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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

FUNCTIONAL MORPHOLOGY OF THE EXTERNAL GENITALIA OF NEARCTIC DAMSELFLIES (ODONATA, ZYGOPTERA)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

LOTHAR EDWARD HORNUFF JR.

Norman, Oklahoma

1968

FUNCTIONAL MORPHOLOGY OF THE EXTERNAL GENITALIA

OF NEARCTIC DAMSELFLIES (ODONATA, ZYGOPTERA)

APPROVED BY

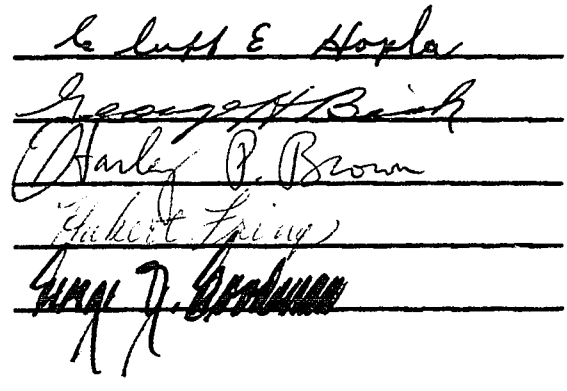


TABLE OF CONTENTS

	Page
LIST OF TABLES	iv
LIST OF ILLUSTRATIONS	v
Chapter	
I. INTRODUCTION	1
II. METHODS	7
III. RESULTS AND DISCUSSION	8
IV. SUMMARY	30
LITERATURE CITED	32

LIST OF TABLES

Table | Page

1. Location of Sperm Material during the Reproductive Sequences 15

LIST OF ILLUSTRATIONS

Figure		Page
1.	Reproductive position, Tandem	2
2.	Reproductive position, Sperm translocation	3
3.	Reproductive position, Copulatory wheel	4
4.	Second abdominal segment of *Argia moesta*	9
5.	Terminal abdominal segments of *Lestes unguiculatus*	12
6.	Mechanism of sperm translocation	18
7.	Male ninth abdominal segment	19
8.	Spermatophores of Zygoptera	21
9.	Spermatozoan of *Enallagma civile*	23
10.	Copulation in *Argia violacea*, lateral view	25
11.	Copulation in *Argia violacea*, dissected view	26

CHAPTER I

INTRODUCTION

The sequence of events in the reproductive behavior of zygopterans is the same for many, if not all, species (Buchholz, 1956; Barra, 1963; Heymer, 1966; Bick and Bick, 1961, 1963, and 1965a; Bick and Sulzbach, 1966; Bick and Hornuff, 1965 and 1966). The behavioral sequences are as follows:

(1) the arrival of single males at water, the mating site, usually during late morning, and the establishment and maintenance of territories associated with suitable perches at or near the land-water interface.

(2) the females arrive at water at midday and are immediately seized by males. A brief tandem flight follows the capture of the female by the male, usually away from water to a suitable perch well above the ground as illustrated in Figure 1.

(3) sperm translocation, or the transferring of sperm by the male from his gonopore on the ventral surface of his ninth abdominal segment to his penis vesicle attached to the posterior end of his second abdominal segment (Figure 2).

(4) copulation (Figure 3) immediately follows sperm translocation and lasts for a varying time interval relative to the particular species.

(5) endophytic oviposition follows copulation and is usually in

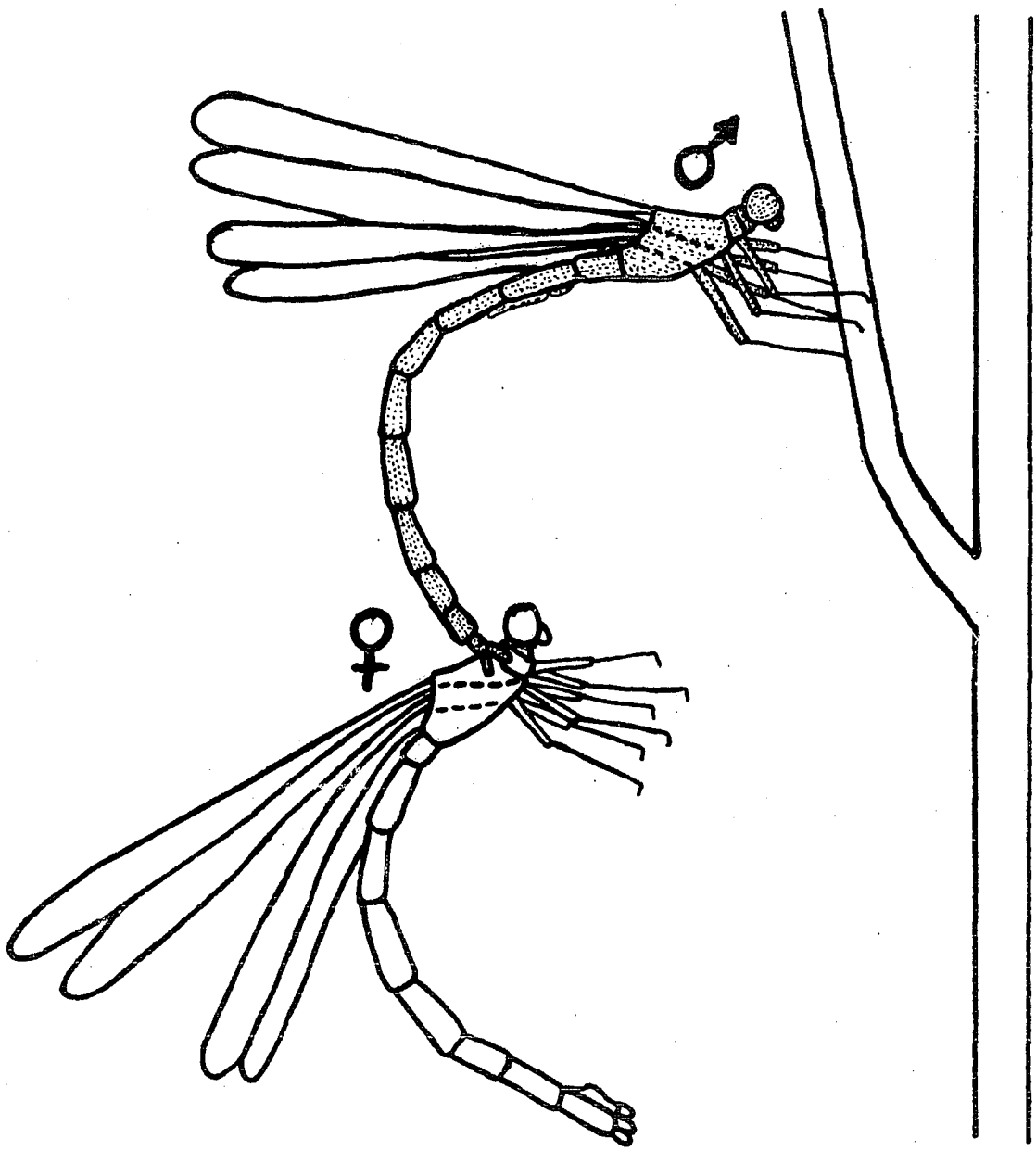


Figure 1: Reproductive position, Tandem.

