DISCUSSION

For the sake of convenience, the discussion portion of the thesis has been divided into two parts:

1. Internal Genital Organs.
2. External Genital Organs.

1. INTERNAL GENITAL ORGANS

(A) MALE

The Testes

Wm. S. Marshall (1914) describes the testes in Libellula quadrimaculata Linn. arising in the third abdominal segment and extending dorsal to the mid-intestine up to the posterior margin of the seventh abdominal segment. Tillyard (1917), George (1928) and Chopard (1949) mentioned that the testes in dragonflies occupy the dorso-lateral sides of the alimentary canal between the fourth and the eighth abdominal segments. Srivastava (1979) states that the position of the testes is different even
in the members of the same subfamily Libellulinae (Anisoptera) in which they extend from the fifth up to the seventh abdominal segments. According to the present investigation, the testes are situated in the posterior half of the seventh and the whole of the eighth abdominal segments only in *Pseudagrion rubriceps* Selys, *Pseudagrion decorum* (Rambur), *Carigrion coromandelianum* (Fabr.), *Ischnura senegalensis* (Rambur), *Ischnura rufoestyla* Selys, *Agriocnemis pygmea* (Rambur) and *Enallagma parvum* Selys. The testes extend slightly forwards beyond the middle of the seventh abdominal segment in *Enallagma malaynum* Selys and remain only in the posterior one-third of the seventh abdominal segment in *Copera marginipes* (Ramb.), besides occupying the whole of the eighth abdominal segment.

The position of the testes in relation to the alimentary canal is dorsal in *Aeschna brevistyla* Ramb. (Tillyard, 1917); sub-dorsal in *Crocothemis servilia servilia* Drury (Srivastava, 1963a); ventro-lateral in *Bradinopyga geminata* Rambur (Prasad & Srivastava, 1964); and lateral to the gut in *Diplacodes trivialis* Rambur (Srivastava, 1979). Midttun (1974) states that the testes lie one along each side of the alimentary canal with their anterior part on the dorso-lateral side of the gut. In passing backwards, they first slope gently ventro-laterally and then ventrally so that the posterior part of each testis comes to lie ventro-lateral to the alimentary canal. However, the testes are situated on the dorsal side of the alimentary canal in all the Zygoptera species investigated except for *Agriocnemis pygmea* (Rambur) and *Enallagma malaynum* Selys in which these lie dorso-laterally to the gut. It is thus evident that the position of the testis is more or less constant in the members of the family Coenagrionidae (Zygoptera) studied by the author, while it seems variable in the Anisoptera species studied by Srivastava (1979) and other workers. Further, the testes are present only in the seventh and the eighth abdominal segments in all the Zygoptera investigated. The testes in Anisopteran species, however, extend from the fourth up to the
eighth abdominal segments. The posterior position of the testes in the Zygoptera appears to be an adaptation due to great elongation of the abdomen and to minimize the possible risk of internal damage to the gonads during its curling for the sperm translocation.

The damselfly testis is an elongated cylindrical structure. Histologically, it consists of a large number of spherical units termed lobules by Marshall (1914) and Tillyard (1917) which contain germ cells inside the investing membrane demarcating them from each other. All the lobules are ensheathed together in a peritoneal membrane which also encloses a longitudinal, common lateral duct within it. The duct receives the openings of the lobular ductules and continues posteriorly beyond the testis as the vas deferens. The germ cells in a lobule are all alike and represent only one stage of spermatogenesis. However, the germ cells in different lobules represent different stages of spermatogenesis, i.e. they may all be either spermatogonia, spermatocytes, spermatids or spermatozoa. A testicular lobule neither exhibits the different zones present in a typical insect testicular follicle namely the germarium, the zone of growth, the zone of maturation and the zone of transformation, nor are these recognizable as such in the testis itself. The germinal epithelium in the adult testes or the lobules is absent. There is no doubt that the testes in all the damselflies studied by the author are 'multilobular', a fact also expressed by many workers like Lillyard (1917), Whedon (1918), Srivastava (1959), Matsuda (1976), Richards & Davies (1977) and Srivastava (1979). Midtun (1974) termed the lobules as cysts and regarded the testis in Somatochlora arctica as 'unifollicular'. According to Snodgrass (1935), Niggleworth (1965) and Eidmann & Kühlhorn (1970), the sex cells contained in a cyst are at the same stage of transformation, while a follicle consists of a number of cysts arranged in an orderly succession along the follicle according to the age of their products. The structure of the
testes in all the species studied by the author reveals that
the lobules are not arranged in an orderly succession along
the testis. Rather, these are irregularly scattered. Therefore,
the testis of a damselfly is not equivalent to a typical
testicular follicle. Moreover, Richards & Davies (1977)
consider the lobes and follicles as synonyms which is clear
from their statement*, "As a rule each testis is a more or less
ovoid body, partly or completely divided into a variable number
of lobes or follicles that show very many variations in form
and arrangement among the different insect species". Further,
the testicular lobules have been observed by the author to open
into the longitudinal common lateral duct, by minute ductules,
especially when ripe. The cysts never possess ducts. These
considerations lead the author to regard the lobules as
equivalent to the lobes or the follicles and hence, the testes
in Odonata are 'multifollicular' and not unifollicular as
reported by Midttun (1974). The term 'lobule' in place of
'lobe' has been used by Odonatologists for the units containing
germ cells in the testis possibly to denote their small size
which in fact, is a reality.

The multifollicular contention of the author for the
testes in damselflies can be challenged due to the absence of
a germinal epithelium and the lack of the successive development
zones in the testicular lobules, both of which are, however,
seen characteristically in insect testicular follicles. Whedon
(1918) reported that the gonad in both the sexes of Lestes are
as fully developed in late larval stages as in the imagines.
George (1928) also found a well developed testis in which the
primary germ cells were clearly marked even in the early
nymphal stage of Agrion. Agreeing with these views, it appears
that the germinal epithelium degenerates early in the nymphal
stages of the damselflies studied, leaving behind only a thin
limiting membrane in the adult stage to enclose the germ cells
which it proliferated. This is an adaptation of the reproductive

system in Odonata, enabling these insects to commence reproduction by mating soon after assumption of the imaginal form, which is usually much shorter as compared to their larval life span.

Tillyard (1917) describes a definite arrangement of the mature and immature lobules in relation to the common longitudinal duct inside the testis. In the present study also, many testicular lobules situated near the common duct in the testis of P. decorum, I. senegalensis, E. malaynum, E. parvum, A. pygmea and C. marginipes contain germ cells in more mature condition (spermatosoa) than those which are located away from the duct. Such a condition in the testis develops due to distension and prolongation of the wall of the ductules of ripe lobules and the passage of the spermatosoa through it into the longitudinal common duct. The ductules themselves become so gorged up with the descending spermatosoa that they swell up considerably and appear like lobules in a transverse section of the testis.

Marshall (1914), Srivastava (1963b), Midttun (1974) and Matsuda (1976) describe the presence of the common duct in the centre of the testes of Anisopteran species in which it runs longitudinally throughout the length of the gonad. In all the species investigated by the author, the common duct of the testis has been found to be laterally situated on the outer side of the gonad but within the peritoneum. In Agriocnemis pygmea (Rambur) and Enallagma malaynum Selys, this duct is slightly displaced towards the dorsal side. It is evident from the above account that the common duct of the testis is centrally located in most of the Anisopteran species while it is situated laterally in the testes of all the Zygopteran Odonata studied.

The Vasa Deferentia

The vas deferens is a bent tube which emerges out posteriorly from the testis near the end of the eighth abdominal segment. In fact, it is the posterior continuation of the
longitudinal lateral duct of the testis which after emerging, turns ventrally and inwards to become ventral to the gut in the middle of the ninth abdominal segment. Tillyard (1917), Midttun (1974) and Srivastava (1979) mention the position of the vas deferens in the eighth and ninth abdominal segments in the Anisoptera species studied by them. According to the present study carried out in the Zygoptera species, the vas deferens lies in the ninth abdominal segment only.

The vas deferens is morphologically as well as histologically divisible into two regions, a proximal region and a distal region in the species *Pseudagrion rubriceps* Selys, *Pseudagrion decorum* (Rambur), *Ischnura senegalensis* (Rambur), *Ischnura rufostigma* Selys, *Enallagma malaynum* Selys and *Enallagma parvum* Selys. There are, however, three morphological divisions in the vas deferens in *Ceriagrion coromandelianum* (Fabr.), *Agrionemis oecum* (Rambur) and *Coptera marginipes* (Ramb.). Marshall (1914) states that a central core of epithelial cells is present in the lumen of the vas deferens in *Libellula quadrivittata*. Midttun (1974) in *Somatochlora arctica* describes the epithelium of the vas deferens as being ciliated. In the present investigation, the author has been unable to confirm the presence of these structures in the species studied.

The vasa deferentia serve to carry the spermatozoa from the testes, where they are produced, to the storage organ, the sperm sac and in the process temporarily store them also. For the purpose of storage, the middle and the distal regions of the duct are modified and enlarged so as to acquire spacious lumen. Asahina (1954) termed the conspicuously dilated middle portion of the vas deferens as vesicula seminalis. In the present study, the vasa deferentia do not show any as prominent dilation to be named as vesicula seminalis. In the adult specimens belonging to *P. rubriceps*, *P. decorum*, *I. senegalensis*, *I. rufostigma*, *E. malaynum* and *E. parvum*, the distal region of
each vas deferens is coloured white to faint red. In post-
teneral and sexually mature specimens of the same species the
colouration in the distal region of the vas deferens changes
to dark brownish-black. As far as the author is aware, this
is a peculiar and new phenomenon connected with the reproductive
system of Odonata which has not been reported by any worker so
far. It has also been found out that the colour darkening
takes place due to accumulation of brownish-black pigment
granules in the cytoplasm of the peritoneal cells. The pigment
is produced possibly as a byproduct during the intensive
glandular activity of the epithelium.

