Role of the petasma and appendices masculinae during copulation and insemination in the penaeoid shrimp, *Sicyonia dorsalis* (Crustacea: Decapoda: Dendrobranchiata)

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Summary

The role of presumed male gonopods in the insemination of females was investigated in the penaeoid shrimp *Sicyonia dorsalis*. Males with partially ablated petasmata or with ablated appendices masculinae did not copulate with females, while control males with exopods removed from the third pleopods copulated frequently and successfully inseminated females. However, males with petasmata altered by blockages at the tip or at the base did copulate with females but were unable to inseminate them. The hypothesis that the petasma of *Sicyonia* is a sperm injection device is rejected. Evidence against this hypothesis includes the structure of the gonopods, the position of the male at right angles below the female during copulation, the brevity of copulation, the frequency of copulation during normal matings, and the ability of males to inseminate only the spermatheca on one side per successful copulation. It is hypothesized that the male uses the petasma, supported by the endopods of the second pleopods, to hook onto the female thelycum, adjusting position so that one erect genital papilla directly injects sperm mass into the aperture of one of the paired spermathecae. It is suggested that female selection on male petasma structure and use has resulted in the complex form of the petasma, rather than a purely mechanical selection for an efficient sperm injection device.

Key words: Copulation, gonopods, insemination, petasma, shrimp

Introduction

In many decapod crustacean species, the inner rami or endopods of the first two pleopods of males are slightly to highly modified from the primitive oar-like natatory form (Bauer, 1986). Located just behind the gonopores, these modified endopods are usually presumed to serve as gonopods in insemination of the female. Experimental studies on two caridean species have demonstrated a role of relatively simple gonopods in the transfer of an adhesive spermatophore during a brief copulation (Bauer, 1976; Berg and Sandifer, 1984). In several decapod species, complex

male gonopods and copulation with a relatively long duration (several minutes to hours) are associated. In a few such species, the direct role of the gonopods in transferring sperm to the female has been described and verified (crayfish *Orconectes limosus*, Andrews, 1911; various brachyurans crabs, Cronin, 1947; Ryan, 1967; Hartnoll, 1969, 1975).

In penaeoid shrimp, the endopods of pleopods 1 and 2 of males are among the most highly modified of any decapod group. The endopods of pleopods 1 join by coupling hooks (cincinnuli) in adult males to form the petasma, highly variable in form and complexity

among penaeoid species. A process, the appendix masculina, is often borne on the endopod of pleopod 2. The petasmata and appendices masculinae have been described in considerable detail because of their importance in penaeoid systematics (e.g., Burkenroad, 1934; Kubo, 1949; Pérez Farfante, 1969; Pérez Farfante, 1985; Bauer, 1991). However, the role of these presumed gonopods of penaeoid males in insemination of females has never been demonstrated (Bauer, 1991). Burkenroad (1934) made detailed hypotheses, based on morphology, about how the petasma might function as a spermatophore grasper in *Penaeus setiferus* or an injection device in *Trachypenaeus similis*. However, these hypotheses have never been tested with observations on or experiments with living animals. Pérez Farfante (1975, 1982) questioned the direct role of the petasma in spermatophore transfer in *Penaeus* (*Litopenaeus*) spp., *Parapenaeus*, and other penaeoid species. Brinton (1975, quoted in Brinton, 1978) suggested that the petasmata of euphausiids and penaeideans might be used as sensory or stimulatory devices during copulation.

The purpose of the present study was to determine if and how the petasma and appendices masculinae of males function during copulation in a penaeoid shrimp, *Sicyonia dorsalis*. Mating behavior, copulation, and variation in insemination success by males have been described in *S. dorsalis* by Bauer (1992, 1996). This previous work has shown that males of *Sicyonia* spp. readily copulate in the laboratory with females which have spermathecae (seminal receptacles) emptied by molting. In this report, alternative hypotheses on the mode of operation of the petasma and appendices masculinae in insemination have been tested. One hypothesis was that the petasma, aided by the appendices masculinae, acts as a sperm injection device. Alternately, it was proposed that the petasma serves in attachment to and/or stimulation of the female during copulation and insemination.

Materials and Methods

Specimens of *S. dorsalis* were collected by otter trawl in Mississippi Sound near Horn Island (30°15′N, 88°45′W) and the Pascagoula Ship Channel (30°20′N, 88°32′W), Mississippi, on several trips during 1991–1993, during the late summer through spring. Shrimps used in experiments were maintained on recirculating water tables with water temperatures from 22–25°C, 30 ppt salinity, and a light-dark cycle of 14h:10h. Preserved specimens were initially fixed in 10–15% seawater formalin, and later transferred to 70% ethanol for permanent storage after a 1–2 h wash in running water and a series of ethanol changes of 25%, 35%, and 50%. Material used for scanning electron microscopy was taken through a graduated series from 70% to 100% ethanol, critical point dried in carbon dioxide, and sputter-coated with a 10–20 nm thickness of gold-palladium. Terminology for the structure of male and female genitalia of *Sicyonia* follows that of Pérez Farfante (1985), except for the shortening (for brevity in this report) of the following terms: "projection of dorsolateral lobule"="dorsolateral projection"; "projection of ventrolateral lobule"="ventrolateral projection." When preserved specimens are viewed under a microscope, the endopods of the anterior pleopods lie horizontally against the body, thus giving rise to the traditional usage in taxonomic descriptions of "dorsal" and "ventral" sides of the petasma and endopods of the second pleopods. I have indicated in parentheses in the text that the "dorsal" and "ventral" sides of these structures correspond to their "anterior" and "posterior" sides, respectively, when the pleopods are moved to a vertical position in living animals.

Observations are reported on the histology of the male duct of *S. brevirostris* of specimens collected in 1987 from the northern Gulf of Mexico (details of fixation, infiltration, sectioning, and staining as for *Trachypenaeus* reported in Bauer and Lin, 1993).

Emission of contents from ejaculatory ducts of males was produced by compressing the posterior of the cephalothorax of living males held in dishes with seawater. The ejaculated contents were placed on slides for observation and photography using transmitted light through a compound microscope.

