Chapter

Positional Relationships among Male Reproductive Organs in Insects

Satoshi Hiroyoshi and Gadi V.P. Reddy

Abstract

The location, morphology and function of male internal reproductive organs in insects have been extensively studied, but the relative positioning of those organs is less understood. Position and morphology of the testis, vas deferens, seminal vesicle, accessory gland and ejaculatory duct determine the migration or ejaculation of sperm and other substances. In species where the testis is connected with the seminal vesicle directly or the seminal vesicle is lacking, males usually store complete sperm in the testis and thus can use them immediately for mating. In contrast, the testis of lepidopteran insects is separated from the duplex (sperm storage organ) via the vas deferens, and the sperm are not mature, requiring morphological development in the vas deferens. Here, we discuss the significance of various positional relationships of male reproductive organs and how this relates to their morphology and function with a focus on sperm.

Keywords: Testis, seminal vesicle, vas deferens, sperm reflux, sperm migration

1. Introduction

The morphology, structure and size of organs have functional significance. Insects are the most abundant of all organisms in terms of species number, resulting in female and male reproductive organs being highly diverse in their structure. While the general pattern of spermatogenesis in insects is basically similar to that in mammals, the morphology, structure, and size of sperm in insects are highly variable [1, 2]. Because available resources are usually limited, the number of sperm produced should be inversely proportional to their size [3]. Although smaller testes do not necessarily produce many sperm, sperm size is closely related to testis size. Among Drosophila groups, there are positive relationships between testis length and sperm length [4–6]. Moreover, sperm length correlates positively with body size in butterfly species [7]. How much sperm a female receives and stores in the spermapheca (female sperm storage organ) should be determined by how many sperm are used for fertilization during the post-mating period. Many insect species are known to over-ejaculate under laboratory conditions but it is unclear whether excessive ejaculation is common in the field.

In general, sperm size in animals including insects is not proportional to body size. Drosophila flies, as is well known, are tiny and thus have small testes, although
D. bifurca have large testes containing very long sperm reaching a length of 5.8 cm [8]. Therefore, the number of giant sperm that they produce is small [9]. This may be due to the size of the testes as well as other reproductive organs. Giant sperm are coiled [10], but their length and thickness must not hinder the movement within the male and female reproductive tract. It is thought that not only the cost of sperm production but also the control of sperm migration would be restricted to make the gamete larger, but in fact some Drosophila sperm have become giant beyond this constraint.

Sperm produced in the testes are usually stored in the seminal vesicles, if they are present. In insects, when present within the male reproductive organs, sperm are either not motile or their motility is more suppressive than when they are retained in the female reproductive organs. Therefore, males need to both store sperm in the seminal vesicles, and limit the energy costs associated with those sperm until mating. Recent studies have revealed that sperm age or die in the spermatheca [11, 12] or male reproductive organs [13], and it is interesting to see how aging affects sperm quality and survival in the seminal vesicles because the morphology of the seminal vesicles may be associated with sperm aging, as mentioned below. Furthermore, a recent molecular biology study indicates that increased expression of seminal fluid protein incorporated in spermatophore genes is correlated with increased sperm viability in the ejaculates [14].

During mating, male insects pass a spermatophore or bolus of seminal fluid to females. In many species, a spermatophore is produced by male reproductive accessory glands, whereas in lepidopteran insects, spermatophores are produced mainly from parts of the simplex (ejaculatory duct). In a nymphalid butterfly, Polygonia c-aureum L., the contents of the simplex are initially ejaculated followed by the contents of the duplex (male sperm storage organ) and then by the accessory glands just before the end of copulation [15]. In the Coleoptera, the accessory glands and seminal vesicles open directly into the ejaculatory duct, allowing seminal fluids in the accessory glands and sperm in the seminal vesicles to ejaculate simultaneously. Molecules transferred from males to females via the seminal vesicles that originated from the accessory glands, seminal vesicle, ejaculatory duct and/or testes affect female physiology, reproductive behavior, and longevity [16, 17]. The shape, size, and weight of the spermatophore made from the seminal fluids are greatly influenced by the structures of both male and female reproductive organs.

