The Functional Morphology of Male Cerci and Associated Characters in 13 Species of Tropical Earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae)

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ABSTRACT

Briceño, R. Daniel, and William G. Eberhard. The Functional Morphology of Male Cerci and Associated Characters in 13 Species of Tropical Earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae). *Smithsonian Contributions to Zoology*, number 555, 63 pages, 97 figures, 1 table, 1995.—We observed courtship and aggressive behavior in males of 13 species in four families of earwigs in order to determine the functional significance of sexually dimorphic morphology of cerci and associated structures in males. Criteria for determining function included appropriateness of design and consistency of use. In 12 species, at least 17 secondary sexual modifications of male cerci and associated structures appeared to serve in aggressive interactions between males, as weapons and/or as display devices. In two species, modifications of male cerci served to clasp females just prior to and during copulation; in one case, they were used to force copulations on females; in the other, they apparently were used as a courtship device. Functions could not be assigned confidently to many minor features, such as positions of teeth on the cerci.

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Contents

The Functional Morphology of Male Cerci and Associated Characters in 13 Species of Tropical Earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae)

R. Daniel Briceño
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Introduction

Earwigs are distinguished from other insects by their hard, unsegmented cerci, which can be closed against each other like forceps (Giles, 1953). They have had highly modified cerci since at least the Jurassic (Carpenter, 1992). The cerci of immatures and females are generally more or less smooth and straight except for inwardly curved tips. In females and immatures, the cerci probably usually function mainly as defensive weapons (Bennett, 1904; Gadeau de Kerville, 1905; Chopard, 1949; Eisner, 1960; Arora and Bhatnagar, 1961; Bharadwaj, 1966; Radesäter and Halldórsdóttir, 1993), and, less often, as offensive weapons for attacking prey (Bennett, 1904; Terry, 1905; Pallister, 1927; Joshi, 1960), offensive weapons in intraspecific battles (Bharadwaj, 1966), touch receptors (Bharadwaj, 1966), and perhaps as implements to help fold and deploy the wings (Gadeau de Kerville, 1905).

In many earwigs the cerci of mature males differ from those of females and immatures in various, sometimes bizarre ways (Figure 1). In some species other portions of the posterior part of the male's body, such as the pygidium and the abdominal tergites, also are modified (Figures 27, 32). Male cercus morphology is often species-specific (e.g., Brindle, 1971, 1976), suggesting that it diverges relatively rapidly, as is typical of characters under sexual selection (Darwin, 1871; West-Eberhard, 1983; Eberhard, 1985). In at least one species, *Forficula auicularia,* males have two forms of modified cerci (Bateson and Brindley, 1892). The form adopted by a given male of this species depends on nutrition during immature stages (Kuhl, 1928). In two others, *Doru taeniatum* and *Paralabella dorsalis,* males do not have two morphs for cercus form (Eberhard and Gutierrez, 1991).

The functional significance of male-specific cercus morphology of earwigs has not been clearly established. Some authors have supposed that male cerci are used to clasp the female during copulation, and thus, apparently, allow the male to force his attentions on her (DeGeer, 1773, in Arora and Bhatnagar, 1961; Goe, 1925, on *Forficula auricularia*). Subsequent observations showed, however, that the male does not hold the female with his cerci either before or during copulation, at least in the species *Labidura riparia* and *Anisolabis maritima* (Gadeau de Kerville, 1905, and references; Bennett, 1904; Arora and Bhatnagar, 1961). Radesäter and Halldórsdóttir (1993) note that in *Forficula auricularia* the male uses his cerci to lift the female's abdomen before copulation, but they do not give details as to which parts of the male contact which parts of the female. Bennett (1904) thought that the asymmetric cerci of *Anisolabis maritima* would make it easier for the male to twist his abdomen to copulate, but he admitted that the variety of forms in the males of other species raise doubts about this possible function. Other authors have speculated that male cercus modifications serve as weapons in intraspecific male-male battles (Bharadwaj, 1966; Radesäter and Halldórsdóttir, 1993), but they gave no supporting evidence. Moore and Wilson (1993) showed that in *Vostox apicedentatus,* secondary sexual characters of male cerci appear to function mainly as

