

PSYCHE

Vol. 102

1995

No. 3-4

THE PROCESS OF INTROMISSION IN THE MEDITERRANEAN FRUIT FLY, *CERATITIS CAPITATA* (DIPTERA: TEPHRITIDIAE)

BY WILLIAM G. EBERHARD¹ AND FLORY PEREIRA²

ABSTRACT

The distiphallus of the male of *Ceratitis capitata* is folded back 180° onto the basiphallus during the early stages of intromission, and is then unfolded within the female. Repeated folding and unfolding may occur within the female. Two membranous sacs on the distiphallus are capable of rhythmic cycles of inflation and deflation. Inflations of the sac near the base of the distiphallus probably help propel the aedeagus deeper into the female, along with periodic stiffening of the basiphallus; inflation of the larger, distal sac may drive the genital rod (which does not transfer sperm) into the ventral receptacle.

INTRODUCTION

Millions of dollars are spent annually in attempts to control the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), but surprisingly little is known regarding many aspects of its basic reproductive biology. Male courtship behavior prior to mounting has been studied in detail (Feron, 1962; Prokopy and Hendrichs, 1979; Arita and Kaneshiro, 1985; Whittier, Kaneshiro, and Prescott, 1992; Briceño, Ramos, and Eberhard, in press), but the process of

¹Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

²Universidad de Costa Rica, Sede del Atlántico, Turrialba, Costa Rica

Manuscript received 2 November 1995.

intromission has received little attention. Intromission would appear to be a relatively difficult task in these flies, because of the female's long, thin, folded vagina, one of the morphological characteristics that permit insertion of the ovipositor (sensu Norrbom and Kim, 1988) deep in to plants. The male intromittent genitalia, or aedeagus, consist of a long, thin, flexible, more or less tubular basiphallus (about 40% of the male's body length), with a smaller, morphologically complex distiphallus at its tip. The process that allows such a long flexible structure to be threaded through the female's cloaca and vagina to her bursa remains unknown.

The pioneer work on genital structure and function in *C. capitata* is the detailed paper of Hanna (1938), and many statements in later publications (e.g., Feron, 1962) are apparently based on this account. Unfortunately, as noted by Griffiths (1972), it is often unclear which of Hanna's statements were based on direct observations, and which were only speculations. Some of his statements are clearly wrong and, as will be shown below, he clearly did not observe portions of the processes he reported. It is thus difficult to interpret Hanna's descriptions without further work.

There are several more recent studies of genitalic functional morphology. Monguira, Salom, and Muñoz (1983) and Valdez-Carrasco and Prado-Beltran (1990) gave descriptions of the female reproductive anatomy of *C. capitata*, and Camacho (1991) described details of the morphology of the spermatheca and the spermathecal duct near the spermatheca. Solinas and Nuzzaci (1984) presented a detailed account in another tephritid, *Bactrocera* (= *Dacus*) *oleae*, of the functional anatomy of female reproductive structures and their mesh with male genitalia after intromission was complete. The genitalic surstyli of male *C. capitata* were found to remain outside the female's body, functioning as clamps with which the male seizes and holds the aculeus of the female in a strong grip (Eberhard and Pereira, 1993). The observations reported here concern the portions of the male's genitalia that enter the female, and the roles they may play in the process of intromission. Sperm transfer will be described elsewhere.

METHODS

All flies were obtained from mass rearing facilities in San José, Costa Rica. The flies were quite tame, and pairs early in copulation

were gently moved from a common cage into individual containers with little or no apparent disturbance. Copulating pairs were immobilized nearly instantaneously with a freezing spray (ethyl chloride) and then fixed in 70% ethyl alcohol. Whole mount preparations of the genital tracts of coupled pairs were examined with the light microscope. Some specimens were soaked briefly in lactophenol before dissection. By sacrificing pairs after known periods of genitalic contact, it was possible to deduce the order of some events during copulation. Specimens were prepared for scanning microscopy and sectioning using standard procedures. The genitalia of some males were pulled forcefully from the female during copulation and immediately fixed in 70% ethanol.

Direct observations of the movements of male genitalia of living flies were made under a dissecting microscope by teasing the aedeagus from its resting place on the abdomen of the male after he had been decapitated to eliminate central control and mounted on a pin. Video recordings of behavior during copulation were made using a National Novicom camera (30 images/sec) with +6 lenses.

RESULTS

A. Basic morphology and movements

The following descriptions emphasize only those parts of male and female morphology that are critical in the process of intromission. Names for external structures are those of Norrbom and Kim (1988).

I. Female

The apical portion of the ovipositor, the aculeus, is a long, curved, apically pointed plate, that extends posteriorly slightly beyond a pair of slightly shorter, smaller ventral plates (8th sternites). The cloaca is located just anterior to the posterior edges of the sternites, and thus lies slightly farther anterior to the posterior tip of the aculeus. There are muscles joining the basal but not the apical portions of the 8th sternites to the aculeus (Valdez-Carrasco and Prado-Beltran 1990), so the female apparently cannot squeeze shut her cloacal opening.

Moving anteriorly, the tubular eversible membrane is joined at its posterior margin with the anterior end of the aculeus, and at its

anterior margin with the posterior edge of the conical sytergosternite 7. When at rest, the ovipositor telescopes, and the aculeus and the eversible membrane lie largely or completely within the sytergosternite 7. Just prior to intromission, the female extends the ovipositor so that the apical portion of the aculeus is exposed, and the male clamps the tip of the aculeus with his surstyli (Eberhard and Pereira, 1993).

Internally, the posterior portion of the vagina loops back on itself when the ovipositor is at rest, and straightens when the ovipositor is extended. A pair of more or less plate-like sclerotized structures (the "stigma" – Fig. 1) are apparently embedded in the wall of the vagina near the posterior end of a small expansion at the anterior end of the vagina (the bursa, or the "insemination pocket" of Solinas and Nuzzaci, 1984) (Figs. 1, 12). Projecting anteriorly from the upper end of the bursa is the ventral receptacle ("fertilization chamber" of Solinas and Nuzzaci, 1984), a smaller, blind-ended, cylindrical structure whose inner-most portion is expanded and covered with smooth, rounded projections (Figs. 1, 2). At the tip of the ventral receptacle is a small, heavily sclerotized extension about the size of a single rounded projection (Fig. 2).