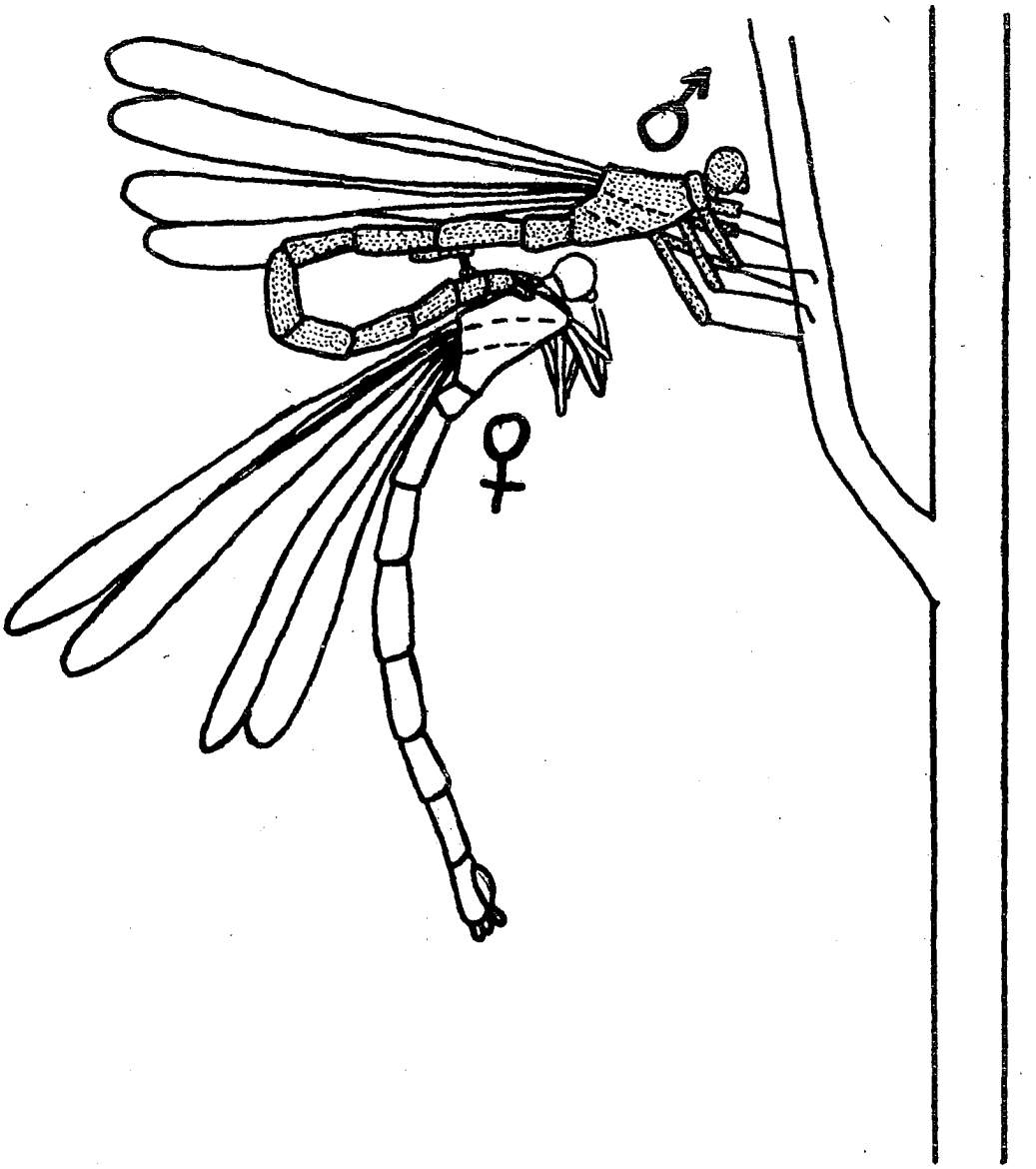


Figure 2: Reproductive position, Sperm Translocation.

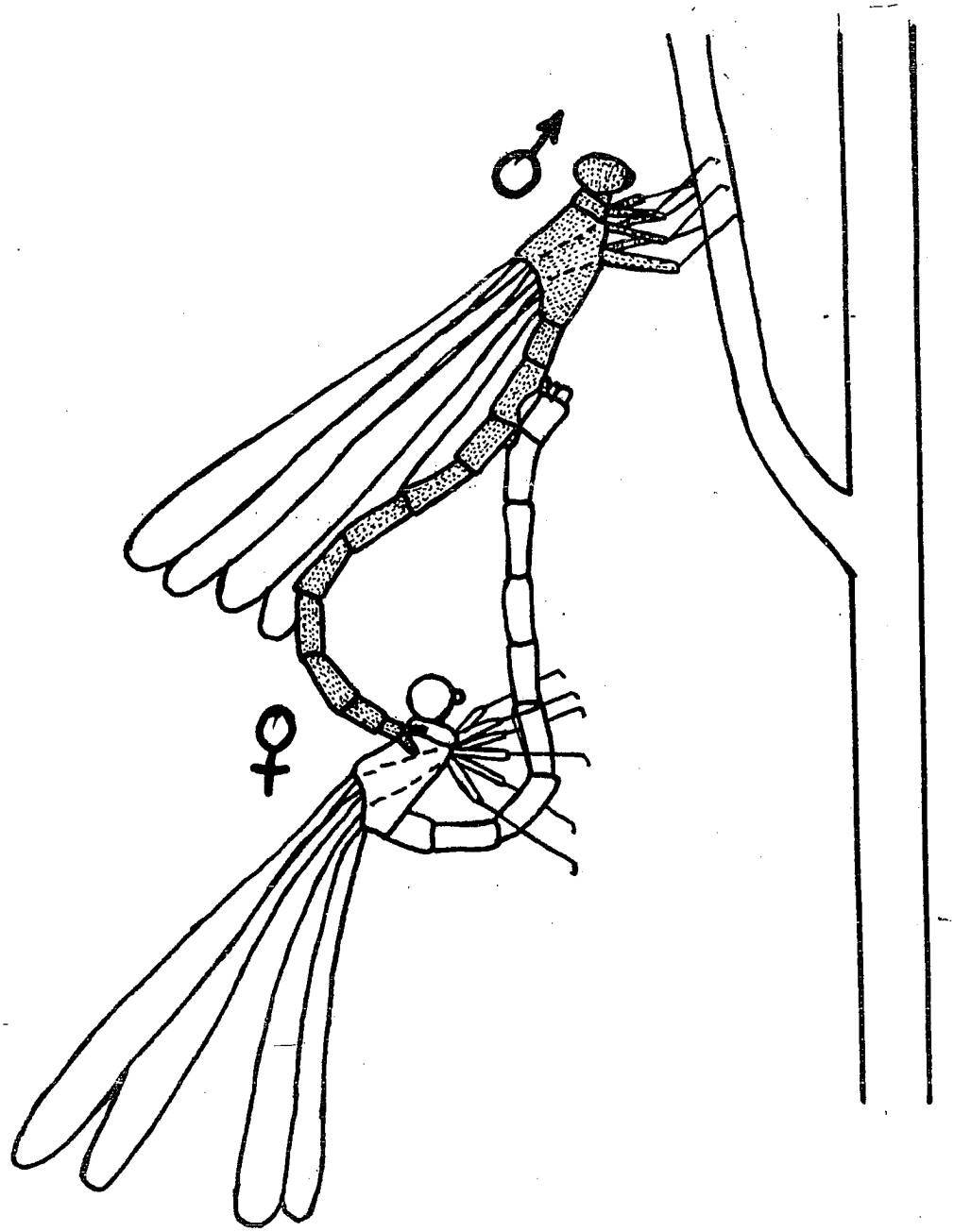


Figure 3: Reproductive position, Copulatory Wheel.

tandem. The length of time and site of oviposition vary with the species. At the completion of oviposition a second attempt at copulation with the female by the same or a different male may be initiated, but, most often, is unsuccessful because of the completely passive or actively uncooperative reaction of the female.

(6) breaking of tandem and the immediate leaving of the reproductive site by the female. The male attempts to re-establish a territory and mate again if a new female is available. The length of time of the complete sequence and the number of other males present at the mating site usually precludes a second mating by the male.

The object of this study was to better explain sperm translocation with descriptions of the nature of the material transferred and the spermatozoa. The time and mechanism of sperm translocation by the male are of interest because they are distinctive in this Order of insects. Speaking of the Anisoptera, which show homologies with the Zygoptera, Tillyard (1917) stated: "The copulatory apparatus of the male Dragonfly is one of the most remarkable structures in the Animal Kingdom. The 'pappal organ' on the pedipalp of the male Spider, and the hectocotylous arm of the Cephalopod Mollusc, extraordinary as they are, do not defy all explanation, since in each case they are modifications of an appendage already present. But the apparatus of the male Dragonfly is not homologous with any known organ in the Animal Kingdom; it is not derived from any pre-existing organ; and its origin, therefore, is as complete a mystery as it well could be." Little is known concerning the mechanism of translocation or the nature of the material transferred by the male. Various accounts in the literature (Alexander, 1964; Davey, 1960 and 1965; Hinton, 1964; Brinck, 1958; Khalifa, 1949;

Whedon, 1919; and Tillyard, 1917) refer to this material as the sperm mass, sperm capsule, or spermatophore. The latter term is most widely used, but there is no clear description as to what constitutes a spermatophore. The broad definition of this term, as used in the present study, is: "a packet, capsule, or mass which contains spermatozoa."

This study also describes the mechanism of "hooking-up" of the male and female during copulation, helping to clarify the role of the complex genital appendages. Most reports are based upon the morphology of the external genitalia and a comparison with the similar structures in the Anisoptera, but there are a number of notable differences in the morphology of the two groups, even though they are considered to be homologous. In his descriptions of differences between the damselflies and dragonflies, Tillyard (1917) noted that the penis of the damselfly is not at all attached to the penis vesicle, as it is in the dragonfly, but its lumen is continuous with the general body cavity, and, also, unlike the dragonflies, there is no external opening through which sperm might pass during impregnation of the female. The penis also apparently lacks muscles, nerves and tracheae in the damselflies. Walker (1953) noted that the penis is separated from the vesicle and stated: "It is not known how the penis functions in conveying the sperm capsules to the female genital aperture." Kennedy (1917) described the penis as the only organ which serves to hold the male and female of Ischnura cervula together during copulation.

CHAPTER II

METHODS

Results are based upon field observations of zygopterans at a number of ponds, lakes and streams in southern Oklahoma in the vicinity of the University of Oklahoma Biological Station at Willis, Oklahoma and in central Oklahoma in the vicinity of Central State College at Edmond, Oklahoma. Additional observations were made at other localities in Oklahoma, Louisiana, and Indiana.

Secected individuals were collected at these sites and returned to the laboratory for additional observations, dissection and study.

CHAPTER III

RESULTS AND DISCUSSION

Male External Genitalia

In zygoptera the gonopore of the male is located on the ventral surface of the ninth abdominal segment, covered by a pair of genital valves. The copulatory organs, however, are located in a genital groove or fenestra along the ventral surface of the second abdominal segment and the anterior portion of the third, and consist of a complex array of structures, Figure 4. Descriptions of the genitalia of Anisoptera havebeen given by Tillyard (1917), Borror (1942), Fraser (1940 and 1956), Gardner (1956), Walker (1953) and Ponnawalla (1966) with brief mention of a few of the similiarities to the Zygoptera. The following description of the copulatory mechanism of the male Argia moesta will serve for all damselflies.

