

**THE POST-OVARIAN GENITAL COMPLEX OF THE
DRAGONFLY, *TRAMEA VIRGINIA* (RAMBUR)
(ANISOPTERA: LIBELLULIDAE)**

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The post-ovarian genital complex (POGC) is ectodermal in origin and confined to the 8th abdominal segment. It consists of a pair of lateral, elliptical spermathecae, a median, spherical bursa copulatrix and a ventral, pouch-like, rectangular muscular vagina. — In the mature female the spermathecae, bursa copulatrix and vagina are lined with a thick cuticular intima. The vagina is externally wrapped in a thick muscle coat formed of four pairs of sternal muscles. The ducts from the spermathecae open anterolaterally into the bursa copulatrix. The latter opens posteriorly into the vagina through a well defined bursa communis. The fertilization pore is a cuticular tunnel formed from a middorsal and two lateral cuticular plates. The common oviduct opens mid-ventrally into the vagina through a spindle-shaped cuticular orifice. — Soon after ecdysis from the penultimate to the last instar larva, a trilobed epithelial structure is formed from a globular mass of epithelial cells present in the middle of the inner surface of the 8th sternum. By the 4th day the bursa copulatrix and vagina are differentiated from the dorsomedian and ventrolateral lobes of the trilobed structure, respectively. The spermathecae bud off from the lateral walls of the bursa copulatrix. The fertilization pore and bursa communis are formed by the 20th day. Prior to the final moult, the post-ovarian genital complex is fully formed but lies in a collapsed state. In the newly emerged adult, the POGC is lined internally with a distinct, thin cuticle and covered externally with a poorly developed muscle coat.

INTRODUCTION

TILLYARD (1917) initially failed to recognize the vagina in *Petalura gigantea* and the spermathecae were variably termed as the accessory sacs (TILLYARD, 1917), spermathecal glands (ASAHINA, 1954), lateral accessory spermathecal sacs (PRASAD & SRIVASTAVA, 1961) and laterale spermateksekker (BJÅNES,

1974). During the last decade extensive work has been carried out on sperm transfer, storage and removal mechanisms in dragonflies, and it is now well-established that the post-ovarian genital complex (POGC) in most Odonata comprises typically the spermathecae, bursa copulatrix and vagina on the 8th abdominal sternum (MIDTTUN, 1976; MILLER, 1982, 1984, 1987, 1988, 1991; WAAGE, 1982, 1984, 1986; SIVA-JOTHY, 1987; MICHIELS, 1989). However, PRASAD & SRIVASTAVA (1961) and SRIVASTAVA & SRIVASTAVA (1992) referred to the POGC as the 8th complex on the basis of its location.

The available literature, moreover, reveals that various morphological and physiological aspects of the POGC are still unexplored, and there is little information on the development of the complex (MATSUDA, 1976). The present work was undertaken to study the structure and development of the POGC in *Tramea virginia*.

MATERIAL AND METHODS

Penultimate and last instar larvae of *Tramea virginia* were collected from local ponds. They were reared in specially designed tubs containing dechlorinated water and covered with mosquito nets (TEMBHARE & THAKARE, 1975) at constant photoperiod (10L: 14D) and temperature $20^{\circ}\text{C} \pm 2^{\circ}\text{C}$. The water was renewed daily. The larvae were fed ad libitum on mosquito larvae and freshly collected zooplankton. Just after ecdysis, the last instar larvae were kept separately and a record of their age was maintained. The life span of the last instar larvae is about 32 days under these conditions.

The post-ovarian genital complex (POGC), along with the 8th abdominal sternum, ovaries and oviducts, was dissected from last instar larvae at four day intervals after ecdysis. Adult females were collected before, during and after copulation and their POGC was immediately dissected. The POGC was fixed in Bouin's fluid for 12-18 hours, dehydrated, cleared in xylene and embedded in paraffin at $60-62^{\circ}\text{C}$. Serial sections of 4-6 μm thickness were cut and stained with Heidenhain's Iron-Haematoxylin-Orange G.

