COPULATION IN *EPHIPPIGER* (ORTHOPTERA, TETTIGONIOIDEA)

by

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Abstract

Observations have been made in a number of *Ephippiger* species from Southern France and the role various reproductive structures play during the copulatory process.

Introduction

A number of species belonging to the genus *Ephippiger* occur in Southern France and in the adjacent parts of Spain and Italy. In some cases these species vicariate geographically, but there are also several instances of overlapping distribution of two or more species. The question has to be raised whether all taxa distinguished as species (e.g. Chopard, 1951; Harz, 1969) are reproductively isolated. In this paper we will investigate whether the interspecific differences in the form of cerci, epiproct, titillators and subgenital plate could function as mechanical barriers possibly operating against interspecific matings. In another, the next, paper the likelihood of interspecific mating is dealt with.

Material and methods

Animals of six species were collected during field trips in August and September, 1977, 1979 and 1980. They were measured and taken to the laboratory where observations were made during the second half of September and during October. In November most animals died. Detailed observations of copulations were made with a stereomicroscope (magnifications 6.5—16×). Some copulations were documented by photography or videorecording.

The species studied and their collecting stations are the following.

Ephippiger ephippiger (Fieb., 1784): Niaux (Ariège) 1977, 1979; Mézel (Ht. Provence) 1979, 1980; Causse de Larzac (Aveyron) 1979; Plan d'Aups (Var) 1979, 1980.

Ephippiger cunii (Bol., 1877): Mont Louis (Pyr. Orient.) 1977, 1979; Canigou (Pyr. Orient.) 1979.

Ephippiger cruciger (Fieb., 1853): Neffiès (Hérault) 1979; Leucate (Aude) 1979.

Ephippiger provincialis (Yers., 1854): Plan d'Aups (Var) 1979, 1980.

Ephippiger terrestris (Yers., 1854)[1]): Mézel and several other places in the vicinity of Digne (Ht. Provence) 1979, 1980, 1981; Fayence (Var) 1980; Col de Braus (Alp. Mar.) 1980; Tende (Alp. Mar.) 1980.

Ephippiger bormansi (Br., 1882)[1]): Col de Tende (Alp. Mar.) 1980; Vallone del Arma (Piemont) 1981.

Some pairs were killed during or just after copulation and preserved to study the position of the genital organs and their elements with respect to each other as well as the position of the spermatophore.

The copulation

Description of the behaviour

The general course of copulation in *Ephippiger* conforms to that in other Tettigonioids, as described by Gerhard (1913, 1914). A short description will be given here emphasizing the details relevant to the questions raised.

A normal copulation will take about half an hour. *Ephippiger* males stridulate during part of the day and night, while sitting on a plant or bush, the height of which generally does not exceed two metres. A sexually motivated female will walk straight to a stridulating male (Busnel & Dumortier, 1954; Duijm & Van Oijen, 1948). On encountering the male the female stops. Both male and female touch each other with the antennae. The male may tremble with his body several times (Busnel et al., 1955). After some time the male will place the extremity of his ab-

[1]) Nadig (1980) considers *E. bormansi* a subspecies of *E. terrestris*, but the conventional classification is retained here for the time being.

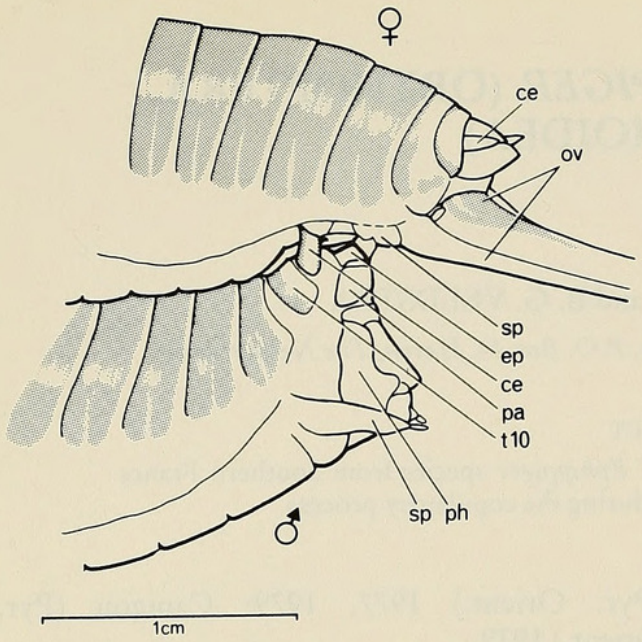

Fig. 1. A pair of *Ephippiger ephippiger* just before the cercal clamp: *ce*, cercus, *ep*, epiproct, *gr*, copulatory groove, *ov*, ovipositor, *pa*, paraproct, *ph*, phallus with: *ll* lateral lobes, *dl*, dorsal lobes and *vl*, ventral lobes; *pl*, pleural region, *sa*, saddle-like part of spermatophore, *sp*, subgenital plate, *st*, stylus, *sx*, spermatophylax, *s6*, sixth sternite, *t9*, ninth tergite, *t10*, tenth tergite.

