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Sexually Reversed Copulatory Courtship Roles and Possible Nuptial Feeding in the Soldier Beetle *Ditemnus acantholabus* (Champion 1915) (Coleoptera: Cantharidae)

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ABSTRACT: Male courtship during copulation is common in insects and spiders, and presumably serves to induce the female to fertilize her eggs with the male's sperm. Fragmentary observations indicate that in *Ditemnus acantholobus*, typical male and female roles are reversed. The female courts vigorously and persistently during copulation while keeping one portion of the male's highly modified pronotum inside her buccal cavity. I propose that female copulatory courtship in this species functions to induce the male to provide material from his pronotum for the female to ingest, and that the species-specific modifications of the male pronotum are courtship devices.
KEY WORDS: Copulatory courtship, sexual selection, *Ditemnus*, Cantharidae

Courtship during copulation ("copulatory courtship") is apparently common in insects and other arthropods, where it may occur in half or more of the species (Eberhard, 1991, 1994; Huber, 1998; Peretti, 1997). Usually it is the male that courts the female. His courtship is thought to serve to influence cryptic female choice, by inducing the female to favor him in reproductive decisions which occur after intromission and which can affect his reproductive success (Eberhard, 1994, 1996). Experimental studies of male copulatory courtship have demonstrated effects on female sperm use, oviposition, and genitalic penetration (Otronen and Siva-Jothy, 1991; Edvardsson and Arnqvist, 2000; Tallamy *et al*., 2002a, b; Ramirez, 2004).

Recent evidence suggests that some females also perform courtship behavior during copulation (see review by Rodriguez, 1998; also Ortiz, 2003; Peretti *et al*., submitted, on a spider; Briceño *et al*., in prep. on a fly). Presumably the function of such behavior is to induce the male to perform behavior that will increase her likely reproductive success. In the micropezid fly (Diptera) *Ptilosphen variolatus*, female copulatory courtship is apparently solicitation of nuptial feeding (Ortiz, 2003). The female taps or hits the male's mouth and head with her front legs, and the male responds by regurgitating a liquid that the female then ingests.

Cantharid beetles (Coleoptera) of the tribe Silini of the subfamily Silinae are unusual in that the male pronotum is often complexly sculptured ("excised") on its dorsal and lateral surfaces (Green, 1966; Moscardini, 1972; Kasantsev, 1994; Ramsdale, 2003). The pronotal modifications in some species include pits (Kasantsev, 1994), which could be secretory pores. Ramsdale (2003) reported that the female of *Ditemnus latilobus* Blatchley clasps the male pronotum for long periods both before and during copulation, and noted that previous authors have proposed that the modified male pronotum in Silini functions to provide an increased surface area for the evaporation of pheromones. The form of the sculpturing apparently diverges relatively rapidly, as it often shows sharp species-specific differences, and in the siline genus *Ditemnus* the male pronota, along with the male

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genitalia, are key characters for distinguishing congeneric species (Green, 1966; Kasantsev, 1994; Ramsdale, 2003).

Materials and Methods

On 28 July 2004, I observed a pair of beetles copulating on the window of a house in an area of second growth with a grassy yard, just South of San Antonio de Escazu, San José Province, Costa Rica, el. 1325 m. The beetles stayed coupled for approximately 15 min on the window, and another approximately 15 min under a dissecting microscope. I filmed just over 12 minutes of behavior with a SONY DCR-TRV50 digital video camera equipped with +9 closeup lenses directly, and through a dissecting microscope. For examination with the SEM, the male's pronotum was dehydrated and dried, then sputter coated with gold.