The Sperm Sac

The sperm sac is a prominent median saccular organ
located in the middle of the ninth abdominal segment. It is
formed by the union of the distal extremities of the vasa
deferentia of the two sides immediately above the male gonopore
and functions as a sperm storage organ. This organ has been
termed seminal vesicle (Marshall, 1914), vesicular sac (George,
1928), vesicule seminalis (Chopard, 1949), vesicula seminalis
(Midttun, 1974), sperm reservoir (Asahina, 1954) and storage
reservoir (Waage, 1979). However, it is popularly termed sperm
sac by a large number of workers namely Tillyard (1917), Bhedon
(1916), Matsuda (1976), Richards & Davies (1977) and Srivastava
(1979).

Srivastava (1965-67) states that a sperm sac is absent
in Aeshnidae contaminata and there is only a horizontal tube
in its position. In other species studied by him (Srivastava,
1959) the sperm sac is in the form of an oval or rounded
in Davidius, and Srivastava (1979) in Diplacodes describe the
sperm sac as a bilobed organ. In the present study also, the
author found a bilobed shape of the sperm sac in Psuedagrion
rubriceps sely, Aeshnidae oxygnea (Ramhur) and Coptera
marginipes (Ramh.). In other species, however, the shape of
the sperm sac varies. It is bulb-shaped in *Pseudagrion decurum* (Hambur), dumb-bell shaped in *Ceriagrion coronandellianum* (Fabr.), spherical in *Ischnura senegalensis* (Hambur), oval in *Ischnura ruffostigma* Selys, pear-shaped in *Enallagma malaynum* Selys and heart-shaped in *Enallagma parvum* Selys. It is only in the *E. parvum* that the caudal end of the fully distended sperm sac projects in the anterior region of the tenth abdominal segment. It is thus evident that the shape of the sperm sac is variable in the species studied and the variation is of great taxonomic importance.

Many workers have expressed contradictory views regarding the nature of the sperm sac. Marshall (1914) discerned an internal cuticular lining in it which is suggestive of the ectodermal origin of the sperm sac. Chopard (1949) states that the "ejaculatory duct is dilated into a seminal vesicle" (sperm sac) and hence it is ectodermal. Tillyard (1917), George (1928), Middlton (1974) and Matsuda (1976) regard the sperm sac as mesodermal in origin. Most of the workers have stated clearly that the sperm sac develops as a result of dilation of the dorsal wall of a short common duct formed by the union of the two vasa deferentia in the middle of the ninth abdominal segment just above the male gonopore. The present investigations by the author reveal that the histological structure of the sperm sac is same as that of the distal region of the vas deferens, thereby establishing beyond doubt an intimate relationship between the two organs. The vasa deferentia are clearly mesodermal in origin. Considering this fact alongwith the similarity of structure between the sperm sac and the vas deferens, and the absence of a chitinous intima in the organ, the mesodermal nature of the sperm sac becomes quite evident. The sperm sac is, therefore, definitely mesodermal in origin, at least in the Zygopteran species studied by the author.

A new and peculiar phenomenon of cumulative pigmentation
associated with the maturity of the insect (damselfly) has been observed by the author in the wall of the sperm sac also in the species Pseudagrion rubriceps Selys, P. decorum (Rambur), Ischnura senegalensis (Rambur), I. rufostigma Selys, Enallagma malaynum Selys and E. parvum Selys. In young and immature specimens, the sperm sac is coloured white to faint red. In post-teneral and sexually mature specimens, the colouration in the wall of the sperm sac changes to brownish-black, a phenomenon similar to that seen in the distal region of the vas deferens. The histological study of the sperm sac shows that the colour darkening is due to accumulation of brownish-black pigment granules in peritoneal wall. It has been noticed by the author that the epithelial cells in the wall of the sperm sac exhibit intense secretory activity and during the process become gradually disorganised. The lumen becomes filled with large amount of secretory material. It is only at this stage that the brownish-black pigment granules appear in the wall of the sperm sac. It seems that the pigment granules are formed as a byproduct during the hectic metabolic activity of the epithelium.

The Ejaculatory Duct

George (1928) while working out the development of the efferent genital ducts in Agriion, stated that an invagination starts from the bases of the gonapophyses of the ninth segment. "This ectodermal invagination, as it extends gradually into the body cavity, meets the fused vasa deferentia, and at a still later stage the invagination extends to the fused vasa deferentia and becomes connected with them. The distended portion of the fused gonoducts at the point where the invagination referred to joins them later develops into the vesicular sac". From this account it is now quite clear that the sperm sac and the ejaculatory duct are different structures. The occurrence of an ejaculatory duct in Odonata has not been clearly stated so far by any reputed morphologist or odonatologist, namely Tillyard (1917), Whedon (1918), Snodgrass (1935), Asahina (1954)
and Richards & Davies (1977) etc. At one place, however, Imms (1957) mentions vaguely about it when he says, "the ectodermal invagination in the Thysanura, Plecoptera and Odonata is little more than a deep cup-like pit".

The ejaculatory duct, as observed by the author, is an inconspicuous tubular organ of microscopic size situated in the cavity of an obliquely placed chitinous structure on the antero-dorsal side of the male gonopore. The ductus ejaculatorius connects the ventral portion of the sperm sac with the genital aperture. It normally gets broken during the dissection of the internal genital organs while the sperm sac is being freed ventrally from the gonopore. However, its structure has been studied from the series of histological sections. The ejaculatory duct possesses a structure similar to that of the sperm sac except that the duct is lined internally by a very thin chitinous intima and the wall is more muscular. It is quite likely that the thick muscular wall of the ejaculatory duct helps in the quick pumping out of the sperms through the genital aperture. The ejaculatory duct is, thus, ectodermal in origin.

The supervisor of this thesis was the first worker to report unambiguously the presence of an ejaculatory duct in Anisopteran dragonflies (Srivastava, 1959). Later on, his findings have been confirmed by Midtun (1974) and Matsuda (1976). In the present study on the Zygopteran species, the author has also found the presence of an ejaculatory duct which is slightly more distinct than that found in the Anisopteran species.

The Accessory Glands

No definite accessory gland has been discovered in connection with the male internal reproductive system of the Zygopteran species investigated. This is in accord with the views of Marshall (1914), Silliday (1917), Whedon (1918), George (1928), Matsuda (1976) and Srivastava (1979). Asahina (1954)
has described a pair of blind glands (supposed to be accessory glands) attached just before the common opening in *Epiophlebia* (Anisomyoptera) in which a sperm sac is absent. He has neither described them in detail nor studied their histological structure. As stated in previous pages, the bilobed shape of the sperm sac is the most common form occurring in Odonata. It is possible that the blind glands in *Epiophlebia* represent the two lobes of the sperm sac which have become greatly elongated and diverticula-like in appearance, a view supported by Matsuda (1976). The glandular function in male Odonata has been, in fact, taken up by the epithelial cells of the wall of the vas deferentia and the sperm sac. Midtun (1974) has convincingly demonstrated the glandular activity of the epithelial cells in the wall of the vas deferens and the vesicula seminalis. It has also been observed in the present study that the epithelial cells in the wall of the vas deferentia and the sperm sac show intense secretory activity. In the epithelium, the cell-boundaries are indistinct, the cytoplasm is granular and highly vacuolated often showing empty spaces at places, and the nuclei are granular and usually nucleolated. The lumen is filled with secretion of two kinds, a granular secretion and a homogeneous secretion. The epithelial layer is reduced when the lumen of the organ is replete with secretion. These changes occur when the damselfly is in the process of attaining puberty. In younger specimens, however, the lumen is narrow, the epithelium distinct and the cytoplasm is of normal consistency. It has also been observed that the secretory activity is reduced in the upper part of the vas deferens.

**The spermatophore**

The occurrence of spermatophores in Odonata has been reported by a large number of workers viz., Marshall (1914), Tilleyard (1917), Whedon (1918), Chopard (1949), Brinck (1962), Hornuff (1968), Corbet (1974), and Richards & Davies (1977). However, Englemann (1970), Tuxen (1970), Wiglesworth (1972) and Matsuda (1976) do not mention about the occurrence of
spermatophore in the group. Asahina (1954) and Chapman (1971) describe the presence of a modified type of spermatophore termed 'spermiozeugma' and 'spermatodeasm' respectively. Srivastava (1959, 1963a & b and 1979); Widdowson (1974); and Pfau (1979)* contradict the occurrence of spermatophores in the Odonata altogether. A spermatophore as defined by Snodgrass (1935) is a "mass of sperms enclosed within a covering or capsule". Accepting it literally, the author has no hesitation to state that the spermatophores are not found in the Zygopteran species studied. However, the seminal fluid to be transferred is itself mucilaginous in which the sperm groups are embedded (Pl. XV, fig. 9). There is no covering, sac or the wall over the structure, nor the seminal fluid is divided into droplets or containers.

Engelmann (1970) while tracing the evolution of sperm transfer mechanism from male to female insects, considers the occurrence of spermatophores to be a primitive feature and a device to ensure safe internal deposition of sperms into the female system. Thysanura, Diplura and Collembola produce spermatophores which are deposited on the substratum to be picked up later by the female. The Odonata is also a primitive order of pterygote insects which, however, lacks a functional 'true penis'. The Odonates are unique in possessing a characteristic secondary copulatory apparatus on the ventral side of the second and third abdominal segments in males. The transference of sperms from the male to the female has to be accomplished indirectly via a spermatophore and by a functional intermittant organ of the secondary copulatory apparatus. It is, therefore, necessary in the male Odonata to translocate the sperms from the genital pore in the ninth abdominal segment to the vesicula spermaliis (penis vesicle) of the secondary copulatory apparatus by curling its abdomen. In order to achieve this successfully and to minimize the hazards during

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such a transfer, the Nature has provided these insects with a thickened seminal fluid of mucilaginous consistency in which sperm groups are embedded. This possibly led earlier odonatologists to misinterpret these sperm groups as 'spermatophores'. Moreover, the functional penis of the male and the '8th complex' of the female are well developed and highly complicated organs which are complimentary and suitably adapted to each other in structure. The bursa of the '8th complex' receives the intromittent organ during copulation ensuring internal deposition of the sperm safely into the spermatheca. Besides this, the definite accessory glands are also absent totally in the males. These facts greatly decrease the necessity of the spermatophore occurrence in Odonata.

