

EVOLUTION OF THE ODONATE COPULATORY PROCESS

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Odonate copulation is almost unique among the Pterygota in that the primary genitalia do not meet during copulation. Previous explanations concerning the evolution of the odonate copulatory process have been influenced by phylogenetic schemes which consider the narrow-winged Zygoptera the most generalized Odonata. However, fossil evidence and the comparative morphology of recent Odonata indicate that the broad-winged Zygoptera represent the most generalized Odonata among recent forms, supporting general evolutionary trends toward male domination of the copulatory process, and toward completion of the copulatory process in flight. One group of scenarios explaining the origin of the odonate copulatory process assumes the original direct transfer of sperm between primary genitalia. These scenarios require that oviposition originally be in tandem, and that sperm transfer to and from the male anterior abdominal sterna originally be accidental. Scenarios assuming the original indirect transfer of spermatophores as in the Apterygota avoid such problems, and lead to an original copulatory sequence which, when slightly modified, is essentially that of existing Odonata. The proposed scenario differs from those previously put forward in that extraordinary postures are not envisioned, the process is originally completed at rest, and development of the odonate tandem hold occurs just prior to sperm transfer. The tandem hold is considered to have developed to prevent female predation of the male while the male guided her to his spermatophores.

INTRODUCTION

Odonata are practically unique among winged insects in that the primary genitalia do not meet during copulation; the only other case of this phenomenon is known in certain advanced Cimicoidea (Hemiptera) (cf. HINTON, 1964). Prior to copulation odonate males transfer sperm to secondary genitalia located on the second and third abdominal sterna from which they are eventually

transferred to the female primary genitalia. The male secondary genitalia consist of paired anterior and posterior hamuli and a medial tongue-like organ of the second abdominal sternum, and an anteromedial organ of the third abdominal sternum. The male terminalia are used to hold the female head or thorax during the copulatory process, thus leading to the formation of the familiar odonate "copulatory wheel". The male terminalia and female head or thorax are generally specifically distinct as are the male secondary genitalia and structures surrounding the female genitalia. Characteristics which are less obviously related to the copulatory process include color and color patterns, and various structural modifications of the tibiae, wings, and abdomen.

Diverse copulatory behavior occurs and ranges from brief in-flight copulations of a few seconds, to lengthy and complex sequences involving displays and guarding. FRASER (1939) and MOORE (*in*: CORBET et al., 1960) illustrated complicated scenarios explaining the evolution of odonate indirect sperm transfer from the direct contact of male and female genitalia employed by other Pterygota. BRINCK (1962) considered the indirect method primitive for the Odonata and suggested an original copulatory sequence similar to that found in the Anisoptera. A comparative evaluation of behavior and morphology, including fossil evidence, indicates that at least two additional scenarios may explain the origin of the odonate copulatory process.

ODONATE PHYLOGENY AND THE FOSSIL RECORD

The odonate phylogeny one follows, will inevitably influence interpretations concerning the evolution of the odonate copulatory process.

KENNEDY (1920) proposed the origin of the Zygoptera from a narrow-winged archetype based on a study of the male penis, and later the discovery of the narrow-winged Permian fossil *Kennedya* led TILLYARD (1925) to propose the origin of the entire Odonata from a narrow-winged ancestor. Phylogenies based on this view are illustrated in FRASER (1954, 1957) and are currently widely accepted, and consequently followed in evaluating odonate reproductive behavior. However, Tillyard's venational interpretations on which his phylogenetic views were based were not adopted by several odonatologists, including Calvert, Needham, Ris, and Williamson (NEEDHAM, 1951). Later TILLYARD (1935) accepted the dual origin of recent Odonata from the Protozygoptera and Protanisoptera first proposed by CARPENTER (1931).

Another possibility was suggested by MARTYNOV (1938) who proposed the origin of the Odonata from more fully veined contemporaries of the Protozygoptera and Protanisoptera. Martynov's view is supported by the absence of the discal brace and reduced longitudinal veins in the Protozygoptera and Protanisoptera. Protozygoptera are also characterized by the extensive basal fusion of A to CuP, and frequent nonalignment of "primary antenodals". In recent Odonata, A is fused to the hind margin of the wing when fused (FRASER, 1938, has even demonstrated fusion of A to the hind margin of the wing in the supposedly ultraprimitive *Hemiphlebia*), and the "primary antenodals" are thickened costal braces when developed which are never nonaligned. The polarity of odonate morphoclines is therefore in doubt, the above evidence supporting the views of early odonatologists such as De SELYS LONGCHAMPS & HAGEN (1854), REDTENBACHER (1886), CALVERT (1893), and NEEDHAM (1903), who considered the Calopterygoidea the most

generalized Odonata. Many Calopterygoidea exhibit complicated reproductive behaviors indicating that evolutionary trends within the Odonata may have been toward a shortening and simplification of the copulatory process.