Mating experiments designed to test hypotheses about petasma and appendix masculina function were composed of five male treatments: (1) control: exopods of third pleopods ablated with microdissection scissors; (2) petasma: distal half to complete petasma ablated; (3) appendices masculinae: endopods (with appendices masculinae) of second pleopods ablated; (4) "distal block": ventral (posterior) side of dorsolateral projections (and space between) coated with cyanoacrylate glue; (5) "basal block": daub of cyanoacrylate glue placed in the space between the basal edges of the ventrolateral lobules, ventral (posterior) side of petasma. To reduce stress during ablations or application of cyanoacrylate glue, males were chilled to 8–12°C from ambient temperature to depress activity. After such treatment, males were allowed to recuperate at least one and usually several days before use in mating experiments. Females used in experiments were maintained in individual containers after collection from the field and checked daily for molting, after which spermathecae are empty and

females are receptive to mating (Bauer, 1991, 1992, 1996). In experimental replicates, two males of the same treatment were placed with a postmolt (1–5 days) female in a recirculating 38 l (10 gal) aquaria with a sand substrate, and ambient conditions as described above for live specimens.

Activities were recorded for 2 days with a time lapse videorecorder system using a low light, infrared sensitive surveillance video camera with an 8.0 or 12.5 mm lens, with recordings made at 24 h (five pictures/s) speed. Day lighting was provided by overhead fluorescent lamps while night observations were illuminated by infrared lamps (880 nm). After the observation period, males and the female were removed, anesthetized by chilling, and preserved. Presence or absence of insemination of the female was determined by dissection, and males were rechecked to observe the state of ablations or cyanoacrylate blockages. Videotapes were viewed to record the number and kind of mating interactions. Median duration of copulation for each replicate was measured from 11 copulations chosen at random; when copulations were less than 11, the duration of all were measured.

Results

Male and female genitalia

The petasma and appendices masculinae of the male are held somewhat near or against the ventral surface of the body (Fig. 1A,B) when pleopods 1 and 2 are not in use in swimming or burrowing. The endopods of the first pleopods are joined dorsally (anteriorly) by stalked coupling hooks, the cincinnuli, to form the petasma (Fig. 1C,D). The lateral lobules of the petasmal endopods are reflexed ventrally (posteriorly) against and fused with the rest of the petasma (Fig. 1E). However, the median edge of each of these ventrolateral lobules projects mesially so that a U-shaped sulcus or groove is formed proximally to distally along their length. Farthest apart proximally, the ventrolateral lobules approach each other distally (Fig. 1E), so that a semi-closed elliptical canal is formed in the distal half of the petasma. The degree of openness depends on the degree of lateral flexion of the pleopodal protopodites to which the petasmal endopods are attached (compare petasmata in Fig. 1A, E). However, the medial edges of the ventrolateral lobules can juxtapose, forming a nearly closed canal at the distal end of the petasma. This space is continuous distally with shallow grooves on the horn-shaped dorsolateral projections whose tips curve mesially

towards each other (Figs. 1E,F). The ventrolateral lobules carry distally hook-shaped projections, the ventrolateral projections, which are bent somewhat dorsally (Fig. 1C,E,F). The cuticle of the lateral lobules, along with that of its projections, is thickened and sclerotized. The dorsomedian lobules are covered by much thinner and more flexible cuticle, as are the articulations between the petasmal endopods and the protopods of the first pleopods.

The bell-shaped appendices masculinae are located on the dorsal (anterior) side of the distal end of a thickened, rigid bar along the mesial edge of the endopods of the second pleopods (Figs. 1A,B; 2A,B). The flattened ends of the appendices masculinae are covered with a thin, soft, flexible cuticle (Fig. 2C,D). On the dorsal (anterior) face of the endopod, that which faces the ventral (posterior) side of the petasma, is a deep sinuous groove with a thin membranous floor between the rigid mesial bar on one side and the sclerotized and thickened lateral side of the endopod (Fig. 2A).

The male slit-like gonopores open at the end of papillae located on the sternum of the last thoracic segment (Fig. 3A,B). The genital papillae, observed in living males as well as in preserved ones, are collapsed mounds composed of a spongy mass of muscular tissue covered by thin, wrinkled folds of cuticle (Fig. 3C,D). Inside the genital papilla is the end of the muscular ejaculatory duct, which lies transversely across the interior of the sternum. The genital papilla joins laterally to the vas deferens which descends ventrally along the sides of the posterior cephalothorax from the dorsally located testis (Fig. 4A–C).

The female genital area, or thelycum, consisting of modified cephalothoracic sternites, is composed of the median plate of sternite 13, the paired lateral bulges of sternite 14, and the posterior thoracic ridge (Fig. 3E). A previously undescribed elliptical area is found on each lateral bulge (Figs. 3E, 4D). These elliptical areas are much more highly calcified than the surrounding lateral bulges (Fig. 4D) during the intermolt. However, for 1–2 days after the molt, the still uncalcified cuticle of these thelycum "windows" appears thinner and membranous compared to that of the rest of the thelycum.