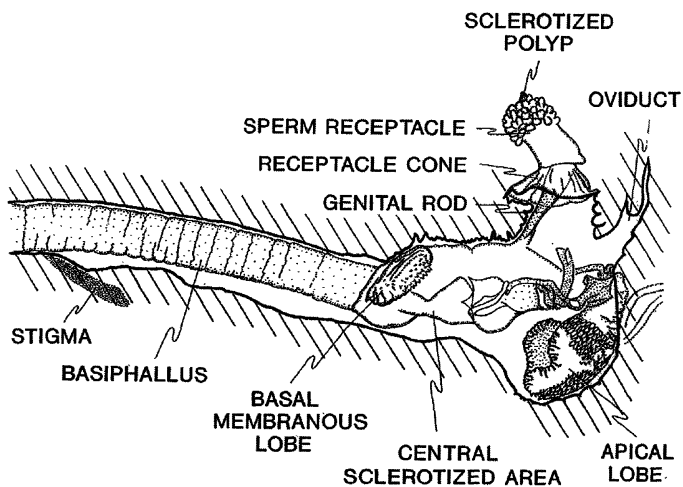


Fig. 1. Diagrammatic cutaway view of positions of male genitalic structures in the female bursa when the male genital rod is inserted in the ventral receptacle of the female (see also Fig. 12).

The wall of the bursa is more sclerotized in the area surrounding the entrance to the ventral receptacle, and has a truncated conical shape (the "receptacle cone" – Figs. 1, 2). The two spermathecal ducts originate near the edge of the receptacle cone. They are long and thin-walled, except at their distal ends where there is a short

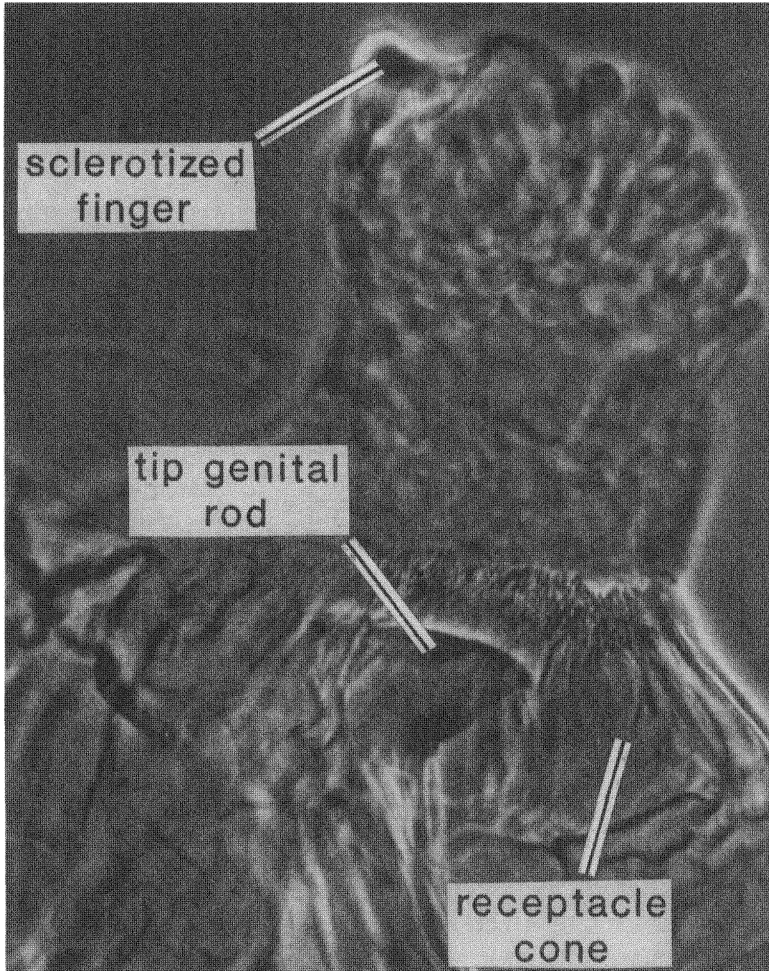


Fig. 2. The ventral receptacle of a female and the sclerotized portion of the vaginal wall (receptacle cone) near its opening, into which projects the tip of the male's genital rod. There are many finger-like projections of the distal portion of the receptacle, and a single sclerotized projection at the tip.

section of strong muscles near the entrance of each teardrop-shaped, highly sclerotized spermatheca (Monguira et al., 1983; Camacho, 1991).

II. Male

Tergite 9 (epiandrium) of the male abdomen is U-shaped, and ventrally forms two pairs of closely associated surstyli that clasp the aculeus when copulation begins. The long aedeagus (about 40% as long as the male's total length) arises from the ventral surface of the abdomen just anterior to the surstyli. The complex distiphallus comprises the tip of the aedeagus; the rest of the aedeagus is the more or less cylindrical basiphallus. Nearly all of the dorsal side of the basiphallus (posterior side of Hanna, 1938) is strengthened by a pair of chitinous strips, while the ventral side is a stiff membrane, with a series of transverse folds (e.g., Figs. 1, 10).

At rest the basiphallus curls spontaneously toward its membranous side, and is kept between folds of the intersegmental membrane between abdominal tergite 5 and the postabdomen (segments 6-8). When the aedeagus of a live decapitated male was teased free, the basiphallus repeatedly straightened partially in brief rhythmic movements about twice/sec.; extensions occurred in synchrony with inflations of the basal sac of the distiphallus (below). The ejaculatory apodeme and sperm sac ("erecting and pumping organ" of Hanna, 1938) may produce increases in fluid pressure within the aedeagus that result in this and other movements of the aedeagus.

The distiphallus at the tip of the aedeagus is complex. At its basal end is a dorsal, basal lobe or eversible sac, with small, conical, scale-like teeth covering part of its surface (Figs. 3, 8) (the "oval bladder" of Hanna, 1938). When the distiphallus was touched persistently with the tip of a pin, the basal sac repeatedly expanded and collapsed. Typical frequencies averaged about two expansions/sec, but there was much variation. As the sac was everted, the direction it projected changed, causing it to move rearward, from a distal to a basal orientation (Fig. 5). Some eversions were "double," with only a partial collapse followed immediately by a second eversion. Eversion of the basal sac was always accompanied by a ventral flexion of the rest of the distiphallus in the region near the base of the sac (upper arrow in Fig. 5).