Results

In the species of this study, *Ditemnus acantholobus* (Champion 1915), the central portion of the male pronotum is deeply indented (central depression in Figs. 1, 2a), and each lateral-posterior margin has a pair of rigid cuticular processes (anterior and posterior processes in Figs. 1, 2). The anterior process is more or less planar, with especially long and dense setae near its postero-lateral edge (Fig. 2b, c). The posterior process is a larger, curved plate that bears on its dorsal surface a deeply wrinkled area that is light in color, contrasting with the red-orange color of most of the rest of the pronotum (Fig. 1a). The wrinkled area has a large, deep postero-lateral aperture (Fig. 2c, d). The posterior process has a dense band of strong setae along its posterior margin (Fig. 2c, d), and scattered strong setae on its ventral surface (Fig. 3a). The surface of the wrinkled area has deep grooves or folds, but no visible pits (Fig. 3b). In a living male observed under a dissecting microscope during copulation, the surface of the wrinkled area was shiny, as if covered by liquid. Near the anterior edge of the posterior process is a sharp, dorsally projecting "spine" (Fig. 2b). Just dorsal to the anterior process is a pore at the tip of a slightly elevated but otherwise unmodified area of cuticle (Fig. 2a, b).

Initial behavioral observations showed that the larger individual (the female) was on the dorsum of the smaller male. Except for two interruptions (see below), the female performed nearly continuous energetic, stereotyped repetitive behavior that appeared to constitute copulatory courtship (see Eberhard, 1994 for criteria). Every approximately 5 sec (mean = 5.24 $\pm$ 2.74 sec, N =35, range 0.40–14.53 sec) she raised herself dorsally, and repeatedly pulled her body anteriorly forcefully, bending the tip of the male's abdomen dorsally and anteriorly (Fig. 4). Each bout of pulling was brief (mean = 1.57 $\pm$ 0.98 sec, $N = 40$), and then the female moved posteriorly again and waited several seconds (mean = 3.63 $\pm$ 1.74 sec, $N = 33$) before again pulling anteriorly. Most pulls were compound movements, and included several smaller, brief pulls. The female's mouth remained in contact with the postero-lateral margin of the pronotum of the male (Figs. 4, 5) during and between bouts of pulling (Figs. 4, 6). Most times when she pulled, the female flexed her head ventrally (Figs. 4, 6), usually several times/bout (mean = 4.3 $\pm$ 0.9 times, $N = 31$, range 3–6) (Fig. 6). The head flexions in a burst were separated from each other by a mean of 0.41 $\pm$ 0.12 sec ($N = 111$, range 0.13–0.77 sec). The female also flexed her prothorax ventrally (Fig. 4). During each anterior movement the female also scrambled with her first and second legs against the sides of the male while her hind legs rested on the substrate (Fig. 4). In most observations I could see only the legs on one side in their entirety; it was clear, however, that bursts of leg movements occurred on both sides of the beetle at

