MORPHO-TAXONOMIC STUDIES OF THE GENITALIA OF A FEW AQUATIC COLEOPTERA

By

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SUPERVISOR'S NOTE

The thesis entitled "MORPHO-TAXONOMIC STUDIES OF THE GENITALIA OF A FEW AQUATIC COLEOPTERA" is a piece of original work of Sri M. Rama Krishna.

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INTRODUCTION

Reproductive organs of aquatic beetles have not been studied in any comprehensive manner. There are some scattered accounts on the morphology of the genital organs of aquatic Coleoptera (Stein 1847, Escherich 1894, Sharp and Muir 1912, Boving 1913, Tanner 1927, Balfour-Browne 1932, Guignot 1933, Feng 1936, Wood 1952, Young 1963, Datta Gupta and Kumar 1963, etc.). However, there is hardly any attempt to assess the bearing of the genital characters on the taxonomy of this group, at the higher categories in particular.

Our knowledge on the entire genital system of these beetles is mainly due to the researches on the *Dytiscus marginalis* (Demandt 1912, Korschelt 1923-'24), which is a European species. It is only very recently that an account of the genital system of an Indian water beetle, *Cybister tripunctatus asiaticus* Sharp, was published by Sidhu (1960a and 1960b).

Aquatic beetles are comparatively less numerous in this part of the country for obvious reasons. Notwithstanding the fact I have undertaken the study of the genitalia of these specially adapted coleopterans. There are interesting structural modifications that have hitherto been known, and such peculiarities should have an important bearing on the taxonomy and the systematics of the group.

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CHAPTER I

External male genitalia:

The male genital complex includes the aedeagus and the genital segments. The aedeagus in Coleoptera is believed to have originated by the fusion of the appendages of the 9th segment (Michener 1944). The genital segments in males and in the females aid in the act of copulation and oviposition respectively (Snodgrass 1935, Michener 1944). In some cases it is only the ninth segment that takes part in the formation of the external genitalia. The ninth segment in most male coleopterans is ring-like and often very much reduced (Gilbert 1952, Lindroth and Palmen 1956). There is wide variation in the genital complex of coleopterans, and the structures have not been compared between the species or groups of species which has led to confusion amongst the morphologists.

In order to understand the homologies of these genital sclerites it is necessary to establish as to which of the segments give rise to the genital sclerites (Michener 1944). To do so a coordinated study of the abdomen and the genitalia in a number of species of any particular group of insects is necessary. Work on this line is that of Stein (1847), Verhoeff (1893-'94), and Michener (1944). In two separate publications i.e. 1893 and 1894, Verhoeff made a survey of the terminal abdominal segments and their appendages in both the sexes of Coleoptera.

Michener's (1944) comparative study of the appendages of the eighth and the ninth abdominal segments of insects is aimed at establishing the inter-ordinal homologies of the genital appendages more accurately and with greater certainity than it was possible in the past. Although his paper was primarily a study of the male genitalia, the structures of the ovipositor of the females were also included.

Sharp and Muir (1912) published an exhaustive memoir on the comparative anatomy of the male genital tube in the order Coleoptera. From the aquatic coleopteran families they examined

3 species representing 2 genera from Dytiscidae,
4 species representing 3 genera from Gyrinidae,
8 species representing 6 genera from Hydrophilidae.

According to Sharp and Muir (1912) the aedeagus of the families Gyrinidae and Hydrophilidae come under 'Byrrhoid type'. Though they included Gyrinidae under 'Byrrhoid type' they were optimistic and stressed the need to find the homologies of the genital structures between the male and the females of Gyrinidae. Later, Michener (1944) studied the male and the female genitalia which, however, was not in relation to Gyrinidae. Recently, Lindroth and Palmen (1956) presented a general description of the male and the female genitalia of Coleoptera, and classified the aedeagus into four main types, as given by Jeannel and Paulian (1944). They are trilobate type, articulate type, vaginate type and annulate type. As the male genitalia of Dytiscidae, Gyrinidae and Hydrophilidae fall under the trilobate and articulate types of aedeagus, it would be important to review the structural details of these two types here.

The trilobate type of aedeagus is symmetrical with well-developed and sclerotized basal piece; median lobe (penis) and basal piece firmly fixed together by the first connecting membrane. This type is similar to the byrrhoid type of Sharp and Muir.

The articulate type of aedeagus is usually asymmetrical with the basal piece unsclerotized or often seemingly absent; lateral lobes (parameres) articulating to the median lobe (penis) by a true condyle. This type is similar to the caraboid type described by Sharp and Muir.

Torsion of aedeagus has been noticed in Adephaga and Staphylionoidea (Lindroth and Palmen 1956). Different observations have been made by authors with regard to its initiation and the degree of torsion (Heberdey 1928, Jeannel and Paulian 1944, Jeannel 1949 and 1955) in the different stages during the life history of the insects.

Heberdey (1928), in Hydroporus ferrugineus (Dytiscidae) found that at the time of emergence of imago from the pupa the genitalia undergo a rotation through 225° in a clockwise direction, when seen from behind. Jeannel (1955) observed torsion in the 'nymph' of Amblystogenium pacificum Pulz (Carabidae).

In Galerucella birmanica Jac. (Chrysomelidae), Verma (1958) observed the genitalia undergoing a torsion through 180° during the post-embryonic development.

Lindroth and Palmen (1956) write that the degree of torsion of the aedeagus can be demonstrated, from the course of the two main tracheal stems. "In most Adephaga", they point out, "there may be a difference of about 90° in the respective positions of the organ when in repose and in activity".

Wood (1952) observed the homologies of the copulatory apparatus in male Coleoptera and, from among the aquatic Coleoptera Rhantus (Colymbetinae: Dytiscidae), Hydrous, and Hydrophilus (Hydrophilidae) were considered.

Pruthi (1924) studied the post-embryonic development and homologies of the male external genital organs of Tenebrio molitor.

Khurana (1964) described the aedeagus of a few species of Dytiscidae, Gyrinidae and Hydrophilidae. Further, she studied their inter-relationship with other families. In her studies in Adephaga, she found the basal piece as gradually reducing in Gyrinidae, Haliplidae, Dytiscidae, Cicindelidae and Carabidae.

Muir (1919) gave a few informative remarks on the male genital tubes and the manner of their functioning. A few details relating to muscles in a couple of 'ring types' were also given. In a comparative study of the musculature of the male external genitalia of the Coleoptera, Pu (1938) has included Cybister japonica and Hydrophilus acuminatus from Dytiscidae and Hydrophilidae respectively. According used to penetrate the hard tissues of plant. Snodgrass (1935) mentions that female insects in which ovipositor is absent have telescopic arrangement of their posterior abdominal segments.

As to the origin of ovipositor, there are two theories. One theory by Verhoeff (1896-1902) states that the ovipositor has originated from abdominal limbs; second theory by Heymons (1896-1899) states that they arise from the sternum.

Interesting observations on the anatomy, the biological adaptations and the mechanism of the ovipositor in the various genera of Dytiscidae were made by Boving (1913).

Tanner (1927), in his paper on a preliminary study of the genitalia of female coleoptera, described the genitalia of 125 genera representing 66 families. He gave the family characters based on the study of three representatives from Dytiscidae, one from Gyrinidae and one from Hydrophilidae.

Young (1963) also gave a brief description of the ovipositor of Laccophilus inagna and L. quadrilineatus, and Jackson (1958) presented an account of the oviposition in some species of Agabus (Dytiscidae). In 1960, Jackson presented a detailed description and diagrams of the female genital complex of Ilybius fuliginosus Fabr. A sclerite homologous to the valvula (vide Scudder 1961a) has been described by her as ovipositor blade.

Scudder (1961a) published an account on the comparative morphology of the ovipositor and the homologies of its structures in the various orders of Insecta. He made no reference to that of Coleoptera, probably because of the general opinion against the presence of an ovipositor in Coleoptera. Scudder (1961a) states that in insects other than Machilidae, the female genitalia have a common plan (Snodgrass 1935).

After a careful examination of the studies of Tanner (1927) Michener (1944) and Scudder (1960, 1961 and 1964), it is found that the sclerites viz., valvifer, coxite and gonocoxa (vide 1 of the Table I) are homologous and hence are synonymous. However, the term coxite of Tanner (1927) is a homonym to the coxite described by Michener. The 'coxite' which Tanner applied to the coleopterans is actually homologous to the valvula or the gonapophysis (vide 2 of the following table of synonyms). Since it is a homonym on the one hand and synonym on the other, it is bound to create confusion. Therefore, I am disinclined to regard the term 'coxite' used by Tanner. However, since it is homologous to the valvula, a sclerite following the valvifer (Michener 1944), I find the term valvula can be used in Coleoptera as well. From the above analysis of the literature it is, now, clear that the valvifer and the valvula of the ninth segment of Coleoptera are homologous to those of Arthoptera, Odonata and Hymenoptera.

Table I : Synonyms of female genital sclerites

1.	Valvifer	(Tanner 1927 : Coleoptera; Michener 1944 : Odonata and Hymenoptera)
	Coxite	(Michener 1944 : Thysanura)
	Gonocoxa	(Scudder 1960, 1961 and 1964 : Thysanura, Orthoptera, Hemiptera, etc.)
2.	Coxite	(Tanner 1927 : Coleoptera)
	Valvula	(Michener 1944 : Odonata and Hymenoptera)
	Gonapophysis	(Scudder 1960, 1961 and 1964 : Thysanura, Orthoptera, Hemiptera, etc.; Michener 1944 : Thysanura)

Male and Female Internal Reproductive Organs

One of the important contributions made in the past on the internal reproductive organs of coleopterans is that of Dufour (1825). Demandt (1912) presented a comprehensive account of the reproductive organs of both the sexes of *Dytiscus marginalis*.

An intensive review of insect gonads was published by Deegener (1928) and Depdolla (1928). These books together with that of Gross' (1903) monograph include literature prior to 1920. Krausse (1946) gave an account of the structure of the reproductive organs of the wood-eating beetle, and his paper also contains a review on the structure of the gonads.

Williams (1945) observed the morphology of the reproductive organs of 27 species representing seven superfamilies and twelve families of Coleoptera. Indeed I appreciate his remark that a complete study of the reproductive organs from too old or dried specimens cannot be made satisfactorily.

Khurana (1964) studied the reproductive organs of beetles belonging to twenty families. Among the aquatic coleoptera she considered two species from Dytiscinae : Dytiscidae, one from Haliplidae, two from Gyrinidae and two from Hydrophilinae : Hydrophilidae.

Internal Male Reproductive Organs

Sharp and Muir (1912) divided the 'genital tube' into two parts:

1. A pair of seminal ducts leading from the testes forms the zygotic portion. This portion with certain glands opening into it was considered to be mesodermal in origin.
2. A long, single, highly irregular tube, folded back and joined to the body wall, forms azygotic portion. This portion along with certain glands are ectodermal in origin.

Escherich (1894) believes the male genital system of *Carabus* is an example of the most simplified type, *Hydrophilus* a more complex type, and *Blaps* somewhat intermediate form.

Bordas (1900) divides the testes in Coleoptera into two main types:

1. those with a simple, tubular testes, and
2. those with a complex testes.

Bordas (1900) has further divided the complex testes of beetles into two kinds namely, fascicular testes and cluster or grape-like testes.

The testes, according to Virkki (1957), is represented by a pair of 'solid slender cylinders' in lower adephagid families : the Carabidae, Cicindelidae, and Dytiscidae. In hydrophilids it is possibly derived from a cylindrical testes by the formation of radial ampules (Virkki 1957, p. 273).

Snodgrass (1935) and Wigglesworth (1965) described that each testes follicle is divided into a succession of zones. They are:

1. germarium or zone of spermatogonia
2. zone of spermatocytes
3. zone of maturation or reduction, and
4. zone of transformation.

Blunck (1912), in his studies on the morphology and physiology of the Dytiscus marginalis explained the formation of spermatophore within the median lobe. Muir (1919) writes that the Dytiscidae, Haliplidae and Pelobiidae produce spermatophores in a similar manner as in Dytiscus. According to him the presence of a funnel shaped median lobe, large median orifice and the absence of a specialized internal sac suggest the production of spermatophores by the beetles having them. In Gyrinidae the median lobe is not funnel shaped and probably for this reason spermatophores are not produced.

Bordas (1899, p. 540) has pointed out the existence of two completely separated ejaculatory ducts in certain longicorns.

Bordas considers that this furnishes an argument in favour of the theory that the terminal parts of the canal were primitively of paired origin. It is possible, however, that this feature is of secondary origin, brought about by the reduction.

Heberdey (1928) choose Hydroporus ferrugineus (Dytiscidae) as primitive type for a study of the development of the male genital system. The male reproductive organs of the genus Rhantus (Dytiscidae) were also studied by him in the same year.

Escherich (1894) made a study of the male reproductive organs of three beetles representing three families. Hydrophilus piceus (Hydrophilidae) is one of them and is said to be having complex type of reproductive organs. With reference to accessory glands the most generally accepted view is the division by Escherich into two categories viz. the mesadenia and ectadenia. The mesadenia are those derived from mesoderm and lack intimal lining; the ectadenia are those derived from ectoderm and with chitinous intima. Escherich's work is later confirmed by Blatter (1897). This terminology of Escherich was subject to criticism by Bordas (1899), who pointed out that since very little is known as to the origin of these glands, the application of these terms cannot be justified. Instead, he preferred to call them 'accessory' or 'annexed glands'. Bordas (1898-99) is of the opinion that where one or more pairs of glands exist, they are mesodermal origin. Pruthi (1924), Nussbaum (1882) and others regard all glands as having been derived from ectoderm. Later Snodgrass (1935)

The number of ovarioles in an ovary varies greatly in different insects (Snodgrass 1935). Robertson (1961) in his review work compiled a list of ovariole numbers in 329 species belonging to 45 families of Coleoptera. The list reveals that the polytrophic adephaga have a range of 4-40 ovarioles. Robertson listed one or two examples from a few subfamilies of Dytiscidae and Hydrophilidae and one example from each of Noteridae and Gyrinidae.

Heberdey (1931), perhaps, is the first to have reported the presence of two genital openings among Coleoptera. Heberdey observed these openings in *Hydroporus ferrugineus* Steph (Dytiscidae) lying one above the other; the upper one leading into the bursa copulatrix and the lower into the vagina.

Again it is not until 1960 another such report was made. Jackson (1960) observed two genital openings in two more genera (*Ilybius* and *Agabus*) of Dytiscidae and she writes, 'It would be of interest to know how widely spread the two genital openings are amongst the Hydradephaga'. So far I have not come across another report of this nature. Jackson further writes, "Heberdey found that the two genital openings in *Hydroporus*, arise as a secondary division of the lumen of the already amalgamated 'Anlage' of the eighth and the ninth segments, the single lumen becoming separated by the formation of a side wall upto the orifice".

Lindroth and Palmen (1956) write that in Coleoptera two main types of female genitalia can be distinguished. They are:

1. The saccular type : without separate bursa copulatrix.
2. The tubular type : with separate bursa copulatrix, usually combined with the development of an ovipositor.

Demandt (1912), and Korschelt (1923-24) presented a detailed structure of the reproductive organs of male as well as female European *Dytiscus*. The morphological studies on the reproductive organs of an Indian *Cybister* were made by Sidhu (1960b) and he pointed out certain important differences with that of *Dytiscus*.

Datta Gupta and Kumar (1963) described and figured the morphology and histology of the female reproductive organs of nine beetles belonging to six families. *Hydrophilus* (Hydrophilidae) is the only representative in this paper from aquatic coleoptera.

Accessory Copulatory Structures (Sexual dimorphic structures)

These structures are developed in the males and are used mainly for holding or coupling the female during coitus. Miall (1912) writes that the males of many land beetles (Carabidae, Cicindilidae, Silphidae and Meloidae) as well as the male dytiscids and hydrophilids possess adhesive suckers in the tarsomeres. They occur on the widened basal three tarsomeres in Dytiscidae. According to Miall, 'Their restriction to males at once suggests that they are accessory reproductive organs'. In some dytiscids these structures arose on the forelegs only, while in others on the middle legs too, though less prominent. They are called adhesive pads.

Simmermacher's (1884) memoir contained a very good account on the 'suckers of insects in general and especially *Dytiscus*. He reports 170 sucking hairs on each foreleg and 1,590 on each middle leg of *Dytiscus marginalis* (Dytiscini : Dytiscidae). While discussing over the circular sucker of foretarsus, Miall writes, 'A similar structure is visible, though much less prominent, in the middle leg of the male'. But in *Cybister tripunctatus asiaticus* (Cybisterini), Datta Gupta and Sidhu (1958) did not report the presence of such a sucker or disc in the tarsus of middle leg. They described the sexual dimorphism in the foreleg.

Miller (1963) presented the sexual dimorphic character in *Paracymus tarsalis* which is peculiar from many other hydrophilids by possessing an acute tubercle on the terminal tarsomere of male.

Bachmann (1959 and 1966) illustrated the forelegs bearing the sexual dimorphic structures in *Andogyrus seriatopunctatus* and *A. anta* respectively (Gyrinidae).

The experimental observation on *Dytiscus* by Lowne (1871) and Blunck (1912) have removed certain misgivings as to the mode of adhesion of the cupules (suckers) to smooth surfaces. Lowne (Miall p. 55) reports the presence of a large sac filled with gelatinous fluid in the cavity of the tarsus. He further states that this fluid travels through the hollow cupules to the area of contact and facilitates adhesion.

Characters of the accessory copulatory structures have been used as an aid in the classification of higher categories of the Dytiscidae by Crotch (1872-73) and Kuhnt (1911).

Taxonomy

The order Coleoptera is divided into two 'natural groups' viz., Adephaga and Polyphaga (Crowson 1960, Imms 1963). The Dytiscidae and Gyrinidae are included under Adephaga while the Hydrophilidae is included under Polyphaga.

Based on the characters of the aedeagus Sharp and Muir (1912) grouped Dytiscidae, Carabidae etc. under Caraboides or Adephaga, and Gyrinidae, Hydrophilidae etc. under Byrrhoidea.

Later, Tanner (1927) on the basis of the characters of female genitalia, grouped Hydrophilidae under Caraboid series along with Dytiscidae, Gyrinidae, etc.

Essig (1947) grouped Dytiscidae along with Cicindelidae, Carabidae, Amphizoidae and Haliplidae under superfamily Caraboidea. Under the Gyrinoidea he included only one family i.e. the Gyrinidae. In this connection Khurana (1964) writes, 'Evidently there is some similarity in their internal reproductive organs. But a careful consideration of the external genitalia in these families would reveal that these families deserve independent status under the suborder Adephaga'.

One of the oldest classifications of dytiscids was that of Crotch (1873), in which the haliplids were included as a subfamily of Dytiscidae.

Sharp (1882) included the dytiscids under two great series viz. 'Dytisci fragmentati' with three subfamilies and 'Dytisci complicati' with six subfamilies.

Lefroy (1909) presented a list of the Indian water beetles under a classification which differs from that of Sharp (vide supra). There is a considerable rearrangement of the groups. The tribes Hydroporini, Methilini which were subfamilies in Sharp's classification are reduced to tribes. The Dytiscinae is probably reduced from its status.

Kuhnt (1911) accepted no subfamilies and, listed only five tribes under Dytiscidae. Later Zimmerman (1920) and Leech (1948) raised these tribes to subfamily level.

The study of Balfour-Browne (1940) (as adopted from Vazirani, 1968) on Dytiscidae of British Isles is a review type. His conclusions on the relationships are given in a chart which stresses the distinctness of Noterinae (Leech 1948). Leech (1948) correctly writes, 'there is at present no unanimity among authors as to the higher categories in the Dytiscidae. Two best known systems proposed are those of Sharp (1882) and Zimmerman (1920 and 1930-35)'. The position is not different even now. This is evident from the following literature. Leech writes that he is not in agreement with all the Zimmerman's grouping of Dytiscidae, but at the subfamily level he seems to be in full agreement with Zimmerman. Brues, Melander and Carpenter (1954) favoured the classification of Sharp (1882). But they excluded the great series proposed by Sharp.

In a recent publication Vazirani (1967) followed Zimmerman's classification upto subfamilies.

A review of the classification of Gyrinidae and Hydrophilidae is omitted owing to inadequate number of species examined from these families. These species are, nevertheless, of great morphological interest.

◆

CHAPTER II

MATERIAL

Altogether 21 species have been studied.

The beetles have been collected from the local water tanks, a few, however, have been picked which were attracted to street lamps. Almost all the dytiscids and hydrophilids are photopositive and can be located near fluorescent street lamps. Except Coelostoma stultum, almost all could be obtained from the cemented reservoirs, the bottom of which contain mud and organic ooze as sediment. The beetles viz. *Guignotus*, *Hyphydrus flavicans* and *Berosus* were located mainly in the mud scooped from the shallow cemented tanks. *Copelatus* sp. were found near the street lamps.

List of the Species Examined

FAMILY DYTISCIDAE

Noterinae

Hydrocanthini

Canthydrus laetabilis Walk.

Laccophilinae

Laccophilus sharpi Regimbart

L. flexuosus Aube

Hydroporinae

Hydrovatini

Hydrovatus acuminatus Motschulsky

Bidessini

Guignotus sp.

Hydroporini

Herophydrus musicus (Klug)

Colymbetinae

Copelatini

Copelatus sp.

Dytiscinae

Eretini

Eretes sticticus (Linn.)

Hydaticini

Hydaticus luczonicus Aube

Cybisterini

Cybister tripunctatus asiaticus Sharp

FAMILY GYRINIDAE

Enhydrini

Dineutes unidentatus Aube

FAMILY HYDROPHILIDAE

Sphaeridinae

Sphaeridiini

Coelostoma stultum Walk.

Hydrophilinae

Hydrobiini

Paracymus evanescens (Sharp)

Enochrus sp.

Hydrophilini

Sternolophus rufipes (Fabr.)

Hydrous indicus Bedel

H. senegalensis Perch

Berosini

Berosus indicus Motschulsky

B. pulchellus M'Leay

B. nr. *nigriceps* (Fabr.)

METHODS

In the laboratory the live specimens which were collected from different places were kept.in the aquarium (6' × 2' × 2') containing small gastropods, tadpoles, small frogs and some water plants. The dissections were made within five days after each collection.

To study the internal reproductive organs of males as well as that of females, the abdomen of fresh beetles was separated from the thorax, then carefully dissected under the sterioscopic dissection microscope at a desired magnification. The magnifications ranged from fifteen to a maximum of one hundred and twenty times the actual size.

The method employed for the study of the organs in minute beetles are as follows: The abdomen was fixed in aqueous Bouin's fluid for about five minutes. From the fixed material the tergal plates and the alimentary canal, which lie dorsal to the internal reproductive organs, were carefully removed. The entire genital system is removed from the abdomen and stained with 0.5% fast green for about 10 seconds and transferred into cavity slide containing a few drops of glycerene. Tracheoles and other unwanted structures associated with the genital system were removed under the dissection microscope.

The aqueous Bouin's fluid makes the transparent and very thin and flexible organs opaque and firm. This makes it easy to distinguish reproductive organs from the tracheoles, fatbody and nerves. Staining with fast green facilitated visibility of the reproductive organs even after transferring to glycerene, and the transfer to this thick fluid has been extremely useful in the physical manipulation of the structures under the microscope.

The beetles for histological studies of the reproductive organs were vivisected in physiological saline solution. The reproductive organs were carefully freed from the thick tracheal tubes taking care to prevent the ovariole sheeth from being damaged. Alcoholic Bouin's fluid and 6% formalin at 40°C were used for fixing the tissues. The ovaries were dehydrated as usual in alcohol but cleared in methyl salicylate or benzene. Xylol is found to be unsatisfactory for this purpose as it greatly crumples the ovaries and makes it difficult for a detailed study. Tissues other than the ovary have been cleared in xylol. All the tissues were prepared for sectioning in the conventional manner, the sections were cut at 5µ.

Regarding the protrusion of the female genitalia Jackson (1960 p. 41) says, "When pressure is exerted upon the abdomen (and sometimes also when the female dies a natural death) the vagina is everted ......". In the present work the above method has been employed for the study of the female genitalia very satisfactorily. However, on many occasions, I left these dytiscids after killing by chloroform, in water for one or two days. Probably due to ingres of water the insects were swollen and as a result of the pressure created inside the body the genitalia were found ejected out in many insects. Occasionally a slight pressure on the abdomen was necessary in order to completely bring the genitalia out. This method was particularly employed to study the position of the bursa copulatrix, vagina, and the location of their external openings. For a clear visibility aqueous Bouin's fluid was poured drop-by-drop on the protruded genitalia till they were sufficiently discernible for description.

Whenever necessary both male and female genitalia and the legs bearing the sexual dimorphic structures were boiled in 10% potassium hydroxide till they were sufficiently clear for a detailed study of the structures. These were then washed with acid water and tap water before making temporary glycerene mounts over the cavity slide. Very transparent structures were, however, stained with fast green before mounting.

The figures were drawn to scale with the aid of camera lucida. There are a few free hand drawings giving the arrangement of the organs, inside the body.

TERMINOLOGY

Aedeagus:

Copulatory organ of male usually consisting of basal piece, median lobe and lateral lobes.

Basal piece:

Unpaired proximal part of tegmen , usually sclerotized.

Endophallus:

Internal tube of median lobe invaginated at the end of the median lobe, receiving ductus ejaculatorius at the anterior end (primary gonopore) and opening apically through phallotreme (secondary gonopore). May be eversible or a permanently phallic structure.

Lateral lobes:

Distal portion of the tegmen. In a generalized tri-lobe type they form two free lateral processes to the median lobe.

Median lobe:

Apical, unpaired part of copulatory apparatus (aedeagus) containing terminal portion and orifice of ejaculatory duct.

Ovipositor blades (Ovipositor):

Functional sclerites which aid in depositing the eggs.

Paraprocts (o and ♀):

Lateral or latero-ventral sclerites of the anus derived from the proctiger or the IX tergum.

Proctiger (o and ♀):

IX tergal sclerite dorsal to the anus among the beetles studied.

Sternite:

A sclerite of the divided sternum.

Sternum:

An entire undivided ventral plate of a segment.

Tegmen (o):

Compound sclerite proximal to median lobe. Usually divided into basal piece and lateral lobes (parameres).

Tergite:

A sclerite of the divided tergum.

Tergum:

An entire undivided dorsal plate of a segment.

Vaginal Sclerites:

Paired or fused sclerites reinforced on either side of the vagina as in <u>Ilybius</u> (vulval sclerite, Jackson 1960), and <u>Laccophilus</u> (saw-like structure projecting from the meso-posterior margin of the eighth sternite, Tanner 1927).

Valvifers (♀):

A pair of sclerites articulating or fusing with the base of the valvulae.

Valvula (♀):

Sclerite extending posteriad from the corresponding valvifer.

Vulva (♀):

Gonopore (genital opening) of the genital chamber or vagina through which eggs are laid during oviposition and median lobe is received during copulation.

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CHAPTER III

ABDOMINAL SEGMENTATION

For the purpose of convenience the segments of the abdomen are grouped into visceral and genital segments (Snodgrass 1935). Those abdominal segments which are not modified in the formation of genital complex are visceral, while those modified so are genital segments.

The total number of segments is nine. There are eight externally visible terga (Pl. I, Figs. 1,6 and 8), each with a pair of distinct spiracles. These terga are non-rectractable (Imms 1963). On the ventral surface, the abdomen has generally six visible and non-retractable sterna (Figs. 2,3,4, etc.). The 1st sternum is absent in all the species of Dytiscidae, Gyrinidae and Hydrophilidae, a condition common to Coleoptera (Jordan 1943, Imms 1963). The 6th visible sternum is the true 7th sternum. Except in gyrinid, the eighth segment is partially retracted into the abdomen. The ninth segment completely retracted into the abdomen in all the species studied.

A few of the anterior sterna are fused sometimes letting them appear as a single sternum (Pl. I, Figs. 2,4, 9,10 and 12). However, in many cases these are distinguished from the subsequent sternum by a distinct suture. With the exception of Telophoridae (Jordan 1943), the fusion of a few anterior sterna is a general feature of Coleoptera and other higher orders (Snodgrass 1935).

The eighth segment is generally divided into tergites and sternites in Dytiscidae, and such a division is absent in Hydrophilidae.

The genital segments are either partially reduced as in some dytiscids (i.e. Hydroporinae) and the girinid, or greatly modified as in Laccophilinae and Dytiscinae (Dytiscidae), and Hydrophilidae in general.

The Table II is self-explanatory in nature and gives an account of the abdominal sclerites.

Explanation of the abbreviations and the signs of the Table II:

B	Partially divided along the axial line
D	Divided along the axial line
P	Proctiger
PP	Modified to form paraprocts
R	Retracted or invaginated into the abdomen
VF	Modified to form valvifers
+	Present
+..........+	Immovably or firmly articulated sclerites
+———+	Sclerites fused, suture either partly or fully obliterated
+⟍	Sternum bearing a posteriorly directed thick spine (Sexual dimorphic structure)
-	Absent

TABLE II: Number of terga and sterna in the abdomen of the male and the female beetles

Species	Sex	Terga Sterna	I 1	II 2	III 3	IV 4	V 5	VI 6	VII 7	VIII 8	IX 9	Remarks
DYTISCIDAE												
<u>Canthydrus laetabilis</u> (Pl. I, Figs. 1 and 2)	Male	Terga	+	+	+	+	+	+	+	+	+R P	VIII tergum with median longitudinal groove
		Sterna	-	+·······	+——	+	+		+	+R D	+R	
	Female	Terga	+	+	+	+	+		+	+	+R D P PP	VIII tergum with median longitudinal groove
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R VF	
<u>Laccophilus flexuosus</u> <u>L. sharpi</u> (Pl. I, Fig. 3)	Male	Terga	+	+	+	+	+	+	+	+D	+R P	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R	
	Female	Terga	+	+	+	+	+	+	+	+D	+R D PP	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R D VF	
<u>Hydrovatus acuminatus</u> Motschulsky	Male	Terga	+	+	+	+	+	+	+	+D	-	VIII tergites elongate and attenuated posteriorly
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R	
	Female	Terga	+	+	+	+	+	+	+	+D	-	--do--
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R	
<u>Hyphydrus flavicans</u> (Pl. I, Fig. 4)	Male	Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R	
	Female	Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R VF	
<u>Guignotus</u>	Male	Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R	Non-retracted sterna dark brown
		Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R VF	
<u>Herophydrus musicus</u>	Male	Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R	Non-retractable sterna dark brown
	Female	Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+——	+	+	+	+	+R D	+R VF	
<u>Copelatus</u> (Pl. I, Fig. 5)	Male	Terga	+	+	+	+	+	+	+	+D	-	
		Sterna	-	+·······	+·······	+	+	+	+	+R D	+R	
<u>Eretes sticticus</u> (Pl. I, Figs. 6 and 7)	Male	Terga	+	+	+	+	+	+	+	+D	+RP D	
		Sterna	-	+·······	+·······	+	+	+	+	+R D	+R	
	Female	Terga	+	+	+	+	+	+	+	+D	+RP D	
		Sterna	-	+·······	+·······	+	+	+	+	+R D	+R VF	

Table II (Contd.)

Species	Sex	Terga Sterna	I 1	II 2	III 3	IV 4	V 5	VI 6	VII 7	VIII 8	IX 9	Remarks
Hydaticus luczonicus	Male	Terga	+	+	+	+	+	+	+	+D	+RP D	
		Sterna	-	+	+	+	+	+	+	+R D	+R	
	Female	Terga	+	+	+	+	+	+	+	+D	+RP D	
		Sterna	-	+	+	+	+	+	+	+R D	+R VF	
Cybister tripunctatus asiaticus	Male	Terga	+	+	+	+	+	+	+	+D	+RP D	
		Sterna	-	+	+	+	+	+	+	+R D	+R	
	Female	Terga	+	+	+	+	+	+	+	+D	+RP D	
		Sterna	-	+	+	+	+	+	+	+R D	+R VF	
GYRINIDAE												
Dineutes unidentatus (Pl. I, Figs.8 and 9)	Male	Terga	+	+	+	+	+	+	+	+	-	
		Sterna	-	+	+	+	+	+	+	+	+R	8th sternum undivided and non-retractable
	Female	Terga	+	+	+	+	+	+	+	+	-	
		Sterna	-	+	+	+	+	+	+	+	+R VF	8th sternum undivided and non-retractable
HYDROPHILIDAE												
Coelostoma stultum (As in Pl. I, Fig. 11)	Male	Terga	+	+	+	+	+	+	+	+	+RP	Paraproct present
		Sterna	-	-	+	+	+	+	+	+R	+R	
	Female	Terga	+	+	+	+	+	+	+	+	+RP	Paraprocts present
		Sterna	-	-	+	+	+	+	+	+R	+R VF B	
Paracymus evanescens (Pl. I, Fig. 10)	Male	Terga	+	+	+	+	+	+	+	+	+RP	Paraproct present
		Sterna	-	+	+	+	+	+	+	+R	+R	
	Female	Terga	+	+	+	+	+	+	+	+	+RP	Paraprocts present
		Sterna	-	+	+	+	+	+	+	+R	+R VF B	
Enochrus (Pl. I, Fig.11)	Male	Terga	+	+	+	+	+	+	+	+	+RP	Paraproct present
		Sterna	-	-	+	+	+	+	+	+R	+R	
	Female	Terga	+	+	+	+	+	+	+	+	+RP	Paraprocts present
		Sterna	-	-	+	+	+	+	+	+R	+R VF D	
Sternolophus rufipes	Male	Terga	+	+	+	+	+	+	+	+	+RP	Paraproct present
		Sterna	-	+	+	+	+	+	+	+R	+R	9th sternum transversely divided by membranous zone
	Female	Terga	+	+	+	+	+	+	+	+	+RP	Paraprocts present
		Sterna	-	+	+	+	+	+	+	+R	+R VF D	
Hydrous indicus H. senegalensis (Pl. I, Fig. 12)	Male	Terga	+	+	+	+	+	+	+	+	+RP	Paraproct present
		Sterna	-	+	+	+	+	+	+	+R	+R	
	Female	Terga	+	+	+	+	+	+	+	+	+RP	Paraprocts present
		Sterna	-	+	+	+	+	+	+	+R	+R VF D	
Berosus indicus B. pulchellus B. nr. nigriceps	Male	Terga	+	+	+	+	+	+	+	+	+RP	Paraproct present
		Sterna	-	+	+	+	+	+	+	+R	+R	
	Female	Terga	+	+	+	+	+	+	+	+	+RP	Paraprocts present
		Sterna	-	+	+	+	+	+	+	+R	+R VF D	

CHAPTER IV

EXTERNAL GENITALIA OF MALES

Family Dytiscidae

Species examined:

Canthydrus laetabilis Walk.

Laccophilus sharpi Regimbart
L. flexuosus Aube

Hydrovatus acuminatus Motschulsky
Hyphydrus flavicans (Regimbart)
Guignotus sp.
Herophydrus musicus (Klug)

Copelatus sp.

Eretes sticticus (Linn)
Hydaticus luczonicus Aube
Cybister tripunctatus asiaticus Sharp

In all the dytiscids studied the VIII tergum is the last visible sclerite of the nonretractable terga. It is demarcated into two sclerotized patches by a median thin longitudinal strip of desclerotized zone. The 8th sternum is retracted into the abdomen and is not visible externally. It is divided into two distinct sternites and both these sternites remain connected by an intermediate membrane. But in *Copelatus* and all the Dytiscinae their anterior margins are confluent and bordered. The ninth segment is entirely retracted into the abdomen and greatly varied. The IX tergum is not sclerotized in some members of the Dytiscidae. But in dytiscids where it is present, it is often divided into two sclerites. The 9th sternum is present in all the dytiscids studied, and show considerable variation.

The basal piece (BP) is reduced or in some species absent. The median lobe (ML) is hollow, usually arcuate with an anterior or antero-dorsal median formation (MF). The lateral lobes (LL) are largely connected to an articular process (CON) (true condyle as described by Lindroth and Palmen 1956) of the median lobe. The distal tip of the lateral lobe is often provided with setae (S).

Measurements:

Abbreviations used for the structures measured are given below. The setae or spines at the extremities of the insect parts are excluded from the measurements. The measurements of both the lateral lobes are given only when they are unequal. All the measurements are taken in millimetres.

Key to the abbreviations used in the text:

IL	Insect length
IW	Insect width
EL	Elytral length
AE L	Length of aedeagus
L ML	Length of medial lobe
L LL	Length of lateral lobe
L EDL	Length of eu-dextral lateral lobe
L ESL	Length of eu-sinistral lateral lobe

Subfamily : Noterinae

Canthydrus laetabilis Walk. (Pl. II, Figs. 1 to 4)

IL	2.57	IW	1.32	EL	1.84
L ML	0.52	L EDL	0.28	L ESL	0.24

The IX tergum forms an oval ring around the aedeagus. The 9th sternal plate smaller and sclerotized, lie ventral to aedeagus and extends slightly behind the IX tergum. The 9th sternum with six prominent spine-like setae on the posterior margin. Its anterior edge oblique (Fig. 1).