2. Function and structure of testes

Testes function is to produce sperm and in turn intake or excrete the various substances including nutrients and hormones for spermatogenesis. In species lacking seminal vesicles, mature sperm are stored in the testis near the vas deferens. The shape of the testis is circular, oval or elongated, perhaps corresponding to sperm length, probably because sperm develop greatly during spermiogenesis (from the spermatid to the sperm) [5]. The testes are usually paired and the numbers vary widely from species to species. The color of the testes also varies greatly depending on the species; for example, many lepidopteran insects have white, yellow, red, or purple testes. Although the pigments that are no longer needed in the body may be deposited in their testes, their function and evolutionary significance have not been clarified.

In P. c-aureum, the testis is completely covered with a yellow membrane from the last instar larval stage to the early adult stage while spermiogenesis is positively occurring [18]. Although the composition and function of this membrane are unknown, it is possible that it actively protects the testis and sperm cells from
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ultraviolet rays and/or various substances in the hemolymph, that are unsuitable or toxic to spermatogenesis. Alternatively, this membrane may positively improve the nutritional and/or humoral conditions for spermatogenesis. Interestingly, the time when this membrane begins to degenerate coincides with the time when adult development of wings is almost complete, the scale of spermatogenesis and testis size begin to shrink, and sperm begin to migrate from the testes to the vas deferens [18–20]. These synchronous events are strongly suspected to be associated with hormones in the hemolymph, such as ecdysteroid. Interestingly, it is shown in *Calpodes ethlius* Stoll (Lepidoptera, Hesperiidae) that the testis is surrounded by the yellow pigment [21].

Testis development including spermatogenesis is affected by developmental stages, temperatures, nutritional conditions, and hormones [22, 23]. In the yellow dung fly *Scathophaga stercoraria* (L.), the testes atrophy after mating [24]. Similarly, in *Drosophila melanogaster* Meigen, there was a significant reduction in the testes size after five successive matings [25]. In general, testis development is closely related to spermatogenesis [26], and testis size usually increases as spermatogenesis becomes more active [27]. However, the relationship between testis size and spermatogenesis depends on the species and developmental stage.

3. Sperm polyphenism

Sperm polymorphism is apparent in the various insect orders [1, 2]. Generally, one sperm is long whereas the other is short; giant sperm have been observed in some *Drosophila* and beetles. Giant sperm fertilize the eggs and short sperm do not participate in fertilization [28, 29], although contradictory findings raise the possibility that both morphs of sperm can fertilize [30]. In lepidopteran insects, there are fertile nucleated eupyrene sperm and infertile non-nucleated apyrene sperm [31–35]. Eupyrene sperm fertilize the eggs, whereas apyrene sperm cannot fertilize the eggs because they lose their nuclei during meiosis [36]. In general, apyrene sperm are produced more or transferred to females more than are eupyrene sperm [37–39], although spermatogenesis of eupyrene and apyrene sperm is not markedly different in the diamondback moth *Plutella xylostella* [40]. This seems to be related to the fact that apyrene sperm are shorter than eupyrene sperm and the former is generated later in development.