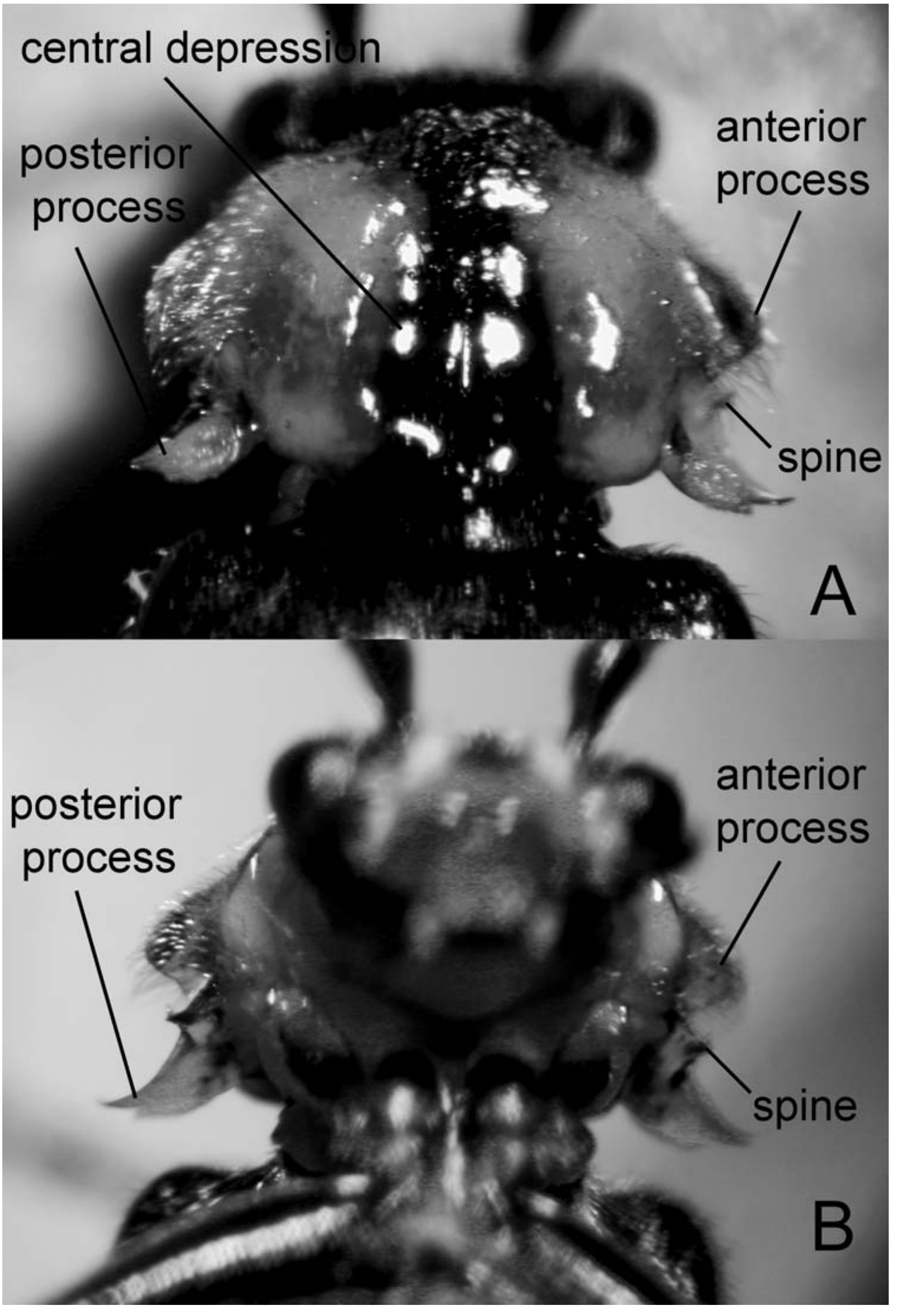

Fig. 1. Dorsal (A) and ventral (B) views of male pronotum of *Ditemnus acantholobus*, showing the large central cavity, the setae on the posterior portion of the anterior processes, the light-colored area on the dorsal surface of the plate-like posterior processes (maximum width of prothorax is 1.87 mm).