The aedeagus 1/5 length of the insect length, asymmetrical and exhibits torsion of 90°. The entire aedeagus inclined rightward and crescentic. Basal piece absent. As a result of the inclination of the aedeagus the left lateral lobe comes to lie dorsad while the right one ventrad. The eusinistral (original left) lateral lobe triangular with rounded corners, and its euventral edge inflected (Fig. 2). The lateral lobe articulates with its narrow end to the proximal region of the median lobe and lacks setae on the posterior margin. It, however, bears about a dozen short spine-like setae, at about the middle of its posterior half. The eudorsal lateral lobe differs from its counterpart in being broader at its anterior end and narrow posteriorly. Its antero-euventral margin produced into a long and narrow projection (Fig. 3). The posterior edge bears a large number of long setae (s), probably sensory in function. Inner surface of this lateral lobe bears an obliquely placed spatulate structure around which globular bodies are present. The eudextral lateral lobe articulates with the basal articular process of the median lobe.

Median lobe (Fig. 4) arcuate, somewhat flattened and grooved. A small basal articular process present. The groove of the median lobe shallow with anteriorly directed minute spines (SPN) at its posterior end. The antero-euventral margin of the median lobe produced into a process.

The process somewhat rectangular and directed anteriad. The median lobe bears four distinct crenulations on its euventral surface. The median lobe broader posteriorly before narrowing to form a round (blunt) tip.

Subfamily : Laccophilinae

Laccophilus sharpi Regimbart (Pl. II, Figs. 5 to 8)

IL 3.88 IW 2.10 EL 3.14
L ML 0.98 LL 0.40

The 8th sternites triangular. IX tergum large, posteriorly narrow and bifid; anteriorly wide unequally bifurcated and inflected downward so as to lie ventral to the proximal portion of aedeagus, thus encirculing the aedeagus. The 9th sternum smaller than the corresponding tergum, attached to the posterior margin of the inflected tergum (Fig. 5); on the inner surface with a longitudinal groove, or the corresponding outer surface a wedge; tip acicular.

Aedeagus about 1/4 the body length, asymmetrical and exhibits torsion of 90°. The entire aedeagus inclined rightward and arcuate; basal piece absent; lateral lobes about half the length of median lobe, laminate; eu-sinistral lateral lobe (Fig. 6) cordate in outline, its ventral margin not entirely concave; and the articular process is actually at the anterior one-third of that lateral lobe; eudextral lateral lobe (Fig. 7) slightly longer than that of eusinistral one, and arcuate; the articular process of eudextral lateral lobe arises from the middle of the euventral margin; both the lateral lobes have a thin tuft of equally long hairs (S) at their distal end.

Median lobe (Fig. 8) completely sclerotized stout arcuate, left margin concave; anterior end forked forming apodemes, median formamen antero-eudorsal, distal end with conspicuous emargination, a ridge (or carina) traverses from the base of median foramen (MF) on the eudorsal surface to the distal extremity on the eusinistral surface. At the distal one-third of the eusinistral surface is a narrow patch of closely set minute setae. The gonopore (GPR) is terminal.

<u>Laccophilus</u> <u>flexuosus</u> Aube (Pl. II, Figs. 9 to 12)

IL	4.31	IW	2.24	EL	3.50
L ML	1.02	LL	0.42		

The structure and position of the ninth segment (Fig. 9) to a great extent is similar to that of <u>L. sharpi</u> Regimbart.

Aedeagus about 1/4 the body length, torsioned (90^o) and not so asymmetrical as that of <u>L. sharpi</u> Regimbart; basal piece absent; lateral lobes laminate not identical, inclined rightward and less than half the length of median lobe; margins inflected and the inner surface thereby concave; posterior tip with a tuft of long hairs, length of hairs in eudextral lateral lobe shorter; anterior euventral margin with an articulating process for the proximal end of median lobe (Fig. 12) well sclerotized, hollow, elongate, arcuate, and flattened; its concave margin i.e. euventral margin now turned to the left side; carina absent; anterior end with a pair of apodemes (termed aedeagal apodemes by Snodgrass 1935); entrace of ejaculatory duct is eudorso-proximal. The euventrodistal margin emarginate; distal one-fourth part with a number of dehiscently arranged minute black spines indistinct even at × 100 magnifications; genital opening distal.

Subfamily : Hydroporinae

Hydrovatus acuminatus Motschulsky (Pl. II, Figs. 13 to 14)

IL	2.82	IW	1.85	EL	2.80
L ML	0.84	LL	0.82		

VIII tergites differ from all the rest of the species in that they are longer than broad, and attenuated posteriorly; 8th sternites not distinctly sclerotized. IX tergites indistinct; 9th sternum resembles somewhat an inverted Y, the two posterior processes unequal, the left one longer than the right, and extend dorsally over to the apex of the aedeagus (Fig. 13).

Length of aedeagus between 1/4 and 1/3 the body length; aedeagus with no torsion, symmetrical. Basal piece (BP) reduced and rod-like. Lateral lobes laminate, cover the median lobe laterally; antero-ventral process of lateral lobes meet each other and articulate with the ventral articular process of the median lobe; posterior end of the lateral lobe hook-like and the bend is ventro-mesad, apex acute. Median lobe (Fig. 14) as usual hollow, dorso-ventrally flattened (depressed), arcuate with ventral concave surface, sclerotized laterally; the dorsal and the ventral surfaces membranous; the dorsal surface grooved lengthwise; proximal end bifid forming apodemes; distal tip acute, curved ventrally and hook-like. Articular process (CON) of median-lobe well sclerotized and with truncate tip. Two longitudinal rows of setae present at the distal one-third of the ventral surface of the median lobe. Endophallus (EDP) distinct and with rough surface. Gonopore (GPR) sub terminal.

Hyphydrus flavicans (Regimbart) (Pl. III, Figs.1 to 4)

IL	4.45	IW	2.80	EL	3.30
L ML	0.92	LL	0.77		

Each of the 8th sternite (Fig. 1) narrow anteriorly and broad posteriorly, forming an L-shaped sclerite with both the limbs of equal length. Its posterior margin fringed with setae. IX tergum membranous and the corresponding sternum very much reduced forming a thin semicircular ring around the aedeagus.

Aedeagus (Figs. 2 and 3) about 1/5 the body length, complex, bilaterally symmetrical, arcuate; no torsion; basal piece absent; lateral lobes identical, distal half wide with two or three curved ridges (Fig. 4), narrows posteriorly, tip acute, posterior one-fourth of the ventral margin fringed with setae. Anteriorly the lateral lobe is thin and divided into two unequal processes; the inner process articulates with the side of the median lobe slightly dorsad, the other travels ventrad and unites firmly with its counterpart just under the mid-ventral line of the median lobe. Median lobe arcuate, with ventral concavity and dorsal convexity. The anterior end is deeply bifid and the apodermal expansions wide; the ejaculatory duct travels between these expansions. The posterior end is four lobed; two large dorsals and two small ventrals, each lobe fringed dorsally with small spine-like process, highly sclerotized and dark coloured. Ventral surface of median-lobe bears a oval process, beneath which the two lateral-lobes unite with each other. Gonopore on the dorsal surface.

Guignotus sp. (Pl. III, Figs. 5 to 7)

IL	2.82	IW	1.33	EL	2.03
L ML	0.56	LL	0.50		

8th sternites triangular with rounded corners (Fig. 5); IX tergites membranous, 9th sternum oval with a small median strut (MS) encircling the aedeagus (Fig. 6).

Aedeagus (Fig. 7) about 1/5 the body length, exhibits torsion of about 90°. Basal piece (BP) as in Hydrovatus acuminatus. Lateral lobes identical, slightly shorter than median lobe, delicate and flexible at the middle. The flexible middle portion less sclerotized and appear membranous (M); anterior half laminate and broad, euventral margin inflexed and articulate proximally to the euventral condyle of the median lobe; posterior half of the lateral lobe thin and margins inflexed forming a groove, thereby semicylindrical; distal end spatulate and fringed with small setae. Lateral lobes cover the median lobe and lie closely appressed on either side of it.

Median lobe (ML) cylindrical arcuate, eudorsal surface convex; two apodemes at the anterior extremity; median foramen (MF) eudorso-proximal; ejaculatory duct (DEJ) passes between the apodemes and enters median lobe on the antero-eudorsal surface, euventral surface membranous at the middle region, attenuated posteriorly, the posterior one-fifth of the median lobe on the eudorsal surface bears minute anteriorly directed setae, tip rounded; gonopore appears to be distal.

<u>Herophydrus musicus</u> (Klug) (Pl. III, Figs. 8 to 10)

IL	2.40	IW	1.65	EL	1.90
L ML	0.47	LL	0.37		

8th sternites L-shaped (Fig. 8); IX tergites membranous, 9th sternum thin and ring-like with no strut attached. Aedeagus about 1/5 the body length, symmetrical and with no torsion; basal piece absent; Lateral lobe laminate, antero-ventral corner elongated, porrect and beak-like, ventral margin inflexed and elongated into a process at the proximal one-third to meet the ventral knob of the median lobe. The inflexed strip at the posterior half bears a single row of setae. Median lobe somewhat cylindrical, sickle-shaped; ventral surface concave, proximal end broad with a ventral rounded knob to which lateral lobes articulate; median lobe deeply bifid at the proximal end dorming a pair of apodemes. Apodemes a little anterior to the condyle (CON) and median foramen lies anteriorly between these three processes; posterior one-fourth of median lobe attenuated, tip rounded; gonopore terminal.

Subfamily Dytiscinae

Eretes sticticus (Linn) (Pl. III, Figs. 14 to 18)

IL 12.08 IW 6.62 EL 9.08
L ML 1.96 LL 2.26

8th sternites somewhat triangular, proximal margin bordered and continuous (Figs. 14 and 18); ninth segment ring-like and encircles the aedeagus; IX tergites triangular. The IX tergites small distinct and bear the anus. 9th sternites form a major part of the ring and join the tergites above the posterior end of the aedeagus.

Aedeagus about 1/5 the body length, no torsion, symmetrical; basal piece (Fig. 16) dorsal to the median lobe, but found underneath the tubular membrane that connects the ninth segment to the aedeagus. Its distal forked end fused with the membrane. Proximal end depressed and serves for attachment; lateral lobes 0.3 mm longer than median lobe, margins inflexed mesad giving grooved appearance, proximal end somewhat bicornuate, antero-ventral cornu short truncate and meet its fellow medially beneath the ventral knob (true condyle) of the median lobe. Lateral lobes attenuated posteriorly, distal end rounded and inflexed. Posterior one-third of each lateral lobe on the outer surface bears a large number of short closely set spine-like setae (S), those on the margin increasingly larger towards posterior end. The inflexed margins of lateral lobes connected with their counterpart by thick membrane forming a sac. At the median posterior end, this sac further thickened to form a somewhat sclerotized dorsally grooved spatulate or tongue-like structure (Fig. 7). Thin antero-mesally directed spine-like setae present in and on either side of this groove. This conjunctival membranous sac lies aoove the median lobe and hence described as dorsal sac (DS).

Median lobe (Fig. 15) narrow and elongate slightly inclined to the right; proximal extremity forked forming apodemes while that of distal end bifid; median foramen (MF) mid-dorsal, two highly folded membranous sacs (SCM) arose from its dorsal surface and lie underneath the bigger dorsal sac, posterior end of this sac attenuated and one-fourth of the posterior end of this sac fringed with microtrichia (MT), and extend beyond the median lobe; tip acute collapsed and depressed when at rest. The lumen of these sacs continues into that of dorsal sac. Two chitinuous strips, probably skeletal supports of the ejaculatory duct, extend from the median foramen. Gonopore subterminal and opens ventrally.

Hydaticus _luczonicus_ Aube (Pl.III, Figs. 19-21;
Pl. IV, Figs. 1 to 2)

IL	13.83	IW	7.69	EL	11.01
L ML	2.20	LL	2.20		

8th sternites as in _Eretes_ _sticticus_ (Linn). A triangular less sclerotized seteferous area present mesad to each of the 8th sternite; a few of these setae, however, join together forming a fringe (HF). The ninth segment is ring-like (Fig. 21), the tergum distinct, divided into two tergites, sternum semicircular and connected to the antero-lateral margin of its tergite, a small spiny process present on its right limb while its left limb flat and wider. The aedeagus and the ninth segment connected by a membranous tube (Fig. 19), its lumen continuous with that of dorsal sac (DS). Thus the lumen of the body cavity continuous with that of the dorsal sac of aedeagus.

The aedeagus about 1/5 the body length, bilaterally symmetrical and exhibits torsion of about 45°, so that its original (morphological) ventral surface tends to turn leftward. The basal piece (Fig. 20) rod-shaped thin flat and widened at both ends, shorter than lateral lobes by about 0.3 mm; posterior end connected to the inside of the dorsal membrane of the dorsal sac (DS); anterior end projects into the abdomen beyond the base of median lobe. Lateral lobes slightly longer than median lobe (Fig. 19), twisted at the middle, connected with each other by dorsal and ventral conjunctival membranes, and form the lateral supporting structures of the dorsal sac (Pl. IV, Fig. 1). A stout arm extends mesad from the anterior end of each lateral lobe to join the antero-ventral condylar region (CON) of the median lobe (ML). Midventrally the posterior end of the dorsal sac forms a grooved sclerotic sheath (SH). Distal end of each lateral lobe with a short cylindrical setose stylus (STY). The median lobe hollow, compressed, and lies underneath the dorsal sac. Ejaculatory duct enter into the median lobe antero-dorsally. Proximal one-fourth of median lobe well sclerotized and bears a baso-ventral articular condyle (CON). The dorsal and the ventral margins of the posterior three-fourth of this lobe less sclerotized leaving between them a still less sclerotized area. A little posterior and dorsal to the median foramen, a pair of flat membranous sacs (ventral sacs) of the median lobe (SCM) join with the dorsal sac. Ventral sacs (SCM) closely attached to the posterior two-thirds of the median lobe and extend on either side of it. The paired ventral sacs communicate with the dorsal sac, ventrally by a common aperture. The posterior part of the median lobe extends upto the ventral sheath of the dorsal sac. This sheath receives the tip of the median lobe when at rest. The distal portion of the median lobe setose; the posterior part of all the three sacs and the ventral sheath profusely fringed with microtrichia or aculiae; the posterior half of each lateral lobe denticulate on its outer margin.

Cybister tripunctatus asiaticus Sharp (Pl.IV, Figs.3 to 5)

IL	24.93	IW	13.43	EL	19.78
L ML	5.65	LL	4.82		

8th sternites fused anteriorly by a horizontally flattened horse-shoe shaped sclerite (Fig. 3). IX tergites conspicuous and the 9th sternum ring-like and well sclerotized (Sidhu 1960a).

Aedeagus (Fig. 4) about 1/4 the body length, symmetrical, exhibits torsion of 90°, elongate arcuate, euventral surface concave and facing left side. Basal piece thin and well sclerotized rod lying on the proximal one-third of the median lobe, closely appressed on the eudorsal surface of the aedeagus, distal end forked and fused with the membrane that connects the aedeagus to the last (i.e. ninth) genital segment. Lateral lobe laminate, slightly shorter than median lobe, broad proximally and attenuated posteriorly, anterior euventral margin inflexed and articulates with its proximal end to the mediab lobe, the euventral and eudorsal margins of each lateral lobe connected by a membrane making it tubular; about one-third of the posterior euventral margin and the apex fringed with long hair-like setae (S); the distal end of the membranous inner surface with a short setae. Median lobe (Fig. 5) sabre-shaped, not uniformly sclerotized, proximal and distal ends bifid, antero-euventral surface with a knob (CON) with which lateral lobes articulate; median foramen at the anterior one-fourth of the eudorsal surface. Arising eudorsally from the median lobe is a membranous sac (SCM) that gets supported by a pair of sclerotized ribs which extend lengthwise, its posterior tip is divided to form two narrow and tubular projections; gonopore (GPR) not terminal but lies hidden at the base between the sac (SCH) and the median lobe proper.

Family Gyrinidae

Species examined

Dineutes unidentatus Aube

In the specimen examined, VIII tergum is the last visible sclerite; correspondingly on the ventral surface is the 8th sternum. Tanner (1927) in the females of the Gyrinus consobrinus Lec. found the eighth segment as the last non-retractable segment. The ninth segment is partially reduced.

Aedeagus symmetrical. Basal piece absent. Lateral lobes as long as, or longer than the median lobe (Sharp and Muir 1912). Basally the median lobe articulates with the lateral lobes through dorsal surface.

Dineutes unidentatus Aube (Pl. IV, Figs. 6 and 7)

IL	6.86	IW	3.74	EL	4.87
L ML	1.44	LL	1.50		

The last nonretractable segment is the eighth. Ninth segment is invaginated and partly reduced; the IX tergum membranous and as in dytiscids bears the anus. 9th sternum well developed and encloses the aedeagus (Fig. 6).

Aedeagus between 1/5 and 1/4 the body length, symmetrical, exhibits no torsion, elongate, and straight. Basal piece absent. Lateral lobes fused with each other at their narrow base forming a transverse bridge-like structure dorsal to the base of the median lobe, the distal three-fourth horizontally flattened, almost with uniform width, apex ovate; posteriorly the outer margin and apex fringed with setae (S). Median lobe as long as the lateral lobe. Median lobe cylindrical anteriorly and grooved ventrally on the posterior; anterodorsal apex of the median lobe acts as the articulating surface and receives the base of the lateral lobes, distal one-fourth attenuated, apex rounded. Endophallus (EDP) tongue-like and visible through the ventral groove. Gonopore ventral.

Family Hydrophilidae

Species examined:

Coelostoma stultum Walk
Paracymus evanescens (Sharp)
Enochrus sp.

Sternolophus rufipes (Fabr.)
Hydrous indicus Bedel
Hydrous senegalensis Perch
Berosus indicus Motschulsky
B. pulchellus M'Leay
B. nr. nigriceps (Fabr.)

In all the hydrophilids examined VIII tergum is the last externally visible sclerite. The last of the non-retractable sterna is the true 7th sternum. The rest of the sclerites i.e. the 8th sternum and the ninth segment are retracted into the body and are not visible externally. None of the genital segments is divided into tergites or sternites. There is no reduction in the tergum or sternum of the ninth segment. On the other hand the IX tergum gives rise to an extra sclerite viz. paraproct. IX tergum bears the anus. 9th sternum is elongate and usually not divided.

The aedeagus is of trilobate type, symmetrical and has a well developed basal piece. Lateral lobes are inwardly connected by membrane. Anteriorly the membrane of the lateral lobes is continuous with the proximal end of the median lobe. Median lobe is hollow and usually cylindrical; anteriorly it has a pair of apodemes (APD) and serve for the attachment of muscles (Pu 1938). Ejaculatory duct travels through the basal piece and median lobe, and opens externally by gonopore.

Subfamily Sphaeridiinae

Coelostoma stultum Walk (Pl. IV, Figs. 8 and 9)

IL	4.20	IW	2.84	EL	2.84
AE L	0.85	LML	0.65	LL	0.81

Paraproct undivided thin and flexible, arises from the anterior margin of the IXth tergum (Fig. 8) and extends ventrad to the base of the 9th sternum; 9th sternum elongate and undivided (Fig. 9).

Aedeagus stout, length about 1/5 the body length; basal piece very short, one-third of the lateral lobes in length, plate-like, covering the bases of the lateral lobes ventrally, no reflexed margins, the anterior margin not bordered, but drawn into a narrow flat projection, directed proximad. Lateral lobes bent inward and close to each other and proximal ends fused ventrally and lie between the basal piece and the base of the median-lobe. Median lobe shorter than lateral lobes by 0.15 mm, exposed dorsally, and partially covered by lateral lobes ventrally; anterior end wide and produced into two stout apodemes (APD), postero-dorsal surface concave, median foramen and gonopore at the proximal and distal extremities.

Subfamily Hydrophilinae

Paracymus evanescens (Sharp) (Pl. IV, Figs. 10 and 11)

IL	1.91	IW	1.20	EL	1.50
AE L	4.00	L ML	0.27	LL	0.27

Paraproct present and extend ventrad.

Aedeagus about 1/5 the body length, elongate; basal piece conical shorter than lateral lobe with anterior narrow and posterior broad ends, the lateral lobes connected to each other by an antero-mesal projection just over the base of the median lobe. Lateral lobe slightly broader at the base than the distal half, the posterior extremity tends to bend inward; median lobe as long as the lateral lobe, funnel-shaped, two segmented, anterior end broad, attenuated distally; from the proximal end two apodemes arise, one on either side of its axis; a small piece of transparent projection, the second segment, lies immediately next to gonopore; gonopore subterminal and ventral.

Enochrus sp. (Pl. IV, Figs. 12 to 14)

IL	3.14	IW	1.71	EL	2.16
AE L	0.78	L ML	0.35	LL	0.40

Anterior margin of IX tergum remain sclerotic inspite of partial desclerotization of the tergum. The anterior sclerotic patch of this tergum extends ventrally forming a thin ribbon-like paraproct (PP). 9th sternum elongate and undivided.

Aedeagus (Fig. 14) about 1/4 the body length; basal piece desclerotized except along margins, transparent, and in length equal to the lateral lobe, its proximal half uniformly narrow and distal half almost uniformly wide; lateral lobes larger than median lobe, broad proximally and attenuated posteriorly. Lateral lobes join each other by means of a conical antero-mesal projection, distal portion bent laterad. Median lobe gives three segmented appearance and the posterior segments decreasingly smaller, the distal segment is very transparent and acute. Gonopore subterminal.

Sternolophus rufipes (Fabr.) (Pl. V, Figs. 1 to 3)

IL	10.20	IW	5.23	EL	7.60
AE L	1.70	L ML	1.04	LL	1.02

Anterior margin of the IX tergum (Fig. 1) modified to form a wide paraproct that extends ventrad; paraproct not separated from IX tergum. 9th sternum elongate and, owing to desclerotization, transversely divided into an anterior and a posterior sclerites (Fig. 2).

Aedeagus (Fig. 3) about 1/6 the body length, elongate basal piece slightly more than half the length of lateral lobe; distal end twice as wide as proximal end, and membranous, which extends medially between the sclerotized area, thereby appearing somewhat triangular, postero-lateral margins reflexed, then bent mesad and connected to each other by membrane. Lateral-lobes inflexed giving boat-shaped appearance. Proximally the ends of the lateral lobes meet dorsally, and join ventrally by a narrow bridge; the posterior end slightly curved inwards. Median lobe tubular, slightly shorter or as long as lateral lobe, dorsal surface sclerotized forming a supporting plate, anterior margin of this plate crescentic, the two ends of which produced into two apodemes; proximal half with inflexed lateral margins, ventral surface membranous, posterior half of the sclerotized median lobe wider than the opening of the gonopore; gonopore subterminal and ventral, tip of median lobe membranous.

Hydrous indicus Bedel (Pl.V, Figs. 4 and 5)

IL	29.45	IW	13.80	EL	23.25
AE L	5.00	L ML	3.05	LL	3.20

Paraproct undivided and ribbon shaped, extends laterad but do not reach the 9th sternum. 9th sternum elongate and undivided.

Aedeagus about 1/6 the body length, basal piece ventral lamellate, three-fourths of the lateral lobe in length, less sclerotized posteriorly, edges reflexed but do not meet each other dorsally, connected by membrane, anterior end narrow with truncate edge, posteriorly articulating with the anterior edge of the lateral lobe. Lateral lobe inflexed and boat-like, dorsally appears triangular in outline, proximal half wide and distal half narrow, postero-lateral end produced into a short spinous projection, posterior extremity indistinctly clavate.

Median lobe tubular, slightly shorter than lateral lobe, but longer than basal piece, consists of dorsal and ventral sclerites supporting the otherwise less sclerotized membranous median lobe, dorsal sclerite (DSC) at the anterior one-fourth is divided and U-like with two apodemes on either side of the axis, posterior half attenuated and tip slightly clavate, ventral sclerite (VSC) is thin and extends from about the middle of the median lobe upto the gonopore. Gonopore sub-terminal, ventral and with 'authine' shaped sclerotic boarder.

Hydrous senegalensis Perch (Pl.V, Fig. 6 and 7)

IL	37.30	IW	18.25	EL	31.00
AE L	7.60	L ML	3.44	LL	3.68

Paraproct undivided ribbon shaped and can be seen distinctly arising as a result of de-sclerotization. It extends laterad but do not reach the ventral surface to meet the 9th sternum. 9th sternum elongate and undivided.

Aedeagus about 1/5 the body length, elongate; basal piece one and quarter times longer than the lateral lobe, inverted V-shaped, sclerotized laterally otherwise membranous both dorsally and ventrally. The proximal one-sixth of the basal piece sclerotized lamellate and ventral; the entire basal piece is thus a wider tube through which the posterior part of the ejaculatory duct travels before entering the median lobe; distally it articulates with the proximal end of the lateral lobe along its outer convex region. Lateral lobe mainly sclerotized on the dorsal surface, lamellate, wider at the region of articulation with the basal piece, attenuated towards either end; the proximal (attenuated) ends of lateral lobes truncate, join with each other on the median line; the posterior narrow portion cylindrical, the ventral surface non-sclerotized and membranous except the sclerotized mesal margin. Lateral lobes saccular and in repose lie closely adpressed to the median lobe.

The median lobe membranous, funnel-like and supported dorsally by a Y-shaped sclerite (DSC), the two antero-laterally directed process of this sclerite being the apodemes, Posterior tip of this sclerite spatulate. Gonopore subterminal, ventral and bordered by 'authine' shaped sclerotic ring, from the proximal end of which extends approximally directed short and thin sclerite.

Berosus indicus Motschulsky (Pl.V, Figs.8 to 12)

IL	4.12	IW	1.84	EL	3.25
AE L	1.50	L ML	0.98	LL	0.97

Paraproct undivided, arises from the antero-lateral margin of the IX tergum and extends ventrally close to the 9th sternum. 9th sternum elongate and undivided.

Aedeagus slightly less than 1/3 the body length, elongate; basal piece shorter than lateral lobe by 0.1 mm, and the anterior edge bordered. The lateral lobe bent inward posteriorly, broader at the base and gradually narrowed distad, the apex rounded and bears ventrally a few scattered spinules.

Median lobe tubular equal or slightly longer than lateral lobes; dorsal surface less sclerotized, proximal one-third slightly narrow, with a pair of apodemes; a pair of inflexed sclerotic blades on ventral surface; each inflexed blade come very close to its counterpart distally and somewhat widely separated proximally (Fig. 11). Inflexed blades and distal tip of the median lobe with spine-like setae, the ventral surface of this region grooved and encloses the bifid endotheca, the latter fringed with microtrichia at the tip; gonopore terminal.

Berosus pulchellus M'Leay (Pl. V, Figs.13 and 14)

IL	2.35	IW	1.37	EL	2.06
AE L	0.65	L ML	0.39	LL	0.32

Genital complex as in B. indicus.

Aedeagus between 1/3 and 1/4 the body length; basal piece shorter than lateral lobe by 0.05 mm, the anterior margin bordered; lateral margins reflexed and dorsally come close at the middle and connected by very transparent membrane. Lateral lobes laminate wide shorter than median lobe, posterior end rounded, anterior margin oblique and wavy.

Median lobe with proximal and distal bifid ends, the former more deep and wide than the latter, the anterior half darker than the posterior due to differential sclerotization; the dorsal surface sclerotized, the postero-lateral half non-sclerotized and fringed with anteriorly directed minute setae. The ventral surface also setose but conspicuous at the posterior half and arranged lengthwise. Gonopore terminal.

Berosus nr. *nigriceps* (Fabr.) (Pl.V, Figs. 15a and 15b)

IL	2.94	IW	1.50	EL	2.27
AE L	0.75	L ML	1.25	LL	0.52

Genital complex as in *Berosus indicus* Motschulsky.

Aedeagus about one-fourth the body length, elongate; basal-piece shorter than lateral lobes by 0.12 mm, the anterior margin bordered; lateral margins reflexed, unlike B. pulchellus widely separated and connected by membrane. Lateral lobes laminate as in *B. pulchellus*, wide but shorter than median lobe, posterior tip blunt, anterior margin oblique and more wavy than *B. pulchellus*. Lateral lobes articulate with the proximal end of median lobe besides their attachment to the basal-piece. A few minute setae scattered at the middle of each lateral lobe.

Median lobe longer than the entire length of the aedeagus, the anterior region deflexed to give U-shaped bend which probably formed out of the apodemes of median lobe; proximal end hook-like, and further drawn into a long posteriorly directed median strut (MS) which lies in between lateral lobes; the posterior one-fourth of the median lobe with anteriorly directed spine-like setae; and the distal half with uniform thickness; gonopore (GPR) an elongated slit and subterminal.

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CHAPTER V

EXTERNAL GENITALIA OF FEMALES

Family Dytiscidae

Species examined:

Canthydrus laetabilis Walk.

Laccophilus flexuosus Aube
L. sharpi Regimbart

Hydrovatus acuminatus Motschulsky
Hyphydrus flavicans (Regimbart)
Guignotus sp.
Herophydrus musicus (Klug)

Eretes sticticus (Linn)
Hydaticus luczonicus Aube
Cybister tripunctatus asiaticus Sharp

In all the above species, eight terga and six sterna are externally visible. The rest of the sclerites are invaginated and take part in the formation of the female genital complex. A sclerite tentatively named as intermediate sclerite is present between the 7th and the 8th sterna of the *Laccophilus* species and the *Eretes sticticus* (Linn), *Hydaticus luczonicus* Aube and *Cybister tripunctatus asiaticus* Sharp.

The 8th sternum is divided into two sternites as in the males.

A functional ovipositor has been observed in Laccophilinae (Tanner 1927, Young 1963), Colymbetinae (Jackson 1958a and 1960) and Dytiscinae (Demandt 1912, Miall 1912, Sidhu 1960a, etc.). Such an ovipositor is absent in the Hydroporinae.

Among the beetles having ovipositor, the ninth segment is entirely seen, but greatly modified in the formation of ovipositor, while in others it is reduced and only the sternites are traceable. The 9th sternum is modified to form valvifers (VLF) and valvulae (VVL). Tanner (1927) considered valvifers as portions of the 9th sternites.

In all dytiscids other than Dytiscinae double genital openings are present, the bursal ostium (BO) is always dorsal to the ovipore (OVP).

Valvulae (VVL) are present in all the dytiscids other than Hydroporinae.

Subfamily Noterinae

Canthydrus laetabilis Walk. (Pl. VI, Fig. 1)

IL 2.67 IW 1.37 EL 1.88

Medially the VIII tergum bears a shallow groove instead of a thin desclerotized zone. 8th sternum divided into two triangular sternites.

Ovipositor not well developed. The IX tergites less sclerotized and go un-noticed if not carefully observed. Valvifers very elongate extending deep inside the abdomen, twice as long as valvula, and attached with muscles on their anterior end. Valvula articulates by its emarginate margin to the posterior tip of valvifer. Valvula awl-shaped. The mesal edges of the valvulae on the posterior half and their outer surface setose, setae short and spine-like. At the bases of these valvulae lies the bursal ostium. Ovipore not enclosed by valvulae, located ventral to bursal ostium a little anteriorly.

Subfamily Laccophilinae

Laccophilus flexuosus Aube (Pl. VI, Figs. 2 and 3)

IL 4.49 IW 2.35 EL 3.65

The eighth and the ninth segments of the abdomen modified to assist in the oviposition. The former relatively less modified than the latter. VIII tergum bears a median longitudinal de-sclerotized zone, 8th sternum divided along its axis as in other dytiscids resulting in a pair of triangular sternites. A small and thin sclerotized piece (IS) arises from the corea between the 7th sternum and the 8th sternites, and this sclerite connects with the paired vaginal sclerites at their mid-ventral margin. The vaginal sclerites free and widely separated towards the anterior half and fused at the posterior half along their dorsal margins forming a Y-shaped structure; anterior end of each vaginal sclerite provided with muscles, the ventral margin of the posterior half free and serrate; each margin with about seventeen teeth. These sclerotic plates contain the ovipore and enclose the vagina.

The IX tergum somewhat reduced and divided into three sclerotic areas; one above and two on either side of the anus. According to their position these plates are called proctiger and paraprocts respectively (Tanner 1927). The proctiger much less sclerotized than paraprocts and indistinct. The valvifers paired, separate from each other, broad and oval in outline. A sword-shaped valvula containing the bursal ostium arises from the antero-ventral corner of each valvifer. Each of the valvula (homologous to the second valvula of Orthoptera and Hemiptera) one-third distance from the distal tip bears an acute short inwardly bent projection on the dorsal margin and meets its fellow; another acute projection arises just a little posteriorly. The tip of the valvulae acute. Conjunctival membrane holds the valvulae together along the margins thereby forming a distally closed tube. Bursal orifice dorsal to the ovipore.

Laccophilus sharpi Regimbart

IL 3.75 IW 2.11 EL 3.07

The intermediate sclerite more distinct than in *Laccophilus flexuosus* Aube, flat and bottle-shaped in outline with a narrow neck. Ovipositor and the position of the genital openings as in *L. flexuosus*.

Subfamily Hydroporinae

Hydrovatus acuminatus Motschulsky (Pl.VI, Figs.4 to 6)

IL 2.87 IW 1.87 EL 2.84

8th sternum divided and retracted into the abdomen.

The female genitalia consist of two sclerotized structures, the ventral less sclerotized and dorsal well sclerotized, and both of them long and semi-tubular. The dorsal sclerite attenuated posteriorly, and with a few scattered denticles on either side; dorsal surface convex and ventral surface concave, anteriorly divided to form two thin apodemes (rami) which project laterad at right angles. The ventral structure thick leathery dorsally, sclerotized along the ridges on either side of its ventral groove and lie enclosed in the groove of the dorsal structure. The dorsal sclerite appears to be the modified 9th sternum, while the ventral sclerotized structure the bursal extension.

Hyphydrus flavicans (Regimbart) (Pl. VI, Figs.7 and 8)

IL 4.17 IW 2.80 EL 3.20

The 8th sternum divided into two sternites and when at rest lie retracted inside the last non-retractable sternite i.e., the true 7th. The IX tergum absent. A pair of valvifers present on either side of the bursal ostium. Each valvifer well sclerotized elongate plate with bordered margins; the distal margin rounded and fringed with setae; the proximal outer margin drawn into a strong shaft which projects anteriad. Valvulae and ovipositor absent. Two genital openings present. Bursal ostium dorsal to the ovipore and lies between the valvifers.

Guignotus sp. (Pl.VI, Figs.9 and 10)

IL 2.63 IW 1.39 EL 1.99

The 8th sternum divided into two sternites, and lie retracted inside the last nonretractable 7th sternum (apparent 6th). IX tergum absent. Valvifers elongate flat weakly sclerotized spatulate, anterior two-third thin while the posterior one-third broad. Posterior margin fringed with nearly 13 setae. The entire valvifer including setae 0.3 mm long.

The broader portion of the valvifer with two processes, one outer and the other inner. Valvulae and ovipositor absent. Two genital openings present. Bursal ostium dorsal to the ovipore.

Herophydrus musicus (Klug) (Pl.VI, Figs. 11 and 12)

IL 3.28 IW 1.93 EL 2.42

8th sternum as in Hyphydrus flavicans. Valvifers broad and truncate at the distal end, attenuated forming a thin elongated shaft at the proximal end; distal tip partially fringed with closely set short setae, while the proximal tip provided with muscular attachment. Valvifers between bursal ostium and ovipore. Valvulae and ovipositor absent. Location of genital openings as in Guignotus sp.

Subfamily Dytiscinae

Eretes sticticus (Linn) (Pl.VI, Fig. 13)

IL 13.01 IW 7.07 EL 10.05

The 7th and the 8th sterna broadly separated by corea. A small area of the intersegmental membrane (corea) with a triangular sclerotic patch immediately posterior to the 7th sternum, and named intermediate sclerite extending half way in the membrane. 8th sternites somewhat rectangular with longer mesal edge. When at rest the 8th sternites lie between the 7th sternum and the valvifers; when extended they assume a vertical position and lie on either side of the base of the ovipositor. Ninth segment greatly modified to form the ovipositor. Its tergites small and lie above the anus while the sternites (valvifers) arise from the outer edge of their corresponding tergites. Valvifers thin elongate and slightly sinuate. Distal end of the valvifers connected to the valvulae which constitute a functional ovipositor. Vulva lies enclosed ventrally by the valvulae. Ovipositor blade a composite structure formed as a result of the fusion of two valvulae on their dorsal surface. Valvulae broad proximally and attenuated distally, fringed with minute scattered setae, tip of valvulae bifid and slightly curved dorsad. The apex bears a fringe of setae directed posteriad. This composite valvular sclerite has a ventral lobe which lies enclosed in its ventral groove when in repose.

Hydaticus _luczonicus_ Aube (Pl.VII, Fig. 1)

IL 14.27 IW 8.23 EL 11.61

The 7th sternum and the 8th sternites widely separated from each other by a very distinct intermediate sclerite, the sclerotized patch of the corea. The IX tergites present. Valvifers flat, wide at the centre and attenuated on either end, ventral margin (in extended ovipositor) bordered, posterior end slightly raised, rounded and well sclerotized and joins the valvula. Valvula of either side fused along the dorsal margin, slightly curved dorsad, broad and attenuated distad, distal end rounded with an oval patch of non-sclerotized area which contains a tuft of setae. Valvula encloses the ventral lobe, ventral lobe uniformly sclerotized, gonopore terminal, distal end not pointed.

Cybister tripunctatus asiaticus Sharp (Pl. VII, Fig. 2)

IL 24.38 IW 14.53 EL 20.55

The general pattern of the female genital complex similar to the other members of Dytiscinae. Intermediate sclerite not so distinct as in Eretes sticticus and Hydaticus luczonicus. Valvifers thin and long, arise from the outer edge of the IX tergites and come to lie on either side of the eversible tip of the abdomen; posteriorly the valvifers articulate with the proximal part of the valvula. Valvula sclerotized, narrowed at both ends, tips blunt. A ventral lobe present at the base of the valvula. The ventral lobe is distinct owing to the sclerotization of the distal end of the vagina. Gonopore terminal.

