MORPHOHISTOLOGY AND THE FUNCTIONAL ASPECTS OF THE COMPONENTS OF THE '8TH COMPLEX' IN FEMALE *ISCHNURA RUFOSTIGMA* SELYS (ZYGOPTERA: COENAGRIONIDAE)

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The eggs of *I. rufostigma* are produced in the ovarioles and passed down the common lateral ducts into the lateral oviducts that posteriorly open into a common median oviduct (oviductus communis). This ultimately leads into the '8th complex' restricted to the 8th segment of the abdomen. The components of the '8th complex' are the vagina, its evagination the bursa copulatrix, and the spermatheca, the subsequent evagination of the bursa. The sperms are deposited by males into the bursa copulatrix, which together with the spermatheca stores them. The anteriormost part of the vagina has an oval-shaped lumen into which the oviductus communis and the bursa copulatrix open and where the fertilization of eggs takes place. Two accessory glands, present in the 9th segment, open into the posterior part of the vagina — the genital atrium — and pour a secretion which bathes the eggs passing for oviposition. The musculature associated with the '8th complex' was studied with the intent of observing its functional abilities.

INTRODUCTION

MARSHALL (1914), TILLYARD (1917) and GEORGE (1929) are among the earlier workers who investigated the female internal genitalia of odonates. They were unable to give an elaborate account of the bursa copulatrix, spermatheca and vagina perhaps because of their close positioning and small size. These three organs together were termed '8th complex' by B.K. SRIVASTAVA (1959) since they were found to be restricted to the 8th segment of the abdomen in all odonates investigated by him. This terminology was later employed by PRASAD & SRI-VASTAVA (1961), V.K. SRIVASTAVA (1980) and SRIVASTAVA & SRIVAS-

TAVA (1989a, 1989b). As the bursa copulatrix, spermatheca and the vagina are enveloped by musculature and an almost continuous mass of adipose tissue rendering them nearly indiscernible one from the other, it is convenient to frame the three components together into a single comprehensive unit — the '8th complex'. The three organs can, of course, be identified by sectioning the '8th complex' in various planes and studying them anatomically and histologically.

Apart from morphological studies, an attempt is also made to trace the fate of the deposited sperm inside the '8th complex', and to track the course of the ovum during fertilization and until oviposition; and also to examine the musculature associated with the activity of the '8th complex'.

MATERIAL AND METHODS

The females were netted around Sagar Lake, Sagar, where they were present nearly through the year, but were most plentiful during the post-monsoon period, i.e. September to November. The study lasted four years (1977-1980). Five categories of females were selected for investigation: (a) virgin, (b) mating, (c) just mated, (d) mated some time back, and (e) ovipositing. The mark-recapture technique (SRIVASTAVA & BABU, 1985) was employed for identifying the specimens released in the open area.

The specimens were dissected in Ringer solution for morphological examination of the internal genital organs. The '8th complex' was found to be pulsating in many cases. Whole mounts of the '8th complex' were also prepared by warming it in 5% KOH solution for about 10 min (which dissolved the surrounding tissue leaving only the chitinous intima intact without much affecting the stored sperm), washing and dehydrating, and staining with Picro-indigo-carmine and clearing with Cedar-wood oil. For histological examinations the relevant tissues were fixed in Aq. Bouin's fixative, embedded with Paraffin-celloidin, sectioned serially (6-8 μm thick) in transverse, horizontal and longitudinal planes, and stained with Delafield's haematoxylin and Eosin.

The musculature was studied by adding Bouin's to the Ringer, which made it conspicuous. Activity of the muscles was observed while the tissue, exposed by dissection, was still in Ringer. The observations were also supplemented by pulling the muscles with forceps.

Oviposition behaviour was observed through powerful field binoculars and notes were recorded on a portable tape recorder. Some females caught while ovipositing continued egg-laying even on the petri-dish during the dissection.

GENERAL ORGANIZATION
OF THE FEMALE INTERNAL GENITAL ORGANS

There are two long, pale, mud coloured ovaries above the gut, conjoined by a median dorsal ligament. The gonads extend from the base of the abdomen up to the middle of the 7th segment. A delicate, expansile, lateral duct runs throughout the length of each ovary on the ventro-lateral side. Numerous compactly placed ovarioles are attached to the duct along the dorso-mesal side. The ovaries are each suspended in the abdomen anteriorly by an apical filament, formed by the coalescence of the terminal filaments of a few anterior ovarioles, while filaments of all the remaining ovarioles are embedded in the median dorsal ligament. Tracheoles, nerve ramifications and adipose tissue are present over the surface of the ovaries.