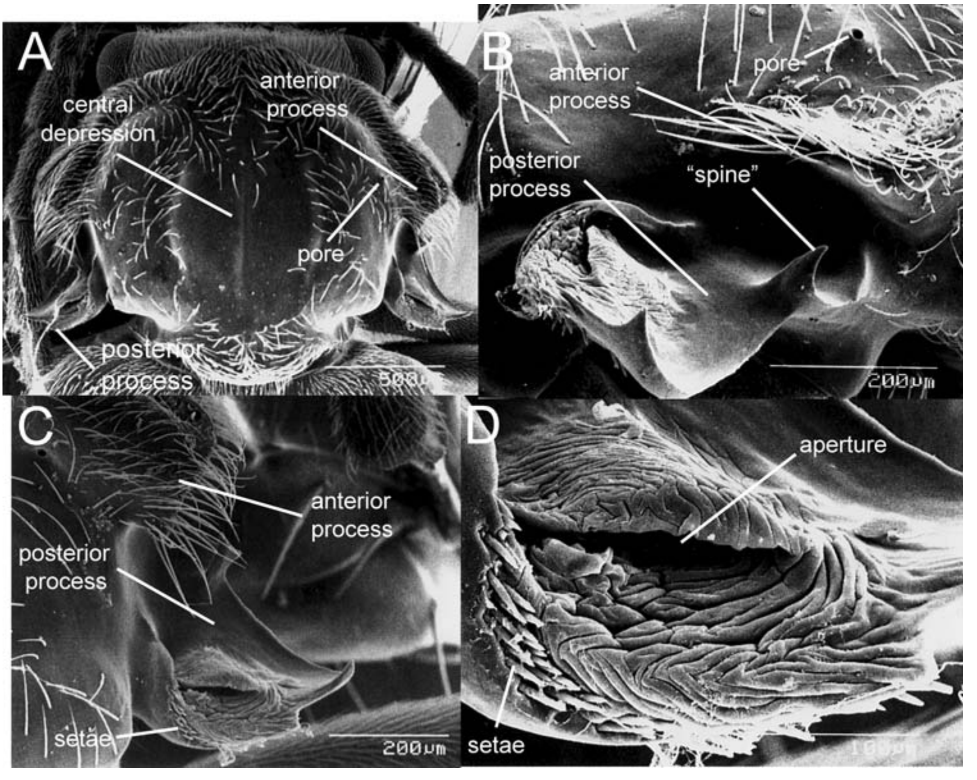

Fig. 2. SEM images of the male prothorax. A) dorsal view of pronotum. B) Lateral view of anterior and posterior processes. C) postero-dorsal view of anterior and posterior processes. D) closeup view of wrinkled area on dorsal surface of posterior process.

approximately the same time, although one side sometimes began up to 0.2 sec before the other. During some pulls the female folded her antennae ventrally and somewhat posteriorly, but this detail was inconsistent.

Further observations under the microscope revealed that part of the modified pronotal margin of the male, almost certainly the plate-like posterior process, was apparently inserted into the female's buccal cavity. The tip of one of the female's mandibles was in the central dorsal depression on the male's pronotum, while the tip of her other mandible hooked the ventral portion of the lateral surface of his pronotum (Fig. 5). Her maxillary palps were on the dorsal surface of his pronotum, just anterior to her head, while her labial palps were on the rear surface of the male's pronotum, and projected more or less ventrally.

The female's mandibles did not hold the male's pronotum while she was flexing her head ventrally. Instead, during each bout of forward movements the female opened and closed her mandibles several times, repeatedly seizing and then releasing the male's pronotum. On average she gripped him 4.2 $\pm$ 0.6 times ($N = 20$, range 3–5) during each forward movement. Her mandibles were open rather than closed most of the time during each sequence of biting (open for 0.29 $\pm$ .08 sec, $N = 75$; closed for 0.10 $\pm$ .05 sec, $N = 61$). Instead of holding the male with her mandibles while she flexed her head, the female opened them just before at least some head flexions (in others the angle of view did not permit certainty on this point). During some pulls the rear margin of the female's head capsule was pulled into her prothorax at the apex of the ventral flexion of the head,