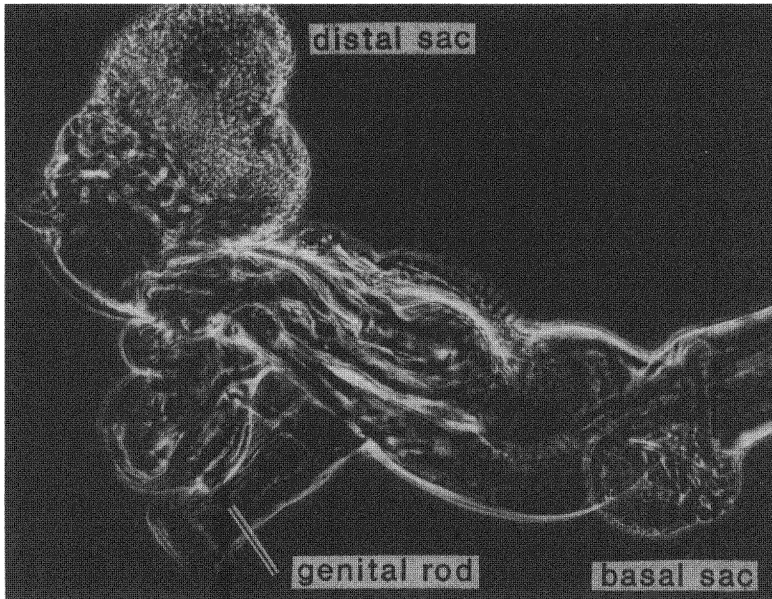


Fig. 3. The distiphallus of a male *Ceratitidis capitata*.

Distal to the basal sac is the exceedingly complex central portion of the distiphallus (Fig. 3), covered by a relatively smooth, featureless membrane (Fig. 4). A single rod-like sclerotized structure (the "genital rod" of Hanna, 1938) extends dorsally from the central sclerotized area (Figs. 1, 3, 4). The tip of the rod flares, somewhat like the bell of a trumpet, and is more flexible than the rest of the rod (compare Figs. 1–4 and 13). The rod is apparently hollow (Fig. 3), and its tip is covered with a featureless membrane (Fig. 6).

Near the tip of the distiphallus is a large distal lobe or sac (the "toothed bladder" of Hanna, 1938) (Figs. 3, 4). The conical teeth that are especially prominent on its ventral and lateral surfaces are similar to but generally larger than those on the basal sac. The distal sac was always partially inflated both in slide preparations of copulating pairs and in living males (contrary to the description of Hanna, 1938). In living flies the sac repeatedly inflated and

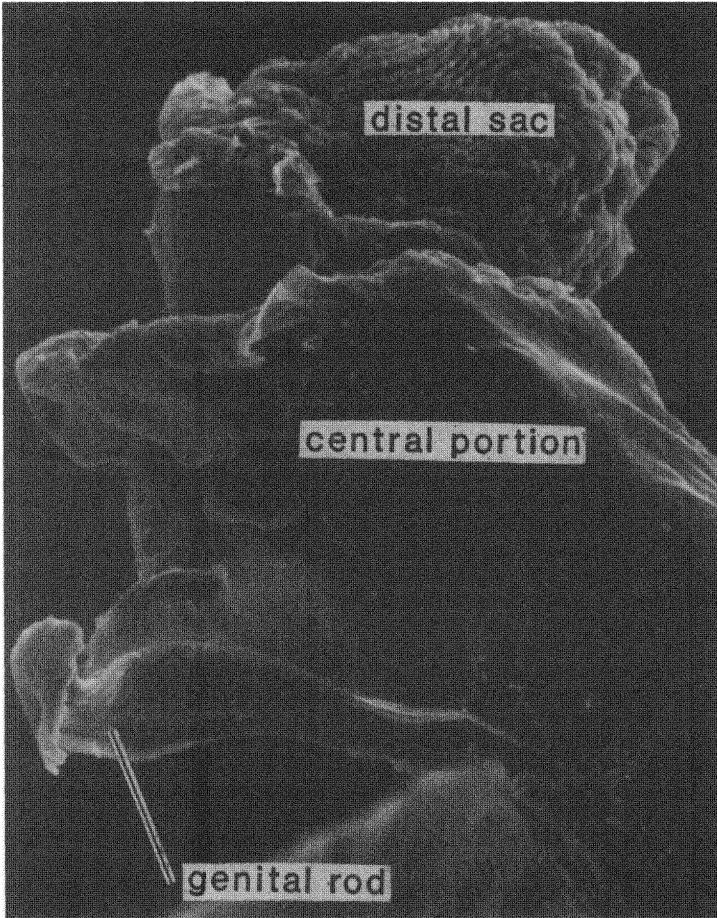


Fig. 4. Scanning electron micrograph of the distiphallus of a male *Ceratitidis capitata*.

deflated. Maximum inflation increased the diameter an estimated 50-100% over that when the sac was minimally inflated.

Inflation of the distal sac caused it to expand mostly in the ventral direction (away from the central portion of the distiphallus) rather than basally or distally. Inflation of the distal sac was not synchronous or coordinated in any obvious way with that of the basal sac. The two sacs are apparently hydraulically independent. When pricked with a pin, the distal sac of a living male deflated

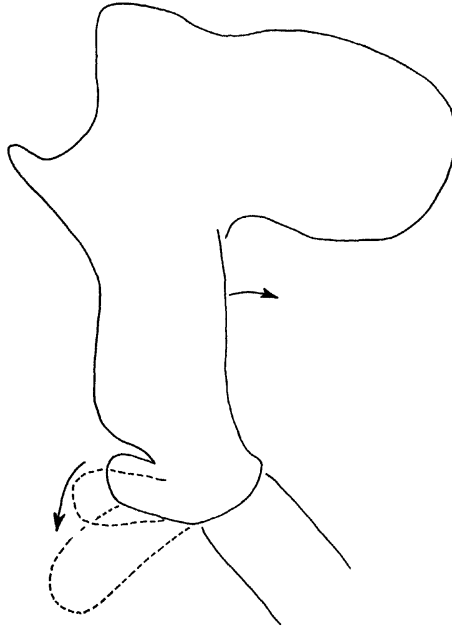


Fig. 5. Diagrammatic representation of the movements of the basal sac of the distiphallus when it inflates (dotted lines). As the sac inflates the distiphallus moves in the opposite direction (arrow).

immediately and permanently (and much more completely than in any other preparation), and released a drop of fluid. The basal sac continued to inflate and deflate as before.

