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THE EVOLUTION OF MATING BEHAVIOUR IN ARTHROPODS

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Introduction

MATING behaviour comprises the events surrounding *fertilisation* in animals in which sperm and eggs meet outside the female's body, or *insemination* in animals in which sperm and eggs meet inside the female's body. These events may be divided roughly into: (1) the specific events of either external gamete release or insemination, which in either case may involve a copulatory act or coupling between male and female, (2) the events leading up to and responsible for bringing about either external fertilisation or insemination (aggregation, pair formation, courtship), and (3) the events immediately following external fertilisation or insemination (specialised staying together), responsible in some animals for subsequent fertilisations or inseminations or for making the preceding ones effective.

Attempts to understand and reconstruct the evolution of mating behaviour in any animal group bring to mind a constellation of problems that can be approached conveniently from either of two ends of a spectrum. On the one hand, one may be concerned principally with the relationship of mating behaviour to speciation, and to the various kinds of isolation that are the causes and effects of divergences among populations. On the other hand, one may search for evidence of long-range evolutionary changes in mating behaviour, and for such phenomena as convergence and parallelism, or reversibility and irreversibility. Certain questions give orientation to both approaches: When are changes in mating behaviour the result of selection bringing about greater efficiency in association with particular habitats, climates, or modes of life; when do they represent trends toward greater communicative efficiency among the individuals of a species; and when do they result from the disadvantageous effects of time, energy, and gametes being wasted in interactions between individuals of similar species that live together? How can one detect traces of the results of these different kinds of selective action and ascertain their importance in the make-up of monophyletic groups at different taxonomic levels and of differing antiquities?

The sources of evidence are comparative morphological, physiological, and behavioural study of modern species, and extrapolation from the morphology of fossil arthropods and from phylogenetic relationships inferred from fossil and other evidence. Arthropods are a prime group for this kind of behavioural reconstruction. Their many species and the ease with which they can be studied comparatively and experimentally provide almost innumerable opportunities for investigating speciation and its related problems. Their behavioural stereotypy provides for a high degree of reliability in relating evolutionary changes in structure to evolutionary changes in function.

Until recently, there had been almost total ignorance concerning the nature of mating behaviour in many of the major groups of arthropods. Fortunately, several investigators have undertaken specifically to fill some of the gaps in our knowledge. Schaller (1952-1955), Klingel (1956, 1960), Schömann and Schaller (1955), and Stürm (1952, 1956) have studied myriapods and primitively wingless hexapods; Brinck (1956, 1957) has written extensively on the mating behaviour of Ephemeroptera and

Plecoptera; and Stürm (1958), A. J. Alexander (1957–1962), Crane (1941), Schuster (1962), Ucluda (1932), Mitchell (1957), Kew (1912, 1930), Vachon (1938), and others have studied various crustacean and arachnid groups.

There have been only a few attempts at synthesis. Outstanding examples are Turner (1916), Gerhardt (1913), and Boldyrev (1915) on the Orthoptera; Richards (1927) on sexual selection in insects; Khalifa (1949) and Davey (1960) on spermatophores, their origins and functions; Spieth (1952, 1958) on *Drosophila*, and on isolating mechanisms and mating behaviour; Thorson (1950) on reproduction in various marine invertebrates; Ghilarov (1958) and Brinck (1958) on the evolution of modes of insemination in arthropods; and A. J. Alexander and Ewer (1957) on the evolution of modes of insemination in spiders and other arachnids.

Arthropod phylogeny and major habitat changes

Figure 1 shows the probable relationships of major groups of arthropods and their relatives, and indicates some prominent characteristics and the range of habitat variation for each group. With regard to mating behaviour, the following statements can be made about the groups listed:

1. All species in the terrestrial and secondarily aquatic groups have internal fertilisation, and therefore some specialised means whereby the female is inseminated. Most have some sort of spermatophore, its traces, or male glands believed to be modified spermatophore-producing glands. Direct coupling, or copulation, is known in all of the major terrestrial and secondarily aquatic groups, and the positions, circumstances, and phylogenies indicate that many independent origins are involved.

2. All primitively aquatic groups include some members with external fertilisation; in some primitively marine groups (e.g., Xiphosura and some polychaete groups), all species examined so far have external fertilisation. Among species with external fertilisation, some possess spermatophores (Crustacea), some appear never to have

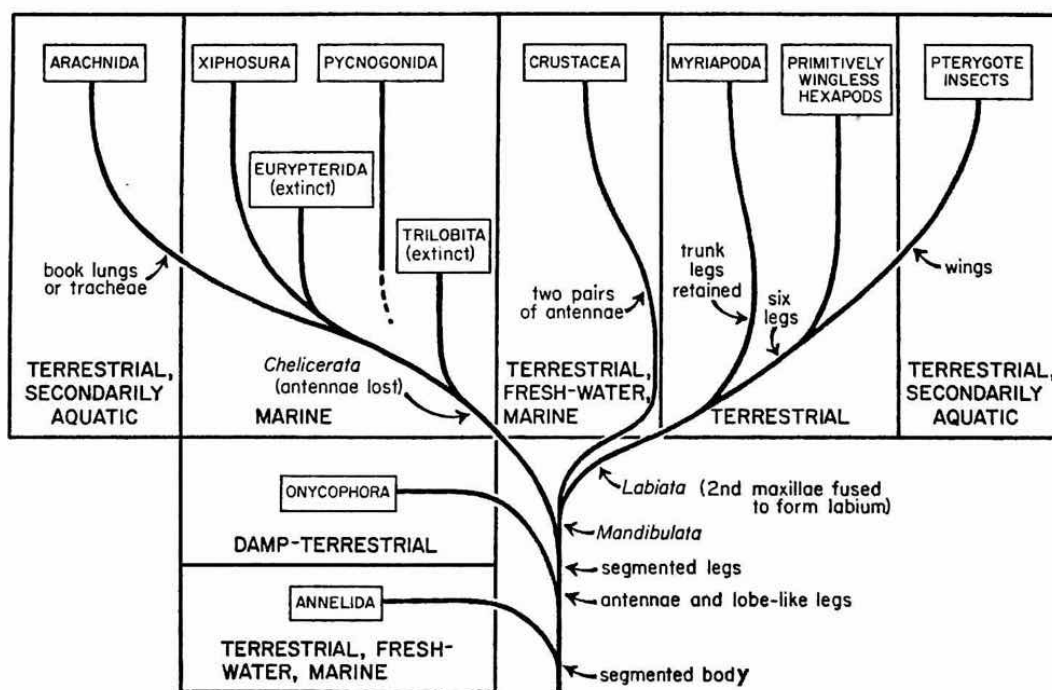


FIG. 1.—Diagram of the probable relationships of major arthropod groups and their relatives, indicating some prominent structural changes and showing ranges of habitat variation (modified from Ross, 1956). Some eurypterids may have lived in fresh water.

