

ON COPULATION AND INSEMINATION IN THE COCKROACH
PERIPLANETA AMERICANA (LINN.).

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INTRODUCTION.

The structure and development of male and female genitalia in different groups of Orthopteroid Insects have been studied by a number of workers. Observations on copulation have also been recorded in several instances; and it is now established that a spermatophore is formed within the genital organs of a male in the various families of Orthoptera, and that insemination is accomplished by transference of a spermatophore from the male to the female. Our knowledge regarding copulation and insemination in cockroaches is meagre. A spermatophore has no doubt been observed in *Blatta orientalis* by Zabinski (1933), and Qadri (1938), but little is known of the exact function of the different parts of the male and female genitalia during the process of copulation. Snodgrass (1937) writes: 'Considering how intimate some of the cockroaches are with us, it is disconcerting to find how little we know of their private lives.' The following account incorporates the observations on the various aspects of copulation and insemination in *Periplaneta americana*, and also deals with the exact working and function of the component parts of the male and female genitalia during the act of copulation.

MATERIAL AND TECHNIQUE.

Large number of nymphs of cockroaches were reared in the laboratory and a complete record of the date and time of their final moult was maintained. The adults were removed from the common stock soon after their emergence and males were segregated from the females. For observing copulation, the male and female cockroaches were brought together in large glass dishes covered with gauze. In some cases several females and one or two males and in others several males and a few females were kept in the same dish. In the event of their not copulating, and also when it was not possible to watch the process, care was taken to separate the males from the females.

Ordinary methods of killing the copulating individuals, with interlocking of their genitalia intact, did not prove successful. However, hot water was found very useful for killing such insects. The copulating pair was led into a beaker

or a tall glass dish and sufficient quantity of hot water at about 70°C. was poured over them. This resulted in quick and simultaneous death of the pair with all their parts in the copulating position. In case immediate dissection was not required, a small incision on the sides of the body of the animals was made and the pair was preserved in 70% alcohol to which a few drops of glycerine were added. After watching progressive stages of copulation, it was found advisable to kill the animals about 45 minutes after the beginning of copulation, since that is the time when they are completely engrossed in the act and do not easily separate.

OBSERVATIONS ON COPULATION.

It has been observed that under laboratory conditions, cockroaches copulate only during night from March to September. On an average the process of conjugation lasts an hour and a half but under disturbed conditions it may get prolonged to two hours or even more. In many cases the males were found excited after six days of their last ecdysis and a few did even copulate with females of the same age. In no case either a male or a female copulated earlier than six days, although, both Zabinski and Qadri are of opinion that at least the females are ready to copulate just after their final moult. Both the males and females copulate several times during their lifetime; the male is capable of copulating at intervals of six to seven days but the female less frequently since the latter, after copulation, gets busy depositing cocoons. The female cockroach becomes once more ready for copulation only when its store of sperms in the spermatheca is exhausted during cocoon-formation. A few of these were observed to copulate even as early as three to four hours after the cocoon-laying was over.

Unlike some other insects there is no evidence to show any kind of courtship in *P. americana* and female in particular gives no indication of its desirability for the action. An excited male, whose abdomen becomes extended, genitalia partly extruded, and the cerci stretched out, bustles about in search of a female and runs after other cockroaches touching their bodies by means of its antennae. On approaching a female, it attempts to insert its abdomen beneath that of the female, and also tries to catch hold of the female genitalia. This is done usually from behind, sometimes from one side, while Wille's remark, 'the male brings the end of its abdomen close to the head of the female,' indicates that it tries to do so from in front. An unwilling female avoids the male and quietly walks away leaving the latter alone on the spot. Rarely does a male find itself readily acceptable to the female, and in this connection Qadri's statement, 'the young males avoid the females and flee away if the latter approach them', gives a wrong impression that the female rather than the male is initially excited. A male in search of a companion may, in the heat of the moment, insert its abdomen beneath that of another male but on finding it one of the same sex, it soon withdraws from there. At times, after a few minutes attempt, it is able to catch hold of a part of the genitalia of a female but in case the latter is unwilling a tussle ensues and the two separate.