The lateral borders of the genital groove are the ventro-lateral margins of the second abdominal tergite. Attached to this tergite, along its anterior half, by means of a membranous connection, is a "U"-shaped sclerite, the anterior lamina, which forms a ventral shelf for this part of the groove. The bend of the "U" is continuous with the intersegmental membrane of the first and second segments. The arms of the "U" are notched on their medial margins at a point a third of the distance from the anterior ends. At these grooves there are membranous hinges in the lamina, dividing it into an anterior and two

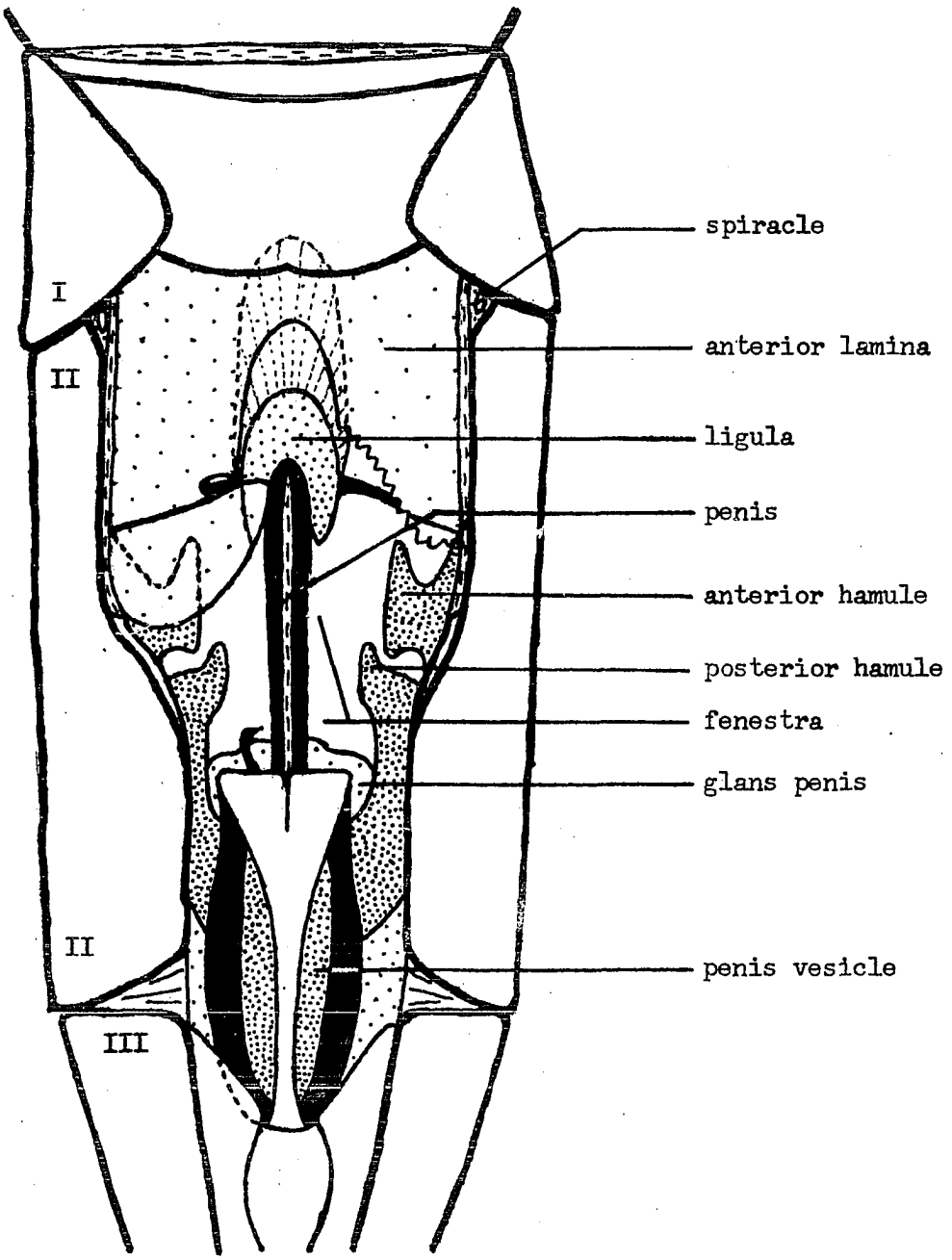


Figure 4: Ventral view of second abdominal segment of Argia moesta, showing the male external genitalia.

smaller posterior regions.

In the posterior portion of the genital groove and overlapping the anterior part of segment three is a sac, the penis vesicle, which serves as a storage place for the sperm material from the testes. The vesicle is attached to the roof of the fenestra near the posterior end of the second segment by a very narrow membranous connection, as illustrated in Figure 6. Two sclerites located along the ventro-lateral regions of the vesicle are the sole supports of the sac and the membrane between them allows the vesicle to be distended when filled. Ventrally at the anterior end is a slit-like opening from the cavity of the sac to the outside through which the sperm material passes.

Attached to the roof of the fenestra near its middle and extending anteriorly to the first segment is the membranous ligula, the lamina batilliformis of Poonawalla (1966). It is concave posteriorly and serves as a sheath for the penis. The penis, unlike that of the anisopterans, is not attached to the penis vesicle, but is connected to the roof of the genital groove immediately posterior to the ligula and is supported by two transverse sclerotized extensions of the main body of the penis imbedded in the body wall. The body of the penis is the most prominent of the external genitalia. At the distal end is the membranous glans penis, supported by sclerites that are hinged to the main stalk. Basally the glans and its supports are broad and strongly recurved, ventrally. A groove can be seen in this portion of the glans along its ventrally directed dorsal surface. The terminus of the glans is greatly prolonged into a pair of filamentous extensions. The penis lacks an opening to the outside. Its lumen communicated directly with the general abdominal cavity. Tillyard (1917) stated that the penis

lacks nerves, muscles and tracheae. Its action, therefore, must be under the control of changes in the blood pressure in the abdomen. Normally the penis at rest lies within the fenestra with its distal glans dorsal to the anterior end of the penis vesicle. During copulation it is exserted ventrally.

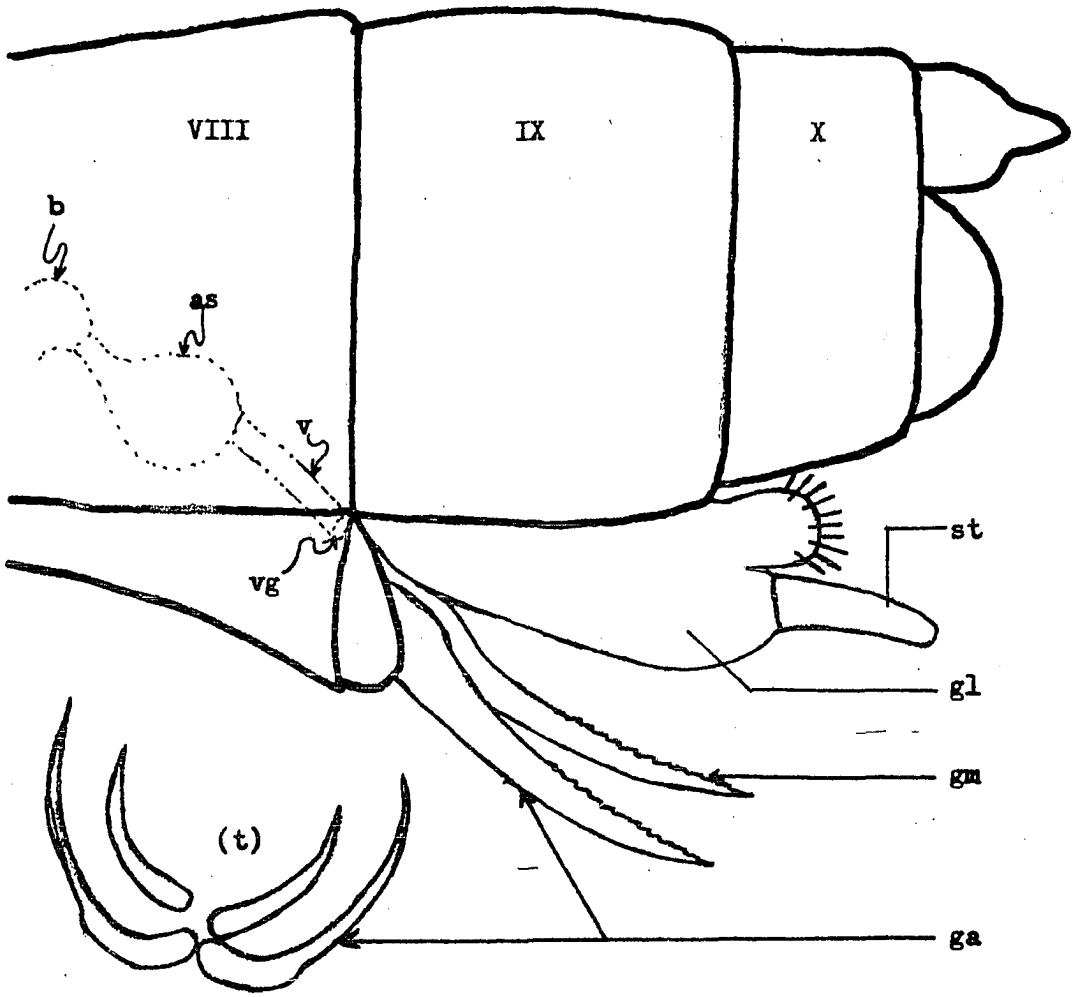
Along the central margins of the genital groove are membranous ridges bearing on each side a pair of projections, the anterior and the posterior hamules, which are directed medially and anteriorly.