For scanning electron microscopy, the POGC of adults was fixed in 70% ethanol, dehydrated, dried and coated with gold. The preparations were examined in a stereoscan 250 MK III electron microscope. Histological measurements were made using a lanometer. No fewer than 25 readings were taken to determine the mean value and standard error. The nomenclature of SIVA-JOTHY (1987) is used for the muscle bands of the vagina.

ANATOMICAL ORGANISATION

In the post-copulated female *T. virginia*, the POGC consists of a pair of lateral, elliptical, milky-white spermathecae, a mid-dorsal spherical bursa copulatrix and a large ventral vagina (Fig. 1). The spermathecae are invested ventrally, and the bursa copulatrix laterally, in the external muscle coat of the POGC. Each spermatheca communicates independently with the bursa copulatrix by a short spermathecal duct. The bursa copulatrix opens into the vagina dorsally, while the median oviduct enters the vagina ventrally. The vagina is a large, long, laterally folded sac-like structure. It extends anteriorly to form a small anterior vaginal pouch (anterior genital chamber) and terminates posteriorly in a vulva. The vulva opens

to the exterior at the base of the 8th abdominal sternum. A rectangular cuticular plate (or collar) with arms, is embedded mid-dorsally in the external muscle coat over the region between the bursa copulatrix and vagina.

HISTOMORPHOLOGY

The wall of all the components of the POGC is basically identical in histological structure and it is composed of outer muscular, middle epithelial and inner cuticular layers.

SPERMATHECAE. — The epithelial layer is composed of tall columnar cells measuring $22.5 \pm 6.55 \mu\text{m}$ in length and $6.64 \pm 1.35 \mu\text{m}$ in width. The internal cuticular lining is annulated, sclerotized and $5.7 \pm 2.15 \mu\text{m}$ thick (Fig. 2). In histological preparations, differentiation of the cuticular lining into 3 or 4 sub-layers is evident. The wall of the spermathecal duct consists of a thin ($4.5 \pm 0.6 \mu\text{m}$), annulated cuticular intima (Fig. 3) and the epithelium is composed of small cells measuring $10.4 \pm 2.56 \mu\text{m}$ in length and $5.8 \pm 1.15 \mu\text{m}$ in width. In post-copulated females, the spermatheca, spermathecal duct and bursa copulatrix are filled with sperm (Fig. 4).

BURSA COPULATRIX. — The epithelial layer is composed of columnar cells measuring $15.2 \pm 3.56 \mu\text{m}$ in length and $8.4 \pm 1.5 \mu\text{m}$ in width. The epithelium is lined internally with a thick cuticular intima. Due to enormous cuticular folds, the dorsal and lateral walls of the bursa copulatrix are deeply grooved (Fig. 5). In the posteroventral region, the cuticular layer becomes thick and forms a slit, the bursa communis. This bears denticles on its inner and outer surfaces. It opens into the vagina at the anterior end of the fertilization pore (Fig. 6).

VAGINA. — The wall of the vagina varies in thickness from one region to another (Tab 1). The cuticular intima is heavily wrinkled laterally (Fig. 7). Paired hollow cuticular processes project into the outer muscle coat just above the fertilization pore and form the dorsal cuticular pockets (Fig. 6).

The lumen of the vagina is expanded and rectangular anteriorly but is greatly reduced in the middle and becomes conical or 'T'-shaped posteriorly (Fig. 8).