possessed spermatophores (Xiphosura, Pycnogonida, Annelida), and none (apparently), gives evidence of having lost a spermatophore. Most or all primitively aquatic groups with internal fertilisation (Annelida, Crustacea) have spermatophores or their traces, and most or all have some members with direct copulation.

Origin of arthropod spermatophores

The term spermatophore, has been used, with respect to both vertebrates and invertebrates, to include any kind of bag, sack, or other container of sperm, formed by the internal organs of the male and enclosing the sperm after they have passed outside the male's body. In some cases stalks or threads supporting droplets of sperm appear to be modified spermatophores. The origin of arthropod spermatophores is problematical (Khalifa, 1949; Davey, 1960); apparently, all are produced by glands in the vasa deferentia or outpocketing from them, and it is still possible that arthropod spermatophores are all either homologous or else secondarily developed following loss of an original spermatophore.

The presence of a spermatophore is usually associated, in both vertebrates and invertebrates, with the transition to terrestrial life (Khalifa, 1949). What this association really amounts to is that spermatophores occur universally and are most elaborate in those animals which we think most closely resemble, either structurally or in their general habitat or mode of life, the first terrestrial animals of each group that took up land living—the salamanders among vertebrates, the primitively wingless hexapods and myriapods among labiates, and the scorpions, pseudoscorpions, and amblypygids among arachnids. But spermatophores and internal fertilisation are also prominent among many kinds of both primitively and secondarily aquatic animals—both marine and fresh-water. The distribution of spermatophores among the groups shown in figure 1 indicates that arachnids, crustaceans, and labiates, as well as annelids and onychophorans, all possessed spermatophores prior to their emergence to land-living. As Davey (1960) points out, internal fertilisation seems to be the actual prerequisite for terrestrial existence, and spermatophores probably just happened to be the particular method of internal fertilisation employed by most groups while they were making the transition. The terrestrial isopods, as one example, may not have possessed a spermatophore during or after the time that they were becoming terrestrial (Schöbl, 1880; Lueken, 1963).

Spermatophores are in the second place often described as alternatives to mating or copulation, and this by extension has also been described or implied to be the context of their origin (A. J. Alexander, 1962b). This attitude appears to stem from the fact that the most elaborate spermatophores and the most striking or outlandish uses to which they are put often involve almost complete dissociation of individual males and females, with each sex reacting to the spermatophore itself rather than to each other. Males of some mites, pseudoscorpions, millipedes, and springtails deposit spermatophores without relation to the presence of females, and the females pick up spermatophores without relation to the presence of males (Lipovsky, Byers, and Kardos, 1958; Kew, 1930; Schömann and Schaller, 1955; Schaller, 1954a). However, such remarkable alternatives to direct interaction between the male and the female could scarcely evolve until *after* a spermatophore had developed—after it had been elaborated at least to a point where it could be an intermediary—an *object* to which the attention of the female could be directed. Although the males of some arthropods direct their attention to freshly deposited eggs (Xiphosura), no female is known to respond directly to sperm unenclosed in any kind of spermatophore. The closest known examples are the female polychaetes which are stimulated to exude their eggs when sperm have been released in the water around them (Thorson, 1950). It would be difficult to postulate a selective advantage for clumping of the sperm in

such animals without first evolving a closer association between individual males and females.

On the basis of the distribution and functions of spermatophores, then, it would seem that we must look to aquatic animals to find the selective advantages accounting for their actual origin—and that we must look, not for animals in which there is *dissociation* between male and female during gamete release (or even, necessarily, external fertilisation), but rather to animals in which there is *close association*, perhaps the closest in existence at the time in each evolutionary line in which a spermatophore developed.

Decapod crustaceans are apparently the only arthropods which have external fertilisation and utilise a spermatophore. Burkenroad (1947), for example, describes mating behaviour in an aquatic decapod, *Palaemonetes vulgaris*, in which the spermatophore never enters the female's body. Males respond (as a result of tactual contact) only to females that: (1) have molted to breeding form, (2) either have not "mated" or have mated within the past 20 minutes, and (3) have not spawned. Spermatophores are pinched off from a continuous column in the vas deferens. They are briefly adhesive to any part of the female's integument, but only those placed near the female's genital opening are effective. These dissolve shortly before spawning, apparently as a result of a chemical released by the female. The sperm are non-motile (otherwise known among arthropods only in other Decapoda and in Isoptera and Diplopoda (Vandel, 1949)) and Burkenroad thinks the eggs envelop them, with all egg and embryonic membranes being formed subsequently. This species may illustrate a primitive function of spermatophores—retaining sperm briefly at the specific location from which the eggs are to be extruded. Spermatophores could originate in a situation such as this as a replacement for the male in an act such as occurs in *Limulus*, where synchronous emission of eggs and sperm is accomplished by the male himself hooking on behind the female and remaining with her until egg deposition (Pomerat, 1933). The principal alternative seems to be that the spermatophore evolved because it increased efficiency of sperm transfer in an animal with internal fertilisation and no intromittent organ.