The apertures to the spermathecae are slits located between the posterior components of the median plate of sternite 13 and the anterior edges of the lateral bulges of sternite 14 (Fig. 3E, 4D). Each aperture leads into a tri-lobed spermatheca located inside the cephalothorax dorsal to the lateral bulges of the thelycum (Fig. 3F).
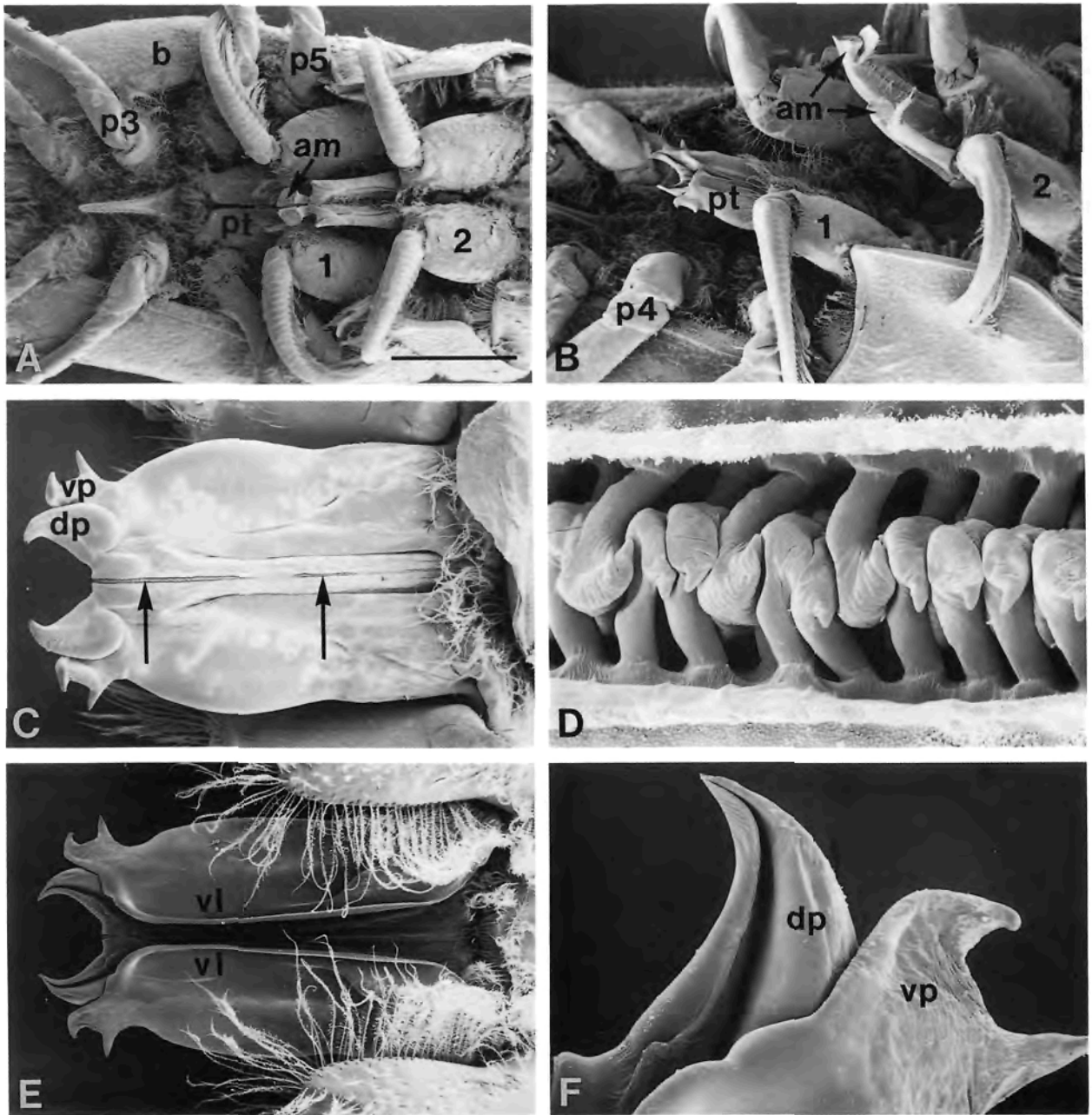
Fig. 1. Male gonopods in *Sicyonia dorsalis*. A: Ventral view of male, anterior to left. B: Ventrolateral view of male from right side, with pleopods 1 and 2 partially lowered from ventral surface. C: Petasma, dorsal (anterior) view; arrows show line of juncture of petasmal endopods. D: Cincinnuli joining medial edges of petasmal endopods. E: Ventral (posterior) view of petasma. F: Grooved dorsolateral and hook-like ventrolateral projections, ventral (posterior) view. am, appendix masculina; b, branchiostegite of carapace; dp, dorsolateral projection; p3,4,5, pereopods 3,4,5; 1,2 protopods of first, second pleopods; pt, petasma;; vl, ventrolateral lobule; vp, ventrolateral projection. Scale bar in A and B: 2 mm; C: 1 mm; D: 20 μm; E: 1 mm; F: 225 μm.

Observations on sperm emission from male gonopores

When males are made to ejaculate by pressure on the sides of the cephalothorax, a short cord of ejaculatory duct contents is emitted through the genital papilla (Fig. 5). The cord is composed of a mass of sperm surrounded by a very thin transparent sheath. Immediately after ejaculation, the ejaculatory ducts fill
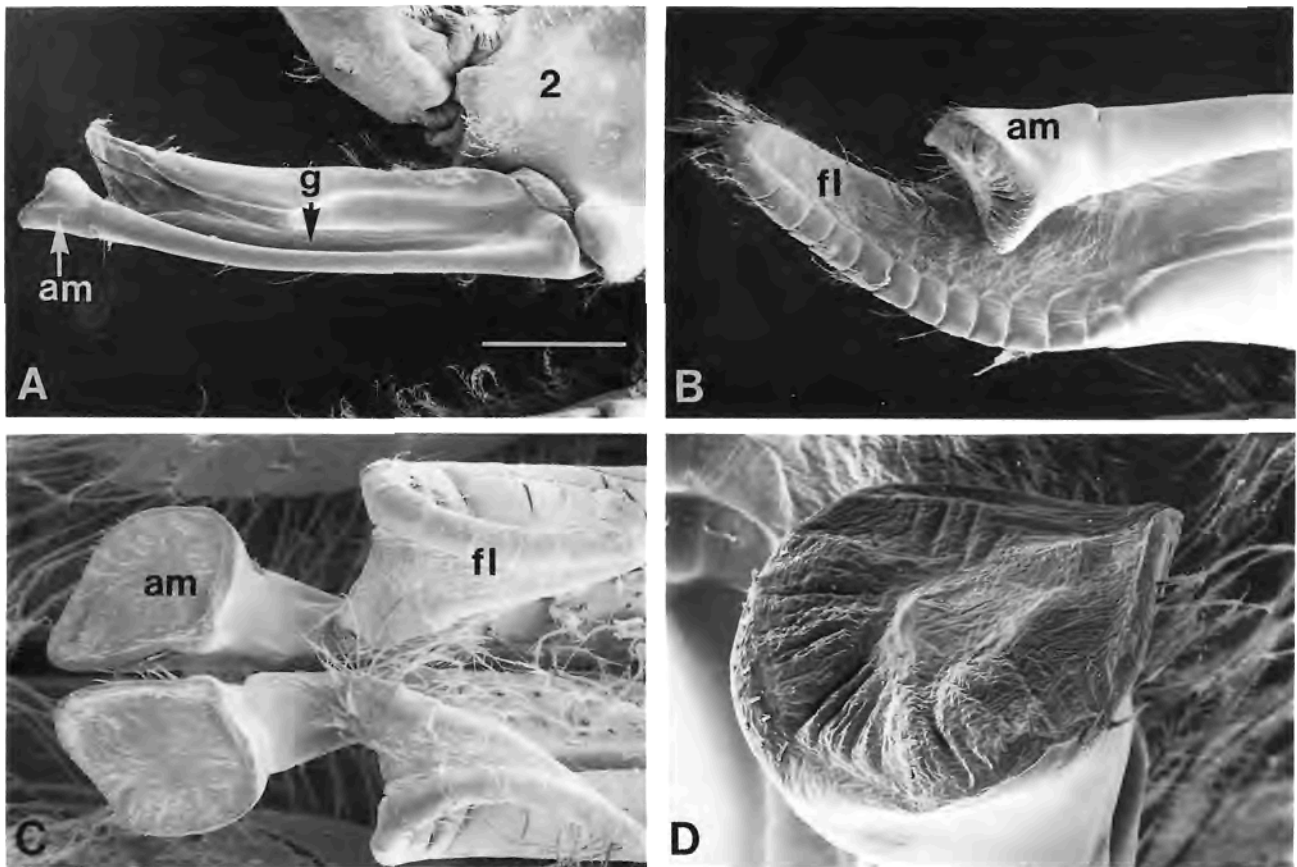
Fig. 2. Endopod of male pleopod 2 with appendix masculina in *S. dorsalis*. A: dorsal (anterior) view of endopod of male pleopod 2 of right side, showing the appendix masculina and deep endopodal groove. B: End of endopod, left pleopod 2, dorsal (anterior) view, with appendix masculina next to semi-segmented but flexible distolateral tip. C: Ventral (posterior) view of endopods with appendices masculinae. D: Distal view of membranous end of an appendix masculina. am, appendix masculina; fl, flexible distolateral tip of endopod, pleopod 2; g, groove; 2, protopod of pleopod 2. Scale bar: A: 830 μm; B: 330 μm; C: 280 μm; D: 125 μm.