FOSSIL EVIDENCE

Fossil evidence concerning morphologic specializations related to the odonate copulatory process is incomplete, but adequate enough when taken together with the morphology of recent forms to establish a polarity for several morphological and behavioral sequences.

It appears that the original odonatoid tandem hold was achieved by clasping the male cerci between the female prothorax and mesothorax, the male epiproct and paraprocts being valvelike as in recent females. This is the condition in male Protodonata (= Meganisoptera) and various Zygoptera including the Polythoridae. Additional support for an original tandem hold on the female thorax is found in the protodonate occipital region, which is not specialized to receive the male terminalia. Therefore, the original dichotomy of Odonata possessing the discal brace (Zygoptera, Anisozygoptera, and Anisoptera) was likely between a zygoteroid group in which the male terminalia were applied to the female thorax, and an anisopteroid group in which the male terminalia were applied to the female head. The zygoteroid group includes the Zygoptera, and the Tarsophlebiidae and Sieblosidae (= Amphipterygidae) of the "Anisozygoptera". The anisopteroid group includes the Anisoptera and remaining "Anisozygoptera" of FRASER (1957).

In place of the transverse action of the cerci used to effect the primitive zygopyteroid hold, the anisopteroid tandem grip employs a dorsal-ventral action of cerci and epiproct. A dorsal-ventral action has also been developed in some Zygoptera with elongated paraprocts, suggesting a possible intermediate condition in early anisopteroid evolution. This condition is indicated in fossil Isophlebiidae in which the male cerci are suited for embracing the posterior surface of the female head and the paraprocts are suited for embracing the dorsal surface of the head. The divaricate epiproct of primitive anisopteroid groups has therefore apparently functionally replaced elongate paraprocts.

The anisopteroid tandem hold may be related to the establishment of the copulatory position in flight. This is apparently accomplished with the aid of the hind legs, and requires that expanded male hind wings be notched proximally for clearance as in Heterophlebioidea, Epiophlebioidea, and most Anisoptera. The Anisoptera are unique in that they possess auricles¹ which may be used to guide

¹ Anisopteran auricles are derived from lateral swellings anterior to the antecostal suture of abdominal segment two; possibly analogous structures in the Euphaeidae are derived from the lateral carinae of this segment. WILLIAMSON (1904) suggested that auricles may serve "as a guide to the female in bringing her vulva in contact with the male genitalia". TILLYARD (1917) suggested that auricles functioned in conjunction with the anal angle of the hind wings in controlling flight, but FRASER (1943) adopted the view of Williamson.

the male hind legs in grasping and manipulating the female abdomen. The spines on the hind tibiae of male Anisoptera are reduced, presumably related to contact with the male body. Anisoptera which have lost the auricles have also lost the notched male hind wing margin, and have the abdomen strengthened by longitudinal carinae (except in *Anotogaster*). Tibial keels are also developed in most Anisoptera and may be used in male-female conspecific recognition just prior to the establishment of the tandem hold, the tibial keels presumably oriented to the female compound eyes in a specific manner while the male grasps the female head.

Fossil evidence concerning the male secondary genitalia is scarce, being unknown for Palaeozoic forms. HAGEN (1866) has illustrated the secondary genitalia of *Tarsophlebia* and *Stenophlebia*. In *T. eximia* Hagen the posterior hamuli, sperm vesicle, and penile shaft were depicted and resemble those of the Zygoptera. In *S. aequalis* Hagen the anterior and posterior hamuli were depicted and are of a distinctly anisopteroid type. The elongate posterior hamuli of *S. aequalis* and the notched margin of the female abdominal sternum eight in *S. phryne* Hagen actually suggest the condition in *Epiophlebia*.

The penis of recent Odonata is not homologous; in the Zygoptera it is developed from the medial organ of segment two, and in the Anisoptera from the medial organ of abdominal segment three. A unique arrangement occurs in *Epiophlebia* where elongate posterior hamuli apparently act in conjunction with the relatively small medial organs of sterna two and three to effect sperm transfer.