Family Gyrinidae

Species examined:

Dineutes unidentatus Aube

Eight terga and seven sterna are externall visible. The last visible sternum is the true 8th sternum (Tanner 1927). Unlike Dytiscidae this sternum is nonretractable and undivided. The part of the abdomen posterior to this is invaginated. IX tergum is membranous as in the male, and the corresponding part of the ventral surface, i.e. the 9th sternum is modified to form a pair of valvifers.

Subfamily Enhydrinae

Dineutes unidentatus Aube (Pl. VII, Fig. 3)

IL 7.38 IW 3.85 EL 5.32

The 8th sternum undivided, nonretractable and connected to the proximal margin of the valvifers. As in males tergum of the ninth segment absent while paired valvifers present with the vulva opening at their median proximal end. Each valvifer is a depressed plate, somewhat rectangular, length twice its maximum width, inner posterior corner rounded, outer posterior half and distal margins fringed with long tufts of setae; proximal margin bordered and has a pair of anteriorly directed long processes or apodemes. The outer apodeme longer than mesal. Proximal ends of all the four apodemes connected with muscles. Valvula and ovipositor absent.

Family Hydrophilidae

Species examined:

Coelostoma stultum Walk

Paracymus evanescens (Sharp)
Enochrus sp.
Sternolophus rufipes (Fabricius)
Hydrous indicus Bedel
H. senegalensis Perch
Berosus indicus Motschulsky
B. pulchellus M'Leay
B. nr. nigriceps (Fabr.)

In all the hydrophilids studied there are eight externally visible terga. Except in Coelostoma stultum and

Enochrus sp. in which there are only five externally visible sterna, the rest of the hydrophilids exhibit six such sterna. Among the dorsal sclerites only the paraprocts and the IX tergum are invaginated. From the ventral sclerites only the 8th and the 9th sterna are invaginated. Usually none of the invaginated terga and sterna, except the 9th sternum i.e. the valvifer, tend to bifurcate longitudinally. The IX tergum bears the anus. Anteriorly this tergum is divided giving rise to paraprocts (PP) as in the case of males. But in females the paraprocts are paired and without fail extend ventrally to articulate with the base of the corresponding valvula. The valvifers may be confluent anteriorly or divided completely. The vagina (VAG) opens as vulva (V) at the base of the valvifers. Anteriorly the valvula is flat wide inverted U-shaped and extend from the proximal end of the valvifers or sternites. The valvula is two segmented, posterior portion long and tubular. In all the species the posterior area of the valvulae have setae all around, while the tip of the second segment bears long setae (S).

Subfamily Sphaeridiinae

Coelostoma stultum Walk (Pl. VII, Fig. 4)

IL 4.11 IW 2.69 EL 2.99

The IX tergum more wide than long, evenly sclerotized; paraprocts extend from either side of the tergum to latero-ventral surface of the genital tube and articulate with the proximal end of the valvulae. 9th sternum widely and deeply cleft leaving a thin confluent area anteriorly. Posterior margin of the two ninth sternal limbs emarginate and bears no setae. Valvulae flat anteriorly and tubular posteriorly, bent in the shape of inverted U. A small sclerite present at the proximal end of its articulation with the 9th sternum. Valvula two segmented as in other hydrophilids; the first and the second segments separated by means of a non-sclerotized tubular structure; the tip of the last segment bears a few short setae.

Subfamily Hydrophilinae

Paracymus evanescens (Sharp) (Pl. VII, Fig. 5)

IL 2.08 IW 1.26 EL 1.58

IX tergum retracted, evenly sclerotized and bears paraprocts on each side; paraprocts usually slender flat and join the base of valvulae. The 9th sternum partly divided forming two valvifers by deep anterior and posterior clefts, anterior end of valvifer pointed, posterior end emarginate resulting in a pair of processes. The valvula two segmented; first segment bears setae posteriorly, second segment separated by a short cylindrical and membranous portion from the first; setae present at the tip of the second valvular segment.

Enochrus sp. (Pl. VII, Fig. 6)

IL 3.09 IW 1.78 EL 2.31

IX tergum retracted; paraprocts present and extend from either side of the IX tergum. Valvifers paired widely separated anteriorly and posteriorly, anterior end of each valvifer pointed, posterior end deeply emarginate resulting in a pair of pointed processes. Anterior end of valvula broad, inner margin notched. The ventral process of paraproct articulates with the spinous process on the anterior margin of the base of valvifer.

Sternolophus rufipes (Fabr.) (Pl. VII, Figs.7 and 8)

IL 10.38 IW 5.33 EL 7.65

The IX tergum rectangular and its posterior corners rounded. The paraprocts extend from either side of the IX tergum as in other hydrophilids, but ventrally they widen to form broad triangular plates whose anterior and mesal margins bordered. Ventrally the paraprocts articulate with the anterior margin of the valvulae, and the valvulae in turn articulate with the anterior margin of the valvifers. The valvifers remain united with each other at the basal portion; posterior end of each valvifer bifid and each lobe long and pointed which bends towards each other; the mesal lobe longer than the outer lobe, posterior margin seteferous. Valvulae broad and articulate with the anterior margin of each valvifers which are tubular long and two segmented; the first segment provided with minute setae and the tip of second segment bears a terminal fringe of setae.

Hydrous indicus Bedel (Pl. VII, Figs. 9 and 10)

IL 32.64 IW 15.29 EL 25.39

IX tergum hexagonal, corners rounded, irregular patch of long non-sclerotized area in the middle; lying on either side of this tergum is a sclerotized strip known as paraproct.

It extends upto the ventral surface between the 8th sternum and the valvifers and articulates with valvula. Each valvifer weakly sclerotized, tip acuminate, posterior margin and the tip fringed with setae. Each valvula articulates with the anterior end of the corresponding valvifer, broad at the base, travel a little to the anterior, bend dorsally to finally swingback posteriorly as an elongated slender tubular process. Valvula two segmented, the proximal segment provided with minute setae, the distal segment bears a terminal fringe of fine setae.

Hydrous senegalensis Perch (Pl. VII, Figs. 11 and 12)

IL 39.02 IW 18.86 EL 30.85

IX tergum longer than wide; uniformly sclerotized; paraprocts extend latero-ventrally on either side of the IX tergum, their anterior margin more sclerotized and hence appear bordered, the ventral longitudinal process of paraprocts united anteriorly, posterior end abruptly widened with which the paraprocts articulates with the base of the valvula. Valvifers separated from each other by a membrane. Posterolaterally each valvifer is emarginated, emarginated margin bears a row of closely set fine setae. From the base of each valvifer arises a flat valvula which extends latero-dorsally (in extended condition) and then travels posteriad as a long tubular process. The valvula two segmented; the first segment long, thickly pitted on the posterior one-thirds, each pit bears a short spiny seta; the second segment short, fringed with tuft of setae distally.

Berosus nr. *nigriceps* (Fabr.) (Pl. VII, Fig. 15)

IL 3.51 IW 1.77 EL 2.88

IX tergum invaginated and undivided. The ventral extension of paraproct flat and wide, bordered anteriorly and more pronounced than its latero-dorsal (when extended) process; it articulates with the base of valvula by means of distinct spine-like process. Valvifers and valvula similar to those of *B. pulchellus*.

* * *

CHAPTER VI

INTERNAL REPRODUCTIVE ORGANS OF MALES

Family Dytiscidae

Species examined:

Canthydrus laetabilis Walk.

Laccophilus flexuosus Aube
L. parvulus Aube
L. sharpi Regimbart

Hydrovatus acuminatus Motschulsky
Hyphydrus flavicans (Regimbart)
Guignotus sp.
Herophydrus musicus

Copelatus sp.

Eretes sticticus (Linn)
Hydaticus luczonicus Aube
Cybister tripunctatus asiaticus Sharp

The testes (TES), the epididymides and the vasa deferentia (VD) are paired and the first two are formed as a result of the coiling of a single long mesodermal tube. The terminal part of this tube in many of the dytiscids (Pl. VII, Figs. 16, 17, etc.) separates from the coiled testis forming a short finger-like process. The coiled testis is usually separated from the epididymis (EPDD) by non-coiled portion of vas deferens. The testis is the site of spermatogenesis while the epididymis stores the spermatozoa which are ready for discharge. The testes and epididymides are enveloped by the peritonial membrane. The vas deferens of each side joins the anterior end of the corresponding

Key to the abbreviations in the text

L AC GL : Length of accessory gland
L L D : Length of lateral ejaculatory
L EJ D : Length of ejaculatory duct

All the measurements are in millimetres.

Subfamily Noterinae

Canthydrus laetabilis Walk. (Pl. VII, Fig. 16)

L AC GL: 1.00, L L D: 0.18, L EJ D: 0.40

Epididymis confluent with the coiled testis. The lateral ejaculatory ducts (LEJ) long and about the length of the common ejaculatory duct (DEJ). The glands (ACGL) long and stout, and lie on either side of the axial line of the body. The gland has seven prominent twists.

Subfamily Laccophilinae

Laccophilus flexuosus Aube (Pl. VII, Fig. 17)

L AC GL: 3.50, L L D: 0.40, L EJ D: 1.00

Epididymis not separate from testis. The vas deferens (VD) of each side opens at the junction of accessory gland with lateral ejaculatory duct. Lateral ejaculatory duct less than half the length of the ejaculatory duct; ejaculatory duct with a ring-like convolution. Accessory gland about three-fourths the body length; lies on either side of the axial line, and bears only one prominent bend that directs the gland posteriorly.

An unpaired gland opens at the proximal end of the median lobe. It contains a number of short blind tubules opening into a central efferent duct which continues poste-

-riorly as a long duct.

Laccophilus parvulus Aube (Pl. VII, Fig. 18)

L AC GL: 1.40, L L D: 0.25, L EJ D: 1.50

Externally the epididymis not separate from testis. The ejaculatory duct is approximately of the same length as the accessory gland. Length of lateral ejaculatory duct about one-sixth that of ejaculatory duct. The accessory glands stout and lie on either side of the axial line and bent ventro-posteriorly in the form of a circle. The apex of each gland comes to lie at the junction of vas deferens with accessory gland. An unpaired gland (PCGL) similar to that of *L. flexuosus* is present.

Laccophilus sharpi Regimbart (Pl. VII, Fig. 19)

L AC GL: 2.80, L L D: 0.50, L EJ D: 1.40

Epididymis and testis confluent. Lateral ejaculatory duct about one-thirds the length of the ejaculatory duct. Accessory glands lie on either side of the axial line, and two-thirds the body length. A single prominent convolution of the accessory gland present at its middle. This convolution sends the gland ventrad and the tip of the gland comes to lie on either side of the bulbous proximal end of the ejaculatory duct. An unpaired gland present similar to that of *L. flexuosus*.

Subfamily Hydroporinae

Hydrovatus acuminatus Motschulsky (Pl. VIII, Fig. 1)

L AC GL: 3.80, L L D: 0.10, L EJ D: 0.50

The testis and the epididymis coiled and confluent. Vas deferens opens at the tip of the lateral ejaculatory duct. Lateral ejaculatory duct about one-fifth the length of the ejaculatory duct. Accessory glands lie on either side of the axial line and longer than the body length. Each gland is much contorted and has six prominent twists.

Hyphydrus flavicans (Regimbart) (Pl.VIII, Fig.2)

L AC GL: 3.70, L L D: Nil , L EJ D: 0.50

The testis and the epididymis indistinguishably united with each other forming a single bundle. The vasa deferentia open at the anterior tip of the ejaculatory duct. Hence the lateral ejaculatory ducts are absent. The glands also open directly at the anterior end of the ejaculatory duct. Accessory glands long and very stout occupying greater part of the abdomen; glands longer than the body length and lie on either side of the axial line of the body and has four distinct twists.

Guignotus sp. (Pl. VIII, Fig. 3)

L AC GL: 1.20, L L D: Nil , L EJ D: 0.60

The vasa deferentia and the glands open at the anterior end of the ejaculatory duct and hence the lateral ejaculatory ducts not present as in _Hyphydrus flavicans_. Accessory gland less than half the body length. Each gland exhibits a single prominent bend at its middle. This bend (twist) brings the terminal portion of each gland posteriorly so that the tip comes to lie ventrad to the base of the left gland.

Herophydrus musicus (Klug) (Pl. VIII, Fig. 4)

L AC GL: 3.20, L L D: 0.20, L EJ D: 0.45

The testis and the epididymis separated from each other by a non-coiled part of vas deferens. Vas deferens opens into lateral ejaculatory duct. The accessory glands stout and longer than body length and lie on either side of the axial line of the body and twisted mainly at three places. Ventrally at the base of the accessory gland the terminal portion of the two glands touch each other.

Subfamily Colymbetinae

Copelatus sp. (Pl. VIII, Fig. 5)

L AC GL: 1.55, L L D: 0.15, L EJ D: 1.70

The testis and the epididymis separated by a short non-coiled vas deferens. Each accessory gland with four twists. The vas deferens joins at the anterior end of the lateral ejaculatory duct. Accessory gland shorter than ejaculatory duct (DEJ) and lie on either side of the ejaculatory duct.

Subfamily Dytiscinae

Eretes sticticus (Linn) (Pl. VIII, Figs. 6a and 6b)

L AC GL: 7.00, L L D: 0.85, L EJ D: 0.95

Testis and epididymis separated by a non-coiled vas deferens. Vas deferens joins at the anterior end of the lateral ejaculatory duct where the accessory glands also join. The lateral ejaculatory duct is only slightly shorter than ejaculatory duct. Ejaculatory duct much shorter than the accessory glands and with no ring-like convolutions. Unlike other dytiscids the right and left glands come to lie one above the other (Fig. 6b), the right dorsal to the left. Both these glands adhere to each other and travel in the same direction. Each gland has five twists. The terminal portion of the gland ultimately comes to touch the basal portion of the accessory gland.

Hydaticus luczonicus Aube (Pl.VIII, Fig.7)

L AC GL: 7.00, L L D: 0.70, L EJ D: 1.00

Testis, epididymis, lateral ejaculatory duct, ejaculatory duct, and the position of the accessory glands as in Eretes sticticus. But the accessory gland exhibits only three twists. The left gland lies dorsal to the right one, and both the glands exhibit similar convolutions.

Cybister tripunctatus asiaticus Sharp (Pl.VIII, Fig.8)

L AC GL: 25.00, L L D: 2.00, L EJ D: 1.70

Testis and epididymis as in Eretes sticticus. The vas deferens opens at the anterior end of the lateral ejaculatory duct. Lateral ejaculatory duct slightly longer than the ejaculatory duct, ejaculatory duct with a ring-like convolution. The accessory glands long thin and bent several times (about eight). The glands lie one on either side of the axial line. Length of accessory gland equal to or slightly longer than the body length.

Family Gyrinidae

Species examined:

<u>Dineutes</u> <u>unidentatus</u> Aube

Striking features of the internal reproductive organs are the presence of a common epididymis and a pair of long lateral ejaculatory ducts.

For a key to the abbreviations used vide p.76.

<u>Dineutes</u> <u>unidentatus</u> Aube (Pl. VIII, Figs. 9 and 10)

L AC GL: 4.50, L L D: 4.00, L EJ D: 1.20

Testis composed of a single long highly coiled blind tube. It lies on either side of median line. The vasa deferentia of both the testes join to run side by side throughout. They travel to-and-fro from left to right resulting in a conjoint inverted U-like bundle of epididymis on the median line just dorsad to the genital ducts. From the left side of the ventral surface of the epididymis travels a pair of conjoint vasa deferentia and separate just before they open at the anterior tip of the lateral ejaculatory ducts exactly opposite to the opening of the accessory gland. The two lateral ejaculatory ducts come close posteriorly and join at the anterior end of the ejaculatory duct. The terminal end of each lateral ejaculatory duct swollen to form a very small bulb which receives the duct of the accessory gland from one side and the vas deferens from the other. The lateral ejaculatory ducts and the accessory glands highly muscular and coiled. The glands and the middle portion of the lateral ejaculatory ducts are spindle-shaped. The ejaculatory duct is much shorter than the lateral ejaculatory ducts. The distal end of each accessory gland is connected by a strand of tissue to the eighth segment.

Family Hydrophilidae

Species examined:

Sternolophus rufipes (Fabr.)
Hydrous indicus Bedel
H. senegalensis Perch

All the beetles examined consist, as usual, a pair of testes with testis follicles (TESF). Each testis follicle opens at the distal end of the vas deferens by means of vas deferens. The vas deferens is a long tube and just before opening into the proximal tip of the ejaculatory duct, enlarges to form seminal vesicle (VSM) where the spermatozoa congregate. Generally two pairs of glands i.e. one pair of opaque glands (OPGL) (ectadenia) and another pair of transparent glands (TRGL) (mesadenia) are present opening at the anterior end of the ejaculatory duct (DEJ). The ejaculatory duct is a long tube.

Subfamily Hydrophilinae

Hydrous indicus Bedel (Pl. VIII, Fig. 11)

Opaque gland with appendix	: 23.00	(20.00 + 3.00)
Transparent gland	: 17.00	
Ejaculatory duct	: 12.00	
Length of testis	: 4.00	

Testis mulbary fruit shaped and consists of a large number of fine elongated follicles which open radially around a central hollow tube viz. vas deferens. The vas deferens of each side continues posteriorly and opens at the base of the opaque gland. Seminal vesicle present but comparatively less thick than that of Sternolophus rufipes . Both the types of accessory glands present. The transparent gland not branched as in the preceding beetle. The transparent glands and the vasa deferentia of each side are connected just before they join the anterior end of the ejaculatory duct. The opaque glands differ from those of the preceding insect in the manner of convolutions. Appendicular gland (APGL) present and covered by opaque gland. The appendix of opaque gland bears transverse ring-like folds all along. The anterior 3 mm of the ejaculatory duct greater in diameter than the rest of the 7 mm long ejaculatory duct.

Sternolophus rufipes (Fabr.) (Pl. VIII, Fig. 12)

Opaque gland with appendix : 6.00 (5.20 + 0.80)
Transparent gland : 6.50
Ejaculatory duct : 4.30

Testis follicles concentric around the tip of the vas deferens. The vas deferens of each testis thin and very long, swollen greatly to form seminal vesicle just before joining the anterior end of the ejaculatory duct. Opaque accessory gland long and coiled like a watch spring and bears at its tip a short annulated tubular gland - the appendicular gland. A transparent gland joins the anterior end of the ejaculatory duct, opposite to the seminal vesicle. This gland lies between the opaque glands of each side. The ejaculatory duct longer than the accessory glands and the apical half much broader than the distal half.

Hydrous senegalensis Perch (Pl.VIII, Fig.13)

Length of opaque gland with appendix : 40.00 (33.00 + 7.00)
Length of transparent gland long branch : 28.00
short branch : 4.50
Length of ejaculatory duct : 21.00
Length of testis : 9.50

Testes, vasa deferentia, seminal vesicles, opaque glands and ejaculatory duct as in the preceding insect. The transparent gland long and thin and divided mainly into two unequal branches opening at the anterior tip of ejaculatory duct by a common duct. The anterior half of the longer branch lies enclosed in the loop of the opaque gland. The longer branch at about its middle bears a very short projection. Bulbous swellings mark the junction of the branches of transparent glands. Two such swellings present on each transparent gland. Unlike the preceding insect the seminal vesicle opens separately into the ejaculatory duct. The anterior half of the ejaculatory duct wider than the posterior half. At about the middle, this duct enlarges forming a bulbous structure.

HISTOLOGY OF THE INTERNAL REPRODUCTIVE ORGANS OF MALES

Species examined:

Eretes sticticus (Linn) (Dytiscidae)
Dineutes unidentatus Aube
Hydrous indicus Bedel

Bordas (1900) and Escherisch (1894) classified coleopteran testes into two types, and both these types of testes are observed in the present study; the simple tubular type in the Dytiscidae and the Gyrinidae, and the complex follicular type in Hydrophilidae. In all the above three species the testis is covered over by peritoneal sheath.

Spermatogonial cells at different stages of development are present at the distal end of the single sperm tube in Dytiscidae and Gyrinidae. In the Hydrophilidae such stages of spermatogenesis are located in each of the testis follicles. In both the types, the area of spermatogenesis could be differentiated into all the four zones described by Wigglesworth (1965). They exist in the following sequence from distal to proximal end.

Zone of spermatogonia
Zone of spermatocytes
Zone of maturation and reduction
Zone of transformation

Efforts to trace the apical cell have proved fruitless.

The zone of spermatogonia consists of primordial germ cells lying among somatic mesodermal cells. The second zone i.e. the zone of spermatocytes consists of spermatocytes in cyst. The third zone consists of spermatids. The fourth zone has spermatids in the final stages of the transformation, and the spermatozoa.

Testis can be distinguished by the presence of developmental stages of spermatozoa, and the epididymis by the mature spermatozoa.

It is well known that the testis and the ejaculatory duct have originated from mesoderm and ectoderm respectively. But, there is difference as to the origin of other structures associated with the internal reproductive system of insects. The vasa deferentia are primarily mesodermal but in some insects the posterior part of it is ectodermal while in some others they are entirely ectodermal (Snodgrass 1935, p. 592). The ejaculatory duct, the genital ducts or the forked anterior end of the ejaculatory duct are ectodermal in origin (Snodgrass 1935, p. 572).

Two types of glands, ectadenia and mesadenia (Escherisch 1894) have been observed. There is a pair of ectadenia in Eretes sticticus, and Dineutus unidentatus. Demandt 1912 and Korschelt 1923-24 described similar glands as 'ectadenien' in Dytiscus marginalis.

In Hydrous indicus two pairs of glands are present; one pair of ectadenia and the other of mesadenia. The ectadenia in all the three species are opaque and the mesadenia which are present in Hydrous indicus are transparent. Similar structures are reported by Escherisch (1894) on Hydrophilus piceus. In both the types of glands the columnar cells are secretory in nature. Secretion is observed in the glands.

Eretes sticticus

Testis: (Pl. IX, Fig. 1)

The testis coil is enveloped by the peritoneal sheath which is composed of a row of cuboidal cells. The epithelial layer of the sperm tube is very thin. The cells of this layer, at the zone of growth have granular cytoplasm and the cell walls are not distinct. The epithelial cells at the posterior end of the testis coil have (well defined) distinct cell walls. All the stages of spermatogenesis have been observed, and the zones could be distinguished. Several bundles of spermatozoa are seen towards the posterior half of the testis coil.

Vas deferens (between testis and epididymis): (Pl.IX, Fig.2)

It consists of an outer cuboidal layer of peritonium (PSH) and an inner layer of columnar cells. In between these two layers is a covering of epithelial sheath. The lumen has spermatozoa (SPZ) which are on their way to the epididymis.

Epididymis:

In a section of the epididymis a number of portions of the convoluted vas deferens are seen. The entire epididymis like the testis is covered by a peritoneal sheath. Spermatozoa have congregated in the epididymis throughout its length. The lumen of the vas deferens of the coiled epididymis is packed throughout with spermatozoa. Here, the wall of the vas deferens is thin and the epithelium is not distinct.

Vas deferens (between epididymis and the ejaculatory duct): (Pl. IX, Fig. 3)

A thin layer of circular muscle fibres (CM) forms the outer covering of the vas deferens. The inner layer of the vas deferens is formed of columnar epithelial layer (EP). There is no intimal lining.

Lateral ejaculatory duct:

The outer layer of longitudinal muscle fibres is followed by the columnar epithelium which is secretory in nature. Intervening them is the basement membrane. Intima lines the epithelial layer.

Ejaculatory duct: (Pl. IX, Fig. 4)

A thin layer of longitudinal muscle fibres (LM) forms the outermost covering. The epithelial layer is formed of columnar cells and has a basement membrane (BM). The nuclei are round and situated at the bases of the columnar cells. The intercellular walls are not distinct and the cytoplasm is granular. The lumen is lined by a thick intima which is secreted by the epithelium.

Accessory gland (opaque gland): (Pl. IX, Fig. 5)

The gland consists of an outer layer of longitudinal muscle fibres and an inner layer of columnar epithelium (EP). There is a basement membrane intervening these two. The columnar cells are granular and vacuolated (VCL) suggesting their secretory nature. The gland is lined by a thin intima (ectadenia) which has been found broken at places. The secretions of these glands is viscid and are acedophilic (eosin stained).

Dineutes unidentatus

Testis:

As in Eretes sticticus, in a longitudinal section of the testis are seen many portions of the convoluted sperm tube. A portion of the extreme anterior end is separated forming a finger-like projection and is containing spermatogonia. All the stages of spermatogenesis are present as in the above dytiscid. The testis coil is covered by peritoneal sheath and the sperm tube has an outer epithelial covering. The posterior end of the testis coil has spermatozoa ready to travel into the common epididymides.

Vas deferens: (Pl. IX, Fig. 6)

The short vas deferens that lies between testis and the common epididymis is slender and has an outer peritoneal sheath and inner epithelial layer. A transverse section of the vas deferens between epididymis and the lateral ejaculatory duct is quite different from that of the *Eretes sticticus*. It is covered by two layers of muscle fibres. Of these two, the outer is the longitudinal and branched muscle layer, while the inner is the circular muscle layer. Beneath the circular layer is the cuboidal epithelium. Intima is absent.

Lateral ejaculatory duct: (Pl. IX, Fig. 7)

Each lateral ejaculatory duct is longer than those of dytiscids and has an outer lattice of muscular layer. The inner epithelial layer is granular, highly vacuolated and the nuclei are largely located at the base. This layer has a basement membrane and the lumen is lined by a very thin intima. The intima is broken up at places facilitating the escape of secretions into the lumen. In between the basement membrane and the outer lattice of muscular layer is a layer of circular muscles.

Ejaculatory duct: (Pl. X, Fig. 1)

The ejaculatory duct has an outer layer of circular muscles and an inner layer of epithelial cells. At some places the epithelial layer is thrown into folds into the lumen. The intimal lining is thin.

Accessory gland: (Pl. X, Fig. 2)

The gland has three distinct layers. The outer layer is formed of longitudinal fibres. The inner layer is the epithelium and the cells are columnar. The nuclei in these cells are located at the bases of the cells. The cytoplasm of the columnar cells is highly granular at their apex and vacuolated towards the base. The epithelium has a basement membrane. The layer between basement membrane and the outer muscle fibres is that of circular muscles and very conspicuous. A very thin intima forms the lining of the lumen.

Hydrous indicus Bedel

Testis: (Pl. X, Fig. 3)

The testis belongs to the complex type of testis. It is composed of a large number of follicles arranged around the distal end of the vas deferens. The follicle is covered by a thin epithelial layer. The epithelial cells are not distinct at the anterior end of the follicles, while they are traceable towards the posterior end. Each follicle is a unit having all the stages of spermatogenesis in the sequence (vide supra).

Vas deferens: (Pl. X, Fig. 4)

The vas deferens has an outer syncytial sheath (SSH) and an inner cuboidal epithelial layer. Between these two is a thin layer of circular muscle fibre. Intima (IT) is absent. The nuclei of the epithelial cells are oval and are placed at the base. Each nucleus has a very distinct nucleolus. The nuclei of the outer syncytial sheath are oblong or elongated.

Seminal vesicle: (Pl. X, Fig. 5)

The wall of the seminal vesicle consists of an outer layer of circular muscles and an inner layer of epithelial cells. The circular muscle layer is slightly less thick than the inner epithelial layer. Basement membrane (BM) is present at the base of the inner epithelial layer. The intimal lining is thin. The lumen is packed with spermatozoa.

Ejaculatory duct: (Pl. X, Fig. 6)

Ejaculatory duct has a thick outer compactly arranged circular muscle layer and an inner thin epithelial layer. The lumen is considerably reduced, and is lined by a thick intima. A few spines from the intima are projecting into the lumen.

Accessory glands:

Opaque gland: (Pl. X, Fig. 7)

The opaque gland has an outer layer of longitudinal muscles (LM). Following this layer is the circular muscle layer (CM). The inner epithelial layer is septate and only the basement membrane extends into the septa (SEP). The epithelial cells are columnar, highly granular and secretory in nature. The interseptal spaces are filled with coarse granules and highly vacuolated. The lumen of the duct is lined by intima and the secretions are seen escaping through it into the lumen. The lumen is filled with secretions which are acedophilic (taking eosin).

Appendix of the opaque gland: (Pl. X, Fig. 8)

The appendicular gland has an outer longitudinal layer of muscles followed by a layer of circular muscles. There is a distinct basement membrane from which the inner layer of columnar epithelial cells arise. The cells of this epithelium appear to be in more than one tier. Cytoplasm of these cells contain vacuoles and fine granules. The nuclei are situated at base, and the nucleoli are distinct. Unlike in opaque glands septa are absent. The lumen is much obliterated and the intima is not distinct.

Transparent gland: (Pl. X, Fig. 9)

This gland has a single layer consisting of epithelial cells and the nuclei are situated at their base. The cytoplasm is highly granular and the cell walls facing the lumen are not distinct. The lumen is filled with granular secretions. Intima is absent.

* * *

INTERNAL REPRODUCTIVE ORGANS OF FEMALES

Dytiscidae

Species examined:

Canthydrus laetabilis Walk.

Laccophilus flexuosus Aube
L. sharpi Regimbart

Hyphydrus flavicans (Regimbart)
Guignotus sp.
Herophydrus mucicus (Klug)

Eretes sticticus (Linn)
Hydaticus luczonicus Aube
Cybister tripunctatus asiaticus Sharp

In Dytiscidae two types of reproductive organs are observed; one type opens to the exterior by a single genital opening, namely the vulva (V) and the other type opens to the exterior with double genital openings namely the ovipore (OVP), and the bursal ostium (BO). Reproductive organs with double external genital openings are common among ditrysian Lepidoptera (Klots 1956, Imms 1963).

Amongst the coleopterans double genital openings are so far reported only in three genera belonging to Hydroporinae and Colymbetinae of Dytiscidae (Heberdey 1931, Jackson 1960). Apparently such a condition is now found to be common among the dytiscids studied except those of Dytiscinae.

The ovarioles per ovary range from 8 in *Canthydrus laetabilis* to a maximum of 30 in *Cybister tripunctatus asiaticus*.

This range almost closely agrees with that given by Robertson (1961). The ovarioles in the reproductive organs of dytiscids are polytrophic and are in accordance with the established characters of Adephaga (Imms 1963). In both the types the lateral oviducts unite forming a common oviduct. The common oviduct joins the vagina (VAG). The spermatheca (SPT) opens at the junction of the vagina and the common oviduct. In dytiscids having single external genital opening, the vagina opens at the end of the ninth segment, while in beetles having double external reproductive apertures, the vagina has been transformed to serve the function of bursa, while another duct that arises from the anterior end of the 8th sternite joins at the junction of the common oviduct and spermatheca. This new duct opens at the base of 8th sternites and discharges the eggs during oviposition. Hence it is functionally known as vagina. The original vagina of the beetle having double genital openings is transformed into bursa copulatrix (BC). The bursa anteriorly gives rise to a duct known as bursal duct (BD). In the different genera the bursal duct may directly open into the vagina or may open into a spermatheca. In the latter case, the spermatheca may open either through a long, or a short tubular connection namely the spermathecal duct (SPTD). The bursa is always dorsal to the ovipore, unlike in Ditrysian Lepidoptera. Thus among Dytiscidae two types of female reproductive organs are found (vide supra).

Key to the abbreviations used in the text:

C OVD	Length of common oviduct
L VA	Length of vagina

L BD	Length of bursal duct
L SPD	Length of spermathecal duct
L B	Length of bursa

All the measurements are taken in millimetres.

Canthydrus laetabilis Walk. (Pl.XI, Fig.1)

C OVD 0.1, L VA 0.27, L BD 2.00

Each ovary consists of eight polytrophic ovarioles; common oviduct about one-third the length of the vagina. The vagina opens outside as ovipore and the ovipore lies at the base of the 8th sternites. The bursal duct opens at the junction of the common oviduct and the vagina. Bursal duct about three times the length of the vagina; bursal duct typically convoluted as in the figure, and lies above the vagina just anterior to the bursa (BC). Bursa about 0.32 mm long and opens dorsal to the base of the valvulae. Spermatheca absent.

Laccophilus flexuosus Aube (Pl.XI, Fig. 2)

C OVD 0.20, L VA 0.45, L BD 1.60

A total of 41 polytrophic ovarioles present in the ovaries. Common oviduct about half the length of vagina. The vagina opens outside by ovipore which lies at the base of the 8th sternites, supported by vaginal sclerites and the intermediate sclerite (vide p.61). Bursal duct three to four times longer than vagina, highly convoluted forming a bundle which lies above the vagina. Bursa 0.55 mm long and opens at the base of the valvulae. Spermatheca absent.

Laccophilus sharpi Regimbart (Pl.XI, Fig.3)

C OVD 0.20, L VA 0.55, L BD 1.00-1.65

A total of 38 ovarioles are found in both the ovaries. Common oviduct about one-third the length of vagina. The position of ovipore as in L. flexuosus. Pseudospermatheca (PSPT) present and the duct between the pseudospermatheca and the bursa is 1.00 to 1.65 mm long. The duct between the pseudospermatheca and the vagina longer than the bursal duct. Bursa 0.7 mm long, longer than vagina, and opens as in L. flexuosus. The spermathecal duct much longer than bursal duct.

Hyphydrus flavicans (Regimbart) (Pl.XI, Fig.4)

C OVD 0.35, L VA 0.25, L BD 0.70

A total of 36 polytrophic ovarioles present in the ovaries. Common oviduct slightly longer than vagina; vagina with no supporting sclerites but opens outside at the base of the 8th sternites. Spermathecal duct joins at the junction of the common oviduct and the vagina by a broad duct. Bursa copulatrix S-shaped anteriorly, stout elongate and longer than vagina. Bursal duct joins the spermatheca. Spermatheca highly sclerotized and tube-like with subterminal openings; spermathecal duct one-thirds the length of the bursal duct.

Guignotus sp. (Pl.XI, Fig.5)

C OVD 0.15 L VA 0.15

Ovarioles polytrophic, length of common oviduct equal to that of vagina; vagina with no supporting sclerites as in

Hyphydrus flavicans, and opens to the exterior at the base of the 8th sternites. Spermathecal duct absent and the spermatheca directly connected to the common oviduct. Bursa copulatrix wide and opens at the end of the valvifers. Bursal ostium dorsal to the ovipore; bursal duct several times longer than vagina and probably about four times the body length, highly coiled forming a thick bundle and lies above the vagina, spermatheca highly sclerotized and conspicuous.

Herophydrus musicus (Klug) (Pl.XI, Fig.6)

C OVD 0.12, L VA 0.3, L BD 1.00

Ovaries consist of a total of 36 polytrophic ovarioles. Common oviduct between one-third to half the length of the vagina. Vagina with no supporting sclerites as in Hyphydrus flavicans, and opens at the base of 8th sternites. Bursa copulatrix highly sclerotized, hollow hemisphere with a rim, and 0.45 mm long. Position of genital openings same as in the above species. Bursal duct slender and coiled, slightly over three times the length of the vagina. Spermatheca present and covered by thin layer of muscles. Spermathecal duct short (0.1 mm long) and approximately equal in length to that of common oviduct.

Eretes sticticus (Linn) (Pl.XI, Fig.7)

C OVD 0.16 L VA 0.3

A total of 54 polytrophic ovarioles present in the ovaries. Terminal filaments of the ovarioles of each ovary come close forming an apical ligament (TL). A peritoneal sheath envelops the ovaries. The ligaments (TL) extend anteriorly through the thorax into the head probably attach to the oesophagus. Common oviduct about half the length of the vagina. Vagina opens to the exterior at the base of valvulae as vulva. Spermatheca globular with a spermathecal gland. The spermatheca joins at the junction of common oviduct and the vagina by a short (0.1 mm) duct. Separate bursa, bursal duct and double genital openings absent.

Hydaticus luczonicus Aube (Pl.XI, Fig.8)

Total of fifty ovarioles present. No appreciable variation from Eretes sticticus is noticed in the rest of the internal reproductive organs.

Cybister tripunctatus asiaticus Sharp (Pl.XI, Fig.9)

C OVD 1.00 L VA 7.5

Total of 60 polytrophic ovarioles present. Terminal filaments join and extend as in Eretes sticticus. Common oviduct one-seventh to one-eighth the length of the vagina; opening of vagina as in the above insect. Spermatheca cylindrical and bears a gland at the distal end. Spermatheca opens at the junction of common oviduct and vagina. Spermatheca and its duct about 6 mm long. At the junction of these three ducts a pair of closely adhering accessory glands (ACGL) observed (Sindhu 1961). Separate bursa, bursal duct and double genital openings absent.

Gyrinidae

The ovarioles are polytrophic as in Dytiscidae. Seventeen ovarioles per ovary are found. In _Dineutes discolor_ Aube, Robertson (1961) found 25 ovarioles per ovary. The spermathecal gland is externally indistinguishable from the spermatheca.

For a key to the abbreviations used in the text vide pp. 95-96.

Dineutes unidentatus Aube (Pl.XI, Fig.10)

C OVD 0.75 L VA 1.45

A total of 34 polytrophic ovarioles present. Common oviduct about half the length of the vagina, bent at the middle and the bend attached with a muscle strand. The bursa copulatrix and the spermatheca together slightly longer than the vagina. The anterior part of the bursa enlarged forming spermatheca and its gland.