A willing female permits the male to insert its genitalia within her vestibulum. The two soon become joined by their posterior ends and remain connected together in a tail-to-tail position till insemination is normally completed. After their mutual union is established, the male becomes perfectly passive while the female takes an active part and moves about dragging the male behind her in search of some dark cosy place. Having secured one, the pair remains stationary and they do not indicate any movement for some time. After about an hour of their union they tap each other by their hind or fore-legs, apparently indicating the climax of the operation. It has been ascertained by dissecting a number of copulating pairs, forcibly separated during the process, that the spermatophore is not discharged from the male within at least an hour from the beginning of copulation. This has also been made sure that even after the deposition of a spermatophore, the pair remains

connected together for about fifteen minutes after which the male withdraws its genitalia and the two separate. The female remains motionless for some time while the male retires from the spot.

SEX-ATTRACTION.

Observations on the mating habits of *P. americana* show that there is no sex-attraction in cockroaches; these appear to be guided mainly by instinct. Wille has demonstrated in *Blatella germanica* that the secretion of two pairs of glands, dorsally situated at the ends of sixth and seventh tergites of adult males, serves to attract the females at the time of mating. He writes: 'When a male encounters a female, it raises the wings at right angles to the body and exposes the depression of its back to the female, who being soon attracted to them, first explores them with her palpi and then proceeds to lick them with her mouth parts.' Rau (1924), Zabinski, and Qadri in their observation on *B. orientalis* agree with Wille on this point and further record that the male attracts the female on its back and extends the abdomen below her to secure a hold on the ovipositors. I, however, failed to observe in *P. americana* any attempt on the part of the male to attract a female on its back, nor have I found the female exploring and licking the glands on the back of the male. Only a pair of dorsal glands,¹ equally developed in both the sexes, occurs in nymphs as well as in adults of *B. orientalis* and *P. americana* and I regard these as odour producing glands as suggested by Hasse (1889) and Oettinger (1906). I therefore feel sure that these have nothing to do with sex-attraction, there being no such phenomenon in these insects.

INTER-RELATIONSHIP OF GENITALIA² AND OTHER PARTS OF MALE AND FEMALE DURING THEIR UNION.

A male cockroach, prior to getting an actual hold on the female pulls down the gynovalvular portion of the seventh sternite of the female by the tip of its protruded titillator. This action of the male releases the ovipositors of the female and their free distal ends are then pushed up by the male genitalia to widen out the entrance of the female genital pouch (gynatrium), into which the male inserts its genitalia. In firmly united specimens, the distal portion of the ninth sternite of the male comes to lie above the gynovalvular portion of the seventh sternite of the female and the styles of the male press hard against the notches of the seventh sternite of the female. The cerci of the female lie beneath those of the male, the two resting in a cross-wise manner on either side. The wings of the male usually come to lie beneath those of the female. The epiprocts of the male stretch beneath those of the female, press against the paraprocts of the latter and also get bent upon themselves.