The polarity of the various morphoclines leading to the development of the secondary genitalia remains problematic. One possibility is that the shaft of the zygopteran penis originally developed as a guide for the female primary genitalia in obtaining sperm from the vesicle on sternum three, with the head of the zygopteran penis and the anisopteran penis developing secondarily. Zygopteran posterior hamuli act in association with the dorsal surface of the penile shaft (cf. MILLER & MILLER, 1981) which is involved in sperm transfer, indicating a possible first step toward the involvement of the posterior hamuli in sperm transfer and eventually leading to the condition found in *Epiophlebia*. Following this view, the anisopteran penis developed through an anterior extension of the sperm vesicle between the posterior hamuli and posterior to the zygopteran penile shaft.

FEATURES OF THE ODONATE COPULATORY PROCESS

The fundamental odonate copulatory process begins with the establishment of a male territory encompassing a suitable oviposition site (T), male-female conspecific recognition which may involve a male courtship display and a female acceptance posture (R), securing a tandem hold on the female and tandem flight (t_1), the union of male secondary and female primary genitalia followed by the

indirect transfer of sperm (I), and male guarding behavior which may involve tandem oviposition (t_2). Therefore the odonate copulatory process may be expressed (T, R, t_1 , I, t_2). Transfer of sperm between male primary and secondary genitalia occurs between steps t_1 and I (e.g. BICK & BICK, 1965a), although the author has occasionally observed anisopteran males apparently transferring sperm to the secondary genitalia during step T. The male penis is also believed to function in removing previously deposited sperm from the female reproductive tract prior to the transfer of sperm (cf. WAAGE, 1979; MILLER & MILLER, 1981; MILLER, 1981). Although considerable variation of the copulatory process exists, the direct transfer of sperm (D) between the primary genitalia does not occur in the Odonata.

Previous perceptions concerning the evolution of copulatory related behaviors within the Odonata (cf. HEYMER, 1972, 1974) have been biased by adherence to phylogenetic schemes which consider the Calopterygidae the most specialized Odonata. Considering the Calopterygoidea the most generalized Odonata supports a reverse polarity for various odonate behaviors, particularly those involving territories, recognition, and guarding. Relatively variable factors such as the nature of preferred oviposition sites have undoubtedly influenced the copulatory process leading to considerable parallel and convergent evolution. However, a general trend reflected in the theory herein proposed is increased male domination throughout the copulatory process.

TERRITORIALITY

The territory defended by odonate males varies considerably with the nature of oviposition sites; in general the more local the oviposition site, the smaller and more constant the male territory. Support for localized oviposition sites among early Odonata is found in the almost exclusive small-stream habitats of the Calopterygoidea (with oviposition sites generally restricted to sunlit portions), and in the endophytic oviposition and the habit of male perching while on territory throughout almost all Zygoptera. Perching near an oviposition site also seems to be the primitive method in the Anisoptera, being found throughout the Gomphidae and Petaluridae and in the more primitive genera of other families such as *Zoraena* of the Cordulegastridae and *Gomphaeschna* of the Aeshnidae. Exceptions include many Libellulidae which have apparently regained the habit of perching on territory possibly in response to their invasion of lentic habitats, and the "mating flight" of *Epiophlebia* which according to ASAHINA's (1950) illustration is similar to the patrol and search flight pattern of *Cordulegaster*. This pattern is typical of Anisoptera whose preferred oviposition sites are arranged somewhat continually along streams and includes species of *Cordulegaster*, *Boyeria*, *Somatochlora*, and *Macromia*. Such behavior typically creates a dynamic procession of male "territories" moving in an upstream direction, the

orderliness of which is disrupted by wild chases when one male gets too close to another. Search and patrol flight patterns are also utilized by lentic species of genera such as *Aeshna*, *Somatochlora*, and *Tetragoneuria*, but hovering tends to be more pronounced. A somewhat similar searching behavior has developed among the narrow-winged Zygoptera (e.g. BICK & HORNUFF, 1966). Comparison with archaeognathan Apterygota indicates that evolutionary trends during the territorial segment of the odonate copulatory process have been away from the male's defense of a territory to which females are attracted, and toward the male's active search of females and defense of only the immediate search area.

