–			

On the left phallic elements Roth & Gurney (1. c.) distinguished an element (designated as *L1b*) from the *L1*. Roth (1973) further separated the remainder of L1 into upper *lobe of L1 (UL)* and lower *lobe of L1 (LL) (see* Table 6).

The senior author (Mizukubo, 1981) proposed several new terms in the male genitalia of *Blattella*, which are applicable to the sclerites of the Blattellinae-type. *R2* was divided into three parts and designated as "*R2d*", "*R2v*", and "*R2l*", respectively. And *R1* and *V* (= ventral phallomere) which were overlooked by the McKittrick (1. c.) were recognized in this study. The latter structure was divided into two parts and termed " *Vd*" for the dorsal element and " *Vv*" for the ventral element. Vv is further divided into three parts ; "*Vvl*", "*Vvm*", and "Vw", respectively.

These attempts were essential for taxonomic studies and are useful to denote the sclerites in restricted taxa. However, in discussing the phylogeny of the entire group of Blattaria, these works were of less use, since they were created independently amending the system of McKittrick and naturally do not cover the full range of the Blattaria.

The homologies in McKittrick's system itself, upon which recent studies were based, has never been tested. McKittrick did not indicate her procedure of homologization : it was scarcely shown how certain sclerites of simple condition in the reference species, for example L2, were applicable to the sclerites of different modes of genitalia dividing it further into such as *L2-vm, L2-v, L2-d* despite their remarkable shift in forms, numbers and positions. Furthermore, we think, there is little basis for her selection of *Cryptocercus* as a reference type. Probably, she meant the basic plan or proto-type of the male genital structures, selecting the reference type for identification. Although, for selection of the reference type, she firstly based on the fact that corresponding female genitalia was primitive, we do not think this would always determine a primitive condition of the male genitalia. As widely admitted, evolution of organs are principally different from those of species themselves : and the same may be true of the genitalia of the opposite sexes in the same species. Despite the strict functional relation between them, two organs in a species would not always evolve, in morphogenetical aspects, simultaneously or in the same direction. The second basis is also hardly applicable, since the simplest organ does not represent the primitive condition or basic plan of the structure, and since she did not demonstrate why the male genitalia of *Cryptocercus* showed no evidence of reductions. In our opinion, it is unlikely to appear the basic or ancestral plan of complex organ of the fairly higher taxa holding its complete condition in the existing species. We consider, for these reasons, that the results of McKittrick and her followers requires further examination.

The descriptive terms used by various investigators to indicate the three distinctive types of genitalia, are presented in Tables 1 to 6.

(3) **Terminology of the male genitalia**

External genitalia of existing species of Blattaria have been characterized by the marked asymmetry of the structures. Each half of asymmetrical pairs typically represent five modes of structures represented respectively by the right and left phallomeres of the Blattidae, the right and left phallomeres of the Blattellinae, and left phallomere of the Blaberidae. We believe that, at the period of formation of the order, the early Blattaria had symmetrical genitalia. It is clear that the left phallomere or penis valve of the Blattellinae essentially agrees with the right phallomere of the Blaberidae ; this suggests that genital structures of the early Blattaria may have been symmetrical and thereby had possessed the potential to differentiate similar structures in the different phyletic lines of the Blattaria. With this in mind, we looked for corresponding SRs between the opposite phallomeres or penis valves in the same species. All the genital sclerites of the Blattaria have been assigned to the three units or phallomeres according to the views of Snodgrass and his followers, even though the

Table 3. Historical review of terminology (3). *Blattella* (Blattellinae) right phallomere.

Present work	Mizukubo (1981)	Walker (1922)	Snodgrass (1937)	McKittrick (1964)
D1d	R1			R2
*D1m	–			
*D1l	–	–	–	–
*D1vm		–		–
D1v	R2d	clasper	sclerotic fold of wall of right phallomere	R2
D2d				
D2v	R2v	–	–	
D2l	R2l	dextral paramere (ectoparamere)	right phallomere	
D3	R3	base of paramere (endoparamere)	apodeme of right phallomere	R3
Vd	Vd	–	–	–
v v	v v	–	–	–

Table 4. Historical review of terminology (4). *Blattella* (Blattellinae) left phallomere

Present work	Mizukubo (1981)	Walker (1922)	Snodgrass (1937)	McKittrick (1964)
D1d	L2		–	L2
*D1m	–		–	
D1l	L2v			L2-v
D1v	L3	sinistral paramere	left phallomere	L3
*D1vm	–	–		–
D2d	L2vm			–
D2v	L2d	virga	virga	L2 d
*D2l	–	–	–	–
D3	L2vm		endophallic apodeme	L2 vm
Vd	Vd			
Vv	Vv			

same nominal phallomeres of the different groups often consist of apparently different sclerites. One need not accept the "*phallomere*" as a paradigm of the study but start from the assumption that any independent sclerites scattered in the various regions of the genital pouch are themselves unique elements or SRs in the entire genital structure.

For reference, these sclerites are categorized, according to their relative positions, into the major genital regions that were assumed independently of the recognized lobes. In order to avoid confusion, we found it useful to postulate a new system of terminology by combining the following two proceeding systems : Quadri's conception of the genital plan involving paired structures of the organ and the McKittrick's system of terminology which has been used fairly widely by researchers and seems to be the simplest way to denote the sclerites. The customary *phallomere* is used, but here

Table 5. Historical review of terminology (5). Blaberidae right phallomere.

Present work	Walker (1922)	McKittrick (1964)	Roth & Gurney (1969)	Roth (1970, 73)
D1d	–			
*D1m				–
D1l				–
*D1vm				–
D1v	right paramere	R2	R2	R2
D2d	virga	–	L2d	prepuce
D2v		L2-d	L2bp	L2d
D2l			–	–
D3	–	L2-vm	L2vm	L2vm
*Vd		–	–	
*Vv	–	–		–

Table 6. Historical review of terminology (6). Blaberidae left phallomere.

<table>
<tr><th>Present work</th><th>Walker
(1922)</th><th>McKittrick
(1964)</th><th colspan="2">Roth & Gurney
(1969)</th><th colspan="2">Roth
(1970, 73)</th></tr>
<tr><td>*D1d</td><td>–</td><td>–</td><td colspan="2">–</td><td colspan="2"></td></tr>
<tr><td>*D1m</td><td></td><td>–</td><td colspan="2">–</td><td colspan="2">–</td></tr>
<tr><td>*D1vm</td><td></td><td>–</td><td colspan="2"></td><td colspan="2">–</td></tr>
<tr><td>D1l</td><td>dorsal flap</td><td>–</td><td rowspan="4">L1</td><td>L1b (?)</td><td rowspan="4">L1</td><td>L1b (?)</td></tr>
<tr><td>D2d</td><td rowspan="3">left paramere</td><td rowspan="2">L1</td><td rowspan="3"></td><td>LL</td></tr>
<tr><td>D1v</td><td></td></tr>
<tr><td>D2v</td><td>–</td><td>UL (?)</td></tr>
<tr><td>*D2l</td><td>–</td><td>–</td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>D3</td><td>–</td><td>–</td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>*Vd</td><td>–</td><td>–</td><td colspan="2">–</td><td colspan="2">–</td></tr>
<tr><td>*Vv</td><td></td><td></td><td colspan="2">–</td><td colspan="2">–</td></tr>
</table>

it is applied only to denote entire structural units of both sides (e. g. "*right phallomere*" for the right unit). The use of *ventral phallomere* is avoided as a descriptive term, because it dose not indicate homology when the entire Blattaria is considered.

There are 11 sclerites or SRs in the each right and left phallomeres (Fig. 1), and their terminology is as follows :

D : dorsal region
Dl : first major region of D
Dld : dorsal SR (subregion) of Dl
Dlm : medial SR of D1
Dlv : ventral SR of D1
Dlvm : ventro-medial SR of D1
D1l : lateral SR of Dl
D2 : second major region of D
D2d : dorsal SR of D2
D2v : ventral SR of D2
D2l : lateral SR of D2
D3 : third major region of D
V : ventral region
Vd : dorsal SR of V
Vv : ventral SR of V

In order to indicate symmetry adequately, we applied equal terms to right and left phallomeres. The opposite homologues were, if necessary, distinguished by leading them with the capital letter, "R" or "L", respectively.

When a SR was supposedly membranous, it was expressed by leading it with the symbol "*".

4. EXTERNAL MORPHOLOGY

(1) ***Periplaneta fuliginosa***

Snodgrass (1935, 37) gave an excellent description of the genital structure of *Blatta orientalis* (Figs. 15, 18) which is taxonomically close to *Periplaneta fuliginosa* here examined. Crampton (1925) also gave clear picture to the genitalia of *P. americana* (Figs. 11, 13). These have a similar structural plan, but have minor structural differences.

The epidermis of the genital cavity of the Blattidae has a strong sclerotic texture, and is armed with elaborate prongs, hooks, and lobes distally (Figs. 10, 12). Dorsalmost genital cavity in *P. fuliginosa* is the trifurcate RD1 (Fig. 14) which is distinguishable into five SRs and lies dorso-medially above the genital opening ; the dorsal wall (RD1d) armed ventrally with strong prong is produced on the right, where it hinged to the posterior margin of RD21 and sunken into deep right pocket ; just below RD1d produced elongate convex sclerite (RD1m) with posterior spine curved inwardly; further below RD1m, the third similar prong or spine (RD1l) occurs ; ventral sclerotic wall of RD1 (RD1v, Fig. 17) is convex, which is the belowmost SRs of RD1 described above ; ventrally all the SRs are firmly fused into an elongate, twisted, and oblique capsule (Fig. 17) ; the lateral wall of this capsule is partially occupied by a membrane surrounded by the ventral RD1v, the antero-dorsal RD2l, and the postero-dorsal D1l. Beneath RD1 is a strongly convex sclerite (RD2d, Figs. 10, 14) which distally fused to arched sclerite comprising RD21 dorsally and RD1v ventrally ; the posterior margin of RD2d is continuous with ventral wall of RD1 (RD1v) through the narrow intervening membrane ; and antero-ventrally it may directly articulate with, and normally is closed by RD2v (=*valvular sclerite* : Snodgrass, 1937) ; thus, together they form a deep transverse oval cavity. RD3 (=*apodemal plate*: Snodgrass, 1937) is short, broad, and extensively sclerotized, supported laterally by RD21 and medially by D2v which articulates with its lower lip (Figs. 10, 14, 17).

On the left between the dorsal and ventral wall of RD1 is an oblique transverse membranous fold (sensu Snodgrass, 1937) or RD1vm which goes upward and is continuous with the anterior margin of LDlvm (Figs. 10, 16). Between the lower end of this fold above and base of the ventral phallomere below is a large genital opening or *phallotreme* (Snodgrass, 1937). The genital exit passage contains a sclerite (R+LVd) in its wall (Fig. 16). RVv (= *ventral phallomere* : Snodgrass, 1935) is a simple broad lobe projecting rightward from beneath RD3 (Fig. 12).

On the left side of the genital cavity is a fasces of sclerites or pot-like structure (Fig. 19) whose basal opening constricted by the surrounding sclerites and sunken into the left pocket. Dorso-laterally the fasces is largely occupied by a strong framework (LD3 plus LD21, Fig. 27) ; LD3 arches anteriorly about the opening of the fasces ; dorsally LD2l extends posteriorly and decurves ventrally, terminating in a posteriorly produced lobe. Outermost lobe (LD2d, Fig. 27) is produced from below the frontal margin of LD3, is much elongated and bends inwardly at the middle portion then tapers and terminates in a bifurcate apex which is strongly turned to the right. Ventrally the fasces is occupied by four irregular sclerites (Figs. 25, 26); the outer proximal ones are thick and small (LD2v) and thin and larger (LVv); the outer distal elongate hook (LD1v); and an inner elongate (LD1vm); all are connected to each other through intervening membranes. Antero-ventrally LDlvm is deeply folded into the genital cavity and forms the inner ventral wall of the fasces. Ventro-medially the fasces is occupied by a flat lobe which is free from the fasces distally (Figs. 19, 23, 24). This lobe consists of three SRs; the dorsal (LD1d), the median (LD1l), and the ventral (LD1m) which takes form of elongate hook in *P. fuliginosa*.

(2) ***Blattella* spp. *(germanica, karnyi, & subvittata)***

General appearance of the blattellan male genitalia is the conical membranous cavity surrounded by sclerites (Figs. 37, 38, 41).

The dorso-posterior face of the genital cavity is much expanded and produced, forming a cone-like structure, on which the apical virga (LD2v) is projected posteriorly. Snodgrass (1937) called this structure *penis* in a functional sense since, when protracted, it was considered to form an intromittent organ as later ascertained by Khalifa (1950). The conical membranous *penis* is dorsal to the median reversible sac (= *endophallic sac* of Snodgrass, 1937) which is a secondary invagination at the mouth of genital exit passage. The ejaculatory duct opens at the bottom of the endophallic sac.

The male external genitalia of *B. karnyi* (Fig. 41) contains eleven sclerites which are allocated in the right and left phallomeres. On the right, the genital pouch forms a wider but shallower pocket (*right phallic pouch* of Snodgrass, 1937) containing a convoluted sclerite on the inner wall. Apparently this is composed of two SRs: the proximal small and straight (RD2d) and the distal broad and crescentic (RD1v). The ventral wall of right phallic pouch is continuous with the posterior margin of RD3 along its posterior two branches and with the anterior margin of RD2v, while the dorsal wall (RD1m) of the same runs downward and is continuous with the ventral wall (RD1l) of the posteriorly produced hollow lobe which contains a long, strong RD2l laterally and small thin RD1d anteriorly. RD1d is rather large and strong in *B. subvittata,* and is armed ventrally with a large spine (Fig. 51). Beneath the convoluted sclerite (RD2d plus RD1v) a broad and flat sclerite (RD2v) occupies the medial dorsal surface of the genital pouch. A broad membranous region between RD2v and LD2v may indicate SR of RD1vm. A long and robust apodeme (RD3) projects anteriorly within the genital pouch and forks in the right distal wall of the genital cavity producing a branch at the base of RD2l. Another branch is sent through the medial wall of the pouch to RD2v above the base of penis.