No obvious openings through which sperm could emerge from the distiphallus were seen in either light microscope or SEM preparations. There were sperm on the surface of the distiphallus in two SEM preparations of male genitalia that had been pulled from females after about 30 min of copulation. In both cases the sperm were in the same area, near the base of the genital rod, where multiple fine folds (Figs. 6, 7) may have concealed opening(s) from which sperm could emerge.

No structures were observed that even remotely resembled several of those described by Hanna (1938), including the heavily sclerotized ductus ejaculatorius, the valve, the large triangular sclerite to keep the genital rod in place, and the relieving bladder.

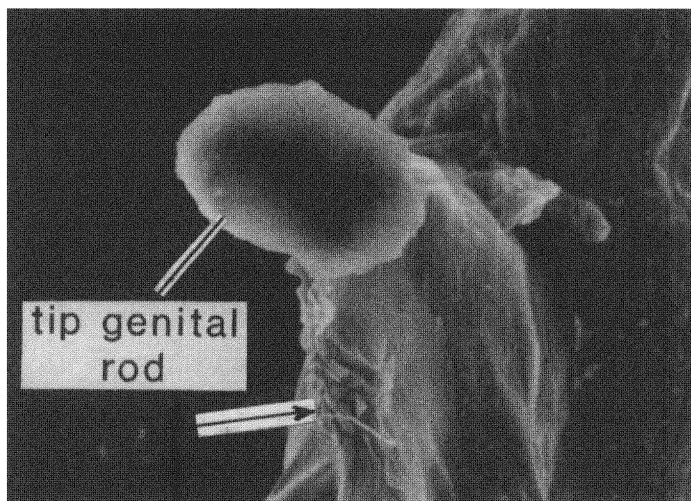


Fig. 6. Scanning electron micrograph of the tip of the genital rod, showing the membrane covering its tip. The arrow indicates the area where sperm may emerge (see Fig. 7).

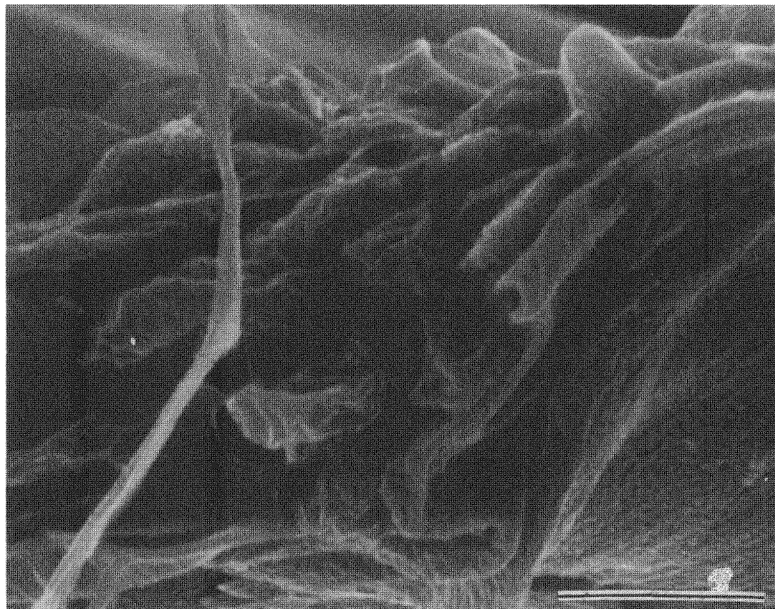


Fig. 7. Scanning electron micrograph of the distiphallus near the base of the genital rod, showing possible apertures through which sperm may emerge.

B. Behavior of genitalia during intromission

Following elaborate courtship behavior (e.g., Feron, 1962; Briceño et al., in press), the male mounted the female, and in successful pairings seized the female aculeus with his surstyli when she extended it (Eberhard and Pereira, 1993; Headrick and Goeden, 1994). In two pairs observed dorsally under a dissecting microscope at the moment the exposed aculeus was clamped, the male's distiphallus was in clear view as the female's ovipositor was extended. The distiphallus quickly flipped ventrally, where it was lost from sight (Eberhard and Pereira, 1993). Presumably it was positioned near the tip of the aculeus, as it was in this position in three of the four males frozen 0.5-2.0 min after pairing had begun and in which the male separated from the female after being placed in alcohol, indicating that intromission had not yet occurred (Fig. 8).

Typically the male then appeared to pull posteriorly repeatedly, so that the female's ovipositor was further extended. Soon after achieving intromission the female's ovipositor was extended until the eversible membrane had entirely emerged from syntergosternite 7 and the aculeus had nearly completely emerged from the eversible membrane. Probably this extension caused the female's normally S-shaped vagina to straighten, and may have facilitated the movement of the male's aedeagus to her bursa. The male also made repeated pushing or thrusting movements with his abdomen that caused the female ovipositor to fold or buckle briefly. The tibiae of the male's middle and hind legs were often crossed and pressed against the ventral surface of the syntergosternite during these movements.

An alternative interpretation, that the female actively extends her ovipositor rather than having it pulled by the male, cannot be discarded with complete confidence, but pulling seems more likely for two reasons. Observations under a dissecting microscope showed that in some cases the anterior portion of the female's abdomen was also extended to about twice its resting length, implying that the male had pulled forcefully. In addition, when a male mounted a female but failed to clamp her aculeus, he often performed repeated "pulling" movements by raising the tip of his abdomen and moving it rearward (see also Eberhard and Pereira, 1993).