MALE-FEMALE RECOGNITION

Male-female conspecific recognition is often elaborate in the Calopterygoidea, suggesting that predacious habits required precontact conspecific recognition in early Odonata. Courtship displays have been described for species of *Libellago*, *Dysphaea*, *Calopteryx*, *Chlorocypha*, *Rhinocypha*, and *Platycypha* (cf. POULTON, 1928; LIEFTINCK, 1948; HEYMER, 1972; WAAGE, 1973; ROBERTSON, 1982), and in primitive genera of other zygopteran groups including *Hemiphlebia* (TILLYARD, 1917) and *Platycnemis* (BUCHHOLTZ, 1956). In the Coenagrionoidea and Anisoptera male-female conspecific recognition is generally much more subtle (e.g. BICK & BICK, 1966; HEYMER, 1974).

The author has observed what may be a subtle display in an attempted heterospecific pairing between a male *Nehalennia irene* Hagen and a female *Enallagma hageni* Walsh. The male hovered before the female, flew over her head, seized her head and thorax with his legs, and affixed his terminalia to her thorax. Upon flying off and finding the female still on the perch, the male again hovered briefly before the female, etc.; the sequence was repeated three times before the male lost interest.

Female rejection-acceptance displays occur in the Zygoptera (e.g. BICK & HORNUFF, 1966; WAAGE, 1973), but are apparently rare in the Anisoptera. Increased visual acuity (cf. SHERK, 1978) is probably responsible for rapid recognition in the Anisoptera, being supported by the taxonomic significance of thoracic color patterns in large genera such as *Aeshna* and *Somatochlora*. Therefore, the trend is apparently toward increased efficiency in male-female recognition achieved through increased male initiative.

TANDEM FORMATION

Odonate male terminalia are variously developed for grasping the female following recognition and seizure. Zygopteran males use the feet to initially grasp the wings, thorax, or head of perched females, and then affix the cerci, or cerci and paraprocots to the thorax. Anisopteran males use the feet to catch females in flight by either the abdomen, thorax, or head, and then eventually affix the cerci

and epiproct to the female head. WILLIAMSON (1918) concluded that in *Archaeogomphus* both the female head and thorax are engaged by only the dorsum of abdominal segment ten of the male. In *Aphylla* the posterior edge of sternum ten has functionally replaced the male epiproct. Also, pairs of the Gomphidae and Cordulegastridae will at least occasionally fall to a surface before the tandem hold is established. The anisopteran method is apparently followed in *Epiophlebia* (cf. ASAHINA, 1954). As previously stated, the zygopteran method is here considered the more primitive. Throughout the Calopterygoidea the male cerci are used in the primitive forceplike manner and are relatively unspecialized. For example, the cerci of the polythorines are quite similar to those of Jurassic Tarsophlebiidae (cf. HAGEN, 1866). Similarity in cercal form among related species is apparently related to reliable precontact recognition, evidenced by the diversity of wing coloration, or male and female displays, or both, in the Calopterygoidea and Libellulidae. The diversity of cercal shapes in many Coenagrionoidea and Anisoptera indicate that female recognition (acceptance) has been shifted to tandem formation.

This is indicated in several heterospecific pairings observed by the author. For example, a male *Enallagma aspersum* Hagen captured in tandem with a female *E. traviatum* Selys was found to have several eggs deposited in the genital fossa of abdominal segment two. In another instance a female *Boyeria grafiana* Williamson rejected and was freed by a male *B. vinosa* Say immediately following establishment of the tandem hold. Female rejection has also been observed as the male grasps the female head in attempted heterospecific pairings among species of *Macromia* and *Tetragoneuria*, indicating that the different lengths of tibial keels within these genera may enable females to recognize conspecific males at this time.

SPERM TRANSFER

Sperm transfer to male secondary genitalia in the Zygoptera apparently occurs at rest only after establishment of the tandem hold (cf. BICK & BICK, 1965a), but in the Anisoptera has been observed by the author only during flight and either before or after pairing. In all cases observed by the author, establishment of the copulatory position has been at rest in the Zygoptera, and in flight in the Anisoptera. *Epiophlebia* probably achieve the copulatory position in flight, although the absence of auricles does not support this. The author's observations of *Gomphus desertus* Banks and *Tetragoneuria cynosura* Say following pairing indicate that anisopteran hind tibiae are placed over the auricles as the male abdomen is flexed downward, thus accounting for the wide gap between the auricles and the notched inner border of the hind wings. The female abdomen is grasped and guided to the male genital fossa by the male legs (hind tarsi) which are apparently pulled dorsally by an upward movement of the abdomen. Anisopteran males may also use the hind legs during intramale sperm transfer.