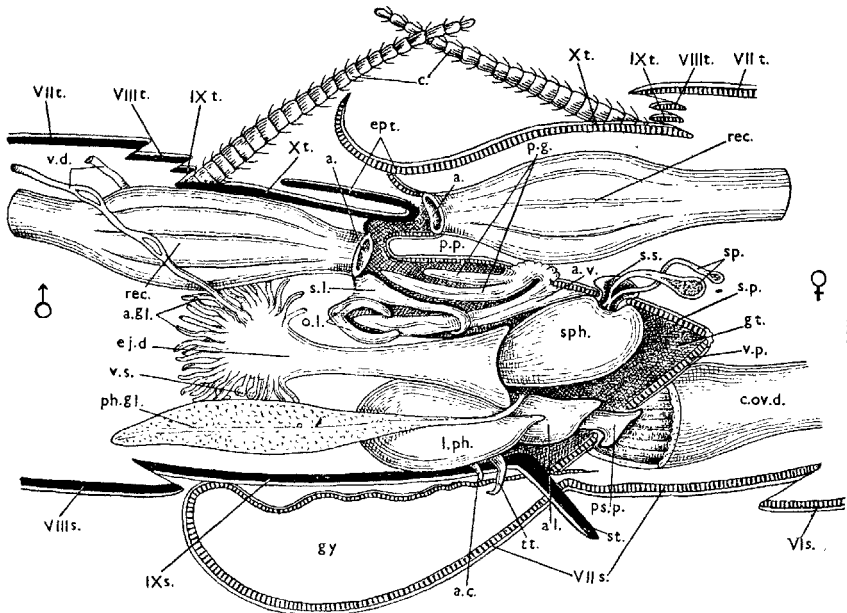
The right phallomere³ of the male genitalia occupies almost a median dorsal position within the gynatrium and is situated between the posterior gynapophyses and the ejaculatory duct, the former taking no part in the actual process of copulation. The distal extremity of the serrate lobe of the phallomere reaches the bases of the anterior valvulae of the ovipositor. The curved spine of the right limb of serrate lobe entangles the left valvula while the two prong-like processes of its left limb hold the right valvula. The right and left anterior valvulae come to lie above the left⁴ and ventral⁵ phallomeres respectively. These valvulae extend back to the opposing lobes which open to allow the entry of the former into the space enclosed between themselves. The opposing lobes soon tighten their hold to grasp firmly

¹ Dorsal glands were described in *Periplaneta* by Minchin (1889-1890).

² The terminology has been adopted from Crampton (1925) and Snodgrass (1937).

³, ⁴, & ⁵ The right, left and ventral phallomeres are equivalent to the *Right Dorsal*, *left* (combined dorsal and ventral), and *Right Ventral penis valves* respectively (Qadri, 1938, 1940).

these valvulae between their lips. It will thus be seen that the anterior valvulae are the only parts of the female genitalia that are held tightly by those of the male



TEXT-FIG. 1. Sectional view (Schematic) of the tail-ends of a copulating pair of *P. americana* showing the interlocking arrangement of their genitalia.

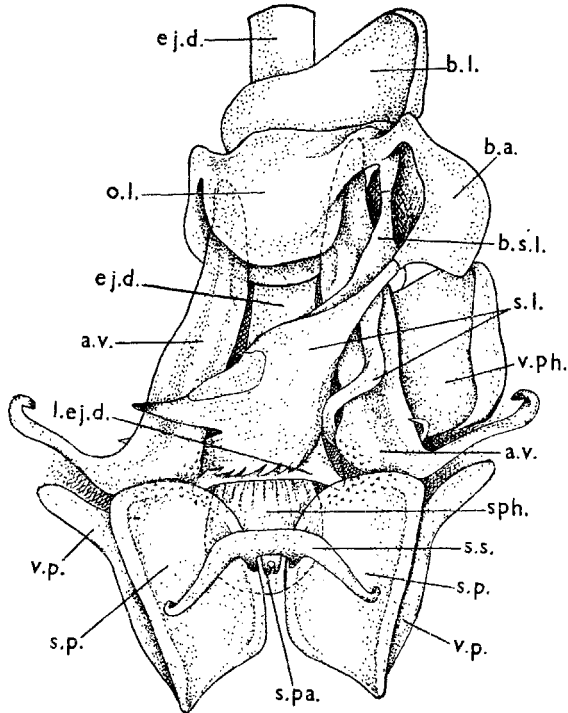
a., anus; *a.c.*, acutolobus; *a.gl.*, accessory glands; *a.l.*, asperate lobe; *a.v.*, anterior valvula; *c.*, cerci; *c.ov.d.*, common oviduct; *ej.d.*, ejaculatory duct; *ep.t.*, epiproct; *gt.*, gynatrium; *gv.*, gonopore; *l.ph.*, left phallosome; *o.l.*, opposing lobes; *p.g.*, posterior gonapophysis; *ph.gl.*, phallic gland; *p.p.*, paraproct; *ps.p.*, pseudopenis; *rec.*, rectum; *s.l.*, serrate lobe; *sp.*, spermatheca; *s.p.*, spermathecal plate; *sph.*, spermatophore; *s.s.*, spermathecal sclerite; *st.*, style; *tt.*, titillator; *v.p.*, vulvular plate; *v.s.*, vesicula seminalis; *VI s.*, *VII s.*, *VIII s.*, *IX s.*, sixth, seventh, eighth and ninth sternites; *VII t.*, *VIII t.*, *IX t.*, *X t.*, seventh, eighth, ninth and tenth tergites.