On the left, a broad flat sclerite (LD1d) occupies the dorso-lateral region of the genital cavity. Below LD1d, the genital pouch is produced into a deep pouch (= *left phallic pouch* : Snodgrass, 1937) or membranous sheath which may be formed through the combination of LD1vm and LD1m. Basally, the sheath contains a small, convex, thin sclerite (LD1l) and a distal elongate hook (LD1v). LD1v is protracted from the sheath during copulation, and works as a real hook against the female copulatory organ (Khalifa, 1950). LD2l may be a membrane occupying the lateral side of the genital pouch. An elongate medial apodeme (LD3) arises from the base of LD2v and penetrates into the genital cavity. LD2v (= *virga*: Walker, 1922 ; Snodgrass, 1937) is fused anteriorly to the posterior end of LD3, taking the form of a conical hollow sclerite in *B. karnyi* and narrow and solid sclerite in *B. germanica.* LD2v in *Blattella subvittata* appears somewhat separated from LD3, though it is actually linked with the latter by a narrow transparent sclerotic needle. Ventro-laterally close to LD2v of *B. karnyi* is a somewhat conical hollow sclerotic cap (LD2d) which fuses anteriorly to the posterior end of LD3. Although the senior author erroneously identified this sclerite as a part of LD3 or *LZ-vm* (McKittrick, 1964 terminology) in the previous work on *Blattella* taxonomy (Mizukubo, 1981), he has changed his mind after further examination. This is certainly identical with the *prepuce* (Roth, 1969 terminology) in the Blaberidae and clearly is different from LD3. LD2d may fuse firmly, but inconspicuously to the base of LD3, even in *B. germanica.*

The terminal part of the endophallic sac in *B. karnyi* contains two opposed sclerotizations (R+LVd and R+LVv, Figs. 39, 40). Each of them is considered here as a composite of their right and left equivalents. Vd is located in the ventral wall of the exit opening, has a flat and elongate shape, and is fringed posteriorly with four long bundles of hairs. Vv is a more elongate and robust structure located posteriorly to adjacent Vd in the endophallic sac, and forks in the wall latero-ventrally sending its anterior apodemal portion into the body cavity. Vd in the other *Blattella* is absent, and Vv may be present in the form of minute pieces of sclerites in the ventral wall of the genital cavity (LVvr, LVvl in Figs. 37, 45).

(3) ***Opisthoplatia orientalis***

The male genitalia of *Opisthoplatia* is similar to that of *Blattella* in general appearance and has a large membranous region. Essentially this is a mirror image of the latter. The right phallomere of *Opisthoplatia* generally is consistent with the left phallomere of *Blattella,* but is simpler, and its left phallomere generally has the same plan as the right of *Blattella,* though it is transformed into a reversible structure (Figs. 52, 59).

The sclerites of the right phallomere are similar to the left phallomere of *Blattella.* However, it lacks several sclerites : the elongate RD2v at the posterior end of RD3 is not seen, rather its rudiment is present ; RD2d (=*prepuce*: Roth, 1970 terminology) which is commonly observed below RD2d in most species of Blaberidae, is absent in *Opisthoplatia.* A large membranous area just below the base of RD3 may represent this SR. The convex plate at the fronto-lateral portion of the genital cavity is considered here to be a composite of RD1d and RD21, while in *Blattella,* the sclerite in the corresponding position is regarded as composed solely of LD1d. RD3 in this species assumes a very interesting form. It is not completely detached from the wall of the endophallic sac (Fig. 55), and may show a process such as a LD3 observed in *Blattella.* Other structures, such as RD1l and RD1v are similar to those of the corresponding left structures in *Blattella* (explanations of these are omitted).

The left side of the genital cavity is a deep and wide pouch in which all the sclerites of left phallomere are contained (Fig. 59). Roth's (1970) photographs of the genital structures of some Blaberidae species do not give a clear picture of the structures, since the left phallomeres were observed in the retracted condition. When the sclerites are extended they are arranged around and at the bottom of the membranous cylinder. LD1v occupies the distal half of its bottom, and at the right (or proximally) it fuses to LD2d and takes form of a distorted "5". LD2d is opposite to small LD2v which is located in the right wall of the cylinder and unites ventrally with the arm of LD3. LD3 is an apodeme which penetrates into the cylinder, its posterior half broadening in the ventral wall and extending the two lateral arms. To the left it articulates with the left edge of LD1v and fuses to the right with LD2v. LD1l is above and close to LD1v but separated from it by a narrow membrane postero-medially, occupying the latero-dorsal area of the cylinder. LD21 is assumed to be part of the membranous left upper wall, and the right upper wall may correspond to SR of Dlvm. The dorsal anterior wall of the cylinder may be formed by LD1m SR. The sclerotic LD1d is not seen ; possibly, this SR may be a part of the wall of anterior area of genital cavity.

5. THE MUSCULATURE

The observed muscles are categorized according to the customary treatment as : sternal extrinsic (S), tergal extrinsic (T), and the genitalia proper (m.). Within the different categories, the muscles were serially numbered for reference. However, since numbering was made at random, the same numerals in the different types do not indicate homology of muscles.

For each species, all muscles observed are listed as follows :

(1) *Periplaneta fuliginosa* (Figs. 16, 28-36)

Right phallomere

Extrinsic

A. Sternal muscles

S1. ST9-RD1d (Figs. 28, 30) : A flat muscle originating laterally on the anterior edge of the right apophysis of sternite IX and inserted on the dorsal middle edge of RD1d.

S2. ST9-RD3 (Figs. 30, 35) : A massive muscle arising medio-dorsally on the lateral portion of sternite, running up and attached to the right dorsal edge of RD3 (= muscle 4 of Snodgrass, 1937).

s3. ST9-RD3 (Figs. 28, 30, 35): A massive muscle arising on the anterior edge of the right apophysis of sternite IX, attached to the middle dorsal edge of RD3 (=muscle 3 of Snodgrass, 1. c.).

s4. ST9-RD3 (Figs, 28, 30, 35) : A massive and long muscle originating on the anterior edge of the left apophysis and running obliquely down to attach to the left dorsal edge of RD3 (=muscle 2 of Snodgrass, 1. c.).

S5. ST9-(R+L) Vd (Fig. 30) : A long and slender muscle arising on the anterior edge of the right sternal apophysis and running downward to attach Vd (=muscle 10a of Snodgrass, 1. c.).

S6. ST9-RVv (Fig. 30) : A long muscle originating on the anterior edge of left sternal apophysis and attached to the left anterior edge of RVv.

B. Tergal muscles

T1. T9-RD1d (Fig. 35) : A massive bundle arising near the right margin of tergite IX and inserted dorsally into the right portion of RD1d.

T2. T9-RD1d (Figs. 28, 35) : A massive bundle originating near the left margin of tergite IX and inserted dorsally into the left portion of RD1d (= muscle 1 of Snodgrass, 1. c.).

Genital proper

m.1. RD3-RD1v (Fig. 28) : A muscle originating along the right lateral edge of RD3 (Fig. 29), and attached dorsally on RD1v (= muscle 6 of Snodgrass, 1937).

m.2. RD3-RD1d (Figs. 28, 35) : A long muscle originating laterally on RD3 like m. 1, but more submarginally (Fig. 29), passing over RD2d and inserted into the bottom of RD1d (=muscle 7 of Snodgrass, 1. c.).

m.3. RD3-RD2d (Figs. 28, 35) : An exceedingly massive muscle, originating amply on the median portion of RD3 (Fig. 29), and inserted dorsally on RD2d (=muscle 5 of Snodgrass, 1. c.).

m.4. RD1v-RD2l (Figs. 28, 35) : A muscle within a capsule of right SRs' composite, running between the ventral surface of RD21 and RD1v (= muscle 8 of Snodgrass, 1. c.).

m.5. RD1d-RD1v (Fig. 35) : A muscle arising on the dorsal inner margin of RD1v, inserted on the bottom of RD1d at its medial portion.

m.6. RD2v-RVv (Figs. 16, 35) : A short muscle running from the right margin of RD2v to the right upper margin of RVv (= muscle 15 of Snodgrass, 1. c.).

Left phallomere

Extrinsic

A. Sternal muscles

s7. ST9-LD1vm (Figs. 30, 31) : A broad muscle originating inwardly on the left sternal apophysis and inserted on the frontal margin of LDlvm.

S8. ST9-LD3 (Figs. 30, 31) : A muscle arising outer-medially on the apex of the left sternal apophysis and attached to the frontal margin of LD3 (= muscle 9 of Snodgrass, 1. c.).

S9. ST9-LD3 (Figs. 30, 31) : A broad muscle arising posteriorly on sternite IX, inserted anteriorly on the frontal margin of LD3 (=muscle 11 of Snodgrass, 1. c.).

S10. ST9-LD1d (Figs. 28, 36) : A long muscle originating anteriorly on the apex of right apophysis of sternite IX, running down to attach to the frontal edge of LD1d(=muscle 10 of Snodgrass, 1. c.).

Genitalia proper

m.7. LD2v-LD2d (Figs. 31, 33, 34): A muscle within the lateral hook (LD2d), arising on LD2v and inserted directly into LD2d to attach on its inner wall (=muscle 12 of Snodgrass, 1. c.).

m.8. LD3-LD2d (Figs. 31, 33, 34) : A muscle originating on the frontal margin of LD3, inserted into LD2d and attached on its outer wall (=muscle 12 of Snodgrass, 1. c. ; this was not distinguished from the above muscle).

m.9. LD3-LD2d (Fig. 31) : A small fan arising on the frontal margin of LD3 and attached to the anterior margin of LD2d.

m.10. LD2l-LD1vm (Fig. 31) : A massive bundle of fibers attached distally on LD21 and proximally on the anterior portion of LDlvm.

m.11. LD2l-LD1m (Figs. 31, 32) : A massive fan attached posteriorly to the posterior angle of LD21 and anteriorly to the dorsal face of the inner ridge formed at the base of LD1m.

m.12. LD2l-LVv (Fig. 32) : A flat muscle from the posterior margin of LVv to LD21.

m.13. LD2l-LD1m (Fig. 32) : A thin bundle of fibers between the bottom of LD21 and the right face of the basal ridge of LD1m.

m.14. LD1m-LD1l (Fig. 36) : A small bundle of fibers attached distally on LD1l and proximally on the dorsal face of the basal ridge of LD1m.

m.15. LD1m-LD1v (Fig. 32) : A small bundle of fibers between basal ridge of LD1m and LD1v.

m.16. LD1vm-LD1m (Figs. 32, 36) : A muscle between the anterior portion of LDlvm and ventral face of the basal ridge of LD1m.

m.17. LD1vm-LD1v (Fig. 32) : A slender muscle originating on the posterior wall of LDlvm and inserted into the distal hook of LD1v.

m.18. LVv-LD1v (Fig. 32) : A flat muscle running between the posterior margin of LVv and the proximal (anterior) base of LD1v.

m.19. LD1vm-LVv (Fig. 32) : A short and broad muscle connecting LDlvm with LVv.

m.20. LD1vm-LD1v (Fig. 32) : A slender muscle originating on the middle wall of LD1vm and inserted near the base of LD1v.

(2) ***Blattella* spp. (*germanica, karnyi, & subvittata*)** (Figs. 42-51)

Right phallomere
  Extrinsic
    A. Sternal muscles
      S1. ST9-RD3 (Figs. 42, 43, 49) : A short muscle originating on the apex of the right apophysis of sternite IX, inserted on the apex of RD3.
      S2. ST9-RD3 (Figs. 43, 49) : A long muscle originating laterally on the apex of the right apophysis of sternite IX, inserted laterally along the right side of RD3.
      S3. ST9-RD3 (Figs. 43, 49) : A short fan arising on the base of the right apophysis of sternite IX, inserted on the posterior proximal branch of RD3.
    B. Tergal muscles
      T1. T9-RD1d (Figs. 42, 46, 51) : A slender muscle originating on tergite IX, inserted proximally on RD1d.
  Genitalia proper
      m.1. RD3-RD1d (Figs. 42, 46, 50, 51) : A long muscle arising dorsally on the apex of RD3, inserted distally on RD1d.
      m.2. RD3-RD1v (Figs. 42, 46, 49, 50, 51) : A long muscle arising ventrally on the apex of RD3, inserted ventrally on RD1v.
      m.3. RD2l-RD1d (Fig. 51) : A short muscle between RD1d (distal portion) and RD21 (anterior portion) (observed only in *subvittata*).
      m.4. RD1d-LD2v (Fig. 46) : A slender muscle from RD1v (or RD2d) to the anterior portion of RD2v (found only in *karnyi*).
      m.5. Vv-*RDlvm (Fig. 46) : A long muscle from the apex of Vv to the bottom of the membranous genital pouch near *RD1vm (found only in *karnyi*).
Ventral elements (composite of right and left phallomere)
  Extrinsic
    A. Sternal muscles
      s4. ST9-RVv (Figs. 43, 45) : A muscle originating on the apex of left apophysis of sternite IX, inserted on the right anterior margin of Vv (in ***kaarnyi*).** In *germanica*, on the other hand, a muscle which is tentatively identified with the former arises on the right apophysis of sternite IX and inserted on the ventral wall of the genital pouch near RD3.
      s5. ST9-*RVd (Figs. 42, 43) : A flat and short muscle arising on the apex of the right apophysis of sternite IX, attached anteriorly on the ventral wall of the ejaculatory duct at the base of the pouch of the ejaculatory duct (observed in ***germanica,*** but not in *karnyi*).
      S6. ST9-*LVd (Fig. 45) : Very fine fibers originating on the left sternal apophysis and attached posteriorly at the ventral wall of the ejaculatory duct (observed in ***germanica,*** but not in *karnyi*).
      S9. ST9-Vv (Figs. 43, 45, 46, 47) : A fairly massive fan originating postero-

rightwardly on sternite IX just posterior to the right apophysis, running up to converge on the anterior extremity of Vv (in *karnyi*). Unlike *karnyi*, the muscle tentatively labeled S9 in ***germanica*** arises on the apex of the left sternal apophysis and is inserted on the very minute sclerite (LVvr) at the ventral wall of the genital pouch.