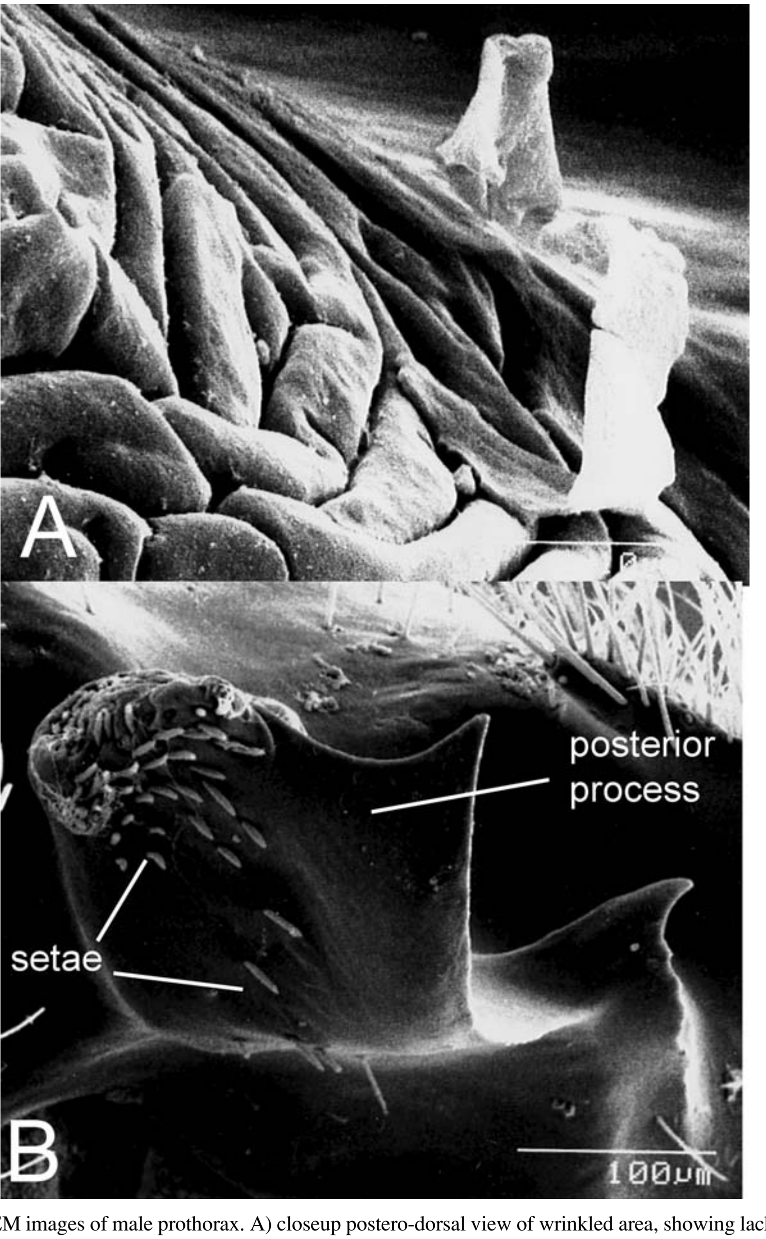

Fig. 3. SEM images of male prothorax. A) closeup postero-dorsal view of wrinkled area, showing lack of pores, and two very small dorsal projections. B) ventral view of posterior process, showing setae at its posterior margin and ventral surface.

indicating that force was exerted by muscles (presumably in her prothorax). When she moved posteriorly, the female maintained her grip on the male's pronotum with her mandibles until the next forward movement. The female's other mouthparts were immobile, or at least relatively quiet.

Details in the video recordings indicated that the scrabbling movements of the female's front and middle legs represented rubbing movements on the male's lateral surface rather