In the more primitive "at rest" method of the Zygoptera the male only lifts the female upward and forward (e.g. JOHNSON, 1961; WAAGE, 1973) at which

time the female effects genital contact. However, the use of the hind legs by male Zygoptera in a manner suggesting the apparent anisopteran method has been described (e.g. BICK & BICK, 1965b; MILLER & MILLER, 1981).

If the zygopteran penis originally developed as a guide for the female genitalia, then it is likely that sperm removal via the zygopteran penis head was the original method of removal. The anisopteran penis would then have developed posterior to, and gradually replaced the zygopteran penis in both sperm removal and transfer. The reduced condition of the homologue of the zygopteran penis in *Epiophlebia* is regarded as a specialization related to the peculiar function of the posterior hamuli, which apparently act as a sperm channel (cf. ASAHINA, 1954). (The posterior hamuli of *Leptogomphus* may also act in part as a sperm channel). Specialization of the epiophlebiine secondary genitalia is also supported by the unique anterior hamuli and surrounding area which apparently engages the male terminalia (posterior edge of sternum ten and ventral prongs of the epiproct) in order that the uniquely elongated primary genitalia may be positioned to inject sperm between the posterior hamuli. Copulation generally occurs at rest in the Odonata and can last for several hours (e.g. KRIEGER & KRIEGER-LOIBL, 1958). However, many Libellulidae commonly complete the entire copulatory process in flight; for example, in-flight copulation lasts for about 5 min in *Tetragoneuria cynosura* Say (KORMONDY, 1959), and only for about 3 sec in *Plathemis lydia* Drury (JACOBS, 1955).

MALE GUARDING

Male guarding behavior has been described for several Zygoptera (e.g. JOHNSON, 1961; BICK & HORNUFF, 1966; BICK & SULZBACH, 1966; WAAGE, 1973) and probably represents the original odonate postcopulatory behavior (originally females were "guarded" while ovipositing in the male's territory). Fidelity to a single female is low in the Calopterygoidea and reaches a zenith in species which oviposit in tandem as in many Lestidae and Coenagrionidae. FRASER's (1939) erroneous generalization that "throughout the whole of the more primitive suborder Zygoptera, the male accompanies the female during oviposition, firmly linked to her prothorax" has apparently led several authors to conclude that tandem oviposition represents the primitive odonate mode (e.g. HEYMER, 1974).

Tandem oviposition has apparently evolved in response to changes in the nature of preferred oviposition sites which may, for example, expose ovipositing females to predation if not held by an alert male. Tandem oviposition also ensures that the most recently deposited sperm will not be removed before oviposition and has apparently led to a decreased importance of complete sperm removal as evidenced by reductions in the penis head. Tandem oviposition is uncommon in the Anisoptera, but is found in species of *Anax* and several

libelluline genera. In *Tramea* the male releases the female to briefly oviposit, and then reestablishes the tandem hold in flight without first grasping the female head with the feet.

Guarding behavior with the male hovering near the female occurs in species of *Libellula*, *Plathemis*, *Perithemis*, *Belonia*, and *Orthetrum*; and in *L. flavida* (which inhabits seepage pools) the males will often guard a female from a nearby perch. However, MOORE (1952) suggested that male dragonflies are only attracted by ovipositing females, and that their short pursuits after intruding males are aborted attempts at mating. Moore did not explain the increased defense of the female (male hovering much closer to the female) with the approach of conspecific males. As in other segments of the odonate copulatory process the general trend seems to be toward increased male domination of the reproductive process.

EVOLUTION OF THE ODONATE COPULATORY PROCESS

PREVIOUS SCENARIOS

Three scenarios have been advanced explaining the evolution of the odonate copulatory process: the "sexual perversions" theory of FRASER (1939), the complete female immobilization theory of MOORE (1960) and the vaguely described in-flight indirect transfer theory of BRINCK (1962).