Each ovariole is panoistic, elongate and directed antero-dorsally. It is narrow apically but broad basally, containing a moniliform string of developing ova, of which the oldest is situated at the base.
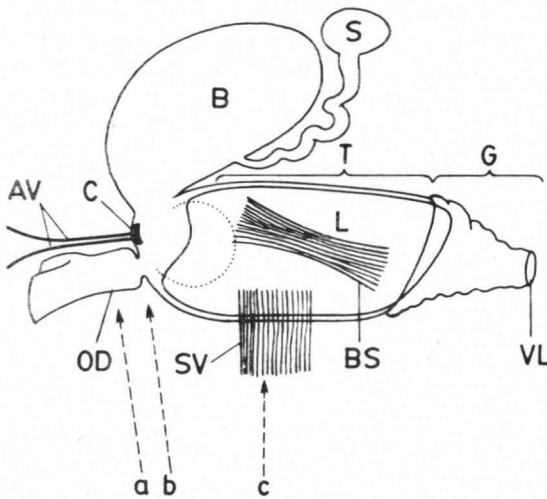
Fig. 1. *Ischnura rufostigma*, diagrammatic representation of the '8th complex' and its associated musculature (lateral view from the left, dorsal upwards). The genital atrium (G) of the vagina opens externally through the vulva (VL). Section-planes of the transverse section figures 3, 6, 8 indicated respectively as *a, b, c* by arrows.

The ovariole is differentiated into a terminal filament, germarium and vitellarium, all wrapped in a membranous epithelial sheath. The terminal filament is long, thread-like prolongation of the epithelial sheath in which cellular differentiation is not evident. The germarium is a small middle region, in which a mass of actively proliferating cells is formed in the centre, which differentiates into primordial germ cells and oocytes. The vitellarium is a large basal region attached to the lateral duct. The epithelium of this region, the follicular epithelium, has a distinctly cellular organization. It grows inwards to enclose each differentiated oocyte in a follicle. The largest follicle is at the base of the ovariole containing the fully developed ovum, around which a hard covering of chorion is secreted by the follicular epithelial cells. The ovum then becomes ready for transference from the ovariole to the lateral duct of the ovary.
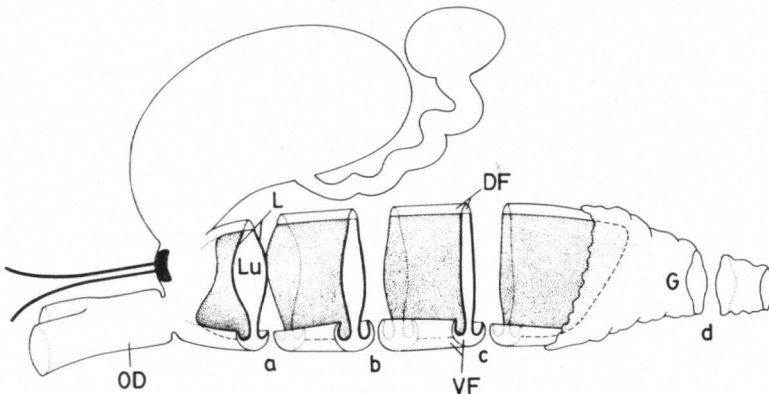

Fig. 2. *Ischnura rufostigma*, 3-dimensional schematic diagram of the vagina along with other organs of the '8th complex' (view from the left, dorsal upwards). The common median oviduct (OD) opens into the wide, oval shaped portion of the lumen (LU) of the tubular portion of vagina. The tubular portion is cut in vertical transverse section-planes at 3 levels: anterior (*a*), middle (*b*), and posterior (*c*). The lumen (LU), between the lateral plates (L), is widest at plane *a*, and the ventral membranous fold (VF) and its evaginations are largest at the plane *b*. The genital atrium (G), also cut in V.T.S. at the plane *d*.

The lateral ducts are thin walled, distensible and they continue posterior to the gonads as a pair of oviducts having similar characteristics. Walls of both ducts have an inner epithelial and an outer muscular layer comprising longitudinal fibres. The oviducts, which do not bear ovarioles, have thicker musculature and a wider lumen. The oviducts initially located dorso-laterally to the gut, gradually turn sidewards and ultimately reach beneath the gut during their course, forming an oblique ring around the alimentary canal. The two oviducts posteriorly open together into a short median oviductus communis (Figs 1,2 [OD]) lying underneath the 8th abdominal ganglion (8G). The common median oviduct has a much wider lumen than that of the oviduct, and is the only part of the internal genitalia described hitherto having the lumen lined by a chitinous intima (CH), secreted inwards by the epithelium (Fig. 3). The ova produced in the ovarioles are released into the lateral ducts, from where they descend down the oviducts and reach the oviductus communis for entry into the vagina of the '8th complex'.