Hydrophilidae

Species examined:

Sternolophus rufipes (Fabr.)
Hydrous indicus Bedel
H. senegalensis Perch

The ovarioles are telotrophic as characteristic of Polyphaga to which this family belongs (Imms 1963). The terminal filaments are joined with each other forming a short suspensory ligament. Anteriorly each lateral oviduct is expanded forming receptacle known as calyx (Snodgrass 1935). At the base of the calyx (CLX) long tubular glands (ACGL) are observed (Datta Gupta and Kumar 1963). Snodgrass writes that among insects the oviducts are generally simple tubes without accessory structures of any kind, though in the Acrididae the anterior end of each is prolonged into a tubular gland. A bursa copulatrix with terminal spermatheca and spermathecal gland is present as a diverticulum of the wall of the vagina (Imms 1963, p. 763). The vagina opens exteriorly by vulva (copulatory as well as ovipositing aperture). Vulva is at the end of ninth segment.

For a key to the abbreviations used in the text vide pp. 95-96.

<u>Sternolophus</u> <u>rufipes</u> (Fabr.) (Pl. XI, Fig. 11)

C OVD 0.9 L VA 0.2

Each ovary with 25 telotrophic ovarioles, terminal filament united forming a short ligament, ovarioles stalked and arranged around a short calyx. From the apex of the calyx arise about eight glands, branched slender and transparent in nature. From the base of the calyx arise four long tubular accessory glands. Common oviduct four to five times longer than the vagina. Vagina opens at the end of the ninth segment as vulva. Bursa (BC) fusiform and several times longer than vagina. Spermatheca small globular body attached to the bursa by a duct. Spermathecal gland shorter than bursa, stalked and opens at the anterior end of spermathecal duct.

Hydrous indicus Bedel (Pl. XI, Fig. 12a,b,c,d)

C OVD 1.50 L VA 1.30

Each ovary with 55 telotrophic ovarioles; arrangement of ovarioles as in Sternolophus rufipes; a few ovarioles branched (Fig. 12b; Datta Gupta and Kumar 1963), maximum oocytes observed is two. Branched structures (Fig. 12c), probably similar to the branched glands of Sternolophus rufipes, arise at the distal end of the calyx, but shorter than those of the preceding insect. Base of calyx with four long tubular accessory glands. Common oviduct and vagina almost equal in length. Vagina opens outside as vulva at the posterior end of ninth segment. Bursa (BC) about two times the length of vagina, cylindrical, anteriorly narrow. Spermatheca as in Sternolophus rufipes. Length of spermathecal gland almost equal to the bursa.

Hydrous senegalensis Perch (Pl.XI, Fig. 13)

C OVD 1.60 L VA 1.00

Each ovary consists of 60 telotrophic ovarioles; ovarioles arranged serially on either side of the calyx, calyx long; four long tubular glands (not longer than the ovary) demarcate the calyx from the lateral oviduct. Common oviduct longer than the vagina. Opening of vagina as in the other hydrophilids studied. Bursa about four times longer than the vagina, cylindrical with broad anterior end. The position of spermatheca subterminal on the bursa and opens into it by a spermathecal duct. Spermathecal gland opens into the spermathecal duct. The gland equal or slightly longer than the bursa copulatrix.

HISTOLOGY OF THE INTERNAL REPRODUCTIVE ORGANS OF FEMALES

Species examined:

Eretes sticticus (Linn) (Dytiscidae)
Dineutes unidentatus Aube (Gyrinidae)
Hydrous indicus Bedel (Hydrophilidae)

Eretes sticticus (Linn)

The ovariole is polytrophic (Pl. XII, Fig. 1). It is enveloped by an outer syncytial layer (SSH). An inner single layer of follicular epithelial cells encircle the developing eggs. The follicular epithelium (FEP) near the basal well developed egg is consisting of flattened follicular cells. At its anterior most region, the germarium consists of a large number of primordial germ cells. Posteriorly the germarium has a few nutritive cells (NRCL). The primordial germ cells (OGN) are smaller than the nutritive cells. The nucleus of nutritive cells is larger than those of the primordial germ cells and occupies a greater part of the cell leaving very little cytoplasm. The nucleus of nutritive cells is strongly basophilic. In the ovariole, groups of nutritive cells alternate with the oocyte. Each oocyte is arranged singly and its ooplasm is acedophilic. The nutritive cells are absent anterior to the well developed egg. Inter-follicular cells (IFC) are very distinct.

The lateral oviduct (Pl. XII, Fig. 2) is composed of a single layer of columnar epithelial cells. A few scattered longitudinal muscle fibres are found around the epithelial layer. The epithelial layer is lined by intima. The intima bears spines which project into the lumen. The longitudinal muscles too extend into the folds. The intima is thin and spinous.

The spermatheca (Pl. XII, Fig. 3) has an outer layer of circular muscles followed by an inner of columnar epithelium. Lining the epithelial layer is the intima. The lumen has spermatozoa (SPZ).

The spermathecal gland (Pl. XII, Fig. 4) has an outer thin layer of muscles and an inner columnar epithelial layer. The epithelium at some places is seen forming short folds. The cytoplasm of these cells is granular. Intima is present.

The vagina (Pl. XII, Fig. 5) has a thin layer of longitudinal muscles followed by a thicker layer of circular muscles. The epithelium is thrown into folds which extend into the lumen. The lumen is obliterated by these folds. The epithelial layer is lined by wavy intima.

Dineutes unidentatus

The ovariole is polytrophic as in Eretes sticticus.

The wall of the lateral oviduct is very thin and mainly consists of a single layer of cuboidal epithelium. The nuclei of each cell is round and has a distinct nucleolus. This epithelium has a basement membrane. The longitudinal muscle fibres if present are few and found scattered. They grouped together to form a compact layer. The intima strongly appears to be absent.

The common oviduct (Pl. XII, Fig. 6) has two distinct layers; the outer thin layer of circular muscle fibres and inner folded epithelial layer. The cells of the epithelial layer are columnar and have distinct nuclei. This layer is thrown into many folds which extend into the lumen.

The spermatheca is an elongated bladder-shaped structure. Separate spermathecal gland is absent. The spermatheca has an outer layer of circular muscles. The inner epithelium is drawn into short folds. The epithelial cells secrete a thick layer of intima. The posterior end of the spermatheca is drawn into a duct which is distinct only in a longitudinal section.

The bursa (Pl. XIII, Fig. 1) has an outer circular muscle layer and an inner epithelial layer. The latter gives rise to folds which completely obliterate the lumen. Intima is very thick.

Hydrous indicus

The ovariole is telotrophic. The nutritive cells are placed at the anterior end of the ovariole (Pl. XIII, Fig. 2a). Terminal filament is present. The entire ovariole is covered by two layers. The thinner syncytial sheath (SSH) is the outer one (Fig. 2b, and 2c). Beneath the layer is the cuboidal epithelial layer (EP). The developing eggs have been surrounded by follicular cells (FEP). The follicular cells are also present between the egg chambers in the ovariole. Towards the posterior end, the germarium has developing follicular cells (PFC)

A transverse section of the accessory gland (Pl. XIII, Fig. 3) of the lateral oviduct is composed of an outer thin layer of circular muscle fibre which is broken at some places. The epithelial layer is evaginated from these broken places to form small projections. This layer is made up of columnar cells. These cells have compactly arranged granules and are basophilic. The cells are seen pouring merocrine secretions (SE) into the lumen. Intimal lining is absent.

Datta Gupta and Ravindra Kumar (1963) reported the presence of intima in the lateral oviduct of Hydrophilus olivacius. The lateral oviduct has an outer scattered longitudinal muscles followed by a layer of circular muscles. The epithelium is thrown into folds which extend into the lumen.

The spermathecal gland is an elongated sac-like structure. The wall of the gland is thickened by three or four tiers of cells (Pl. XIII, Fig. 4). The lumen is lined by thin intima. The secretions are eosinophilic. The stalk of the gland has around it the circular muscles and the lumen is lined by thick intima. The epithelial cell layer is much obliterated. As a result they are indistinct. The spermatheca is a hard and round body. It is devoid of any muscular covering (Pl. XIII, Fig. 5). The outer thick layer is columnar and compactly arranged to a greater extent except for the occurrence of intercellular spaces at a few places. The lumen of the spermatheca is lined by a thick intima, and packed with spermatozoa. The spermathecal duct has an outer circular muscle layer, inner epithelial layer and intima (Pl. XIII, Fig. 6). The same three layers are present in case of bursa, but greatly pronounced. The epithelial folds are projected into the lumen and the folds are further branched, partly reducing the lumen of the bursa.

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CHAPTER VIII

ACCESSORY COPULATORY STRUCTURES

In this chapter sexual dimorphic structures of the males, which are used in holding the female during coitus are studied.

In Dytiscidae the cupules are restricted to the basal three tarsomeres; in Dineutes indicus they are present on all the five tarsomeres of the foretarsi, and in hydrophilids they are present on the basal three tarsomeres. For convenience of description the cupules are divided into two types viz. microcupules and macrocupules. In the former, the adhesive disc of the cupule is equal or longer than the stalk, while in the later it is shorter. Each cupule has a tubular stalk and a terminal disc-like expansion. According to Lowne (1871), the expanded part of the tarsus in Dytiscus is hollow and contains a large sac, and the bases of the cupules open into this sac (Miall 1912). These cupules pour out glutinous secretion when applied to the smooth surface. It has been proved beyond doubt that these cupules assist the male in firmly holding the female during copulation (Lowne 1871, Blunck 1912, Imms 1963, Borror and DeLong 1964). I have found to my satisfaction that all the species selected at random (the species of Laccophilus, Hyphydrus flavicans, Herophydrus musicus, Eretes sticticus, Hydaticus luczonicus, Dineutes unidentatus and Berosus species) left glutinous secretion on the micro slides wherever it is touched by the cupules. This adhesive nature of these cupules and the restriction of the cupules mostly to the males is taken to be sufficient to include a study of these structures in the present work under the chapter 'accessory copulatory structures'.

The disc-like expansion of the cupules is an elastic transparent structure stiffened by radiating ribs, which in many ditiscids are observed projecting beyond the edge. The cupules are located on the ventral surface of the tarsomeres.

With regards the description of the tarsomeres, the surface orientation of Snodgrass (1935) is followed.

Dytiscidae

Species examined:

Canthydrus laetabilis Walk.

Laccophilus flexuosus Aube
L. sharpi Regimbart

Hydrovatus acuminatus Motschulsky
Hyphydrus flavicans (Regimbart)
Guignotus sp.
Herophydrus musicus (Klug)
Copelatus sp.
Eretes sticticus (Linn)
Hydaticus luczonicus Aube
Cybister tripunctatus asiaticus Sharp

In most males of dytiscids the basal three tarsomeres of the pro and mesotarsus, are either incrassate or widened forming a flattened platform (tarsal pad) from where the cupules arise. The tarsal pad may be circular or oval or elongate. The pads are generally fringed with stiff pointed setae on the proximal, anterior and posterior margins of the pad while the distal margin is usually devoid of such setae.

Canthydrus laetabilis Walk.

Tarsus with no adhesive pads, and no cupules; not different from female.

Laccophilus sharpi Regimbart

Protarsus: (Pl. XIV, Fig. 1)

Tarsus arcuate (sickle-shaped), five segmented, thinner towards distal end. Proximal three tarsomeres incressate and the ventral surface with indistinctly flattened transverse zones; on each zone a transverse row of microcupules present. The basal tarsomere with two transverse rows of cupules, each row containing four cupules; the second and the third tarsomeres each with only one transverse row of four distally placed cupules. Cupules directed distad and each bears an oval disc. The base of the stalk fits into a socket. Setae in the vicinity of the cupules thin. The dorsal surface medially possesses a row of long hair-like setae.

Mesotarsus:

The arrangement and the number of cupules remains same as in that of male protarsus.

Laccophilus flexuosus Aube

Protarsus: (Pl. XIV, Fig. 2)

Tarsus arcuate with five distinct segments; basal three segments incrassate and bear a large number of clearly visible globular sacs inside. Tarsus bears four transverse rows of cupules; two rows on the first tarsomere, and one on each of the second and the third tarsomeres. The first row differs from that of L. sharpi in having five microcupules. A row of medially placed long hair-like setae present on the dorsal surface.

Mesotarsus:

Same as above.

Hydrovatus acuminatus Motschulsky

Protarsus: (Pl. XIV, Fig. 3)

Tarsus five segmented, basal three tarsomeres widened, ventral surface flat and bears scattered cupules; first tarsomere with four to five microcupules; second and third tarsomeres with two or more microcupules each. A few tube-like adhesive structures, probably tenent hairs (Packard 1912) also present. Second and third tarsomeres consists of about four and eight tenent hairs respectively. A few marginal setae located on either side of the first three tarsomeres. Third tarsomere deeply bifid at the distal end and conceals the shorter fourth tarsomere. The dorsal surface of the enlarged tarsus bears a row of longitudinally arranged hair-like setae. At the mid-length, the fifth tarsomere bears an anteriorly directed distinct spine-like seta. The females lack such seta.

Mesotarsus:

Mesotarsus five segmented, basal three tarsomeres widened and bear adhesive structures ventrally.

like setae on the dorsal surface. Fourth tarsomere shorter than any one of the tarsomeres and concealed by the distal lobes of the third tarsomere. Last tarsomere with no anteriorly directed ventral seta.

Mesotarsus:

As in the protarsus.

Herophydrus musicus

Protarsus: (Pl. XIV, Fig. 6)

Tarsus consists of four tarsomeres; basal three tarsomeres flattened ventrally and bear a number of compactly set microcupules; first tarsomere bears the microcupules all along the ventral surface while the second and the third bear them only at the anterior half; middle tarsomere of the tarsal pad smaller than the other two; third tarsomere deeply bifid. The dorsal surface of all these tarsomeres bears a median longitudinal row of hair-like setae. Terminal tarsomere shorter than the preceding tarsomere, and bears a single subterminal anteriorly directed seta which is absent in female. The ungues sharply pointed at the tip unlike those in females where they are blunt.

Mesotarsus:

As in protarsus.

Copelatus

Protarsus: (Pl. XIV, Fig. 7)

Tarsus five segmented; first three tarsomeres expanded forming an elongated tarsal pad. The dorsal surface of this pad convex while the ventral surface more or less flattened. Posterior margin of the tarsal pad with thicker growth of hair-like setae than on the anterior. The first tarsomere with two rows of microcupules, each row bearing four microcupules, one row at the disto-ventral margin while the other a little proximal to the latter. The second and the third tarsomeres with a single row of four disto-ventrally placed microcupules. Protarsus consists of a total number of sixteen cupules.

Mesotarsus:

As in protarsus.

Eretes sticticus

Protarsus: (Pl. XIV, Fig. 8)

Protarsus five segmented; basal three greatly flattened forming a circular tarsal disc containing many cupules on its ventral surface. Basal tarsomere contains two macrocupules and three patches of microcupules; each patch consists of about four microcupules; one patch lies at the anterior and the other at the posterior margin, the third patch lies on the median line. The second and the third tarsomeres each with approximately 120 microcupules. Anterior and posterior margins of the tarsomeres of the pad are of identical length. Around the entire margin of the tarsal pad a row of slightly curved spine-like setae present.

Mesotarsus:

Five segmented and devoid of tarsal pad and cupules.

Hydaticus luczonicus

Protarsus: (Pl. XIV, Fig. 9)

Tarsus five-segmented; basal three tarsomeres greatly flattened and plate-like together forming a circular pad bearing cupules and setae. The anterior and the posterior margins of the tarsomeres of the pad with unequal length. The anterior, the posterior and the proximal margins of the tarsal pad bear single row of setae. These setae are closely set on the proximal and the posterior margins of the first tarsomere while the remaining marginal setae of the pad somewhat dehiscently placed, some of these setae stout. Ventrally the first tarsomere bears nine submarginal cupules, two of the proximal cupules larger than the rest. The second and the third tarsomeres bear seven and six microcupules respectively. The cupules from the first tarsomere to the third tend to be gradually smaller in size. Tarsal pad mostly with macrocupules except for a few distally placed microcupules; four of the cupules on the median axis of the basal tarsomere much larger than any of the rest. Dorsally the first tarsomere bears two rows of black minute spine-like setae. An oblique row of minute spines extend on the dorsal surface of the second and the third tarsomeres. Tarsal pad with no hair-like setae on the dorsal surface.

row formed of eighteen cupules; basal half of this tarsomere with a triangular patch of closely arranged spine-like setae; second tarsomere bears a single row of twenty cupules; third tarsomere consists of a row of eighteen cupules.

Mesotarsus:

Tarsus five segmented and devoid of tarsal pad or cupules.

Gyrinidae

Species examined:

Dineutes unidentatus

Unlike in dytiscids all the five tarsomeres of the protarsus of the male widened forming an elongated tarsal pad, which is fringed with cupules. Such a tarsal pad is present in _Gyrinus_ (Miall 1912), also in _Andogyrus_ (Bachmann (1959 and 1966). The forelegs are prehensile in both male and female and are suitable for their predatory habit. Miall writes that in male the 'suckers' of the tarsal pad are believed to be of use to grasp the female. Unlike in dytiscids the second paid of legs are greatly flattened for swimming and bear no accessory copulatory structures (Miall 1912).

Dineutes unidentatus

Protarsus: (Pl. XIV, Fig. 12)

Protarsus five segmented; all the segments widened (while they are normal in female) forming a tarsal pad; tarsal pad elongate first four tarsomeres wider than long; all the tarsomeres fringed with numerous compactly set microcupules.

Mesotarsus:

Flattened and oar-like; no accessory copulatory structures.

Hydrophilidae

Species examined:

- *Coelostoma stultum* Walk
- *Paracymus evanescens* (Sharp)
- *Enochrus* sp.
- *Sternolophus rufipes* (Fabricius)
- *Hydrous indicus* Bedel
- *Hydrous senegalensis* Perch
- *Berosus indicus* Motschulsky
- *B. pulchellus* M'Leay
- *B.* nr. *nigriceps* (Fabr.)

Both protarsus and mesotarsus are examined for the accessory copulatory structures. The examination revealed that such accessory structures are not common to all hydrophilids and when present they are restricted only to the protarsus. However, some sexual dimorphic structures which appear to be the accessory copulatory organs are present in a few of the hydrophilids (ex. *Paracymus evanescens* and *Hydrous indicus*) and hence they are also described. About all other types of sexual dimorphic structures on the tarsus which apparently do not aid in coupling the sexes are just indicated only to tell that they do not conform to the title of this chapter. The accessory copulatory structures are distinct in *Berosus* species.

Hydrous indicus Bedel

Protarsus: (Pl. XV, Fig. 2)

Tarsus five segmented; sexual dimorphic structures present. Tarsus of female of uniform breadth throughout while that of male gradually increases distad; disto-ventral surface of the fifth tarsomere bears a patch of stout short blunt and black spine-like setae. Cupules absent.

Mesotarsus:

No sexual dimorphism.

Hydrous senegalensis Perch

Protarsus: (Pl. XV, Fig. 3)

Tarsus five segmented as in the female; last tarsomere somewhat wider than that of female. Cupules absent.

Mesotarsus:

Sexual dimorphism absent.

Berosus indicus Motschulsky

Protarsus: (Pl. XV, Fig. 4)

Tarsus bears four apparent segments; first and second tarsomeres fused (In female the protarsus consists of five distinct segments, the first four tarsomeres bear on their ventral surface two rows of spine-like setae). The basal two tarsomeres bear a number of compactly arranged micro-cupules on their disto-ventral surface. On the first tarsomere they extend more than half of its length; last tarsomere longer than any one of the other segments.

Mesotarsus:

No such structures observed.

Berosus pulchellus M'Leay

Protarsus: (Pl. XV, Fig. 5)

The number of tarsomeres and their arrangement as in B. indicus. But the cupules arise anteriorly in less than half the length of the tarsomere. On either side of the patch of cupules spine-like setae present.

Mesotarsus:

No dimorphism noticed.

Berosus nr. nigriceps (Fabr.)

Protarsus: (Pl. XV, Fig. 6)

Tarsus with four tarsomeres; position and arrangement of cupules as in B. pulchellus; spine-like setae present on either side of the patch of cupules.

Mesotarsus:

No sexual dimorphism noticed.

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CHAPTER IX

DISCUSSION

ABDOMINAL SEGMENTS

Dytiscidae

The reports on the number of abdominal segments from Dytiscidae show certain differences. Tanner (1927) observed ten abdominal segments in the female Laccophilus macularus (Germ). In Dytiscus marginalis, Demandt (1912) and Korschelt (1923-'24) label the last visible and undivided sternum as the 8th. Grasse (1965) incorporated this figure without alteration.

However, my studies on more than a dozen species of adult dytiscids have revealed a total of only nine segments in the abdomen. I have, in all these beetles, found the last nonretractable sternum to be the 7th sternum in contrast to the observations made by Demandt and Korschelt. The 8th sternum is divided into a pair of sternites.

Peytoureau (1894) (as adopted from Newell 1918) observed nine abdominal somites in Dytiscus. According to Peterson (1953), only nine abdominal segments have been observed in the larval stages of most species of Dytiscidae and further, the ninth segment is usually greatly reduced in size.

Balfour-Browne (1932) labels the last of the non-retractable sterna of Dytiscus as the 7th and the divided sternites as the 8th. My observations are in agreement with his with regard to the assignment of numbers to the sterna. However, Balfour-Browne (1932) illustrates a very conspicuous first sternum of the abdomen, although, in the text, he clearly mentions the first segment as absent or very much reduced. This segment is actually absent in Coleoptera or if present is vestigial (Jordan 1943, Imms 1963).

Seemingly, there is some confusion as to the presence of connation in the anterior sterna of the abdomen of certain dytiscids. In the male of _Hyphydrus_ _flavicans_, Vazirani (1968) reports the 2nd abdominal 'sternite' as having a small spine directed backward. But, I have found the spine on the 4th sternum. It is probable that Vazirani thought it to be the 2nd for the reason that the visible 2nd and the third sterna (i.e. true 3rd and the 4th sterna) are fused with each other completely obliterating the suture between them.

Gyrinidae

In present observations on _Dineutes_ _unidentatus_, it is seen that the first visible sternum is actually the composite sclerite formed owing to the fusion of the 2nd and the 3rd sterna. This composite sternum is larger than the succeeding sterna. The suture between these sterna is greatly obliterated. Similarly, the larger first visible sternal plate of _Dineutes_ _americanus_ (Say) (Borror and DeLong 1964) and _Gyrinus_ sp. (Grasse 1965) seem to be a composite sclerite of 2nd and 3rd sterna with the intermediate suture absent. The last non-retractable sternum is the 8th sternum and is somewhat triangular (Tanner 1927, Grasse 1965, Borror and DeLong 1964, Bachmann 1959 and 1960).

9th sternum is supposed to be the basal piece of Byrrhoid or Trilobate type, the lateral lobes and the median lobe should be firmly articulated (Sharp and Muir 1912) to the preceding sclerite (i.e. 9th sternum) as in Byrrhoid type of aedeagus of Hydrophilidae.

Thus, the sclerite which lies anterior to the aedeagus, and ventral to the membranous IX tergal region, should truly represent the 9th sternum. It has been ascertained in the present work, that the so-called basal piece of gyrinids (Sharp and Muir 1912) truly represents the 9th sternum and, therefore, I am disinclined to agree with Sharp and Muir in considering this sclerite as the basal piece.

Hydrophilidae

There is difference in the number of externally visible or non-retractable abdominal sterna in Hydrophilidae.

Newport (as quoted by Packard 1903) illustrated only five non-retractable sterna in the abdomen of _Hydrous piceus_. Pu (1938) states the abdomen of _Hydrous acuminatus_ as consisting of five visible sterna.

My observations on _Hydrous indicus_, _H. senegalensis_ and further, on five species belonging to three genera of Hydrophilidae, have revealed the existence of six visible and non-retractable sterna in the abdomen. However, the first visible sternum (i.e. 2nd sternum) is so small and fused that it can easily escape the attention if not carefully looked at. It is probable that a careful re-examination of _H. piceus_ and

H. acuminatus taking into consideration the corresponding terga, would prove fruitful.

Borror and DeLong (1964, p. 281) distinctly featured six abdominal sterna in Hydrophilus triangularis (Say). In his figure the first visible sternum (i.e. the true 2nd) is apparently as large as the 2nd visible (i.e. the true 3rd) sternum. But, none of the beetles examined here show such a large 2nd sternum. However, the presence of 2nd sternum is by no means a common feature of Hydrophilidae. In Coelostoma stultum and Enochrus sp. the 2nd sternum is totally absent.

There is lack of consistency with regard to the total number of abdominal segments. Peytoureau (1894) reported only eight abdominal segments from Hydrophilus sp. Packard (1903, p. 181) and Newell (1918) observed ten abdominal segments in Hydrophilus piceus and H. triangularis respectively. Tanner (1927) has featured ten segments in the female of Hydrophilus triangularis.

My observations have revealed the existence of only nine abdominal segments in either sex among the hydrophilids, and agree with those of Pu (1938) and Wood (1952) on Hydrous acuminatus and Hydrous trangularis respectively.

The IX tergum in either sexes of the hydrophilids studied here is transversely divided giving rise to a single paraproct in males, and a pair of paraprocts in females. In males the paraproct is located anterior to the IX tergum, while in females it is divided and each one comes to lie on either side of the IX tergum and extend without fail ventrally to the base of the valvulae.

Origin and evolution of paraprocts with reference to Hydrophilids

The paraprocts lie on either side of the anus. Snodgrass (1935) generalises them as a pair of lobes of the XI tergum, and in position ventrolateral to the anus of insects.

Crampton (1925) has suggested that the paraprocts of the beetles may be a part of the IX tergum (Tanner 1927). Even after an extensive study of the female genitalia, Tanner (1927) could not definitely establish the relationship of the paraprocts to the IX tergum. Tanner, however, suspects them to be a part of the IX tergum.

In the present study variations in ninth segment of hydrophilids show successive stages in the formation of the paraprocts from the IX tergum. The paraproct has come into existence as a result of the division of the IX tergum.

In Sternolophus rufipes (Pl. XV, Fig. 7) a narrow desclerotized zone extends from the lateral margins of the IX tergum towards the middle, where the desclerotization is incomplete, thereby preventing the anterior end of IX tergum from separation. In Hydrous senegalensis (Pl. XV, Fig. 8) the IX tergum is very much desclerotized, completely cutting off an anterior ribbon-shaped sclerite.

The ribbon-shaped anterior sclerite of the IX tergum extends ventrad on either side of the 9th sternum as in Hydrous indicus. It further extends ventrally (Sternolophus rufipes Pl. XV, Fig. 9) to meet the lateral margins of the anterior part of the 9th sternite forming a perfect but undivided paraproct.

The females have well developed paraprocts than the males and are homologous to the paraprocts of males. In females the paraproct is completely divided and each one lies on either side of the IX tergum (Pl. XV, Figs. 10 and 12). On the ventral surface, the ends of each paraproct come close to each other and enlarged into a broad triangular plate as in *Sternolophus rufipes* (Pl. XV, Fig. 11) or elongated (Pl. XV, Fig.13) forming a longitudinal strip as in *Hydrous senegalensis* and *H. indicus*.

The 9th sternum is undivided in males. In females it is either partially divided (*Coelostoma stultum*) or completely divided as in most other hydrophilids to form the female genitalia.

AEDEAGUS

Dytiscidae

The aedeagus of dytiscids belongs to the articulate type (type articule of Jeannel and Paulian 1944 or adephagid type of Sharp and Muir 1912). There are a large number of illustrations of the aedeagus of the aquatic beetles. A description of every new species, almost always, is accompanied by an illustration of its aedeagus. It is apparent from the literature that for such studies the aedeagus is generally taken either from a dried specimen or from long preserved specimen, and consequently they fail to give details of the thin basal piece and the soft parts associated with the aedeagus of certain dytiscids.

My studies on the male genitalia of fresh specimens have revealed the presence of aedeagal sacs (vide p. 44 to 48) whose functional significance is perhaps not known. Their association with the aedeagus clearly indicates their role in copulation.

Table III : Inter-relationship between the aedeagus of *Eretes sticticus*, *Hydaticus luczonicus* and *Cybister tripunctatus asiaticus*

Eretes sticticus	*Hydaticus luczonicus*	*Cybister tripunctatus asiaticus*
No torsion	Torsion about 45°	Torsion 90°
Basal piece reduced and rod-like flattened anteriorly and forked posteriorly	Basal piece reduced and rod-like, flattened at both ends	Basal piece reduced and rod-like
Lateral lobes connected by a large dorsal sac	As in *Eretes*	Lateral lobes not connected by a large dorsal sac
Lateral lobes with prominent stout spine-like setae on the outer surface and not uniform	Lateral lobes with uniform spine-like setae	Lateral lobe with long setae at the posterior end
Median lobe J-shaped	Median lobe J-shaped and laterally compressed	Median lobe sabre-shaped
Median lobe with two free sacs	Sacs largely attached to the median lobe	Median lobe with a single sac on its dorsal surface. The sac folded and has two posterior arms
Gonopore subterminal but lies near the distal end	As in *Eretes*	Gonopore lies hidden dorsally between median lobe and its sac

There are three sacs in Eretes sticticus and Hydaticus luczonicus (Table III). Two of these sacs are small and associated with the median lobe and are called ventral sacs while the remaining one (the dorsal sac) is larger and connects the lateral lobes. The ventral sacs in Eretes are free from the median lobe while in Hydaticus they are largely attached to the median lobe. In Cybister tripunctatus asiaticus only the dorsal sac is present.

It is apparent from the above table that the aedeagus of Eretes and Hydaticus are more closely related to each other than to Cybister.

Torsion:

Torsion has been observed among Coleoptera and in most Adephaga, and there may be a difference of 90° (Lindroth and Palmen 1956). Torsion is observed in seven of the eleven species of Dytiscidae studied here.

Heberdey (1928) noted that even in the 'younges imagines' of Hydroporus ferrugineus Steph. (Dytiscidae) the genitalia were asymmetrical and the ductus ejaculatorius winding, while in pupa the genitalia were symmetrical and the ductus ejaculatorius straight.

Hydrovatus acuminatus, Hyphydrus flavicans and Herophydrus musicus exhibit no torsion of the aedeagus. Though to a large extent torsion is absent in Eretes sticticus the median lobe is slightly inclined rightward. In Hydaticus luczonicus the aedeagus is inclined at 45° in the clockwise direction when viewed from behind. In *Canthydrus laetabilis* *Laccophilus* species, *Guignotus* sp. and *Cybister tripunctatus* torsion is 90°.

Table IV : Information on the symmetry, torsion and basal piece of the aedeagus of the dytiscids studied

Species	Symmetry	Torsion	Reduced basal piece
Canthydrus laetabilis	Asymmetrical	90°	Absent
Laccophilus	Asymmetrical	90°	Absent
Hydrovatus acuminatus	Symmetrical	Absent	Present
Hyphydrus flavicans	Symmetrical	Absent	Absent
Guignotus sp.	Symmetrical	90°	Present
Herophydrus musicus	Symmetrical	Absent	Absent
Copelatus	Symmetrical	90°	Doubtful
Eretes sticticus	Symmetrical	Absent	Present
Hydaticus luczonicus	Symmetrical	45°	Present
Cybister tripunctatus	Symmetrical	90°	Present

A basal piece is either absent or greatly reduced. Among those in which it is absent are *Canthydrus laetabilis*, both the species of *Laccophilus*, *Hyphydrus flavicans*, and *Herophydrus musicus*. A simple sclerotized rod-like remenant of basal piece is observed in *Hydrovatus acuminatus* and *Guignotus* sp.

A reduced basal piece is present in *Rhantus flavogriscens* Cr. (Wood 1952) and *Ilybius aedescens* (Sharp and

Muir 1912). A re-examination of Copelatus sp. might reveal the existence of reduced basal piece. My study on this insect is based on a single specimen. The basal piece among these beetles belonging to Colymbetinae is akin to that of Dytiscinae, in that it is slightly widened at the posterior extremity. In Hydaticus luczonicus the basal piece is widened posteriorly while in Eretes sticticus and Cybister tripunctatus it is forked.

Gonopore:

The position of gonopore is not constant among the species and can be of taxonomic value.

Gyrinidae

The aedeagus of Dineutes belongs to the 'articulate type'. The lateral lobes conjointly articulate to the dorsal surface of the proximal tip of the median lobe (vide p. 48).

Hydrophilidae

In all the hydrophilids the aedeagus is symmetrical. The aedeagus is trilobate. Sharp and Muir (1912), Jeannel and Paulian (1944) and Lindroth and Palmen (1956) considered this type of aedeagus as the primitive.

The basal piece among the hydrophilids, except in Coelostoma stultum, is beyond the anterior end of the median lobe and compared to that other hydrophilids is large. In Coelostoma stultum the basal piece is comparatively small and lies below the anterior portion of the median lobe and the lateral lobes.

In Eretes, Hydaticus and Dytiscus marginalis (Balfour-Browne 1932), the dorso-ventral position of the accessory glands is due to torsion of the aedeagus. As a result of torsion, the beetles having short ejaculatory duct have their accessory glands twisted and in the process keep them one above the other.

Laccophilus, Guignotus and Cybister have long ejaculatory ducts and thick accessory glands. Among these beetles the torsion of aedeagus could only bring a loop-like bend of the ejaculatory duct and, further, no change is noticed from the lateral position of the accessory glands.

Lateral ejaculatory duct:

The occurrence of two completely separated ejaculatory ducts is reported by Bordas (1899) in certain longicorn beetles. Later on similar reports are made by Sharp and Muir (1912), and Williams (1945). Sharp and Muir explain that such a feature can be of secondary origin. Metcalfe (1932) based on the developmental studies of insects describes the ejaculatory duct as unpaired in origin.

Snodgrass (1935) while describing the male organs of insects in general, contends that "though the ejaculatory duct is always described as unpaired in its embryonic origin, its anterior end is frequently forked, especially when the accessory glands arise from it".

In Dytiscus marginalis the tube a little below where the vas deferens unites has been considered to be the accessory gland by Balfour-Browne (1932). In Cybister tripunctatus asiaticus, Sidhu (1960b) labels that part of the tube as the genital duct.

I believe in the term, lateral ejaculatory duct, expressed by Bordas, Sharp and Muir for the following reasons

(a) that it serves in ejecting the spermatozoa mixed with the secretions of the accessory glands

(b) it is known in general that the vasa deferentia join at the anterior end of the ejaculatory duct and the accessory glands arise from the anterior end of the ejaculatory duct or from short divergent anterior branches of the duct (Snodgrass 1935).

However, histological studies of this lateral ejaculatory duct of Eretes sticticus and Dineutes unidentatus revealed that the epithelial cells are equally glandular as those of the accessory glands. Hence, this is actually the forked part of the ejaculatory duct, but lined with glandular epithelial cells of the type observed in accessory glands.

The lateral ejaculatory ducts are absent among the hydrophilids which have more than one pair of accessory glands arising from the anterior end of the ejaculatory duct. The lateral ejaculatory ducts are short among dytiscids and very long in Dineutes unidentatus (Gyrinidae). In these two families each accessory gland opens at the anterior end of the corresponding lateral ejaculatory duct.

Ectodermal and Mesodermal origin:

The mesodermal origin of ovaries and the testes and the ectodermal origin of the vagina and the ejaculatory duct is universally agreed upon. However, there is considerable difference in insects as to the origin of the remaining parts of the internal reproductive organs (Metcalfe 1932).

Escherisch's classification of the accessory glands, viz. that one pair of glands is mesodermal origin (the mesadenia) and the other of ectodermal origin (the ectadenia), is generally accepted.

In spite of some differing opinions of some authors (vide p. 14), the Escherich's classification of accessory glands is still followed, very much with regard to Coleoptera (Demandt 1912, Imms 1963, Khurana 1964).

Apparently accessory glands in the dytiscids and Dineutes unidentatus are ectadenia. In the hydrophilids there are two pairs of glands - the opaque, and the transparent glands. The opaque glands are ectadenia while the transparent glands are mesadenia.

The following table shows the ectodermal and the mesodermal nature of the various parts of the male internal reproductive system, based on the presence or absence of intima among the three representatives of the families.

Table V : Ectodermal and mesodermal nature of the male reproductive organs of Eretes, Dineutes and Hydrophilus

	Eretes	Dineutes	Hydrophilus
Accessory gland	Ectadenia	Ectadenia	One pair ectadenia and the other pair mesadenia
Vas deferens	Mesodermal	Mesodermal	Mesodermal except the seminal vesicle. Seminal vesicle ectodermal

Balfour-Browne (1932) described the two accessory glands in the males of Dytiscus marginalis as vescular seminales. Sidhu (1961) examined the microtomy sections of this gland in Cybister and found no spermatozoa. Spermatozoa are obviously absent in the accessory glands of Eretes sticticus and in fact these accessory glands do not serve the function of seminal vesicles.

Bordas (1900) observed two types of testes in Coleoptera. Tubular type of testis is found in Dytiscidae, Gyrinidae while the complex testis (with many follicles) is found in Hydrophilidae.

The testis in some dytiscids is confluent with the epididymis while in Dytiscinae the two are widely separated by an uncoiled part of the vas deferens. Thus there is considerable variation in the male reproductive organs within the family Dytiscidae.