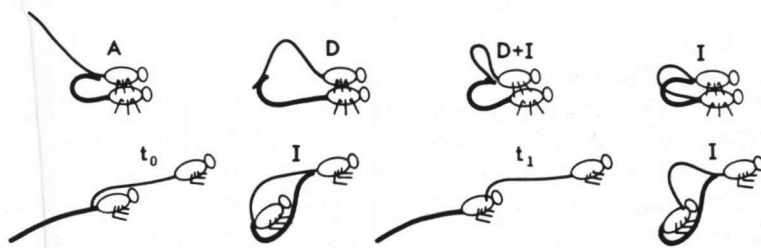


Fig. 1. Fraser's scenario illustrating the evolution of the odonate copulatory process: (A) male alighting upon female, — (D) direct sperm transfer, — (I) indirect sperm transfer, — (t_0) tandem hold not currently existing, and — (t_1) tandem hold currently existing; females designated by thicker abdomen, wings omitted for clarity, flight indicated by position of legs.

Fraser's scenario (Fig. 1) begins as the male alights on the female thorax, "the female curling up her abdomen in strong dorsi-flexion to facilitate coitus". The primary genitalia of the two sexes "are brought into close association with the 2nd segment of the male" accompanied by a still greater dorsal flexion of the female abdomen. A genital fossa is formed beneath abdominal segment two of the male, and the primary genitalia of the male are eventually "quite unable to effect normal coitus with the female", so that "the male contracted the habit of

masturbating in the genital fossa". The male being finally altogether excluded from the original mode of copulation grasped the base of the female abdomen, which was then followed by "tandem-flight with the male gripping the female by the base of the abdomen". After tandem oviposition, the female in attempting to copulate "found that by curling her abdomen downwards and forwards in ventri-flexion instead of dorsalwards as usual she was able to consummate the act of copulation". Eventually the male shifted his point of initial seizure from the base of the female abdomen to the constriction between the head and thorax to avoid "the fluttering wings of the female". Fraser's scenario can be expressed (D, I, t_0 , I, t_1 , I) where t_0 denotes a tandem hold not found in existing Odonata.

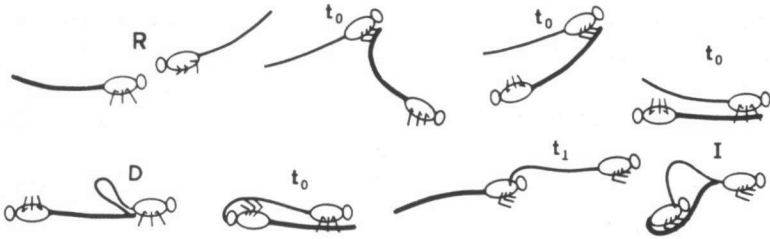


Fig. 2. Moore's scenario illustrating the evolution of the odonate copulatory process: (R) male courtship display,— (t_0) tandem hold or tandem position not currently existing,— (D) direct sperm transfer,— (t_1) tandem hold currently existing, and— (I) indirect sperm transfer; females designated by thicker abdomen, wings omitted for clarity, flight indicated by position of legs.

Moore's scenario (Fig. 2) assumes "that the rapacity of the female dragonfly was originally overcome by a male display" which puts the female in a state of catalepsy with the abdomen raised. The male grasps the apex of the female abdomen with his legs and flies off carrying her upside down and backward. The pair lands with the female on her back and after the male bends his abdomen forward so that the primary genitalia are in close proximity at a point below his second abdominal segment, he "inserts sperm into the female's genital opening, being aided by the second and third abdominal segments and their respiratory movements". The male straightens his abdomen touching the legs of the female and "the reflex clutching movements evoked" in the female. The apex of the male abdomen is bent around the female head and "when he flies the female is carried off in the tandem position". Copulation is attempted in the tandem position and is successful because of sperm left on the abdomen by previous copulation, and copulation is "perfected by the original mating movement turning into the filling of the accessory genitalia" which precedes the new mode of copulation. Moore's scenario can be expressed (R, t_0 , D, t_1 , I).

Brinck (1962) suggested that direct sperm transfer between the primary genitalia was never developed in the Odonata. Because apparently all male Apterlygota deposit spermatophores which are picked up by females, Brinck

reasoned that this may have been the method employed by early Pterygota. After the evolution of wings, Brinck postulated reduced population densities and the spending of a large portion of the insect life span in flight, therefore necessitating a better contact between males and females to ensure sperm transfer. In most Pterygota this was accomplished by placing spermatophores on the female body which eventually led to the direct contact of the primary genitalia, whereas in the Odonata spermatophores were placed on abdominal sterna 2 and 3 of the male.