domen in front of the female's head; the female will then touch the male's somewhat ventrally curved abdomen with her maxillary palps. Moving forward slowly, continually touching, she finally mounts the male's back. When the female has entirely mounted, the male bends his abdomen dorsally, extends the lobes of the phallus and turns his subgenital plate downward. The titillators are now visible between the phallus lobes. The cerci are extended and spread in a laterodorsal direction. The female is now sitting on the back of the male with her head above his pronotum and the median planes of both partners have to coincide at this point. In the female the caudal part of the ventral abdominal wall is contracted, the ovipositor making an angle of 20—45° with its longitudinal axis (fig. 1). Only in this position the female's subgenital plate is situated between the male's cerci in such a way that the copulation may proceed. The male circles with its cerci caudally and medially. Suddenly the inner teeth of the cerci get a grip on the female's subgenital plate and at the same time the cerci clamp the female tightly. Clamping does not occur randomly, but only on two small grooves — the copulatory grooves — which are easy to distinguish by their dark colour, owing to extra sclerotisation. By adducting the cerci the male pulls the female firmly against its body. In this position the epiproct pushes dorsocaudally against the female's subgenital plate and provides one of the factors for determining the position of the male abdomen with respect to the female's. At the same time, pushing the epiproct against the female subgenital plate results in the lifting of the caudal part of the subgenital plate from the female gonotrema. By this action the gonotrema will be opened up and exposed. Immediately after being clamped, the female brings the ovipositor downward very rapidly to such a position that it fits in the emargination of the caudal rim of the subgenital plate and contacts the styli (fig. 2). After some seconds the ovipositor returns to its normal position. The function of this action is not clear. Perhaps in this way a final check is made to determine whether the partners are in the correct position to enable the next step in the copulation procedure, viz., the rotation. In this position the male will extend and contract the phallus alternately. The female now makes a few steps forward, the male meanwhile somersaulting until he gets hold of the female's ovipositor with his fore and middle legs (fig. 3). In doing so, the male is rotated about an axis through the inner cercal teeth. This rotation is only possible when the cerci are tightly clamped. The position of the male is now entirely fixed with respect to the female and evidently in the only one in which the spermatophore can be deposited. When extended the phallus now reaches the basis of the ovipositor. The phallus makes pulsat-

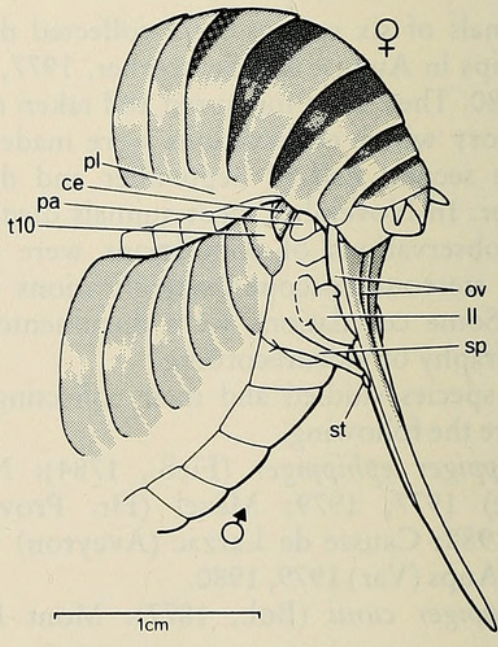

Fig. 2. The position of male and female *E. ephippiger* immediately after the cercal clamp, the female having lowered the ovipositor to contact the male's subgenital plate and styli. See fig. 1 for explanations.