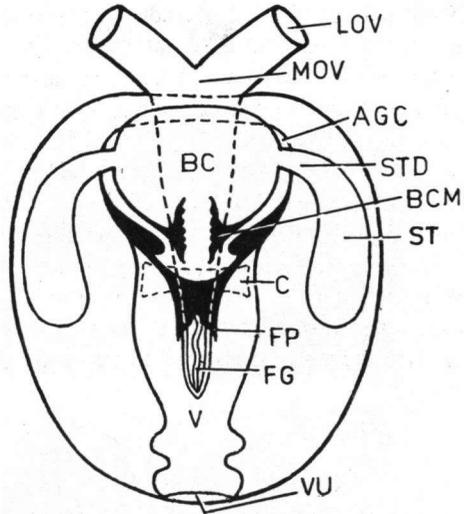
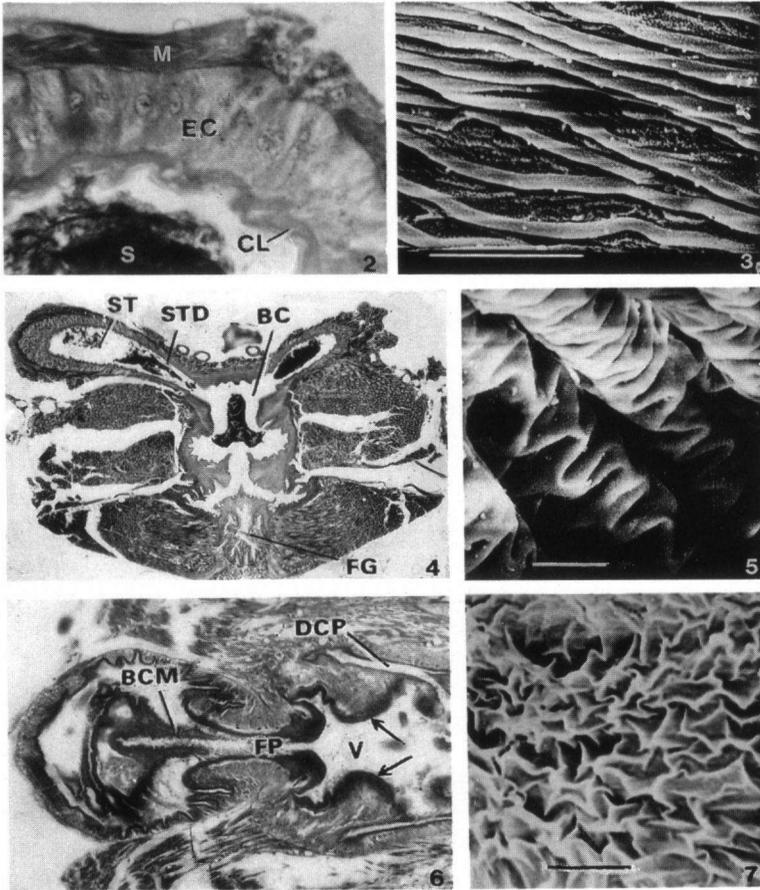


Fig. 1. *Tramea virginia*: Gross anatomy of the post-ovarian genital complex (POGC). [AGC = anterior genital chamber (anterior vaginal pouch); — (BC = bursa copulatrix; — BCM = bursa communis; — C = collar; — FG = female gonopore; — FP = fertilization pore; — LOV = lateral oviduct; — MOV = median oviduct; — ST = spermathecae; — STD = spermathecal duct; — V = vagina; — VU = vulva].



Figs 2-7. *Tramea virginia*: (2) Transverse section of a spermatheca showing the histological structure of the wall and sperm (S) in the lumen. CL = cuticular lining; EC = epithelial cells; M = muscle coat [Iron haematoxyline Orange - G (FeH-OG), $\times 330$]; - (3) SEM of inner surface of a spermathecal duct showing the annulated cuticular lining [Scale bar = $10 \mu\text{m}$]; - (4) Transverse section of the POGC showing female gonopore (FG) and darkly stained sperm in the spermathecae (ST), spermathecal ducts (STD) and bursa copulatrix (BC) - [FeH-OG, $\times 40$]; - (5) SEM of inner surface of the bursa copulatrix showing folded cuticular lining. [Scale bar = $10 \mu\text{m}$]; - (6) Longitudinal section of the mid-region of the POGC showing bursa communis (BCM), fertilization pore (FP), vagina (V), dorsal cuticular pocket (DCP) and lateral vaginal plates (arrow) [FeH-OG, $\times 90$]; - (7) SEM of inner surface of the vagina showing wrinkled cuticular lining [Scale bar = $10 \mu\text{m}$].