THE '8TH COMPLEX'

The '8th complex' (Figs 1, 2, 4, 5), situated beneath the alimentary canal just behind the 8th ganglion, is a translucent and highly muscular structure of composite nature. Its components are vagina (V), bursa copulatrix (B) and spermatheca (S), all assembled within the posterior two-thirds of the 8th abdominal segment. In the '8th complex' rhythmic spontaneous pulsations were observed occasionally, which were of two kinds: (a) all components pulsating synchronously, (b) the components pulsating individually. No reason could be ascertained as to why the former take place. But the occurrence of the latter is associated with the transfer or movement of sperm to and fro between the bursa copulatrix and spermatheca. The '8th complex' is ensheathed by adipose tissue interspersed with muscle fibres, thus attaining a fluffy appearance. It is also supplied with tracheoles and nerve ramifications. The histological features of the '8th complex' are most easily studied in teneral specimens.

THE VAGINA

The vagina is a prominent tubular organ on the mid-ventral side composed of an anterior tubular portion (T) and a genital atrium (G).

The ANTERIOR TUBULAR PORTION forms the main part of the vagina, along each dorso-lateral side of which a nerve cord runs posteriorly. Its major part is dorsally hidden by the bursa copulatrix and spermatheca. In the anterior tubular portion (Fig. 2) the lumen (LU) is large, usually compressed, distensible and lined prominently by chitinous intima. The lumen for the most part — except anteriorly — is flanked on each side by a thickened, cuticular, lateral plate (L). The lateral plates are oblong, lamellate, vertically placed, and they bear several pores along their mid-line, especially in the posterior part. They have concave anterior margins. The lumen swells anteriorly, becoming wide and oval shaped in the anterior part of the vagina where it is partly enclosed by the anterior portions of the lateral plates. Here the lumen receives the openings of the common
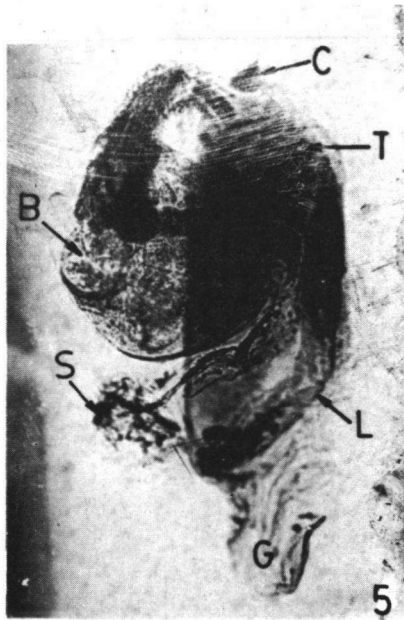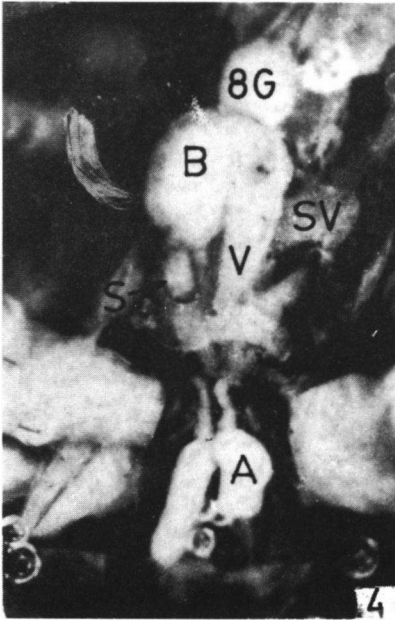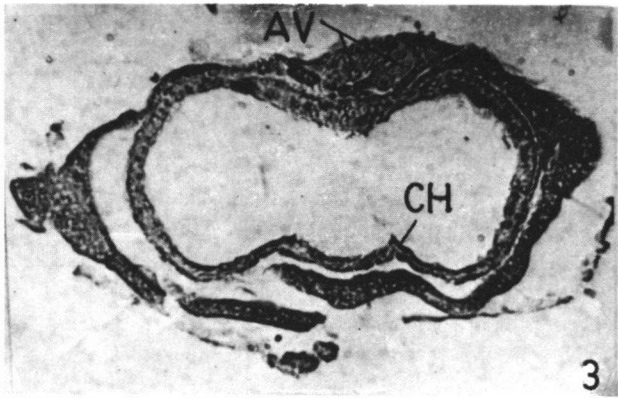
Figs 3-5. *Ischnura rufostigma*: (3) Transverse section of the common median oviduct showing a wide lumen lined distinctly by chitinous intima (CH). The two fasciculi of the anterior vaginal muscles (AV) running along the common median oviduct, are present on its dorsal surface (x 200). — (4) Dissection showing the '8th complex' behind the 8th ganglion (8G), and two accessory glands (A) in the 9th segment of abdomen. The '8th complex' comprises bursa copulatrix (B), spermatheca (S) and vagina (V). Right dorsal view (x 30). — (5) KOH-treated preparation of the '8th complex' showing anterior tubular portion (T) and genital atrium (G) of vagina, bursa copulatrix (B), and spermatheca (S). Sperm present within bursa copulatrix and spermatheca. Oblong lateral plate (L) and collar (C) distinct in the tubular portion of the vagina. Lateral view (x 60).

median oviduct on its antero-ventral and of the bursa copulatrix on its antero-dorsal sides (Figs 1, 2). The opening of the common median oviduct (Fig. 6 [O]) is 'T'-shaped due to infolding of the wall, which is provided with a marked ring of circular muscles forming a sphincter-like structure. The rhythm of the sphincter is neurogeneous. The sphincter allows only one ovum at a time to enter the oval shaped lumen in the vagina, where the sperm stored also enters from the sperma-theca via the base of the bursa copulatrix. An internally projecting, thick, hard cuticular collar (C) lies embedded in the wall in the anterior end part of the vagina between the openings of the common median oviduct and the bursa copulatrix. The collar comprises a central part placed in an obliquely vertical way bearing an anterior process, and a broad lateral arm on each side.