Eventually (after about 1-10 min) the aculeus moved anteriorly and was partially engulfed by the tubular eversible membrane; the

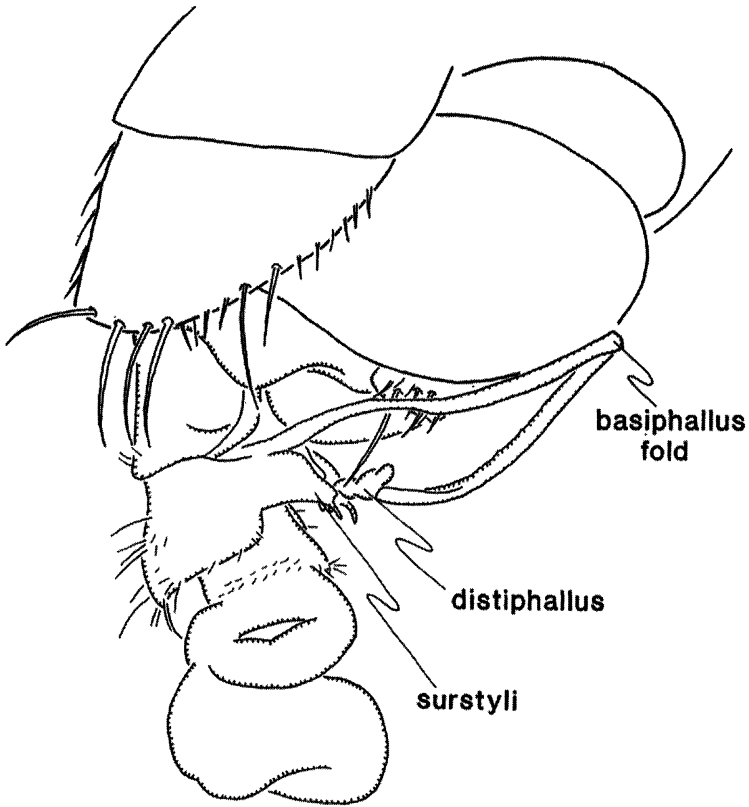


Fig. 8. Posterior portion of the abdomen of a male which was frozen 30 sec after he established genital contact with a female. The male fell free of the female, indicating that he had not introduced his aedeagus in the female's vagina or had achieved only very shallow intromission. His basiphallus was sharply bent, and the distiphallus (not folded back on the basiphallus—compare with Fig. 10) was positioned between the surstyli, near the site of the genital opening of the female when her aculeus was held by the surstyli.

eversible membrane remained completely outside sytergosternite 7. This was the position during most of copulation. The male often made long series of "thrusting" movements of various rhythms and magnitudes (Fig. 9). With each "thrust" the female aculeus moved anteriorly, deeper into the tubular eversible membrane. In at least some pairs it appeared (from a slight increase in the degree of extension of the male's abdomen as the aculeus returned to its

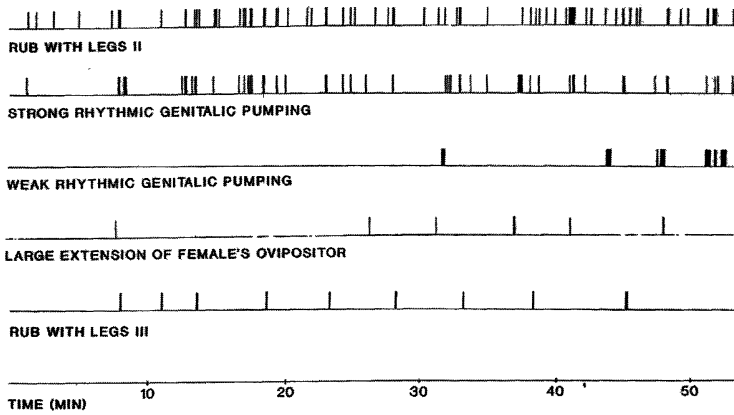


Fig. 9. Male behavior during a copulation lasting 54 min. The widths of the bars indicate the duration of different activities.

original position) that the “thrusts” were actually brief, rhythmic *pulls* on the aculeus, and that after each pull the aculeus was retracted by the female(?) back into her body. Occasionally the male pulled forcefully and extended her ovipositor briefly (Fig. 9).

The internal events associated with intromission were deduced from 33 different pairs frozen at different times after original genitalic contact in which the aedeagus was at least partially inserted in the female’s vagina: 2 after 30 sec; 1 after 1 min; 8 after 2 min; 8 after 3 min; 6 after 5 min; and 8 after 10 min.

Penetration did not follow a strict timetable. The genitalia of three males frozen after 2 min had reached the inner end of the bursa, while those of another male were still short of the stigma after ten min. In eight cases the distiphallus was folded back on the basiphallus (Fig. 10). In three of the pairs with the distiphallus folded back the male’s genitalia were still substantially short of the stigma, while in three others they had passed the stigma, and were within the bursa. In one case the basiphallus was short of the stigma and apparently in the process of unfolding (Fig. 11).

In all eight cases in which the male genitalia was not folded back and had not entered the bursa, the distal sac of the distiphallus was flexed anteriorly, so that it was the leading portion of the male’s genitalia (Fig. 12, Left).

In all 10 cases in which the male's distiphallus was not folded back and had not passed the stigma, the genital rod was pressed against the side of the central portion of the distiphallus (as in Fig. 12, Left). In contrast, in 12 of the 16 cases in which the male's genitalia had entered the bursa, the genital rod was flexed at least 30° from the axis of the central portion (Fig. 12, Right); in 3 of these pairs its tip was within the ventral receptacle (Fig. 1). The soft tip of the genital rod apparently folded back on itself as the rod entered the receptacle (Fig. 13).