S10. ST9-Vv (Fig. 45) : A muscle originating on the apex of the left apophysis of sternite IX, inserted on the left apical margin of Vv (in *karnyi*). In ***germanica,*** however, the muscle tentatively identified with the former is inserted on the minute sclerite (LVvl) which is situated at the side of a similar, minute sclerite on which S9 is inserted.

Genitalia proper

m.6, 12. Vv-Vd (Fig. 48) : Short muscles between the posterior branches of Vv and the postero-lateral margin of Vd, which is opposite the former.

m.7, 11. Vv-Vd (Figs. 46, 48) : Elongate and stout muscles originating latero-ventrally on the neck of Vv and inserted posteriorly on the latero-posterior portion of Vd. It is possible to conceive of homology of these with S5 and S6 in ***germanica,*** respectively, but this homology is equivocal at present.

m.8. Vv-Vd (Figs. 46, 47) : A muscle originating dorsally on the anterior portion of Vv and inserted on the anterior margin of Vd.

m.9. Vv-Vd (Fig. 46) : A short muscle running between the anterior end of Vd and the posterior fork of Vv.

m.lO. Vv-Vd (Fig. 46) : A muscle running between the middle portion of Vd and the posterior fork of Vv.

Left phallomere

Extrinsic

A. Sternal muscles

S7. ST9-LD3 (Figs. 43, 44) : An extensively massive fan arising broadly on the central portion of sternite IX, running up to converge on the anterior end of LD3.

S8. ST9-LD3 (Figs. 42, 44, 45, 46, 47) : A muscle arising on the apex of left sternal apophysis, inserted on the anterior end of LD3.

S11. ST9-*LD2l (Figs. 43, 44, 45): A flat and long muscle arising on the anterior extremity of the left sternal apophysis, inserted on the minute sclerite (LD21) which lies freely, latero-ventrally near LD1d (in *germanica*).

B. Tergal muscles

T2. T9-LD1d (Figs. 42, 44) : A slender muscle originating laterally on tergite IX, inserted on the anterior margin of LD1d.

Genitalia proper

m.13. LD3-Vd (Figs. 42, 44, 46) : A small bundle of fibers from the wall of the ejaculatory duct (just anterior to its pouch) to the anterior extremity of LD3 in ***germanica.*** In *karnyi* this is a muscle between the anterior end of Vd and anterior end of LD3.

m.14. Vd-LD2d (Fig. 46) : A muscle connecting the postero-dorsal face of Vd and anterior narrow groove of LD2d (in *karnyi*).

m.15. Vv-LD2d (Fig. 46) : A long muscle arising to the left on Vv and inserted medially on the narrow groove of LD2d (in *karnyi).*

m.16. LD3-LD1l (Figs. 44, 47) : A massive muscle arising on the anterior extremity of elongate LD3, runs downward and inserted on a thin small sclerite, LD1l which is situated at the base of the hook (LD1v).

m.17. LD3-LD1d (Figs. 44, 46) : A massive muscle within the left phallomere, originating on LD1d and inserted posteriorly on the apex of LD2d (in *kamyi).* In germanica, this muscle is also inserted on LD2d which is reduced and firmly fused to LD3.

m.18. LD3-*LD1vm (Fig. 44) : An elongate and slender muscle originating on the anterior end of LD3, inserted on the proximal wall of the left phallic pouch (LD1vm), but may be absent in *karnyi*.

m.19. LD1l-LD1v (Fig. 44) : A small muscle within a hook or LD1v, arising on the LD1l and inserted into LD1v (usually difficult to observe).

m.20. LD1l-*LD1m (Fig. 44) : A slender muscle from the dorsal wall of the left phallic pouch to LD1l (usually difficult to observe).

m.21. LD1d-*LD1m (Figs. 44, 46) : A slender muscle from the posterior margin of LD1d to the outer wall of the left phallic pouch.

(3) ***Opisthoplatia orientalis*** (Figs. 53, 54, 56-58, 60-62)

Right phallomere

Extrinsic

A. Sternal muscles

Note : The broad apodemal plate which is provided with muscles is identical with the lateral apodemes of sternite IX in *Blattella* spp., although in *Opisthoplatia*, the two apodemes are detached from the base of sternite IX and are anteriorly fused together to form an inverted “V”.

S1. ST9-RD2l (Figs. 53, 54, 56): A muscle originating to the right on the apodemal plate, inserted on the ventral margin of the combined plates of RD21 and RD1d.

s2. ST9-RD3 (Figs. 53, 54, 57) : A muscle arising on the right apical margin of the apodemal plate and inserted on the anterior end of RD3.

S3. ST9-*RVv (Figs. 53, 54, 56) : A muscle originating just posterior to the position of the S2 origin on the apodemal plate, inserted on the ventral membrane (RVv) of the genital pouch.

s4. ST9-*RVv (Figs. 54, 56, 57) : A muscle arising medially on the anterior margin of the apodemal plate, inserted on the minute sclerite (RVv) which situated in the ventral wall of the genital pouch.

B. Tergal muscles

T1. T9-RD2l (Fig. 53) : A muscle originating on tergite IX, inserted at RD2l (though fused to RD1d) on its anterior margin.

T2. T9-RD1d (Fig. 53) : A muscle arising to the right of tergite IX, inserted on the anterior margin of RD1d.

Genitalia proper

m.1. RD3-*RVv (Fig. 57) : A narrow muscle from the anterior end of RD3 to the ventral membrane of the genital pouch (RVv).

m.2. RD3-dej (*RVd ?) (Fig. 53) : A muscle from the anterior end of RD3 to the wall of the ejaculatory duct (*Vd 2).

m.3. RD3-RD11 (Figs. 53, 58) : A stout muscle from the anterior end of RD3 to RD11.

m.4. RD3-RD1v (Fig. 58) : A slender muscle from the anterior end of RD3 to the outer wall of the hook-like RD1v.

m.5. RD11-RD1v (Fig. 58) : A small muscle within a hook (RD1v), arising from the inner wall of RD11, inserted on the inner wall of RD1v.

m.6. RD3-RD21 (Fig. 57) : A slender muscle from the anterior end of RD3 to the ventral margin of RD21.

m.7. RD3-*RD2d : A muscle from the RD3 to the posterior conical membranous wall (RD2d) near the base of RD3.

m.8. RD3-*RD1m (Fig. 58) : A muscle from the medial portion of RD3 to the anterior wall of membranous sheath (RD1m) which contains the hook (RD1v).

m.9. RD3-*RD1vm (Fig. 58) : A muscle from the posterior portion of RD3 to the posterior wall of the membranous sheath (RD1vm) of the hook.

m.10. *RD2d-RD1d: A muscle from the posterior conical membranous wall of the genital pouch (RD2d) to RD1d.

Left phallomere

Extrinsic

A. Sternal muscles

s5. ST9-dej (*LVd ?) (Figs. 53, 54) : A muscle originating to the right on the apex of apodemal plate and inserted on the wall of the ejaculatory duct.

S6. ST9-*D1vm (Fig. 60) : A long muscle originating medially on the apex of apodemal plate, inserted on the inner wall of left phallic pouch which contains sclerites.

S7. ST9-LD3 (Figs. 61, 62) : A long muscle originating medially on the apex of the apodemal plate, inserted postero-proximally on the neck of LD3.

S8. ST9-LD3 (Figs. 60, 61, 62) : A muscle arising medially on the apex of apodemal plate, inserted dorsally on the anterior extremity of LD3.

S9. ST9-LD3 (Figs. 60, 61, 62) : A muscle originating anteriorly on the left margin of the apodemal plate, inserted dorsally on the anterior portion of LD3.

S10. ST9-LD3 (Fig. 60): A muscle originating on the left margin of the apodemal plate, inserted broadly along the left basal margin of LD3.

S11. ST9-LD3 (Fig. 60) : A muscle running parallel to S10, originating on the portion of the apodemal plate just posterior to the attachment of S10, inserted on LD3 just posterior to the insertion of S10.

s12. ST9-LD11 (Figs. 60, 61, 62) : A muscle arising medially on the anterior portion of apodemal plate, inserted on LD11.

B. Tergal muscles

T3. T9-*LD1d (Fig. 53) : A muscle arising on tergite IX, inserted on LD1d.

Genitalia proper

m.11. LD3-LD1v (Figs. 60, 61) : A muscle arising ventrally on the anterior margin of LD3, running posteriorly to attach to the recurved portion of LD1v.

m.12. LD3-LD2d (Fig. 61) : A muscle arising anteriorly on the right or proximal margin of LD3, inserted on LD2d.

m.13. LD2d-LD2v (Fig. 60) : A short muscle between the two opposed sclerites, LD2d and LD2v.

m.14. LD1l-LD2d (Figs. 60, 62): A short muscle between the anterior projection of LD2d and LD1l.

m.15. LD2v-*LD1vm (Fig. 62) : A massive muscle originating on the basal wall of the genital pouch (LDlvm), inserted on the anterior margin of LD2v.

6. HOMOLOGY OF THE SCLERITES

(1) D1

D1 is designated to substitute for R1 of McKittrick (1964). It includes five SRs or elements which are labeled RD1d, RD1m, RD1v, RDlvm, and RD1l, respectively. The typical association in D1 elements of the Blattaria appear to be similar to that of RD1 of the Blattinae (Figs. 1, 2), although some exceptions exist in the different types. Due to the proper associations among them, any sclerites or SRs can be defined by the constant number of surrounding SRs which come out in order in the same direction. For instance, RD1m is defined by clockwise association with RD1v, RD1l, RD1d, and RDlvm.

RD1 in *Periplaneta fuliginosa* is a twisted capsular sclerite, while it is represented by five more or less distinct sclerites in *P. americana* or *Blatta orientalis* which were described elaborately by Walker (1922), Crampton (1925, Fig. 13), and Snodgrass (1937, Figs. 15, 18). We assume that in *P. fuliginosa,* some distinct SRs of RD1 fuse firmly into a single sclerite, although RDlvm of this species does not participate in the sclerite (Figs. 6, 10, 16). There are six muscles that run into RD1 of *P. fuliginosa* : S1 from the ninth sternite ; m.4 from RD2l ; m.1, m.2 from RD3 ; and T1, T2 from the ninth tergite and within RD1, a muscle m.5 between RD1d and RD1v (Fig. 6, 28, 35). This observation also suggests that RD1 in this species may consist of at least three sclerites in view of Snodgrass' (1935) claim that a single movable sclerite had been originally provided with two antagonistic muscles. Here, RD1m is defined by the clockwise association with RD1v, RD1l, and RD1d by fusion, and to *RDlvm by adjacency (Fig. 2).

In the Blattinae, the region of LD1 may migrate from its ordinary location at the dorso-medial portion of genital cavity to the inner or right side position of the fasces of left sclerites. In the drawings of *Periplaneta* spp. by Walker (1922, cf. Figs. 20, 21, 22) and *Blatta orientalis* by Snodgrass (1937, his Figs. 13E, 14A) it is apparent that *L1* of McKittrick (1964) is a composite of three sclerites (or small lobes). In *P. fuliginosa* (Figs. 19, 23) as well, *L1* of McKittrick(1964) is observed to be formed by three components : a lobe which is a composite of two sclerites, and to its right a long spine. These are labeled LD1d, LD1l, and LD1m in the present system of terminology (Table 2). There are also two sclerites that were labeled *L2v* by McKittrick ; a basal, ample, elongate sclerite (LD1vm) and an apical narrow sclerite that terminates in a long and slightly curved spine (LD1v) in species of the Blattinae (Figs. 13, 19, 20, 21, 22). They are distinct in *P. fuliginosa* and may unite into a common sclerite in *Blatta orientalis* [in the drawings of Walker (1922) and Snodgrass (1937)]. LD1d receives a sternal muscle (S10) as in RD1d (Figs. 6, 28, 36). However, there is no muscle from LD3. The association pattern between the sclerites of LD1 is consistent with that in RD1. For example, LD1m associates counterclockwise with LD1v (by adjacency), LD1l (by adjacency), LD1d (by articulation), and Dlvm (by articulation) (Fig. 2).

Sclerites of RD1 are highly reduced in *Blattella* spp. RD1d of *B. germanica* is a thin, small plate in the dorsal front of RD21 (Fig. 37). Like *P. fuliginosa,* RD1d of *B. germanica* receives muscles from tergite (T1) and from RD3 (m.1) (Fig. 8). However, unlike *P. fuliginosa* a muscle between RD1d and RD21 is not observed in this species. This muscle is present in the congeneric *B. subvittata*; in this species the hook-like RD1d is located at the corresponding position (m. 3 : Fig. 51). In *Blattella* RD1v is a crescent-shaped sclerite which unites with a narrow small RD2d to form a convoluted sclerite (Figs. 37, 38, 41). Other sclerites of RD1 such as RD1m, RD1l, RDlvm may take part in the dorsal membrane of the right phallic pouch and other dorsal membranes of the genital pouch. There, *RD1m may associate clockwise by adjacency with RD1v, *RD1l, RD1d, and *RD1vm (Figs. 3, 4).

LD1d in *Blattella* is a broad sclerite lying on the frontal region of the genital pouch and is provided with a muscle T1 anteriorly (Figs. 7, 8, 42, 44). Posterior to this sclerite is a membranous sheath or left phallic pouch (sensu Snodgrass, 1937). There is a small flattened LD1l at the base of the terminal hook or LD1v. LD1m and LD1vm may correspond respectively to the outer and inner parts of the membranous sheath of the hook, where m.20 and m.21 attach to the former, and m.18 to the latter (Figs. 7, 42, 44). *LDlm associates counterclockwise by adjacency with LD1v, LD1l, LD1d, and *Dlvm (Figs. 3, 4).