Srivastava (1959), Kalla and Nath (1970) and Midttun (1974) mention the occurrence of free spermatozoa in the seminal fluid in Anisopteran species, where the functional penis is joined directly to the penis vesicle (vesícula spermalis) thereby reducing considerably the hazards during the sperm transfer. In the Zygoptera species investigated by the author, the functional penis does not communicate directly with the vesícula spermalis, thereby increasing the probabilities of sperm loss during the transference. Therefore, in Zygoptera the seminal fluid possessing sperm groups ('Spermidozeugma' of Hallowitz, 1916 & 1918) has become thickly mucilaginous so that it does not flow out easily. Further, the males of higher insect species generally transfer free spermatozoa into the female (Engelmann, 1970 and Schaller, 1971). On this account also the Zygoptera, in which sperm groups are involved in the transference, seem to be more primitive than the Anisoptera where free spermatozoa are transferred. This is in accord with the evolutionary position of the Zygoptera and Anisoptera, the former being primitive than the latter. It is thus evident that the method of sperm transfer is an indirect one in Odonata, occurring through a 'spermatophore-like mechanism' which is primitive as well as greatly modified, a fact consistent with the evolutionary position and high specialization of these insects.
(B) FEMALE

The Ovaries

Among the Anisoptera, Marshall (1914) states that the ovaries in Libellula quadrinaculata Linn. extend from the first abdominal segment unto the middle of the sixth abdominal segment. Tillyard (1917) describes the ovaries in Petalura gigantea Leach running separately*, from the base of the abdomen down to the anterior region of the seventh abdominal segment, dorsally on either side of the digestive tube. In Davidius, the anterior ovarian end begins at about the second abdominal segment and ends posteriorly at the level after seventh abdominal segment (Asahina, 1954). According to Prasad & Srivastava (1961), the ovaries in Pantaia flavescens Fabr. are situated between the first and the fifth abdominal segments only. In the Anisosygopteran species, Epiphebia superates Selys studied by Asahina (1954), the ovaries extend from the first abdominal segment unto the seventh abdominal segment. Among the Zygoptera, Whedon (1918) mentions the presence of the ovaries from the base of abdomen unto the posterior part of the eighth abdominal segment in Celopteryx. Asahina (1954) reports the position of the ovary in Mnaia between the abdominal segments one and eight. According to Johnson (1973), the ovaries in Arga extend from the first abdominal segment unto the seventh abdominal segment. In the present work, however, the position of the ovaries is different from these accounts as they extend from the base of the abdomen unto the middle of the seventh abdominal segment in all the Zygopteran species studied.

The above description evidently shows that the ovaries in Zygoptera usually extend from the base of abdomen posteriorly beyond the sixth abdominal segment often projecting into the eighth segment, than the ovaries in Anisoptera which reach unto the end of the sixth abdominal segment or slightly more. The

* Shown by Tillyard in the "Biology of Dragonflies" (1917) on page 220, figure no. 97.
position of the ovaries in the third and fourth abdominal segments described in *Agrion* by George (1926) is an exception and needs confirmation. It is also interesting to note that the position of the ovaries is more or less constant, at least in all the members of the family Coenagrilliidae studied by the author, a finding similar to that observed with the testes also.

The ovary comprises numerous panoistic ovarioles which are attached to a common lateral duct running throughout the length of the gonad. Tillyard (1917) and Matsuda (1976) state that the ovarioles are held closely together by a thick sheath. In the present study the author has not been able to find any sheath enclosing the ovaries which are, however, held together by adipose tissue filling the interovariolar spaces in the ovary. Moreover, the ovaries of the two sides are joined together by loose connective tissue, possibly rich in nutrients, forming a median dorsal ligament extending from the metanotum upto the dorsum of the ninth abdominal segment on the mid-dorsal side of the alimentary canal.

Prasad & Srivastava (1961) state that the ovarioles are arranged longitudinally on the ventral side of the lateral oviduct in the Anisoptera species *Pantala flavescens*. Johnson (1973) reports that each ovariole is attached by a pedicel to the medial side of the lateral oviduct in the Zygopteran *Argia moesta*. In the present investigation the ovarioles are attached to the dorso-mesal side of the common lateral duct, which has been named so to differentiate it from the portion of the oviduct without ovarioles.

The Oviducts

The common lateral ducts, as observed by the author, extend posteriorly beyond the ovaries to continue as short thin-walled oviducts, each lying on either side of the alimentary canal. Each oviduct arises subdorsally in the posterior part of the seventh abdominal segment and turns ventrallywards and
inwards. The oviducts of the two sides ultimately meet each other in the anterior part of the eighth abdominal segment below the alimentary canal to form a common median oviduct. The oviduct is not lined internally by a chitinous intima and hence, is mesodermal in origin. The author's findings regarding the position and nature of the oviducts are in conformity with the views of Marshall (1914), Whedon (1918), George (1928), Prasad & Srivastava (1961), Johnson (1973) and Matsuda (1976).

Whedon (1918) states that only one egg at a time, passes down the oviduct in Regaloperpus coeruleus while two or more eggs move through it in Calopteryx maculata. In the present study, however, up to a maximum of four eggs have been observed to descend down together in the oviduct at a time, especially in Pseudagrion rubriceps Selys, Ceriagrion coromandelianum (Fabr.), Ischnura rufostigma Selys and Enallagma parvum Selys.

The Common Median Oviduct (Oviductus Communis)

In all the species investigated, the oviducts of the two sides meet each other in the anterior part of the eighth abdominal segment below the alimentary canal to form a common median oviduct. The oviductus communis is a short thick-walled duct concealed from view by the presence of the eighth abdominal ganglion. The existence of a common median oviduct in Odonata has also been reported by Marshall (1914), Whedon (1918), George (1928), Prasad & Srivastava (1961), Johnson (1973) and Matsuda (1976). Tillyard (1917) and Richards & Davies (1977) are, however, silent on this point.

George (1928) in Agrion, Prasad & Srivastava (1961) in Pantaia and Matsuda (1976) in Mnaia describe the common median oviduct as a mesodermal structure. Snodgrass (1935) defines the oviductus communis as a median invagination of the body-wall into which open the lateral oviducts. The genital chamber, or the vagina, are derivatives of the posterior part of this median
oviduct. According to Tuxen* (1970) also, the common oviduct is "the ectodermal part of oviduct, from fusion of paired oviducts to gonopore", which is vulva. Evidently, the common median oviduct, genital chamber, vagina etc. are ectodermal in origin and, therefore, always provided with a chitinous intima. The common median oviduct in all the damselflies studied displays undoubtedly a histological structure similar to that of the oviduct but in addition, its lumen is lined internally by a distinct chitinous intima. The common median oviduct is, therefore, ectodermal in origin and not mesodermal as reported by Prasad & Srivastava (1961) and Matsuda (1976).

The '8th Complex'

Since the vagina, the bursa copulatrix and the spermatheca are not distinctly visible morphologically and only a microscopic study reveals their true identity, the author has named these organs collectively as the '8th Complex' after Prasad and Srivastava (1961) simply for the sake of convenience in description. As observed by the author, the '8th Complex' is a translucent white structure of composite nature situated beneath the alimentary canal in the posterior half of the eighth abdominal segment. It comprises a ventral tubular vagina, a dorsal saccular bursa copulatrix and a spermatheca arising from the latter. The assemblage of these organs is coated with adipose tissue which makes them indiscernible. Srivastava (1959) reports that the '8th Complex' shows rhythmic movements in the living condition of the insect, a finding which the present author has not been able to confirm in the species studied by him.

The Vagina

Tillyard (1917), Whedon (1918) and Johnson (1973) make no mention of the presence of a vagina in their descriptions of the odonate female reproductive organs. On the contrary,

Tillyard (1917), Whedon (1918), Chopard (1949) and Richards & Davies (1977) state that the two oviducts open into a large pouch-like spermatheca or bursa. Asahina (1954) also makes no reference to the presence of the vagina in the text, though he has shown its occurrence in the Table-15 given by him. In the present study, the author has observed the presence of a distinct tubular passage, termed vagina, on the ventral side of the '8th Complex', a finding in conformity with Asahina (1954), Prasad & Srivastava (1961) and Matsuda (1976). This is in agreement with the views of Snodgrass (1935) who regards the vagina, bursa copulatrix and spermatheca as separate morphological derivatives of the posterior portion of oviductus communis, i.e. the 'ectodermal invagination'. The early odonatologists perhaps due to lack of facilities and the minute size of these structures, mentioned simply the existence of a pouch-like structure at the posterior end of the female reproductive system which they termed bursa. In the present study, vagina has been observed to be composed of an anterior tubular portion and a posterior, genital atrium.