again with a sperm mass moving down from the vas deferens (Fig. 4C,D). In seawater, the cord of sperm retains its form for several minutes, slowing expanding from a cylindrical to a flattened globular mass in 10–20 min (Fig. 5). No accessory male secretion was observed in the ejaculatory duct or associated with the sperm mass after ejaculation.

Copulation experiments

Males in the control treatment, in which the exopods of the third pleopods had been removed, copulated frequently with females in all replicates ($n=$ 12, Fig. 6A), with successful insemination of one ($n=$ 3) or both ($n=7$) spermathecae (Fig. 6B). Males from petasma and appendices masculinae ablation treatments only attempted copulation in 1 and 2 replicates, respectively, and no females were inseminated (Fig. 6A,B). Males with petasma blocked distally or

basally with cyanoacrylate glue did copulate with females, sometimes frequently (Fig. 6A). However, the median number of copulations accomplished by males of these treatments were significantly different (lower) than that for the control group (rank sum test; basal block vs. control, $P=0.002$, distal block vs. control, $P=0.003$). No females were inseminated in the distal petasma block treatments. In two replicates of the basal block treatment, females were inseminated (Fig. 6B). However, at the end of the observation period, one of the two males in each of these two replicates was observed to have lost the cyanoacrylate blockage treatment.

The duration of copulation was measured and compared among the control, distal block, and basal block treatments (Fig. 6C). Median duration of copulation was greater in the control treatment than in either the distal or basal block treatments. The differences in median duration of copulation were
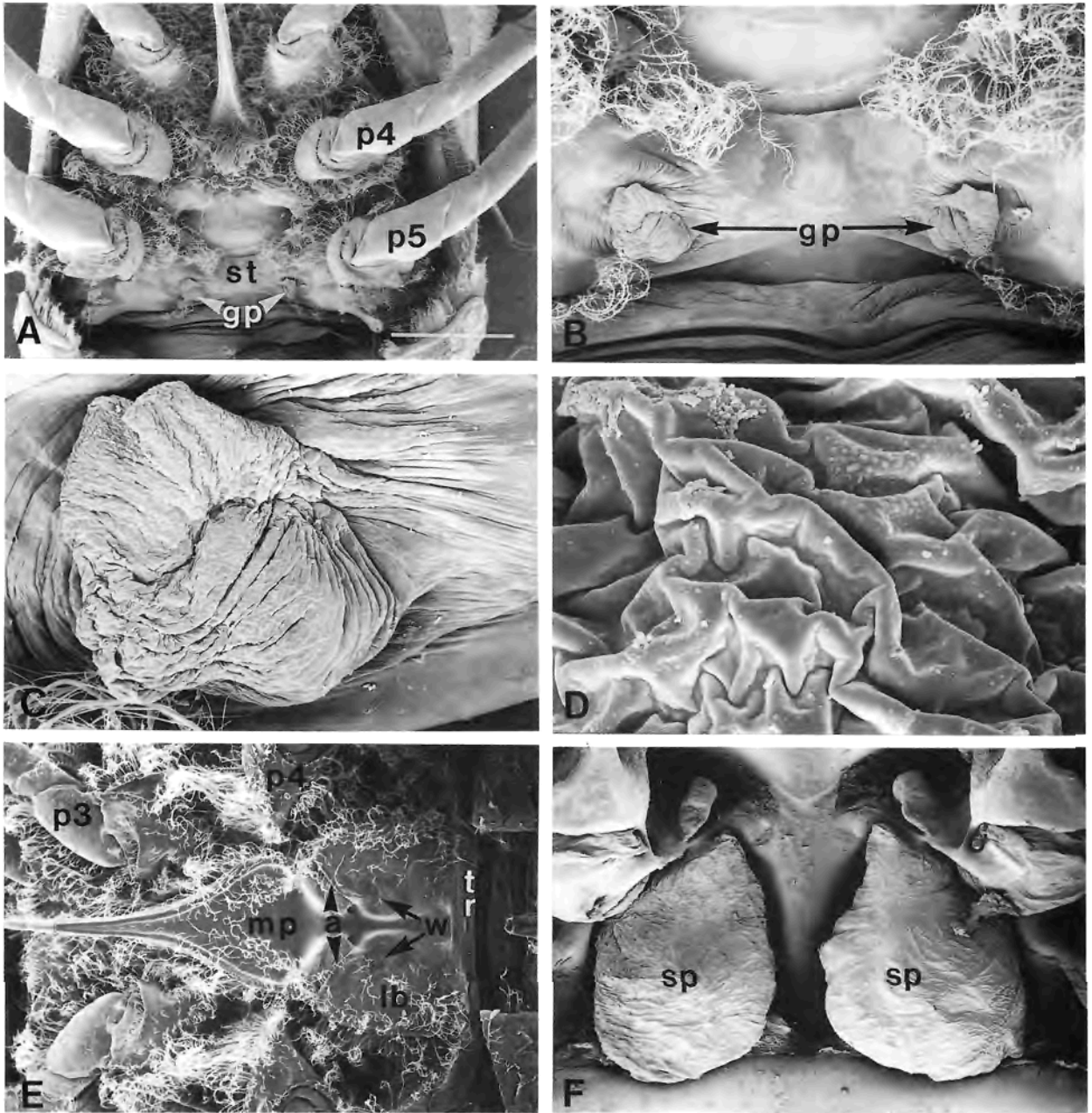
Fig. 3. Male and female genitalia, *S. dorsalis*. A: Ventral view of male, anterior pleopods removed from abdomen to expose posterior of cephalothorax, anterior at top of figure. B: Sternum of male segment XIV with genital papillae. C: Closeup of genital papilla on right side of male. D: Higher magnification of wrinkled, flexible cuticle of a genital papilla. E: Ventral view of posterior cephalothorax of female (anterior to left of figure), showing thelycum with median plate, lateral bulges, apertures to the spermathecae, and posterior thoracic ridge. F: Interior of cephalothorax, dorsal the thelycum, of segment 14, KOH cleaned female, showing dorsal view of spermathecae. a, aperture to spermatheca; gp, genital papilla; mp, median plate; lb, lateral bulge of right side; p3,4,5, pereopods 3,4,5; sp, spermatheca; st, sternum of segment XIV; tr, posterior thoracic ridge; w, "windows" (areas of darker tone) of lateral bulges. Scale bar: A: 1.9 mm; B: 550 μm; C: 130 μm; D: 5 μm; E: 1.2 mm; F: 800 μm.