In *Opisthoplatia orientalis,* the form of RD1 is similar to LD1 of *Blattella* species. RD1d of the former is firmly fused to RD2l which occupies a ventro-lateral position in the genital pouch. RD1v of 0. *orientalis* is, as in LD1v of *Blattella,* transformed into slender retractable hooks. RD1m and RDlvm may take part in the membranous sheath or right phallic pouch containing a hook or RD1v (Fig. 55). Muscles m.8 and m.9 are inserted respectively on the supposed RD1m and RDlvm (Figs. 9, 58). Then *RDlm associates clockwise by adjacency with RD1v, RD1l, RD1d, and *RDlvm (Fig. 5).

In the left phallomere of 0. *orientalis,* as in the right phallomere of *Blattella,* the Dlv fuses with D2d and forms a convoluted sclerite. The concrete shape of Dlv plus D2d in the right phallomere of *Blattella* shows a strong similarity to the 5-shaped corresponding structures in *Opisthoplatia*, if they were reversed and inverted. LD1l is located just anterior to RD1v when the left phallic pouch is protruded (Fig. 59). However, other SRs of LD1 such as LD1d, LD1m, and LDlvm are reduced and membranous. They may be parts of the dorsal wall of the left phallic pouch or other dorsal regions of the genital cavity. The massive m.15 (Figs. 9, 61, 62) from LD2v and S6 (Fig. 60) that is attached to the frontal base of the left phallic pouch may indicate Dlvm SR. T3 is attached to the membranous region at the dorsal base of the genital cavity and may suggest that this SR represents Dld of the left phallomere. In this species, *LDlm may associate counterclockwise by adjacency with LD1v, LD1l, *LD1d, *LD1vm, LD2v, and LD2d (Fig. 5). Association between LD1v and LD1vm may be lost due to intervention of LD2v and LD2d.

(2) **D2**

D2 is designated here as a substitute for R2 of McKittrick (1964). It includes three sclerites or SRs which are held between the dorsal D1 and ventral D3.

In *Blatta* and *Periplaneta* species, RD2 elements are well developed and show a typical arrangement. RD2d is a thick rounded capsular sclerite, whose lower lip is hinged to the upper lip of RD2v and fused to the anterior portion of RD2l laterally (Figs. 14, 15, 17, 18). Then RD2d of these genera are defined by the clockwise association with RD2l (by articulation or close adjacency), RD1v (by fusion), RD1vm (by adjacency), RD2v (by articulation), and RD3 (by adjacency) (Fig. 2).

LD2d of the same (Fig. 27) is a long and free hook which projects outwardly from the posterior position of LD3 ; LD2l is the dorsalmost sclerite out of those which form right wall of the fasces of the left phallomere; LD2v is a small sclerite situated ventrally at the base of LD2d. Then LD2d associates counterclockwise by adjacency with LD2l, LD1v, LD2v, LVv, and LD3 (Fig. 2). LD1vm loses association with LD2d due to intervention of LD1v between them.

RD2d in *Blattella* unites with RD1v to form a common convoluted sclerite which is located on the membrane between RD3 and RD1 (Figs. 37, 38, 41, 46, 51). RD2v loses the hinges with RD2d; it is a triangular flat sclerite beneath the convoluted RD2d plus RD1v and articulates ventrally with the proximal branch of RD3 (Figs. 49, 50). RD2d associates clockwise with RD1v (by fusion), *RD1vm (by adjacency), RD2v (by adjacency), and RD3 (by weak adjacency) (Figs. 3, 4). Association between RD2d and RD2l may be lost.

In the right phallomere of 0. *orientalis*, D2d element probably participates in the membranous region at the apex of genital cavity just ventral to D2v plus rod-like D3 (Fig. 55), since the corresponding regions are heavily sclerotized in the Blaberidae species shown by Roth (e. g. 1969) and in *B. karnyi*. *D2l* of 0. *orientalis* and *Blattella* are held in a different manner. In *B. germanica*, *LD2l* is a membranous region in the ventro-lateral side of LD1d where it receives a muscle S1l (Figs. 8, 45), while in 0. *orientalis*, RD2l is assumed to be fused to RD1d, since too many muscles S1, T1, T2, m.6, m.10 attach on this single plate (Figs. 9, 56, 57). D2v of the mentioned phallomere of these species (Figs. 45, 55) is situated dorsally on the endophallus or phallotreme, where it unites to the posterior end of D3 and is more or less projected posteriorly. LD2d of *Blattella* associates counterclockwise with *LD2l, LD1v, LD1vm, by adjacency, and to LD2v and LD3, by fusion (Figs. 3, 4). *RD2d of 0. *orientalis* may associate clockwise with RD2l, RD1v, RD1vm, *RD2v, and RD3 commonly by adjacency (Fig. 5).

Connections and forms of LD2 SRs in 0. *orientalis* are maintained as in RD2 of *Blattella* ; LD2d associates counterclockwise with *LD2l (by adjacency), LD1v (by fusion), to *LD1m, *LD1vm by adjacency and to LD2v, LD3 by articulation (Fig. 5). Association between LD1m and LD2d is obscure. Like *Blattella* species, LD2d unites with LD1v to form a single convoluted sclerite ; LD2v almost completely fused to proximal margin of LD3 ; LD2v and LD2d are separated from each other by a narrow membrane; a small sclerite located anterior to LD3 is labeled LD1l.

In all of the species studied, D2 elements are provided with comparatively few muscles. The muscles between D2d and D3 are rather commonly observed : RD2d in *P. fuliginosa* is connected by m.3 (Figs. 6, 35) to RD3 ; LD2d of same is an elongate lateral hook and receives m.8 and m.9 from LD3 (Figs. 6, 31) ; LD2d of 0. *orientalis* receives m.12 from LD3 (Figs. 9, 61). Unlike other Blaberidae species, RD2d of 0. *orientalis* is a soft membranous region about the base of the middle rod but is provided with m.7 from RD3 (Fig. 9). However, RD2d of *Blattelh* receives no muscles from RD3 ; LD2d of the same has no muscle from LD3 due to its fusion to the base of rod-like LD3. Other common muscles are rare : muscles between D3 and Dlv are found in the right phallomere of *P. fuliginosa* (m.1 in Figs. 6, 28), the crescent-shaped RDlv of *Blattella* (m.2 in Figs. 7, 8, 46, 50), and in the right phallomere of 0. *orientalis* (m.4 in Figs. 9, 58) ; those between D21 and Dld are found in the right phallomere of *P. fuliginosa* (m.5 in Figs. 6, 35) and in the right phallomere of *B. subvittatu* (m. *3* in Fig. 51).

(3) **D3**

D3 serves as an axis among the sclerites or SRs of the phallomere. Of the dorsal elements or "D", it occupies the ventralmost area and thereby receives sternal muscles which may control the movement of the entire dorsal elements (D), and further provides the other dorsal sclerites with muscles. Between the ninth sternite and D3 there is constantly observed at least a single muscle ; S2, S3, S4 in RD3 of *P. fuliginosa* (Fig. 6) ; S8, S9 in LD3 of the same ; S1, S2, S3 in RD3 of *Blattella* spp. (Figs. 7, 8) ; S7, S8 in LD3 of the same ; S2 in RD3 of 0. *orientalis* (Fig. 9) ; and S7, S8, S9, S10, S11 in LD3 of the same. Again, in several forms, D3 provides the principal elements of D1 and D2 with common muscles. There is also observed muscles between D3 and D2d denoted as m.3 in RD3 of *P. fuliginosa* (Fig. 6) ; m.8 and m.9 in LD3 of the same ; m.7 in RD3 of 0. *orientalis* (Fig. 9); m.12 in LD3 of the same, except in LD3 of *Blattella* species which completely fuses to LD2d. Between D3 and D1 elements, we can find a few muscles : m.1, m.2 in *P. fuliginosa* ; m.1, m.2, m. 16, m.18 in *Blattella* spp. ; m.3, m.4, m.8, m.9, and m.11 in 0. *orientalis*, though they vary in number attached to elements of D1.

The association patterns of the elements around D3 are surprisingly similar throughout the three genera examined as : (1) RD3 of *Blatta* and *Periplaneta* articulates with RD21 at the lateralmost position, then associates clockwise with RDlv (by adjacency), RD2d (by adjacency), RD2v (by articulation), and RVv (by adjacency) (Fig. 2). Similar associations are present in the left phallomere of the same genera. LD3 associates counterclockwise with LD21 (by fusion), LDlv (?), LD2d (by adjacency), LD2v (by adjacency), and LVv (by adjacency). (2) RD3 of *Blattelh* associates clockwise with D21 (by articulation), RDlv (by adjacency), RD2d (by adjacency), RD2v (by articulation), and Vv (by weak adjacency). Of these, the association with RD2d and Vv is rather weak but no intervening structure was recognized between the sclerites (Figs. 3, 4). LD3 of the same also shows a common association pattern : it associates counterclockwise with *LD2l (by adjacency), LDlv (by weak adjacency), LD2d (by fusion), LD2v (by fusion), and Vv (by adjacency). (3) RD3 and associated sclerites in the right dorsal region of 0. *orientalis* resembles those of the left dorsal region of *Blattella* in form and accordingly associate the same way (Fig. 5) : it associates clockwise with

RD21 (by adjacency), RD1v (by adjacency), RD2d (by weak adjacency), RD2v (by fusion), and RVv (by adjacency). LD3 of the same associates counterclockwise with *LD2l (by weak adjacency), LD1v (by articulation), LD2d (by adjacency), LD2v (by fusion). Association between LD3 and Vv in *Opisthoplatia* is not determined because of the large intervening membrane and membranous condition of LVv. As seen above, both RD3 and LD3 in the three genera commonly have five associated sclerites which are arranged in the same order around them and provide definition of D3.

It is interesting to observe that LD3 of *Blattella* and RD3 of 0. *orientalis* are commonly modified as a slender rod that fuses at its base with D2v in the dorsal area of the phallotreme (Figs. 41, 55). RD3 of 0. *orientalis,* however, attaches along its most left side to the wall of the endophallic sac or endophallus and is separated only proximally (Fig. 55). This may represent an intermediate condition during the specialization of a completely free, rod-like LD3 as commonly observed in the Blattellinae from the general LD3 in the ancestor. This may further suggest that the rod-like structure is identical with the Vd element. But we do not stand the latter view, for the present, considering the entire association pattern and musculature. If the rod-like structure is Vd, R+LVv and R+LVd in *B. karnyi* may be transfered to LD3 and LD2v, respectively. Several veiws are possible, and further examination of many species of the genera other than studied here may provide with reliable homology of the structures.

(4) Vd

Crampton (1925) and Snodgrass (1937) had recognized a piece of sclerite about the aperture of the ejaculatory duct in *Periplaneta americana* and *Blatta orientalis*. Crampton called the portion on which the sclerite lies "penis" regarding it as equivalent to the aedeagus of other insect orders. Based on the presence of this sclerite, Snodgrass considered this portion as a phallic invagination on the endophallic sac to which the true ejaculatory duct is continued. He named the sclerite itself as *"endophallic sclerite"* or *"sclerite of endophallus"*.

In *Blattella karnyi*, the terminal ventral wall of the genital exit passage contains a sclerotization which is opposite to another conspicuous structure at the posterior ventral wall of the genital pouch (Fig. 41). Because of its location, the former is possibly homologous with the endophallic sclerite of the Blattinae. The latter may be identical with the ventral phallomere of the Blattinae since it is located below the endophallus. As far as we know, these structures are peculiar to the Blattidae and Blaberidae.

The attachment of the sternal muscles may suggest Vd SRs in the wall of the phallotreme. At least a single muscle is observed between Vd and ninth sternite : S5 in R+LVd of *P. fuliginosa* (Figs. 6, 28, 30) ; a flat muscle or S5 to the pouch of ejaculatory duct of *B. germanica* (Figs. 8, 42, 43) ; a fiber or S6 to the ventral wall of the phallotreme of the same (Figs. 8, 45) ; S5 to the phallotreme of 0. *orientalis* (Figs. 9, 53). In Vd of *B. karnyi*, however, there is no sternal muscle.

We think that the unique structure around the genital exit passage of *B. karnyi* may be the significant link between the two types of the genitalia represented typically by *Blattella germanica* and *Blatta orientalis* in the study of Snodgrass (1. c.). Vd which had existed in the ancestral plan of the Blaberoidea genitalia may have been gradually lost (except for the Polyphagidae) during the organ's evolution.

(5) **Vv**

As stated in the "Historical review and problem", it was Snodgrass (1935) who first gave the ventral lobe of the Blattinae genitalia equal status with the lateral two lobes, giving it the term *"ventral phallomere"*.

On the other hand, Quadri (1940) pointed out that the rudiments of the male genitalia in species of *Blatta* and *Periplaneta* started as a paired structure, then divided horizontally into four lobes which he called *"penis valves"*. According to Quadri, the right ventral penis valve developed to occupy the ventral middle position of the genitalia in the adult, while the left ventral penis valve emigrated from its original ventral position to a dorso-proximal position in the adult genitalia. However as discussed previously in the section of "D1", the left ventral penis valve in the adult obviously corresponds to LD1 in the present terminology. Admitting the view of Quadri, there is a noticeable discrepancy between the connections of the "left ventral penis valve" and the surrounding structures in the early nymphal stages and in the adult.

Undoubtedly, the observed "ventral phallomere" of the adult in the Blattinae is identical with the ventral element of the right phallomere (RVv) as pointed out by Quadri. Here, RVv associates clockwise by adjacency with RD3, RD2v, RVd, and LVv (Fig. 2).