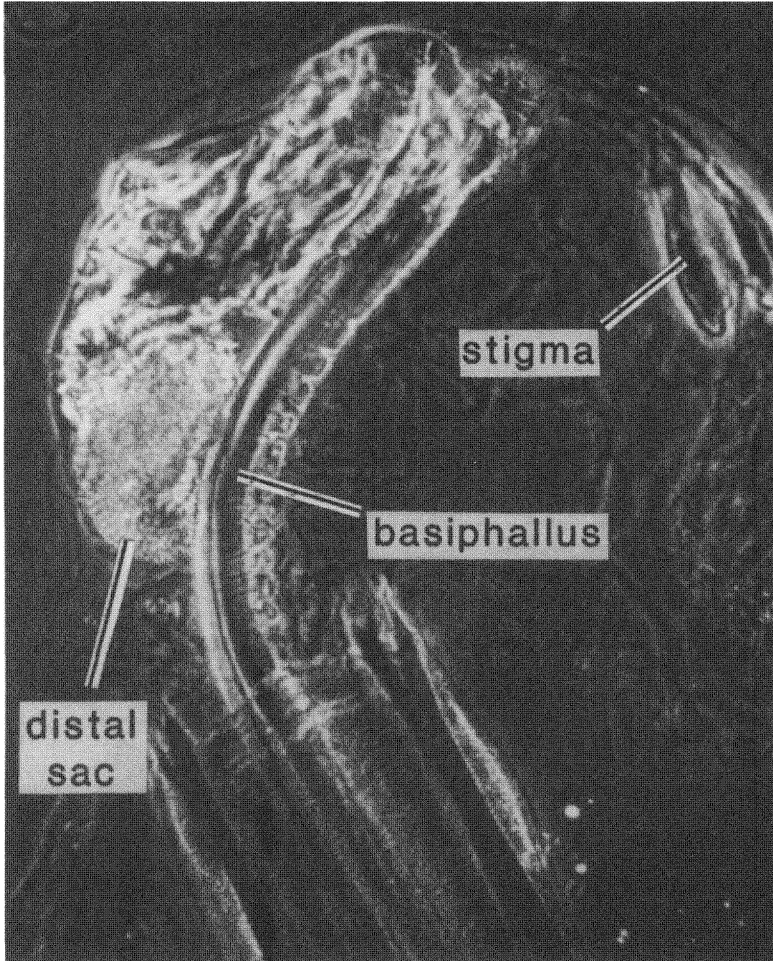


Fig. 10. Wholemount of the aedeagus of a male in the vagina of a female posterior to the stigma after 2 min of genital contact. The male's distiphallus is folded back 180° to lie along the terminal portion of the basiphallus.

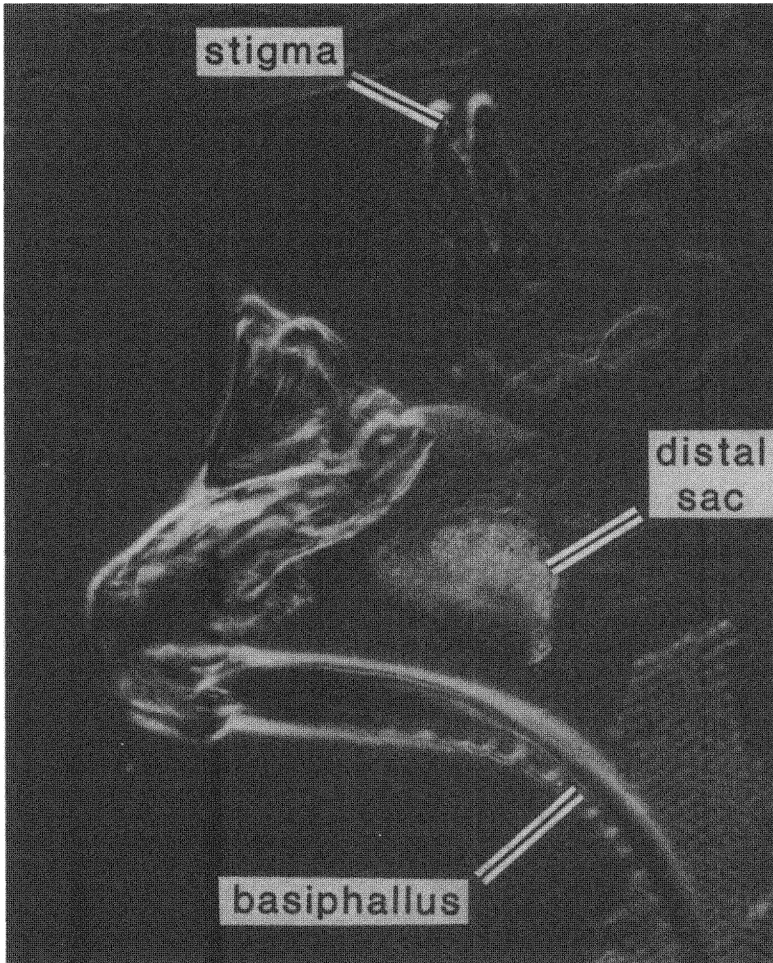
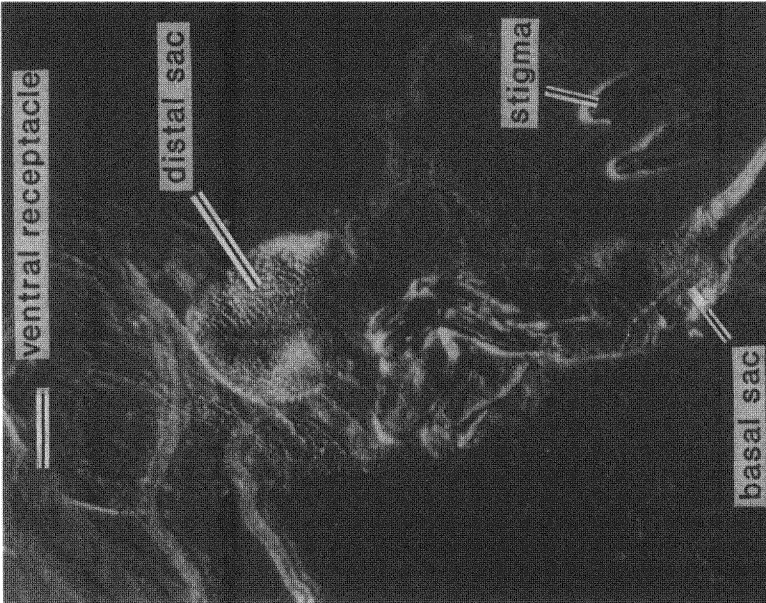
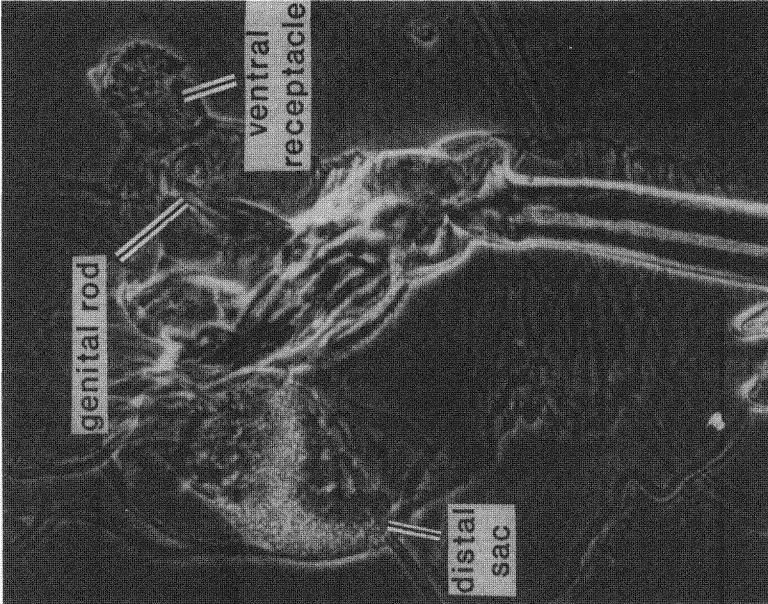