The lateral plates are connected both dorsally and ventrally by thick, folded, cuticular membranes bounding the lumen. The dorsal membranous fold (DF) is small and uniform all through, while the ventral membranous fold (VF) is large, sending the lumen into prominent, upcurved lateral evaginations running through the length of plates (Figs 2, 8). The inner margins of the evaginations are supported by upcurved extensions of the ventral edge of the lateral plates. The ventral membranous fold and its evaginations are largest in the middle part, and extenua-ting toward the anterior and posterior ends. When the lateral plates are pulled apart the folds allow much widening of the space on the ventral side, giving a triangular appearance in transverse section. The chitinous intima layer is secreted by an epithelium lying on the outer side which stands on a basement membrane. The epithelial cells are single layered, short and cuboidal, each bearing a large spherical nucleus. Muscle fibres and interspersed adipose tissue are present over the epithelium.

The GENITAL ATRIUM is a short, membranous, wrinkled, pouch-like, posterior extension of the vagina (Figs 1, 2, 5). Its front margin forms a rim or collar-like structure in which a small region of the tubular portion is sunk. The genital atrium is copiously surrounded by adipose tissue in teneral specimens only. Muscles are altogether absent from the region. The epithelium is thin, single layered and the cells have a large nucleus each. The chitinous intima is also thin, and uneven. Posteriorly the genital atrium opens externally through the vulva (VL), located ventro-medially between the sternites 8th and 9th.

THE BURSA COPULATRIX

The bursa copulatrix (Figs 4, 5) is a cylindrical, sac-like evagination of the antero-dorsal wall of the vagina, with which it is connected by a narrow base. In teneral and virgin specimens the bursa lies to one side in a flattened and wrinkled condition. Histologically the bursa is similar to the anterior tubular portion of the vagina. Its chitinous intima is usually thrown into irregular folds, except in the basal region, where it is thicker and produces numerous postero-

-ventrally directed spines on the ventro-lateral wall. The non-secretory epithelium consists of a single row of cuboidal cells having prominent rounded nuclei. The musculature is thick, comprising longitudinal fibres. The adipose tissue forms a regular and complete layer on the outer side, through which a few muscle fibres project and attach to the vagina and spermatheca.

The lumen of the bursa copulatrix − narrow in virgins − receives the male ejaculate (containing sperms embedded in seminal fluid of thick consistency). It serves both as a copulatory pouch for mating and as a temporary sperm storage organ. In just mated females the lumen is found to be considerably swollen to accommodate a large volume of sperm (Figs 6, 8); the spermatozoa are mostly in the form of groups or bundles. The other sperm storage organ, the spermatheca, does not receive spermatozoa at the time of mating when only the bursa is inseminated. The pulsations of the bursa copulatrix drive a part of its contained sperm to reach the spermatheca for storage. The storage capacity of the sperma-theca is less than that of the bursa and most of the sperm volume is retained by the bursa copulatrix.

THE SPERMATHECA

The spermatheca (Figs 4, 5) is a long posteriorly directed bursal evagination which is attached near the middle on the ventral side of the bursa copulatrix. It consists of a proximal duct and a distal sac, which exhibit no histological differen-tiation. The spermathecal duct (SD) runs sinuously, with slightly increasing diameter along the ventro-medial surface of the bursa (Fig. 8); and upon reaching the end dilates into a sac, which seems to be a continuation of the bursa. The sac is faintly red in colour and oval to rounded in shape. The spermatheca lies quite close to the bursa copulatrix, both being fastened together by a thick layer of adipose tissue.

The cellular organization of the spermatheca is most easily seen in virgin individuals (Fig. 7), in which the lumen is narrow, compressed and without sperm. The chitinous intima, bounding the lumen, is thick and traversed by numerous fine ridges and canals. The epithelium (E), single layered, is composed of cuboidal cells. A large oval nucleus possessing a nucleolus and several deeply-staining granules, is situated in each cell near the basal end. The epithelium of the spermatheca is secretory in nature, as suggested by the granulated and vacuolated cytoplasm. Its secretion has thin consistency. The musculature, outside the epithe-lium and responsible for rhythmic pulsations of the spermatheca, comprises a thin layer of circular muscle fibres which is slightly thicker in the duct region. The spermatheca is connected with the bursa copulatrix and the underlying vagina by a few strands of longitudinal muscle fibres.