Comparison of the patterns of associations between the sclerites around Vv shows that a small flat sclerite just below LD3 in the present terminology, or *"L2d"* of McKittrick (1964) must represent the ventral SR of the left phallomere (LVv), although, so far, none of the former investigators had named this sclerite. The association patterns are somewhat more complex than the right one due to some secondary associations between the sclerites : LVv associates counterclockwise by adjacency with LD3, LD1v, LD2d, D2v, Vd, and RVv (Fig. 2).

The Vv elements are in most cases lost or much reduced in the Blattellidae and the Blaberidae. The rudiment of the structure could not be traced back even in the early nymphal stages of *Blattella germanica* (Snodgrass, 1937). While a conspicuous ventral structure in *Blattella karnyi* is supposed to be a composite of right and left ventral SRs (RVv+LVv), and therefore may not be completely homologous with the observed ventral phallomere of the Blattinae. In *B. karnyi*, RVv associates clockwise with RD3, RD2v, and RVd by adjacency, and LVv by fusion (Fig. 3). LVv associates counterclockwise with LD3, LD2v, and LVd by adjacency, and RVv by fusion. The two patterns are consistent with that of RVv of *P. fuliginosa*. In most Blattellidae and Blaberidae, the Vv elements are reduced in both phallomeres, into very minute sclerites or they may be participate in the membranous ventral wall of the genital pouches.

The attachment of the sternal muscles may suggest Vv SRs in the ventral wall of genital pouch. Between the ninth sternite and Vv, there is generally at least a single muscle : S6 in RVv of *P. fuliginosa* (Figs. 6, 30) ; S4, S9, and S10 in (R+L) Vv of *B. karnyi* (Figs. 7, 46, 48); S4 to the right ventral wall of the genital cavity of *B.*

germanica (Figs. 8, 43, 45); S9 and S10 inserted respectively on the two minute sclerites (LVvr and LVvl) at the medial wall of genital cavity of the same (Figs. 8, 45) ; S4 to a minute sclerite at the middle of the ventral wall of genital cavity and S3 to the wall just rightward of the former in 0. *orientalis* (Figs. 9, 56, 57). The attachment of the sternal muscle of LVv in *P. fuliginosa* is shifted to the neighboring LD1vm (Figs. 6, 31 : S7).

7. SUMMARY

(1) Male genitalia of five species of the Blattaria, namely *Periplaneta fuliginosa* (Blattidae : Blattinae) ; *Blattella* spp. (*germanica, karnyi*, and *subvittata*) (Blattellidae : Blattellinae) ; and *Opisthoplatia orientalis* (Blaberidae : Epilamprinae) were examined. In addition, the drawings of *Periplaneta americana* figured by Crampton (1925), and those of *Blatta orientalis* by Snodgrass (1937) (both Blattinae) were referred to for the comparisons. The three subfamilies referred to above were considered to represent three variations of the genital structures: 1) strongly sclerotized, with the ventral outstanding lobe (= Blattinae type for the superfamily Blattoidea) ; 2) largely membranous, with the left retractable hook (= Blattellinae type for the family Blattellidae with a few exceptions) ; 3) largely membranous, with the right retractable hook and left retractable sclerites (= Epilamprinae type for the family Blaberidae).

(2) The homology of membranous regions as well as sclerites were studied, assuming that the entire genital pouch could be divided into subregions (SRs) which correspond to the observed structures whenever sclerotic or not. It obviously dues to a great degree of replacement of sclerites with membrane that the Blattellinae type and Epilamprinae type are hardly relatable to the Blattinae type.

(3) Eleven SRs are commonly recognized bilaterally throughout the examined species. They are grouped into the dorsal (D) and ventral (V) major regions in the genital pouch. D is divided into D1, D2, and D3 ; V includes Vv and Vd as its components ; D1 includes Dld, Dlm. Dlv, Dlvm, and D1l ; in D2, there are D2d, D2v, and D2l. D3, Vv, and Vd are not divided.

(4) There are three kinds of neighboring relations (= associations) between SRs: association by fusion, by articulation, and by adjacency. Even when two sclerites are interrupted by a membrane, unless largely separated, a week adjacency between them is recognizable. They are applied in a plane graph of association pattern to show relationships of the entire SRs.

(5) The association pattern of the sclerites (SRs) is introduced as a useful tool for identification of the genital sclerites. The pattern involves the rule of arrangement of the sclerites in the entire structural complex. Undoubtedly, it is more stable than the concrete form of the sclerites themselves. The graphs of association pattern in the different types are very similar, although they do not completely agree in detail.

(6) Musculature is of less importance in the identification of the male genital sclerites, but is helpful only supplementally. The muscles among the various types studied are inconsistent in number and points of attachment on the sclerites. The almost exclusive reception of the sternal muscles on the rod-like structures observed in the middle in the Blattellinae and Epilamprinae types strengthens their identi-

fication with D3 or apodemal sclerites of the Blattinae type.

(7) The outermost hook of the left phallomere of the Blattinae type and retractable hooks of the Blattellinae and Epilamprinae types, which often, had been suggested as homologous, are considered to be derived from different SRs' and thus not to be homologous structures.

(8) As suggested by Quadri (1940), the male genitalia of the Blattoidea is concluded as a paired structure. The current view that the genitalia of the Blattoidea (Blattinae type) is comprised of three principal lobes or phallomeres (Snodgrass, 1935) is rejected here. The outstanding ventral phallomere (the third phallomere) in the type is shown to be a ventral element of the right phallomere (RVv). On the other hand, the left ventral element (=LVv) of this type was retained as a small flattened sclerite set ventrally in the fasces of the left phallomere.

(9) Three types of genitalia may have arisen independently from a symmetrical ancestral type. The Blattellidae and Epilamprinae types are almost mirror images of each others suggesting that there had existed symmetrical basic plan which had possessed potencial to differentiate similar structures.

8. ACKNOWLEDGMENTS

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REFERENCES

Asahina, S. 1961. A revised list of the Japanese cockroaches of sanitary importance (Insecta, Blattaria). *Jap. J. M. Sc. and Biol.*, *14: 147-156.*

Asahina, S. 1981a. Notes on the *Blattella* species of Taiwan I. What is "*Phyllodromia humbertiana* Karny 1915"? *Jap. J. sanit. Zool., 32 (3)* : 215-219. (In Japanese, with English summary)

Asahina, S. 1981b. ditto, II. What is "*Ischnoptera sauteri* Karny 1915"? *Jap. J. sanit. Zool., 32 (4)* : 255-259. (In Japanese, with English summary)

Chopard, L. 1920. (in Snodgrass, 1937). Recherches sur la conformation et le developpment des derniers segments abdominaux chez les Orthopteres. 352 pp. Rennes.

Crampton, G. C. 1925. The external anatomy of the head and abdomen of the roach, *Periplaneta americana. Psyche, 32* : 195-220, 5-7 pls.

Guthrie, D. M. and A. R. Tindall 1968. *The biology of the cockroach.* Edward Arnold Ltd., London, 408 pp.

Hebard, M. 1929. Studies in Malayan Blattidae (Orthoptera). *Proc. Acad. nat. Sci. Philadelphia,* 81:

1-109, 6 pls.

Khalifa, A. 1950. Spermatophore production in *Blattella germanica* L. (Orth.: Blattidae). *Proc. Roy. ent. Soc. Lond.* **(A)** 25: 53-61.

Matsuda, R. 1976. *Evolution of insect abdomen. 533* pp. Pergamon Press, Oxford.

McKittrick, F. A. 1964. Evolutionary study of cockroaches. *Mem.* Cornell Univ. *Agr. Exp. St., 389* : 1-197.

Mizukubo, T. 1981. A revision of the genus *Blattella* (Blattaria : Blattellidae) of Japan. I. Terminology of the male genitalia and description of a new species from Okinawa Island. *Esakia, (17)* :149-159.

Princis, K. 1969. Pars 13 Blattaria ; Subordo Epilamproidea, Fam. Blattellidae. *In "Orthopterorum* Catalogus, ed, by M. Beier pp. 712-1038. Junk, 's-Gravenhage.

Quadri, M. A. H. 1940. On the development of the genitalia and their ducts in orthopteroid insects. Trans. *Roy. ent. Soc. Lond., 90:* 121-175.

* Remane, A. 1956. Die Grundlangen des nattirlichen Systems der vergleichen Anatomie und der Phylogenetik, Leipzig.

* Remane, A. 1961. Gedanken zum Problem : Hmologie und Analogie, Präadaptation und Parallelität. *Zoologischer Anzeiger, 166 : 447-465.*

Roth, L. M. 1969. The male genitalia of Blattaria. I. *Blaberus* spp. (Blaberidae : Blaberinae). *Psyche, 76* : 217-250.

Roth, L. M. 1970. The male genitalia of Blattaria. II. *Poeciloderrhis* spp. (Blaberidae : Epilamprinae). Psyche, 77 :104-119.

Roth, L. M. 1973. The male genitalia of Blattaria. XI. Perisphaerinae. *Psyche, 79* :305-348.

Roth, L. M. 1977. A taxonomic revision of the Panesthiinae of the world I. The Panesthiinae of Australia (Dictyoptera : Blattaria : Blaberidae). *Aust. J. Zool. Suppl. Ser.* (48) :1-112.

Roth, L. M. 1979. ditto, II. The genus *Salganea* Stal, *Microdina* Kirby and *Caeparia* Stal (Dictyoptera : Blattaria : Blaberidae). *Aust. J. Zool. Suppl. Ser. (69)* : 1-201.

Roth, L. M. 1985. A taxonomic revision of the genus *Blattella* Caudell (Dictyoptera, Blattaria: Blattellidae). *Ent. scand. Suppl. No. 22. 221* pp.

Roth, L. M. and A. B. Gurney 1969. Neotropical cockroaches of the *Epilampra abdomennigrum* complex ; a clarification *of* their systematics (Dictyoptera, Blattaria). Ann. *ent. Soc. Amer., 62* : 617-627.

Snodgrass, R. E. 1935. *Principles of insect morphology.* McGraw-Hill, New York, 667 pp.

Snodgrass, R. E. 1937. The male genitalia of orthopteroid insects. *Smithson. misc. Coll., 96 (5)* :1-107.

Walker, E. M. 1922. The terminal abdominal structure of orthopteroid insects: a phylogenetic study (Part II). *Ann. ent. Soc.* Amer., 15: 1-76, 11 pls.

*Not seen by the authors.

Plate III

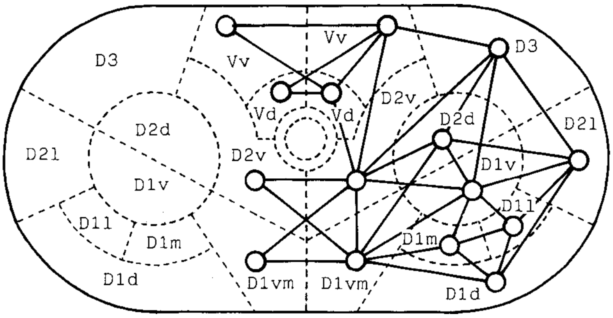
Fig. 1. Schematic map of male genitalia of Blattaria showing the basic arrangement and association pattern of SRs. (Frontal view: Dorsal is to the bottom of figure)

Fig. 2. *Periplaneta fuliginosa* ; association pattern of SRs. Broken lines indicate weak adjacency or supposed associations ; single lines for adjacency ; double lines for articulation ; and triple lines for fusion.

Fig. 3. *Blattella karnyi* ; association pattern of SRs.

Fig. 4. *Blattella germanica* ; association pattern of SRs.

Fig. 5. *Opisthoplatia orientalis* ; association pattern of SRs.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Vv
Vv
D3
D2v
Vd
Vd
D2d
D21
D2d
D21
D2v
D1v
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D1m
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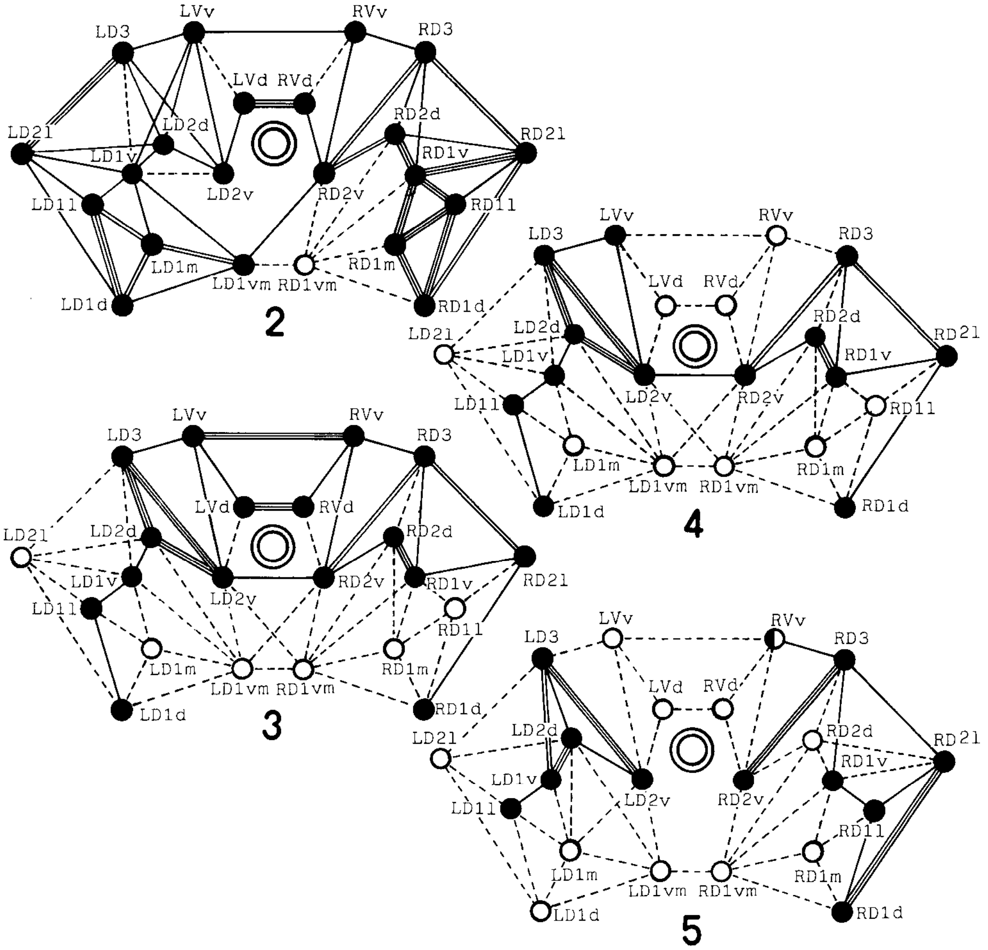
D1d
D1vm
D1vm
D1d