statistically significant between the control and distal block treatments ($P=0.001$), as well as between the distal and basal block treatments ($P=0.004$), but not between control and basal block treatments ($P= 0.079$).
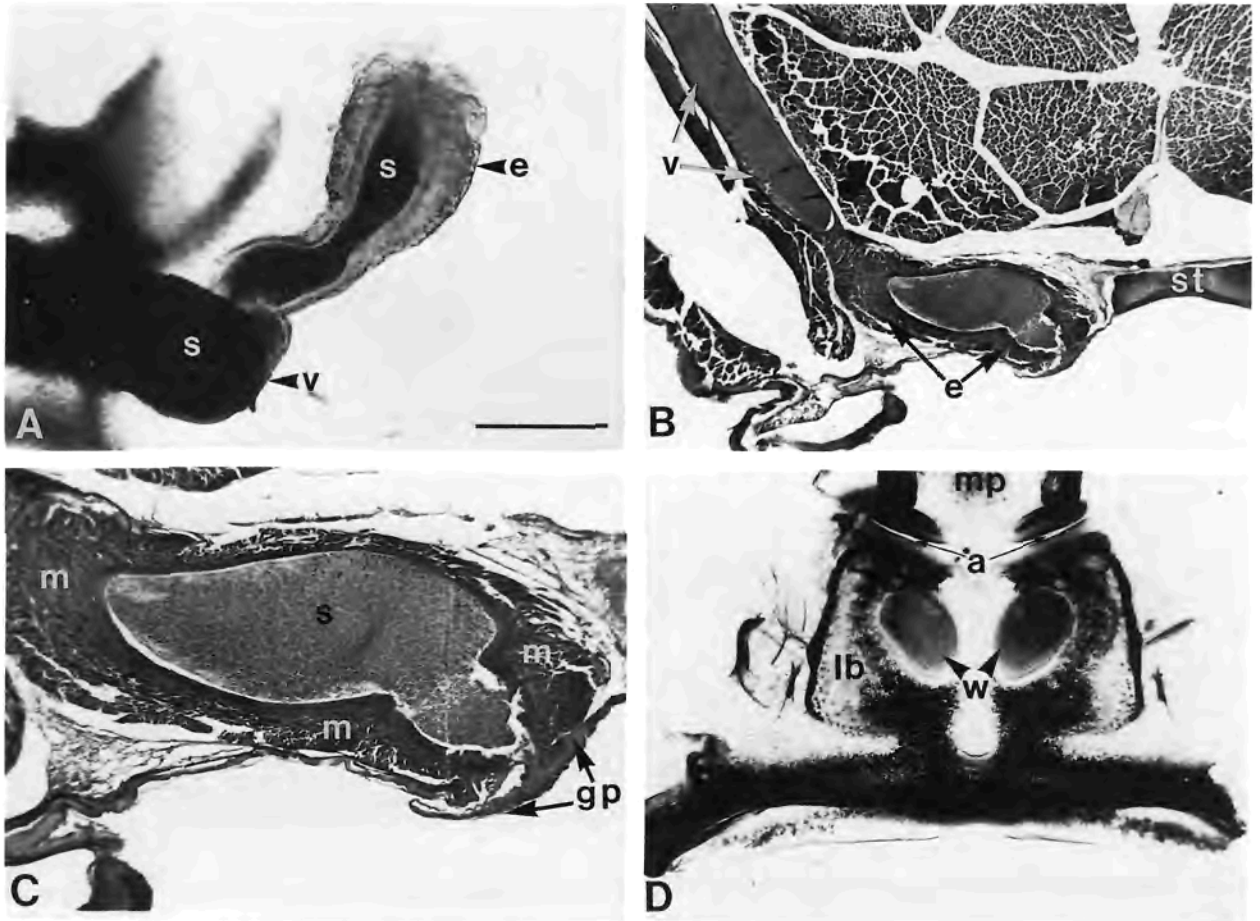
Fig. 4. Ejaculatory duct (A–C) and thelycum characters (D) in *Sicyonia* spp. A: Ejaculatory duct at the distal end of the vas deferens of a male *Sicyonia dorsalis*, dissected from a fresh specimen. B: Histological section through the last cephalothoracic segment of *S. brevirostris*, posterior view, left side, showing the left vas deferens descending into the left ejaculatory duct. C: Closeup of ejaculatory duct shown in B, showing sperm mass, muscular coat of duct, and collapsed genital papilla. D: View with transmitted light of exuviae of exterior of thelycum of a female *S. dorsalis*, showing areas of heavy calcification which become membranous ("windows") in females just after ecdysis. a, aperture to spermatheca; e, ejaculatory duct; gp, genital papilla; lb, lateral bulge of right side, m, muscle coat; mp, median plate; s, sperm mass; st, sternum; v, vas deferens; w, thelycum "window". Scale bar: A: 500 μm; B: 1.2 mm;, C: 500 μm; D: 1.5 mm.

Discussion

The sum of evidence from this study and from previous work on *Sicyonia* mating favors rejection of a sperm injection function for the petasma and appendices masculinae. Results of this study and comparative work on other decapods support acceptance of the alternative hypothesis that the genital papillae directly introduce a sperm mass into the spermathecae of the female. The petasma and appendices masculinae may serve (a) to temporarily connect male and female genitalia during copulation and (b) to adjust the position of a male genital papilla relative to the aperture of a spermatheca. Additionally, the petasma and appendices masculinae might serve to stimulate the female and as sensory devices providing information to the male, although there is no direct evidence from this study. Below, arguments are marshalled for and against the sperm injection and the alternative hypothesis. A model of the mechanics of insemination is proposed.