In both the species of Hydrous the follicular testis is mulbary fruit shaped. Similar structure has been observed by Escherich in Hydrophilus piceus. Unlike in Hydrous the follicular testis in Sternolophus is Chrysanthymum flower shaped (Pl. VIII, Fig. 12).

The mesadenia in Hydrous senegalensis are branched and such a condition is observed by Escherich in Hydrophilus piceus. In Hydrous indicus and Sternolophus rufipes they are unbranched.

Except for the above there is no significant difference in the general structure of the male reproductive system compared to Hydrophilus piceus.

INTERNAL FEMALE-REPRODUCTIVE ORGANS

Ovarioles:

Observations regarding the number of ovarioles in Canthydrus laetabilis agree closely with that of Noterus crassicornis Müll. reported by Stein (1847).

In Laccophilinae, the number of ovarioles ranges between 18 and 21 per ovary and perhaps the first report from Laccophilinae.

In Hydroporinae 18 ovarioles are observed in each ovary. Stein (1847) observed 14-16 ovarioles in Hydroporus palustris L., (Hydroporini) and Hyphydrus ovatus (Hyphydrini).

Among the Dytiscinae studied here, the number of ovarioles ranges from 25 to 30. Stein (1847) and Henneguy (1904) reported 30 to 40 ovarioles in Acilius sulcatus L., and 30 ovarioles in Dytiscus marginalis respectively.

Ultimately the number of ovarioles in an ovary of the family Dytiscidae falls within the range given by Robertson (1961) and the range given by Robertson is 6-40 (Noteridae - Dytiscidae). But, the average number of ovarioles came down to 21 as against the 25 given by Robertson.

In Hydrophilidae the maximum number of ovarioles recorded by Robertson (1961) is twenty in Hydrophilus obtusatus Say. Datta Gupta and Kumar (1963) observed fifty-four ovarioles in Hydrophilus olivaceus Fabr. In the present study the maximum number of ovarioles has reached to sixty per ovary in Hydrous senegalensis.

The arrangement of the ovarioles in Hydrous indicus and H. senegalensis strikingly differs from each other. In Hydrous indicus the receptacle (calyx) is a hollow coniform and stout structure around which the ovarioles open. In H. senegalensis the ovarioles open serially on either side of the calyx with the result the calyx is greatly elongated. Incidentally the ovary reminds us the condition in grasshoppers (Snodgrass 1935) to some extent.

Snodgrass (1935) points out that the number of sperm tubes in a testis is generally less than the number of egg-tubes in the ovary. In all the hydrophilids studied here they outnumber the ovarioles.

Spermatheca:

In Dytiscidae the spermatheca may be absent or present.

A 'funnel-shaped median organ' is described by Feng (1936) from the female genitalia of Bidessus licenti and B. trasserti Feng. In a closely related genus i.e. Guignotus, the spermathecal capsule attached anteriorly to the dorsal surface of the vagina is somewhat similar to the 'funnel-shaped organ'. It is likely that this is the spermathecal capsule. Two distinct varieties of spermatheca are observed.

(a) Highly chitinized and not covered by distinct muscular layer (ex. Subfamily Hydroporinae).

(b) Chitinized and covered by distinct muscular layer (ex. Dytiscinae).

While the spermatheca and the spermathecal gland is distinct in Dytiscinae, they are indistinct from the bursa copulatrix in Dineutes unidentatus (Gyrinidae).

Bursa Copulatrix:

In the Dytisci-di-orificia, the bursa copulatrix opens directly to the exterior by bursal ostium, while in mono-orificia the bursa is not distinct from vagina. The bursa copulatrix in Herophydrus musicus differs from the rest of the 'Dytisci-di-orificia by its entirely sclerotized hemispherical nature.

The female reproductive organs of Dineutes unidentatus differ from that of Dytiscinae in that the bursa is a diverticulum, in the former.

Accessory Glands:

Long branched tubular structures, which are probably the accessory glands are seen attached to the anterior end of the calyx (Pl. XI, Figs. 11-12e). As far as I am aware this is the only case of such glands joining the anterior end of the calyx. However, in acridids the anterior end of the calyx is drawn into a single tubular gland (Snodgrass 1935).

In Hydrous indicus similarly branched but short tubular structures are present but their true nature is not known.

Variations in the female reproductive organs of Hydrous and Hydrophilus:

The female reproductive organs of Hydrophilus olivaceus are described by Datta Gupta and Kumar (1963) and Khurana (1964). Though Hydrous and Hydrophilus are closely related genera the female internal reproductive organs of these two beetles show much difference in the structure.

Table VI : Variations in the female internal reproductive organs of Hydrophilus olivaceus and Hydrous indicus

Hydrophilus olivaceus	Hydrous indicus
--------	Long tubular branched structures at the anterior end of the calyx
Lateral oviduct with five accessory glands (Datta Gupta and Kumar 1963, Khurana 1964)	Lateral oviduct with four accessory glands
One gland associated with common oviduct (Datta Gupta and Kumar)	No such gland
'Bursal sac' absent (Khurana 1964)	A prominent bursa copulatrix present
Spermathecal gland absent (Khurana 1964)	Spermatheca and spermathecal gland present

Snodgrass (1935) points out that "the oviducts are generally simple tubes without accessory structures of any kind, though in Acrididae the anterior end of each prolonged into a tubular gland". However, the occurrence of accessory structures on the lateral oviducts, seem to be a general feature in Hydrophilidae. All the three species of Hydrophilidae examined have revealed the existence of long tubular glands at the anterior end of the lateral oviduct. Similar structures have been reported by Datta Gupta and Kumar (1963) in Hydrophilus olivaceus.

In Hydrophilus olivaceus the number of accessory glands is give (Datta Gupta and Kumar 1963, Khurana 1964). In Sternolophus rufipes, Khurana (1964) observed five accessory glands. My observations on Sternolophus rufipes, Hydrous indicus and H. senegalensis have revealed only four accessory glands.

Histological studies disclosed that they produce merocrine secretions (Pl. XII, Fig. 3). The secretion of these glands is white, viscous sticky, and very likely used by the beetle in spinning the silky cocoon during oviposition. Most species spin some sort of cocoon by the silk secreted from the silk glands (Miall 1912, Imms 1963, Miller 1963).

Datta Gupta and Kumar (1963) observed a gland associated with the common oviduct in Hydrophilus olivaceus but made no mention of the spermatheca. In the same beetle, Khurana (1964) observed a spermatheca but failed to point out the accessory gland that was observed by Datta Gupta and Kumar.

While Datta Gupta and Kumar made no mention of the bursa, Khurana points it to be absent.

In *Sternolophus rufipes* according to Khurana (1964) (a) 'the five accessory glands of either side open into a common short tubular gland before joining the lateral oviduct; (b) the common oviduct is very short; (c) spermatheca is long narrow and approximately of uniform diameter throughout its length; (d) the spermathecal gland and the bursal sac are absent'.

A re-examination of this beetle revealed important differences in the structure of the reproductive organs. The accessory glands of the oviduct open individually into the lateral oviducts; common oviduct as long as the lateral oviduct; spermatheca globular; spermathecal glands and bursal sacs very distinct.

The following table shows the ectodermal or mesodermal nature of the various parts of the internal reproductive system, based on the presence or absence of intima among the three representatives of the families.

Table VII : Ectodermal and mesodermal nature of the female reproductive organs of *Eretes*, *Dineutes* and *Hydrophilus*

	Eretes	*Dineutes*	*Hydrophilus*
Lateral oviduct	Ectodermal	Mesodermal	Ectodermal (Datta Gupta and Kumar 1963)
Median oviduct	Ectodermal	Mesodermal	Ectodermal
Spermathecal gland	Ectodermal	Ectodermal	Ectodermal
Accessory glands of lateral oviducts	---	---	Mesodermal

FEMALE GENITALIA

The occurrence of two external genital openings is a very rare phenomenon amongst Coleoptera. Double genital openings have been described only in Hydroporus ferrugineus Steph. (Heberdey 1931) and in Agabus and Ilybius (Jackson 1960) of Dytiscidae among coleopterans.

My observations for the first time have revealed two genital openings in the subfamilies Noterinae and Laccophilinae; and for the second time in Hydroporinae. The first report being that of Heberdey (1931) in Hydroporinae.

Terminology of certain female structures:

Snodgrass (1935) labelled the external opening of bursa (i.e. the copulatory opening) as vulva. The term vulva, here, is not an apt term as it has been used in insects having a single external genital opening. Hence, I followed the terminology used by Eidmann (1929-'31). The same terminology is however used by Klots (1956), Wigglesworth (1965), Jackson (1960) and Davey (1965). All these workers correctly called the copulatory opening as the bursal ostium and the vaginal opening through which the eggs are laid as the ovipore.

As a result of the discovery of double genital openings and the absence of vulva in certain dytiscids the old term i.e. the 'vulvar sclerite' (Boving 1913) or 'vulval sclerite' (Guignot 1933, Balfour-Browne 1950, Jackson 1960) need to be changed. Boving (1913) and Jackson (1960) studied this sclerite in Ilybius in which it is now (Jackson 1960) found that there is no vulva. In such a situation the name vulvar sclerite or vulval sclerite has no meaning and its retention would only mislead the morphologists to think the presence of vulva.

In the species of <u>Laccophilus</u> I have observed sclerites homologous to the vulval sclerites of <u>Agabus</u> and <u>Ilybius</u> (Jackson 1958 and 1960). Due to the reasons mentioned above I preferred to call these sclerites as vaginal sclerites since they are on either side of the ovipore (vaginal orifice).

Feng (1936) ascribed dorsal position to the saw-like vaginal sclerites ('dorsal chitinous piece') and ventral position to the vulvulae ('ventral chitinous piece'). In his description of the female genitalia of <u>Laccophilus</u> <u>uniformis</u>, Feng omitted the 8th sternite whereas in some other genera the same has been described as 'ventral chitinous piece'. Thus Feng's description is inconsistent and incomplete.

Judging by my observations and by those of Tanner (1927), I find that what Feng describes as the dorsal chitinized piece in <u>Laccophilus</u> is actually the vaginal sclerite belonging to the 8th segment, and is ventral. Further, the so-called 'ventral chitinized piece' is homologous to the valvula and is dorsal.

Except in <u>Laccophilus</u> <u>uniformis</u> and <u>Hydrovatus</u> <u>equalis</u>, the position ascribed by Feng (1936) to the female genital sclerites is consistent with my observations. Further, the structure of the female genitalia belonging to Laccophilinae and Hydroporinae basically agrees with those studied by me.

In Hydroporinae the broad 8th sternite ('ventral chitinized piece' - Feng) and the valvifer 'dorsal chitinized piece' - Feng) are generally setose on the posterior margin. The valvifer is thin as compared to the 8th sternite, and elongate, its anterior end narrow and posterior end wide, posterior margin seteferous.

It would be of taxonomic interest to study the inter-relationship between the female genitalia of Agabus, Ilybius (Colymbetinae) and Laccophilus (Laccophilinae).

Table VIII : Inter-relationship of the female genitalia of Agabus, Ilybius and Laccophilus

	Agabus Jackson (1958-'60)	Ilybius Jackson (1960) Feng (1936-'37)	Laccophilus
1.	Valvulae are not the functional ovipositor blades	Valvulae are the functional ovipositor blades	Valvulae not analogous to those of Ilybius
2.	Valvulae awl-shaped and without cutting teeth	Valvulae awl-shaped and with cutting teeth along the dorsal margin	Valvulae sword-shaped slightly arcuate and without cutting teeth
3.	Vaginal sclerites not as much developed as in Laccophilus, but slightly better developed than in Ilybius. Vaginal sclerite not the functional ovipositor blade.	Vaginal sclerites not well developed. Vaginal sclerite not the functional ovipositor blade	Vaginal sclerites well developed fused along their dorsal margin on the posterior half, and modified to form ovipositor with cutting teeth on the posterior half of the ventral margin.
4.	Valvulae bear sensory hairs	Valvulae bear sensory hairs	Valvulae without sensory hairs

(Contd.)

Table VIII (Contd.)

	Agabus Jackson (1958-'60)	*Ilybius* Jackson (1960) Feng (1936-'37)	*Laccophilus*
5.	Median sclerotic strip indistinct	Median sclerotic strip present	Intermediate sclerite homologous to the median sclerotic strip present
6.	Anus supported by sclerotized area of valvifer (valvifer+paraproct)	Anus supported by sclerotized area of valvifer (valvifer + paraproct)	Anus supported by paraprocts
7.	Spermatheca present	Spermatheca present	Spermatheca absent
8.	Valvulae (ovipositor blades) bear the bursal ostium, while the ovipore is supported by vaginal sclerites (vulval sclerites)	As in *Agabus*	As in *Agabus*

The above observations on female genitalia support the inclusion of *Agabus* and *Ilybius* under one subfamily (the Colymbetinae), and the *Laccophilus* in a separate subfamily (the Laccophilinae), because the *Agabus* and *Ilybius* (Colymbetinae) differ from Laccophilinae in the points 2, 3, 4, 6 and 7 of the above table.

INTER-RELATIONSHIP OF THE SPECIES OF HYDROPORINAE

Four species of Hydroporinae have been studied. Zimmermann (1920) included *Hydrovatus* in Hydrovatini, *Hyphydrus* in Hyphydrini, and *Herophydrus* in Hydroporini. The genus *Guignotus* is raised in 1934 by Houlbert and is grouped in dessini.

In the present study the presence of four segmented pro- and meso-tarsus, and a short duct connecting the bursa with the vagina in Hyphydrus and Herophydrus musicus suggest their close relationship with each other.

Both these beetles differ from Guignotus (Bidessini) in that the latter has 5-segmented pro- and meso-tarsus and a long coiled duct connecting bursa with vagina.

The Hyphydrus flavicans and the Herophydrus musicus differ from Hydrovatus acuminatus, in that the later has five segmented pro- and meso-tarsus; elongate VIII tergites which gradually taper distad; spermatheca structurally quite different; greatly modified female genital sclerites (vide p. 62-63), long accessory glands with more convolutions; apodeme on the 9th sternum of male (Pl. II, Fig. 13); reduced rod-like basal piece; elytra with pointed posterior tip.

But Hydrovatus resembles Guignotus in that, pro- and meso-tarsus 5-segmented; 9th sternum with an anterior process (apodeme); and the presence of basal piece.

The above similarities bring the Hydrovatus and Guignotus close to each other. However, Hydrovatus has the following unique characters by which it differs from the rest of the Hydroporinae studied here.

VIII tergites elongate and attenuate posteriorly; 9th sternites in females fused with each other and attenuate posteriorly, forming what it seems to be an ovipositor blade. The distal end of the vagina supported by chitinized sclerites.

However, all the four beetles have important common characters (Table XIII, Nos. 3, 5, 6, 8, 11, 15 and 17) justifying their inclusion under Hydroporinae.

Sequence in the secondary appearance of the 3rd and the 4th sternal suture among Dytiscidae:

Jordan (1943) writes that, 'the number of connate sterna (firmly soldered sterna) having been found consistent in some families. Erichson (1848) and other after him made use of this distinction in their classification of the Coleoptera'.

In Adephaga connation has be-n observed (vide chapter I) between the 2nd and 4th sterna (Jordan 1943). There is difference in the extent of connation between 3rd and 4th sterna of Dytiscidae. In Hydroporinae and Noterinae the suture between 3rd and 4th sterna is totally indistinct (Pl. I, Figs. 4 and 2). In Laccophilinae this suture has secondarily appeared and is partly visible (Pl. I, Fig. 3). In Colymbetinae (Leech and Sanderson 1956) and Dytiscinae the suture is completely visible (Pl. I, Figs. 5 and 7) but the two sterna involved still exhibit connation.

Thus it can be noticed that the suture has secondarily appeared in gradual sequence in Laccophilinae, Colymbetinae and Dytiscinae.

ACCESSORY COPULATORY STRUCTURES

It has been held that the tenent hairs are the modified setae (Packard 1903). It occurs to me that the microcupules have evolved (Pl. XVI , Figs. 14, 15 and 16) from the tenent hairs by the development of a membranous cup-like structure which is supported by radiating ribs and folds at their tip. Further variation in the size of this cup-like structure has resulted in the macrocupules. Thus the macrocupules seem to be more efficient adhesive structure than the less specialized tenent hairs and microcupules.

Sequence in the occurrence of the accessory copulatory structures on the tarsi of the dytiscids:

Adhesive setae or tenent hairs are present in many of the males of the families (Carabidae, Cicindelidae) of Adephaga (Miall 1912). Probably, owing to the increased efficiency in the adhesive capacity of the adhesive structures, they are gradually restricted to the protarsi only. Such a gradual sequence can be demonstrated among the dytiscids as follows.

The Hydroporinae have tenent hairs and microcupules in both the sexes but they are restricted to the basal three segments of the pro- and meso-tarsus.

In Noterinae (Vazirani 1968), Laccophilinae, Colymbetinae and Dytiscinae the cupules are restricted to the males only. Noterinae, Laccophilinae, and Colymbetinae have only microcupules while the Dytiscinae have either micro- or macropules or in some cases both the types. According to Vazirani (1968) the Noterinae have small circular or oval suckers (microcupules) on the underside of the basal segments of the pro-tarsus.

In *Eretes sticticus*, Vazirani (1968) observed a total of only 28 cupules on the protarsal pad. But, in the specimens collected from Pilani, there are about 240 cupules. Such a great variation in the number of cupules in the same species is indeed noteworthy.

The number of protarsal cupules in *Hydaticus luczonicus* (Pl. XIV, Figs. 9 and 10) is 22, while that of mesotarsal cupules is 15.

The cupules of the protarsal pad of *Cybister* are arranged in four distinct rows. The first two on the basal tarsomere, the remaining two rows, one on each of the 2nd and 3rd tarsomeres. The total number of cupules is about 72. The protarsal pad of *Cybister* is distinct from the rest of the genera of the Dytiscinae examined in the following respects:

(a) macrocupules absent,
(b) micro-cupules arranged in distinct transverse rows,
(c) basal segment has a triangular patch of setae.

Gyrinidae

In Gyrinidae (Miall 1912, Bachmann 1959-'66) the protarsus is widened and the cupules are borne on all the tarsomeres. The cupules are invariably the microcupules. The mesotarsus does not bear the accessory copulatory structures.

Hydrophilidae

With regards to the accessory copulatory structures of hydrophilids it is apparent that cupules are not present in all. However, there are certain stout setae ventrally near the claws among a few hydrophilids (ex. Hydrous, Paracymus evanescens and P. tarsalis Miller). It is likely that these structures together with the ungues would be of help in firmly holding the notal margins of the females during copulation. However, this argument needs to be supplimented by careful examination on the use of these structures during the mating.

Among hydrophilids examined I came across microcupules only in the genus Berosus.

Common characters in the three families studied:

1. A total of nine abdominal segments present.
2. There are eight non-retractable terga.
3. The sternum-1 is absent.
4. In females the 9th sternum is either partially or fully divided forming valvifers.
5. In males the 9th sternum is undivided.

Table IX : Inter-relationship of the families : Dytiscidae, Gyrinidae and Hydrophilidae

Dytiscidae	Gyrinidae	Hydrophilidae
1. VIII tergum longitudinally divided except in *Canthydrus laetabilis* (Canthydrinae).	VIII tergum undivided.	VIII tergum undivided.
2. When present the IX tergum, in males is either longitudinally divided or undivided. In Canthydrinae) (*Canthydrus laetabilis*) and Laccophilinae it encircles the aedeagus.	IX tergum membranous.	IX tergum in males, transversely divided at anterior end giving rise to an undivided paraproct.
3. In females, the paraprocts are present in Canthydrinae (*Canthydrus laetabilis*) and Laccophilinae, absent in Hydroporinae.	In females the paraprocts absent.	In females the paraprocts absent.
4. 8th sternum retracted into the abdomen and divided to form a pair of sternites.	8th sternum not retracted into the abdomen and not divided to form sternites.	8th sternum retracted into the abdomen but not divided to form sternites.
5. In males: 9th sternum either plate-like as in Canthydrinae (*Canthydrus laetabilis*) and Laccophilinae; or ring-like as in Hydroporinae, Colymbetinae and Dytiscinae.	In males: the 9th sternum is a broad plate with reflexed lateral margins covering the basal half of the aedeagus.	In males: 9th sternum is a single plate neither ring-like nor with reflexed lateral margins.
6. In females: 9th sternum divided forming valvifers. Valvulae often present except in Hydroporinae (In *Ilybius* and *Agabus* of Colymbetinae the ovipositor blade and valvifer respectively: Jackson 1960 and '58), correspond to the valvulae of Canthydrinae (*Canthydrus laetabilis*) and Laccophilinae.	In females: 9th sternum divided forming valvifers. Valvulae absent.	In females: 9th sternum either partially (*Coelostoma stultum*) or fully divided forming either fused or separate valvifers. The valvulae two segmented.
7. The 2nd, 3rd and the 4th sterna are immovably joined to each other. The suture between the 2nd and 3rd sterna is distinct.	The 2nd, 3rd and the 4th sterna are immovably joined to each other, the suture between the 2nd and 3rd sterna is partly obliterated.	All the non-retractable sterna are firmly articulated to each other.
8. Aedeagus adephagid type.	Aedeagus adephagid type.	Aedeagus byrrhoid type.
9. Simple tubular testis.	Simple tubular testis.	Follicular testis.

(Contd.)

Table IX (Contd.)

	Dytiscidae	Gyrinidae	Hydrophilidae
10.	A pair of laterally placed epididymis present. In Dytiscus marginalis they come close and appear to be connected by a common peritoneal membrane (Korschelt).	A common epididymis present and placed medially above the lateral ejaculatory ducts.	Epididymis absent, instead a pair of seminal vesicles present.
11.	Lateral ejaculatory ducts usually present and short.	Lateral ejaculatory ducts abnormally long.	Lateral ejaculatory ducts absent.
12.	Common ejaculatory duct either long or short.	Common ejaculatory duct short.	Common ejaculatory duct long.
13.	Only one pair of ectadenien accessory glands.	As in Dytiscidae.	Both the ectadenien and the mesadenien glands present.
14.	Ovarioles polytrophic.	Ovarioles polytrophic.	Ovarioles telotrophic.
15.	Lateral oviducts without accessory glands.	Lateral oviducts without accessory glands.	Lateral oviducts with accessory glands.
16.	Reproductive organs either saccular or di-orificid (p. 169).	Tubular type.	Tubular type.
17.	Generally the basal three pro-tarsomeres of males bear cupules. The tarsomeres may bear either macro- or microcupules, or both.	All the five pro-tarsomeres of males bear microcupules.	Only in a few male hydrophilids the cupules are present. When present the basal three protarsomeres bear the microcupules.
18.	Several dytiscids have cupules on the mid-tarsus also.	No cupules on mid-tarsus.	No cupules on the mid-tarsus.

All those who included them in Dytiscidae have done so because the Noterinae are closer to Laccophilinae than to any other subfamilies (Vazirani 1968).

Most authors seem to agree to the subfamily status of Noterinae, Laccophilinae, Hydroporinae, Colymbetinae and Dytiscinae. However, some dytiscids are separated from these subfamilies and were included under new subfamilies by Sharp (1882), Brues et al. (1954). Kuhnt (1911) divided the Dytiscidae into only five tribes and these tribes are later raised by Zimmerman (1920) to the subfamily level (vide Table X)

Leech (1948) points out the lack of unanimity among the authors as to the higher categories in the Dytiscidae. The position is not different even to this date. Crowson (1955) is of the view that if Colymbetinae, Dytiscinae and Laccophilinae are accepted as subfamilies, to be consistent, the Noteridae and the Hydroporidae should be accepted as families.

Vazirani (1968) accepts in principle that a raise in the status of Noterinae should be followed by an increase in the status of Hydroporinae too. However, he preferred to wait before making change in the status of the existing subfamilies.

Thus the status of Noterinae and consequently that of Hydroporinae has remained uncertain. Vazirani (1968) writes that the status of Laccophilinae is also a matter of controversy. Despite the differing opinions on the classifications of Dytiscidae, the most generally followed classification at

Table 1 : Classifications of the family Dytiscidae proposed or followed by different authors with special reference to the subfamilies

Crotch 1873	Sharp 1882	Maxwell Lefroy 1909	Kuhnt 1911	Zimmerman 1920 Feng 1936-'37	Brues Melander and Carpenter 1954	Leech 1948 Vazirani 1957-58
Subfamily Haliplides	I. Dytisci fragmentati	I. Hydroporides	Hydroporini	I. Noterinae	Noterinae	Noterinae
		Hydroporini	Noterini	Notomicrini		
		Hydrovatini		Suphicini	Vatellinae	
Subfamily Dytiscides	Noterinae	Methlini	Laccophilini	Noterini		
				Hydrocanthini		
	Vatellinae		Colymbetini			
		II. Noterides		II. Laccophilinae	Laccophilinae	Laccophilinae
Ereteni	Laccophilinae		Dytiscini			
Hydroporini		III. Laccophilides		III. Hydroporinae	Hydroporinae	Hydroporinae
Noterini				Vatellini		
Agabini	II. Dytisci complicati	IV. Dytiscides		Hydrovatini		
Dytiscini				Hyphydrini		
				Bidessini	Methlinae	
	Hydroporinae	Colymbetini		Hydroporini		
		Hydaticini		Methlini		
	Methlinae	Thermonectini		IV. Colymbetinae	Colymbetinae	Colymbetinae
	Colymbetinae	Eretini		Copelatini	Cybisterinae	
	Dytiscinae	Cybisterini		Agabini		
	Hydaticinae			Colymbetini	Hydaticinae	
	Cybisterinae			V. Dytiscinae	Dytiscinae	Dytiscinae
				Eretini		
				Hydaticini		
				Thermonectini		
				Dytiscini		
				Cybisterini		

the subfamily level is that of Zimmerman (1920). Further, there is no well accepted phylogenetic classification among Dytiscidae.

All the beetles belonging to Noterinae, Laccophilinae, Hydroporinae, Colymbetinae are found to have two genital openings. (As I have no fresh material of *Hydrovatus acuminatus*, I dissected preserved specimens). In *Hydroporus ferrugineus* of Hydroporinae (Hyberdey 1931) and in *Agabus* and *Ilybius* of Colymbetinae (Jackson 1960) also there are two genital openings. An ad hoc examination of more random unidentified species belonging to Laccophilinae, Hydroporinae has also revealed the occurrence of 'di-orificid' type of female reproductive organs (vide infra). Apparently double genital openings are common to subfamilies Hydroporinae, Noterinae, Laccophilinae and Colymbetinae. It occurs to me that the double genital openings is a significant character so far as the grouping of the series is concerned.

Significantly, all the beetles (including *Dytiscus*) belonging to Dytiscinae have only a single genital opening (the vulva) on the ninth segment and thus they are quite different from the rest of the subfamilies of Dytiscidae.

The beetles having double genital openings have 'di-orificid' type of female reproductive organs while the series Dytisci-mono-orificia have saccular type of female reproductive organs.

On the lines of Monotrysia and Ditrysia of Lepidoptera (Imms 1963), I find it apt to propose the division of Dytiscidae into two series viz. Dytisci-di-orificia and the Dytisci-mono-orificia (Table XI). The series Dytisci-di-orificia includes Noterinae, Laccophilinae, Hydroporinae and Colymbetinae; while the series Dytisci-mono-orificia includes only the Dytiscinae.

Table XI : Contrasting characters of the two proposed series of Dytiscidae

Dytisci-mono-orificia	Dytisci-di-orificia
Single genital opening	Double genital openings
Functional ovipositor present	Functional ovipositor present or absent
A distinct spermathecal gland attached to the spermatheca	A distinct spermathecal gland not found attached to the spermatheca
Valvulae present but fused dorsally	Valvulae frequently present, absent in Hydroporinae
Aedeagus with reduced basal piece	Aedeagus with or without reduced basal piece
Aedeagus with distinct sacs	Aedeagus without sacs
Basal three segments of the protarsus forming either a circular or oval disc	Basal three segments of the protarsus neither circular nor oval, but have adhesive structures with the exception of Canthydrinae in which sexual dimorphism is absent in the tarsi
Macrocupules generally present (absent in <u>Cybister</u>)	Macrocupules absent. Microcupules present generally.
The male accessory glands (ectadenia) lie one on either side of the axial line of the abdomen	The male accessory glands generally lie one above the other (except in <u>Cybister tripunctatus asiaticus</u>). In <u>Dytiscus marginalis</u> too they lie one above the other (Balfour-Browne 1932).
Spermatheca present	Spermatheca present or absent
Testis and epididymis separated by vas deferens	Testis and epididymis separate or confluent

beetles lay their eggs in the incisions made on the plant stems. The well sclerotized intermediate sclerite, the ovipore and vaginal sclerites lie at the antero-mesal end of the 8th sternites. In Agabus (Colymbetinae), the 8th and the 9th sterna come close as in Ilybius (vide infra). The posterior end of the two genital ducts viz. bursa and vagina remain separate (Jackson 1960). The valvifers and the paraprocts are fused and the area of paraproct is represented by a small projection of the valvifer (Fig. 4). The valvulae are not stout and lack the serrate cutting edge and the beetles are devoid of functional ovipositor. Consequently, they deposit their eggs generally on the leaf surface. The vaginal sclerites are very much reduced, but remain slightly larger than that of Ilybius. Thus Agabus (Agabini) represents a condition between Laccophilus (Laccophilinae) and Ilybius (Colymbetini).

In Ilybius (Colymbetinae), the two sterna i.e. the 8th and the 9th come very close due to the shortening of the intersegmental membrane. As a result, the two genital openings come very close and according to Jackson (1960) the circular muscles around the ventral wall of the bursa encloses the vagina. However, they are separated by a partition. The valvifer is fused with the paraprocts and the intervening suture is absent. (The paraproct has been described by Jackson as the 'area of valvifer lying near anus'. A comparison with that of Laccophilus has revealed this sclerotized area as the paraproct fused with valvifer). In Ilybius fuliginosus (Fig. 5) the awl-shaped valvulae, as in segment is closed and the opening at the end of the ninth segment serves both for copulation and discharge of eggs.

However, in the majority of Lepidoptera (Snodgrass 1935, Klots 1956) the primary anterior aperture is retained at the posterior end of the 8th sternum.

Homologous apertures are observed among some dytiscids. But the position of these apertures in dytiscids is slightly different from that in Panorpoid Lepidoptera.

The two 8th sternites in dytiscids are separated by an intervening membrane and due to the shrinkage of this membrane at the anterior end of the ovipore, a change is brought in the original position of the ovipore which now comes to lie at the antero-mesal portion of the 8th sternum.

Based on the wide differences (Table XII) as well as on many other morphological features of the two groups of insects (Lepidoptera and the Coleoptera), I presume that the beetles (Dytisci-di-orificia) and the lepidopterans having double genital openings shared no common ancestor.

The re-occurrence of double genital openings derived from the genital chamber is a specialized feature, and their presence in Lepidoptera and in Coleoptera is a striking example of parallel occurrence.

Significantly enough, the double genital openings derived from genital chamber arose in a few of the spermatophore producing insects. Spermatophore production is reported in some dytiscids (Muir 1912, Jackson 1960) as well as in Panorpoid Lepidoptera (Davey 1965). Incidentally, I observed a long spermatophore being ejected when pressure is applied on the abdomen of *Herophydrus musicus*. A teased preparation when examined under microscope revealed spermatozoa in it.

PROBABLE ORIGIN OF DIORIFICID TYPE OF REPRODUCTIVE ORGANS (Pl. XVI)

It is very likely that the diorificid type of reproductive organs have originated from the saccular type (vide p.170) of female reproductive organs of the Coleoptera. Khurana (1964) has described the female reproductive organs of several Adephagid coleopterans which are saccular type.

Based on the developmental studies of female genital ducts, Heberdey (1931) explains that the two genital openings in *Hydroporus* (Hydroporinae) arise as a secondary division of the lumen of the already amalgamated "Anlage" of the eighth and the ninth segments.

It is possible that during development of dytisci-diorificid beetles, the genital chamber arising from the amalgamated eighth and ninth segments (Pl. XVI, Fig. 7) is secondarily divided (Fig. 8) into two pouches and each pouch grows anteriorly to join with the common oviduct. Thus the genital chamber gives rise to double genital ducts (Fig. 9) and their openings. Later, the dorsal genital duct is elongated (Fig. 10) and the two openings are separated by the de-amalgamation of the eighth and ninth segments. The dorsal duct serves the function of receiving and transporting the spermatozoa to the posterior end of the common oviduct. The posterior part of this duct enlarges to receive the median lobe during copulation and hence called the bursa copulatrix, while its duct is called the bursal duct, thus reaching the condition in Canthydrinae and Laccophilinae.

In some insects (*Hyphydrus flavicans*) the anterior end of the bursal duct is enlarged and heavily sclerotized forming the spermathecal capsule (Fig. 11).

GROUPING THE FEMALE INTERNAL REPRODUCTIVE ORGANS OF THE ORDER COLEOPTERA

Lindroth and Palmen (1956) distinguished only two types of female reproductive organs in Coleoptera.

1. The saccular type: without separate bursa copulatrix
2. The tubular type: with separate bursa copulatrix, usually combined with the development of an ovipositor.

The reproductive organs of the subfamily Dytiscinae fall under the first type, while those of *Dineutes unidentatus* (Gyrinidae) and Hydrophilidae come under the second type.

Lindroth and Palmen (1956) seemingly did not give due importance to the observations of Heberdey (1931), and contended that the bursa opens exceptionally at the terminal end (dorsad) of the vagina giving the suggestion of a double genital opening. However, in *Hydroporus*, Heberdey has observed a complete separation of the vagina from the bursa copulatrix, and both these open to the exterior by two distinct genital openings.

My observations reveal that in all the species having double genital openings, the vagina is completely separated from the bursa. Moreover, the bursal ostium is located in the ninth segment dorsal to the 9th sternum, and the ovipore at the meso-proximal end of the 8th sternum.

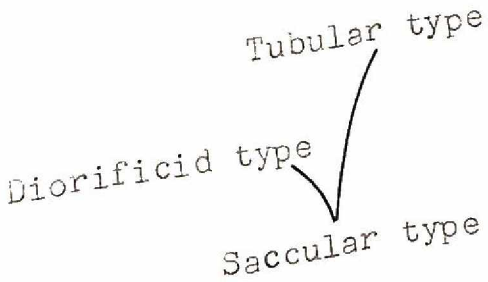
In the light of these observations (vide supra), it becomes necessary to rearrange the types of female reproductive organs given by Lindroth and Palmen (1956) so as to give place to the type of reproductive organs having double genital openings.

Hence, I make the following modifications and rearrangement:

I Mono-orificia:	Reproductive organs with a single external opening. Ex: All beetles excepting Dytisci-diorificia
i. Saccular type:	Reproductive organs without separate bursa copulatrix. Ex: Dytiscinae
ii. Tubular type:	Reproductive organs with separate bursa copulatrix usually combined with the development of an ovipositor. Bursa copulatrix not opening to the exterior. Ex: Gyrinidae, Hydrophilidae
II Di-orificia:	Reproductive organs with double external openings. Bursa opening to the exterior by bursal ostium. Ex: Dytisci-di-orificia.

PROBABLE EVOLUTION OF THE BURSA COPULATRIX IN THE ORDER COLEOPTERA

With the present observations revealing a new kind of female reproductive organs, the number of the major types of reproductive organs in the order Coleoptera as a whole is increased from two viz. saccular and tubular types (Lindroth and Palmen 1956), to three (vide supra). All these three types are observed in the aquatic beetles that I studied. It is possible to draw a distinct evolutionary path of these types as follows:



The saccular type represents the simple type of reproductive organs among Coleoptera, in that it has no separate bursa, and further the tubular vagina is simply an elongated genital chamber with a spermatheca and spermathecal gland at its anterior end. The vagina in this case serves both for receiving the medium lobe and discharging the fertilized eggs. Thus, it is both a functional bursa copulatrix and vagina.

The tubular type of reproductive organs arose as a further development of a separate bursal diverticulum (a blind tube) from the vagina (Pl. XVI, Figs. 12 and 13).

The diorificid type of reproductive organs are said to have developed from the saccular type (p.167) as a result of the secondary division of the genital chamber in the early developmental stages. In this type, the bursa opens directly to the exterior by a bursal ostium.

Table XIII: Suggesting the subfamily characters of the Hydroporinae, Noterinae, Laccophilinae, Colymbetinae and Dytiscinae

	Noterinae	Laccophilinae	Hydroporinae	Colymbetinae	Dytiscinae
1	The suture between 3rd and 4th sterna completely obliterated	The suture between 3rd and 4th sterna partly obliterated	The suture between 3rd and 4th sterna obliterated or at least not very distinct	3rd and 4th sterna immovably united and the intermediate suture distinct	3rd and 4th sterna immovably united and the intermediate suture very distinct
2	VIII tergum with longitudinal groove but not divided into two distinct tergites	VIII tergum with longitudinal thin desclerotized zone and divided into two distinct tergites	As in Laccophilinae	As in Laccophilinae	As in Laccophilinae
3	8th sternum completely divided into two triangular sternites	8th sternum completely divided into two sternites, these sternites often triangular	8th sternites completely divided into two sternites. Often not triangular	8th sternites anteriorly bound together by a continuous bordered margin	8th sternites bound together by a continuous bordered margin.
4	Vaginal sclerites absent	Vaginal sclerites (the functional ovipositor) stout and fused at the posterior half	Vaginal sclerites absent	Vaginal sclerites weak and small	Vaginal sclerites absent
5	IX tergum in males thin ring-like and encircles the aedeagus	IX tergum, in males enlarged, broader than in *Canthydrus laetabilis* and encloses the aedeagus. Unlike in *Canthydrus* it is deeply bifid anteriorly	IX tergum absent in both the sexes	Males: IX tergum generally present	IX tergum in males divided into a pair of tergites
6	Posterior end of the 9th sternal plate fringed with spine like setae	9th sternal plate grooved and posterior end spine-like	9th sternum never plate-like, thin, semi-circular and partly encircles the aedeagus	9th sternum in males thin and semicircular	9th sternum semicircular and united on either side of the IX tergites
7	Basal piece absent	Basal piece absent	Basal piece rod-like or absent	Basal piece rod-like and broad at the posterior tip	Basal piece rod-like and generally broad at the ends
8	Aedeagus asymmetrical and exhibits torsion	Aedeagus asymmetrical and exhibits torsion	Aedeagus symmetrical; all species do not exhibit torsion	Aedeagus symmetrical and exhibits torsion	Aedeagus symmetrical and in Dytiscinae, has aedeagal sacs. Torsion present or absent

able XIII (Contd.)