In support of the postulated odonate method, Brinck called attention to the archaeognathan method of depositing spermatophores on a thread attached near the male genital opening. Body contact between males and females was supposedly enhanced to prevent the loss of spermatophores when the male abdomen was raised in enabling the male's feet to grasp the female prothorax. However, Brinck noted that it was possible that the male terminalia were already modified to grasp the female, and cited the grasping antennae of sminthurine Collembola as an example of grasping organs among early insects. Brinck's scenario was not illustrated or explained in detail, but it is evident that he considered the establishment of the tandem hold and copulatory position to have originally occurred in flight as in most Anisoptera.

ALTERNATIVE SCENARIOS

Assuming as do Fraser and Moore that the primitive mode of odonate sperm transfer was direct, three variations of an additional scenario seem likely (Fig. 3). The basic scenario can be expressed (T, R, D, t_1 , I, t_2), and the variations involve

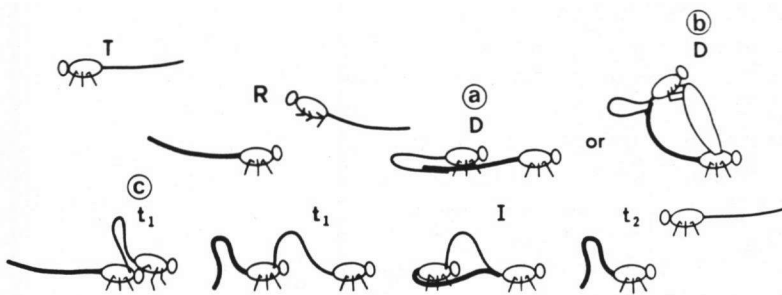


Fig. 3. Alternative scenario illustrating the evolution of the odonate copulatory process from direct sperm transfer: (T) establishment of a male territory near a suitable oviposition site,— (R) male-female conspecific recognition,— (D) direct sperm transfer,— (t_1) existing tandem hold,— (I) indirect sperm transfer, and—(t_2) male guarding behavior;— (a and b) possible positions during direct sperm transfer,— (a and c) possible positions during which sperm is accidentally transferred to male anterior abdominal sterna; females designated by thicker abdomen, wings omitted for clarity, flight indicated by position of legs.

three explanations for the initial transfer of sperm to the male anterior abdominal sterna. Transfer could have occurred in place of direct sperm transfer (Fig. 3a), during direct sperm transfer (Fig. 3b), or during the establishment of the tandem hold (Fig. 3c).

The first possibility seems reasonable because the male could mistake his own abdomen for that of the female. Fraser and Moore have envisioned extraordinary postures to accommodate the second possibility, but such explanations are unnecessary if the wings were held vertically at rest enabling the male to hold the female wing tips. In support of the third possibility WILLIAMSON & CALVERT (1906) reported that males of *Calopteryx*, *Argia*, and *Enallagma* transfer sperm to the secondary genitalia immediately after the female is captured. Furthermore, BICK & BICK (1965a) concluded that sperm transfer in all Zygoptera probably occurs in tandem immediately prior to copulation. However, the abandonment of direct sperm transfer once established seems unlikely, and each proposed scenario requires the original mode of odonate oviposition to be in tandem and for sperm transfer to and from the male anterior abdominal sterna to be accidental, which also seems unlikely. ALEXANDER (1964) commented that recognizing indirect rather than direct sperm transfer to be the forerunner of odonate copulation will lead to simpler and more reasonable hypotheses than the "fantastic schemes" proposed by Fraser and Moore.

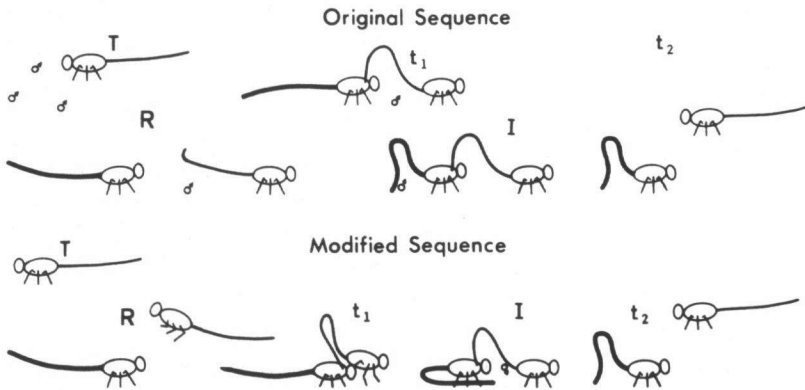


Fig. 4. A scenario illustrating the possible evolution of the odonate copulatory process without assuming an original direct transfer of sperm between the primary genitalia: (T) establishment of a male territory near a suitable oviposition site,—(♂) spermatophore,—(R) male-female conspecific recognition,—(t_1 of original sequence) male guiding female with cerci,—(t_1 of modified sequence) existing tandem hold and transfer of spermatophore to male secondary genitalia,—(I) indirect sperm transfer,—(t_2) male guarding behavior during oviposition; females designated by thicker abdomens, wings omitted for clarity, flight indicated by position of legs.