Female External Genitalia

The following description of the terminal abdominal appendages of Lestes unguiculatus will serve for all damselflies. The female external genitalia are located on the ventral surface of the eighth and ninth abdominal segments, Figure 5. In the zygoptera these organs serve a dual function. The female uses them to pierce vegetation during endophutic oviposition, for which they are well adapted. Observations of these structures during copulation showed that they also functioned as a means by which the female ninth abdominal segment and the male second abdominal segment were held together during copulation, and together with the male organs form the passageway by which sperm material is conducted from the male to the female. Tillyard (1917) and Walker (1953) described the female organs, but differed as to terminology. The terminology of Tillyard is employed.

The terebra consists of two pairs of medially located and posteriorly directed, pointed processes, the gonapophyses, which compose the ovipositor. The anterior pair, the anterior gonapophyses, are grooved posteriorly and are attached to the posterior margin of the

Figure 5: Terminal abdominal appendages of Lestes unguiculatus, lateral view. (as - assessory gland; b - bursa; ga - anterior gonapophyses; gl - lateral gonapophyses; gm - medial gonapophyses; st - stylus; t - terebra; v - vagina; vg - gonopore)



eighth abdominal segment. The posterior pair, the median gonapophyses (the posterior gonapophyses of Walker, 1953) are also grooved and attached medially to the anterior end of the ninth abdominal segment immediately posterior to the anterior pair in the grooves of which the posterior processes are fitted. A third pair of processes, the lateral gonapophyses or genital valves, are flaps attached along the lateral margins of the ninth sternum, extending posteriorly beneath the tenth segment, and each terminating in a hard, black stylus. These at rest form a ventral covering beneath the terebra, which is normally retracted within the ventral groove of the ninth abdominal segment. During copulation and oviposition the terebra is extended from the groove.

Sperm translocation

Some authors refer to sperm transfer as the process by which the male impregnates the female. Others use this term to describe the means by which the male transfers sperm from the gonopore on the venter of the ninth abdominal segment into the penis vesicle on the venter of the second and third abdominal segments prior to copulation. In this study sperm translocation is used to describe the latter filling of the penis vesicle.

Buchholtz (1956) reported that she believed sperm translocation had occured prior to the capture of the female in about 75% of the males, the remainder after capture, and described a stage in the copulatory behavior during which, "the male flexes his abdomen ventrally so as to make the female's head and antennae touch his accessory genitalia." I have never seen such contact, but the description fits exactly the event

of sperm translocation as had been observed often in the field. Robert (1958) described a similar occurrance in which "the male bends his abdomen without loosening the female and touches many times the ventral surface of his second abdominal segment with that of the ninth segment." This is also undoubtedly sperm translocation.

Corbet (1963) stated that it is not known whether copulation occurs only once with a single translocation of sperm by the male. Bick and Bick (1963 and 1965b) are convinced that, necessary or not, sperm translocation occurs prior to each copulation in Zygoptera. I have very often observed sperm translocation in the following: Lestes unguiculatus (Bick and Hornuff, 1965), Enallagma aspersum and E. exsulans (Bick and Hornuff, 1966), E. civile, E. ebrium, Ischnura verticalis, Argia apicalis, A. violacea, and A. immunda. In every case where I noted initial seizure, sperm translocation prededed copulation. During this study I observed sperm translocation in E. civile 27 times during four hours of observations split between two consecutive days. In every instance it occurred in tandem with the female after initial seizure and was followed immediately by copulation.

In many species there was often a second attempt at copulation with a female that had just completed oviposition. These second attempts were usually brief and most often unsuccessful (Bick and Bick, 1963 and 1965a; and Bick and Hornuff, 1966). A second attempt at sperm translocation has not been reported.

In order to determine the necessity of sperm translocation prior to copulation, I collected 207 single males which are listed in Table I and represent 14 species of 7 genera. All were perched at or near water, the mating site. These were all at the stage prior to the be-

TABLE 1.-Location of Sperm Material during the Reproductive Sequences. (p.v. - penis vesicle; S.T. - sperm translocation; Cop. - copulation; Ovi. - oviposition; gona. - gonapophyses; (+) - full structure; (-) - empty structure)

SPECIES	SEQUENCE									
	'Single	♂ p.v.	'S.T.	♂ p.v.	'Cop.	♂ p.v.	'Ovi.	♂ p.v.	'♀ gona.	
	+	-	+	-	+	-	+	-	+	-
Enallagma										
civile	2*	38**	27	0	50	5	0	34	5	17
basidens	0	14	-	-	4	0	0	8	1	1
Argia										
sedula	0	11	-	-	-	-	0	39	-	-
plana	0	8	0	1	6	0	0	18	0	3
immunda	0	12	-	-	5	0	1*	7**	0	3
moesta	0	36	-	-	3	1	0	16	0	4
apicalis	0	12	-	-	-	-	0	8	-	-
nahuana	0	20	-	-	2	0	-	-	1	1
violacea	0	11	-	-	-	-	-	-	2	1
Ischnura										
verticalis	0	12	-	-	-	-	-	-	-	-
Hetaerina										
americana	0	24	1	0	7	0	1*	4**	-	-
Calopteryx										
maculatum	0	4	-	-	-	-	-	-	-	-
Lestes										
disjunctus	0	3	-	-	-	-	-	-	-	-
Archilestes										
grandis	0	2	-	-	1*	1**	-	-	-	-
TOTAL										
All species	2*	207**	28	1	78	7	2*	136**	9	30

* - Individuals only half full.

** - Includes a number of half empty individuals equivlaent to the number of half full individuals.

gining of mating. The penis vesicles of all were opened and their contents noted. In all (except 2 individuals of E. civile) the vesicles were empty. In the vesicles of these two individualsmasses of sperm material were found (verified by microscopic examination) equivalent to less than half of the capacity of the vesicle. These could have resulted from incomplete or unsuccessful copulation.

Twenty-nine males were collected immediately following sperm translocation, while still in tandem with females, but prior to the begining of copulation, including 27 individuals of E. civile and one each of Argia plana and Hetaerina americana. In all (except A. plana) dissection and microscopic examination of the contents of the penis vesicle revealed a mass of sperm material filling the vesicle to the point of distention.

Random collection of 84 males during copulation showed 77 individuals with penis vesicles filled with sperm material, 6 empty, and a single individual with a half-filled vesicle. The time and intensity of collection, which probably included mostly early copulation, would account for the great number of males with filled vesicles. The 6 males with empty vesicles could have been in copulation for some time prior to their being collected. The glans penis of practically all the above individuals overlaid the slit at the anterior end of the penis vesicle instead of being positioned dorsal to the vesicle as it was in all the single males examined. During the examination of five of the above males, sperm material was found in a groove formed by the membranous anterior end of the penis vesicle and the glans penis. This discovery led me to the examination of the external genitalia of 39 females collected during copulation. In nine of these individ-

uals sperm material (verified by microscopic examination) was found in the groove formed by the anterior and median gonapophyses. I believe that sperm material would have been found in more females if copulation had been allowed to proceed for a longer period of time.

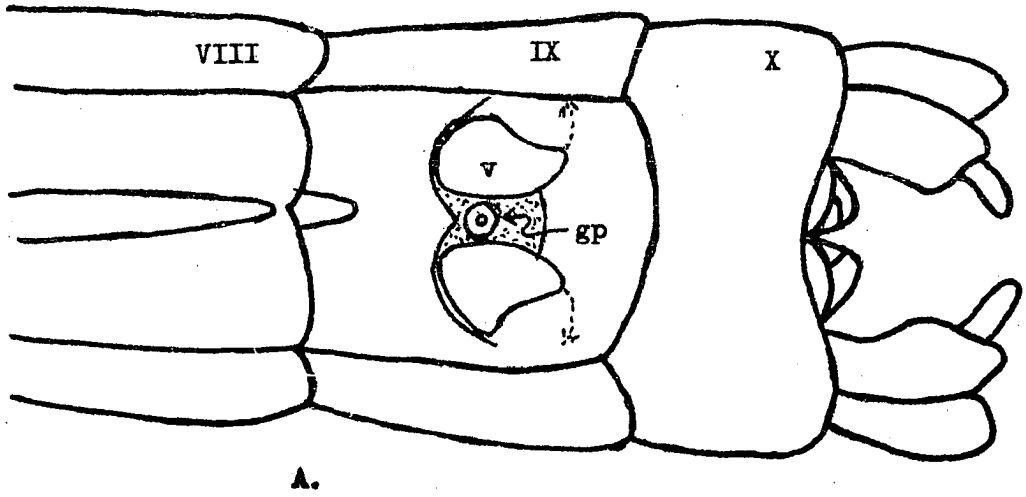
Dissection and examination of the penis vesicles of 136 males taken during tandem oviposition, which indicated that copulation was complete, revealed 134 empty vesicles and 2 with the remains of sperm material.