I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LVv
RVv
RD3
LVd
RVd
LD21
LD2d
RD2d
RD21
LD1v
RD1v
LD2v
RD2v
LD11
RD11
LD1m
RD1m
LD1vm
RD1vm
LD1d
RD1d

2

3

4

5

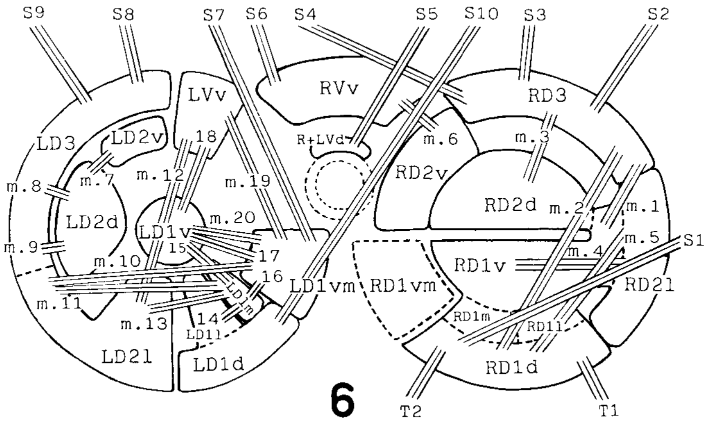
Plate IV

Fig. 6. *Periplaneta fuliginosa*; schematic map of the male genitalia with indication of musculature. (Frontal view : Dorsal is to the bottom of figure)

Fig. 7. *Bluttella karnyi*; schematic map of the male genitalia. (Frontal view : Dorsal is to the bottom of figure)

Fig. 8. *Bluttella germanica*; schematic map of the male genitalia. (Frontal view : Dorsal is to the bottom of figure)

Fig. 9. *Opisthoplatia orientalis*; schematic map of the male genitalia. (Frontal view : Dorsal is to the bottom of the figure)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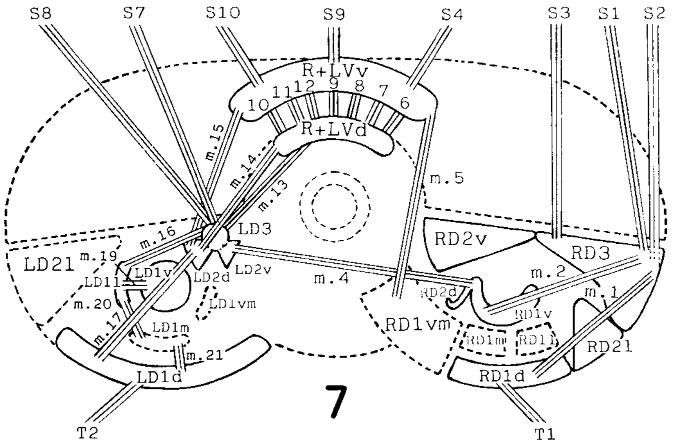
S8
S7
S6
S4
S5
S10
S3
S2
S1
LVv
RVv
RD3
LD3
LD2v
R+LVd
m.6
m.3
18
m.12
m.19
RD2v
m.8
m.7
LD2d
RD2d
m.2
m.1
LD1v
m.20
15
m.9
17
m.10
m.4
m.5
RD1v
16
LD1vm
RD1vm
RD21
m.11
LD1m
14
m.13
RD1m
RD11
LD11
LD21
LD1d
RD1d
T2
T1

6


S8
S7
S10
S9
S4
S3
S1
S2
R+LVv
10
11
12
9
8
7
6
R+LVd
m.15
m.14
m.13
m.5
m.16
LD3
RD2v
RD3
LD21
m.19
LD1v
LD2d
LD2v
m.4
m.2
LD11
LD1vm
RD2d
m.1
m.20
RD1v
RD1vm
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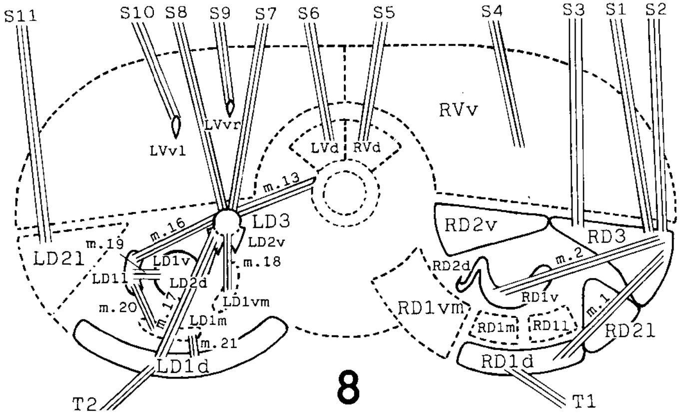
LD1d
RD1d
T2
T1

7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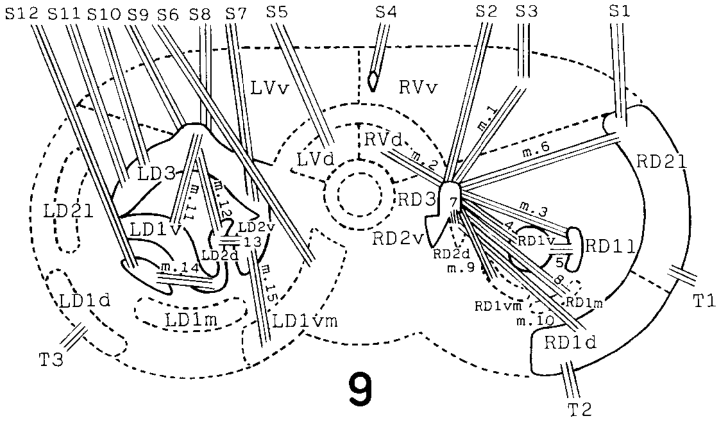
S10
S8
S9
S7
S6
S5
S4
S3
S1
S2
RVv
LVvl
LVvr
LVd
RVd
m.13
LD3
RD2v
RD3
m.16
LD2v
LD21
m.19
m.18
m.2
LD1v
RD2d
LD11
LD2d
RD1v
LD1vm
RD1vm
m.20
m.17
LD1m
m.1
RD1m
RD11
m.21
RD21
LD1d
RD1d
T2
T1

8


S12
S11
S10
S9
S6
S8
S7
S5
S4
S2
S3
S1
LVv
RVv
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LVd
RVd
m.6
m.2
RD21
LD3
m.11
m.12
RD3
7
LD21
m.3
LD1v
LD2v
RD2v
13
4
RD1v
RD11
LD2d
RD2d
5
m.9
m.14
m.15
8
LD1d
RD1vm
RD1m
m.10
LD1m
LD1vm
RD1d
T1
T3
T2

9

Plate V

Fig. 10. *Periplaneta* ***fuliginosa*** ; entire male genitalia, dorsal view. (Posterior is to the bottom of the following figures)

Fig. 11. ***P. americana*** ; entire male genitalia, dorsal view. (Redrawn from Crampton, 1925)

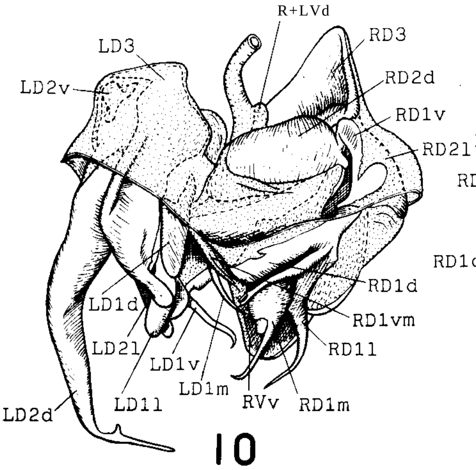
Fig. 12. ***P. fuliginosa*** ; entire male genitalia, ventral view.

Fig. 13. ***P. americana*** ; entire male genitalia, ventral view. (Redrawn from Crampton, 1925)

Fig. 14. *P.* ***fuliginosa*** ; right phallomere, dorsal view.

Fig. 15. *Blatta orientalis* ; right phallomere, dorsal view. (Redrawn from Snodgrass, 1937)

Fig. 16. *P.* ***fuliginosa*** ; ventral lobe (=Vv and Vd), dorsal view.



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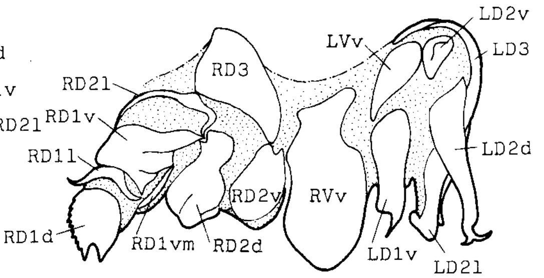

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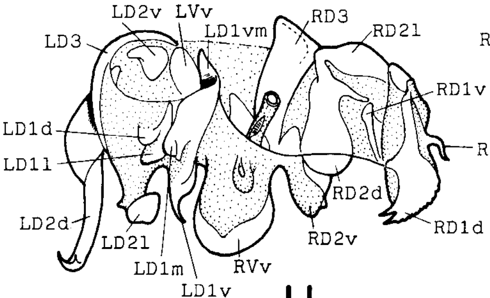

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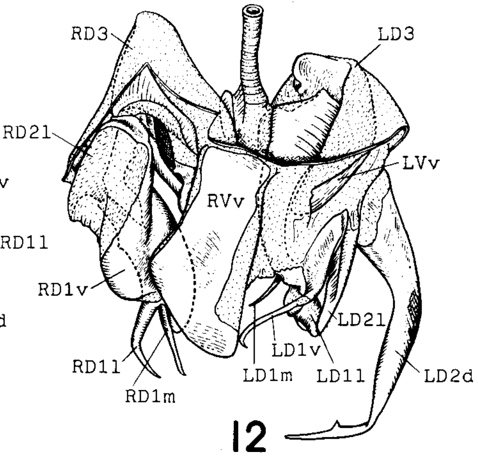

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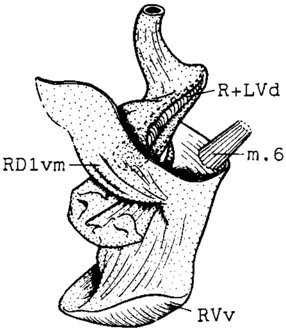

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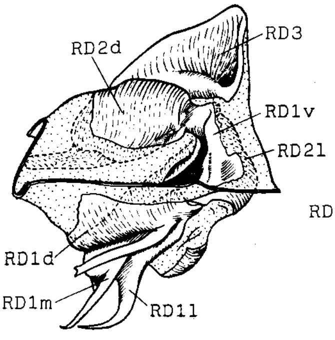

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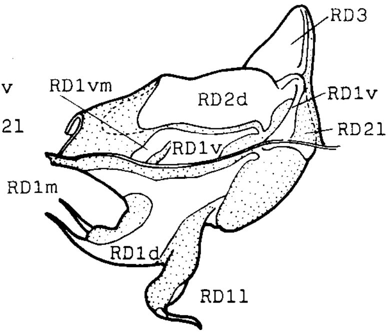

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Plate VI

Fig. 17. *Periplaneta fuliginosa* ; right phallomere, ventral view.

Fig. 18. *Blatta orientalis* ; right phallomere, ventral view: (Redrawn from Snodgrass, 1937)

Fig. 19. *P. fuliginosa* ; entire left phallomere, inner view.

Fig. 20. *P. americana* ; entire left phallomere, inner view. (Redrawn from Walker, 1922)

Fig. 21. *P. burnnea* ; entire left phallomere, inner view. (Redrawn from Walker, 1922)

Fig. 22. *P. fuliginosa* ; entire left phallomere, inner view. (Redrawn from Walker, 1922)

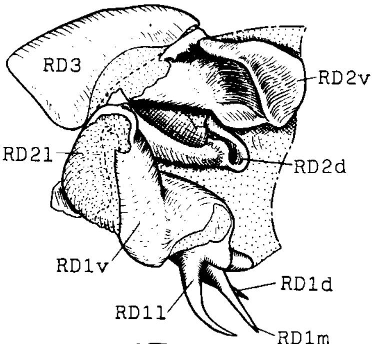
Fig. 23. Same ; LD1d and LD1l.

Fig. 24. Same ; inner sclerites of the left phallomere, ventral aspect.

Fig. 25. Same : inner sclerites of the left phallomere, dorsal aspect. LD1d and LD1l are removed.

Fig. 26. Same ; outer and ventral sclerites of left phallomere, inner aspect. Inner sclerites are removed.

Fig. 27. Same ; outer and ventral sclerites of left phallomere, outer aspect.