The following sequences of change seem to account for the situations now existing with regard to mating and spermatophores in the major groups of arthropods and their relatives. First, an early divergence (or early divergences), perhaps among marine ancestors of annelids, arthropods, and onychophorans, led on the one hand toward increased synchrony of gamete release through external triggers, and loss of or failure to elaborate interactions between individual males and females. Such a trend has given the modern polychaete worms in which mass breeding is famous, and in which seasonal, lunar, and daily cycles are all utilised, both in synchronising sexual behaviour in males and females of the same species and in causing similar species living together to perform sexually at different times (Thorson, 1950; Smith, 1958). Evolutionary lines diverging from this one have led toward increased association between *individual* males and females at the time of gamete release—to, for example, situations such as described above for *Palaemonetes* and *Limulus*. Only in such evolutionary lines, where individual males are stimulated by individual females, and to one extent or another, vice versa, is the opportunity present for the development of internal fertilisation, and thus, copulatory acts of various sorts and complexities and the elaboration of sexually dimorphic behaviour. Some animals may have been able to develop an intromittent organ directly and by-pass a spermatophore-passing stage; there seems to be no specific evidence that this has occurred among arthropods, but it has not been eliminated as a possibility.

Spermatophore-passing, wherever it occurred, provided the opportunity for another set of changes. In one trend, exemplified only in surface-dwelling arthropods and in secondarily aquatic arachnids derived from surface-dwelling terrestrial species, the spermatophore has been elaborated as an indirect transfer device, all semblance

of copulation has been lost, and interactions between individual males and females have waned. In a second case, the spermatophore has been elaborated among some terrestrial insects as a hypodermic device attached externally by the male, and injecting the sperm almost directly into the female's spermatheca. Crickets and their relatives (Orthoptera : Tettigonioidea) represent the extreme of this trend. Finally, spermatophore-transferring behaviour, perhaps whenever it has appeared, has given rise to evolutionary lines developing partway or all the way toward intromittent copulation, loss of the spermatophore, and delivery of free sperm. Along with internal fertilisation, this seems to be an irreversible trend in mating behaviour, perhaps in all animals. It has happened repeatedly in marine, fresh-water, and terrestrial arthropods, as well as in vertebrates in all three of these habitats. Two unusual kinds of intromittent copulation for which the antecedents are not entirely clear are: (1) the haemocoelic insemination of bedbugs and their relatives (Cimicoidea) (Mellanby, 1939; Hinton, this volume) and (2) the indirect act of Odonata (Buchholtz, 1956; Fraser, 1939; Moore, 1960). The history of intromittent copulation in Odonata is particularly interesting because of the central role it may play in understanding the history of winged insects (see below and Alexander and Brown, 1962).

Trends toward dissociation between male and female

Extreme dissociation between male and female during indirect spermatophore transfer is known only in terrestrial and secondarily aquatic Arachnida and terrestrial Labiata (Kew, 1930; Lipovsky, Byers, and Kardos, 1957; Mitchell, 1958; Schaller, 1954b). Such behaviour must always have been preceded by a closer interaction, at least during the origin and early evolution of the spermatophore. Progressive dissociation could have become possible only when the female actively began to pick up the spermatophore. This does not occur in any of the animals that transfer spermatophores in what seems to be a primitively close association between male and female (Onycophora, Hirudinea, Decapoda), and it may have appeared only in surface-dwelling, terrestrial arthropods. One possible avenue of change toward dissociation is that created by the functioning of dense aggregations at the time of spermatophore transfer, as are seen today in some collembolans and mites. In such aggregations, it is not difficult to perceive a selective value in females picking up any spermatophore encountered, and as a corollary, of males depositing spermatophores independently of stimulation from individual females. Subsequent steps in such procedures could be for aggregations of minimal size to become the necessary stimulus for both deposition and pickup of spermatophores, and finally, for the climatic or environmental events responsible for developing the aggregation to become sufficient to cause spermatophore deposition and pickup, with or without the presence of other conspecific individuals of either sex being involved. One wonders how many times such trends toward dissociation have occurred, and which, if any, of the male-female pairings known among arachnids and labiates actually evolved as reversals of dissociation, leading, in a sense, back toward a copulatory act. If, in its extreme, dissociation becomes an irreversible trend, it would seem possible for it to be principally responsible for limiting the radiation and evolutionary specialisation of a group.

Origins of arthropod copulatory acts

All or nearly all arthropod copulatory acts have evolved from indirect spermatophore-transferring acts. Two special examples of the importance of understanding this are illustrated by the papers of Brinck (1958, 1962) and Alexander and Ewer (1957). By recognising that indirect spermatophore transfer instead of intromittent copulation was the most probable forerunner of the bizarre copulatory acts occurring in modern Odonata (dragonflies and damselflies) and Araneida (spiders), respectively, they have been able to replace the fantastic schemes otherwise necessary to explain

these acts (Fraser, 1939; Moore, 1960; Bristowe, 1929) with simpler and more reasonable hypotheses.

Direct copulation, or insertion of either a spermatophore or free sperm directly into the female, occurs in Arachnida, Crustacea, and Labiata, as well as in Annelida and Onychophora. The kinds of acts and their distribution indicate that copulatory acts have evolved independently in the three arthropod groups: (1) in the water in Crustacea, (2) on land (Phalangida, Solpugida, Araneida, Acarina) and in the water (Acarina) in Arachnida, and (3) on land in Pterygota and Diplopoda.

Crustacea. All copulatory acts known in terrestrial crustaceans (Decapoda, Isopoda) occur with the male and female venter-to-venter, and all apparently evolved before the emergence to land life. Venter-to-venter positions are also known in secondarily aquatic mites (Acarina) (Ucluda, 1932; Mitchell, 1957) and judging from the prevalence of indirect spermatophore transfer *via* the substrate among terrestrial mites, and its occurrence in aquatic mites (Mitchell, 1958), the aquatic groups may have evolved copulation since re-entering the water. Otherwise, among all arthropods, venter-to-venter mating positions in which the male and female gonopores are brought together have been reported only in Acarina (André, 1949) (in which the pair face in opposite directions), Hymenoptera (*Apis*) (see Ribbands, 1953, for discussion), and Diptera (Richards, 1927).^{*} Histories of the acts in Acarina are uncertain, but the last two acts are definitely modifications of previous copulatory acts which took place in a different position, probably end-to-end. Venter-to-venter copulation with the pair facing in the same direction has probably evolved as a primitive mating position in arthropods only among aquatic Crustacea and terrestrial Diplopoda.