Table I

Variation in the size of the wall-epithelia and cuticle layers in the different regions of the vagina of *Tramea virginia*

Region	Epithelial Cells		Cuticular layer Thickness (μm)
	Length (μm)	Width (μm)	
Anterior vaginal pouch	7.22 \pm 2.45	5.7 \pm 0.86	7.6 \pm 0.42
Antero-dorsal	42.6 \pm 5.6	7.5 \pm 1.25	26.6 \pm 4.45
Mid- and postero-dorsal	22.8 \pm 4.26	7.8 \pm 1.25	74.0 \pm 18.75
Antero-lateral	35.6 \pm 6.65	7.5 \pm 1.84	13.4 \pm 2.24
Mid- and postero-lateral	30.9 \pm 7.45	7.8 \pm 2.15	15.2 \pm 5.75

\pm Standard error

The lumen of the anterior vaginal pouch is narrow anterolaterally and posterolaterally due to immense deposition of cuticle, and bears a large number of thin, finger-like cuticular processes or stubs (Fig. 9).

The fertilization pore is formed in the vagina due to a unique arrangement of a mid-dorsal and the lateral cuticular plates (Fig. 10). The mid-dorsal plate lies over the lateral plates to form a tunnel-like fertilization pore. The inner surface of the tunnel is lined with spines of variable length (5.7-13.4 μm) (Fig. 11). There are fine denticles on the bursa communis facing the anterior opening of the fertilization pore (Fig. 12). The lateral regions of the vagina facing the posterior opening of the pore comprise thick, cuticular, semicircular, lateral vaginal plates (Fig. 6).

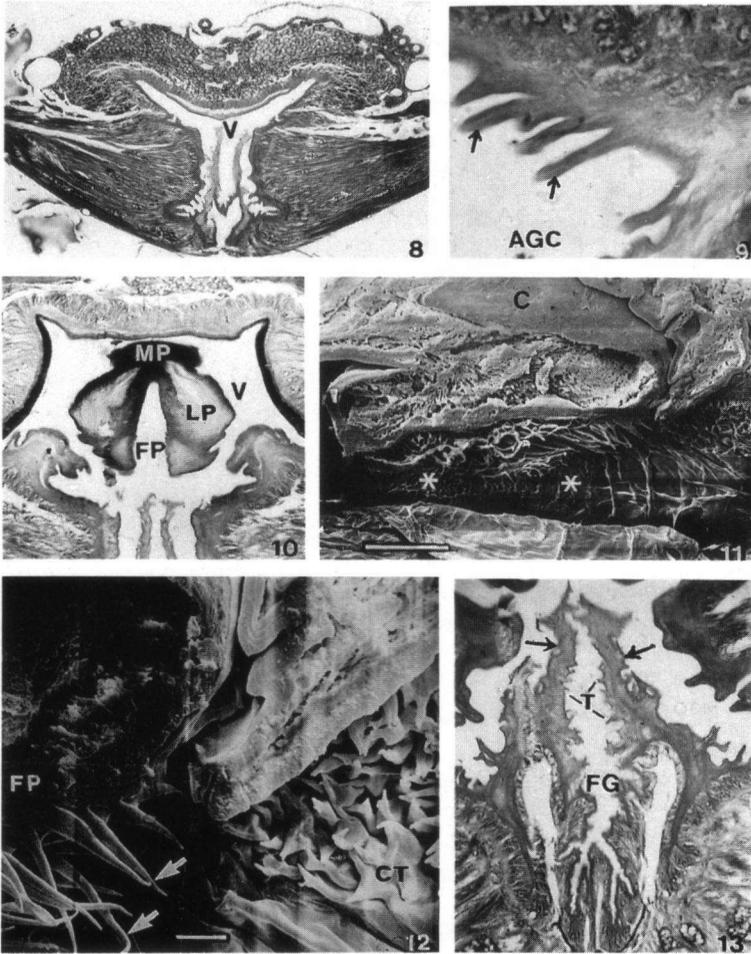
The median oviduct opens ventrally inside the vagina through a spindle-shaped orifice, the female gonopore. This orifice is encircled by a cuticular rim bearing fine denticles (Fig. 13).