The sperm, received from the bursa copulatrix, may be stored for a long period in the spermatheca. The secretion of the spermatheca gets interspersed with the
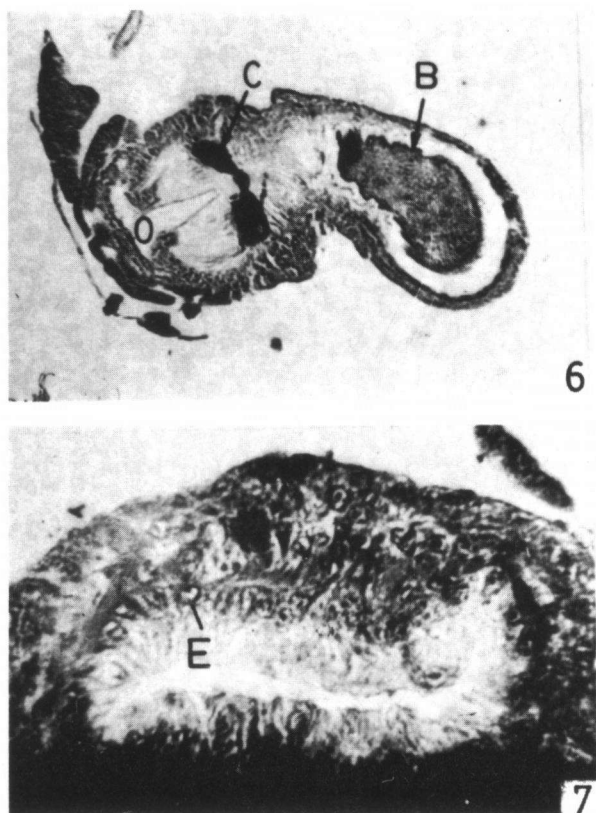
Figs 6-7. *Ischnura rufostigma*, transverse sections through: (6) The anterior end part of the vagina, showing collar (C) situated between the opening (O) of the common median oviduct and the base of the bursa copulatrix (B), both of which open into the anterior oval shaped lumen of the tubular portion of the vagina (x 100). − (7) The spermathecal sac of a virgin individual containing no sperm in its lumen. The epithelium (E) of the spermatheca is secretory (x 450).

sperm. The secretion not only provides viability to the sperm, but also a suitable medium to facilitate sperm movement. The increased number of separate spermatozoa in the spermatheca, suggests that the groups of sperms are partly segregated here. The sperm of the spermatheca passes through the base of the bursa copulatrix into the oval shaped lumen of the vagina where fertilization takes place. The sperm was found to be present in the spermatheca of all mated females, suggesting that the spermathecal sperm is not removed by successively mating males.
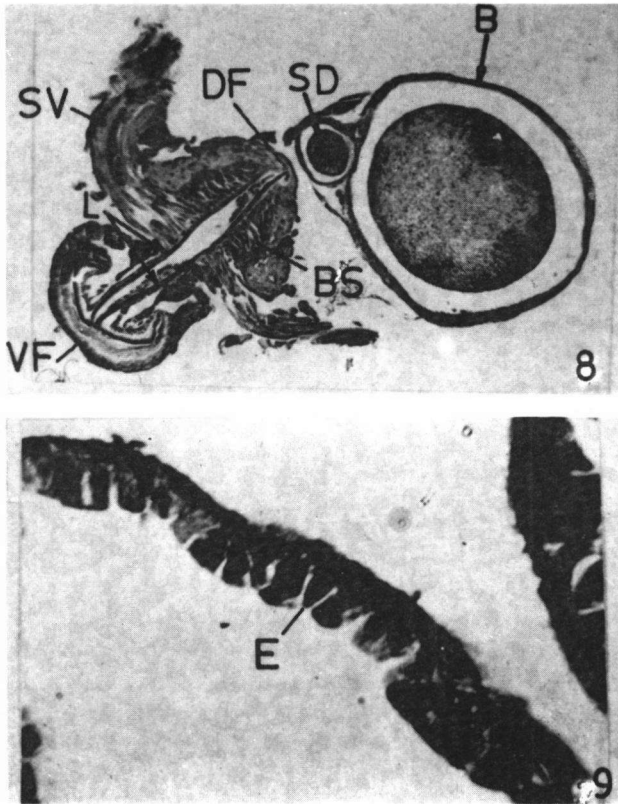
Figs 8-9. *Ischnura rufostigma*: transverse sections through: (8) The '8th complex' through the middle, showing sperm filled bursa copulatrix (B) and spermathecal duct (SD), and the anterior tubular portion of the vagina. The vaginal lumen there is flanked by lateral plates (L), which are connected dorsally by a dorsal membranous fold (DF) and ventrally by a ventral membranous fold (VF). Paired bow-shaped muscles (BS) and sterno-vaginal muscles (SV) seen (x 100). — (9) A portion of the sac of the accessory gland, having prominently secretory epithelium (E) (x 450).