Numerous aquatic crustaceans have external fertilisation, apparently all with a spermatophore, which is either inserted into a seminal receptacle, marsupium, or brood pouch on the female's venter, from which the sperm are later expelled as the eggs are extruded, or placed on the outside of the female's body near or attached to the genital opening (Schöne, 1961). In species with internal fertilisation, insemination is accomplished by direct apposition of the genital openings or by means of various thoracic or abdominal appendages of the male. Apparently no crustacean group has evolved the kinds of indirect spermatophore transfer *via* the substrate that are widespread among both Arachnida and Labiata.

Arachnida. All of the 18 species of Scorpionida, Pseudoscorpionida, and Pedipalpi for which insemination has been described transfer the spermatophore indirectly *via* the substrate, but their behaviour during spermatophore transfer gives strong clues as to the origins of some of the kinds of copulatory acts that occur in Araneida, Acarina, and Phalangida. In 11 of the 18 cases the male and female face one another during the act. In one amblypygid (*Trithyreus sturmi*), the female catches on to the male from behind (Stürm, 1958). In another (*Admetus barbadensis*), the male faces the female until she has been "passified" by preliminary touching and tapping, turns away from her to deposit the spermatophore stalk and turns back to load it with sperm, and then backs away from the loaded spermatophore and (apparently by his actions) causes the female to walk forward and pick up the sperm (A. J. Alexander, 1962b).

In three pseudoscorpions (*Chthonius* spp.), males place spermatophores on the ground with or without females present, and the latter inseminate themselves, apparently without reference to the presence or absence of males. In these three pseudoscorpions the spermatophore stalk is very long and the male walks forward off it; in the other five pseudoscorpions studied, as with all other cases in which pairings occur with male and female facing one another, the male backs away from the deposited spermatophore (Kew, 1912, 1930; Vachon, 1938).

Among the 13 cases involving pair formation, only two amblypygids (*Damon variegatus* and *A. barbadensis*) carry out the act with no mating grasp. In one

^{*} See Addenda, p. 90.

pseudoscorpion, *Dendrochernes cyrneus*, the male holds only one of the female's chelifers during the preliminaries, and then releases it during the later portions of the act. Males of this latter species possess large anteriorly-projecting ventral organs, apparently organs of display, called "ram's horn organs". Only in the schizomid, *T. sturmi*, does the female hold the male, this from behind, as already mentioned.

The female is solely responsible for actual pickup of the spermatophore in all of the above cases except that of *D. latreillii*, in which the male seizes the edges of the female's genital opening with his first walking legs and pulls them down over the sperm droplet. In another pseudoscorpion, *D. cyrneus*, the male's head goes under the female's body during the "embrace" that occurs between inseminating acts, and according to A. J. Alexander (1962b), the male of *A. barbadensis* sometimes touches the genital region of the female with his anterior legs during the preliminaries to insemination. In the solpugids observed, the male picks up the spermatophore from the ground and introduces it into the female with his chelicerae (Millot and Vachon, 1949). Similar acts occur in mites (Acarina) (André, 1949) and have been reported for a springtail (Collembola) (Lie-Patterson, 1900). As A. J. Alexander and Ewer (1957) point out, the relationship is obvious between such acts and the process of "sperm induction" in spiders (Araneida) whereby the male fills a syringe-like device on his pedipalp, usually from sperm deposited on a web, and later injects the sperm into the female (Locket, 1926, 1927; Bristowe, 1926, 1929; Bristowe and Locket, 1926). The observations of Kew (1930), Nuttall and Merriman (1909), and A. J. Alexander (1962b) on pseudoscorpions, ticks, and amblypygids, respectively, indicate that sensory functions of the anterior appendages of the male during insemination probably preceded manipulative and inseminating functions.

Most indirect spermatophore-transferring acts are dominated by the male. A. J. Alexander (1957) points out a possible inefficiency in this arrangement when the male does not have direct contact with the actual pickup of the sperm by the female. In the scorpion, *Opisthophthalmus latimanus*, he may manipulate the female as if she has picked up the sperm when she has in fact not been able to obtain it. Two kinds of changes might be expected to reduce such inefficiency. First, the female may come to dominate the act, either as in *Trithyreus* or by dissociation of the pair during the actual pickup so that the female is solely responsible for success in this part of the act. This is one possible way that selective action could promote progressive dissociation of the male and female following the development of active pickup of the spermatophore from the substrate by the female. Second, the male may become more directly involved in the actual pickup of the spermatophore by the female, by the utilisation of either his anterior appendages or mouthparts (in acts where the partners face one another) or by the development of a closer association between the deposition or extrusion of the spermatophore and its insertion into the female.

Phalangida mate with the male and female facing one another, utilising a long, anteriorly-projecting male intromittent organ (Berland, 1949). Both genital regions, although located on the eighth post-oral segment as in all Arachnida and Xiphosura, some Crustacea, and some Collembola, are directed anteriorly. It is likely that the Phalangid copulatory act evolved from indirect spermatophore transfer occurring in an anterior-to-anterior position, as described above for Scorpionida, Pseudoscorpionida, and Amblypygida, and as probably preceded sperm induction in spiders and insemination by means of the anterior male appendages in mites. This position in indirect spermatophore transfer is characteristically associated with anterior location of the genital openings, and we can predict that the Symphyla, in which mating behaviour is totally unknown, either transfer a spermatophore with the male and female facing one another or lack any kind of direct interaction between the sexes in connection with insemination. Beginning with an indirect spermatophore transfer *via* the substrate, the position of the partners has usually evolved in one of two directions—facing one another or with one individual turned 180°. The amblypygid

species, *Admetus barbadensis*, illustrates a possible transitional stage by utilising both positions in sequence during insemination (A. J. Alexander, 1962b). The eventual position of the gonopores may be determined by the direction taken at this point in evolution, and the phylogenetic significance of the multiplicity of conditions found among labiates in this regard (Brinck, 1958), may be comprehensible only as a result of understanding the nature and history of spermatophore-transferring acts within the various labiate groups.