4. Storage and migration of sperm

The production and storage of sperm can be a lifelong event for males. There are four types of sperm migration within the male reproductive organs. First, sperm formed in the testis move to the vas deferens or the seminal vesicle. In lepidopteran insects, sperm migration occurs from the testis to the duplex via the vas deferens, with a circadian rhythm. Second, sperm move from the seminal vesicle through the ejaculatory duct to the female reproductive tract during mating. Third, there is a process called sperm reflux. In *P. c-aureum*, the accessory glands open into the duplex, but not into the ejaculatory duct, thus when the accessory gland material passes the duplex, it ejaculates all sperm present. This prevents sperm from being preserved in the next copulation. Thus this butterfly regurgitates excess sperm in the duplex into the vas deferens during mating. Finally, sperm migration sometimes occurs immediately after mating. Male sweetpotato weevils *Cylas formicarius* (F.) can mate several times a night, and sperm migrate from the testes to the seminal vesicles immediately after mating [41, 42]. This may be due to the fact that the
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semenal vesicles are adjacent to the testes, that spermatogenesis is active during the adult stage, and that sperm production is completed in the testes. Thus, the positional relationship between the testes and the seminal vesicles, the degree of sperm perfection in the testes, and the stage at which sperm are formed determine the male ejaculation pattern.

Sperm migration from the testis to the duplex via the vas deferens has been well studied in lepidopteran insects. Conversely, many dipteran insects do not have the seminal vesicles, which are sometimes called sperm reservoirs, however the distal end of the testis stores sperm. Their sperm are functionally complete. However, in lepidopteran insects, sperm are not mature in the testis and change morphologically when passing through the vas efferens from the testis to the vas deferens. It has been demonstrated that eupyrene sperm migration occurs in a circadian rhythm even in cases of in vitro culture of the testis-vas deferens-duplex complex [43]. It has also been reported that there is a circadian rhythm in the secretory activity of the upper vas deferens [44]. Although the reasons for sperm migration in lepidopteran insects being rhythmic are unclear, sperm migration is a time-consuming and energy-intensive process and thus it is reasonable to expect to be time managed.

Sperm formed in the testes are stored in the seminal vesicles until mating. At the time of mating, sperm are ejaculated into the female along with spermatophore. Interestingly, when *Heliothis virescens* (F.) are irradiated at the early adult stage, the sperm are not incorporated into the spermatophore because the sperm in the duplex has not moved to the simplex where the spermatophore is formed, resulting in no transfer of sperm [45]. Some studies have revealed that the so-called ‘mating failure’ often occurs in insects [46–48]. That is, they may mate but not pass spermatophore or sperm to females.

In *Drosophila melanogaster* Meigen, proteins within the seminal fluid of the male accessory gland are required for efficient accumulation of sperm in the female’s sperm storage organs, and morphological changes in the shape and position and tissues within the female reproductive tract may be needed for successful sperm storage [49]. In species with a long life span, for example, the wood-feeding cockroach, *Cryptocercus punctutatus*, sperm are viable in the spermatheca for at least three years [50]. In these cases, female condition as well as the longevity of sperm is important for sustaining their survival.

Although the function of the seminal vesicles is to store and protect sperm, it is known that organs other than the seminal vesicles also store sperm. In lepidopteran insects, several species have a dilated part, also called a secondary seminal vesicle, between the lower vas deferens and the duplex [46, 51–53] Even if all the sperm in the duplex are ejaculated during mating, these stored sperm can be replenished immediately from the secondary seminal vesicle. In addition, even species with a large swelling in the middle vas deferens may store sperm there to some extent temporarily [54], and may transfer sperm to the duplex after mating to prepare for subsequent matings. In species with these functions, sperm reflux would not be present.

5. Insemination

In insects, a spermatophore is passed into the female reproductive organs during mating directly or indirectly. The system of insemination varies greatly from species to species, the main cause of which is species diversity and complexity of the female reproductive organs. Probably, the female complex of reproductive organs have co-evolved with the male complex of reproductive organs.
The timing of transfer of sperm to females during mating varies greatly from species to species. Copula duration also varies widely, from minutes in parasitoid wasp and mosquitoes [55] to days in stick insects [17], but in the latter the ejaculation duration could be shorter than the copula one. The post-mating guard guarantees female oviposition behavior and ovarian development. It has been suggested that sperm progression to the spermatheca is supported by the activity of the muscles and nerves of the male and female reproductive organs in addition to sperm motility [56].