MUSCULATURE ASSOCIATED WITH THE '8TH COMPLEX'

Though the musculature forms a regular layer outside the epithelium in the vagina, bursa copulatrix and the spermatheca, a few strands of muscle fibres interconnect these three organs. The tubular portion of the vagina offers an attachment for several more muscles (paired) which are (Fig. 1):

(a) Bow-shaped muscles (BS): — These muscles run lengthwise on each side of the vagina (Fig. 8) with both ends attached to the tubular portion of the vagina itself. The muscle on each side is attached antero-dorsally to the region of

the oval shaped lumen and postero-ventrally near the posterior end of the lateral plate.

(b) Sterno-vaginal muscles (SV): − These are a pair of strong muscles (Figs 4, 8), one on each side. One end is attached to the lateral plate near the middle of the tubular portion of the vagina, and the other is extended ventro-laterally to attach to the sternum of the 8th segment.

(c) Anterior vaginal muscles (AV): − These are also paired muscles whose fibres are arranged into two filamentous fasciculi attached to the front end of the vagina at the anterior collar. The fasciculi extend forwards running close together along the mid-dorsal surface of the common median oviduct (Fig. 3). Upon reaching the anterior end of the common oviduct the two fasciculi separate out. Each then further extends forwards along the mesal margin of the oviduct of its side and finally attaches to the 7th sternite.

THE ACCESSORY GLANDS

Two accessory reproductive glands (Fig. 2 [A]), located in the 9th segment of the abdomen, are seen on removal of the rectum. The glands, of unequal size, lie almost parallel and extend posteriorly. Each is whitish and consists of a proximal duct and a distal sac. The sac is cylindrical, somewhat dorso-ventrally flattened and possesses a spacious lumen lined by chitinous intima. The lumen is empty in teneral and sexually immature damselflies, but is filled with a secretion in the mature females − especially those who have just mated and are about to oviposit. The secretion comes from cuboidal epithelial cells (Fig. 9 [E]) which are arranged in only one row. Each cell has highly granulated, vacuolated cytoplasm and a spherical nucleus. Sometimes empty spaces are seen between the epithelial cells and also deposits of secretion near the apical end of cells. The epithelium is bounded by a thin basement membrane, which is itself surrounded by a thin layer of circular muscle fibres. The outermost layer is formed by thin pieces of adipose tissue adhering sparingly. The duct of the accessory gland is thread-like and is histologically very similar to that of the sac in the arrangement of layers. Its chitinous intima is thicker, the epithelium non-secretory, and the musculature relatively thicker. The duct opens on the dorso-lateral side of the hind part of the genital atrium in the proximity of the vulva. The duct conveys the gelatinous secretory material of the sac to the genital atrium where the secretion is then poured over the eggs passing for oviposition. The secretion, frothy in appearance and with sticky properties, gets applied all over the egg.

THE OVIPOSITION

The egg, fully ensheathed by the secretion of the accessory gland, leaves the genital atrium to emerge from the vulva. The vulva is enclosed by the base of

two pairs of valvulae of the ovipositor which are interlocked together forming an ovipositor canal; the eggs slide down through this canal. Prior to this, the blades of the valvulae have already carved a hole into the vegetation below the water surface. The eggs pass one after the other and are neatly placed in the holes. The eggs are invariably laid with their posterior obtuse end coming out first from the vulva, so that after oviposition the anterior pointed end is orientated outwards. The secretion ensheathing the egg fixes the egg in its place.

DISCUSSION

The bursa copulatrix, spermatheca and vagina are the three components of the '8th complex' in female *Ischnura rufostigma*. The vagina lies on the ventral side, being evaginated antero-dorsally into the bursa copulatrix which is itself evaginated posteriorly into the spermatheca. The presence of bursa copulatrix, spermatheca and vagina (all confined within the 8th abdominal segment) in the female system is reported in most odonates (SRIVASTAVA, 1959; PRASAD & SRIVASTAVA, 1961; PFAU, 1971; MIDTTUN, 1976; WAAGE, 1979, 1984; SRIVASTAVA, 1980; MILLER, 1982, 1987; SRIVASTAVA & SRIVASTAVA, 1989a, 1989b), with a few exceptions amongst the suborder Zygoptera. A bursa copulatrix and a vagina are not reported present respectively in *Mnais strigata* (ASAHINA, 1954; MATSUDA, 1976) and *Argia moesta* (JOHNSON, 1973), whereas in *Lestes vigilax* the presence of a spermatheca is questioned by WAAGE (1982, 1984).