Some spermatophore-transferring acts among arachnids apparently occur but once when a pair has been formed, but in other cases (e.g., *D. cyrneus*) several successive inseminations are the rule. In such cases, the importance of describing the entire sequence of interactions associated with insemination is obvious: activities and positions may vary widely from courtship to copulation or insemination and post-copulatory or inter-copulatory behaviour. As with *A. barbadensis*, characteristics of these different events as they occur in sequence can give important clues concerning pathways of evolutionary change.

Labiata. All of the pterygote insects copulate (except, in a direct sense, Odonata) but all other labiates in which insemination is known transfer spermatophores indirectly. With the possible exception of the mites (Acarina), more variations in manner of copulation occur among the Pterygota than among all other Arthropoda combined (Table I). This is surprising in view of the fact that copulation may have evolved but once in this group, but not so surprising in view of the antiquity of pterygotes, their million or so species, and their many different modes of life.

Most authors (e.g., Richards, 1927) assume that some kind of male-above position is primitive in the Pterygota. However, comparisons of ranges of variation in the mating positions of different orders, the antiquity of groups showing various kinds of mating positions (Table I), and changes in position during mating and among groups within orders (figs. 2, 3), indicate instead that the primitive position was either female-above, or male-side, in either case with the male reaching under the female's abdomen. These positions are the most prevalent among different orders today, and, as Ghilarov (1958) and Brinck (1958) point out, they are compatible with the probable derivation of pterygote mating from an act involving indirect spermatophore transfer *via* the substrate and a ventral female genital opening. A female-above position may have been the only position occurring at the time of separation of the older orders, except for the aberrant male-above position of the Odonata, which involves pre-copulatory transfer of sperm(atophores?) by the male to an intromittent organ developed at the base of the abdomen (Fraser, 1939; Buchholtz, 1956).

Comparison of spermatophore transfer methods among primitively wingless labiates give definite indications as to how pterygote copulation may have originated. Collembola transfer spermatophores *via* the substrate in ways not differing greatly from those described above for various Arachnida (Schaller, 1952a, 1952b, 1954; Lie-Patterson, 1900). Aggregations are formed in some species without close interaction between individuals; in other species, males ride on females for long periods by means of special antennal grasping organs, and then apparently pull the female over the spermatophore. Lie-Patterson thought the male of one species used its mouthparts and forelegs to inseminate the female. Diplura transfer spermatophores *via* the substrate (Schaller, 1954a), as do Chilopoda (Klingel, 1956, 1960). Pselaphognath millipedes and some centipedes utilise webs which assist the female in locating the spermatophore (Schömann and Schaller, 1955; Klingel, 1960). In chilognath millipedes, the male transfers the spermatid fluid from his gonopore on the third body segment to modified walking legs (gonopods) on the seventh or the penultimate body segment and then places it into the female's gonopore on the third body segment (Causey, 1943; Evans, 1910).

Thysanura are believed to be more similar to the pterygote ancestor than any

other primitively wingless labiates, and their inseminating behaviour substantiates this belief and demonstrates how pterygote copulation could have originated.

In Lepismatidae (*Thermobia*, *Lepisma*), the male deposits a spermatophore on the ground, and directs the female in its pickup by spinning "signal" threads near it (Stürm, 1956). In Machilidae, the male deposits sperm droplets directly on a thread extending from the tip of his abdomen to the substrate or to some object (Stürm, 1952). The male twists his body around the female and with his antennae and cerci guides her genitalia into a position to pick off the sperm droplets. This act is very close to being true copulation—all that is needed is to bring the male and female genitalia progressively closer together and eventually have the spermatophore attached to her genital opening or partly inserted. In such case the male would be contacting the female from below or from the side and using his cerci and antennae as guiding and manipulating devices, all of which directly links the act to the kind of copulation occurring today in nearly all of the older pterygote orders. One thysanuran, *Nicoletia tergata* Mills (1940), possesses in the male a dorsal abdominal gland—a fact of special interest because in the thousands of orthopteroids and other pterygotes which mate with the female mounting upon the male's back (Table I), there is nearly always some special gland or visual, auditory, or tactual stimulus inducing her to assume this position. Alexander and Brown (1963) have suggested, on account of this correlation between the origin and nature of pterygote copulations and the timing of wing origin, that there may be a close relationship between mating behaviour and the early elaboration of the tergal flaps that eventually became wings. Ghilarov (1958) and Brinck (1958) suggest that the appearance of flight was causal in the development of direct copulation in the Pterygota, but it seems as likely that copulation preceded flying ability in the ancestor of the Pterygota.

A female-above position is also the easiest kind of act from which to derive the other pterygote mating positions. For example, figure 2 superimposes mating positions on a phylogenetic tree of orthopteroid insects. The female-above act recurs in every group except three, sometimes in almost identical form (Tettigoniidae, Gryllidae, Blattodea). It is easy to see that the so-called false male-above position of Acridoidea, Mantodea, and Phasmodea could have evolved from a female-above position through movement of the male out from under the female, and the development of grasping and holding devices. In each case the male has come to search out, leap upon, and hold the female, and has developed an intromittent organ by which the spermatophore is inserted directly into the female. In general, these changes have accompanied the evolution of this kind of male-dominated act in whatever group it is known, vertebrate or invertebrate.

At this point, the evidence suggests that all female-above mating acts in arthropods are primitive, except for: (1) the female-above venter-to-venter act reported by Hiatt, (1948), in the lined shore crab, *Pachygrapsus crassipes* Randall, which must be derived from the usual male-above, venter-to-venter act prevalent among Decapoda, and (2) the female-above venter-to-venter acts reported for honey bees and some flies (see Ribbands, 1953; Richards, 1927).* With the exception of phalangid anterior-to-anterior and decapod venter-to-venter acts, a female-above position may also have been primitive in all groups now exhibiting other kinds of acts such as male-above and end-to-end (Pterygota and Acarina). Mitchell (1957) thinks that the ancestor of the water mite subfamilies, Pioninae and Thysaninae, mated venter-to-venter with the female-above and the male and female facing in opposite directions. Brinck (1929) postulates a primitive anterior-to-anterior, female-above copulatory act in spiders.