Fertilization efficiency also affects the number of ejaculations. As is well known, ants and wasps can efficiently fertilize many eggs with a small amount of sperm. For example, in a parasitoid wasp *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae), males have small (several hundred) numbers of sperm in the seminal vesicle and the fertilizing efficiency of stored sperm in the female genital organs is extremely high [57], although in the majority of insects the ratio of fertilized eggs/stored sperm is low due to polyspermy at fertilization. Orthopteran insects can ejaculate a bit at a time, probably because their seminal vesicles and accessory glands have an elongated gland-like structure and open separately into the ejaculatory duct. Therefore, in the desert locust, spermatophore and sperm can be gradually transferred to females gradually during mating from the proximal part of the gland near the ejaculatory opening. Because sperm migration starts to occur actively several days after adult emergence, it seems likely that new sperm are constantly stored near the entrance of the seminal vesicles and ejaculated into the females (Hiroyoshi, unpublished). This might be related to sperm aging and sperm competition. In the migratory grasshopper *Melanoplus sanguinipes* (F.), several spermatophores are passed to females in a single mating [58]. If the accessory glands and seminal vesicles were not elongated, it would be difficult to transfer spermatophore and sperm a bit at a time.

6. Positional relationship

The arrangement of male internal reproductive organs of various species is listed in Table 1. Figure 1 shows the positional relationship between reproductive organs. Alphabetical order does not represent the phylogenetic relationship between species. Most probably other formats of organ positioning are yet to be discovered. Some insects lack the accessory glands. Of particular importance is the positional relationship between the testes, vas deferens, seminal vesicles, accessory glands, and ejaculatory duct, because the placement of these organs is important for ejaculation.