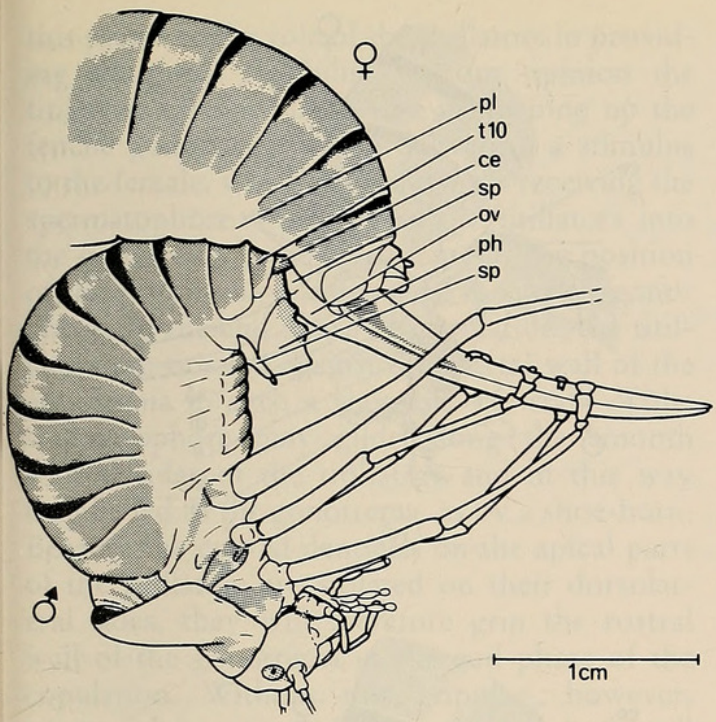

Fig. 3. The relative position of male and female after the rotation in *Ephippiger*. See fig. 1 for explanations.

ing movements during which its dorsal lobes, together with the apical parts of the titillators, will glide over the basis of the ovipositor. After a number of very intensive pulsating movements the apical parts of the titillators will be put into the female's gonotrema at the basis of the ovipositor. Thereafter, the pulsating movements of the phallus will continue for a while but less intensively: meanwhile the titillators in the gonotrema are moved backward and foreward. They are dorsocaudally directed and their apices reach the roof of the genital chamber, where the female's genital lobes are situated. Possibly these genital lobes are expanded during this phase. After some time the pulsating movements stop, the phallus being in a maximally extended position. The phallus lobes part and the spermatophore is extruded (fig. 4a). The globular caudal part of the spermatophore bears dorsally a saddle-like structure. With the aid of the phallus the male pushes the spermatophore with the saddle against the ventral valves of the ovipositor (fig. 4b). The saddle is sticky so that the spermatophore adheres to the ovipositor for some time.

The phallus is then contracted, especially its dorsal lobes (fig. 4c). In this phase the stalk of the spermatophore is inserted into the gonotrema. At the same time the female will make sculling movements with the ovipositor by moving the right and left valves with respect to each other rostrally and caudally, respectively. Apparently the female is playing an active role while receiving the spermatophore. At the end of this phase the extremity of the stalk of the spermatophore is firmly held by the genital lobes in the genital chamber.

After some seconds follows the deposition of the spermatophylax, a rather voluminous gelatinous mass (fig. 4d). Meanwhile the male withdraws the phallus from the spermatophore. The titillators have been withdrawn from the gonotrema and are visible again. The female will now make some strides, the cerci will loosen and the partners part. The male's phallus is contracted and the subgenital plate closed. The female will soon begin to eat parts of the spermatophylax and ultimately, after an hour or so, also the spermatophore. In the meantime sperm from the spermatophore has had ample opportunity to enter the female's spermatheca. The openings of the sperm canals in the spermatophore-stalk are situated just opposite the entrance to the spermatheca.

Experiments

The role of the inner cercal teeth was verified by carefully cutting them away. This was done in males of *E. ephippiger* and *E. terrestris*. Five copulation attempts by these experimental males were observed, all showing the same course. After mounting, the female performed downward movements with the ovipositor without however reaching the male's subgenital plate. Although the male tried to grasp the female with his cerci, he never succeeded. It is concluded that the inner cercal teeth are essential for providing a hold on the female. Furthermore, these experiments showed that the fully deflected position of the ovipositor will only be realised as a reaction to the accomplishment of the cercal clamp.