Because intromittent organs are in nearly all pterygotes restricted to species with male-above or end-to-end positions, any explanation other than the above one would have to include accounting for loss of intromittent organs, an event possibly unknown

* See Addenda, p. 90.

among all animals. Among the pterygote groups shown in Table I, only the Tettigoniodea and Blattodea include species lacking intromittent organs, and in all cases, elaboration of an intromittent organ seems linked to male domination of the act and trends leading toward a male-above copulatory position or some kind of linear position. A notable exception is *Boreus* (Mecoptera) in which the male holds the female on his back with tong-like wings, and in which there is an elaborate intromittent organ and no spermatophore (Cooper, 1940). Although it is difficult to make positive generalisations, the Diptera, Siphonaptera, and Mecoptera may lack spermatophores in all species; the orthopteroids, Lepidoptera and Ephemeroptera

TABLE I.—Copulatory positions of pterygote insects (*Zoraptera* omitted because of lack of information). Ages of oldest fossils approximated by combining information from Carpenter (1953), Jeannel (1949), Dodson (1960) and Kulp (1961). Interpretation should take into account the fact that the male hypopygium in some Diptera and Hymenoptera is twisted during development (Richards, 1927)

Pterygote Insect Groups	Approx. age of oldest fossils (millions of yrs.)	Variation in copulatory positions							Venter to venter (facing same way)
		♀-above venter to ♂ dorsum	♂-side reaching under ♀	false		End-to-end			
				♂-above reaching under ♀	♂-above venter to ♀ dorsum	♂ abdomen slightly twisted	♂ abdomen strongly twisted	♂ inverted (lying on back)	
Siphonaptera	50	×
Diptera	160	×	×	×	×	×	×	×	×
Lepidoptera	50	.	×	.	.	×	×	.	.
Trichoptera	160	.	×	.	.	×	.	.	.
Mecoptera	275	×	×	.	.	.	×	.	.
Hymenoptera	160	.	×	×	×	×	×	.	.
Coleoptera	240	.	×	×	×	×	×	.	.
Neuroptera	275	×	×	.	.	.	×	.	.
Thysanoptera	240	.	.	×	.	.	×	.	.
Anoplura	1	×
Mallophaga	.	×
Psocoptera	275	×	×	.	.
Homoptera	220	.	×	×	×	×	×	×	.
Hemiptera	275	.	×	×	×	×	×	×	.
Plecoptera	240	.	×	×
Embioptera	50	.	×	×
Phasmodea	60	.	.	×
Acridoidea	60	.	×	×	.	.	×	.	.
Tettigoniodea	300	×	.	.	.	×	×	×	.
Isoptera	50	×	.	.
Dermaptera	160	×	.	.
Mantodea	50	.	.	×
Blattodea	320	×	×	.	.	×	.	.	.
Odonata	275	.	.	.	×
Ephemeroptera	275	×

Probable Transitional Relationships

The diagram illustrates probable transitional relationships between copulatory positions. It consists of several horizontal lines with arrows and brackets indicating evolutionary paths. From top to bottom, the relationships are: 1) A line with a right-pointing arrow (>) above it. 2) A line with a left-pointing arrow (<) above it and a right-pointing arrow (>) below it. 3) A line with a left-pointing arrow (<) above it and a right-pointing arrow (>) below it. 4) A line with a left-pointing arrow (<) above it and a right-pointing arrow (>) below it. 5) A line with a right-pointing arrow (>) above it. 6) A line with a right-pointing arrow (>) above it and a left-pointing arrow (<) below it. 7) A line with a right-pointing arrow (>) above it and a left-pointing arrow (<) below it.

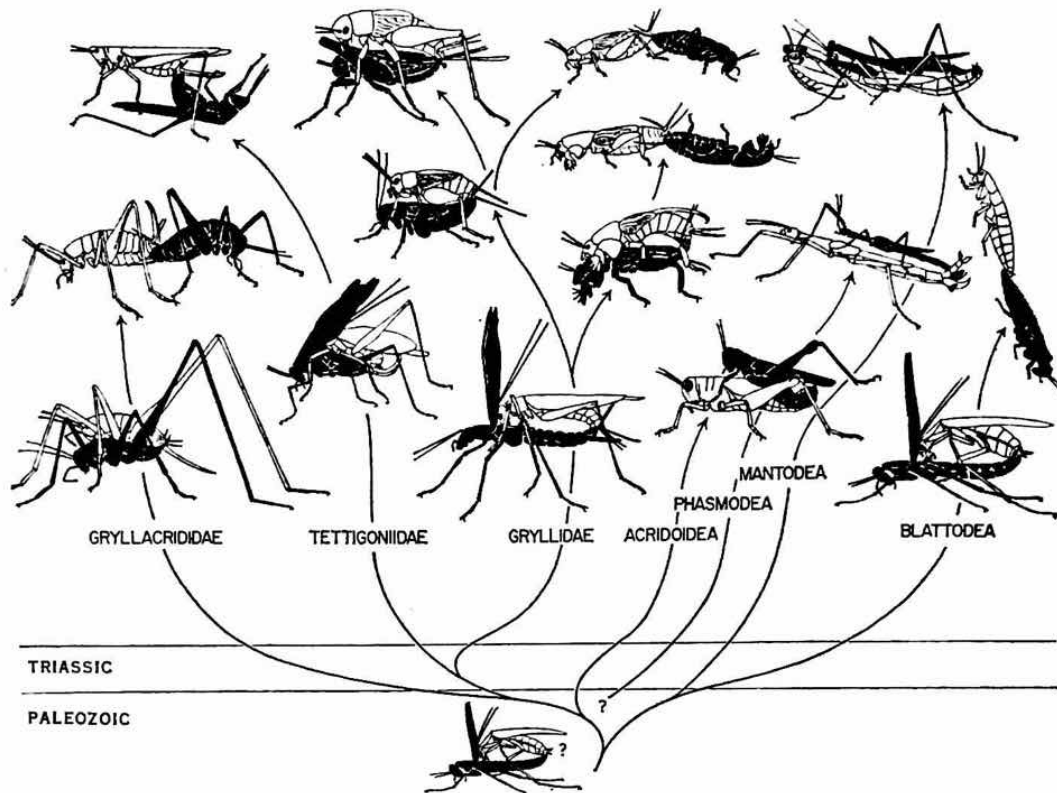


FIG. 2.—Diagram of the probable relationships of major groups of Orthoptera and positions assumed during copulation. Males black, females white. Most positions shown are in some species the only position assumed. Arrows between positions both connect positions which are in some species assumed in sequence during copulation, and suggest evolutionary relationships (except in the field crickets and mole crickets—see text and fig. 3).

probably possess them in all species; and other groups studied have species with spermatophores and species without them (Khalifa, 1949; Davey, 1960; Ghilarov, 1958).