In type A, ejaculates reach the seminal vesicle or duplex form the testis via the vas deferens, to which the accessory glands are open. Thus far, all lepidopteran insects studied represent type A. As the accessory gland material passes through the duplex during mating, it flushes out all sperm and semen in the duplex. This relies on constant daily sperm replenishment form the testis to support multiple matings. Type B is similar to type A, but the seminal vesicles differ in that they connect to the ejaculatory duct along with the accessory glands. Type B is common in the homopteran, coleopteran and dipteran insects. In these insects, sperm production is typically completed in the testes, and in contrast to the Lepidoptera, the sperm do not require the vas deferens to mature. Type C lacks the seminal vesicles, but is basically the same as type B and more common in dipteran insects. Similarly, mature sperm can immediately be ejaculated from the testes during mating. Type C is an effective arrangement for multiple matings by adult males. Type D is found in some weevil species, where both the seminal vesicles and accessory glands are connected
| Order       | Family               | Scientific name                        | Type | References |
|-------------|----------------------|----------------------------------------|------|------------|
| Thysanura   | Lepismatidae         | Ctenolepisma campbelli                 | F    | [59]       |
| Ephemeroptera| Leptophlebiidae      | Miroculis amazonicus                   | H    | [60]       |
| Plecoptera  | Taeniopterygidae     | Oibietyx sp.                           | B    | [61]       |
| Perlida     |                      | Perlesta placida                       | G    |            |
| Dermaptera  | Labiduridae          | Labidura riparia                       | H    | [63]       |
| Anisolabidida|                      | Euborellia brunneri                   | H    | [64]       |
| Isoptera    | Termitidae           | Silvestritermes eumagnathus            | H    | [27]       |
| Blattodea   | Blattidae            | Leucophaea maderae                     | E    | [65]       |
| Mantodea    | Liturgusidae         | Cidfinia klasi                         | E    | [66]       |
| Orthoptera  | Caelifera            | Orphulella punctata                    | E    | [67]       |
| Tettigidae  | Tetrixarenosa angusta|                                       | E    | [68]       |
| Pygomorphida|                      | Poekilocerus pictus                   | E    | [69]       |
| Psocoptera  | Psyllipocidae        | Dorypteryx domestica                   | H    | [70]       |
| Psolliidae  |                      | Psolilla marginepunctata               | H    | [71]       |
| Homoptera   | Delphacidae          | Peregrinus maedis                      | B    | [72]       |
| Cicadellida |                      | Graminella nigrifrons                  | B    | [73]       |
|             |                      | Bothrogonia ferruginea                 | B    | [74]       |
| Cicadoidea  | Colletidae           | Colletes rufipes                       | F    | [79]       |
| Hemiptera   | Reduviidae           | Rhodnius prolixus                     | B    | [76]       |
| Pentatomida | Aphididae            | Perillus bioculatus                    | B    | [77]       |
|             |                      | Acyrthosiphon pisum                    | C    | [78]       |
| Hymenoptera | Colletidae           | Colletes rufipes                       | F    | [79]       |
| Andrenida   |                      | Ozaea flavencers                      | F    | [79]       |
| Megachilida |                      | Anthidium manicatum                   | B    | [79]       |
| Apidae      |                      | Centris violacea                      | F    | [79]       |
| Eulophidae  |                      | Dahlbominus fascipennis               | B    | [80]       |
| Formicidae  |                      | Solenopsis invicta                    | F    | [81]       |
| Neuroptera  | Chrysopidae          | Chrysopa oculata                      | B    | [82]       |
| Ithonidae   |                      | Polystochotes punctatus                | B    | [83]       |
| Nemopterida |                      | Pambippena sp.                        | B    | [84]       |
| Megaloptera | Corydalidae          | Perachauliodes continentalis          | B    | [85]       |
| Coleoptera  | Rhysodidae           | Yamatosa nipponensis                  | B    | [86]       |
|             |                      | Rhysodes comes                        | B    | [87]       |
| Carabidae   |                      | Campalita chinense                    | C    | [88]       |
|             |                      | Damaster frustorferi                  | C    | [88]       |
|             |                      | Leistus prolongatus                   | C    | [88]       |
| Tenebrionida|                      | Perastizopus armaticeps                | B    | [89]       |
| Trogossitida|                      | Bolbocerosoma farctum                 | B    | [90]       |
|             |                      | Menacanthus contracta                 | B    | [90]       |
| Chrysomelida|                      | Galericella birmanica                 | B    | [91]       |
|             |                      | Leptinotarsa decemlineata             | B    | [92]       |
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...to the ejaculatory duct via the vas deferens. Type E is found in cockroaches and orthopteran insects, and through the testes the vas deferens leads to the tubular accessory glands and tubular seminal vesicles, both of which lead to the ejaculatory duct. In Type F, the testes open into the vas deferens or seminal vesicles and then the ejaculatory duct. Some hymenopteran insects belong to type F. Types G and H represent those insects that lack the accessory glands.

7. Conclusion

The position, as well as the morphology, structure and function of the male internal reproductive organs, is presumably adaptive, probably for successful
Figure 1.
Simple illustration of each type of configuration of male internal reproductive organs. TS, VD, SV, AG, and ED indicate testis, vas deferens, seminal vesicle, accessory gland, and ejaculatory duct, respectively. Arrow indicates the direction of ejaculates (semen or sperm).
reproduction. The complex folds of these organs, which are surrounded by the tracheae and fat bodies, suggests that they require large amounts of oxygen and nutrients. However, until now, research on the arrangement of the reproductive organs has not been prioritized. We hope that this chapter will serve as an opportunity and foundation for studying not only the morphology, structure and function of reproductive organs, but also their positional relationships.

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Author details

Satoshi Hiroyoshi\textsuperscript{1*} and Gadi V.P. Reddy\textsuperscript{2}

1 Kawagoe, Saitama, Japan

2 USDA-ARS-Southern Insect Pest Management Research Unit, Stoneville, MS, USA

*Address all correspondence to: satoshi_hiroyoshi@yahoo.co.jp

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