Fig. 11. Wholemount of male genitalia in the vagina posterior to the stigma after 2 min of copulation. The distiphallus appears to be in the process of unfolding.

Fig. 12. Positions of the male aedeagus in the female's vagina. Left. The distiphallus is just passing the stigma, with the genital rod pressed against the central portion of the distiphallus, and the distal sac positioned so that it penetrates the female most deeply. Right. The distiphallus is deeper in the female, at the anterior end of the bursa. The tip of the genital rod is within the receptacle cone, and the distal sac presses against the opposite wall.



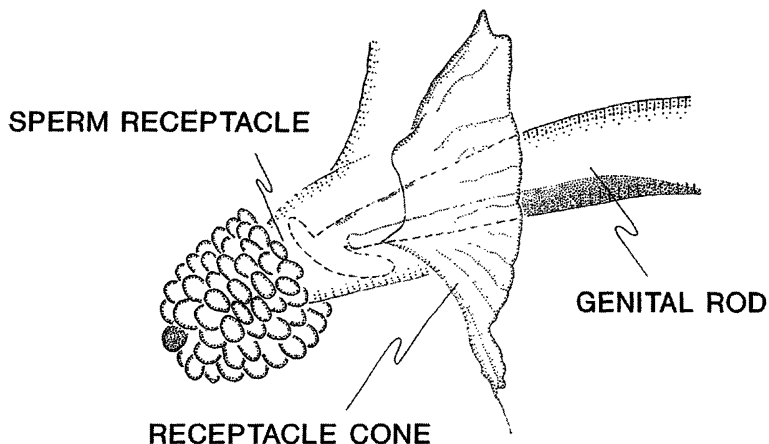


Fig. 13. Diagrammatic view of the male genital rod inserted into the female's ventral receptacle. Note the distortion of the tip of the rod (compare with Figs. 1-4).

DISCUSSION

A tentative sequence of the events in a successful intromission can be deduced from these observations and previous publications. The male first clamps the female aculeus with his surstyli. The male's median prensisetae are inserted between the lateral edges of the female's aculeus and her 8th sternites (Eberhard and Pereira, 1993), probably thereby lifting the distal portions of the sternites from the aculeus and exposing the cloacal opening for insertion of the aedeagus. The male also apparently extends the female's ovipositor by pulling the aculeus posteriorly. While the female's ovipositor is extended, the male flips his aedeagus ventrally. The basiphallus is folded sharply (Fig. 8), perhaps by catching the distiphallus between his surstyli or on the aculeus. Probably the next step is the insertion of the folded distiphallus and the tip of the basiphallus into the female's cloacal opening, but the details of this process are not clear.

The distiphallus is subsequently unfolded after entering the female. Unfolding occurs when the male genitalia have still not reached the bursa, and it is possible that there are several cycles of folding and unfolding as the male's genitalia move deeper into the female. Unfolding may be accompanied by the male pulling his

basiphallus posteriorly, and refolding may occur as he thrusts it anteriorly. The genital rod is pressed against the central portion of the distiphallus, and the distal sac is oriented directly anteriorly in the female. The movement of the male's genitalia deeper into the female is probably brought about by a combination of periodic stiffening and straightening of the basiphallus, inflations of the basal sac (Fig. 5), and pulls with the surstyli on the aculeus that extend the ovipositor. The teeth on the basal sac may reduce slippage as the distiphallus is pushed up the vagina.

The deepest penetration of the male genitalia is to the anterior end of the bursa. Here various parts of the distiphallus are reoriented. The genital rod folds away from the central portion, and is at least sometimes inserted into the ventral receptacle. The receptacle cone in the bursal lining may serve to guide the rod into the receptacle. The distal sac is expanded in the opposite direction, and its expansion may drive the rod into the ventral receptacle. The apical surface of the central portion of the distiphallus becomes the leading edge of the male's genitalia, and presses against the innermost wall of the bursa.

Several of the genitalic movements seen in living males permit deductions regarding how male genitalia move within the female. Extensions of the basal sac of the distiphallus and the simultaneous flexions of the distiphallus (Fig. 5) seem designed to propel the unfolded distiphallus deeper into the female. The partial straightening movements of the basiphallus temporarily stiffen the basiphallus, and presumably make it easier for the male to push it deeper into the female. The expansions of the distal sac, on the other hand, do not have any obvious relation to deeper penetration of the aedeagus into the female. Once the distiphallus has reached the inner end of the bursa, expansion of the distal sac may drive the genital rod into the receptacle cone and eventually into the ventral receptacle itself. Judging by the distortion of the tip of the rod as it enters the ventral receptacle, appreciable force may be involved. Use of inflatable lobes or sacs to drive genitalic structures into the female is also thought to occur in other insects (Siva-Jothy, 1988).

Our observations of sperm are only very fragmentary, and further study is required. It is worth noting, however, that when the male genital rod is inserted in the ventral receptacle, the area near the base of the rod tentatively identified as the site from which

sperm emerge, probably lies at or very near both the openings of the female's spermathecal ducts and the ventral receptacle.