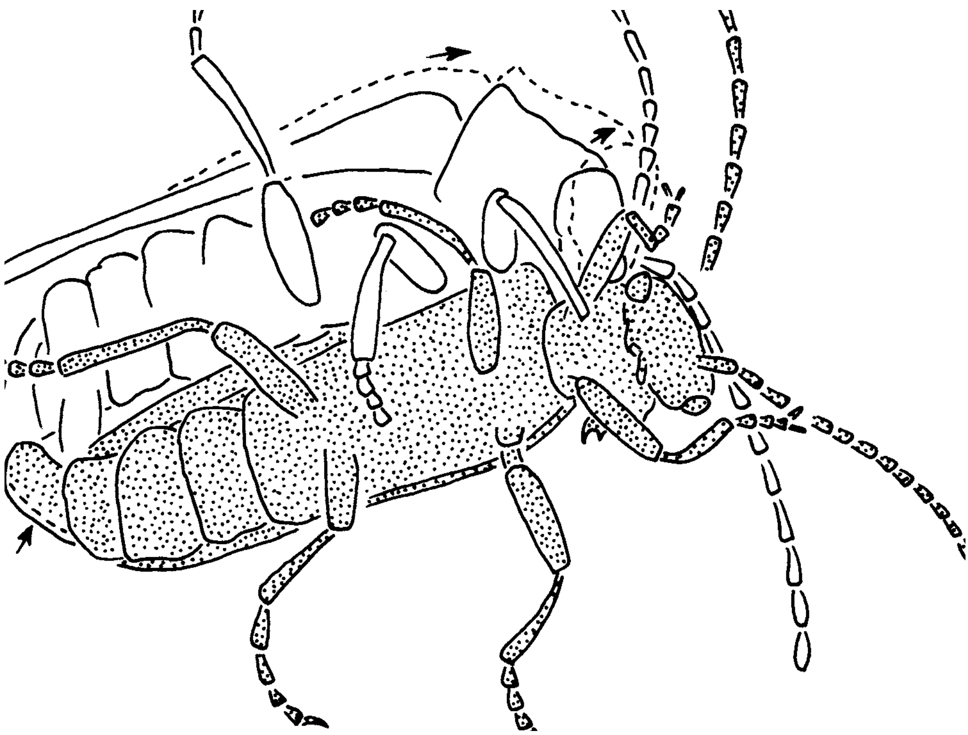

Fig. 4. Diagrammatic illustration of anterior pulling movement of the female on the male (stippled). The second position (dotted lines near arrows) followed the first by 0.13 sec. The female's head and prothorax bend ventrally, lifting the anterior portion of her body away from the male. (drawn from a video recording; body parts that were not in focus are not drawn, and only the head, thorax and abdomen are drawn in the second position).

than pushes against his body to pull herself forward. The coordination between abdominal bending and female leg movements was inconsistent, and the duration of bursts of leg movements was substantially longer than that of abdomen bending (mean = 2.88 ± 2.71 sec, $N = 34$, versus 1.57 ± 0.98 sec) (Fig. 6). Details of the legs' positions also suggested rubbing rather than pushing. The female's middle tarsus was repeatedly dragged passively across the male's pleuron, bending anteriorly as the tibia moved rearward, rather than maintaining an extended position. The front tarsus was often (perhaps the majority of the times) dragged across the surface of the male as it was being raised, instead of being extended. There was no obvious close coordination between the ipsilateral legs or contralateral legs. In sum, the female did not push herself forward using her front and middle legs. It was not clear whether she pulled herself forward by holding the process of the male's pronotum in her buccal cavity and flexing her head and prothorax ventrally, or whether she pushed herself forward with her hind legs, and only bent her head and thorax ventrally to maintain buccal contact with the male's prothorax.

The male performed brief bursts of very rapid, low amplitude quivering, apparently of his entire body, that caused his body to blur in video recordings. These vibrations were only visible under the dissecting microscope.

On two occasions the female released the hold with her mouth on the rear margin of the male's prothorax while their genitalia remained coupled. The first occurred when I disturbed the pair to place them under the dissecting microscope; the second occurred later,