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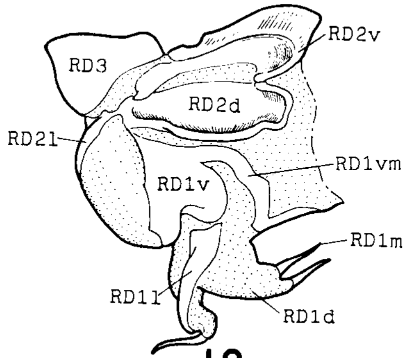

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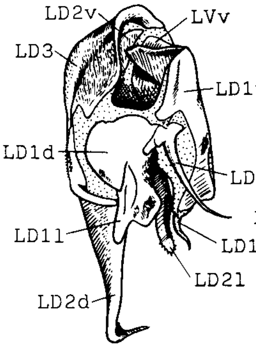

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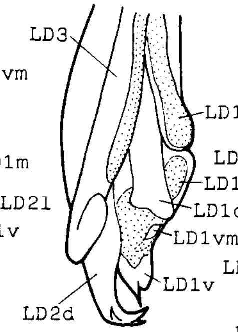

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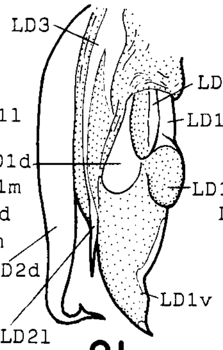

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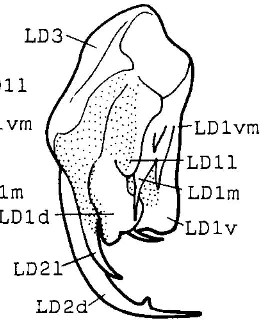

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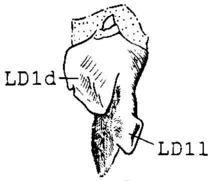

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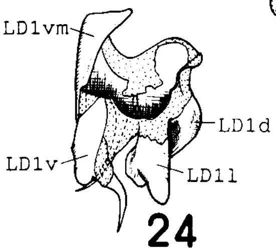

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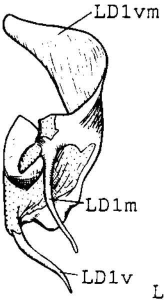

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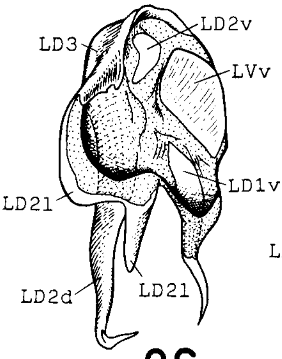

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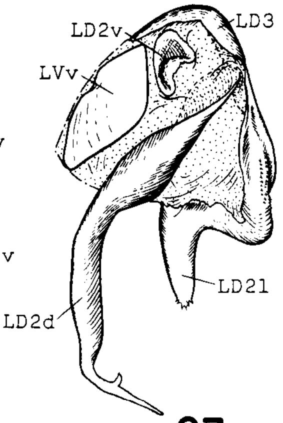

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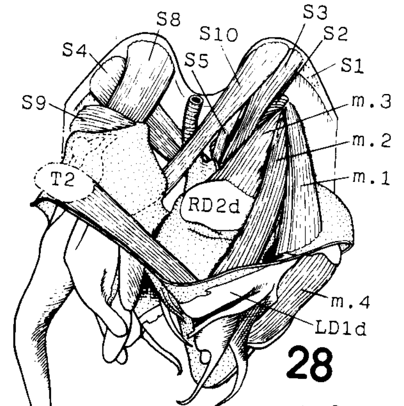
Plate VII (*Periplaneta fuliginosa*)

Fig. 28. Genital musculature, dorsal view. Muscles S1, T1, S6, and S7 are removed.
Fig. 29. Dorsal aspect of RD3 showing the points of attachment of the muscles.
Fig. 30. Genital musculature, ventral view.
Fig. 31. Diagram showing muscles within a left phallomere, inner view.
Fig. 32. Diagram showing ventral muscles beneath the those shown in Fig. 31.
Fig. 33. Diagram showing outer aspect of LD2d along with muscles inserted on it.
Fig. 34. Same, inner aspect.
Fig. 35. Diagram showing musculature in the right pahllomere, dorsal view; the opposite RD2v and RD2d are opened and m.2 is partially cut away to show the m.5.
Fig. 36. Diagram showing muscles of the inner sclerites of left phallomere, ventral view.



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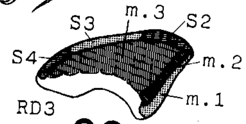

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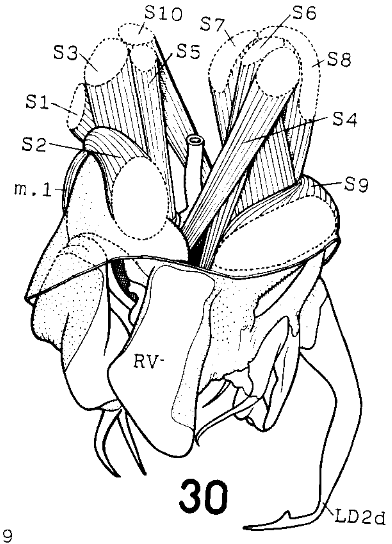

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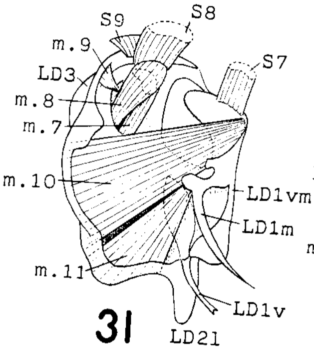

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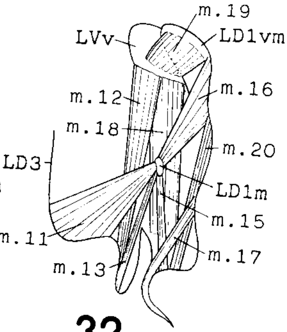

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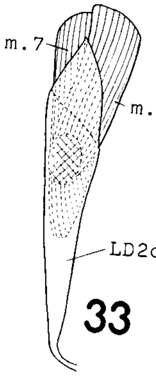

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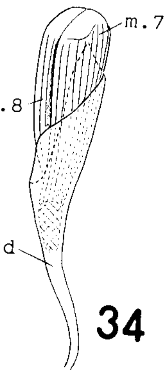

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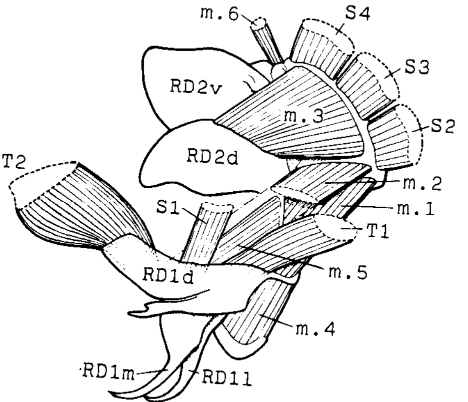

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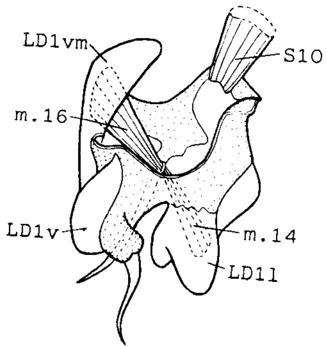

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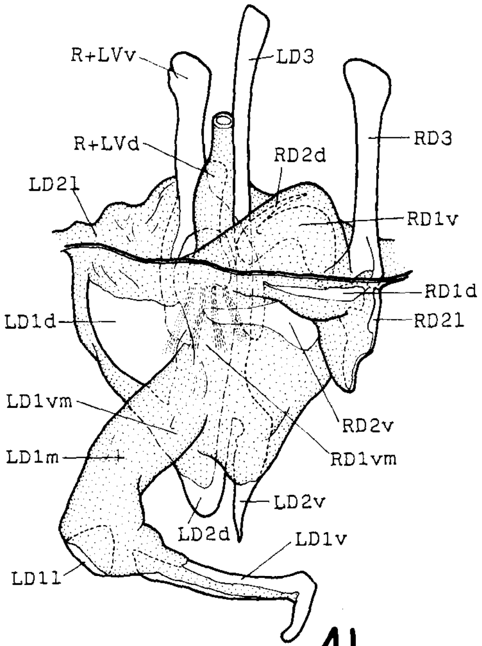
Plate VIII

Fig. 37. *Blattella germanica* ; entire male genitalia, dorsal view.
Fig. 38. *B. subvittata* ; entire male genitalia, dorsal view,
Fig. 39. *B. karnyi* ; ventral sclerites (=Vv and Vd), dorsal view.
Fig. 40. Same ; lateral view.
Fig. 41. Same ; entire male genitalia, dorsal view.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LD3
R+LVd
RD3
RD2d
LD21
RD1v
RD1d
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RD21
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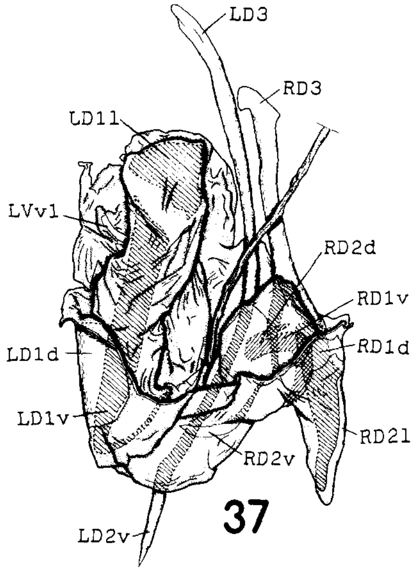
LD1m
LD2v
LD2d
LD1v
LD11

41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LD2v

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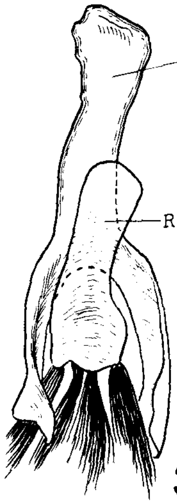
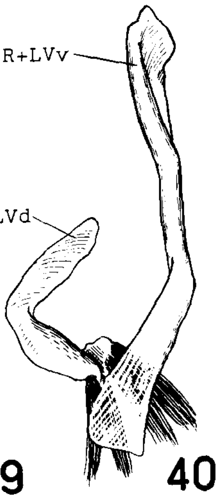

R+LVv
R+LVd

39



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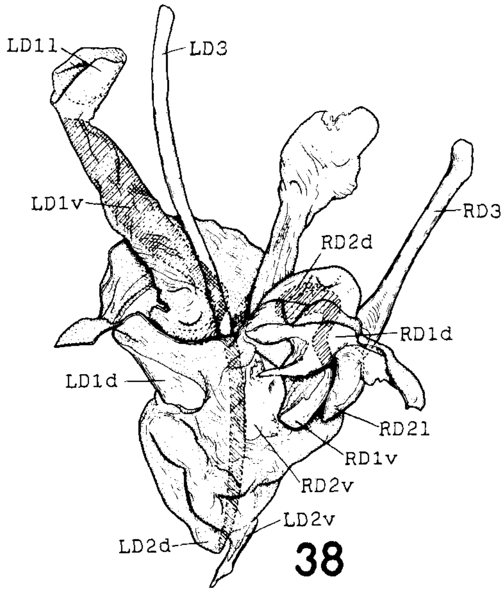
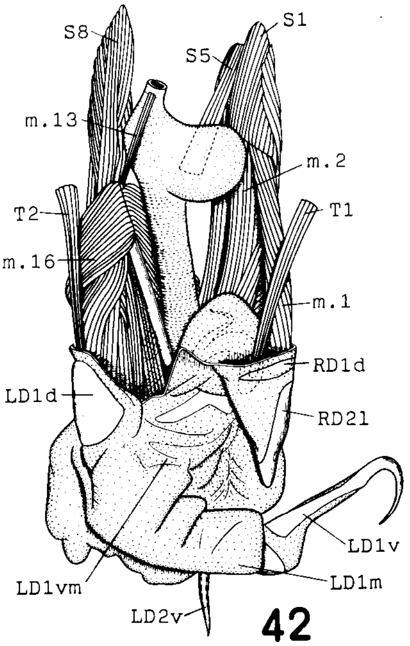

LD11
LD3
LD1v
RD3
RD2d
RD1d
LD1d
RD21
RD1v
RD2v
LD2v
LD2d

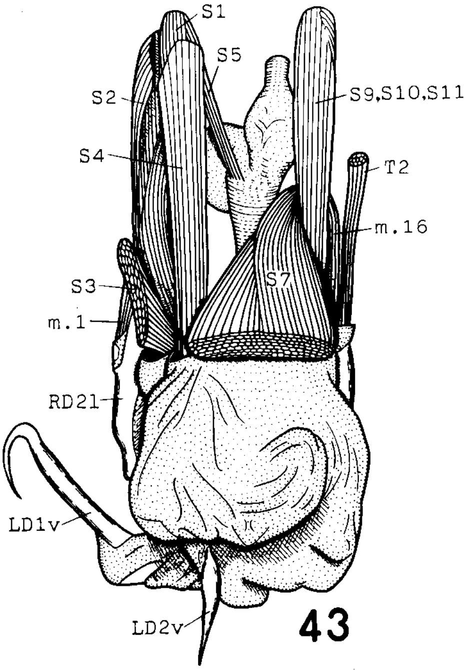
38

Plate IX *(Blattella germanica)*

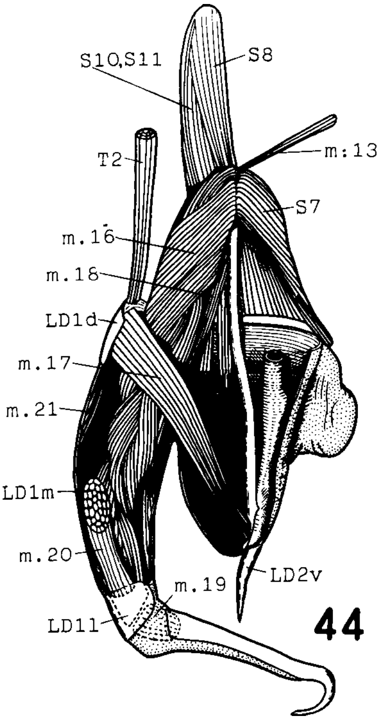
Fig. 42. Entire genital musculature, dorsal view.
Fig. 43. Entire genital musculature, ventral view.
Fig. 44. Muscles within the left phallomere, dorsal view.
Fig. 45. Same, dorsal muscles are removed and middle portion of LD3 is cut away to show the ventral muscles.