The Collar:- Tillyard (1917) mentioned for the first time, the presence of a hard chitinious structure, the 'Collar' projecting internally into the lumen of the pouch-like bursa or spermatheca in Petalura gigantea. Later on, Prasad & Srivastava (1961) and Johnson (1973) confirmed its occurrence in the vagina but assigned no function to this structure. The anterior tubular portion of the vagina as observed by the author, is characterized by strong muscularization externally and heavy chitinization internally. The chitinious intima of the vagina is specially thickened in the anterior wall to form a strongly sclerotized structure termed collar in the damselflies studied. The collar is situated in the anterior wall near the tri-junction of the common median oviduct, vagina and the bursa copulatrix. It

* A Morphological Study of a Relic Dragonfly Epiophlebia superestes Selys (Odonata, Anisocyogoptera), pages 82-83.
comprises a central portion and a pair of postero-ventrally directed, wing-like lateral arms. The antero-ventral end of the central portion is produced forward as a short spiny process, the anterior process of the collar. The author ventures to suggest a function to this organ for the first time. According to him, the central portion of the collar prevents the intrusion of penis into the oviductus communis besides providing surface for attachment of the anterior vaginal muscles. Its lateral arms seem to guide the penis tip to enter into the bursa copulatrix.

The chitinous intima is thickened and strongly developed also in the lateral wall of the anterior tubular portion of vagina forming a pair of laminate lateral plates which are connected dorsally. In addition to giving attachment to the sterno-vaginal muscles, the presence of these lateral plates is also attributed to the necessity of safeguarding the delicate wall against possible abrasion and injury during the entry of male intromittent organ inside the vagina during copulation.

The genital atrium:— As far as the author is aware, a genital atrium has not been described by any worker so far in the female internal genitalia of Odonata. Waage (1979), however, has recently depicted a structure similar to genital atrium in a scanning electron micrograph of the female reproductive tract in Calopteryx. In all the species investigated by the author, the anterior tubular portion of vagina opens posteriorly into a small thin-walled chamber termed genital atrium in the present work. Though lined by transparent cuticle, possibly soft in nature, this organ lies crumpled in the body cavity. The ducts of the accessory glands open into its postero-dorsal wall. The genital atrium is, therefore, a new discovery the function of which appears to hold the egg temporarily before its extrusion through the vulva. In the meantime, the secretion of the accessory glands is poured over the egg which is then laid in the plant tissue.
The Bursa Copulatrix

Snodgrass (1935) defines bursa copulatrix as a genital chamber or its part which acts like a copulatory pouch during mating. Richards & Davies (1977) mention the bursa copulatrix to be a pouch-like modification of the vaginal region. In the present work, a sac-like bursa copulatrix is found situated on the antero-dorsal side of the vagina in all the species investigated. The bursa copulatrix communicates with the vagina by a duct which enters into the vagina from the dorsal side of the collar. The histological structure of the bursa copulatrix is very similar to that of the anterior tubular portion of vagina. The epithelium is non-glandular and the lumen filled with spermatozoa in mated insects. This strongly indicates that the bursa copulatrix is a part of the vagina perhaps an evagination of it, which, in fact is true (George, 1928; Srivastava, 1959).

The bursa copulatrix has been named differently by various workers. It is termed Spermatheca (Tillyard, 1917; Matsuda, 1976; Richards & Davies, 1977); Spermathecal pouch (George, 1928); Median spermathecal sac (Prasad and Srivastava, 1961) and Seminal receptacle (Marshall, 1914). The author has observed, at least distinctly in Ischnura senegalensis (Rambur) (Pl. XVII, figs. 5 & 7) that the distal portion of the penis during copulation enters into the cavity of this sac which evidently acts as a copulatory pouch. Moreover, the diameter of the bursa copulatrix has been found to be nearly equal to the size of the distal portion of the penis in the species investigated. The author, therefore, regards this organ as bursa copulatrix on the basis of its definition given by Snodgrass (1935).

Tillyard (1917) mentions a pouch-like bursa in Petalura gigantea. Pfau (1971) depicts a cylindrical bursa copulatrix in Ischnura elegans. Weage (1979) reports a round shape of the bursa copulatrix in Calopteryx maculata. This account indicates
that the shape of the bursa copulatrix is variable in Odonata. In the present work also, the author has observed that the shape of the bursa copulatrix varies in different species. It is spherical in *Pseudagrion rubriceps* and *Coepa marginipes*; oval in *Pseudagrion decorum*; elliptical in *Ceriagrion coromandelianum*, *Agriocnemis pygmaea* and *Enallagma parvum*; cylindrical in *Ischnura rufostigma*; cylindrical with a tapering apex in *Ischnura senegalensis*; and blindly elongated in *Enallagma malaynum*. The shape of the bursa copulatrix thus appears to be of great taxonomic significance.

The Spermatheca

Tillyard (1917), Asahina (1954) and Richards & Davies (1977) state the presence of pouch-like spermatheca in the female reproductive system of dragonflies confusing it with the bursa copulatrix. The author during the present study has observed the presence of a well developed spermatheca which is quite separate from the bursa copulatrix in all the Zygopteran species studied except *Pseudagrion decorum* (Rambur). The spermatheca is a median organ, blind at the distal end but communicating proximally with the bursa copulatrix. Histologically, the spermatheca possesses a structure very similar to that of the bursa copulatrix and is, therefore considered an outgrowth of the latter.

The shape of the spermatheca varies in the different species investigated. It is bulb-shaped in *Pseudagrion rubriceps* and *Enallagma malaynum*; oval in *Ischnura rufostigma*; mango-like in shape in *Ischnura senegalensis*; conical in *Coepa marginipes*; elongated diverticulum-like in *Agriocnemis pygmaea* and *Ceriagrion coromandelianum*; and club-shaped in *Enallagma parvum*. This finding of the author that the shape of the spermatheca has a taxonomic importance is similar to that of Johnson (1973).

The spermatheca serves as a storage organ for the sperms
received via the bursa copulatrix during mating. This explains the presence of the spermas in the cavity of the bursa copulatrix as well as that of the spermatheca. Prasad & Srivastava (1961) state that spermathecal epithelium is glandular in *Pantala flavescens*. Johnson (1973) mentions that the spermathecal tube is enveloped in a glandular tissue in *Argia moesta*. In the present work also the author has observed the spermathecal epithelium to be secretory in nature. The absence of a spermatheca in *Pseudagrion decorum* is compensated by the fact that the function of storage and secretion has been adopted by the bursa copulatrix whose epithelial wall is distinctly glandular.

**Summarising**, the '8th complex' is an ectodermal structure as all its constituent organs are prominently lined, sometimes heavily, by a chitinous layer. These internal cuticularizations form definite patterns which ensure a safe copulation without any apparent risk of damage to any soft part of the female system and almost perfect internal deposition of the spermatosoma into the bursa and the spermatheca.

**Fertilization**, according to Tillyard (1917) occurs in the oviducts, especially in its upper region. The author, however, differs from this view as he did not find any spermas either in the oviducts or in the common median oviduct. He, therefore, thinks that the fertilization takes place in the '8th complex' just at the place where the oviductus communis and bursa copulatrix open into the vagina.

**The Accessory Glands**

The occurrence of the accessory reproductive glands in Odonata has been a controversial topic among workers. Tillyard (1917) and Whedon (1918) described a pair of elongated sacs opening into the pouch-like spermatheca and regarded them as accessory glands. Chopard (1949), Defossez (1970, 1972) and Richards & Davies (1977) state that the accessory glands open
into the spermatheca by a common duct. The report of the accessory glands opening into the spermatheca does not seem much convincing, both structurally and functionally. This perhaps led Prasad & Srivastava (1961) to state that the accessory glands are absent in the reproductive system of female dragonflies and to regard those organs as accessory spermathecal sacs in which the epithelium is glandular. Further, the accessory glands do not store sperm which are, however, present in the lumen of the accessory spermathecal sacs. The accessory glands, therefore, seem to be absent in Anisoptera.

Among Zygoptera, George (1928) in Ayrton and Matsuda (1976) in Mnais mentioned a pair of glandular structures in the ninth abdominal segment. These structures are morphologically separate and different from those described by earlier workers. However, no detailed account of the morphology or histology of the organs has been given by these workers.

The author in the present work has described for the first time the occurrence of definite accessory glands in Odonata. According to him, a pair of typically glandular organs is present in the ninth abdominal segment beneath the rectum of all the female Odonata investigated. These organs lie almost parallel to each other and open anteriorly into the genital atrium at a point which is very close to vulva. Each gland consists of a distal saccular portion and a proximal duct. The histological study of the saccular portion shows typically a glandular epithelium with secretory activity which possesses highly granular and vacuolated cytoplasm, granular nuclei and a number of empty spaces. The wall of saccular portion of the gland is thinly muscular. On the other hand, the epithelium of the duct is non-glandular and the musculature thick. These findings of the author stand in conformity with the general structure of the accessory glands in other insects. Therefore, the author considers these organs as accessory glands.
2. EXTERNAL GENITAL ORGANS

(A) MALE

The Supra-anal Appendages

A pair of supra-anal appendages termed 'true cerci' (Fraser & Asahina, 1970) are present in both the sexes arising out postero-laterally at the end of the tenth abdominal segment. These appendages consist of hollow, stout and chitinous structures which are situated dorsal to the anus. Each appendage is a subconical structure provided with two spines in *Pseudagrion rubriceps* Selys; tubular rod-like structure bearing three spines in *Pseudagrion decorum* (Rambur); quadrate with a hook in *Ceriagrion coromandellanum* (Fabr.); triangular plate ending in a hook-like process in *Ischnura senegalensis* (Rambur); triangular with a hook-like process and a papilla at the distal end in *Agrionemis pygmea* (Rambur); rounded with a hook in *Ischnura rufostigma* Selys; plate-like with one spine in *Enallagma malaynum* Selys; pistol-shaped in *Enallagma parvum* Selys; and conical structure which is provided with a hook in *Coptera marginipes* (Ramb.). The supra-anal appendages are longer in size than the infra-anal appendages in *P. rubriceps*, *P. decorum*, *A. pygmea*, *E. malaynum* and *E. parvum*; and comparatively short in *C. coromandellanum* (Fabr.), *I. senegalensis*, *I. rufostigma*, *C. marginipes*. Therefore, the supra-anal appendages possess a characteristic shape in all the damselflies investigated which may be regarded specific for the species.