Sperm injection has been indicated as a likely gonopod function in *Sicyonia* based on Burkenroad's hypothesis on the penaeid shrimp *Trachypenaeus similis* and from previous work on other decapods with complex genitalia. Burkenroad (1934) suggested that the spout-like distolateral projections of the petasma might serve to introduce sperm packets and a male plug substance (Bauer and Lin, 1993) into the
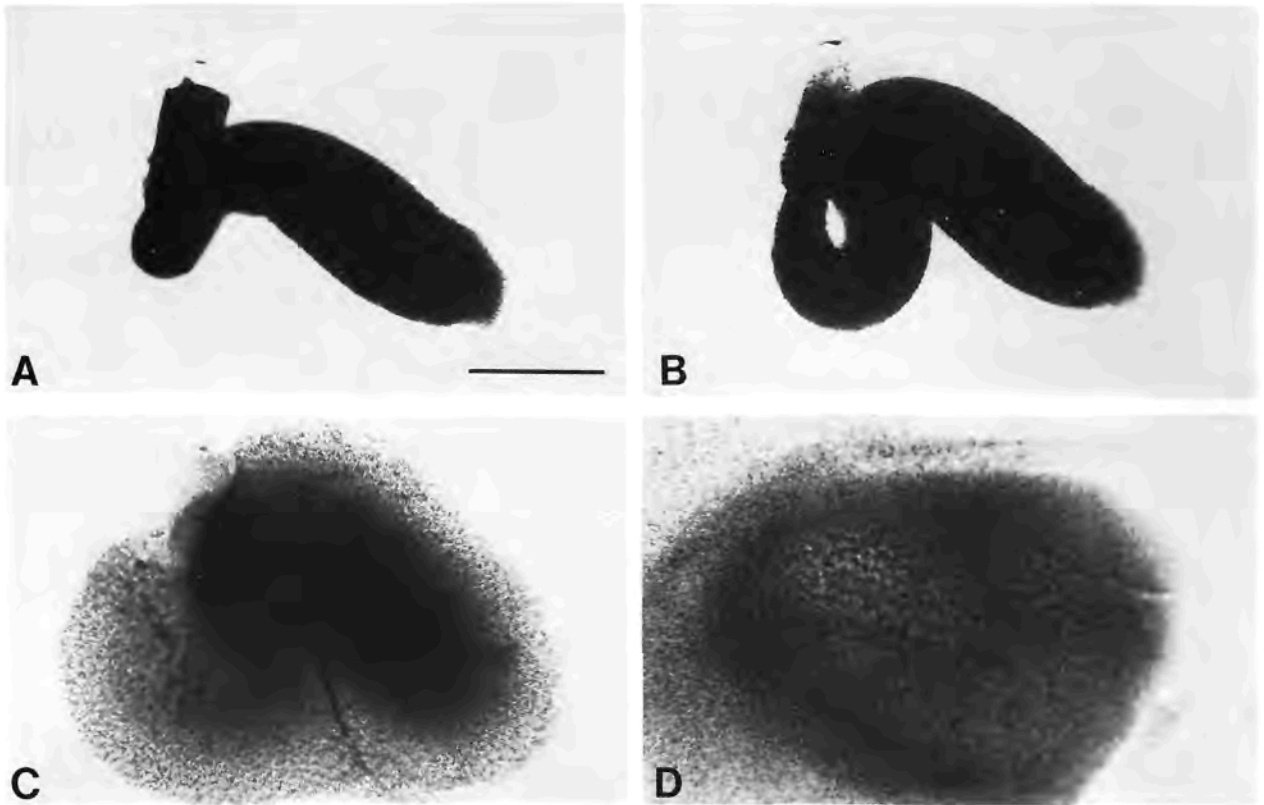
Fig. 5. Artificially ejaculated sperm cord at 1, 3, 10, and 25 min (A, B, C, and D, respectively) after extrusion. Scale bar: A–D: 500 μm.

thelycum during copulation. In the crayfish *Orconectes limosus* (Andrews, 1911) and in the brachyuran crab *Portunus sanguinolentus* (Ryan, 1967), direct observations have demonstrated that genital papillae (= penes) pump sperm mass and male accessory substances into the tube-like or grooved endopods of pleopods 1. Endopods of the second pleopods then push the ejaculated material into female sperm storage structures via these pleopod 1 injection devices.

In *S. dorsalis*, a sperm injection function for the petasma at first seems plausible. There are genital papillae, although relatively short and collapsed in living males. The petasmal endopods do form a semi-enclosed space through which a viscous cord of sperm mass might pass from the genital papillae through the channels of the dorsolateral projections into the apertures of the spermathecae. Taken at face value, results of experimental matings might appear to support such a sperm injection hypothesis. Males with petasmata blocked basally or distally copulated with but did not inseminate females.

However, several kinds of observations cast doubt on a sperm injection hypothesis. Foremost are the observations on *S. dorsalis* and other *Sicyonia* spp.