It is difficult to reconcile some of our observations with those of Hanna (1938). In particular, it is nearly certain that Hanna misdescribed intromission. His claim that the "aedeagus" (=basiphallus) "uncoils and becomes rigid, then ... is introduced into the genital pore of the female and pushed into the vaginal duct ..." (Hanna, 1938: 46) is not credible. Because of the length of the basiphallus, such a maneuver would have to begin with the tip of the female's ovipositor located almost an entire abdomen's length from the tip of the male's abdomen. Direct observations of copulating flies, and of specimens frozen in copulation showed that, on the contrary, the tip of the male's abdomen is always close to the tip of the aculeus.

Some of the observations reported here may be of general significance for other flies. The apparent need for the female ovipositor to be extended if the male is to intromit successfully has also been noted in the tephritids *Rhagoletis mendax* (Smith and Prokopy, 1982) and *Procecidochares stonei* (Green, Headrick and Goeden, 1993), and in the latter the male surstyli apparently hold the aculeus. The male of *Musca domestica* also pulls on the ovipositor and extends it early in copulation (Tobin and Stoffolano, 1973). Caution must be exercised in generalizing however, as illustrated by the finding that the similarly elongate male genitalia of the otitid *Tetanops myopaeformis* do not simply extend along the female vagina, but are coiled in her bursa (Klostermeyer and Anderson, 1976). Basic aspects of genitalic coupling varied even among different species of the sphaerocerid genus *Coproica* (Lachmann, 1994), and the sepsid genus *Archisepsis* (W. Eberhard, in prep.).

ACKNOWLEDGEMENTS

We thank Rafael Lucas Rodriguez for analyses of videos, Hernan Camacho for providing flies, and Al Norrbom for help with morphological terminology. Financial support was provided by the Vicerrectoría de Investigación of the Universidad de Costa Rica, the Smithsonian Tropical Research Institute, and the International Atomic Energy Agency.

LITERATURE CITED

- Arita, L., and K. Kaneshiro. 1985. The dynamics of the lek system and mating success in males of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). Proc. Haw. Ent. Soc. 25:39–47.
- Briceño, R.D., D. Ramos, and W.G. Eberhard. 1996. Courtship behavior of male *Ceratitis capitata* (Diptera: Tephritidae) in captivity. Fla. Ent. 79(2):130–143.
- Camacho, H. 1991. Transferencia de espermatozoides en la mosca del Mediterráneo, *Ceratitis capitata* (Diptera: Tephritidae). Masters thesis, Univ. de Costa Rica.
- Eberhard, W.G., and F. Pereira. 1993. Functions of the male genitalic surstyli in the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). J. Kans. Entomol. Soc. 66:427–433.
- Feron, M. 1962. L'instinct de reproduction chez la mouche Méditerranéenne des fruits *Ceratitis capitata* Wied. (Diptera. Trypetidae). Comportement sexual.—Comportement de ponte. Rev. Pat. Veg. Ent. Veg. 41:1–129.
- Green, J.F., D.H. Headrick, and R.D. Goeden. 1993. Life history and description of immature stages of *Procecidochares stonei* Blanc & Foote on *Viguiera* spp. in southern California (Diptera: Tephritidae). Pan-Pac. Entomol. 69:18–32.
- Griffiths, G.C.D. 1972. The phylogenetic classification of Diptera Cyclorrhapha with special reference to the structure of the male postabdomen. Dr. W. Junk, the Hague 1–340 p.
- Hanna, A.D. 1938. Studies on the Mediterranean fruit-fly: *Ceratitis capitata* Wied. I. The structure and operation of the reproductive organs. Bull. Soc. Fouad Ier Entomol. 1938:39–59.
- Headrick, D.H., and R.D. Goeden. 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1:194–252.
- Klostermeyer, L.E., and A.W. Anderson. 1976. Anatomy, histology, and post-larval development of the reproductive system of the sugarbeet root maggot. Ann. Entomol. Soc. Am. 69:625–631.
- Lachmann, A. 1994. Struktur und Evolution der Fortpflanzungorgane von fünf *Coproica*—Arten (Diptera, Sphaeroceridae). Ph.D. Thesis, Freie Univer. Berlin, Germany.
- Monguira, M.L., F. Salom, and M. Muñoz. 1983. Estudio morfológico del aparato reproductor femenino de *Ceratitis capitata* Wied. (Dipt.: Tephritidae). Bol. Serv. Plagas 9:31–44.
- Norrbom, A.L., and K.C. Kim. 1988. Revision of the *schausi* group of *Anastrepha* Schiner (Diptera: Tephritidae), with a discussion of the terminology of the female terminalia in the Tephritoidea. Ann. Entomol. Soc. Am. 81:164–173.
- Prokopy, R.J., and J. Hendrichs. 1979. Mating behavior of *Ceratitis capitata* on a field-caged host tree. Ann. Ent. Soc. Am. 72:642–648.
- Siva-Jothy, M. 1988. Sperm “repositioning” in *Crocothemis erythraea*, a libellulid dragonfly with a brief copulation. J. Ins. Behav. 1:235–245.
- Smith, D.C., and R. Prokopy. 1982. Mating behavior of *Rhagoletis mendax* (Diptera: Tephritidae) flies in nature. Ann. Entomol. Soc. Am. 75:388–392.
- Solinas, M. and G. Nuzzaci. 1984. Functional anatomy of *Dacus olea* Gmel. female genitalia in relation to insemination and fertilization processes. Entomologica (Bari) 19:135–165.

- Tobin, E.N., and J.G. Stoffolano. 1973. The courtship of *Musca* species found in North America. 1. The house fly, *Musca domestica*. Ann. Ent. Soc. Am. 66:1249–1257.
- Valdez-Carrasco, J., and E. Prado-Beltran. 1990. Esqueleto y musculatura de la mosca del Mediterraneo, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae). Folia Ent. Mex. 80:59–225.
- Whittier, T.S., K.Y. Kaneshiro, and L.D. Prescott. 1992. Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. Ann. Ent. Soc. Am. 85:214–218.



Hindawi

Submit your manuscripts at
<http://www.hindawi.com>