	Noterinae	Laccophilinae	Hydroporinae	Colymbetinae	Dytiscinae
9	---	A gland, probably the prepucial gland present in males only	---	---	---
10	Females with both IX tergites and the paraprocts	Females with paraprocts only. In *Laccophilus maculatus* Tanner (1927) reports the proctiger as present. This proctiger seems homologous to IX tergites	Females without paraprocts	Females: IX tergum partly reduced and partly fused with the valvifers	IX tergum in females distinct and divided into a pair of tergites
11	Females with very long valvifers which extend deep into the abdomen and not connected to paraprocts	Females with short valvifers connected to the paraprocts only	Generally a pair of spatulate valvifers present	Valvifers nearly equal to the length of valvulae	Valvifers longer than valvulae (functional ovipositor) and connected to IX tergites and valvulae
12	Valvulae shorter than valvifers, conical (awl-shaped) and seteferous	Valvulae elongate longer than valvifers, sword-shaped, arcuate and with no setae	Valvulae absent	A pair of valvulae (functional ovipositor blades in *Ilybius*) present	Valvulae long, fused dorsally, broad basally and attenuated posteriorly. Posterior end of valvula fringed with a tuft of setae
	Intermediate sclerite absent	Intermediate sclerite present beneath the ovipore at the base of the 8th sternites	Intermediate sclerite absent	Intermediate sclerite (median sclerotic patch) present beneath the ovipore (Jackson 1960)	Intermediate sclerite slightly shifted to a place between 7th and 8th sternites
13	Double genital openings present	Double genital openings present	Double genital openings present	Double genital openings present	Only single genital opening known as vulva present. Vulval lobe with supported vulval sclerite or sclerites
14	Bursal duct long, conspicuous and with a few convolutions	Bursal duct extremely long, very thin and highly convoluted	Bursal duct present, short or long	Bursal duct present	Bursal duct absent
15	Spermatheca absent	Spermatheca absent	Spermatheca present	Spermatheca (Stein 1847, Jackson 1960) receives the bursal duct from one end and opens into the vagina from the other end	Spermatheca which is a blind tube, opens into the vagina by a spermathecal duct. Spermatheca with a spermathecal gland

Table XIII (Contd.)

	Noterinae	Laccophilinae	Hydroporinae	Colymbetinae	Dytiscinae
16	Ovarioles 6 per ovary	Ovarioles 18-21 per ovary	Ovarioles 18 per ovary	Ovarioles 20-40 per ovary (Stein 1847, Robertson 1961)	Ovarioles 25-30 per ovary
17	Cupules absent: but microcupules said to be present on the basal segments of the tarsi of the males in Noterinae (Vazirani 1968)	A few cupules present on the basal three pro- and meso-tarsomeres of males. Tarsal pad not very distinct (Pl. XIV, Fig. 1)	Several microcupules present on basal three pro- and meso-tarsomeres of males as well as females. The bifid lobes of the 3rd tarsomere of these tarsi conceal the 4th tarsomere when the latter present	In <u>Copelatus</u> microcupules present on the tarsal pad of the basal segments of the pro- and mesotarsus of males; tarsal pad distinct, elongated	Both macro- and microcupules are observed (in the subfamily Dytiscinae) on either pro- or mesotarsus. In some, both pro- and mesotarsus have cupules. Tarsal pad circular or oval

In a review of the 'phylogeny of Coleoptera', Crowson (1960) suggests that the Noteridae (presently included under Dytiscidae), Dytiscidae and Gyrinidae have a common ancestor. He further contends that Noteridae (Herbivorous), Gyrinidae (Carnivorous, adult surface feeding, larva bottom feeding), and Dytiscidae proper are the results of adaptive radiation of the ancestral dytiscids.

The Diorificid type of female reproductive system is in a well developed state in Hydroporinae. It is probable that the intermediate stages in the evolution of Diorificid reproductive system between the ancestral dytiscids and the Hydroporinae are no longer present. The common ancestor of dytiscids, and gyrinids probably had saccular type of internal reproductive system. It is possible to expect such a type of internal reproductive system in the common ancestral group because most adephagids also have it, and further it is the simple and perhaps the primitive type among Coleoptera. The origin of the diorificid type of internal genitalia involves several co-ordinated changes in the physiology of the reproductive organs and the behaviour of either sex. Such changes must have taken place during a long period in the geological time scale which means the Hydroporinae with the well developed di-orificid type of reproductive system probably came into existence during a long period of time from the hypothetical common ancestor of dytiscids and gyrinids. Crowson's (1960) hypothesis that the dytiscids and gyrinids originated from a common ancestor complies closely with the evolution of the female internal reproductive organs that I have suggested

(p. 170), in that the internal reproductive system of Dytiscidae and of Gyrinidae evolved from the saccular type which is probably present in their common ancestor (vide supra).

Though in the Dytiscinae the diorificid type of reproductive system is lacking, they are still supposed to have evolved from Colymbetinae because of their important similarities to Colymbetinae (Table XIII). But, such an evolution must have taken place during a long period of time because the disappearance of separate bursal opening means again a change in many other physiological and ethonological changes in the beetles. Therefore, the dytisci-di-orificians belong to the less specialized group of Dytiscidae and have possibly existed much earlier than the fossil Actea, which has been found in the upper Jurassic period. But we have yet to find a fossil similar to dytisci-di-orificians. Since di-orificid type of reproductive system is not found in Carabidae with which the dytiscids share a common ancestor, it is possible that the common ancestor also does not have such a reproductive system. Since, series Dytisci-di-orificia is the only group among Coleoptera found to have such a type of reproductive system it is reasonable, for the time being, to conceive that this system arose somewhere in the evolution of dytiscids from the aforesaid common ancestral group. Such a common ancestor has existed during the triassic period (vide supra) which means, between 175-200 million years ago.

The evolution of the female external genitalia (p.162), the progressive reappearance of the suture between 3rd and

4th sterna (p. 150), the gradual restriction of the accessory copulatory structures to the protarsi and the evolution of cupules (p.150-51), all in same line suggest the probability of the evolution of the dytiscids in the sequence: Hydroporinae, Noterinae, Laccophilinae, Colymbetinae and Dytiscinae.

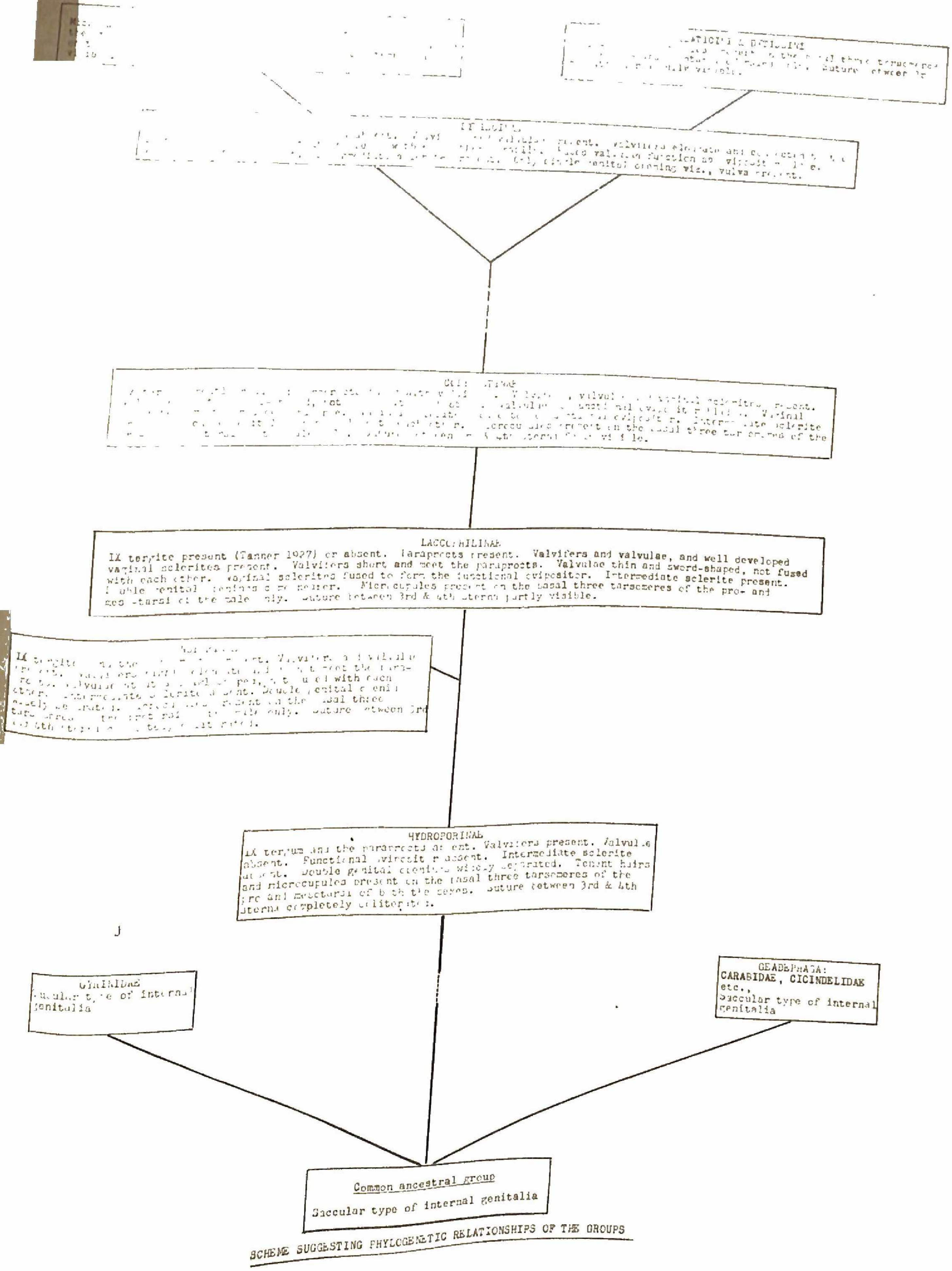
Though the Noterinae deserve a position between Hydroporinae and Laccophilinae, it should however be considered as a group slightly deviating from the main line of the intrafamilial evolution somewhere between Hydroporinae and Laccophilinae owing to the following differences with other dytiscids.

i. The males in Noterinae, at least in some species like *Canthydrus laetabilis*, do not have accessory copulatory structures on the tarsi. When present, they seem to occur on the protarsi only (Vazirani 1968). The structure of tibia at the distal end is different from the rest of dytiscids (Leech and Sanderson 1963).

ii. The valvifers are abnormally elongated and extend deep into the abdomen.

iii. A pair of IX tergites present in addition to the paraprocts.

The following scheme suggests the phylogentic sequence of the adephagid groups with a special reference to the subfamilies of Dytiscidae.



[illegible]

[illegible]

[illegible] present. Valvifers elongate and [illegible] fused valvulae function as ovipositor [illegible] Only single genital opening viz., vulva present.

[illegible]

LACCOPHILINAE
IX tergite present (Tanner 1927) or absent. Paraprocts present. Valvifers and valvulae, and well developed vaginal sclerites present. Valvifers short and meet the paraprocts. Valvulae thin and sword-shaped, not fused with each other. Vaginal sclerites fused to form the functional ovipositor. Intermediate sclerite present. Double genital openings observed. Microcupules present on the basal three tarsomeres of the pro- and meso-tarsi of the male only. Suture between 3rd & 4th sterna partly visible.

[illegible]
IX tergite [illegible] Valvifers and valvulae present. [illegible] with each other. [illegible] Double genital openings [illegible] on the basal three tarsomeres [illegible] male only. Suture between 3rd and 4th [illegible]

HYDROPORINAE
IX tergum and the paraprocts absent. Valvifers present. Valvulae absent. Functional ovipositor absent. Intermediate sclerite absent. Double genital openings widely separated. Tenent hairs absent. Double genital openings [illegible] and microcupules present on the basal three tarsomeres of the pro and mesotarsi of both the sexes. Suture between 3rd & 4th sterna completely obliterated.

GYRINIDAE
Saccular type of internal genitalia

GEADEPHAGA:
CARABIDAE, CICINDELIDAE
etc.,
Saccular type of internal genitalia

Common ancestral group

Saccular type of internal genitalia

SCHEME SUGGESTING PHYLOGENETIC RELATIONSHIPS OF THE GROUPS

SUMMARY

Comparative studies of the abdomen, the genital system of both the male and the female aquatic beetles, and the accessory copulatory structures have been made.

The total number of abdominal segments is found to be nine in all the three families studied viz. Dytiscidae, Gyrinidae and Hydrophilidae. The true 1st sternum is invariably absent. The 2nd sternum is present in the Dytiscidae and the Gyrinidae, and it may be present or absent in the Hydrophilidae.

In Hydrophilidae, the paraprocts have originated from the IX abdominal tergum.

The male genitalia of twenty one species of beetles belonging to Dytiscidae, Gyrinidae and Hydrophilidae are studied. In the dytiscids and the gyrinids the aedeagus is of articulate type while in the hydrophilids it is trilobate type. An examination of the aedeagus from the fresh beetles has revealed the presence of aedeagal sacs in Dytiscinae. The obvious inter-relationship of the aedeagus of three species of the subfamily Dytiscinae have been pointed out.

Studies of the male reproductive organs of Laccophilus have revealed the existence of a prepucial gland attached to the ejaculatory duct at the point where it enters the aedeagus.

The dorso-ventral position of the male accessory glands in Dytiscinae is attributed to the torsion of the aedeagus.

The female internal reproductive system of dytiscids revealed many peculiarities. Mainly based on the female internal reproductive system, the family Dytiscidae is divided into two series viz., Dytisci-diorificia and Dytisci-mono-orificia.

The division of the posterior part of the internal reproductive organs of the Diorificid beetles into two genital ducts is probably the result of the division of the genital chamber into two ducts viz., Bursal duct and the Vagina.

Though the females of 'Dytisci-diorificid' beetles have double genital openings as in Panorpoid Lepidoptera, yet both these groups differ largely from each other.

The internal female reproductive organs of Sternolophus rufipes revealed important differences from the observations made by Khurana (1964).

Based on the variations in the position of the bursa and the spermatheca, the female internal genitalia (internal reproductive organs) of the order Coleoptera were grouped under two types ie. Saccular and Tubular types by Lindroth and Palmen (1956). In the light of the present studies this grouping is revised and reset. As a result, there are at present three types of female internal genitalia viz., Saccular, Tubular and Diorificid types.

There is a gradual change in the occurrence of the suture between the true 2nd and the 3rd sterna in Dytiscidae. In Hydroporinae, it is indistinct and in Dytiscinae it is disinct with intermediate stages in the remaining subfamilies.

The inter-relationships of the subfamilies of Dytiscidae have revealed the possible trend of evolution of the group-Phylogeny of the group Dytiscidae is discussed. The subfamilies of Dytiscidae are arranged in the phylogenic sequence ie. Hydroporinae → Canthydrinae → Laccophilinae → Colymbetinae → Dytiscinae.

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* Originals not seen

KEY TO THE ABBREVIATIONS OF THE FIGURES

ACGL	Accessory gland
AN	Anus
APD	Apodeme
APGL	Appendicular gland
APP	Area of paraproct
BC	Bursa copulatrix
BD	Bursal duct
BM	Basement membrane
BO	Bursal ostium or Bursal orifice
BP	Basal piece
CLX	Calyx
CM	Circular muscle
CON	Condyle
COVD	Common oviduct
DEJ	Ejaculatory duct
DNT	Denticle
DS	Dorsal sac
DSC	Dorsal sclerite
E	Egg
EDP	Endophallus
EP	Epithelium
EPDD	Epididymis
EPSH	Epithelial sheath
FEP	Follicular epithelium
GC	Genital chamber
GPR	Gonopore
GRM	Germarium

HF	Hair fringe
IFC	Interfollicular cells
IM	Intersegmental membrane
IT	Intima
IS	Intermediate sclerite or median scleretic patch
LEJ	Lateral ejaculatory duct
LL	Lateral lobe
LM	Longitudinal muscle
LU	Lumen
M	Membrane
MAC	Macrocupule
MF	Median foramen
MIC	Microcupule
ML	Median lobe
MS	Median strut
MT	Microtrichia
N	Nucleus
NRCL	Nutritive cell
ODL	Lateral oviduct
OPGL	Opaque gland
OV	Ovary
OVL	Ovariole
OVP	Ovipore
PCGL	Prepucial gland
PDCL	Pedicel
PFC	Prefollicular cells
PP	Paraproct
PSPT	Pseudospermatheca

PSH	Peritoneal sheath
R	Rectum
S	Setae
SCM	Sacs of median lobe
SE	Secretion
SEP	Septum
SH	Sheath
SPCT	Spermatocyte
SPG	Spermatogonial cell
SPN	Spine
SPT	Spermatheca
SPTD	Spermathecal duct
SPTGL	Spermathecal gland
SPZ	Spermatozoa
SSH	Syncytial sheath
STY	Stylus
TES	Testis
TESF	Testis follicle
TF	Terminal filament
TH	Tenent hair
TI	Tibia
TL	Terminal ligament
TRGL	Transparent gland
V	Vulva
VAG	Vagina
VAGS	Vaginal sclerite
VCL	Vacuole
VD	Vas deferens

VLF	Valvifer
VS	Vulval sclerite
VSC	Ventral sclerite
VSM	Seminal vesicle
VVL	Valvula
ZM	Zone of maturation
ZTR	Zone of transformation
ZSPC	Zone of spermatocytes
ZSPG	Zone of spermatogonia
I to IX	These roman numerals stand for abdominal terga
2 to 9	These arabic numerals stand for abdominal sterna

PLATE I

Nonretractable segments of the abdomen

Fig. 1 Dorsal view of abdomen of *Canthydrus laetabilis*

Fig. 2 Ventral view of abdomen of " "

Fig. 3 Ventral view of abdomen of *Laccophilus*

Fig. 4 Ventral view of abdomen of *Hyphydrus flavicans*

Fig. 5 Ventral view of abdomen of *Copelatus* sp.

Fig. 6 Dorsal view of abdomen of *Eretes sticticus*

Fig. 7 Ventral view of abdomen of " "

Fig. 8 Dorsal view of abdomen of *Dineutes unidentatus*

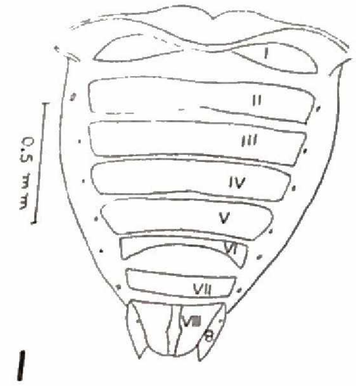
Fig. 9 Ventral view of abdomen of " "

Fig. 10 Ventral view of abdomen of " "

Fig. 11 Ventral view of abdomen of *Enochrus* sp.

Fig. 12 Ventral view of abdomen of *Hydrous indicus*

PLATE. I



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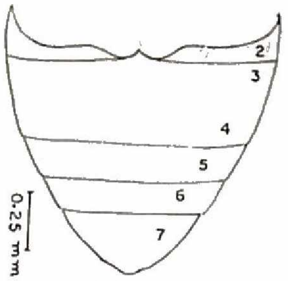

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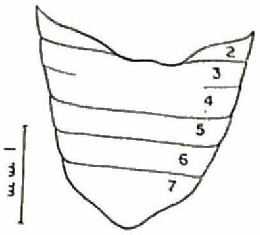

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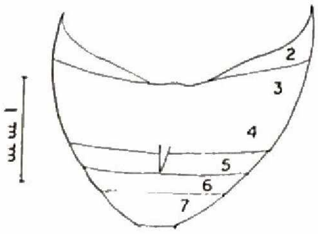

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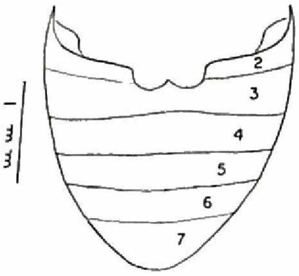

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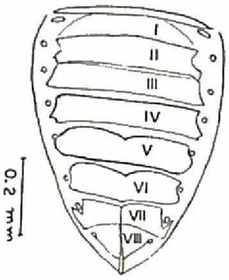

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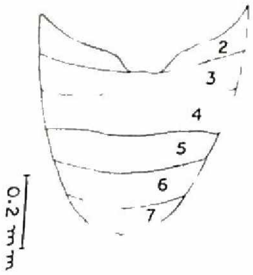

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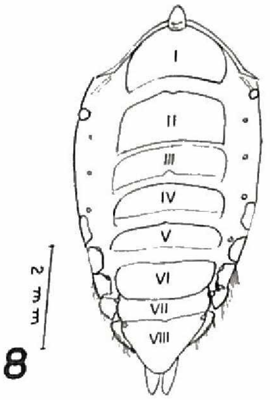

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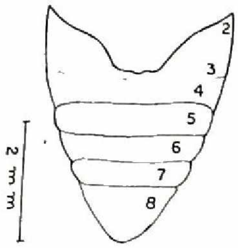

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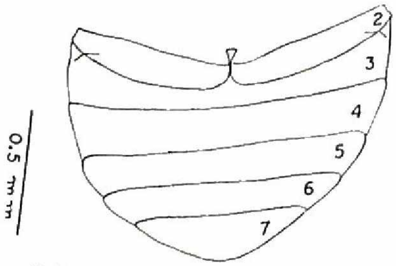

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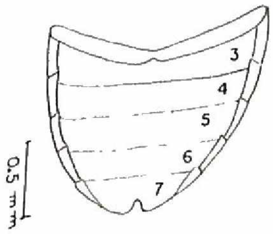

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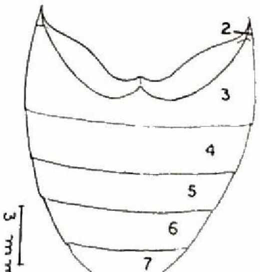

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PLATE II

External Genitalia of Males

Fig. 1	Ninth segment of	*Canthydrus*	*laetabilis*
Fig. 2	Eusinistral lateral lobe of	"	"
Fig. 3	Eudextral lateral lobe of	"	"
Fig. 4	Median lobe of	"	"
Fig. 5	Ninth segment of	*Laccophilus*	*sharpi*
Fig. 6	Eusinistral lateral lobe of	"	"
Fig. 7	Eudextral lateral lobe of	"	"
Fig. 8	Median lobe of	"	"
Fig. 9	Ninth segment of	*Laccophilus*	*flexuosus*
Fig. 10	Eusinistral lateral lobe of	"	"
Fig. 11	Eudextral lateral lobe of	"	"
Fig. 12	Median lobe of	"	"
Fig. 13	Genital complex of	*Hydrovatus*	*acuminatus*
Fig. 14	Ventral view of the median lobe of	"	"

Figs. 4, 6, 7, 8, 10, 11, 12 and 14 are drawn to the same scale of Fig.1

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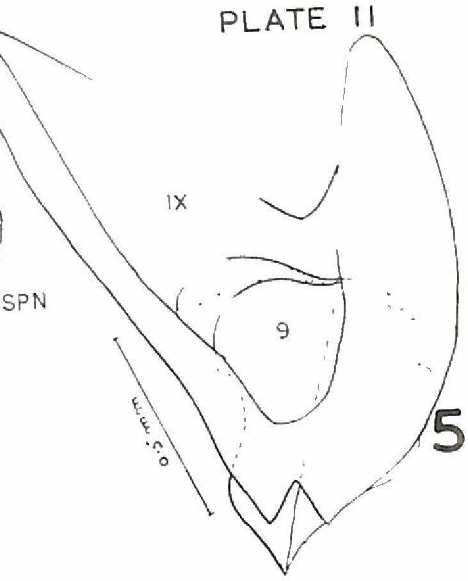

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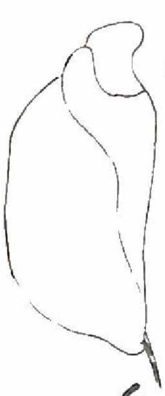

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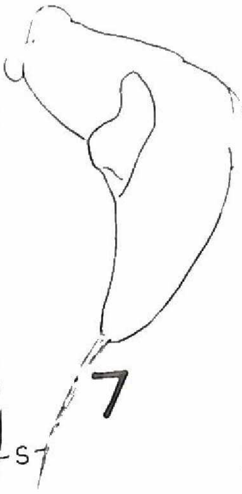

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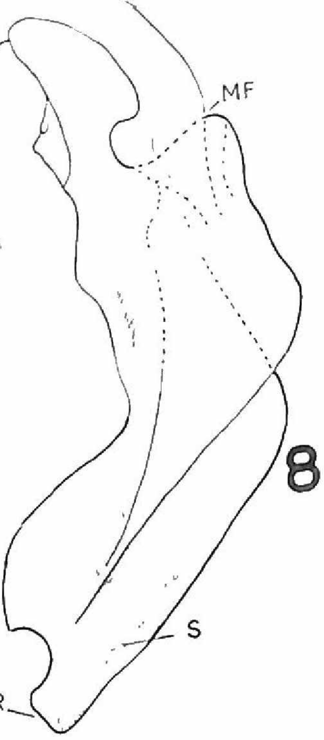

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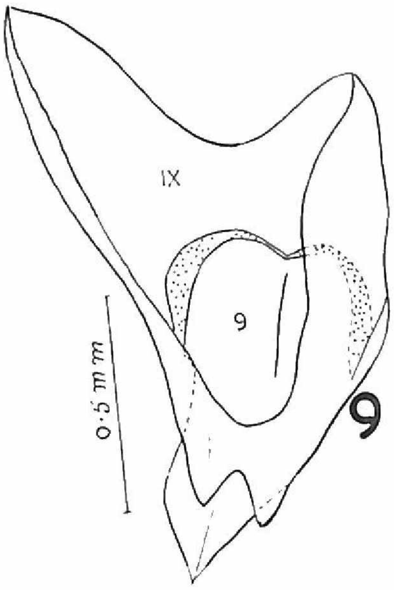

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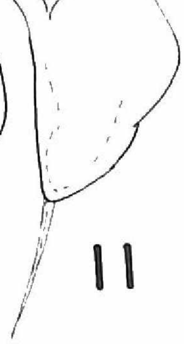

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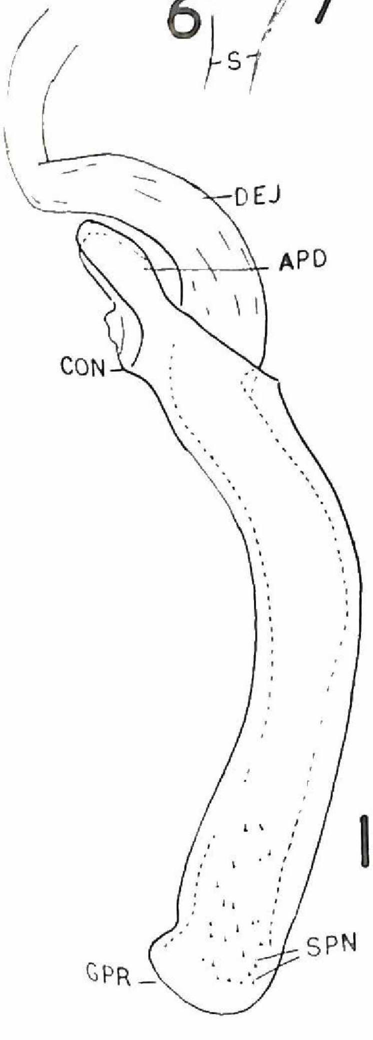

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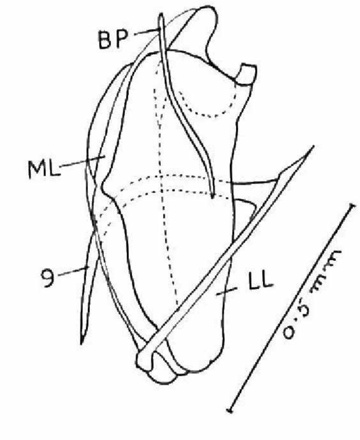

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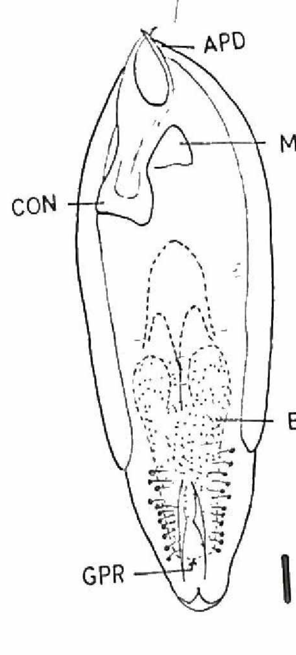

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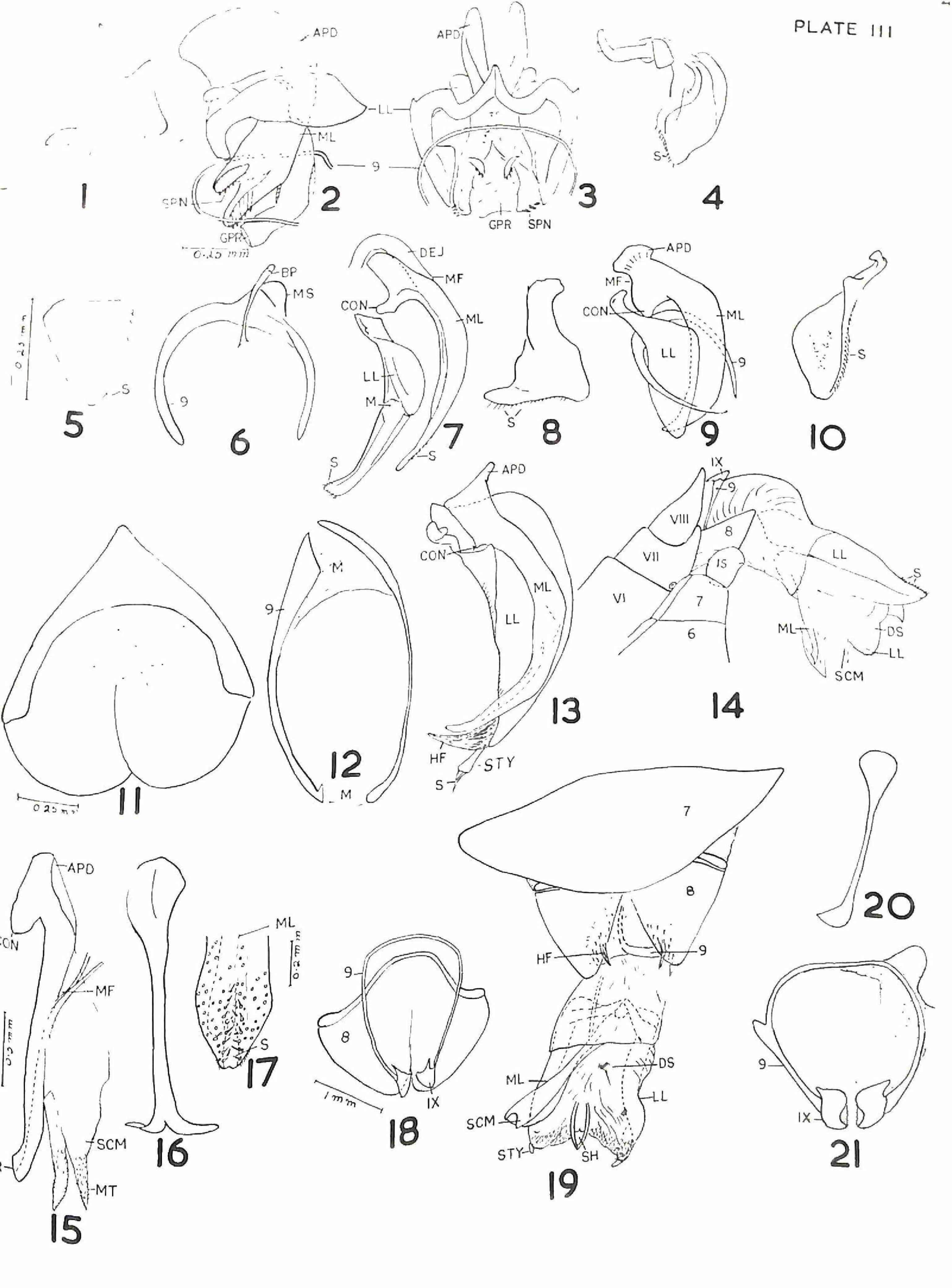
PLATE III

External genitalia of Males

Fig. 1	8th sternite of	*Hyphydrus flavicans*
Fig. 2 Fig. 3	Genital complex (lateral and ventral view respectively) of	" "
Fig. 4	Inner view of the lateral lobe of	" "
Fig. 5	8th sternite of	*Guignotus* sp.
Fig. 6	Ninth sternum with the basal piece	" "
Fig. 7	Aedeagus (lateral lobe and median lobe) of	" "
Fig. 8	8th sternite of	*Herophydrus musicus*
Fig. 9	Genital complex of	" "
Fig. 10	Lateral lobe of	" "
Fig. 11	8th sternum of	*Copelatus* sp.
Fig. 12	Ninth segment of	" "
Fig. 13	Aedeagus (one of the lateral lobes removed of)	" "
Fig. 14	Genital complex (evaginated) of	*Eretes sticticus*
Fig. 15	Median lobe of	" "
Fig. 16	Basal piece of	" "
Fig. 17	Spatulate organ of the sac (dorsal sac of the lateral lobes) of	" "
Fig. 18	Ninth segment along with 8th sternites of	*Hydaticus luczonicus*
Fig. 19	Genital complex (evaginated)	" "
Fig. 20	Basal piece	" "
Fig. 21	Ninth segment	" "

PLATE III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SCM
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SH
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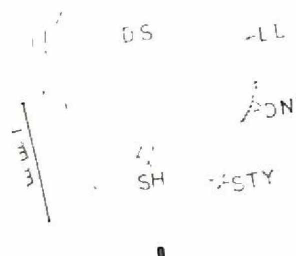
IX
21

PLATE IV

External Genitalia of Males

Fig. 1	Lateral lobes with dorsal sac,	*Hydaticus luczonicus*
Fig. 2	Lateral view of the median lobe of	" "
Fig. 3	8th sternum of	*Cybister tripunctatus*
Fig. 4	Lateral view of the aedeagus of	" "
Fig. 5	Lateral view of the median lobe of	" "
Fig. 6	Aedeagus along with 9th sternum of	*Dineutes unidentatus*
Fig. 7	Aedeagus	" "
Fig. 8	Genital complex (dorsal and ventral views respectively) of	*Coelostoma stultum*
Fig. 9		
Fig.10	Dorsal and ventral views of	*Paracymus evanescens*
Fig.11		
Fig.12	Dorsal and ventral views of genital complex of	*Enochrus* sp.
Fig.13		
Fig.14	Aedeagus/Dorsal view of the	" "