Assuming as does Brinck that the original mode of odonate sperm transfer was indirect, an additional scenario seems likely (Fig. 4). The proposed original sequence is readily derived from that of the Apterygota. For example, STÜRM (1952) reported that in the Machilidae, males deposit sperm droplets on an anchored thread extending from the apex of the abdomen, and then use their antennae and cerci to guide the female genitalia in picking up the sperm droplets.

The placement of the spermatophore on the male or female is probably related to feeding habits, and may reflect a primary ecologic and evolutionary dichotomy in the Pterygota. The odonatoids are obligate predators in contrast to other Palaeoptera, and probably developed the cercal hold to prevent female predation while males guided them to spermatophores. Originally, female Pterygota approached the male from behind, leading to the original female-above male-below copulatory position of the Neoptera (ALEXANDER, 1963). Ephemeroptera also utilize the female-above position and have the male coxites and telopodites (leg homologs) of abdominal segment nine modified for grasping the female abdomen. These same organs are found in palaeozoic Ephemeroptera (*Protereisma*; CARPENTER, 1933) and Palaeodictyoptera (*Stenodictya*; KUKALOVA, 1970), supporting the female-above copulatory position in all nonodonatoid Palaeoptera. It is also noted that the male odonate genital valves and anterior hamuli may represent modified coxites, again indicating the primary pterygote dichotomy to be between the odonatoids and remaining Pterygota.

Predacious habits would also require increased care in male-female conspecific recognition. This probably involved a display of the male terminalia, and it is perhaps significant that both male *Calopteryx* and *Hemiphysalia* display this portion of the abdomen to the female.

Male territories and guarding behavior were also probably included in early odonatoid reproductive behavior because of localized oviposition sites related to endophytic oviposition and the likely small stream habitats of early odonatoids. Fundamental differences between this scenario and that vaguely described by BRINCK (1962) involve the formation of the tandem hold before the placement of the spermatophore on the male, and the formation of the tandem hold and copulatory position at rest.

Modification of the original sequence would occur following the transformation of the male cerci into clasplike organs analogous to male ephemeropteran forceps. This would allow tandem flight and further male domination of the copulatory process by enabling males to sequester females, rather than simply attract them. It is possible that prior to tandem flight males improved their reproductive success by attracting females with displays similar at least in purpose to the "cross display" of *Calopteryx* (e.g. BUCHHOLTZ, 1951; ZAHNER, 1960; JOHNSON, 1962; PAJUNEN, 1966; BEATTY & BEATTY, 1970; WAAGE, 1973; HEYMER, 1974). However, male seizure of the female would inevitably occur and if the wings were held dorsally at rest as in

Ephemeroptera, most Zygoptera, and primitive anisopteroids², the male would probably seize the female wing tips, climb down along the costa, grasp the female head with his legs, and establish the tandem hold, as is often the case in extant species of *Calopteryx*.

It is possible that the female wing spreading in order to discourage male seizure developed early, and formed the basis for both female and male threat displays in recent Zygoptera. Initial association of the spermatophore with the male anterior abdominal sterna probably occurred during step t₁. Males unable to consistently return to their spermatophores, possibly because of interference from rival males, could transfer a spermatophore from the primary genitalia to the anterior abdominal sterna by backing toward the female. The spermatophore could then be placed on the ground as in I of the original sequence (Fig. 4). The modified sequence requires that the male leave the spermatophore attached to abdominal sterna 2 and 3, and that the female accept it from this location as illustrated in the modified step I.

Fossil and recent morphological evidence indicate that the modified sequence was employed at least by the Permian, and considering the well-developed clasping cerci of the Protodonata it was likely developed before the known fossil record of insects.

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² Fossil Isophlebiidae are characteristically found with the wings at least partly folded dorsally, and ASAHINA & EDA (1956) reported that the wings of *Epiophlebia superstes* Selys gradually close at rest.

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