The vagina is enveloped dorsolaterally by a thick and intricate muscle coat, which is formed from 4 pairs of muscles: the anterolateral sternoplate (Alsp), the posterior sternoplate (Psp), the longitudinal sternovaginal (Lsv) and the transverse sternovaginal (Tsv). All are confined to the eighth abdominal sternum. (Figs 14-15).

The anterolateral sternoplate muscle bands are connected to the lateral edges of the median plate (collar) and the anterolateral sternal rim. They encircle the anterior region of the vagina including the anterior vaginal pouch.

The posterior sternoplate muscle bands are connected to the ventral surface of the median plate and the posterolateral sternal rim. The paired bands are fused along the mid-dorsal region of the vagina and bifurcate at the posterior end of the vaginal region.

The longitudinal sternovaginal muscle bands run over the lateral region of the vagina and are connected to the anterior and posterior margins of the sternum. They envelop the vagina laterally from the anterior vaginal pouch to the terminal



Figs 8-13. *Tramea virginia*: (8) Transverse section of the posterior region of the vagina (V) showing 'T' shaped lumen [FeH-OG, $\times 38$]; - (9) Transverse section of the anterior genital chamber (AGC) showing cuticular finger like stubs (arrows) projected in the lumen [FeH-OH, $\times 230$]; - (10) Transverse section of the anterior region of vagina (V) showing a median plate (MP) above the lateral plates (LP) on either side of the fertilization pore (FP). [FeH-OG, $\times 154$]; - (11) SEM showing cuticular collar (C) and spiny tunnel (asterisks) of the fertilization pore [Scale bar = 10 μm]; - (12) SEM of the anterior end of the fertilization pore (FP) showing spines (arrows) and cuticular teeth (CT) of the bursa communis [Scale bar = 10 μm]; - (13) Transverse section of the ventral region of the POGC showing female gonopore encircled by a cuticular rim (arrow) bearing fine teeth (T) [FeH-OG, $\times 154$].

vulva.

The transverse sternovaginal muscle bands are located beneath the longitudinal sternovaginal muscles. They run from the lateral margins of the sternum and are connected to the lateral walls of the vagina. Some of the transverse sternovaginal muscle fibres intersect the longitudinal vaginal muscle fibres.

The anterolateral sternoplate and posterior sternoplate muscle bands together constitute the outer layer, while the longitudinal sternovaginal and transverse sternovaginal muscle bands form the middle and inner layers of the muscle coat, respectively. All muscle bands, except the anterolateral sternoplate, are thick. The spermathecae and their ducts are enveloped by a thin layer of intrinsic muscles.

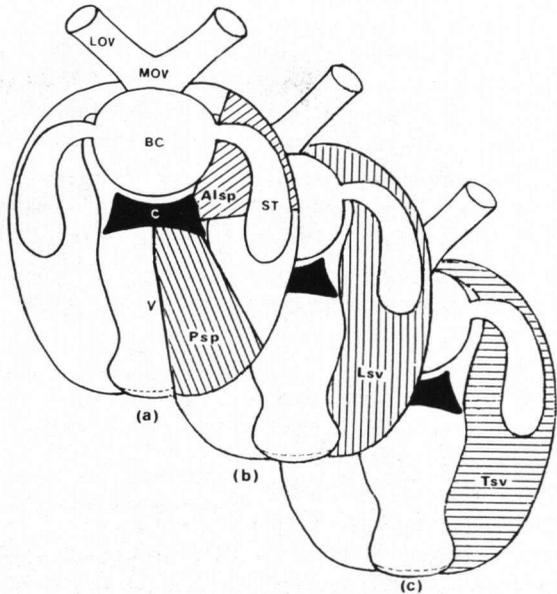


Fig. 14. *Tramea virginia*: diagram of the vaginal muscle coat showing (a) anterolateral sternoplate muscle band (Alsp) and posterior sternoplate (Psp) muscle band as the outer layer (b), longitudinal sternovaginal (Lsv) muscle band as the middle layer (c) and transverse sternovaginal (Tsv) muscle band as the inner (d) layers. [BC = bursa copulatrix; - C = collar; - LOV = lateral oviduct; - MOV = median oviduct; - ST = spermatheca; - V = vagina].