PLATE IV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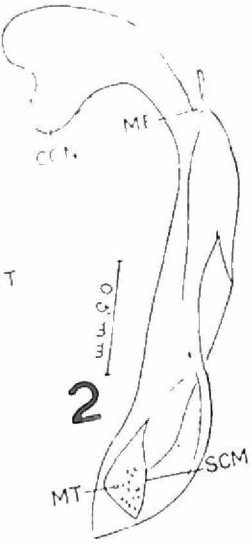
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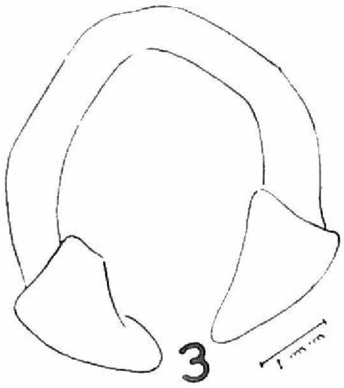
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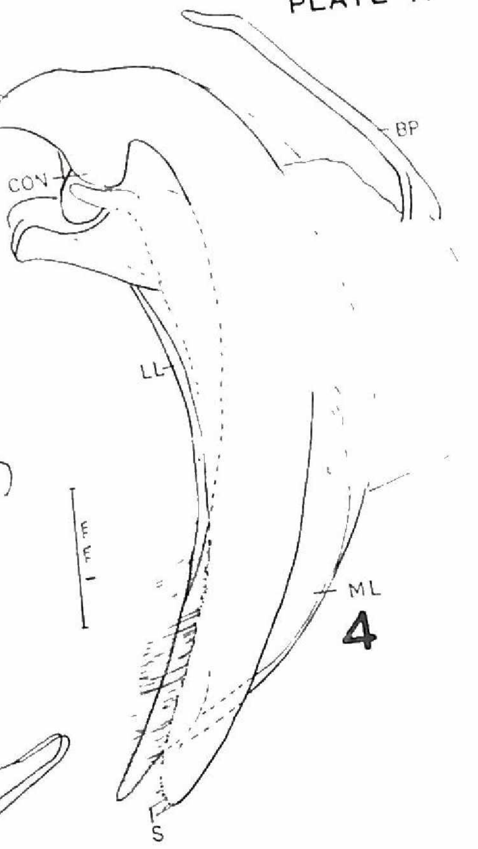
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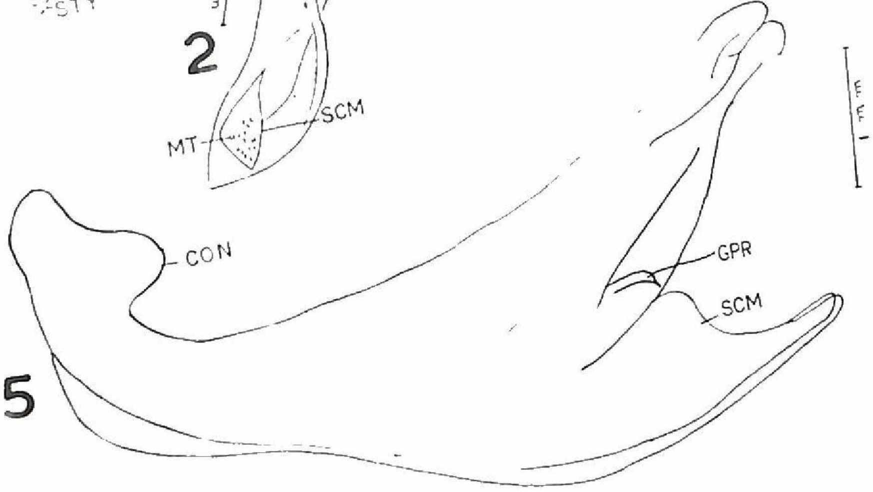
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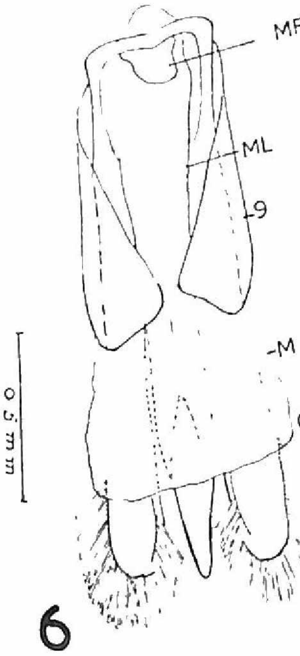
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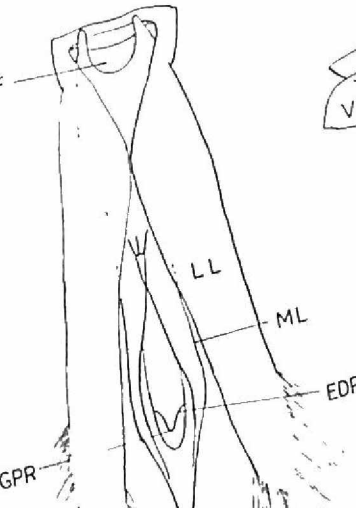
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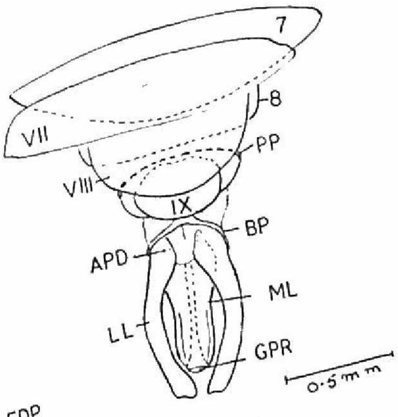
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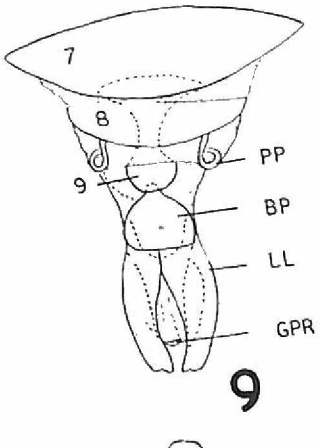
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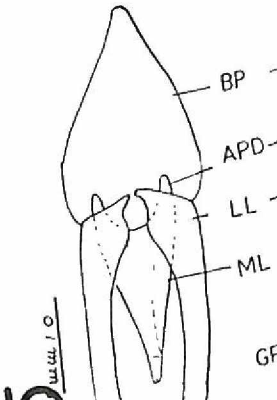
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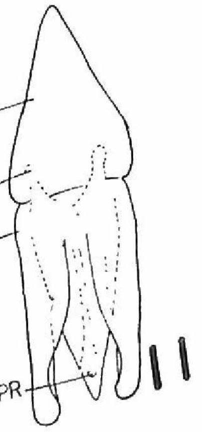
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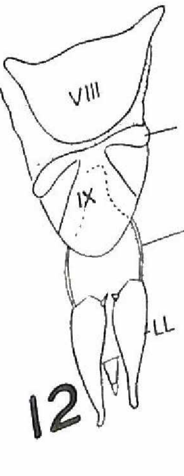
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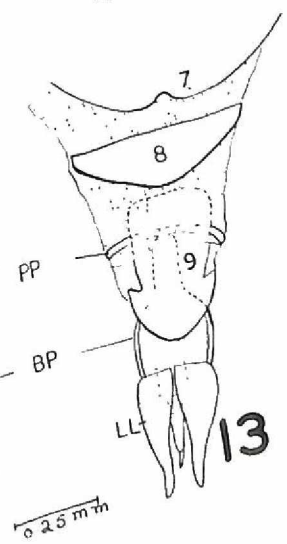
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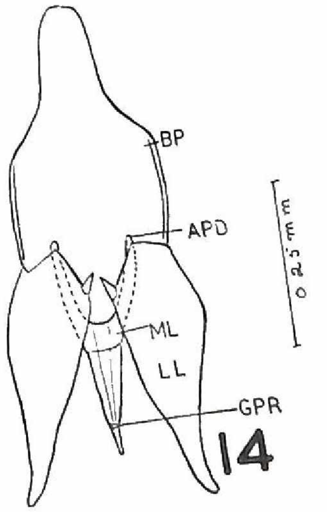
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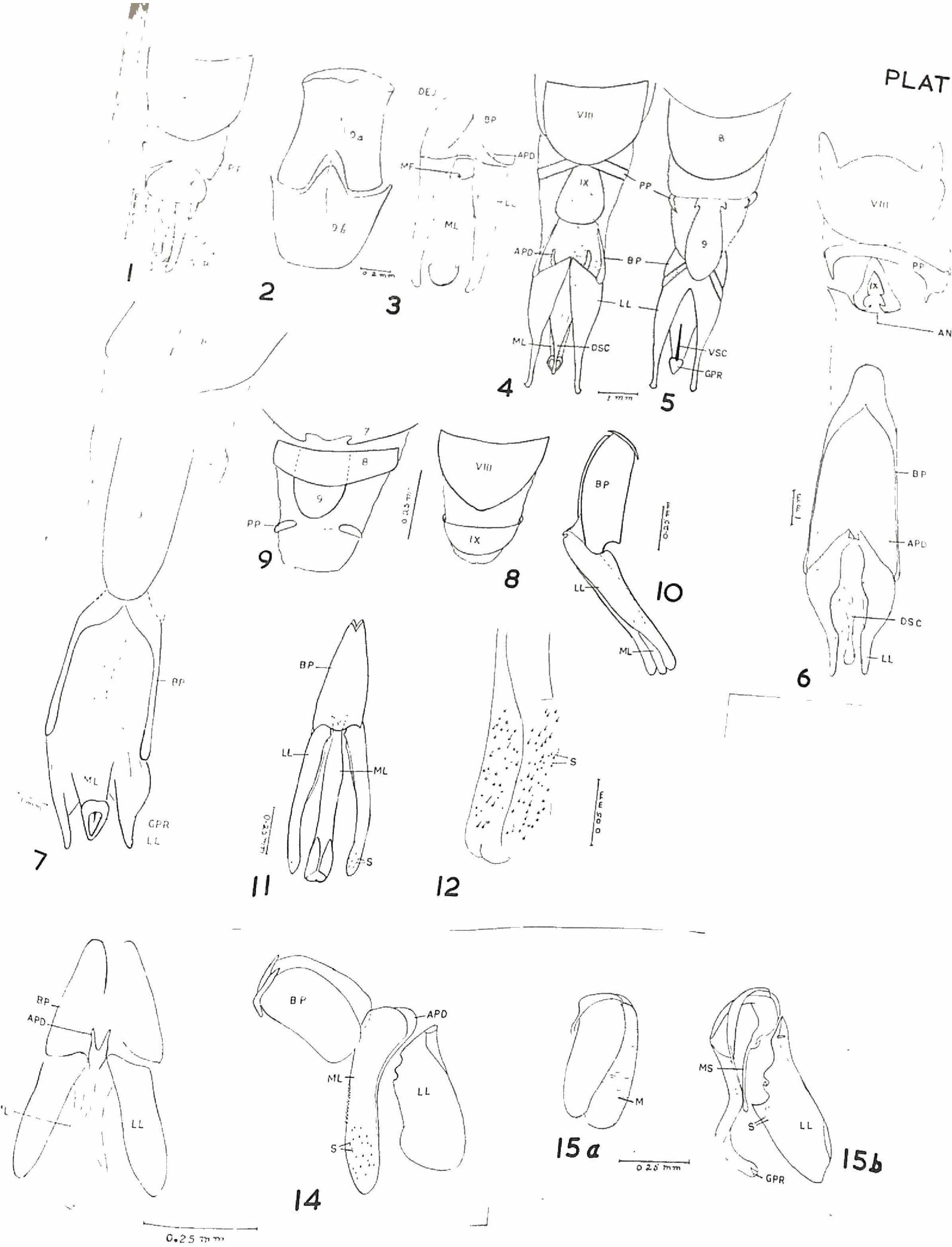
PLATE V

External Genitalia of Males

Fig. 1	Dorsal view of the male genital complex of	*Sternolophus rufipes*
Fig. 2	9th sternum	" "
Fig. 3	Aedeagus	" "
Fig. 4	Dorsal view of the genital complex of	*Hydrous indicus*
Fig. 5	Ventral view of the genital complex of	" "
Fig. 6	Dorsal view of the genital complex of	*Hydrous senegalensis*
Fig. 7	Ventral view of the genital complex	" "
Fig. 8	Dorsal view of the genital complex of	*Berosus indicus*
Fig. 9	Ventral view of the genital complex of	" "
Fig. 10	Lateral view of the aedeagus of	" "
Fig. 11	Ventral view of the aedeagus of	" "
Fig. 12	Distal end of the median lobe of	" "
Fig. 13	Dorsal view of the aedeagus of	*Berosus pulchellus*
Fig. 14	Lateral view of the aedeagus of	" "
Fig. 15a	Basalpiece of	*Berosus* nr. *nigriceps*
Fig. 15b	Lateral view of the median lobe of	" "

PLATE V



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LL
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DSC
1 mm
5
8
9
VSC
GPR
VIII
PP
IX
AN
6
BP
1 mm
APD
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7
BP
ML
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9
7
8
9
PP
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8
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10
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11
BP
LL
ML
S
0.25 mm
12
S
0.05 mm
BP
APD
LL
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14
BP
APD
ML
LL
S
15a
M
0.25 mm
15b
MS
S
LL
GPR

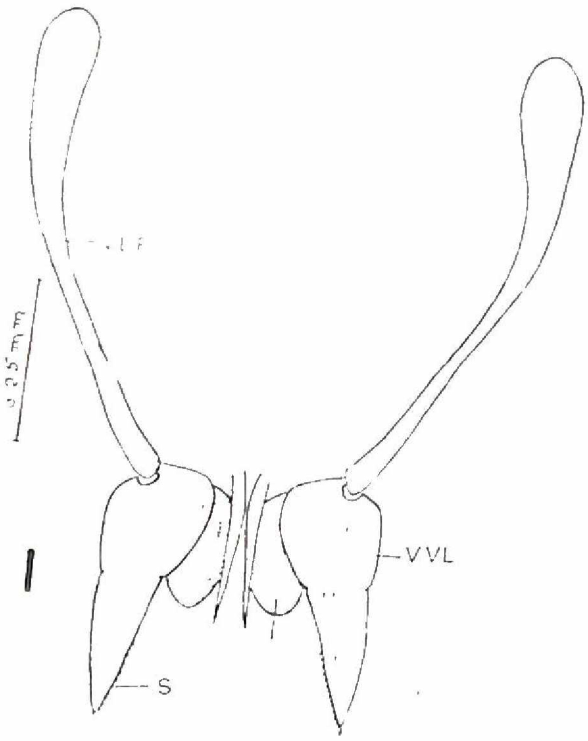
PLATE VI

External Genitalia of Females

Fig. 1	Dorsal view of the external genitalia of females of	*Canthydrus laetabilis*
Fig. 2	Ventral view of the external genitalia of females of	*Laccophilus flexuosus*
Fig. 3	Lateral view of the external genitalia of females of	" "
Fig. 4	VII and VIII terga of	*Hydrovatus acuminatus*
Fig. 5	Dorsal view of the external genitalia of female,	*Hydrovatus acuminatus*
Fig. 6	Ventral view of the female genitalia and spermatheca of	" "
Fig. 7	8th sternite of	*Hyphydrus flavicans*
Fig. 8	Valvifer of	" "
Fig. 9	8th sternite of	*Guignotus* sp.
Fig. 10	Valvifer of	" "
Fig. 11 Fig. 12	The 8th sternite and the valvifers respectively of	*Herophydrus musicus*
Fig. 13	Lateral view of the external genitalia (vaginated) of	*Eretes sticticus*

Figures 4, 5, 6, 7, 8, 9, 11 and 12 are drawn to the same scale of F

PLATE VI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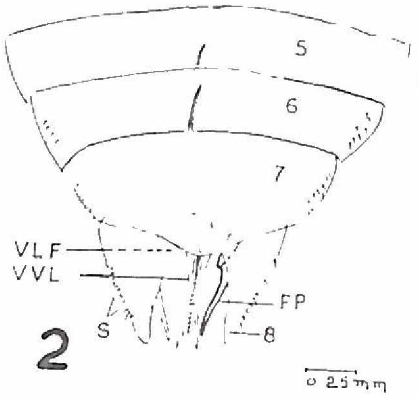
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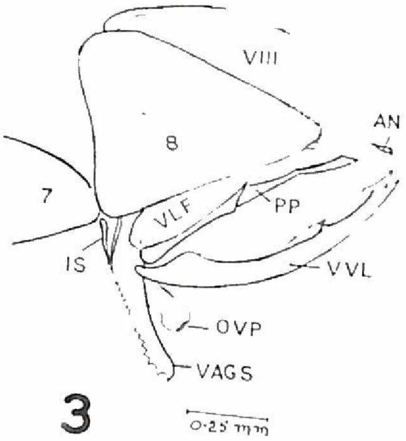
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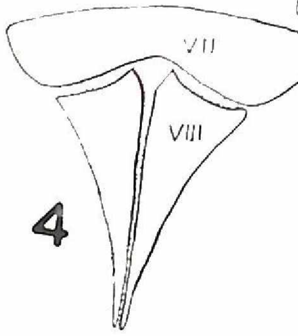
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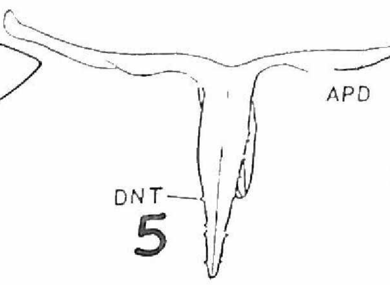
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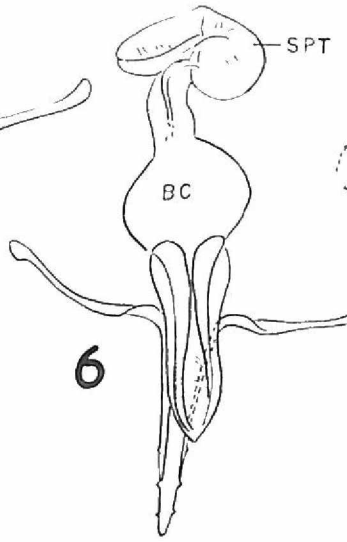
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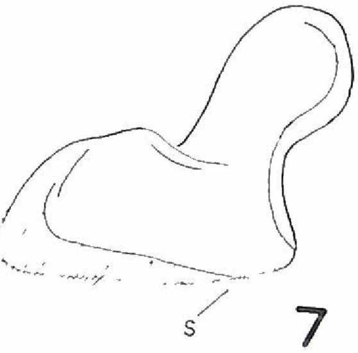
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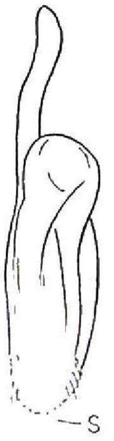
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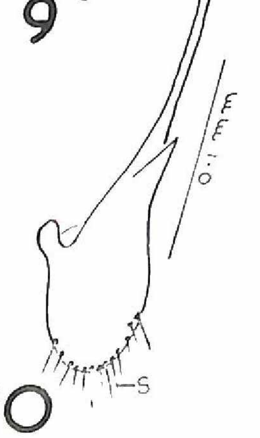
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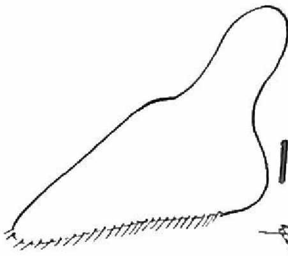
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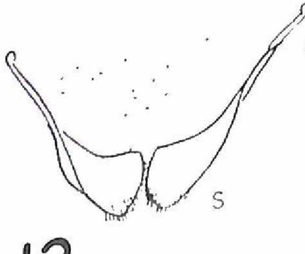
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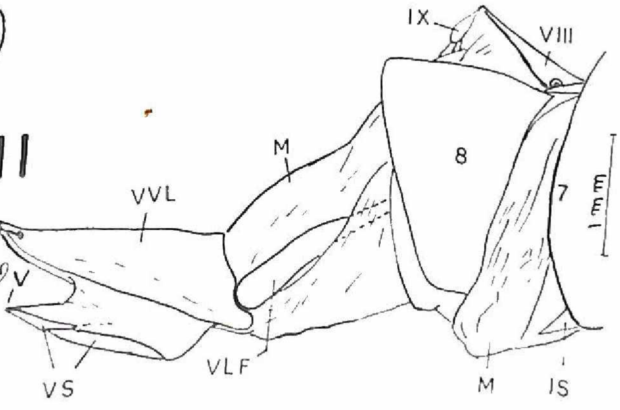
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PLATE VII

Fig. 1	Lateral view of the external genitalia of the female	*Hydaticus luczonicus*
Fig. 2	Lateral view of the external genitalia of the female	*Cybister tripunctatus*
Fig. 3	Dorsal view of the external genitalia of the female	*Dineutes unidentatus*
Fig. 4	Dorsal view of the external genitalia of the female	*Coelostoma stultum*
Fig. 5	Dorsal view of the external genitalia of the female	*Paracymus evanescens*
Fig. 6	Ventral view of the external genitalia of the female	*Enochrus* sp.
Fig. 7 Fig. 8	Dorsal and ventral view respectively of the external genitalia of the female	*Sternolophus rupifes*
Fig. 9	Dorsal view of the external genitalia of the female	*Hydrous indicus*
Fig. 10	Ventral view of the external genitalia of the female	" "
Fig. 11	Dorsal view of the external genitalia of the female	*Hydrous senegalensis*
Fig. 12	Ventral view of the external genitalia of the female	" "
Fig. 13	Ventral view of the external genitalia of the female	*Berosus indicus*
Fig. 14	Ventral view of the external genitalia of the female	*Berosus pulchellus*
Fig. 15	Ventral view of the external genitalia of the female	*Berosus* nr. *nigriceps*
Fig. 16	Dorsal view of the internal reproductive organs of	*Canthydrus laetabilis*
Fig. 17	Dorsal view of the internal reproductive organs of	*Laccophilus flexuosus*
Fig. 18	Dorsal view of the internal reproductive organs of	*Laccophilus parvulus*
Fig. 19	Dorsal view of the internal reproductive organs of	*Laccophilus sharpi*

PLATE VII

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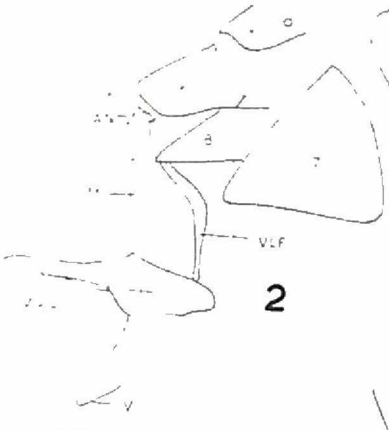

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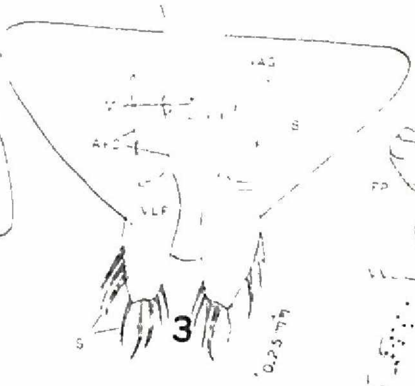

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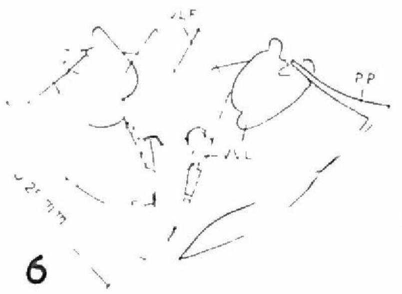

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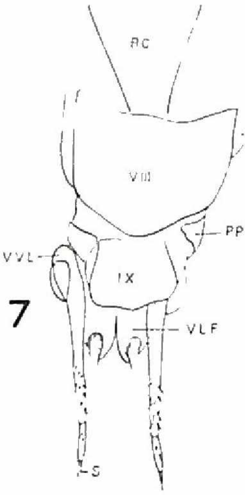

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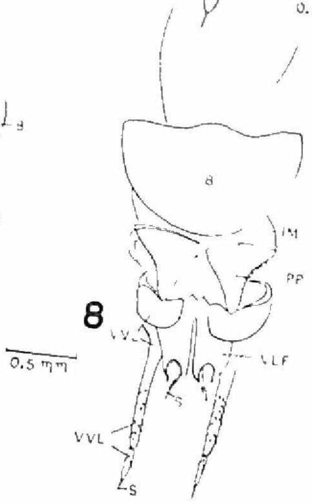

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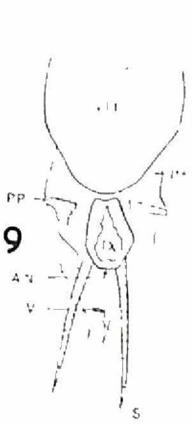

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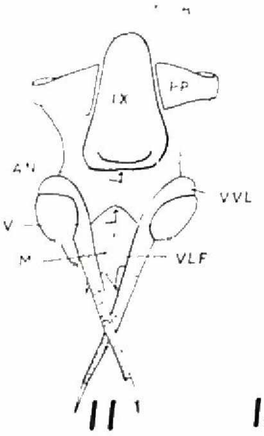

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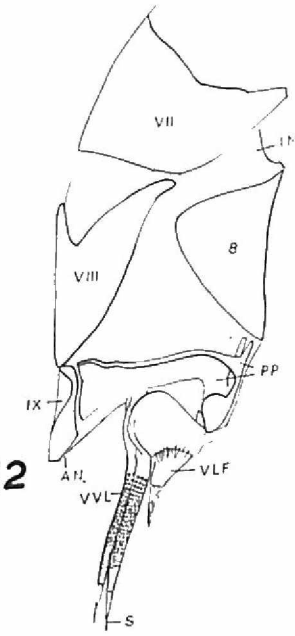

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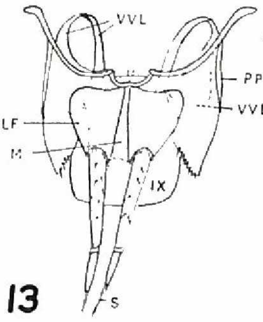

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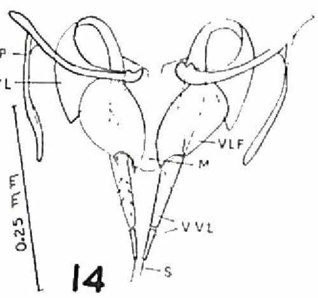

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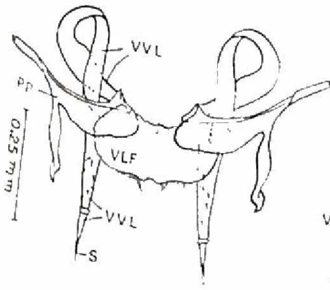

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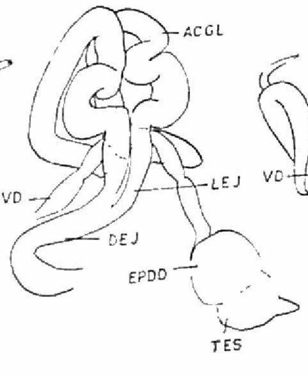

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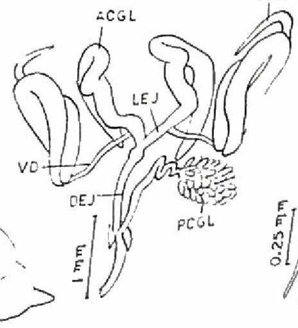

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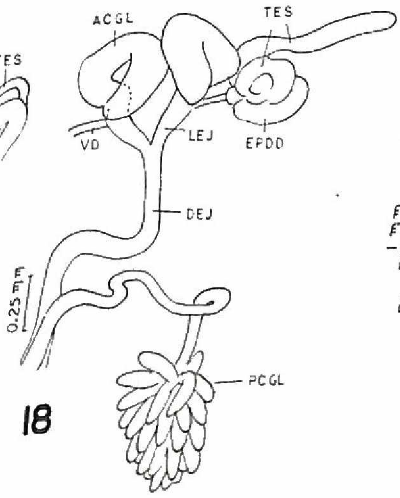

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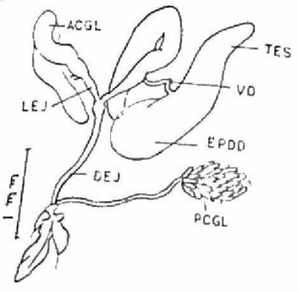

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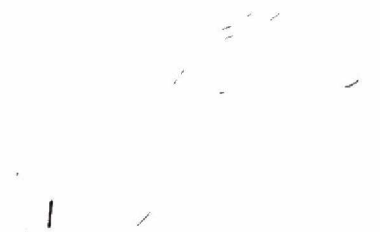
PLATE VIII

Fig. 1	Internal reproductive organs of	*Hydrovatus acuminatus*
Fig. 2	Internal reproductive organs of	*Hyphydrus flavicans*
Fig. 3	Internal reproductive organs of	*Guignotus* sp.
Fig. 4	Internal reproductive organs of	*Herophydrus musicus*
Fig. 5	Internal reproductive organs of	*Copelatus* sp.
Fig. 6a	Internal reproductive organs of	*Eretes sticticus*
Fig. 6b	Showing the convolutions of the accessory glands of	" "
Fig. 7	Internal reproductive organs of	*Hydaticus luczonicus*
Fig. 8	Internal reproductive organs of	*Cybister tripunctatus*
Fig. 9	Internal reproductive organs of	*Dineutes unidentatus*
Fig. 10	Internal reproductive organs of	" "
Fig. 11	Internal reproductive organs of	*Hydrous indicus*
Fig. 12	Internal reproductive organs of	*Stenolophus rufipes*
Fig. 13	Internal reproductive organs of	*Hydrous senegalensis*

PLATE VIII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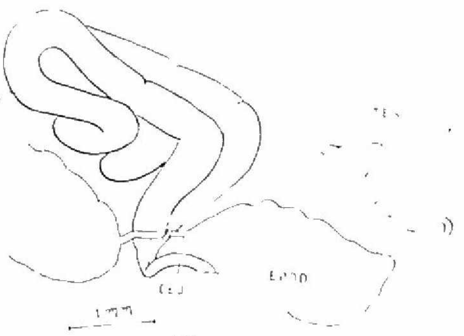
2


3


4

5

6a 6b



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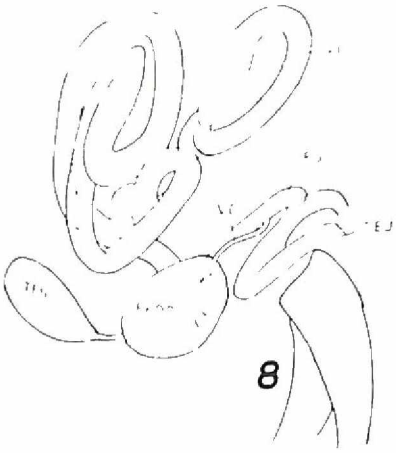

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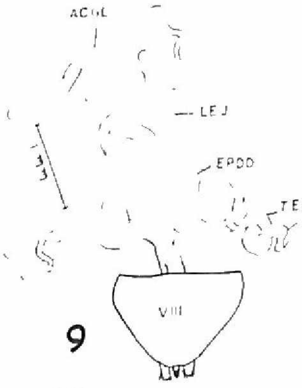

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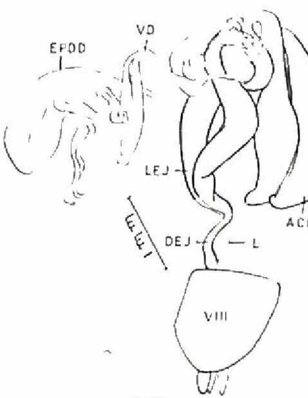

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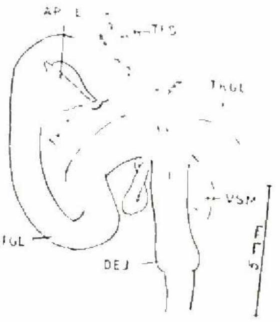

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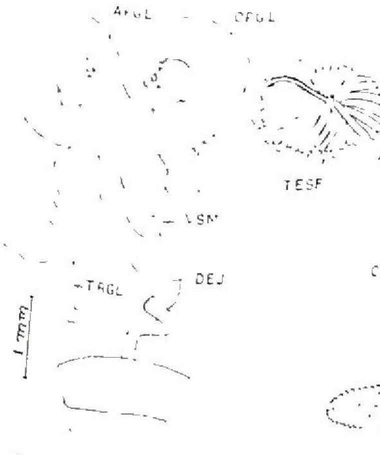

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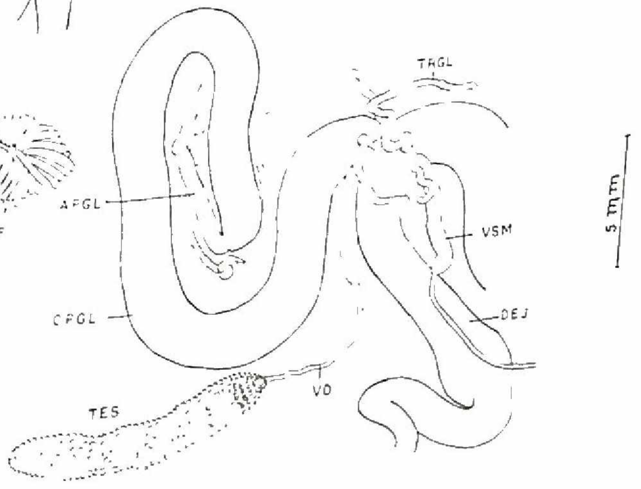


13

PLATE IX

Histology of the Male Internal Reproductive Organs

Eretes sticticus

Fig. 1	L.S. of testis
Fig. 2	T.S. of the vas deferens between the testis and the epididymis
Fig. 3	T.S. of the vas deferens between the epididymis and the lateral ejaculatory duct
Fig. 4	T.S. of common ejaculatory duct
Fig. 5	T.S. of accessory gland

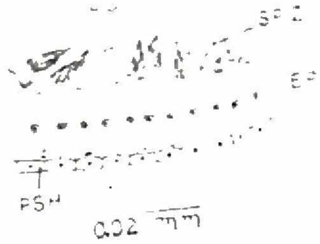
Dineutes unidentatus

Fig. 6	T.S. of the vas deferens
Fig. 7	T.S. of the lateral ejaculatory duct

Figs. 3, 4 and 6 are drawn to the same scale of Fig. 2


T
PSH
EP
SPZ
0.25 mm

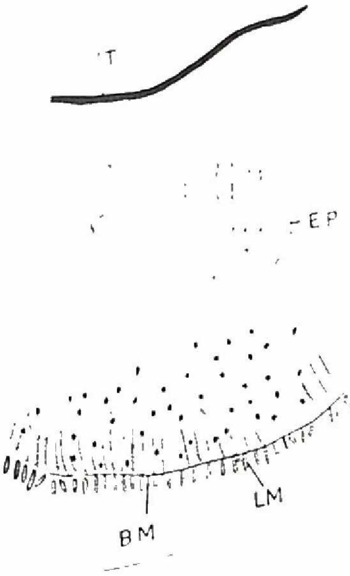
1


SPZ
EP
PSH
0.02 mm

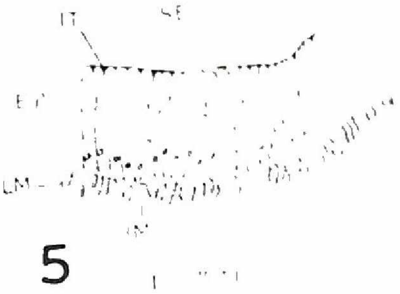
2


EP
CM

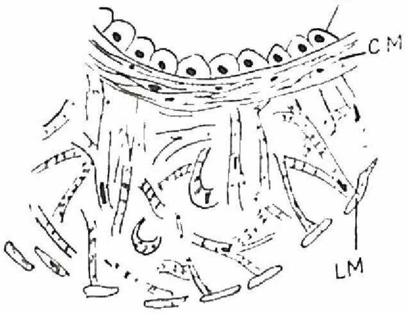
3


IT
EP
LM
BM

4


IT
SE
EP
LM

5


EP
CM
LM

6


U
EP
N
CM
LM
0.05 mm

7

PLATE X

Histology of the Internal Reproductive Organs of Males

Fig. 1	T.S. of the common ejaculatory duct
Fig. 2	T.S. of the accessory gland

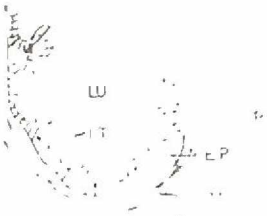
Hydrous indicus

Fig. 3	L.S. of the testis follicle
Fig. 4	T.S. of the vas deferens
Fig. 5	T.S. of the seminal vesicle
Fig. 6	T.S. of the common ejaculatory duct
Fig. 7	T.S. of the opaque gland
Fig. 8	T.S. of the appendicular gland
Fig. 9	T.S. of the transparent gland

Figs. 2, 3, 7 and 8 are drawn to the same scale of Fig. 1.

Figs. 5 and 6 are drawn to the same scale of Fig. 4.