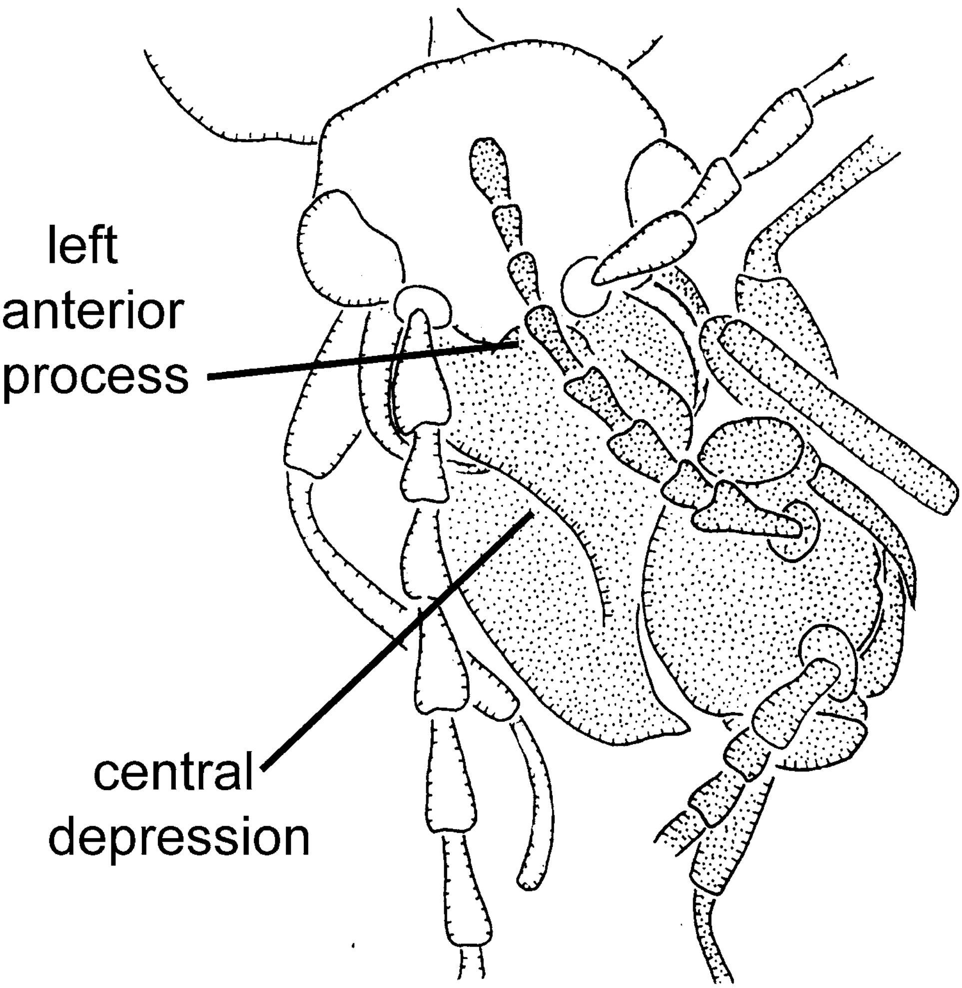

Fig. 5. Diagrammatic closeup of female holding the partially twisted male (stippled) by his prothorax with her mandibles (from a photograph).

without my intervention. In each case the female regained her hold on his prothorax approximately 30–60 sec later. On the first occasion, the female dismounted and the two beetles turned to face opposite directions for approximately 10–30 sec; she then climbed back onto the male's dorsum and seized his pronotum. During the second, the female remained mounted and repeatedly grasped briefly with her mandibles at the male's pronotum and more posteriorly on the dorsal surface of his elytra. Her mandibles were used more as tongs than as pincers; they enclosed the lateral sides of the male's elytra, and their tips did not pinch him.

Discussion

These observations, though fragmentary, leave little doubt that the elaborate pronotal modifications of the male of *Ditemnus acantholobus* contact the female's buccal cavity and areas near her mouth during copulation. The posterior pronotal process almost