The bursa copulatrix in odonates acts like a copulatory pouch during mating by receiving the distal part of the male penis, so that the sperm material is deposited into it. Subsequently the sperm is temporarily stored here. As the bursa copulatrix produces no secretion of its own the storage medium in the bursa is provided by the thick seminal fluid. Some of the sperm volume is transferred to the spermatheca also for storage and the rest is retained by the bursa. There are thus two organs in the damselflies for the storage of sperm — the bursa copulatrix and the spermatheca (SRIVASTAVA, 1980; WAAGE, 1984; MILLER, 1987; SRIVASTAVA & SRIVASTAVA, 1989a, 1989b). Copulating male odonates may be able to remove the sperm of rival males from the bursa, but they are thought not to be able to do so from the spermatheca (WAAGE, 1979, 1982, 1984, 1986; MILLER & MILLER, 1981; MILLER, 1984, 1987; CARLE, 1982). This ability to displace sperm (sperm removal and repositioning) seems to be widespread in odonates, especially amongst the members of the suborder Zygoptera (WAAGE, 1984). However, the sperm from the spermatheca in *Ischnura rufostigma* is not removed during such activity, as suggested by the presence of sperm in the spermatheca in all the mated cases. The spermatheca thus behaves as a true sperm storage organ.

SRIVASTAVA & SRIVASTAVA (1987) have reported that in Zygoptera — including the present species — the sperm material produced, translocated, and

transferred to the female bursa copulatrix, contains spermatozoa in the form of groups or bundles mostly which lie dispersed in seminal fluid, and not in the form of spermatophores. Obviously, to facilitate the fertilization process there is the need to resolve or segregate the groups of sperms into separate individual spermatozoa. In *I. rufostigma*, the glandular secretion of the spermatheca is herewith thought to separate the sperm groups into separate spermatozoa, and also to provide a suitable medium for their movement. The separated motile sperms, driven by rhythmic pulsations of the spermatheca, pass through the base of the bursa copulatrix and reach the anterior part of the vagina where the lumen is oval. It is here that the fertilization occurs.

As in other Zygoptera, the vagina of *I. rufostigma* allows the male penis to reach the bursa copulatrix for insemination. The entry of the penis through the vagina is facilitated by the action of the sterno-vaginal muscles which pull apart the two lateral plates of the vagina, causing widening of the vaginal space. JOHNSON (1973) called these two plates together the collar and the vagina, the bursa copulatrix whereas MILLER (1987) termed the plates the cuticular plates or vaginal plates, whose activity according to him is under nervous influence.

Another cuticular thickening found in the vagina is the "collar". The term "collar" was given by TILLYARD (1917), to a hard chitinized internally projecting structure in the organ (called by him the spermatheca or bursa) in *Petalura gigantea*. A similar collar plate was also noticed by PRASAD & SRIVASTAVA (1961) in *Pantala flavescens*, located on the dorsal side of the '8th complex'. Based on these reports the cuticular piece, embedded in the anterior wall of the vagina between the openings of the common median oviduct and the bursa copulatrix, is herewith termed as the "collar". Nearly at the same location PFAU (1971) has illustrated in *Ischnura elegans* a cuticular place where the muscle MVa is inserted. This muscle according to him, widens the vagina to open the bursa copulatrix and to suck the sperm into it. Our examinations differ markedly with those of PFAU (1971). In *I. rufostigma*, the cuticular piece, the "collar", not only precludes the intrusion of the penis into the common median oviduct, but diverts and guides the distal part of the penis to enter into the bursa copulatrix. The positioning of the collar during such activity is regulated by the action of the anterior vaginal muscles. A similar collar has also been reported by us (SRIVASTAVA & SRIVASTAVA, 1989a, 1989b) for two other zygopterans, *Pseudagrion rubriceps* and *Copera marginipes*. The anterior vaginal muscles also pull the vagina forwards so as to readily accommodate an egg descending from the common median oviduct into the vaginal lumen. The pulsatory activity of the vagina of the '8th complex' is due to the activity of the paired bow-shaped muscles of the vagina. Working in unison, these muscles contract and expand the lumen of the tubular portion of the vagina alternately in the anterior and posterior parts thereby driving the fertilized egg posteriorly.

While passing through the genital atrium the egg is bathed in the accessory

gland secretion which is applied all round the egg, ensheathing it completely. Since the secretion has sticky properties it fixes the fertilized egg into the vegetation lying submerged in water. The eggs of an anisopteran, *Tholymis tillarga* which oviposits epiphytically on submerged leaves, were also found by MILLER & MILLER (1985) to have a coating of secretion.

ACKNOWLEDGEMENT

REFERENCES

ASAHINA, S., 1954. *A morphological study of a relic dragonfly Epiophlebia superstes (Selys) (Odonata: Anisozygoptera)*. Jpn Soc. Prom. Sci., Tokyo.

CARLE, F.L., 1982. Evolution of the odonate copulatory process. *Odonatologica* 11(4): 271-286.

CHAPMAN, R.F., 1971. *The insect structure and function*. E.L.B.S. & Engl. Univ. Press, London.