The absence of sperm material in the vesicles of over 99% of the single males indicates that sperm translocation must precede copulation. This, with the observations of sperm translocation in tandem after capture of the female and prior to copulation, substantiates the observations of Bick and Bick (1965b).

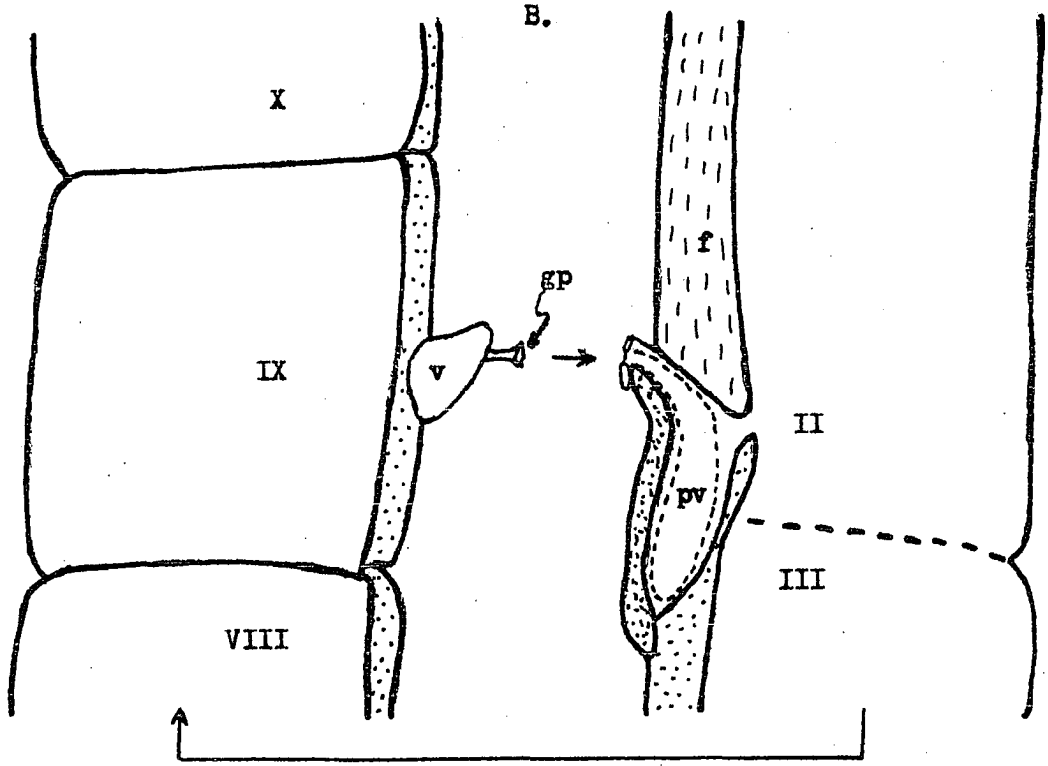
The absence of sperm material in the vesicles of over 98% of the males taken during tandem oviposition indicates that sperm were not retained in the penis vesicle for future mating, and that sperm translocation must occur prior to each copulation.

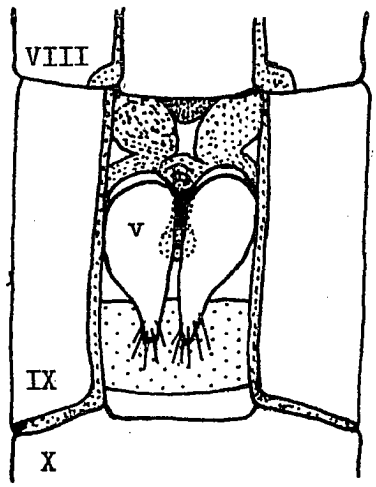
The ventral surface of the ninth abdominal segment of the male was briefly described by Walker (1953) as a "genital aperture, flanked by a pair of small flaps, the genital valves" (Figure 6). These valves vary in shape among the various genera, but are somewhat uniform in closely related species (Figure 7) and, in all cases, are hinged along their antero-lateral margins. During sperm translocation they are opened and held ventrally, parallel to the long axis of the abdomen. The actual passage of sperm material from the male reproductive system into the penis vesicle is accomplished through the ejaculatory duct, the sperm injector of Jurzitza (1966 and 1967), which can be

Figure 6: Mechanism of sperm translocation in Zygoptera. A - Ventral view of the terminal abdominal segments of Enallagma ebrium; B - Lateral dissected view, showing detail of vesicle during translocation. (f-fenestra; gp-gonopore; pv-penis vesicle; v-valve)

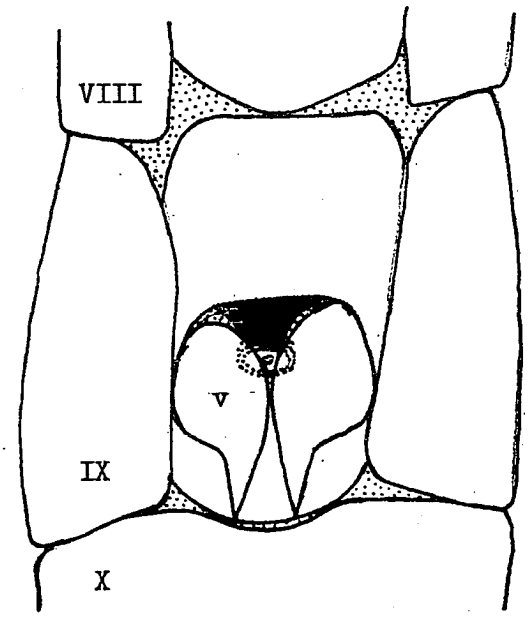


A.

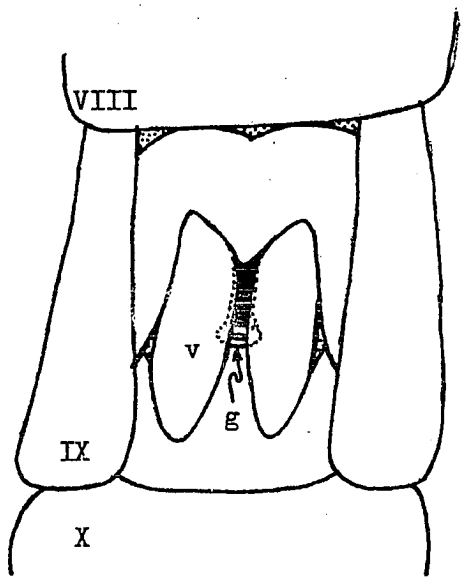




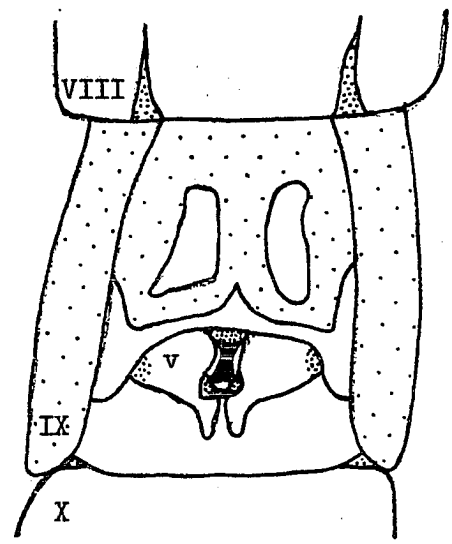
Enallagma civile



Argia violacea



Ischnura verticalis



Hetaerina americana

Figure 7: Ventral view of the ninth abdominal segment in Zygoptera.
(v - genital valve; g - gonopore)

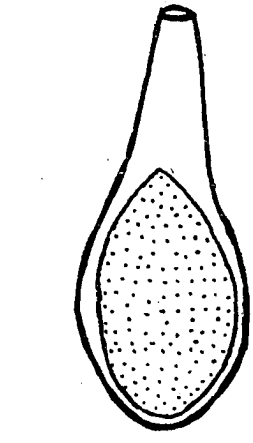
exserted. This is undoubtedly "the vestigial relics of the male penis on the ninth segment" referred to by Fraser (1939). In all species examined the distal end of the exserted duct was expanded. Field observations of the process clearly showed the duct extending between the ninth and second abdominal segments (Figure 2), but the expanded end of the duct was not visible and appeared to be inserted into the slit at the anterior end of the penis vesicle. The soft fluid nature of the sperm material would easily enable it to be passed through the ejaculatory duct and deposited within the vesicle.