(Bauer, 1991, 1992) about the pattern of filling of spermathecae related to male position during copulation. Males copulate with their ventral surface opposed to that of females, as in all decapods, so that the ventrally located male and female genitalia come into contact. But instead of being diametrically opposed to the female, i.e., cephalothorax to cephalothorax, abdomen to abdomen, as in crabs and crayfish, a *Sicyonia* male copulates from below the female with its body at a 90° or somewhat oblique angle to that of the female (Palombi, 1939, Fig. 2; Bauer, 1992, Figs. 2d,e). In addition, repeated observations and experiments have shown that males can only inseminate one spermatheca with a single act of copulation (Bauer, 1991, 1992). When the male, situated below the female during copulation, is projecting out from the female's left side, only the left spermatheca may be inseminated and vice versa. Males must copulate at least once from each side of the female to inseminate both receptacles. In order to use the petasma as a sperm injector, the ventral surface of the male in *S. dorsalis* would have to be diametrically opposed to that of the female, as in crayfish and brachyuran crabs (Andrews, 1991; Ryan, 1967).
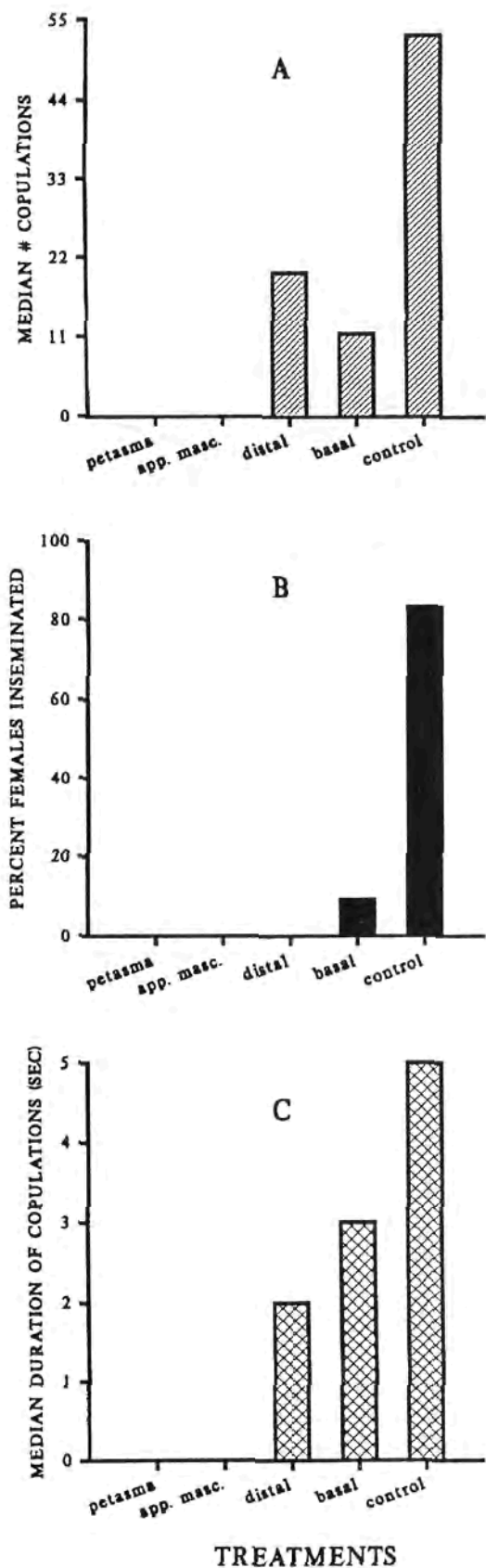
Given the observed perpendicular mating position and pattern of receptacle filling in *S. dorsalis*, only one dorsolateral projection of the petasma could be inserted into only one receptacle during a single copulation. However, in this scenario, sperm mass in the common petasma "canal" would be emitted through the other, unused dorsolateral projection and lost. Decapod species with sperm-injecting gonopods and *S. dorsalis* differ in the duration of copulation. In the former, copulation with seminal fluids transported through male gonopods takes several minutes to several hours (Andrews, 1911; Hartnoll, 1969) as opposed to only a few to several seconds in *S. dorsalis* and other *Sicyonia* spp.(Bauer, 1992; control males in this study).

A model for the roles of the petasma, appendices masculinae, and genital papillae in insemination is proposed for *S. dorsalis* (Fig. 7). When male and female genital areas are opposed as in the typical copulatory position, the crescent formed by the pair of dorsolateral projections may fit or cup around the posterior thoracic ridge of the thelycum. In this position, the genital papilla on the side of the male facing the anterior of the female would be nearer the apertures of the spermathecae, i.e., the left genital papilla if the male is copulating from the female's left side (Fig. 7), the right papilla if the male is facing out the right side of the female. The male papilla which faces the female's spermathecal apertures can only be inserted into the aperture anterior to the petasma, which will block the genital papilla from being inserted into the spermatheca on the other side of the female. Thus, as illustrated in Fig. 7, when the male copulates from the left side of the female, the left genital papilla of the male has access only to the left spermathecal aperture of the female. This model is concordant with observations (Bauer, 1991, 1992) which have shown that only the spermatheca on the side of the female that the male is mating from can be inseminated.

Fig. 6. Results of experimental matings. A: Comparison of median number of copulations of individual females with a pair of males over a two day period in different treatments of mating experiments. The number of replicates (n) and the minimum and maximum number of copulations (between parentheses) for each treatment are: control, n=12 (20,140); petasma ablation, n=12 (0,13); appendices masculinae ablation, n=11 (0,1); distal block, n=15 (1,102); basal block, n=22 (0,76). B: Insemination success in different treatments of mating experiments. C: Comparison of median duration of copulation among three treatments in the mating experiments. Minimum and maximum durations (seconds) were: control, 2,8; distal block, 2,5; basal block, 2,15.
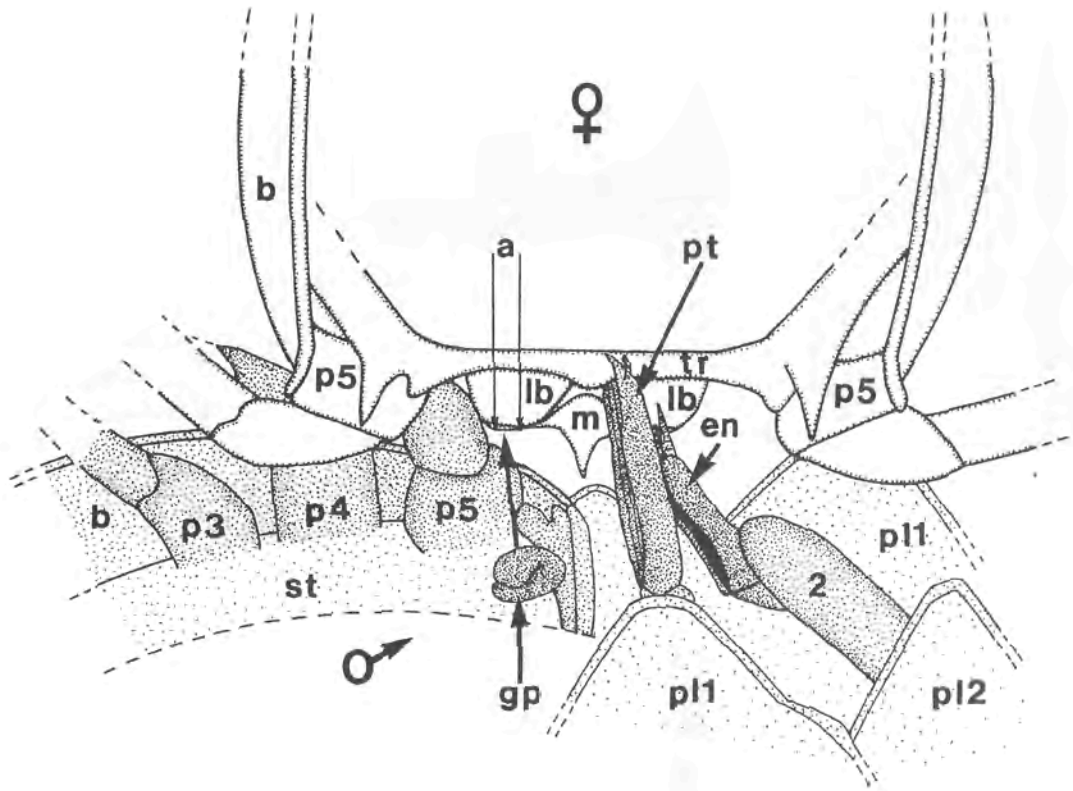
Fig. 7. Proposed model of insemination mechanics in *Sicyonia dorsalis*, in which the petasma of the male, supported by the endopods of the second pleopods, hooks onto the female's posterior thoracic ridge, just behind the thelycum. The arrow from the genital papilla of the male shows the path to the aperture of one of the female's seminal receptacles on the anterior edge of a lateral bulge of the thelycum. In this diagram, the male (upside down, below the female) is mating on the female's left side, i.e., the male anterior end is facing to the left. A cross section of the female cephalothorax (ventral) just posterior to the thoracic ridge and thelycum is viewed in this diagram from the posterior side of the female, so that the female's left side is to the reader's left. As proposed in the model, when the male is mating from the female's left side, only the aperture of the female's left seminal receptacle can be contacted by a genital papilla, that of the male left side. This is reversed when the male is copulating from the opposite direction. The posterior three thoracic appendages (pereopods) and the genital papilla are illustrated for the male's left side (ventral), which is viewed from the male's right side (corresponding right side of male not illustrated in order to expose this view). The complete first abdominal segment of the male is shown, with a lateral (slightly anterolateral) view of the petasma and the endopod of the right second pleopod (left second pleopod, behind right, is omitted for clarity). The female's thelycum (lateral bulges, median plate) actually projects anteriorly (into the page, away from the reader) from the plane of the female cross section shown, and it has been tilted back ventrally out of its proper plane in order to illustrate it (the left genital papilla of the male and the aperture to the female seminal receptacle are both anterior to the posterior thoracic ridge, around which are hooked the dorsolateral projections of the petasma). Male structures are stippled completely, female structures are indicated by a single row of stipple. a, aperture, indicated by tips of arrows, to seminal receptacle of female left side; b, branchiostegite or gill cover (inner side of male left, exterior of female left); en, endopod of the male's right second pleopod; gp, left genital papilla with gonopore; lb, lateral bulges of thelycum; m, median plate of the thelycum; p3, p4, p5; coxae of the 3rd, 4th, 5th pereopods; pl1, pl2; pleural plate of 1st, 2nd, abdominal segment of male; pt, petasma; st, sternum of left side of male; tr, posterior thoracic ridge of female; 2, protopod of male's right second pleopod.