PLATE X



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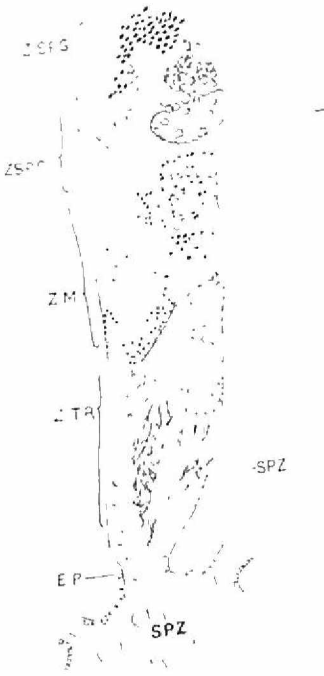

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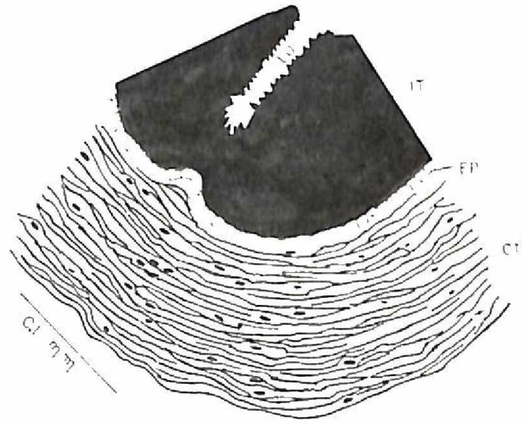

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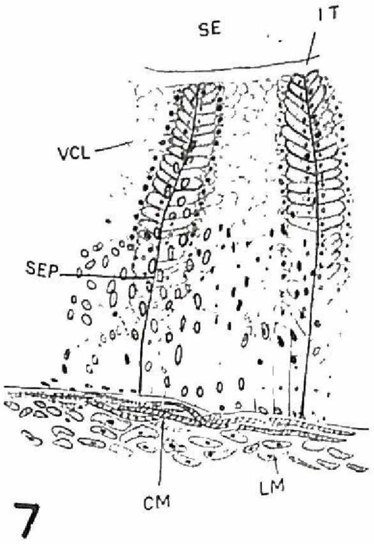

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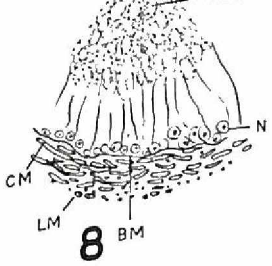

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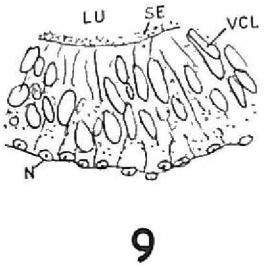

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PLATE XI

Internal Reproductive Organs of Females

Fig. 1	Dorsal view of the internal reproductive organs of	*Canthydrus laetabilis*
Fig. 2	Internal reproductive organs of	*Laccophilus flexuosus*
Fig. 3	Internal reproductive organs of	*Laccophilus sharpi*
Fig. 4	Dorsal view of the internal reproductive organs of	*Hyphydrus flavicans*
Fig. 5	Dorsal view of the internal reproductive organs of	*Guignotus* sp.
Fig. 6	Dorsal view of the internal reproductive organs of	*Herophydrus musicus*
Fig. 7	Dorsal view of the internal reproductive organs of	*Eretes sticticus*
Fig. 8	Dorsal view of the internal reproductive organs of	*Hydaticus luczonicus*
Fig. 9	Dorsal view of the internal reproductive organs of	*Cybister tripunctatus*
Fig. 10	Internal reproductive organs of	*Dineutes unidentatus*
Fig. 11	Dorsal view of the internal reproductive organs of	*Sternolophus rufipes*
Fig. 12a	Dorsal view of the internal reproductive organs of	*Hydrous indicus*
Fig. 12b	Branched ovarioles of	" "
Fig. 12c	Accessory gland from the tip of the calyx of	" "
Fig. 12d	Lateral view of the posterior end of the reproductive organs of	" "
Fig. 13	Internal reproductive organs of	*Hydrous senegalensis*

Figs. 6 and 7 are drawn to the same scale of Fig. 2.

PLATE XI


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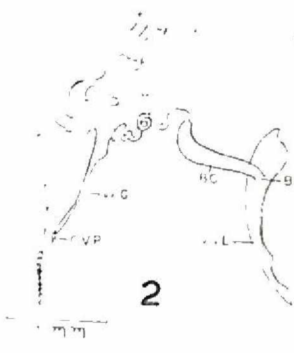

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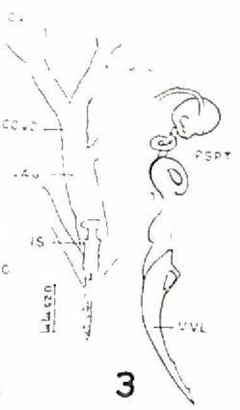

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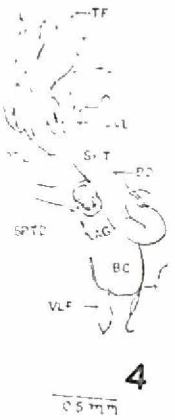

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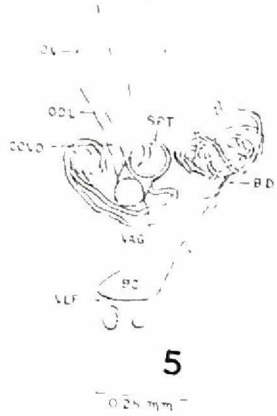

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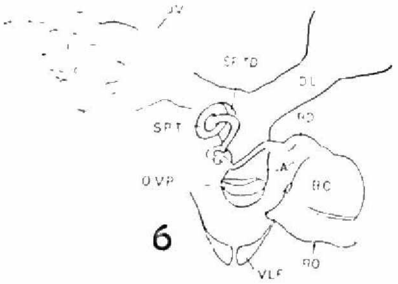

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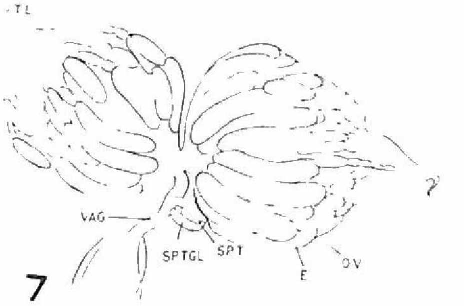

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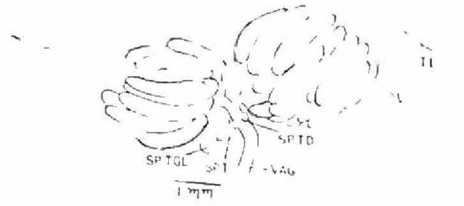

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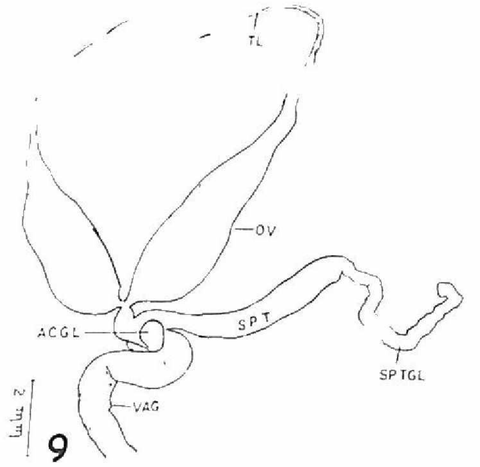

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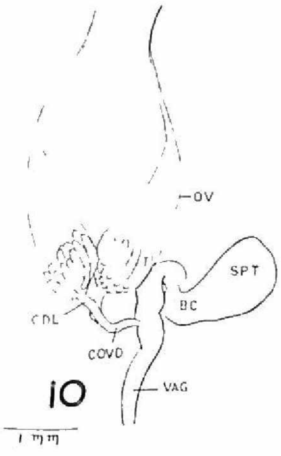

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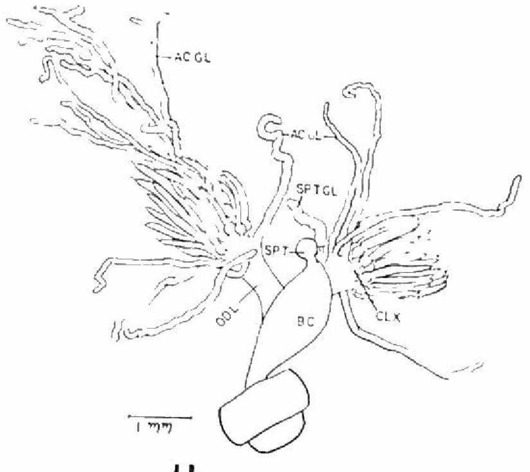

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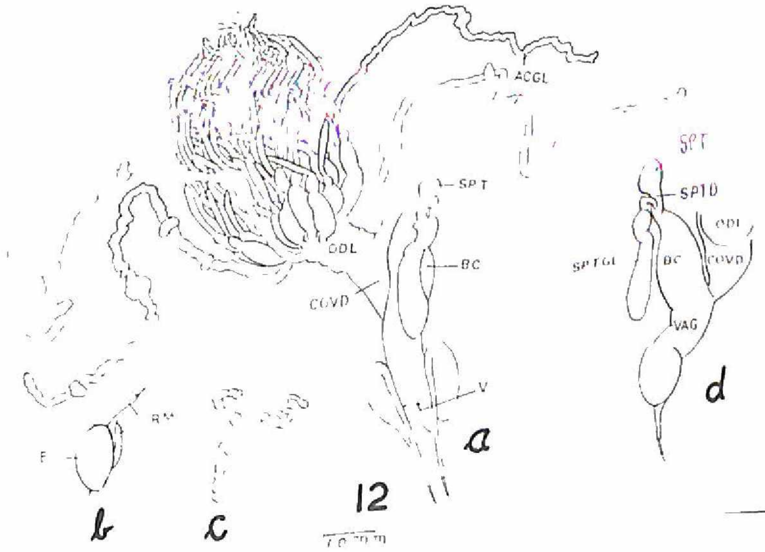

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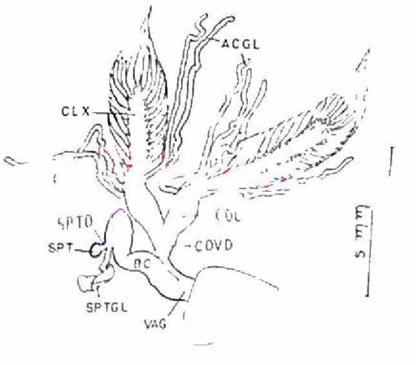

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PLATE XII

Histology of the Internal Reproductive Organs of Females

Eretes sticticus

Fig. 1 L.S. of the polytrophic ovariole

Fig. 2 T.S. of the lateral oviduct

Fig. 3 L.S. of the spermatheca

Fig. 4 L.S. of spermathecal gland

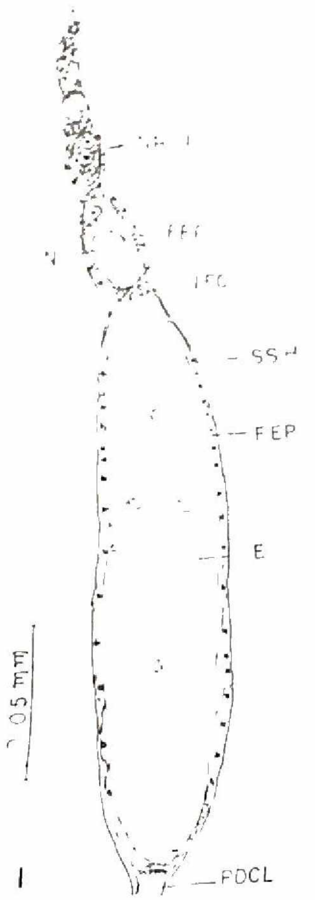
Fig. 5 T.S. of the vagina

Dineutes unidentatus

Fig. 6 T.S. of the common oviduct

Figs. 3, 4 and 5 are drawn to the same scale of Fig. 2.

PLATE XII



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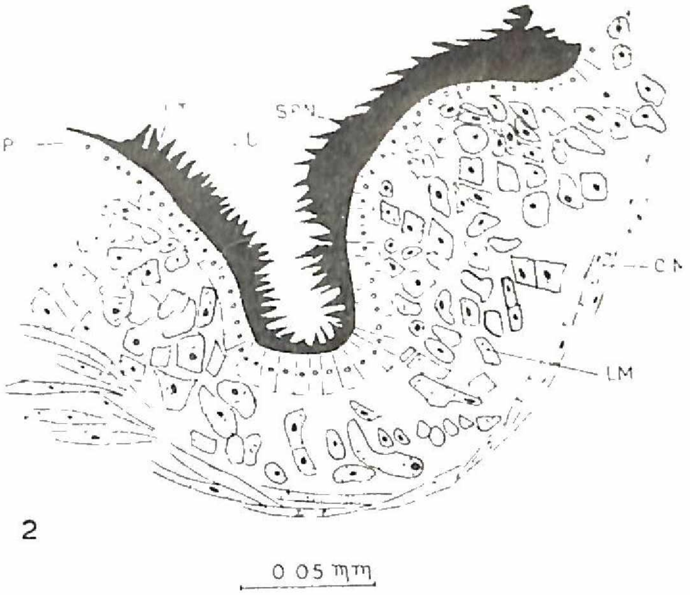

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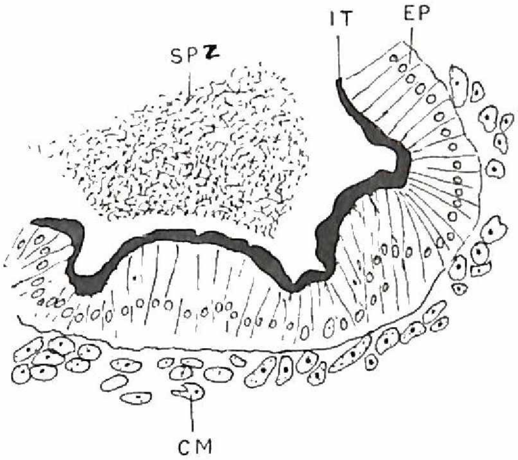

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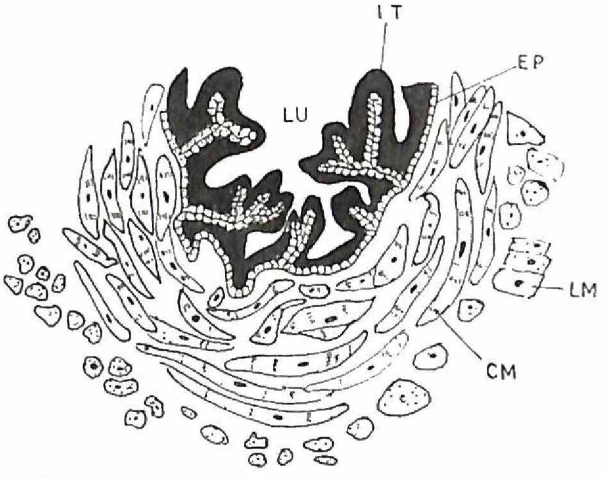

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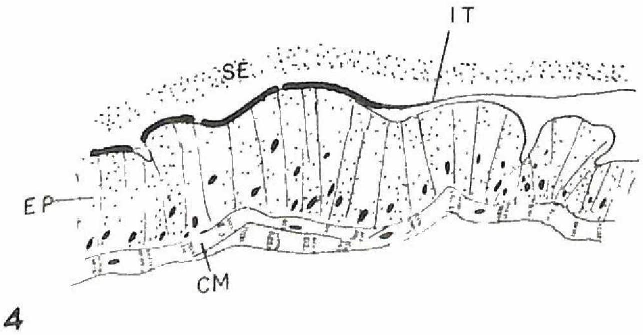

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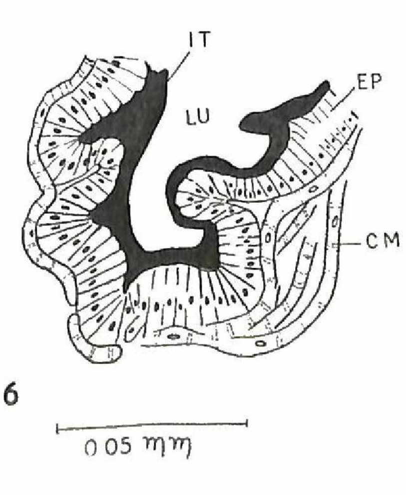

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PLATE XIII

Histology of the Internal Reproductive Organs of Females

Dineutes unidentatus

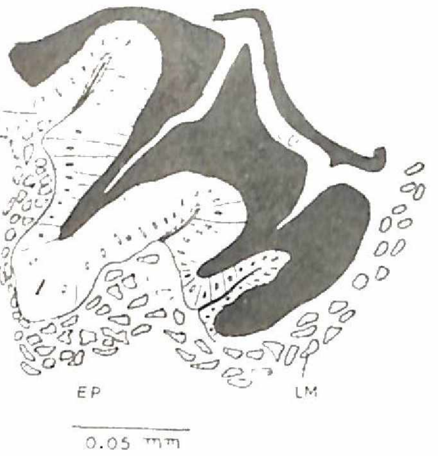
Fig. 1	T.S. of bursa

Hydrous indicus

Fig. 2a	L.S. through the anterior part of the germarium
Fig. 2b	L.S. through the posterior part of the germarium
Fig. 2c	L.S. through the region of the developing egg and the developed egg
Fig. 3	T.S. of accessory gland of the lateral oviduct
Fig. 4	L.S. of the spermathecal gland
Fig. 5	T.S. of the spermathecal capsule
Fig. 6	L.S. of the spermathecal duct

Figs. 2b and 2c are drawn to the same scale of Fig. 2a.

PLATE XIII



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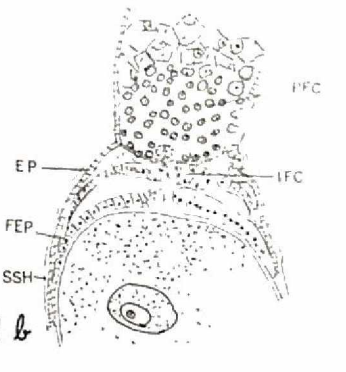

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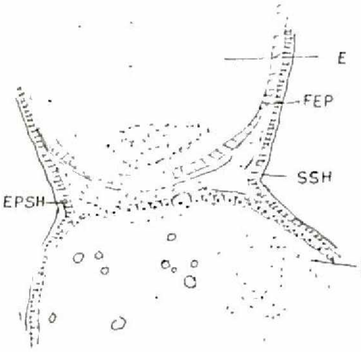

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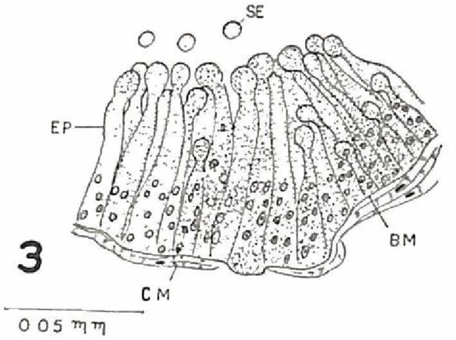

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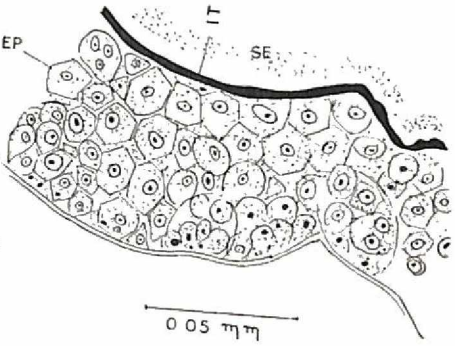

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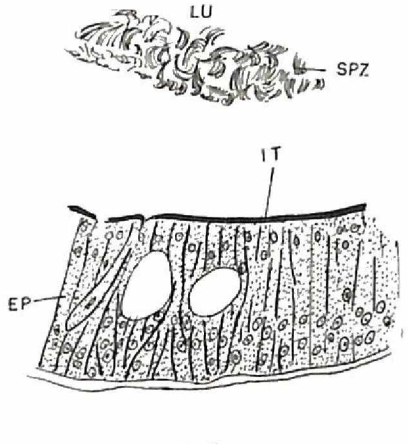

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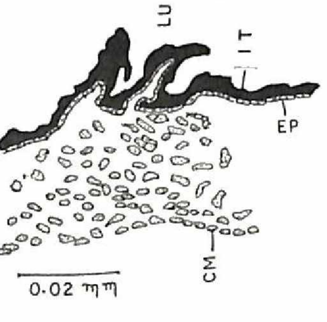

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PLATE XIV

Accessory Copulatory Structures

Fig. 1 Protarsus of *Laccophilus sharpi*

Fig. 2 Protarsus of *Laccophilus flexuosus* (diagrammatic)

Fig. 3 Protarsus of *Hydrovatus acuminatus*

Fig. 4 Protarsus of *Hyphydrus flavicans*

Fig. 5 Protarsus of *Guignotus* sp.

Fig. 6 Protarsus of *Herophydrus musicus*

Fig. 7 Protarsus of *Copelatus* sp.

Fig. 8 Protarsus of *Eretes sticticus*

Fig. 9 Protarsus of *Hydaticus luczonicus*

Fig. 10 Mesotarsus of " "

Fig. 11 Protarsus of *Cybister tripunctatus asiaticus*

Fig. 12 Protarsus of *Dineutes unidentatus*

PLATE XIV

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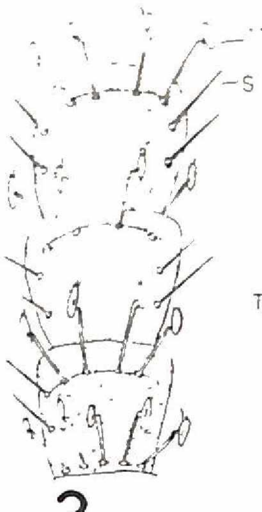

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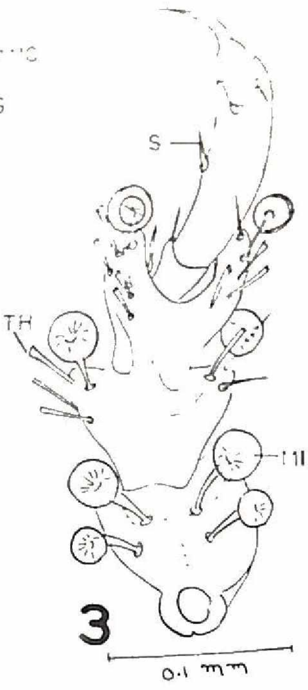

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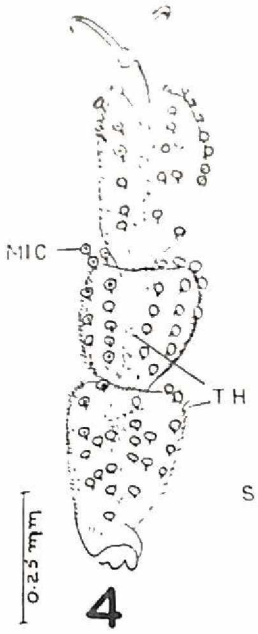

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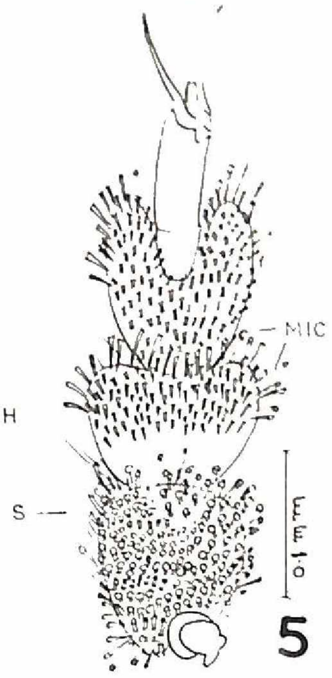

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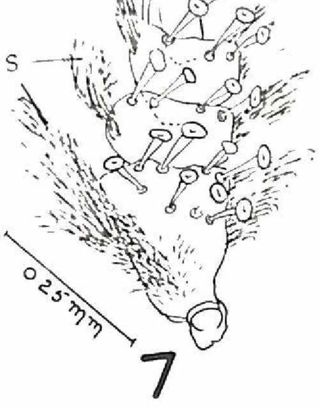

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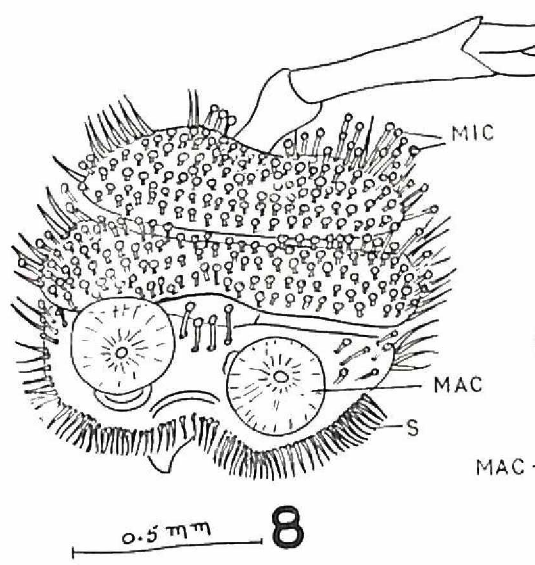

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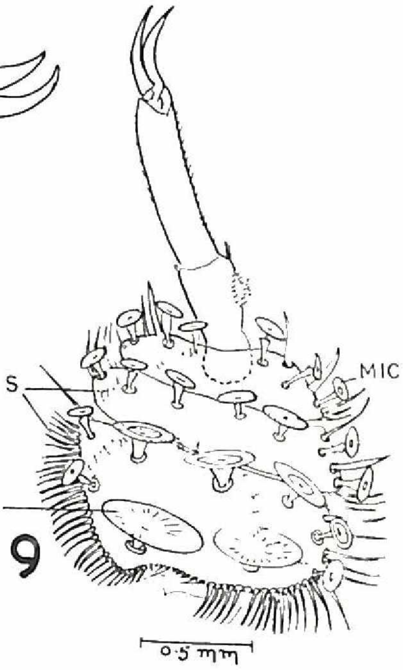

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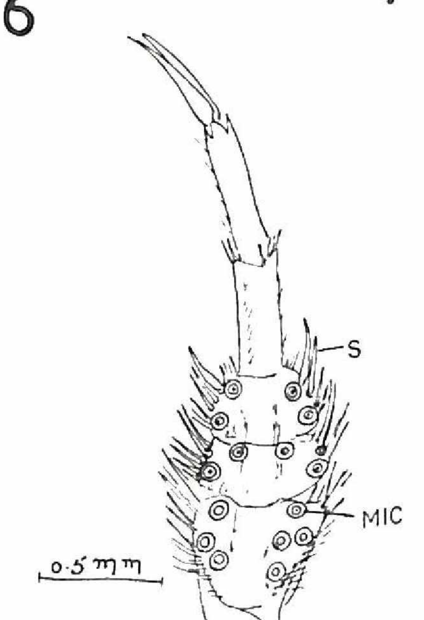

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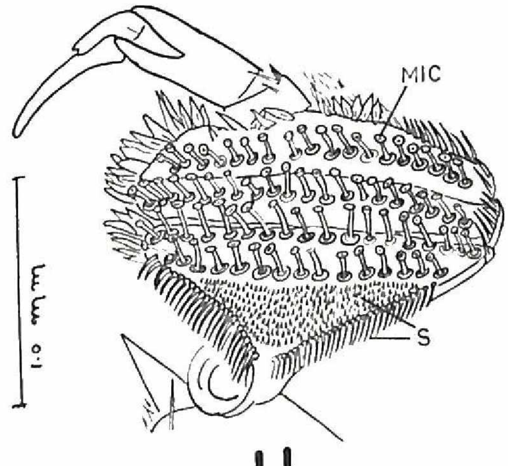

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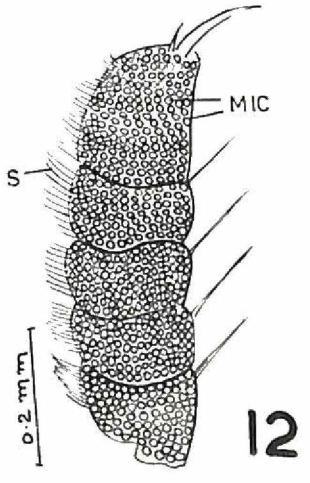

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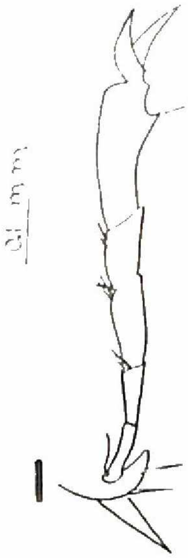
PLATE XV

Accessory Copulatory Structures

Fig. 1	Protarsus of *Paracymus evanescens*
Fig. 2	Protarsus of *Hydrous indicus*
Fig. 3	Protarsus of *Hydrous senegalensis*
Fig. 4	Protarsus of *Berosus indicus*
Fig. 5	Protarsus of *Berosus pulchellus*
Fig. 6	Protarsus of *Berosus* nr. *nigriceps*
Figs.7 to 13	Suggesting the origin and evolution of paraprocts

PLATE XV



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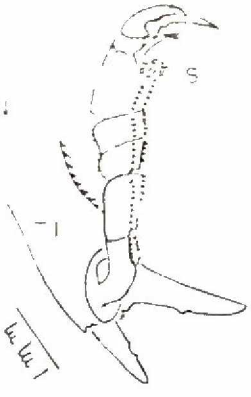

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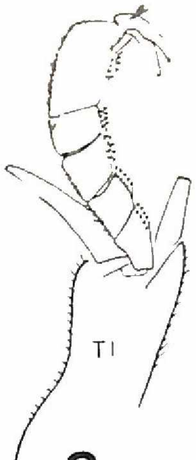

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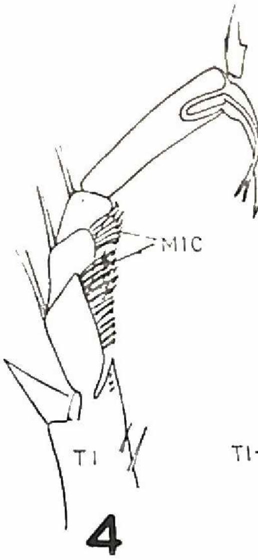

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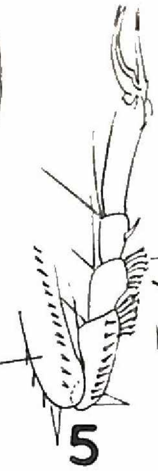

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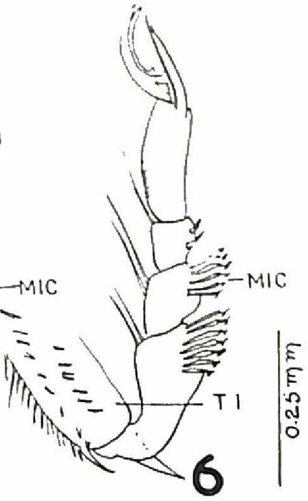

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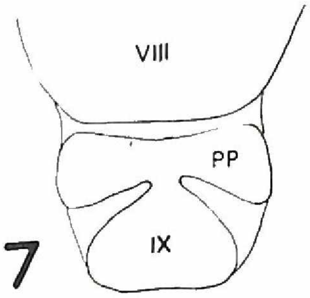

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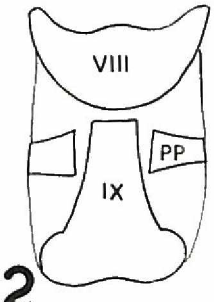

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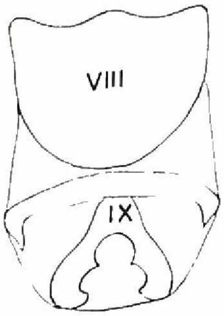

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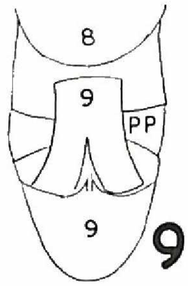

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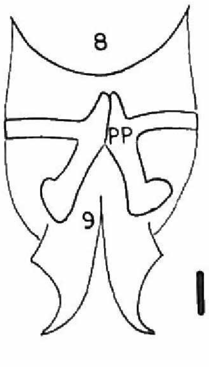

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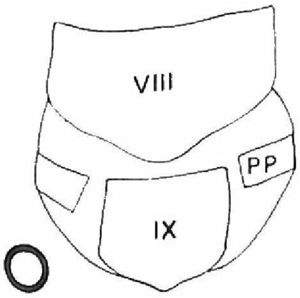

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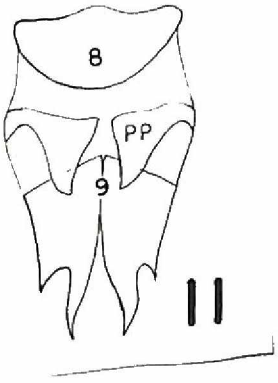

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PLATE XVI

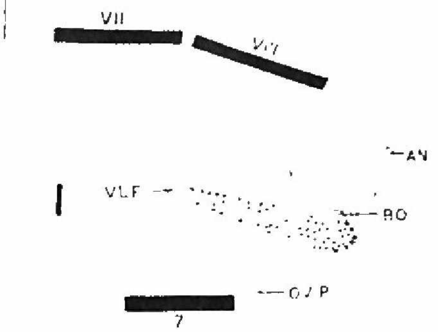
Figs. 1 to 6 : Suggesting the evolution of the female external genitalia

Fig. 1	Representing Hydroporinae	(Diagrammatic)
Fig. 2	Representing Noterinae	(")
Fig. 3	Representing Laccophilinae	(")
Figs.4 and 5	*Agabus* and *Ilybius* of Colymbetinae	(")
Fig. 6	Representing Dytiscinae	(")
Figs.7-11	Figs suggesting the origin of Diorificid type of reproductive organs	
Figs.12-13	(Saccular type), Fig. 12(Diorificid type) and Fig. 13 (Tubular type): Evolution of the three types of reproductive organs observed in Coleoptera	

Figs. 14 to 16 : Figures suggesting the evolution of adhesive setae

Fig. 14	Tenent hair
Fig. 15	Microcupule
Fig. 16	Macrocupule

PLATE XVI



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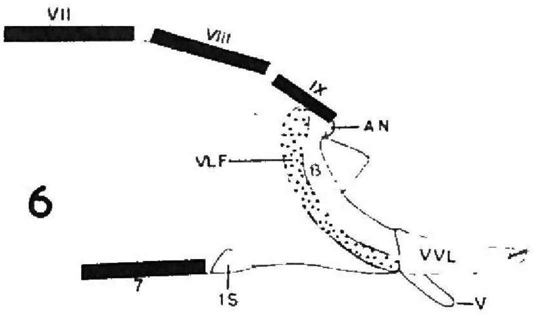

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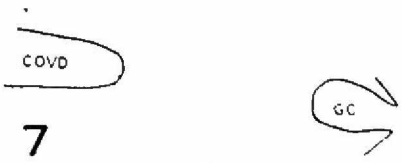

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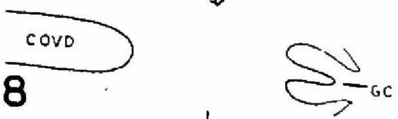

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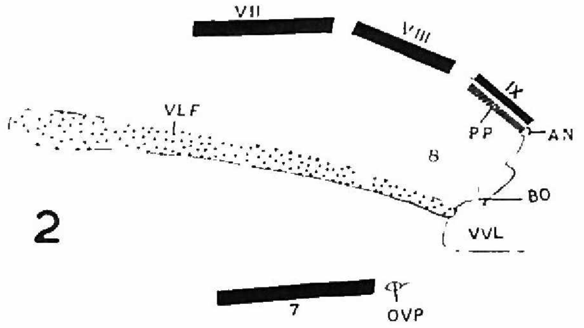

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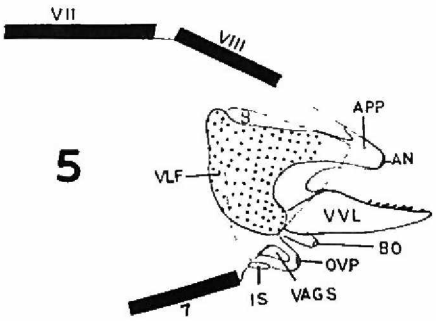

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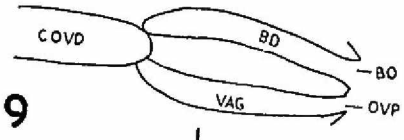

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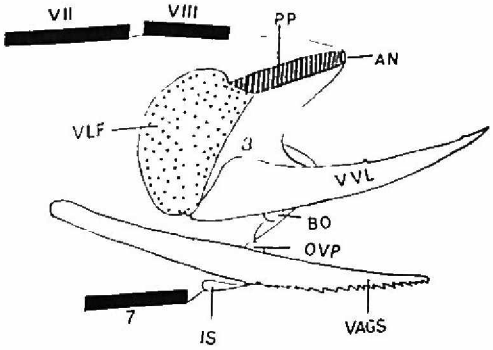

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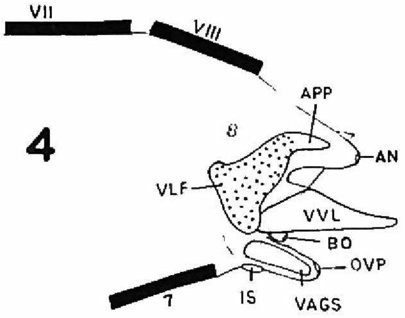

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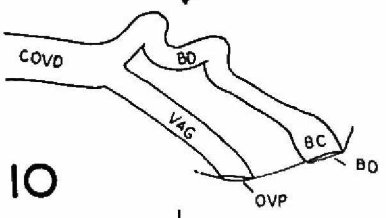

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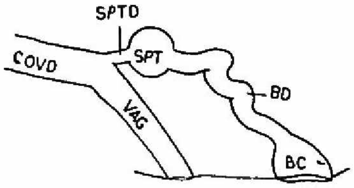

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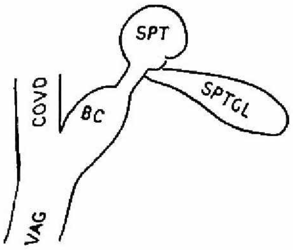

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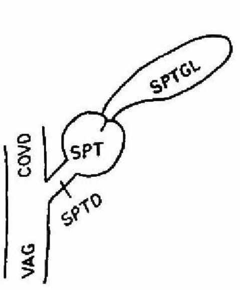

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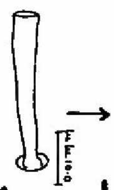

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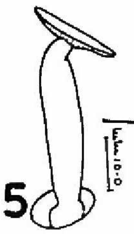

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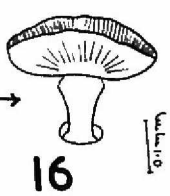

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