The Infra-anal Appendages

The infra-anal appendages comprise a pair of hollow chitinized structures which are characteristically present in the males only on the ventro-lateral side of the anus at the terminal end of the tenth abdominal segment. The shape of the appendage varies in the different species. It is an ungulate structure with a spine in *Pseudagrion rubriceps*; sac-like with an apical spine in *Pseudagrion decorum*; cylindrical with a
blunt spine in *Ceriagrion coromandelianum*; forcipate in *Ischnura senegalensis*; cylindrical forceps-like in *Ischnura rufostigma*; conical and apically serrated in *Agrionemis pygmaea*; hook-like structure provided with a spur in *Enallagma malayanum*; conical with an acute apex in *Enallagma parvum*; and characteristically long and cylindrical with a round apex in *Copera marginipes*. The structure and shape of the infra-anal appendages are, therefore, characteristic for the species investigated.

Prasad & Srivastava (1960 and 1964), Srivastava (1963a 
& b and 1979), Fraser & Asahina (1970), Matsuda (1976) and 
Richards & Davies (1977) state that the infra-anal appendage 
is unpaired in Anisoptera. In all the Zygopterae studied, 
the author has found that the infra-anal appendages are paired. 
The infra-anal appendages are regarded 'paraprocts' by Snodgrass 
(1954) and Richards & Davies (1977), and 'processes on the 
paraprocts' by Fraser & Asahina (1970).

**Function of the Anal appendages:** The supra-anal appendages 
and the infra-anal appendages comprise together the anal 
appendages which are copulatory (clasping) structures in the 
male damselflies. During 'tandem', the male seizes the female 
prothorax by the anal appendages and holds all through the 
mating process in which, the female flexes her abdomen ventrally 
and forwardly and contacts the male secondary copulatory 
apparatus to receive the sperm material. In this process, the 
infra-anal appendages of the male are placed on the dorsum of 
the female prothorax and the male supra-anal appendages are 
pressed against the rear of the female prothoracic margin. 
Since the tandem occurs during flight, a firm grasping of the 
female by the male damselfly is necessary for the copulation 
to take place safely and comfortably. The structure of the 
male anal appendages is supplementary to both sexes and plays 
an important role in achieving sexual isolation (Corbet, 1980).
According to Paulson (1974) if a male tries to grasp a hetero-specific female, the anal appendages fail to engage the appropriate thoracic structures in the female.

Corbet (1962) and Chapman (1971) state that the male appendages are cemented to the female prothorax by a white sticky secretion in several species of Coenagrionidae. The author has not found any secretion either on the male appendages or on the female prothorax in any damselfly investigated. On the contrary, the female prothorax is securely held by the male anal appendages during 'tandem' and the grip is further strengthened by the spines, hooks and processes which are present on them.

The Male Gonopore

The ejaculatory duct opens out to the exterior through a median gonopore which is situated between a pair of coxites on the venter of the ninth abdominal segment. The aperture is elliptical in *Pseudagrion rubriceps* Selys and *Ischnura rufostigma* Selys; circular in *Pseudagrion decorum* (Rambur), *Agrioncemia pygmaea* (Rambur), *Enallagma parvum* Selys, *Ceriagrion coromandelianum* (Fabr.), *Ischnura senegalensis* (Rambur) and *Copaera marginipes* (Ramb.); and oval in *Enallagma malaynum* Selys.  

The 'True Penis':— Tillyard (1917), George (1928), Chopard (1949) and Asahina (1954) do not mention the presence of a penis in the ninth abdominal segment. Fraser & Asahina (1970) state that the penis as found in other insects, is entirely obsolete in Odonata. Matsuda (1976) believes that the penis is represented by paired penis valves (coxites). In Odonata, the occurrence of a rudimentary penis in the ninth abdominal segment has been described in Anisoptera species, *Crocothemis servilia servilia*, *Lathrecista asiatica asiatica*, *Brachythemis contaminata* and *Diplacodes trivialia* by Srivastava in 1963 a & b, 1965-67 and 1979 respectively. In the present study, the rim of the gonopore is strengthened by a sclerotized ring which is
invaginated inside the body to form an anterior chitinous structure in all the species. This structure supports the ejaculatory duct antero-ventrally and has been overlooked by all the previous workers except Srivastava (1959). In the Zygopteran species Agriocnemia pygmaea (Rambur), Enallagma malaynum Selys and Coptera marginipes (Ramb.), the author has observed that during sperm translocation a portion of the chitinous structure (described above) helps in the formation of a small tube which bears the gonopore at the apex. The formation of the tube is facilitated by displacement of the coxites away from each other. Snodgrass (1935) defines penis as a median tubular organ bearing at its apex the gonopore or the external opening of the ejaculatory duct. The author, therefore considers this chitinous structure as rudimentary 'true penis' which appears more distinct in Zygoptera than in Anisoptera. As a result of shifting of the copulatory function from the ninth to the second abdominal segment in the male of the modern odonata, the true penis has become unfunctional and degenerated so as to assume a peculiar form which is very different from the typical penile form of insects.

The Coxites

A pair of sclerotized structures are present on either side of the gonopore on the venter of the ninth abdominal segment. These are termed coxites (Walker, 1922 and George, 1928); valvules (Tillyard, 1917; Chao, 1953 and Asahina, 1954); gonopods (Snodgrass, 1935); genital valves (Walker, 1953; Hornuff, 1968); gonapophyses (Fraser & Asahina, 1970); and penis valves (Matsuda, 1976). A coxite consists of a basal portion which is united with the body-wall and a freely hanging terminal style. The shape of the coxites is variable in the species studied. It is wedge-shaped in Pseudagrion rubriceps; bean-shaped in Pseudagrion decorum and Ischnura senegalensis; rhomboidal in Ceriagrion coromandelianum; pear-shaped in Ischnura rufostigma and Agriocnemia pygmaea; kidney-shaped in Enallagma malaynum; and elliptical in Enallagma parvum and
The shape of the coxites is evidently of great taxonomic importance.

The coxites cause extrusion of the 'penis tube' during sperm translocation and also protect the gonopore which lies surrounded and partly concealed by these structures. In the present work, the term coxite has been retained in accordance with Walker (1922) and George (1928).

The Anterior genital plate and the post-genital plate

Two sclerotized plates have been found comprising the ventral wall of the ninth abdominal segment in all the male damselflies studied. The plate lying anterior to the gonopore is termed the anterior genital plate and the plate lying posterior to the gonopore is called the post-genital plate. The surface of the anterior genital plate is beset with numerous tubercles and hair, while that of the post-genital plate is provided with tubercles only. The presence of these plates has also been reported by Snodgrass (1935) and Srivastava (1979), and are regarded homologous to similar structures in other insects.

The secondary copulatory apparatus

The males of all the damselflies studied are characterised by the possession of a complicated, functional 'secondary copulatory apparatus' on the ventral side of the second and a brief anterior part of the third abdominal segments. The shifting of the copulatory function to the base of the abdomen from the posterior side has been a unique phenomenon in Odonata and unparalleled one in the evolutionary history of the Insects. The secondary copulatory apparatus, therefore, cannot be homologized with any structure of other insects. According to Matsuda (1976), this 'represents a conspicuous case of production of new structures in evolution'.

The secondary copulatory apparatus consists of a set of
organs namely, genital fossa, genital sac, anterior lamina, lamina-batilliformis, paired anterior and posterior hamules, framework, secondary penis (the intromittent organ) and a vesicula spermatis. Structures like oriellets, genital lobes, penis sheath and posterior lamina reported present in the copulatory apparatus of Odonata by other workers (Tillyard, 1917; Chao, 1953; Asahina, 1954; and Srivastava, 1979) are, however, absent in the damselflies investigated.

The Genital Fossa

The genital fossa is a depression on the ventral side of the second abdominal segment in which the organs of the secondary copulatory apparatus are lodged. The fossa is laterally bordered by the ventro-lateral margins of the second abdominal tergite. Thompson (1908) dividing the second abdominal sternum into two parts, states that the anterior portion (sternum) comprises the anterior lamina, anterior hamules, lamina batilliformis and penis whereas the posterior portion (sternellum) is represented by the framework and posterior hamules. The vesicula spermatis is a derivative of the third segment and, thereby overhang the posterior part of the genital fossa. Tillyard (1917), Chapman (1971) and Richards & Davies (1977) describe a connection between the genital fossa and the vesicula spermatis, a finding which the author is unable to corroborate in the species investigated.

The Genital Sac

The genital sac is a large chamber which projects into the interior of the second abdominal segment and opens ventrally in the middle. The wall of the sac is membranous and supported anteriorly by the lamina batilliformis and posteriorly by the median plate of the frame. The lateral support is provided by the vertical and longitudinal bars of the framework. The basal plate of the penis lies incorporated in the roof of the genital sac. The cavity of the sac houses the antero-proximal portion
of the penis. As far as the author is aware, the presence of a genital sac in the secondary copulatory apparatus of male Odonata has been reported by Poonawalla (1966) only.