DEVELOPMENT

The development of the POGC is initiated in the newly moulted last instar larva as a globular epithelial mass elevated at the centre of the inner surface of the 8th abdominal sternite; it is almost completed prior to the emergence of the adult. Within a few hours it is modified into a tiny trilobed structure consisting of a mid-dorsal and a pair of ventrolateral lobes (Fig. 16). The mid-dorsal lobe is connected to the ventrolateral lobes by a stalked lumen which is forked ventrally. The wall of the lobes is made up of tall columnar epithelial cells.

In the 4-day old larva, the spermathecae develop as bud-like spherical, lateral outgrowths of the mid-dorsal lobe. Their walls resemble that of the mid-dorsal lobe and each outgrowth encloses a small central lumen (Fig. 17). The epithelial cells bear prominent basal nuclei and contain stained granules. The epithelium

secretes a thin cuticular intima. The mid-dorsal and ventrolateral lobes form the bursa copulatrix and vagina, respectively. The whole complex is enveloped externally in a mass of mesodermal cells. The formation of a pair of mesodermal plugs attaching the vagina firmly to the sternum is evident.

In the 8-day old larva, the bursa copulatrix and vagina along with their lumina become prominent. The bursa appears as a

small transverse chamber bearing oblong lateral spermathecae. The opening of the bursa into the vagina is also quite distinct. At this stage, the female gonopore is demarkated just below the vagina (Fig. 18). Subsequently, the epithelial cells of the spermathecae enlarge and change from columnar to spheroidal (Fig. 19). Fine muscle fibres are differentiated from the peripheral mass of the mesodermal cells.

By day 12, the epithelium of the lateral sides of the vagina have turned inwards to form a cup-shaped pocket in which heavy deposition of cuticle takes place (Fig. 20). In the 20-day old larva, three cuticular plates, a median and two lateral ones, are formed from the deposited cuticular secretion. These three plates collectively form the fertilization pore in the mid-anterior region of the vagina. Subsequently the cuticle of the mid-posterior region of the bursa copulatrix is modified due to excessive deposition and forms the bursa communis. In the 24-days old larva, the anterior part of the vagina is separated into an anterior vaginal pouch, due to the formation of the fertilization pore. This pouch lies ventral to the bursa copulatrix. The collar is formed above the fertilization pore due to heavy deposition of cuticle, and subsequently the posterior region of the lumen of the vagina tapers and forms a vulva. By 28 days, a cuticular rim around the orifice of the female gonopore becomes distinct.

In the newly emerged imago, the spermathecae, bursa copulatrix and vagina, though completely developed, still exist in a collapsed state and have poorly sclerotized cuticular intima and feebly developed musculature (Figs 22-23).

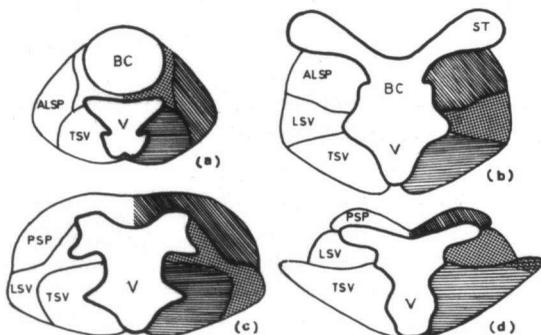


Fig. 15. *Tramea virginia*: diagram of the vaginal muscle coat at different transverse planes: (a) anterior; — (b) mid-anterior; — (c) mid-posterior; — (d) posterior. [ALSP = anterolateral sternoplate muscle band; — BC = bursa copulatrix; — LSV = lateral sternovaginal muscle band; — PSP = posterior sternoplate muscle band; — ST = spermatheca; — TSV = transverse sternovaginal muscle band; — V = vagina].