Spermatophore

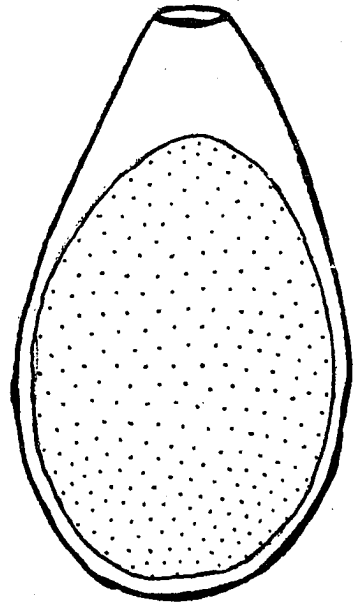
Microscopic examination of the penis vesicle immediately following sperm translocation or during early copulation showed a mass of sperm material which filled the vesicle. In living specimens, I found this material to be rather fluid substance with no definite shape. In fresh specimens it was not the jelly-like structure described for the hemipteran, Rhodnius, by Davey (1965), but my preserved material had the appearance of the spermatophore he described. There was a transparent outer region which was definitely clearer than the remaining center portion, in preserved material. The central posterior region was more dense, being composed of the mass of spermatozoa, as illustrated in Figure 8. In some individuals, especially in the genus Argia, there was a constriction of the clearer outer layer toward the anterior end. In many of the preserved spermatophores there was seen an opening or slit at the very anterior end, or, at least, the end appeared to be torn open.

As stated previously, it was impossible to determine the size and

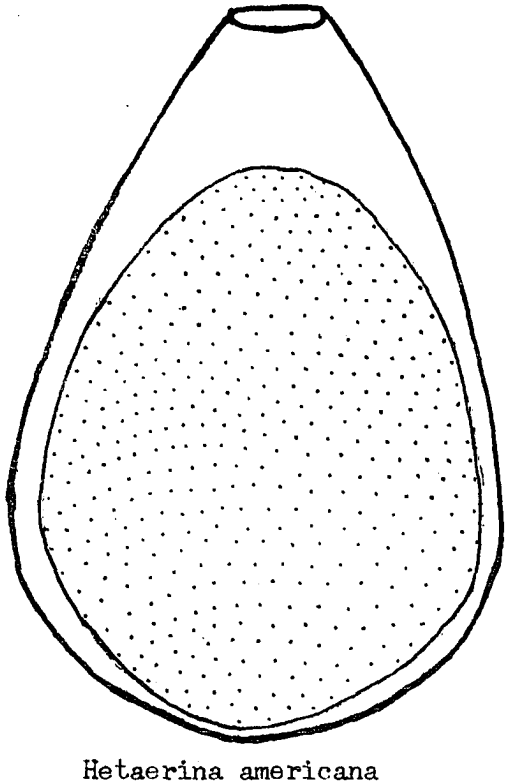
Figure 8: Spermatophores of Zygoptera. Shape indicates the shape of the penis vesicle of the male rather than the spermatophore itself. X 100



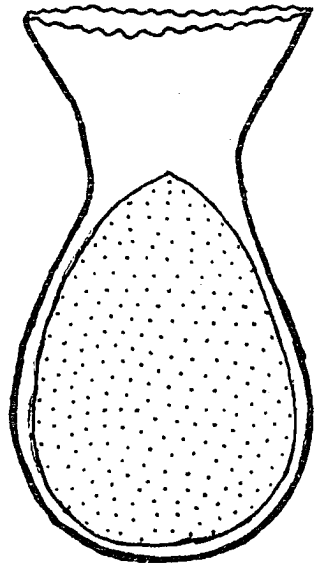
Enallagma basidens



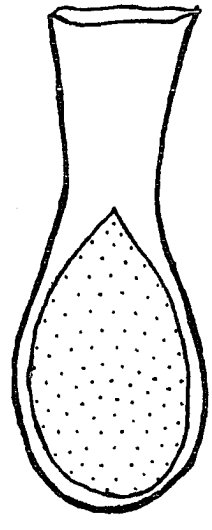
Enallagma civile



Hetaerina americana



Argia plana



Argia immunda

shape of the sperm mass because of its liquid character in living material. However, sperm material from preserved specimens varied in size and shape. Measurements of the preserved spermatophores of 13 individuals of E. civile gave an average of 0.78 mm. X o.42 mm., ranging from 0.68 X 0.32 to 0.90 X 0.50. The shape of the preserved material as shown in Figure 8 was quite variable among the different species and corresponded to the shape of the lining membrane of the penis vesicle rather than that of the spermatophore itself. The constriction in Argia corresponds to a like constriction of the male vesicle. The spermatophore of all species examined were transparent and colorless with the exception of H. americana, which was dull yellow in color.

The spermatozoan of E. civile (Figure 9) is very elongate. The head is approximately one micron in diameter, and ranged from 12.5 to 15.0 micra in length with an average of 14.5 in 18 measured individuals. The tails were over three times the length of the heads, approximately 50 micra, and gradually tapered toward the end from a diameter nearly that of the head.

Copulation

No clear description of the functional roles of the various organs of the external genitalia of the second and third abdominal segments of the male can be found in the literature of this group. Tillyard (1917) stated that since the penis of the zygopterans has no muscles, nerves or tracheae, "it is difficult to say what part a poorly developed organ of this kind can play in copulation," and speculated that it might serve as a means by which the male holds the female gonopore in

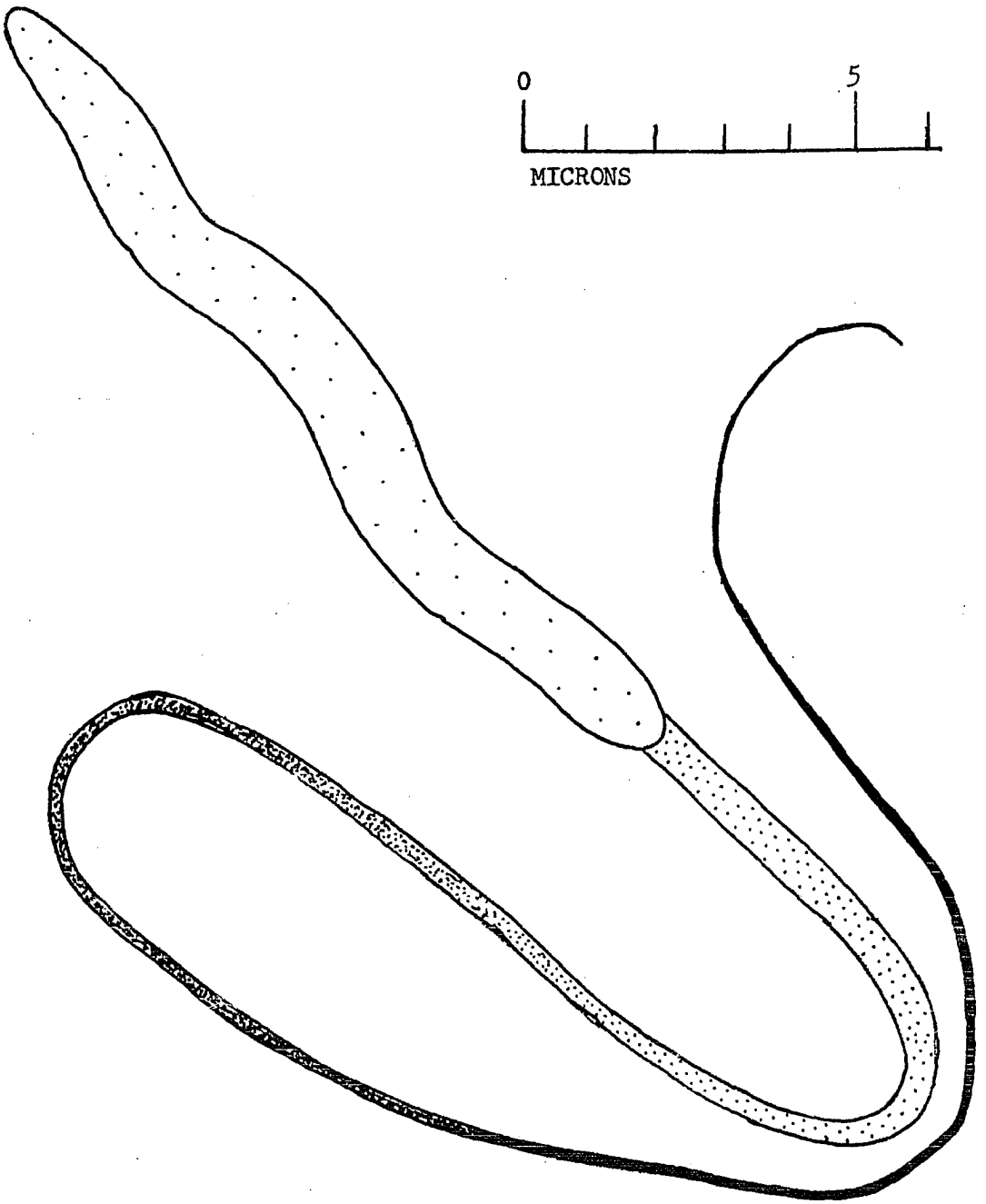


Figure 9: Spermatozoan of Enallagma civile.

contact with his penis vesicle. Kennedy (1917) believed the penis to be the sole clasping organ during copulation. Walker (1953) stated that the function of the penis is not known.