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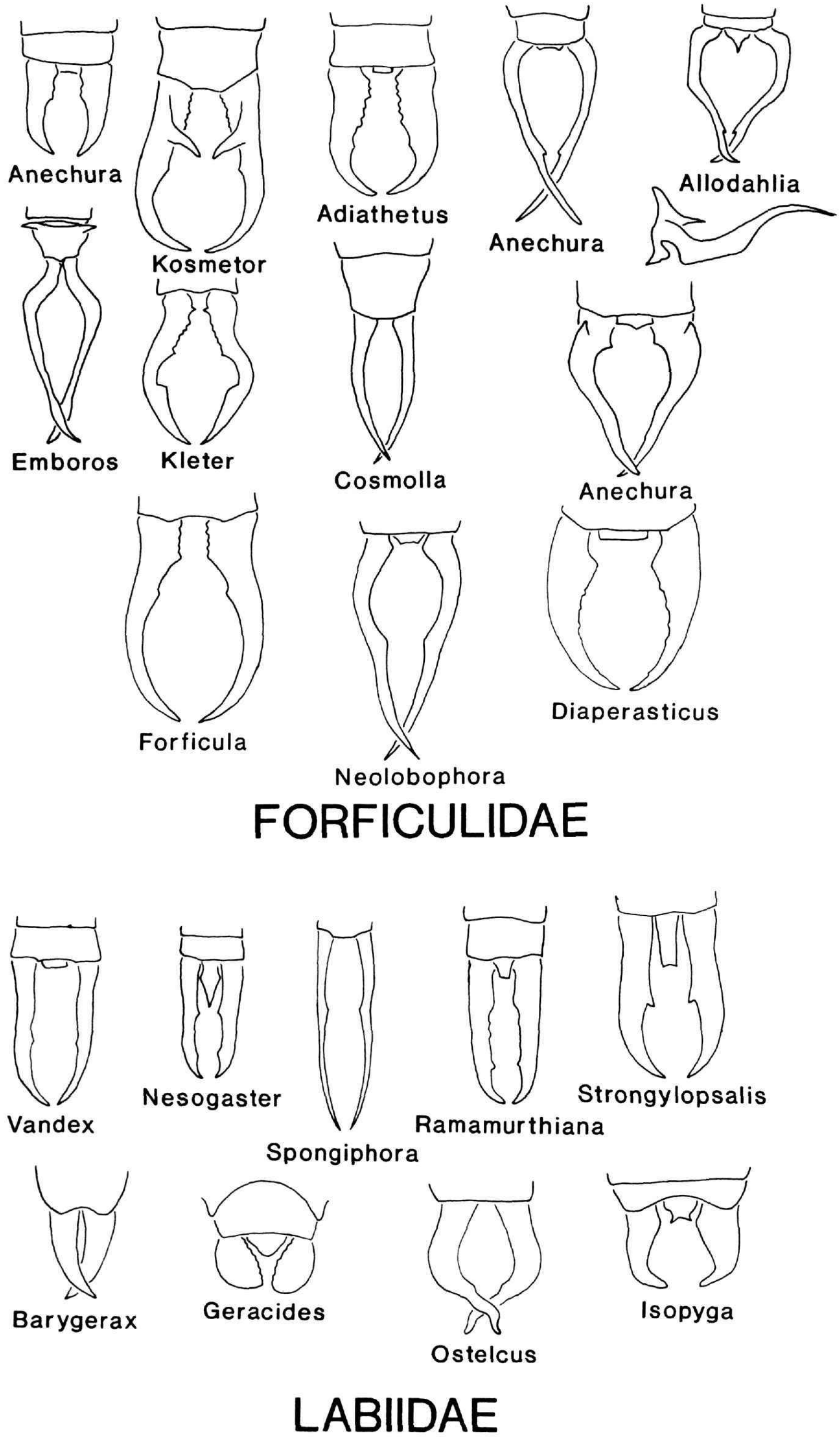