DISCUSSION

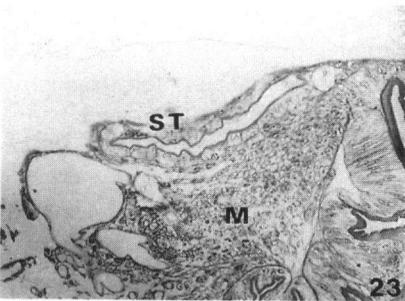
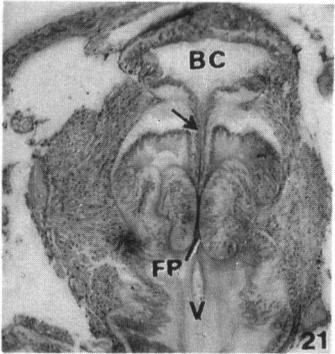
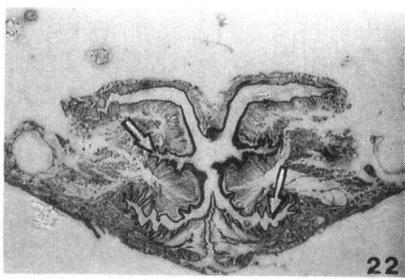
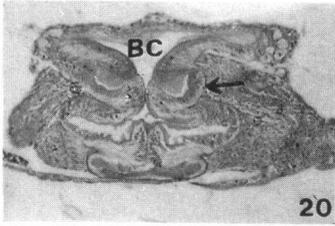
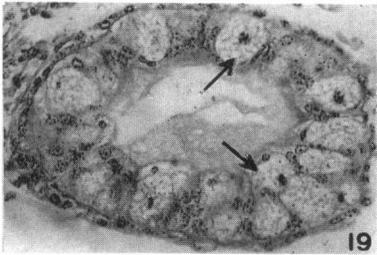
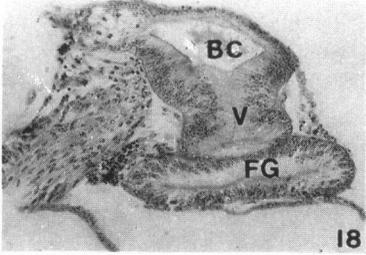
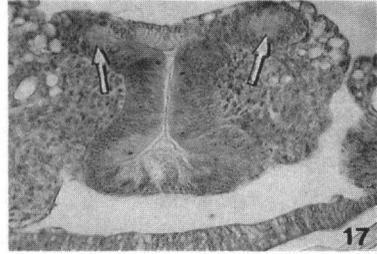
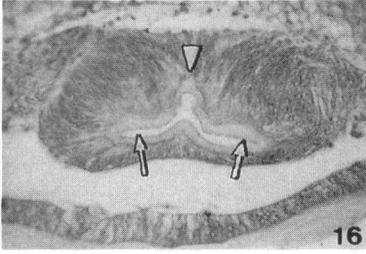
On the basis of pre-existing literature, MATSUDA (1976) concluded that the vagina, bursa and spermathecae originate from various invaginations developed on the 8th sternum. In contrast, the present study indicates that the entire POGC is developed from a single, trilobed invagination of the 8th sternum. The bursa copulatrix develops from the mid-dorsal and the vagina from the ventrolateral lobes of the trilobed invagination. Later, the spermathecae are budded off from the dorsolateral walls of the bursa copulatrix.

In *T. virginia* the spermathecae open independently through distinct spermathecal ducts into the anterolateral region of the bursa copulatrix and thus differ from those of *Epiophlebia superstes* (ASAHINA, 1954) and *Brachythemis leucosticta*, *Zyxomma petiolatum*, *Tholymis tillarga*, *Parazyxomma flaviscans*, *Brachythemis lacustris*, *Potamarcha congener* (MILLER, 1982, 1988, 1991), in which the formation of a common spermathecal duct opening into the bursa has been reported. MATSUDA (1976) reported opening of the spermathecae directly into the vagina.