S8
S1
S5
m.13
m.2
T2
T1
m.16
m.1
RD1d
LD1d
RD21
LD1v
LD1vm
LD1m
LD2v

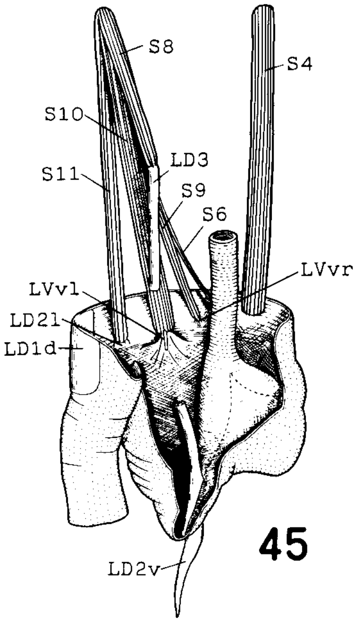
42


S1
S5
S2
S9,S10,S11
S4
T2
m.16
S3
S7
m.1
RD21
LD1v
LD2v

43


S10,S11
S8
m:13
T2
S7
m.16
m.18
LD1d
m.17
m.21
LD1m
m.20
LD2v
m.19
LD11

44


S8
S4
S10
LD3
S11
S9
S6
LVvr
LVvl
LD21
LD1d
LD2v

45

Plate X

Fig. 46. *Blattella karnyi* ; entire genital musculature, dorsal view. m.16 is removed.

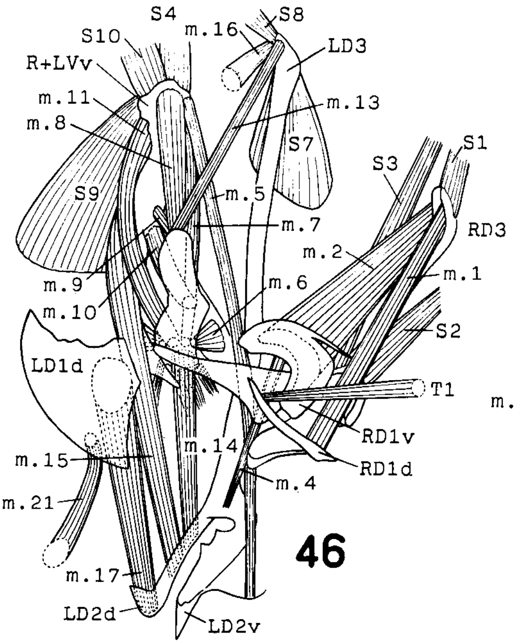
Fig. 47. Same ; ventral aspect of the left phallomere.

Fig. 48. Same ; muscles of Vv and Vd, ventral aspect.

Fig. 49. *B. germanica* ; muscles from the right sternal apophysis to the sclerites of the right phallomere, ventral view.

Fig. 50. Same ; muscles of RD3, ventral view.

Fig. 51. *B. subvittata* ; schematic diagram showing the relationship between sclerites and muscles in the right phallomere. Of the *Blattella* species examined, m.3 is found only in this species.



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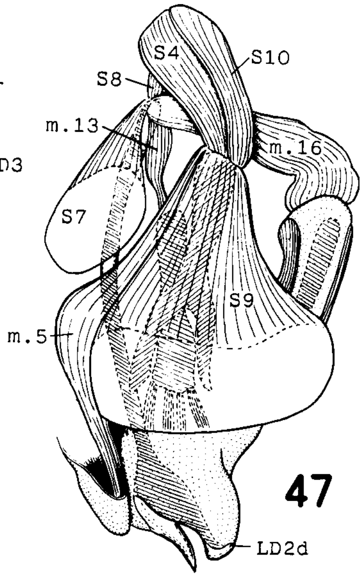

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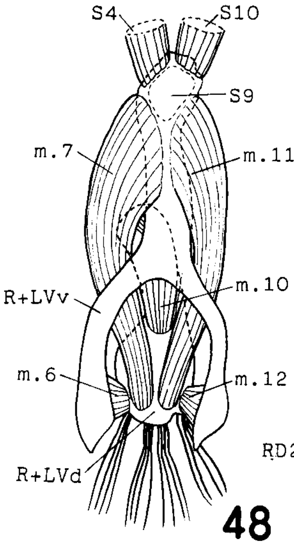
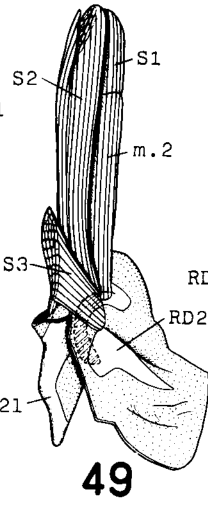


48



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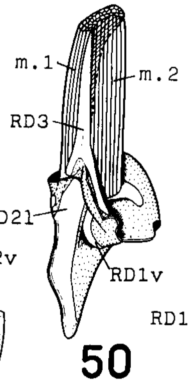

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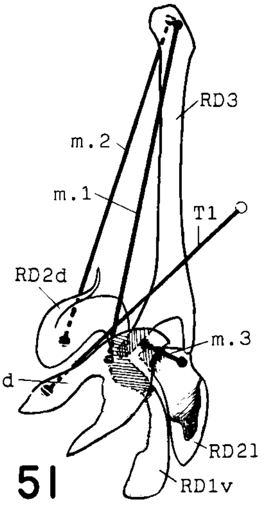


51

Plate XI *(Opisthoplatia orientalis)*

Fig. 52. Entire male genitalia, dorsal view.

Fig. 53. Entire male genital musculature, dorsal view.

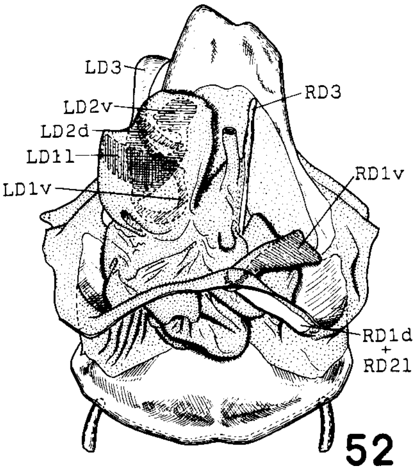
Fig. 54. Ninth sternal apophyses as an inverted “V”, indicating the points of insertion of sternal muscles.

Fig. 55. Right phallomere with hook (RD1v) protracted, dorsal view.

Fig. 56. Right phallomere, showing sternal muscles, ventral view.

Fig. 57. Same, S1 and S3 removed.

Fig. 58. Muscles associated with hook (RD1v).



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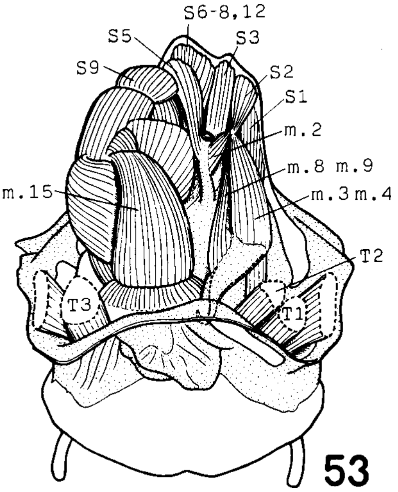

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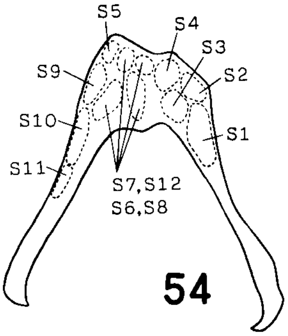

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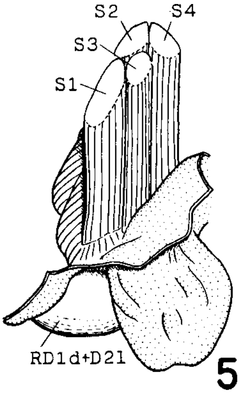

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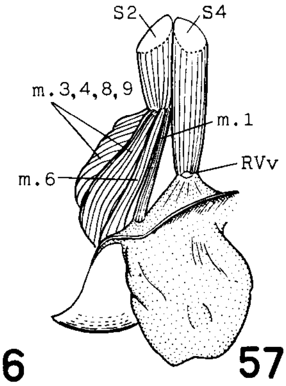

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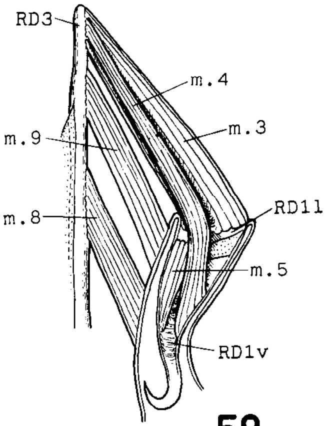

58

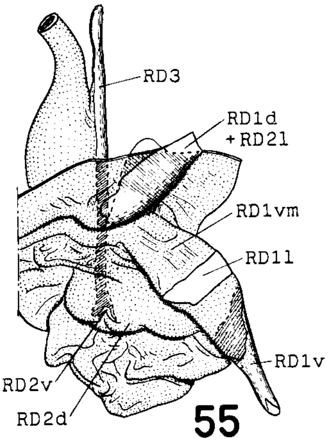

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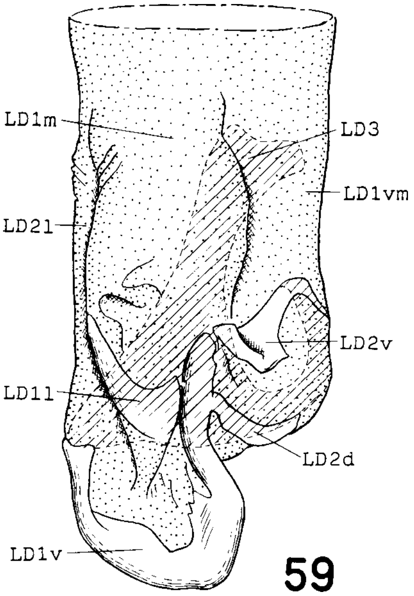
Plate XII (*Opisthoplatia orientalis*)

Fig. 59. Left phallomere in a protracted condition, dorsal aspect.

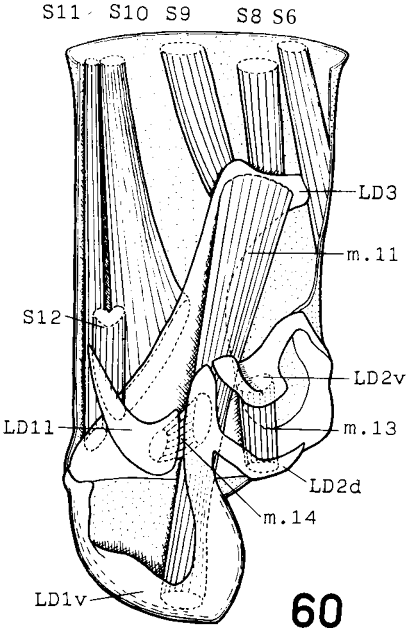
Fig. 60. Left phallomere showing the musculature of dorsal aspect. Muscles S7, m.12, m.15, are throughly removed and S12 is cut away anteriorly.

Fig. 61. Left phallomere showing the musculature of inner aspect. M.6 is not drawn and S10, S11, m.13, and m.14 are removed.

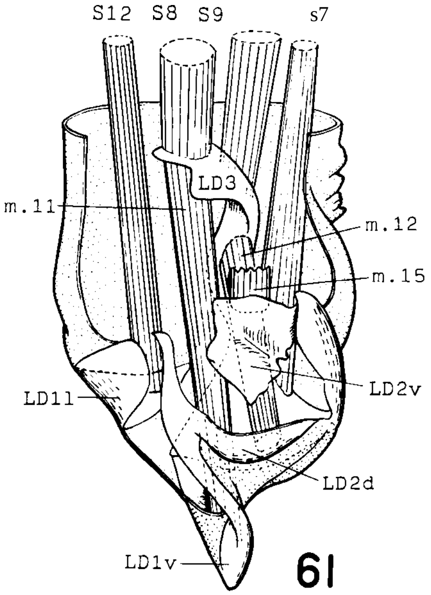
Fig. 62. Left phallomere showing the musculature of ventral aspect. Muscles S6, m.12, and m.13 are not drawn ; m.11 is posteriorly cut away ; and S10 and S11 are removed.


LD1m
LD3
LD1vm
LD21
LD2v
LD11
LD2d
LD1v

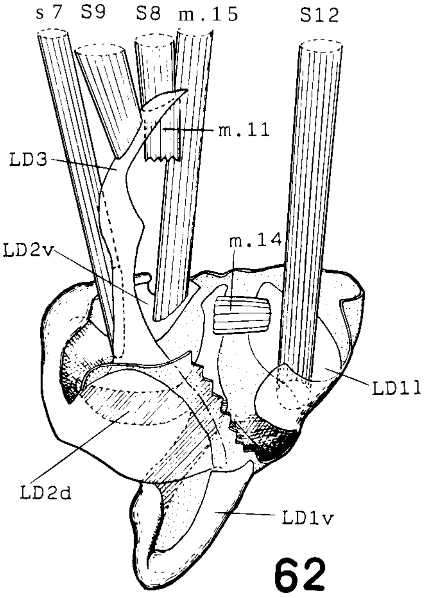
59


S11
S10
S9
S8
S6
LD3
m.11
S12
LD2v
LD11
m.13
LD2d
m.14
LD1v

60


S12
S8
S9
s7
m.11
LD3
m.12
m.15
LD11
LD2v
LD2d
LD1v

61


s 7
S9
S8
m.15
S12
m.11
LD3
m.14
LD2v
LD11
LD2d
LD1v

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