I collected three copulating pairs of damselflies which remained together in the copulatory attitude. These pairs were immediately killed in a cyanide jar and preserved intact in alcohol. The species were Argia violacea, Enallagma geminatum, and Ischnura verticalis. The first two pairs were carefully dissected apart and the positions and attitudes of the various organs of the male and the female external genitalia noted. The third was cleared and mounted whole on a glass microscope slide. The attachment of copulation was found to be the same in all three pairs. The following is a description of the attachment in A. violacea, but the same would apply to the other two species.

In A. violacea (Figures 10 and 11) the anterior and median gonapophyses of the female were inserted into the ventral groove on the ventral surface of the male second abdominal segment with one of each pair on either side of the penis. They were anchored tightly by the anterior laminae of the male. These were the only structures that functioned as clasping organs by either sex during copulation. The lateral gonapophyses of the female were held apart and parallel to the male abdomen and played no part in the attachment. The penis of the male is inserted between the right and left anterior and medial gonapophyses of the female with the proximal portion of the glans penis extending to the posterior bases of both pairs of the gonapophyses in the region of the female genital aperture. The stalk of the penis was fitted into the pair of median grooves of the anterior laminae of the

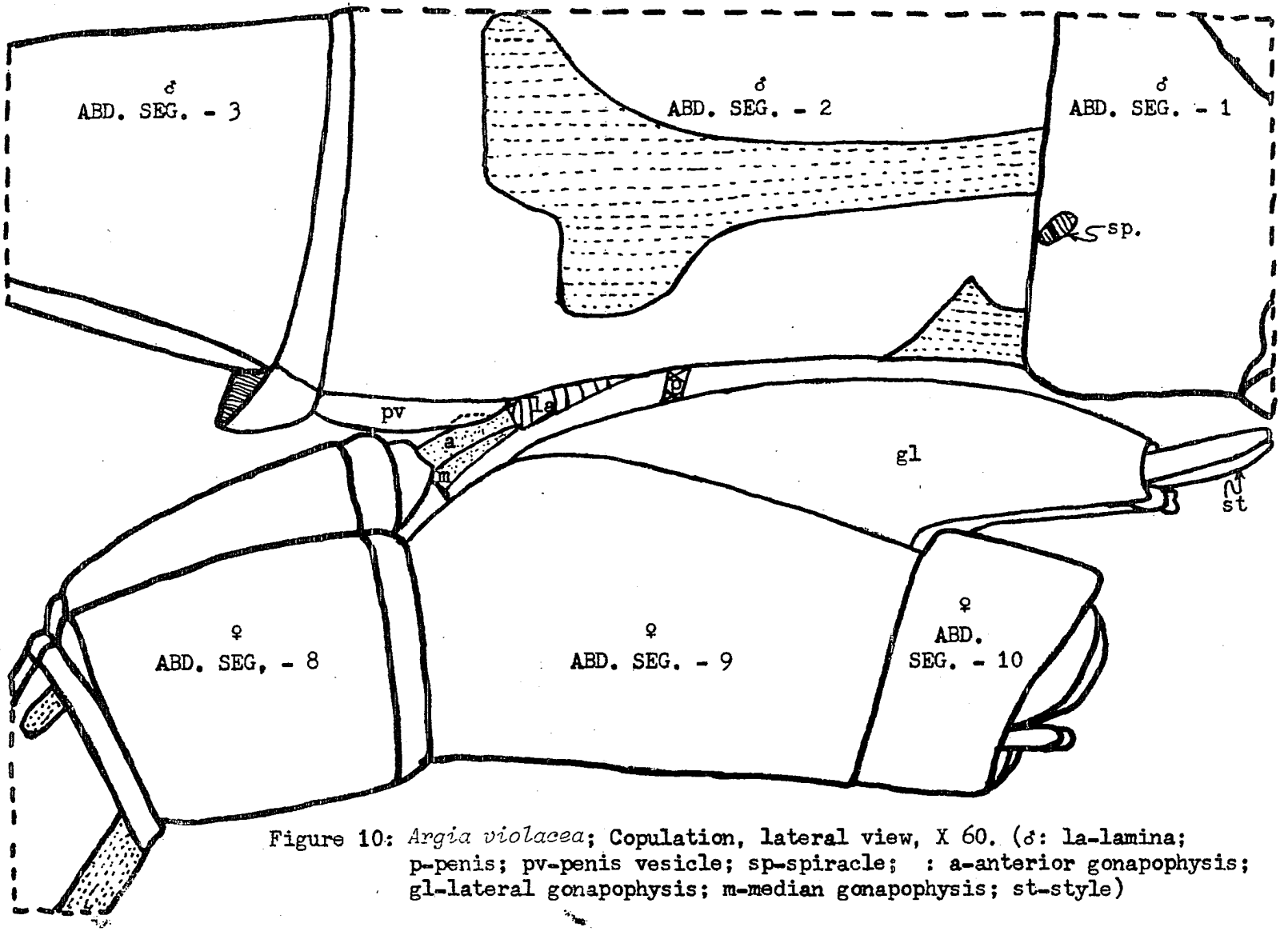


Figure 10: *Argia violacea*; Copulation, lateral view, X 60. (♂: la-lamina; p-penis; pv-penis vesicle; sp-spiracle; : a-anterior gonapophysis; gl-lateral gonapophysis; m-median gonapophysis; st-style)

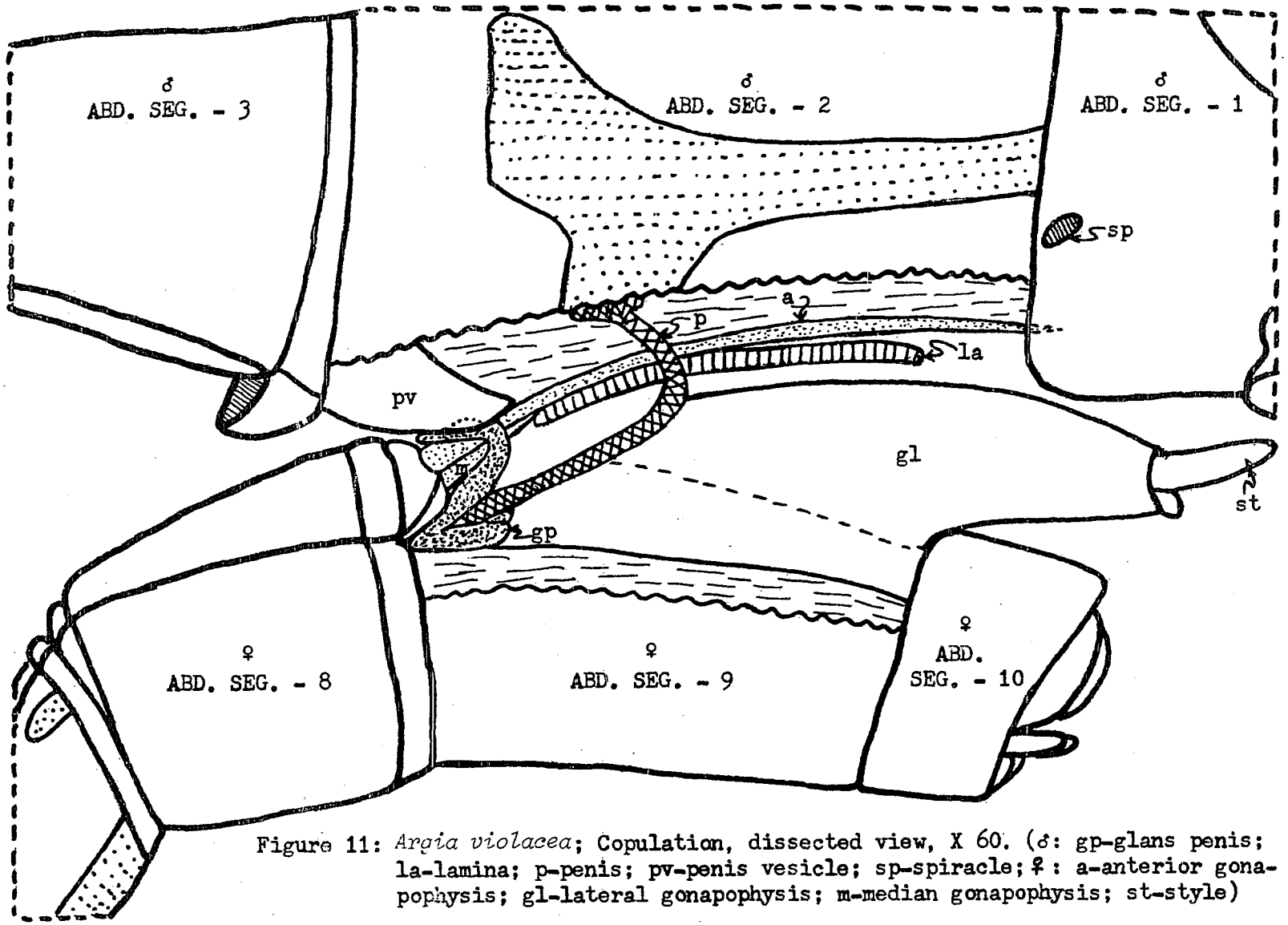


Figure 11: *Argia violacea*; Copulation, dissected view, X 60. (♂: gp-glans penis; la-lamina; p-penis; pv-penis vesicle; sp-spiracle; ♀: a-anterior gonapophysis; gl-lateral gonapophysis; m-median gonapophysis; st-style)

male which appeared to hold it in the exserted position. The distal ends of the glans penis protruded from between the gonapophyses and lay on either side of the slit at the anterior end of the penis vesicle. The anterior opening of the penis vesicle was pressed against the slightly parted bases of the terebra of the female, externally. The hamules of the male play no part in the attachment and were located laterad of the inserted gonapophyses. The posterior hamules fitted against the anterior margin of the anterior gonapophyses and the anterior hamules lie against the posterior gonapophyses. Tillyard (1917) described the hamules of Anisoptera as being complicated in form and functioning as claspers. In the Zygoptera the hamules are merely two pairs of simple finger-like projections located posteriorly near the edges of the ventral groove. They are apparently only sensory structures, or guides to align the terebra in the genital groove of the male or through their sensory function to indicate to the male that the gonapophyses are properly positioned.