Some workers have reported secretory cells in the spermathecal wall (ASAHINA, 1954; PRASAD & SRIVASTAVA, 1961), while MIDTTUN (1976) observed glandular cells in the spermathecal ducts. In *T. virginia*, although the glandular cells in the spermathecal wall of the larva are evident, neither the spermathecae nor their ducts show a glandular structure in the adult stage, supporting the observations of BJÅNES (1974) and SIVA-JOTHY (1987). In *T. virginia* the cuticle of the adult spermathecae and their ducts is modified into annulated cuticle ridges, presumably to facilitate movement of the sperm. Similar ridges are also found in the ducts of *Somatochlora arctica* (MIDTTUN, 1976).

PRASAD & SRIVASTAVA (1961) observed a division of the bursa copulatrix into two parts, but in *T. virginia* it is a single, undivided structure, and its internal cuticular lining forms intricate folds, as found in *S. arctica* (MIDTTUN, 1976).

The bursa communis and fertilization pore are well developed in *T. virginia* and are lined with spines, supporting the observations of MIDTTUN (1976), MILLER (1984) and SIVA-JOTHY (1987). It has been suggested that the penis approaches the bursa copulatrix via the bursa communis and that the sperm released into the former enter the vagina through the fertilization pore (MILLER, 1984; SIVA-JOTHY, 1987). However, in *T. virginia* it appears that the sperm pass from the bursa copulatrix into the bursa communis before passing through the fertilization pore to fertilize the eggs. Information regarding the movement of the egg in the vagina for fertilization is relayed by the lateral vaginal plates in some libellulids (MILLER, 1984; SIVA-JOTHY, 1987). The position, size and shape of these plates in *T. virginia* also indicate a similar functional interrelationship. The anterior vaginal pouch of *T. virginia* is similar to that of *Orthetrum cancellatum* (SIVA-JOTHY, 1987), whereas the dorsal cuticular pocket of the



vagina in *T. virginia* is also found in *S. arctica* (MIDTTUN, 1976). These structures increase the volume of the vagina, and the dorsal pockets also make room for the movement of the cuticular collar. Although spermatophores were reported in the sperm sacs of *Ictinogomphus rapax* (TEMBHARE & THAKARE, 1982) and bursa copulatrix of *S. arctica* (MIDTTUN, 1978), they were not found in *T. virginia*.

The contraction and expansion of the vagina during copulation, fertilization and oviposition is operated by the four paired vaginal muscle bands in *T. virginia*, as in *O. cancellatum* (SIVA-JOTHY, 1987). However, the vaginal muscle coat of *T. virginia* consists of small, thin anterolateral sternoplate and paired posterior sternoplate muscle bands whereas, in *O. cancellatum* the anterior lateral sternoplate muscle bands are large and there is a single, unpaired posterior one (SIVA-JOTHY, 1987). The intrinsic muscles around the spermathecae and their ducts in *O. cancellatum* (SIVA-JOTHY, 1987) are also found in *T. virginia*.

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Figs 16-23. *Tramea virginia*: (Figs 16-20): transverse section through the mid-region of the eighth sternum of the ultimate instar larva [FeH-OG]: (16) Development of a trilobed structure consisting of the mid-dorsal (arrow head) and ventrolateral lobes (arrows), with a well-defined lumen in the newly moulted larva [$\times 200$]; — (17) Differentiation of the spermathecae (arrows) in the four-day old larva [$\times 200$]; — (18) Differentiation of the bursa copulatrix (BC), vagina (V) and female gonopore (FG) in the eight-day old larva [$\times 100$]; — (19) The wall of a spermatheca composed of spherical epithelial cells (arrows) [$\times 600$]; — (20) Secretions of the cuticle in the vaginal pockets (arrows) of the 12-day old larva [BC = bursa copulatrix; $\times 50$]. — (Figs 21-23): (21) longitudinal section showing the formation of fertilization pore (FP) leading into the vagina (V) from the bursa communis (arrow) in the 20-day old larva [BC = bursa copulatrix, $\times 40$]; — (22) Transverse section of the vagina of the newly moulted imago showing enormously folded and collapsed vaginal lumen (arrows) [$\times 40$]; — (23) Transverse section of the mid-anterior region of POGC of newly moulted imago showing collapsed spermatheca (ST) and feebly developed muscles (M) [$\times 100$].

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