Parallelism within a group can reveal how changes in mating position can take place and the taxonomic levels and life contexts in which such changes occur. Four related orthopteroid groups: Gryllidae, Tettigoniidae, Gryllacrididae, and Blattodea, all include species with mating acts beginning and ending with the female mounted on the male's back (fig. 3). All four also have species with mating acts that begin in

Start	Finish	♀-above	♀-above	End-to-end
.	.	.	End-to-end	End-to-end
Gryllidae	.	.	+	+
Tettigoniidae	.	.	+	+
Gryllacrididae	.	.	+	?
Blattodea	.	.	+	+

FIG. 3.—Parallelism in changing mating positions among four groups of Orthoptera.*

this position, but terminate with the pair swivelled so that they are end-to-end. All but the Gryllidae are known to have species with mating acts which begin with the pair end-to-end. This represents a fundamental change from the other acts beginning with the male backing toward the female's head, and we may wonder how it could happen. A clue is present in the nature of the behaviour of crickets that begin

* See Addenda, p. 90.

with the female-above and terminate with the pair end-to-end. In the cricket genus *Miogryllus*, for example, the post-copulatory position is also end-to-end, and contact is maintained, and re-initiated if temporarily lost, by cercal contact rather than the antennal contact characteristic in other cricket genera (R. D. Alexander, 1962). The initial position is female-above, and the male turns out to the side to achieve the linear position. Two other ways that linear positions are derived from female-above positions in these groups are (1) male dropping more or less vertically from the perch in Tettigoniidae that mate on vegetation, and (2) male and female both twisting their abdomens in Gryllacrididae. In Conocephalinae the male engages the female's genitalia in a linear position by walking backward along her body at an angle on a stem. Baumgartner (1905) reported a linear position in the American genus *Neocurtilla* (*Gryllotalpa* of authors), with the male lying on his back. Baumgartner's observation was doubted by Boldyrev (1915), who reported a normal female-above position in European *Gryllotalpa*, but I have confirmed it. The position assumed at the beginning of copulation, however, is still unknown.*

To find in Gryllidae the precise intermediate between an act beginning with the female-above and terminating with the pair end-to-end, and an act beginning with the pair end-to-end, one needs only to locate a cricket in which the first act in a series of copulations begins with the female-above and terminates end-to-end, and in which the second copulation takes place without the pair resuming the female-above position. Such a cricket, as well as one which mates only end-to-end, will probably be discovered eventually, and one can predict that these will both be crevice-dwelling or burrowing species that are either brachypterous or wingless, for these are two principal changes in mode of life that have accompanied development of end-to-end copulation in all four of the above groups.* The importance of recording the entire action sequence for comparative studies is again emphasised by these examples.

Mating behaviour and speciation

Much evidence from recent studies, particularly on various groups of insects, indicates that accelerated change takes place in mating behaviour when recently diverged species become sympatric and synchronic following the extrinsic separation which brought about their divergence (Dobzhansky, 1951; Spieth, 1958; Mayr, 1963). Such active divergence presumably continues until differences that are maximally effective in preventing sexual interactions become established between the species. If one considers the entire sequence of interactions (or "potential" isolating mechanisms) that could feasibly occur between newly formed species, from the initial coming-together of the sexes through courtship, mating, fertilisation and eventually the production of hybrids, then it becomes clear that the most efficient discordances would be those occurring earliest in the sequence (host specificities, diurnal and seasonal cycles, aggregating signals, courtship behaviour). It follows that these early-operating events should diverge rapidly, and provided that their differences are easily observable or measurable they should give the taxonomist his most reliable means of species recognition in any group within a given region (Spieth, 1952; Alexander, 1962). It also follows that, although efficiency in late-operating reproductive isolating mechanisms does not preclude selective divergence in earlier-operating mechanisms, once an early-operating isolating mechanism, such as a sexual signal, effectively begins to keep two species apart, then divergences in phenomena occurring later in the chain of reproductive events can occur only incidentally or in other selective contexts. This suggests that if interspecific and intergeneric barriers to mating can be by-passed in the laboratory, for example by artificial insemination, erratic ability to hybridize might be discovered more frequently than expected among

* See Addenda, p. 90.

relatively unrelated species, perhaps providing an unexpectedly useful tool for geneticists. It also means that positive results in laboratory tests of hybridisation, or even negative results in tests of close-range mating preferences, by themselves have little value in determining the evolutionary status of populations. The geographic, ecological, and temporal relationships of populations must be understood before the evolutionary significance of differences and similarities, or of discordance or lack of discordance in reproductive activities and characteristics, can be evaluated.

Returning to questions asked in the introduction, it is clear that only detailed and extensive comparative study involving many thousands of species can elucidate to what extent the evolutionary directions taken by particular groups with regard to mating behaviour have been influenced by (1) events of speciation, (2) perfection of intraspecific communication, and (3) changes in habitat and climate. Considerable progress has been made in the past decade; it reveals not only how much is yet to be accomplished, but also how drastically our conceptions of evolutionary history may yet have to be revised.

ADDENDA

The following information was acquired while the manuscript was in press.

1. Dr. Norman E. Gary of the University of California (Davis) kindly loaned the manuscript of a paper in press in the *Journal of Agricultural Research* in which he establishes a male-above, male-venter-to-female-dorsum mating position for honeybees.

2. Observations by Mary Jane West, Daniel Otte, and the author of a single complete mating act in *Neocurtilla borealis* (Burmeister) (*Gryllotalpa hexadactyla* Perty of authors) in a burrow with two glass walls confirmed that the act begins as well as terminates with the pair end-to-end and the male on his back. This "completes" the diagram in figure 3, and introduces interesting questions regarding variability and evolutionary changes in mating positions among male crickets, for Boldyrev's (1915) extensive observations positively indicate a female-above position in *Gryllotalpa gryllotalpa* (L.).