The exact function of the penis could not be determined from the specimens, but from its position it would slightly spread the gonapophyses, since the distal ends of the glans protruded from between them near their bases and since the main portion of the penis lay between them. The penis could secondarily aid the anterior laminae in holding the female by pressing the bases of the gonapophyses against the penis vesicle. However, I do not think that the penis functions very efficiently in the attachment, but provides with the terebra the passageway through which the sperm material passes from the male to the female. In E. civile and E. basidens there is a pair of small grooves on either side of the penis into which the gonapophyses fit, and in H. americana

there is a similiarly placed pair of spiral flaps which could engage the gonapophyses, but it does not seem likely that these would be of much benefit for attachment because they are membranous and not sclerotized. With the penis of the male exserted, as it is during copulation, a groove was seen in the terminal glans penis supported by two sclerotized structures which resembled a two-tined fork. The position of the proximal portion of the glans along the grooved posterior side of the terebra formed a tubule through which sperm material could pass to the female gonopore. This was confirmed when sperm material was found in the groove of the gonapophyses of nine females of E. civile taken during copulation. Sperm material was also found outside of the penis vesicle in the groove of the glans of another five males of the same species, also taken during copulation.

I have previously described the fluid appearance of the spermatophore. Its liquid nature would greatly facilitate its movement from the vesicle of the male through the tubule formed by the terminal filamentous lobes of the glans penis and the anterior portion of the vesicle and through the tubule formed by the terebra of the female and the proximal glans to the genital aperture of the female. The spermatophore is apparently moved in a stream from the vesicle into the female, which would account for the relatively long periods of time required by most of the zygopterans during copulation. The fluid spermatophore is thus moved in toto to the female which would account for the empty vesicles in the males collected following copulation while in tandem oviposition with the females.

The pumping action seen during copulation in many species would press the posterior margin of the penis vesicle against the posterior

part of the eighth abdominal segment of the female, which protrudes ventrally because of the attachment of the terebra. This pumping action would aid in the squeezing of the sperm fluid out of the penis vesicle.

CHAPTER IV

SUMMARY

1. Sperm translocation always occurs after capture of the female by the male and immediately prior to copulation.
2. Sperm translocation must occur in the male prior to each copulation and none is stored for future matings.
3. Sperm translocation is accomplished in the male through the exsertion of the ejaculatory duct located in the ninth abdominal segment and the insertion of its funnel-shaped distal end into the anterior opening of the penis vesicle.
4. The spermatophore of Zygoptera is a fluid mass of material which is moved from the penis vesicle of the male into the gonopore of the female in a continuous stream.
5. The spermatozoan of Enallagma civile has an elongate head averaging 1.0 X 14.5 micra and a tail approximately 50 micra in length.
6. The attachment during copulation is achieved by means of the terebra of the female being inserted into the genital groove on the ventral surface of the second abdominal segment of the male and being held in place by the anterior lamina of the male.
7. The penis in Zygoptera is of little use for attachment during copulation, but forms a tubule with the ovipositor of the female for conducting the sperm material from the penis vesicle of the male to the female genital aperture.
8. The remaining organs of the external genitalia of the male and the

female zygopterans are passive structures in attachment between the male and female during copulation.

LITERATURE CITED

Alexander, R. D. 1964. The evolution of mating behavior in arthropods. Symposium No. 2, Royal Ent. Soc. London: 78-94.

Barra, J. 1963. Les odonates ou Libellules. Le Hohneck. Aspects Physiques Biologiques et Humains. l'Association Philomathique d'Alsace et de Lorraine. Strasbourg. A l'Occasion de son Centenaire. pp. 293-300.

Bick, G. H. and J. C. Bick 1961. An adult population of Lestes disjunctus australis Walker (Odonata: Lestidae). Southwestern Naturalist 6(3-4): 111-137.

_____, _____. 1963. Behavior and population structure of the damselfly, "Enallagma civile" (Hagen) (Odonata: Coenagriidae). Southwestern Naturalist 8(2): 57-84.

_____, _____. 1965a. Demography and behavior of the damselfly, "Argia apicalis" (Say) (Odonata: Coenagriidae). Ecology 46(4): 461-472.

_____, _____. 1965b. Sperm transfer in damselflies (Odonata: Zygoptera). Ann. Ent. Soc. Amer. 58(4): 592.

_____, and L. E. Hornuff Jr. 1965. Behavior of the damselfly, "Lestes unguiculatus" Hagen (Odonata: Lestidae). Proc. Ind. Acad. Sci. 75: 110-115.

_____, _____. 1966. Reproductive behavior in the damselflies, "Enallagma aspersum"(Hagen) and "Enallagma exsulans" (Hagen) (Odonata: Coenagriidae). Proc. Ent. Soc. Wash. 68(2): 78-85.

_____, and D. Sulzbach. 1966. Reproductive behavior of the damselfly, "Hetaerina americana" (Fabricius) (Odonata: Calopterygidae). Animal Behavior 14: 156-158.

Borror, D. J. 1942. A revision of the Libellulinae of the genus "Erythrodiplax" (Odonata). Ohio State Univ. Grad. School Studies. Contributions in Zool. and Entom. No. 4, XV + 286 pp.

Brinck, Per 1958. Parningens uppkomst och betydelse hos insekter

och narstaende djurgrupper. Entomologisk Tidskrift. 78(4): 246-264.

Buchholtz, C. 1956. Eine Analyse des Paarungsverhaltens und der dabei wirkenden Ausloser bei den Libellen, "Platycnemis pennipes" und"Pl. dealbata" Klug. Zeitschrift fur Tierpsychologie. 13(1): 13-25.

Corbet, P. S. 1963. A Biology of Dragonflies. Quadrangle Books, Chicago, Ill. 247 pp.

Davey, K. G. 1960. The evolution of spermatophores in insects. Proc. Royal Ent. Soc. London (A). 35: 107-113.

_____. 1965. Reproduction in the insects. W. H. Freeman and Co., San Francisco, Calif. X + 96 pp., 21 figs.

Fraser, F. C. 1939. The evolution of the copulatory process in the order Odonata. Proc. Royal Ent. Soc. London (A). 14: 125-129.

_____. 1940. A comparative study of the penes of the family Gomphidae (Order Odonata). Trans. Royal Ent. Soc. London. 90: 541-550.

_____. 1956. Odonata."In" Taxonomist's Glossary of Genitalia in insects, pp. 25-31. Ejnar Munksgaard, Copenhagen. 284 pp.

Gardner, A. E. 1956. The Biology of Dragonflies. Proc. S. London Ent. and Nat. Hist. 1954-5: 109-134.

Heymer, A. 1966. Études comparées du comportement inne de "Platycnemis acutipennis" Selys 1841 et de"Platycnemis latipes"Rambur 1842 (Odonata, Zygoptera). Ann. Soc. Ent. Fr. (N.S.) 2(1): 39-73.

Hinton, H. E. 1964. Sperm transfer in insects and the evolution of haemocoelic insemination. Symposium No. 2, Royal Ent. Soc. London: 95-107.

Jurzitza, G. 1966. Zur Uebertragung des Spermas auf das Copulationsorgan der Odonatenmännchen. Tombo 9: 15-16.

_____. 1967. Zur Uebertragung des Spermas auf das Copulationsorgan der Odonatenmännchen. Tombo 10: 26-27.

Kennedy, C. H. 1917. Notes on the life history and ecology of the dragonflies (Odonata) of central California and Nevada. Proc. U. S. Nat. Mus. 52: 483-635.

Khalifa, A. 1949. Spermatophore production in Trichoptera and some other insects. Trans. Royal Ent. Soc. London. 100: 449-471.

Poonawalla, Z. T. 1966. The structure and musculature of the secondary male genitalia of the Odonata and the functional significance of the muscular disposition. Ann. Ent. Soc. Amer. 59(4): 810-818.

Robert, P. A. 1958. Les Libellules (Odonates). Neuchatel: Delachaux and Niestle. 364 pp.

Tillyard, R. J. 1917. The biology of dragonflies. Cambridge Univ. Press, xii + 396 pp., 4 pl., 188 figs.

Walker, E. M. 1953. Odonata of Canada and Alaska, Vol. 1. Univ. of Toronto Press, xii + 292 pp., 44 pl.

Whedon, A. D. 1919. The comparative morphology and possible adaptations of the abdomen in the Odonata. Trans. Amer. Ent. Soc. 44: 373-437.