With regard to the role of the titillators the following morphological information is relevant. A male has two symmetrical titillators. Each titillator consists of a basal part, on which two muscles insert, and an apical part, which may protrude from the phallus lobes. The latter enters the female gonotrema during copulation. One muscle inserts on the lateral part of the titillator basis and originates from the apodeme of the 10th tergite. This muscle is probably homologous with the ventral retractor muscle (Snodgrass, 1940). The other muscle inserts on the medial part of the titillator basis and has its origin on the subgenital plate. This muscle is the homologue of Snodgrass's dorsal retractor mus-

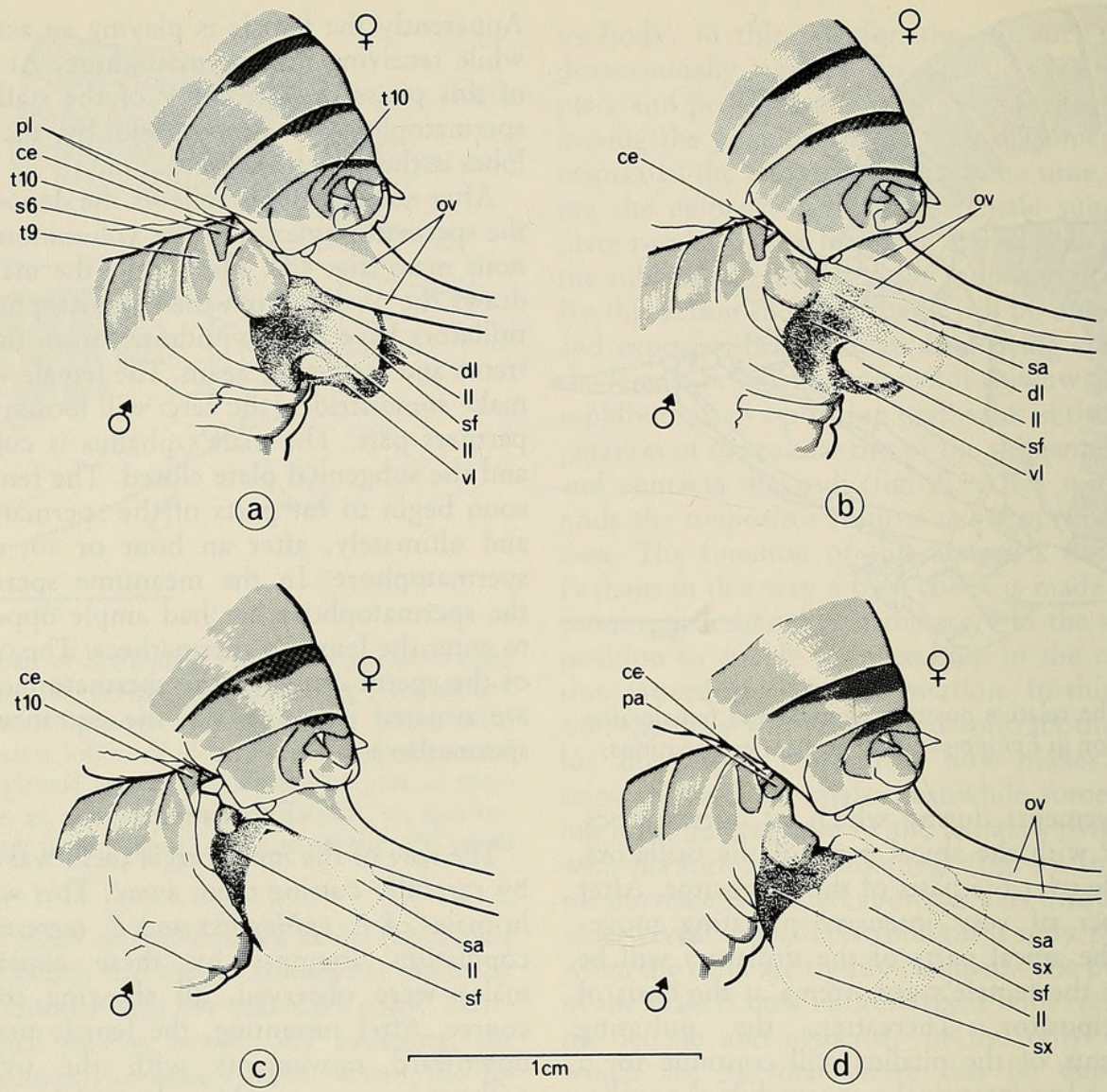

Fig. 4. Production of the spermatophore in *Ephippiger*: (a) the globular part of the spermatophore becomes visible; (b) the saddle-like part of the spermatophore is being pressed against the ovipositor; (c) the dorsal lobes of the phallus are being contracted; (d) the spermatophylax appears. See fig. 1 for explanations.