In this model, the endopods of the second pleopods, bearing the appendices masculinae, are proposed to mechanically support the petasma in setting against or hanging on to the female genital area during copulation. Morphological observations indicate that the free edge of each ventrolateral lobule of the petasma can fit into the sinuous groove on the dorsal (anterior) side of the endopods of the second pleopods,

forming an interlocking unit during copulation. The soft membranous tips of the appendices masculinae would face and perhaps touch the female genitalia.

The internal and external structure of the male genital papilla shows that it is capable of entering the aperture of a spermatheca. The papilla is composed of a spongy mass of muscular tissue surrounding the end of the ejaculatory duct and is covered with thin flexible

cuticle. This morphology suggests that it may be erectile during ejaculation. Due to its pliability, it seems capable of being inserted into the very narrow aperture of the spermatheca.

Results from experimental matings may seem to contradict the hypothesis that the petasma is some sort of attachment and/or stimulatory/sensory device during copulation. According to the model (Fig. 7), the dorso-lateral horns fit against some part of the female genital area. In the distal block treatments, the application of cyanoacrylate glue blocked both flow of sperm through the petasma and perhaps the successful male attachment to or stimulation of the male during copulation. In the basal block treatments, the distal end of the petasma was free to attach to or stimulate the female while possible sperm flow was blocked at the base. However, as in the distal block treatments, insemination was unsuccessful although copulation occurred.

These results might be best interpreted in light of the work of Bauer (1992) and sexual selection on animal genitalia (Eberhard, 1985). In *S. dorsalis*, males paired for one or two days with uninseminated females copulated several to many times but often inseminated only one or neither of the spermathecae (Bauer, 1992; 2 of 12 females in control treatment in this study). As in many animal species (Eberhard, 1985, 1990, 1991; Thornhill and Alcock, 1983), copulation itself may be a form of courtship, in which the female may or may not allow insemination. Females might be testing the fitness of males during copulation, using some criteria of petasma usage. It is suggested here that females may detect even relatively small alterations in the petasma, such as those done in the distal block and basal block treatments. In the mating experiments, the median duration of copulation was shorter in both the basal block and distal block treatments when compared to that by males in the control treatments, an indication that females broke off copulations and/or blocked insemination in some way upon detection of petasmata altered from standard form or usage. Such behavior would be would be a selective mechanism (sexual selection by female choice) on the morphology of the male petasma which might explain the evolution of the complex, often morphologically bizarre, male gonopods of *Sicyonia* and other penaeoid genera.

"Lock and key" hypotheses, in which species-specific male and female genitalic interlocking evolves as a mechanical reproductive isolating mechanism, have been reviewed by Eberhard (1985). This type of hypothesis seems particularly inapplicable to *Sicyonia* spp. Although the male gonopods are complex and do vary among species, the female structure to which the male petasma most likely attaches, the posterior thoracic ridge, is not complex nor obviously variable among *Sicyonia* spp. In addition, it would seem that females could recognize and reject males of another species during the courtship ("following" behavior) that precedes copulation.

The possible role of the petasma and appendices masculinae as sensory and/or stimulatory structures should be considered. Males with petasma or the appendices masculinae ablated failed in most cases to copulate with or even court females, while control males equally traumatized by ablations of other abdominal appendages copulated with and inseminated females. Although sensory setae or sensillae were not observed on the petasma, the soft membranous tips of the appendices masculinae might house tactile receptors which would provide information, e.g., the position of the male relative to the female. Similarly, a stimulatory function of the gonopods might be considered. Both sets of gonopods might be used to touch and prod the female, providing some key stimulation or information about male condition. The thelycum of the female is covered with many fine setae which might be sensory. The thelycum "windows," oval areas which are membranous just after the molt, when mating usually occurs in nature, might be possible sensory areas of the female for receiving male stimuli. An argument against the latter is that females, kept from male contact until long after the windows had become highly calcified and presumably useless for receiving tactile stimuli, copulated with and were inseminated by males (Bauer, 1996).

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