during the act of copulation and are released only after the completion of the act. The remaining sclerites of the right phallosome are only subsidiary and mainly provide attachment to the muscles.

The other parts of the male and female genitalia lie just under the right phallosome of the male and the ovipositors of the female. The vulvular plates which ordinarily lie flat on the seventh sternite become vertically slanting and female gonopore situated between the vulvular plates consequently points obliquely backwards. The lateral spermathecal plates, which in the natural condition superpose the perivulvulars get likewise tilted and thus widen out the vaginal opening. The arms of the median spermathecal sclerite are pulled anteroventrally and all these adjustments cause the spermathecal papilla face vertically downward.

The ventral phallosome, on which the terminal opening of the ejaculatory duct is present, shifts to the right making room for the expansion of the lower lip of the ejaculatory duct. It does not hold any part of the female genitalia while Qadri writes: 'In *B. orientalis* it holds the anterior ovipositor valves tightly.' The ejaculatory duct becomes fully dilated and its membranous upper lip as well as the thick lower lip, both extend up to the entrance of the vagina. The spermatophore is expelled out by the muscular contraction of the wall of the ejaculatory duct and it is directly attached on to the ventrally projecting spermathecal papilla.

The left phallomere which moves at an angle of about 30° from its original position projects towards the right from beneath the ejaculatory duct. The ex-



TEXT-FIG. 2. Dorsal view (semi-diagrammatic) of the male and female genitalia during copulation after the removal of the posterior gonapophyses.

a.v., anterior valvula; *b.a.*, basarcus; *b.l.*, basilamina; *b.s.l.*, basi-serrate lobe; *ej.d.*, ejaculatory duct; *l.e.j.d.*, lip of the ejaculatory duct; *o.l.*, opposing lobe; *s.l.*, serrate lobe; *s.p.*, spermathecal plate; *s.pa.*, spermathecal papilla; *sph.*, spermatophore; *s.s.*, spermathecal sclerite; *v.p.*, vulvular plate, *v.ph.*, ventral phallomere.

panded tip of the pseudopenis enters the female gonopore where it rotates about 90° on its own axis getting an anchorage on the perivulvular sclerites. The asperate lobe lies just above the pseudopenis, a little to the right side, while the opening of the phallic gland is situated immediately adjacent to the opening of the ejaculatory duct. The titillator, which in the very beginning of the process brought about the opening of the female gynatrium to allow the entrance of the male genitalia into it, comes to lie ventrally in a slanting position. The acutolobus is situated above and slightly to the left of titillator and its curved spine presses against a depression on the endogynal plate in the öothecal membrane. The other sclerites are likewise tilted and mainly provide attachment to the muscles.

Rau's, Zabinski's, and Qadri's descriptions of the copulatory process are inadequate and for want of clear and properly labelled sketches an understanding of the inter-relationship of the parts of male and female genitalia is hardly possible. I agree with Zabinski's observations that the removal of the long hooked process (titillator) from the genitalia of a male disables the same to copulate with a female because such a male will not be able even to open out the female gynatrium (vestibulum). Likewise, a normal male will be unable to retain hold on a female cockroach from

whose genitalia the anterior valvulae have been removed,* because this is the only part of a female that is well within the grasp of the male during the act of copulation.