cle. The following movements have been observed: (a) dorsal deflection, (b) lateral deflection. In (a) and (b) the apices of both titillators stay close together pointing in the same direction, whereas when the phallic lobes are maximally extended, the apices may diverge. To obtain some insight into the way the titillators function during copulation the following experiments were performed. In eight males of *E. ephippiger* the apical parts of the titillators were cut off. Both titillators where shortened to the same extent, but the length of the cut parts differed. In the extreme case the entire denticulated part was removed. The operation did not alter sexual motivation or copulatory behaviour. One copulation was observed in each male. In no case were the remnants of the titillators inserted into the female's gonotrema, independent of the length of the remaining part. Probably the cut ends of the titillators cannot readily enter the gonotrema because they lack the rounded apex which is characteristic of the intact titillator. Notwithstanding the lack of insertion, a spermatophore was deposited in all cases. In half of these cases the stalk was brought into the normal position within the gonotremal space. In the remaining cases this did not occur and the female then lost the spermatophore immediately after the copulation. From these observations it follows that the insertion of the titillators is not a prerequisite for completion of the copulation. Evidently the action of the male's phallic lobes together with the action of the female's genital lobes may result in normal reception of the spermatophore stalk. The number of failures was nevertheless high;

this points to the role of the titillators in providing additional reliability. In our opinion the titillators do not play a role in opening up the female gonotrema nor in delivering a stimulus to the female, which is essential for receiving the spermatophore. Insertion of the titillators into the gonotrema probably orientates the position of the gonotrema just opposite the male's gonophore. In the end phase of copulation, the titillators are situated against the rostral wall of the gonotrema in such a way that the stalk of the spermatophore may glide along the smooth ventral sides of the titillators and in this way may be led to the gonotrema, as by a shoe-horn. Because the curved denticles on the apical parts of the titillators are situated on their dorsolateral sides, they will therefore grip the rostral wall of the gonotrema in the end phase of the copulation. Without this gripping, however, successful insertion of the spermatophore still remains possible. In two other males of *E. ephippiger* a part of only one titillator was cut off, the other being left intact. Insertion appeared to be normal in these males during copulation. In one copulation the stalk of the spermatophore was inserted quite normally, in the other case the spermatophore was lost by the female. In the latter case, orientation of the male gonopore with respect to the female's gonotrema was in our view not precise enough to ensure reception of the stalk by the female's genital lobes.

Discussion

The copulatory behaviour in *Ephippiger* consists of two closely interlocked complementary series of movements by male and female. Both female and male copulatory apparatuses function as mechanical systems of considerable complexity. For their successful interaction not only has highly standardised behaviour to be performed, but also the form and dimensions of the various parts in male and female must conform to a high extent. In the course of the copulation a consecutive series of mechanical conditions has to be satisfied after the female has mounted:

(1) do the median planes of both partners coincide?

(2) is the female's subgenital plate situated between the male's cerci?

(3) can the inner cercal teeth get a hold in the copulatory grooves of the female's subgenital plate?

(4) does the ventrally deflected ovipositor fit the emarginated rim of the male's subgenital plate so that their gonopores are just in front of each other?

(5) do the phallic lobes with the titillators reach the female's gonotrema?

Only when all conditions are fulfilled is the cercal clamp carried out correctly and rotation ensues. After this, spermatophore and spermatophylax will be produced and the spermatophore stalk will be inserted into the female's gonotrema when:

(6) the titillators have been introduced in the gonotrema.

Form, position and size of the various parts of the genital apparatus have to correspond; it is analogous to a lock and key system. However, this system does not appear to be very rigorously determined: interspecific copulations may occur occasionally under laboratory conditions. Moreover, not every morphological detail appears to be of decisive importance as is indicated by the experiments with cut titillators.

In the following paper, the differences between species with regard to their genital apparatus and copulatory behaviour will be considered together with the possibility of interspecific matings.

Summary

The course of copulation in the genus *Ephippiger* has been described emphasising the succession of mechanical conditions that must be satisfied for the copulation to be completed. The male cerci play a central role; they have to grasp into the copulatory grooves on the female's subgenital plate with their inner teeth. Only after having successfully clamped the female does the male rotate about the axis through the inner cercal teeth and continues copulation. The titillators appear to be used as shoe-horns for guiding the spermatophore stalk when it is being introduced into the female gonotrema.

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