The Anterior Lamina

The anterior lamina is a large, hood-like chitinous plate forming the ventral shelf of the genital fossa in the anterior part and protecting other organs of the secondary copulatory apparatus especially the lamina batilliformis. The anterior margin of the lamina is bordered internally by a heavily sclerotized transverse bar termed laminar process by Khan (1974 & 1976). In the present study, the bar has been termed transverse apophysis as it gives attachment to anterior apophysial muscle. The posterior margin of the lamina is deeply emarginated in the middle to form an inverted 'V'-shaped cleft which divides the plate into two lateral halves or limbs. The medial sides of the limbs provide support to a membrane which covers the cleft dorsally. The membrane also extends forwards in the interior of the genital fossa forming thereby a sac, termed median laminar sac by the author. The median laminar sac tapers anteriorwards and projects into the first abdominal segment in all the Zygoptera species studied except Periagrion coromandelianum (Fabr.) and Ischnura senegalensis (Hambur). The anterior portion of the median laminar sac is distinctly triangular in Knallagme malaynum Seleys and divided into two processes in Copera marginipes (Camb.). During copulation, the median laminar sac holds the tip of teresbra of the female ovipositor. The median laminar sac is a new feature in the secondary copulatory apparatus of the Zygoptera studied.

The Lamina Batilliformis

The lamina batilliformis is a prominent structure, characteristically present in the secondary copulatory apparatus
of the Zygopterae Odonata only. It is absent in Anisoptera and Anisosygoptera (Pfau, 1971). This structure has not been described by Tillyard (1917), George (1928), Chopard (1949), Richards & Davies (1977) etc.

In all the species studied by the author, the lamina batilliformis is located medially in the genital fossa above the cleft of the anterior lamina and enclosed between the anterior hamuli. Structurally, it consists of an anterior plate and two posterior limbs, each being produced into a cornu. The plate is concave dorsally and arch-like apically. It is tongue-shaped in Ceriagrion coromandelianum (Fabr.) and Enallagma parvum Selys; spoon-shaped in Ischnura rufostigma Selys; triangular in Enallagma malaynum Selys; and scoop-shaped in the remaining species examined. The margin of the plate is not spiny in any of the species investigated by the author, a finding which is contrary to that reported by Khan (1976) in Megalestes major Selys.

The lamina batilliformis provides support to the genital sac, which lodges the antero-proximal part of the penis. It is, therefore a device for protecting the penis in Zygopterae which lacks a penis sheath. In Anisopterae, the penis lies protected by a penis sheath (Pavestava, 1963 a & b). The position of the lamina batilliformis in Zygopterae is same as that of the penis sheath in Anisopterae. Thompson (1908) analogizes this 'chitinized structure between the posterior lobes of the anterior lamina' of Zygopterae with the Anisopterae penis sheath due to similarity in their position. Fraser (1956) also supports this view. Hornuff (1968) termed lamina batilliformis as ligula after Fraser (1956). In the present work, the term lamina batilliformis has been adopted in accordance with Matsuda (1976). The lamina batilliformis appears to guide the terebra of the ovipositor (Matsuda, 1976), to be placed apart on the lateral sides in the space of the median laminar sac during copulation in such a way that the male intromittent organ acquires alignment with the female genital aperture.
The Anterior Hamules

According to Thompson (1908) and Tillyard (1917), the anterior hamules are absent in Zygoptera. However, in all the species investigated the author has found a pair of anterior hamules situated behind the anterior lamina in the anterior region of the genital fossa. Each hamule consists of a movable outer plate and a rigid inner plate, the two being fused together along their mesial sides. The inner plate bears a hook-like structure. The movement of the outer plate automatically causes a simultaneous action for the hook of the inner plate. Asahina (1954), Fraser & Asahina (1970) and Matsuda (1976) state that the anterior hamules are continuous with the anterior lamina in Zygoptera. The present study reveals that the anterior hamules are separate and well developed structures which are, no doubt, movably attached to the anterior lamina.

Among Anisoptera, the anterior hamules are absent in the members of the family Libellulidae (Srivastava, 1963 a & b; Poonawalla, 1966; Fraser & Asahina, 1970) but present in Aeschnoidea (Richards & Davies, 1977). Faulkner (1974) describes in Anisoptera that the shape of the anterior hamules is variable and taxonomically significant. In the Zygoptera studied, the anterior hamules are although present but do not show sufficient variation in shape as could be utilized in the identification of the species.

The Posterior Hamules

Thompson (1908), Tillyard (1917), Srivastava (1959), Poonawalla (1966) and Fraser & Asahina (1970) mention that the posterior hamules are well developed and complicated structures in Anisoptera. Asahina (1954) and Pfau (1971) describe these as 'large, posteriorly extended structures of extra-ordinary importance' in Anisoczygoptera. In the present study on the Zygopteran species, the author has observed that the posterior hamules are small and simple structures. These are only a pair of strongly sclerotized, hollow outgrowths of chitin projecting
ventrally from the apex of the anterior limb of the median plate of framework. The shape of the posterior hamule is triangular in Ceriagrion coromandelianum (Fabr.); rectangular in Ischnura senegalensis (Rambur) and I. rufostigma Selys; knob-like in Ayriocnemia pygmaea (Rambur), Knallagyna malaynum Selys and E. parvum Selys; and club-like in Copera marginipes (Ramb.). At the base of each hamule in Ischnura senegalensis (Rambur), I. rufostigma Selys, Knallagyna malaynum Selys and E. parvum Selys, there is a foramen also which leads into the cavity of the hamule. The surface of the hamule is beset with many long hair. The hamuli posteriores could not be discerned in Pseudagrion rubriceps Selys and I. decorum (Rambur).

According to Asahina (1954) and Pfaul (1971), the posterior hamuli function as intromittent organs in Anisocygotaera. Tillyard (1917), Srivastava (1963 a & b, 1979), and Richards & Davies (1977) describe the hamules as claspers to hold or retain the female genital structures during copulation in Anisoptera and Zygoptera. In the present study, the shape of the posterior hamule does not corroborate to the aforesaid view as it lacks a hook or any likewise structure for clasping. On the other hand, the presence of long bristle-like hair on its surface is suggestive of a sensory nature, perhaps tactile. During copulation, the ventrally projecting posterior hamuli become the first organs of the male secondary copulatory apparatus to touch the female body. The author, therefore believes that in Zygoptera the posterior hamules are sensory organs which serve as guides to the male himself to adjust its copulatory structures and bring them in alignment with the female organs for a proper and effective mating, and not as guides to the female genital organs as suggested by Tillyard (1917), Hornuff (1968) and Richards & Davies (1977).

The Framework

Supporting the genital fossa, the genital sac and the basal plate of penis is a system of chitinous rods which
collectively form a skeleton of framework. It comprises a pair of anterior vertical bars, a pair of lateral longitudinal bars and a posterior median plate. The median plate bears typically a pair of anterior limbs and a pair of posterior limbs arising from the lateral sides. Srivastava (1959) states that the shape of the supporting framework remains more or less constant in the six species of odonates investigated by him. In the damselflies studied by the author, the shape of the median plate (hence framework) varies from species to species. It is 'H'-shaped in *Pseudagrion rubriceps*; provided with a membranous antero-median region in *E. decorum*; half-egg shaped in *Ceriagrion coronandellianum*; 'W'-shaped in *Ischnura senegalensis* and *Ischnura rufostigma*; 'H'-shaped with notched anterior limbs in *Agricnemia pycnæa*; rectangular with a median process on the anterior side in *Enallagyma malaynum*; rectangular but with median process both on the anterior and the posterior sides in *Ophera marginipes*; and 'V'-shaped in *Enallagyma parvum*. It is thus evident that the shape of the framework, especially the median plate is species-specific and of taxonomic value.

**The Penis**

In the modern odonates the copulatory function has been transferred from the ninth abdominal segment to the second abdominal segment, rendering thereby the true penis unfunctional which finally degenerated. The term penis has been adopted in this work for the functional intromittent organ of the secondary copulatory apparatus after a large number of workers in odonatology, viz. Thompson (1908), Tillyard (1917), Kennedy (1916, 1922), Fraser (1940), Chao (1953), Asahina (1954), Prasad & Srivastava (1960, 1964), Poonawalla (1966) and Srivastava (1979). But when accuracy is demanded, the term 'secondary penis' is applicable for this intromittent organ.

According to Goddard (1896), Tillyard (1917), Williamson (1920), Kennedy (1922), Fraser (1940), Chao (1953), Asahina (1954), Prasad & Srivastava (1960), Poonawalla (1966) and
Naravastava (1979), the penis of Anisoptera is three-segmented. Hörner (1942) describes four segments in the penis of _Erythrodiplax_. The Zygoptera penis is reported unsegmented or one-segmented by Kennedy (1916), Tillyard (1917), Garman (1917), Asahina (1954), Fraser (1956) and Gamble (1970). However, Poonawalla (1966) states that the penis in damselflies is composed of three segments while Pfau (1971) mentions only two segments in it. In the present work, the author has found that the penis in all the Zygoptera species consists of a long, stout chitinous organ which is bent twice in opposing directions, first near the proximal end and second time near the distal end. There are no joints in it and hence the penis is evidently unsegmented. The curvature of the penis at two places has, perhaps been misinterpreted by Poonawalla (1966) and Pfau (1971) who consider it segmented. Moreover, the penes in Anisoptera and Zygoptera are not homologous organs (Matsuda, 1976; Jurzita, 1980*). The author, therefore, believes that the penis in Zygoptera species is unsegmented or consists of one-segment only whereas in Anisoptera dragonflies it is distinctly three-segmented.

Thompson (1908) mentions the development of the penis in Zygoptera from the anterior part of the 'sternum' of the second abdominal segment. Pfau (1971) states that it arises from a sternal appendix ('processus caudalis' or 'sternellum') of the second segment. Roberts' (1912) idea that 'the penis is homologous with the fused pair of legs' has long ago been rejected by the morphologists. Matsuda (1976) emphasizes that the homology of the 'secondary penis' never extends beyond the limit of the order Odonata as no such organ occurs in any other group of Arthropods. In the present study, as observed by the author the penis arises from the middle of the genital fossa and is not connected with the vesicles in the damselflies investigated.