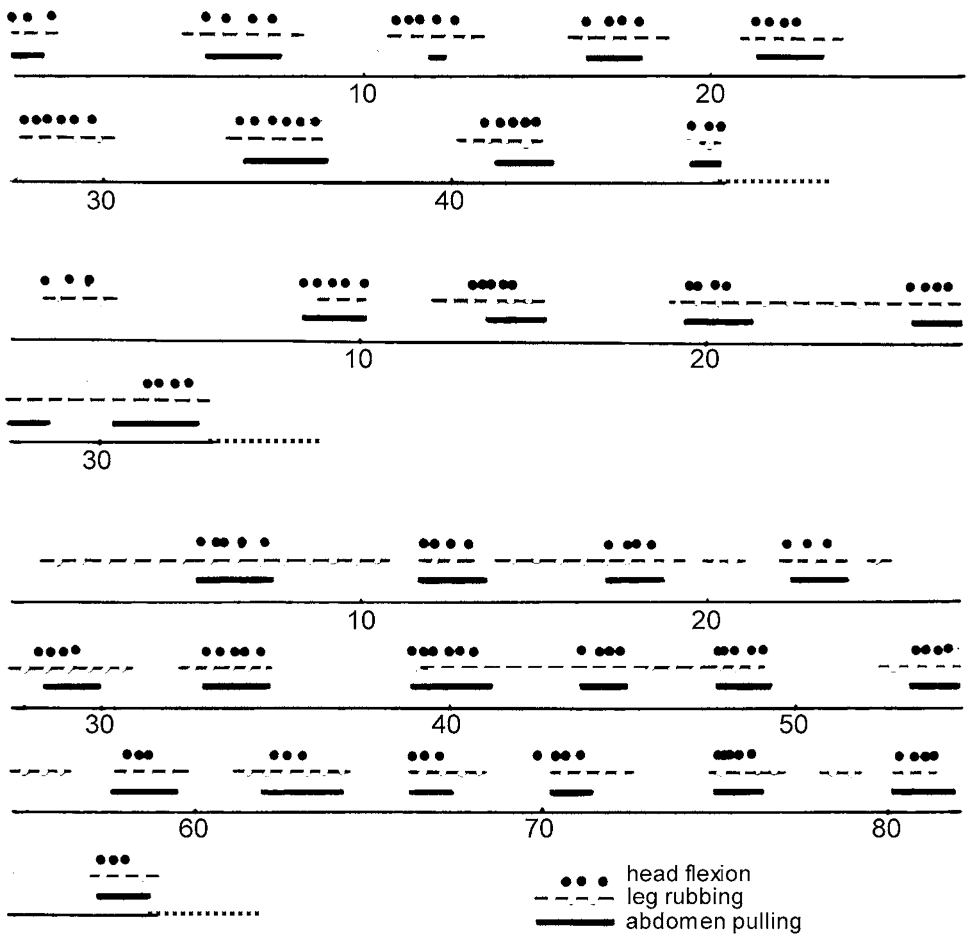

Fig. 6. Graphical representation of the periods of time during which the female performed head flexion, leg rubbing, and forward pulls with the abdomen during copulation (time in seconds; dotted lines indicate breaks in filming).

certainly entered into the female's buccal cavity. There are three suggestions that the wrinkled area on its dorsal surface serves to deliver male secretions to the female: its shiny, "wet" appearance in a living specimen (the possibility that the female's mouthparts wetted the male rather than vice versa cannot be eliminated, however); the deep opening on its surface (Fig. 2d); and the deeply wrinkled surface around this opening, which is typical of surfaces for dispersing liquids in other insects (e.g., the evaporatory area of Heteroptera–Schuh and Slater, 1995). The wrinkled cuticle is also compatible with the non-exclusive alternative that chemical stimuli are dispersed to the female through the air.

The large central depression in the male's pronotum provides one of the female's mandibles with purchase when she seizes his prothorax. Other details of the male pronotum, such as the anterior process with its large setae, the spine-like projection near the anterior margin of the posterior process, and the strong setae on the posterior margin of the posterior process and on its ventral surface, do not have such obvious utilitarian significance. Judging by their designs, they may provide additional stimuli to the female. The setae on the anterior process probably contact the female during copulation just dorsal to her mouth. Similar patches of setae are also associated with the anterior processes of several other species of *Silis* (Kasantsev, 1994). Elaborate male structures with apparently stimulatory designs are common in some other groups in which females obtain nuptial secretions by applying their mouthparts to the male's surface, such as erigoniine and some theridiid spiders (Lopez, 1987) and some millipedes (Haacker, 1971).

The unusual sex role reversal during copulation in *D. acantholobus*, with the female rather than the male performing the most persistent and energetic copulatory courtship, may also be associated with female feeding on secretions from the male's pronotum. Perhaps, as in the micropezid fly *P. variolatus* (Ortiz, 2003), the female stimulatory behavior induces the male to provide more secretion.

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