GEORGE, C.J., 1929. The morphology and development of the genitalia and genital ducts of Homoptera and Zygoptera as shown in the life-histories of Philaenus and Agrion. *Q. Jl microsc. Sci.* 72: 447-485.

JOHNSON, C., 1973. Ovarian development and age recognition in the damselfly Argia moesta (Hagen, 1961) (Zygoptera: Coenagrionidae). *Odonatologica* 2(2): 69-81.

MARSHALL, W.S., 1914. On the anatomy of dragonfly, Libellula quadrimaculata Linn. *Trans. Wisc. Acad. Sci.* 17(2): 755-790.

MATSUDA, R., 1976. *Morphology and evolution of the insect abdomen*. Pergamon Press, Oxford.

MIDTTUN, B., 1976. The morphology of the spermatheca, bursa copulatrix and vagina of Somatochlora arctica (Zetterstedt) (Odonata: Corduliidae). *Norw. J. Zool.* 24(3): 175-183.

MILLER, P.L., 1982. The occurrence and activity of sperm in mature female Enallagma cyathigerum (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica* 11(2): 159-161.

MILLER, P.L., 1984. The structure of the genitalia and the volumes of sperm stored in male and female Nesciothemis farinosa (Foerster) and Orthetrum chrysostigma (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 13(3): 415-428.

MILLER, P.L., 1987. An examination of the prolonged copulations of Ischnura elegans (Vander Linden) (Zygoptera: Coenagrionidae). *Odonatologica* 16(1): 37-56.

MILLER, P.L. & A.K. MILLER, 1985. Rates of oviposition and some other aspects of reproductive behaviour in Tholymis tillarga (Fabricius) in Kenya (Anisoptera: Libellulidae). *Odonatologica* 14(4): 287-299.

MILLER, P.L. & C.A. MILLER, 1981. Field observations on copulatory behaviour in Zygoptera, with an examination of the structure and activity of the male genitalia. *Odonatologica* 10(3): 201-218.

PFAU, H.K., 1971. Struktur und Funktion der sekundären Kopulationsapparates der Odonaten (Insecta, Palaeoptera), ihre Wandlung in der Stammesgeschichte und Bedeutung für die adaptative Entfaltung der Ordnung. *Z. Morph. Tiere* 70: 281-371.

PRASAD, S.N. & B.K. SRIVASTAVA, 1961. The morphology of the female reproductive organs of Pantala flavescens Fabricius (Libellulidae: Odonata). *Proc. natn. Acad. Sci. India* (B) 31: 47-56.

RICHARDS, O.W. & R.G. DAVIES, 1977. *Imms' general textbook of entomology*. Chapman & Hall and Methuen, London.

SNODGRASS, R.E., 1935. *Principles of insect morphology.* McGraw-Hill, New York — London.

SRIVASTAVA, B.K., 1959. *The study of the reproductive system of certain Odonata (Anisoptera).* Ph.D. thesis, Univ. Allahabad.

SRIVASTAVA, B.K. & B.S. BABU, 1985. On some aspects of reproductive behaviour in Chloroneura quadrimaculata (Rambur) (Zygoptera: Protoneuridae). *Odonatologica* 14(3): 219-226.

SRIVASTAVA, V.K., 1980. *The study of the reproductive system of certain Odonata (Zygoptera).* Ph.D. thesis, Univ. Saugar.

SRIVASTAVA, V.K. & B.K. SRIVASTAVA, 1987. On the zygopteran sperm material, with reference to the spermatophore. *Odonatologica* 16(4): 393-399.

SRIVASTAVA, V.K. & B.K. SRIVASTAVA, 1989a. Female internal genital organs of the damselfly Pseudagrion rubriceps Selys (Zygoptera: Odonata). *Folia morphol.* 37(2): 165-171.

SRIVASTAVA, V.K. & B.K. SRIVASTAVA, 1989b. Internal genital organs of female Copera marginipes (Rambur) (Zygoptera: Platycnemididae). *Indian Odonatol.* 2: 27-35.

TILLYARD, R.J., 1917. *The biology of dragonflies.* Cambridge Univ. Press, Cambridge.

TUXEN, S.L., 1970. *Taxonomist's glossary of genitalia in insects.* Munksgaard, Copenhagen.

WAAGE, J.K., 1979. Dual function of the damselfly penis: Sperm removal and transfer. *Science* 203: 916-918.

WAAGE, J.K., 1982. Sperm displacement by male Lestes vigilax Hagen (Zygoptera: Lestidae). *Odonatologica* 11(3): 201-209.

WAAGE, J.K., 1984. Sperm competition and the evolution of odonate mating systems. *In*: R.L. Smith, [Ed.], Sperm competition and the evolution of animal mating systems, vol. 8, pp. 251--290, Academic Press, New York.

WAAGE, J.K., 1986. Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biol. J. Linn. Soc.* 28: 285-300.

WIGGLESWORTH, V.B., 1972. *The principles of insect physiology.* E.L.B.S. and Chapman & Hall, London.