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In the Anisoptera, the 'secondary penis' is continuous with the vesicle which develops from the third sternite (Defoerse, 1972). It is also a fact that the penis sheath is absent in all the Zygoptera species in which its protective function has been taken up by a new organ, the lamina batilliformis described earlier. From this account, it is evident that the 'secondary penis' of Zygoptera is not homologous with the 'secondary penis' of Anisoptera. Further, it can only be compared with the anisopteron penis sheath, a view shared with Tillyard (1917), Asahina (1954), Fraser & Asahina (1970) and Juritzza (1980)*.

Tillyard (1917) states that in Aeschna, an orifice is situated on the convex dorsal side of the second segment of penis. Prasad & Srivastava (1960) describe an orifice dorsally at the end of the third segment of the penis in Pantala flavescens. Poonavalla (1966) also mentions that the penis in Zygoptera is traversed by a slender internal tube which opens out to the exterior through an orifice situated between the glans and the prepuce. The author's finding differs from all these workers as no external orifice of the penis has been observed in any Zygoptera penis studied by him. On the other hand, the internal tube of penis communicates basally with the haemocoele. The flow of the haemocoeleomic fluid into it causes the penis to become turgid and erect, a process which possibly aids in its extrusion out through the orifice of the genital sac.

The lack of any external orifice and a direct connection between the vesicle and the penis in Zygoptera has been very puzzling in respect to its function of sperm transference during copulation. Walker (1953) states that 'it is not known how the penis functions in conveying the sperm capsules to the female genital aperture'. Hornuif (1968) describes that the penis forms a tubular passage in the ovipositor of the female through which the sperm material is passed down. In the present investigation,

* Personal communication to the author dated Jan. 10, 1980
it has been observed that an external dorsal groove is present along the median line in the proximal and middle regions of the penis shaft. The author ventures to suggest that during the process of protrusion and intromission of penis into the vulva of female, the external groove described above comes in contact with the orifice of the vesicula spermatis. The sperms are then poured down through this groove (canal) from the cavity of the vesicula spermatis of the male insect into the bursa copulatrix of the female damselfly. The mucilaginous consistency of the seminal fluid helps in this safe internal deposition of the sperms.

The Vesicula Spermatis

There is an elongated sac-like structure which lies near the anterior end of the third abdominal sternite in all the Zygopteran species investigated. It stores spermatosoma temporarily prior to their transference by the penis to the female body and termed 'penis vesicle' in Anisoptera by all the Odonatologists. It performs the same function of sperm storage in Zygoptera too, and hence named penis vesicle by Tillyard (1917), Hornuff (1968) and Khan (1974 & 1976). The term 'penis vesicle' is suggestive of the notion that the penis is a part of the vesicle or vice-versa. In the Anisopteran species, the penis is undoubtedly a part of the vesicle which accordingly deserves the name penis vesicle. However, the Zygopteran penis bearing no homology to its Anisopteran fellow, is well separated from the vesicle with which it neither communicates nor connects. The term penis vesicle is, therefore, a misnomer for this organ in Zygoptera. The author has for this reason named the vesicle in the present work as 'Vesicula Spermatis' (meaning a vesicle for the sperms) in accordance with Matsuda (1976). There is no doubt that the vesicula spermatis of the Zygoptera is homologous with the penis vesicle of the Anisoptera.

Tillyard (1917), Chapman (1971) and Richards & Davies
(1977) mention that the vesicula spermatis communicates with the genital fossa. Kennedy (1922) and Horner (1942) state that the vesicle opens into the haemocoel. The author has found that the vesicula spermatis communicates neither with the genital fossa nor with the haemocoel in all the species investigated. Kennedy (1922), Fraser (1940), Horner (1942) and Chao (1953) mention that the penis vesicle helps in the erection of penis in Anisoptera. Srivastava (1959) describes elaborately, a process for the erection of penis in the Anisoptera species where the penis vesicle participates actively together with the genital lobes. In the present work on Zygoptera species, it has been observed that the vesicula spermatis plays no role at all in the erection of the penis, which is performed by muscular action (described subsequently). Moreover, the connections of the vesicle with the penis and the genital fossa are also absent here. Further, there are two apodemes associated with the vesicula spermatis and not one as reported by Asahina (1954).

In the dragonflies an external orifice is lacking in the penis vesicle, which communicates directly with the introvert organ (Srivastava, 1979). The vesicula spermatis in the damselflies studied, however, opens out to the exterior through a slit-like orifice which is guarded by a pair of lips.

Functional Morphology of the Secondary Copulatory Apparatus

A characteristic 'secondary copulatory apparatus' is situated on the ventral side of the second and a part of the third abdominal segments of male damselflies. As described earlier, the musculature of the second abdominal segment consists of paired, superior longitudinal tergal muscles, inferior longitudinal tergal muscles, tergo-leural muscles of vesicula spermatis, longitudinal muscles of framework, posterior muscles of framework, anterior muscles of framework, muscles of the anterior lamina, and anterior apophysial muscles. In addition to these muscles another set of paired muscles, the dorso-
ventral apodemal muscles of the vesicula spermalis also take part in the functional mechanism of the copulatory apparatus, though this muscle belongs to the third abdominal segment.

Of all the nine paired muscles associated with the secondary copulatory apparatus, only the anterior apophysial muscles do not take any part in the copulation. However, its movements regulate the elevation and depression of the anterior lamina to help in the respiratory activity. The muscular action of the remaining muscles is concerned directly or indirectly with the copulatory process. The transference of the sperms from the vesicula spermalis of the male secondary copulatory apparatus into the bursa copulatrix of the female is described below on the basis of musculature of the secondary copulatory apparatus.

The muscular action initiates as soon as the ventral surface of the eighth and ninth segments of the female after curling of abdomen, become apposed to the ventral surface of the second and third abdominal segments of the male. The tip of the terebra of the female ovipositor enters the median laminar sac of the male secondary copulatory apparatus through the cleft of the anterior lamina. This causes contraction of the muscles of the anterior lamina which elevate the laminar plate so that the terebra gets fixed firmly and the tandem attachment between the male and the female is accomplished. These muscles do not relax till the sperm transference from male to the female is completed. Later, the longitudinal muscles of framework contract with the result that the anterior vertical bars of the frame are pulled caudad. This also swings the basal plate of the penis backwards, consequently exerting the shaft of the penis ventrad and forward. Normally, the exertion of the penis is checked by the vesicula spermalis which lies beneath the apical portion of the penis. However, the contraction of the superior longitudinal tergal muscles straightens the second abdominal segment, and that of the doro-ventral apodemal muscles of the vesicula spermalis
brings the vesicle slightly caudad. These events also facilitate the exertion of the penis shaft. Once the penis shaft is exerted, its further protrusion is stopped by the ventrally-lying body of the female. The penis then acquires an alignment with the vulva. This is achieved fully by several contractions and expansions of the posterior muscles of the framework which help the penis to readjust its position slightly. A sudden contraction of the anterior muscles of framework brings forward the whole set of the lateral longitudinal bars together with the anterior vertical bars of the frame and basal plate of the penis. This movement jerks the penis to enter through vulva into the vagina of the female. Now, the interior longitudinal tergal muscles and the tergo-pleural muscles of vesicula spermatis contract simultaneously causing a series of events. The third abdominal segment bends due to the contraction of the inferior longitudinal tergal muscles, and the vesicle is brought forward in such a way that the orifice of the vesicula spermatis embraces the beginning of the external median dorsal groove of the shaft situated near the anterior end of the penis. The contraction of the tergo-pleural muscles of vesicula spermatis depresses the front part of the vesicle, an action which automatically lifts upward the hinder part of the organ. The outcome of these events is that the orifice of the vesicula spermatis enters the cavity of the median dorsal groove of penis, and the posterior portion of the membranous dorsal wall of the vesicle becomes pressed against the third abdominal sternite bearing the vesicula spermatis. The compression thus caused to the lumen of the vesicle drives out the contained sperms through the vesicular orifice. Consequently, the sperms flow in a stream along the median dorsal groove of the penis and reach near the opening of the female spermatheca where the penis tip remains abutted. When the transference of the sperms has been completed, all the concerned muscles get relaxed. The penis and the vesicula spermatis become disposed to their normal position at rest. The female is thus unlocked from the copulatory tangle of the male and flies away.
(B) FEMALE

The supra-anal Appendages

The supra-anal appendages in the female damselflies comprise a pair of short sclerotized structures coming out laterally from the postero-terminal end of the tenth abdominal segment above the anus. These are simple in construction and smaller in size than those of the males with which they are homologous. The muscles and the spines are poorly developed in the appendages and hence, these do not seem to participate in the copulatory mechanism. Fraser (1956) mentions that the supra-anal appendages of the female Odonata take part in the oviposition. It is likely that the female supra-anal appendages hold the leaves and the stem filaments in which the eggs are deposited endophytically.

The supra-anal appendages are conical in shape in all the species except Pseudagrion rubriceps males and Pseudagrion decorum (Fambur), in which they are rod-like and cylindrical respectively. As these are the only appendages at the posterior end of the abdomen in the females, they are simply called anal appendages by Tillyard (1917), Chao (1953), Prasad & Srivastava (1961) and Matsuda (1976). The author has termed them supra-anal appendages due to their dorsal position in respect to the anus. Snodgrass (1954), Fraser & Asahina (1970), Matsuda (1976), and Richards & Davies (1977) regard these appendages as cerci.

It is an acknowledged fact that in all the three suborders of Odonata (Zygoptera, Anisoptera & Anisozygoptera), the infra-anal appendages are absent and the supra-anal appendages are short and non-functional in the females. The author considers that this condition of the anal appendages of females is leading towards an evolutionary reduction of structures.
The Female Genital Aperture (Vulva)

Snodgrass (1935) and Tuxen (1970) define vulva as the 'external opening of the genital chamber or of the vagina'. In the present study the vulva is a ventro-median external aperture of the female internal reproductive system between the eighth and the ninth abdominal sternum which lies hidden from view by the base of the valvulae of ovipositor. It leads internally into the genital atrium. Vulva is different than the female gonopore which is the posterior opening of the oviductus communis into the vagina of '8th Complex'. In the thesis, the term female genital aperture has been adopted for vulva after Engelmann (1970) and Richards & Davies (1977).