Qadri (1938) writes: *The right ventral penis valve, which is probably incorrectly referred to as the penis by Zabinski and others, holds the anterior ovipositor valves tightly, while the right dorsal penis valve lies between the anterior valves, and appears to be the main clasping organ. The ejaculatory duct enters from the side and its membranous lip is applied to the bases of the anterior valves where the spermatophore is attached*' (Italics are mine). There appears to be some confusion in the use of the terms left and right dorsal and ventral penis valves in the genitalia of male (Qadri 1940). My observations on *P. americana* are not in agreement with those of Qadri in many respects. The right ventral penis valve, which is equivalent to the ventral phallomere, is plane and simple part incapable of holding anything, still Qadri has assigned to it the function of holding the anterior ovipositor valves which are actually grasped by the right phallomere equivalent to the right dorsal penis valve mentioned by him. The details regarding the functions of the other component parts of the genitalia have not been described by him. The membranous lip of the ejaculatory duct lies below the ovipositor valves and is not applied to the bases of these as pointed out by Qadri and neither is the spermatophore attached to the bases of the anterior valves.

FATE OF THE SPERMATOPHORE.

As already mentioned the spermatophore is expelled out of the ejaculatory duct and it is attached on to the spermathecal papilla of the female where it has been found sticking up to about 21 hours after the copulation. In a freshly mated female, the outer wall of the spermatophore is soft and it is loosely attached to the spermathecal papilla but within about two hours the wall of the spermatophore sets in and hardens so that the spermatophore becomes firmly fixed on to the papilla. After about 18 hours the spermatophore-attachment becomes loose and 3 to 4 hours later it is no more found within the genital chamber of the female. The ultimate fate of the empty spermatophore is obscure, possibly it drops out and is eaten up by the female as is recorded in some other Orthopteroid insects (Gerhardt, 1913, 1914).

Different views have been expressed regarding the place of attachment of the spermatophore and its fate. Zabinski says: 'Copulation in *B. orientalis* results in the attachment of a spermatophore on the papilla of the female containing the spermathecal orifice; the spermatophore is carried by the female for two or three days and is then rejected.' Qadri wrongly criticises Zabinski regarding the initial place of attachment of the spermatophore and writes: 'In just-mated female, the spermatophore is *far* from the spermathecal aperture and lies between the bases of the ovipositor valves. In a male, dissected eight hours after mating, the spermatophore was *shifted* from the ovipositor valves to the interior of the genital cavity in the *vicinity* of the spermathecal aperture.' (Italics are mine). My observations on *P. americana* are in agreement with those of Zabinski since I also find that a spermatophore is attached from the very beginning to the spermathecal papilla. It appears that while Qadri was handling a just mated female, the soft, freshly laid spermatophore which was then loosely attached to the spermathecal papilla got displaced from its original position during dissection and remained attached to the ovipositors which lie just above and press against the posterior part of the spermatophore. It is, otherwise, not possible to explain the deposition of a spermatophore far away from the spermathecal aperture and also its shifting from the ovipositor valves to the interior of genital cavity in the vicinity of the spermathecal aperture as the time advances.

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SUMMARY.

Copulation in cockroaches usually takes place during night from March to September and lasts about an hour and a half. There is no courtship. A male becomes sexually excited when fully formed spermatophore is present in its ejaculatory duct and moves about in search of a female while the latter behaves indifferently and it does not try to mount the back of the male as mentioned by previous workers. There is no glandular secretion to affect sex-attraction. Copulation takes place only six days after the final moult in both the male and female. The males copulate several times at intervals of about seven days while the females less frequently and they can do so even a few hours after laying a cocoon.

During copulation the male and female remain joined together in a tail-to-tail position. The titillator of the male genitalia forces open the female gynatrium thus allowing the entry of the former into the latter. The pseudopenis actually enters the female gonopore and anchors the vulvular plates; the right phallomere works as the main clasping organ since its opposing lobes and the serrate lobe hold the ventral valvulae and their bases. The spermatophore is expelled out and is directly attached on to the ventrally projecting spermathecal papilla.

The secretion of the phallic gland is poured over the spermatophore during its attachment to the spermathecal papilla and hardens to form the outer wall of the former. The spermatophore remains attached to the papilla for about twenty-one hours during which the spermatic fluid within the spermatophore passes into the spermatheca.

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