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DISCUSSION

J. M. Thoday. Amongst the species you have studied, have you seen any signs of intraspecific variation in copulation?

R. D. Alexander. Variations in position seldom occur, except for minor deviations; the patterns are extraordinarily rigid. Some genera, and probably some species, can be identified by the length of time taken in copulation.

J. M. Thoday. If one species characteristically turns around at the last minute, can individuals be found that do not turn?

R. D. Alexander. I know of no variations among the individuals of a species that are similar to the kind which occur among species and genera. But not very many species have been examined in great detail.

G. C. Varley. At what stage does the male start constructing the spermatophore?

R. D. Alexander. In some species shortly before copulation; in others the males seem always to be carrying a spermatophore. This may dry out and become useless, but it is still carried and is only rubbed off or chewed off after an unsuccessful courtship. In two genera (*Anurogryllus* and *Neocurtilla*) spermatophores have not been found in preserved or freshly killed males, although they are present on females after

copulation. I suspect that there is something different here about the time of formation of the spermatophore.

G. C. Varley. You would suggest that formation is directly linked with the beginning of mating?

R. D. Alexander. Possibly, in these cases. If so, this would be a secondary "temporariness", for these crickets are descended from others that formed spermatophores before courtship, and these in turn from ancestors which formed the spermatophore immediately prior to mating.

V. B. Wigglesworth. I suppose that the behavioural differences are correlated genetically with the others, but again it would be difficult to say which came first.

R. D. Alexander. It is sometimes difficult to discover any anatomical basis for behavioural differences. With acoustical patterns, all the external structures, including the auditory organs, may be identical between species, and the differences may lie solely in the nervous system.

P. T. Haskell. It has been supposed that genitalia differences between species are not very important when other good discriminatory mechanisms exist. There are some grasshoppers, for example, where the primary isolating mechanism is the song pattern; but in these same sympatric species, natural hybridisation can and does occur. Will there not be some selection pressure for genitalia differences even here?

R. D. Alexander. Selection for divergence in genitalia can only occur if copulation is *sometimes initiated* between species in the field; otherwise, genitalic differences may be entirely accidental or left over from some time in the past when interspecific copulation was sometimes started. Reproductive isolation which depends upon genitalic incompatibility is inefficient, and we should expect that earlier operating mechanisms (such as discordances during courtship) would quickly replace it. As an example, there are differences in the male genitalia among three species of *Magicicada* which occur together. Interspecific copulation in the field has never been seen. But when the three species were placed together in cheesecloth cages, all possible kinds of interspecific mating took place in a short time, showing that the genitalic differences are probably not the reason for the lack of naturally occurring interspecific copulation. The genitalic differences probably arose as the *result* of isolation, and never functioned as the *cause* of it (Alexander and Moore, 1962).

P. T. Haskell. But surely those species are separated geographically.

R. D. Alexander. No. They are the ultimate in sympatry and synchrony, emerging together by the millions and individually intermixed.

O. W. Richards. It seems dangerous to assume too often that mechanisms as complicated as the genitalia have evolved purely as accidental accompaniments (i.e. pleiotropic effects) of other changes. In bumblebees, the part of the genitalia which shows the biggest differences at the species level does not enter the female but comes into contact only with her seventh sternite which has much the same shape in all species. There seems to be a real problem here.

R. D. Alexander. I did not mean that the *change* in genitalia was accidental, but that the *divergence* between species was accidental. These are two different things. Changes in genitalia may occur solely to produce greater efficiency of mating within the species, as for example the evolution of intromittent organs. These always result in greater efficiency, and I do not know any example of a reversal, or loss of an intromittent organ.

O. W. Richards. How does such divergence come about? If elaborate genitalia are developed, how is selection benefited?

R. D. Alexander. This requires a study of how genitalia are used. It is impossible to predict the use of a particular structure. For instance, the parameres of ground

beetles have been described as prizes, but in some species, at least, they remain outside the female during copulation (Alexander, 1959). The effect of a particular shape or kind of surface on an insect's genitalia may be tactile rather than mechanical, and without direct observation speculation is unprofitable.

J. M. Thoday. Differences in the genitalia of two species need not imply that their associated functional differences are related to copulation. There may be many other functions. For example, in primates with highly-coloured genital apparatus the colour has nothing to do with copulation but brings the sexes together; behaviour mechanisms are involved. To distinguish between selective and non-selective characters may therefore be unrealistic.

H. E. Hinton. An example of this is the fact that in some South American butterflies (Reverdin, 1915), and in one Eupterotid moth (Forbes, 1941) stridulatory organs are present on the male genitalia.

R. D. Alexander. Professor ^{White's} ~~Thoday's~~ remarks would apply both to increased efficiency of mating within a species and to increased efficiency of reproductive isolation between species.

M. J. D. White. It does not follow that because copulation can take place normally between two species whose genitalia are so different, therefore the question of the shape of the genitalia is not of much importance. Any morphological change resulting in successful insemination, even of one or two per cent., is likely to affect natural selection. Therefore, it is entirely natural that there should be a very extended evolution of genital structures. This is not incompatible with the fact that in spite of considerable differences in genitalia it is possible under particular—usually artificial—conditions to get successful copulation between selected species. The essential point is that natural selection can account for the one or two per cent. of cases, whereas the casual observer cannot.

C. E. Dyte. Do you consider that groups with complicated courtship patterns are preadapted to take advantage of a diversity of environments? In the Hawaiian Diptera the two families which have produced most species (the Dolichopodidae and the Drosophilidae) have complex courtship patterns, while those with relatively few species probably have simpler patterns. A species will obviously tend to diverge in its courtship from species with which it does not live, but there will be a particularly strong selective pressure for species to develop effective isolating mechanisms should they become sympatric. Groups which already have a complex courtship pattern might be able to evolve further complexities relatively rapidly under such circumstances.

R. D. Alexander. In closely related sympatric species, very little is known about which differences developed when the species were allopatric and which developed subsequently. Similarly, it is not known what kinds of differences between present allopatric populations may cause incompatibility if the populations eventually came together. These are critical questions in the study of speciation.

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