The Subgenital Plate

Tillyard (1917) describes the presence of a 'ventral spine' in Acrioninae at the base of the ovipositor. Fraser (1933) mentions in female Zygoptera a process of the eighth abdominal sternum termed 'ventral apical spine'. Asahina (1954) reports the presence of a notched spinous process in the Anisozygoptera Epiphanes. Prasad & Srivastava (1961) state that the sternum of the eighth segment is prolonged postero-ward to form a 'vulvar scale' in the Anisoptera species studied by them. Snodgrass (1935) describes that in female insects, the sternum of the eighth segment is enlarged and produced posteriorly beneath the base of the ovipositor forming a subgenital plate. In Ischnura senegalensis, Ischnura rufostigma, Enallagma malaynum and Enallagma parvum, the author has observed that the posterior margin of the eighth abdominal sternite is prolonged caudally beneath the base of the ovipositor to form a plate-like structure. As this plate lies beneath the vulva, it is termed subgenital plate after Matsuda (1976). The subgenital plate is arch-shaped and provided with a median spine in the present work which protects the vulvar opening and the base of the ovipositor.
THE OVIPOSITOR

The structure of Odonate ovipositor has been described by many workers viz. Van der Reeve (1906), Tillyard (1917), Walker (1919), Machotin (1929), Crampton (1929), Chao (1953), Ashina (1954), and Fraser and Ashina (1970). Therefore, the terminology of the different components of the ovipositor has been as varied as the workers. The following is a list of the synonyms of the terms used by different workers, signifying their morphological homology:

First Valvifer - The coxa of abdominal segment VIII. It provides attachment to the first valvule.
Synonym: First valvifer (Snodgrass, 1935)
First gonocoxa (Scudder, 1961)
Basivalvula (Matsuda, 1976)

First Valvule - The process belonging to the first valvifer or abdominal segment VIII.
Synonym: Anterior process (Tillyard, 1917)
First valvule (Snodgrass, 1935; Matsuda, 1976)
First gonapophysis (Scudder, 1961)

Second Valvifer - The coxa of abdominal segment IX which bears a gonoplace (Chapman, 1971). It provides attachment to the second valvule.
Synonym: Lateral process (Tillyard, 1917)
Vulvar scale (Fraser, 1933)
Second valvifer (Snodgrass, 1935)
Second gonocoxa (Scudder, 1961)
Lateral valve (Hakim, 1964)
Lateral valvula (Matsuda, 1976)

Second Valvule - The process belonging to the second valvifer or abdominal segment IX.
Synonym: Median process (Tillyard, 1917)
Second valvule (Snodgrass, 1935; Matsuda, 1976)
Second gonapophysis (Scudder, 1961)
**Gonangulum** - The sclerite attached ventrally to the base of the first valvulae (first gonapophysis) and dorsally articulating with the second valvifer (second gonocoxa).

**Synonyms**: Anterior plate (Anodgrass, 1935)
Gonangulum (Scudder, 1961; Matsuda, 1976)

The first valvulae and the second valvulae together form an aculeus or terebra (Fraser & Asahina, 1970).

Srivastava (1959) mentioned that the ovipositor is greatly reduced in the family Libellulidae. Scudder (1961) states that a well developed ovipositor is present in Zygoptera and Anisomyzoptera and in the members of the Anisopteran families Aeshnidae and Petaluridae. In the present investigation also, a well developed ovipositor has been found in all the species studied. It consists of first valvifers, second valvifers or lateral valves, first valvulae, second valvulae and gonangula all of which are paired. The components are specialized chitinous structures of sternal origin (Scudder, 1971). The distal ends of the first valvulae and the second valvulae are saw-like in structure and hence the ovipositor is adapted for endophasic egg-laying. Hakim (1964) has failed to observe serrations in the valvulae of the ovipositor in *Pseudagrion decorum* (Rambur), *Ischnura rufostigama* Selys and *Lestes umbrina* Selys. Tillyard (1917) mentions that the eggs in *Synlestes weyersi* are laid in groups of three to four. The author has observed that the eggs are laid one by one and singly in each hole in the species studied by him, a finding similar to that of Kumar & Prasad (1977) and Rowe (1978). The eggs are laid in living plant tissue through holes made by the movements of the valvulae, which are strongly chitinized and firmly articulated with their respective valvifers. The tip of the terebra is sharply pointed and digs a hole in the ovipositing surface. The two valvulae are then moved together by muscular action in a saw-like manner and the hole is quickly
enlarged in size by their penetration. The first and the second valvulae are interlocked together by a ridge and groove system which has been termed 'tongue and groove arrangement' by Scudder (1971) and 'olisterhet' by Smith (1969). This type of interlocking mechanism helps in the oviposition as follows:

(i) It prevents independent movement of the components of the ovipositor.

(ii) Avoids buckling of valvulae; if any, during movement.

(iii) Forms a canal-like passage by the apposition of the dorsal groove of the first valvular shaft with the ventral ridge of the second valvular shaft through which the eggs descend.

After egg-laying, the teretre is retracted back in the space enclosed between the pair of lateral valves where it lies well protected when not in use. The tip of the teretre which is not enclosed by the basal portion of lateral valves, is ensheathed by the gonoplace. A stylus is also present near the gonoplace. Scudder (1961) does not regard it to be a true gonostyle and considers it as third valvule (Scudder, 1971). Lillyard (1917) named it as stylloid process or sternorchabdit. The surface of the stylus is covered with hair which also form a dense tuft of short bristle-like structures on the apical side. The stylus is seemingly used as tactile organ for selecting a suitable site for oviposition as it is the first organ of the ovipositor which comes in contact with any surface.

Asahina (1954) and Hakim (1964) describe the presence of a laterotergite in the Zygopteran ovipositor. The author has also observed in the present work that a bar-like laterotergite is situated between the anterior apophysis of second valvifer and the ventro-lateral border of the ninth tergite. It forms a sort of buffer valve between the ninth tergum and second valvifer, and thus facilitates the closing and opening of the second valvifers. Asahina (1954) considers the latero-
tergite as valvifer in *Epiophlebia superba*. Matsuda (1976) regards it as a gonangulum. In the present study, both the laterotergite and the gonangulum are found separately in the same species. The gonangulum is an oblique bar-like structure present ventrally on either side of the median line near the junction of the eighth and ninth abdominal sternites. A gonangulum comprising a triangular sclerite has been mentioned also by Scudder (1961) in *Aeschna grandis*. The author, therefore, considers that the laterotergite and the gonangulum are two different structures, each having separate position and different articulations and are not homologous to each other as reported by Matsuda (1976).

Snodgrass (1935) states that "the ventral body-wall between the bases of the second valvifers sometimes contain sclerites, which are termed intervalvulae". These have been termed differently by various workers, viz. chitinious sclerite-m and intervalvula superior (Mabotin, 1929); posterior intervalvula and post-stermite (Asahina, 1954); and sternal plates (Hakim, 1964). In the present study, the author has found two such sclerites which are situated in the intervalvular membrane extending between the bases of the lateral valves. On the basis of their position, these sclerites are termed anterior intervalvular sclerite and the posterior intervalvular sclerite in the thesis. These structures represent the reduced sternum of the ninth abdominal segment due to the occurrence of ovipositor in the region.

**Functional Morphology of the Ovipositor**

The ninth abdominal segment of the female damselflies possesses a characteristic organ, the 'ovipositor', for egg-laying. The ovipositor is a compound organ consisting of five paired structures, the first valvifers, the second valvifers (lateral valves), the first valvulae, the second valvulae and the gonangula. The muscles of the ninth abdominal segment are concerned with orientation and movement of the various
components of the ovipositor, especially the terebra (first and second valvulae together) during the copulation and oviposition. The shafts of the first and the second valvule of a side are engaged together by a ridge and groove arrangement. The muscular action for the movement of any valvule involves the same and simultaneous muscular action upon the other valvule as well. When the ovipositor is not in use, the terebra is enwrapped by the lateral valves.

The contraction of the unpaired transverse sternal muscle pulls the two lateral valves away from each other so that terebra is set free. To allow the entry of the penis into the valva during copulation the terebra becomes divided into two longitudinal halves, each having a first and a second valvule. This is achieved by the contraction of the anterior intervalvalvular muscles which act upon the second valvulae through the medium of the anterior intervalvalvular sclerite.

The contraction of the anterior apophysial muscles of the lateral valve causes the anterior part of the lateral valve to move upwards. Consequently, the posterior part of the lateral valves bearing the style is erected to become ventrad. This makes the style the first organ of the ovipositor to come in contact with any surface during the selection of the site for oviposition. The contraction of the posterior apophysial muscles of the lateral valve produces an effect which is antagonistic to that of the anterior apophysial muscles of the lateral valve and causes the lateral valves to go back into their normal position. As soon as a suitable site for oviposition has been obtained, the terebra is ejected ventrally by the contraction of the dorsal-ventral muscles of the first valvifer which act upon the first valvulae. The forward and backward movements of the terebra are then regulated in a saw-like manner by the alternate contraction and relaxation of the longitudinal muscles of the first valvifer. A hole is thus made in the plant tissue for the deposition of the egg which slides down through the ovipositor canal formed by the valvulae.
The terebra is retracted back within the sheath of the lateral valves by the action of the muscles of the second valvule. The longitudinal tergal muscles do not participate in any activity involved in the oviposition. However, their contraction results in the straightening of the segment.