FIGURE 1.—Male cerci and pygidia of genera whose behavior has not yet been studied, illustrating the diversity of forms (not drawn to the same scale).

weapons in male-male aggressive interactions. A related possibility is that they function as aggressive display devices in battles between males. A final possibility, in the tradition of Darwin (1871), is that male cerci are courtship devices that males use to stimulate females in ways that increase the chances that the females will accept them as mates.

Except for the incomplete observations of Goe (1925) on *F. auricularia* and those of Moore and Wilson (1993) on *Vostox apicedentatus*, the observations needed to settle this controversy, i.e., detailed accounts of the animals' behavior in different contexts, have not been made. This study is a step in this direction, presenting descriptions of male-male aggressive behavior and male-female courtship in 13 species in 11 genera of 4 families of earwigs. The data suggest that nearly all the hypotheses are correct for at least some species. Modifications of male cerci and posterior portions of their abdomens appear to serve in different species as threats and/or weapons against conspecific males, as courtship devices, and perhaps to restrain females to facilitate copulation and insemination.

MATERIALS AND METHODS

Because the sexual dimorphism and divergent evolution of male cerci suggested a role for sexual selection, we observed males as they battled conspecific males and as they courted females. We paid particular attention to interactions in which the male-specific details of cercus morphology (as compared with the cerci of conspecific females) came into play. We used two criteria to judge whether a given male-specific trait performed a particular function. (1) Appropriate design: the mechanical properties of the male-specific modifications were appropriate to resolve interactions in ways favoring the possessor of the trait (for instance, the trait appeared to make a male more likely to win a battle with another male); and (2) Consistency: interactions in which the trait was involved in this way occurred repeatedly. A third type of data, involving interspecific comparisons of behavior and morphology, also helped in elucidating some traits.

Earwigs are fast, active animals, and they make rapid and finely graded adjustments in response to the behavior of other individuals, both when they are fighting and when they are courting (e.g., Figure 8). In addition, they show gradations in the "intensity" of their behavior. Thus, their behavior shows relatively low levels of stereotypy. As a result, our "consistency" criterion was more difficult to apply than in some other animals, such as horned beetles (Eberhard, 1979), which seem clumsier and less capable of fine behavioral adjustments. Rather than attempt a complete inventory of behaviors (probably a hopeless task in these highly flexible animals), we have described the most common types of behavior seen at different levels or intensities of interactions. Because it is not feasible to give complete, precise verbal descriptions of many of the complex interactions (especially aggression), we have included many illustrations traced from video recordings.

Male and female earwigs were captured in the field and kept in petri dishes with wet sponges, commercial dogfood, and pollen (Briceño and Eberhard, 1987). Animals whose behavior was to be observed were isolated individually for at least a week prior to the observations. Moore and Wilson (1993) showed that 7.5 hrs of isolation in *Vostox apicedentatus* was sufficient to minimize the effects of previous interactions.

Observations began immediately after a pair was placed in a container; usually, however, the animals were disturbed by the transfer and only began to interact several minutes later. All species were observed in small (5.4 cm diameter) plastic petri dishes that were placed on a blue background and covered with a plate of glass, or in shallow circular excavations in wooden boards, also covered by glass plates, and all were illuminated from above. Four species (*Doru taeniatum, Anisolabis maritima, Vostox quadripunctatus,* and *Paralabella dorsalis*) also were observed in tunnels carved in wood or sponge and covered with a glass plate. All observations were at room temperature (~20°–24°C). All behavior was videotaped with a National Nevicon Omnipro camera equipped with +6 closeup lenses at 30 frames/s and subsequently was analyzed frame by frame. The movements of fighting animals were so rapid that the unaided eye was unable to detect many details of the interactions.

In male-male interactions we paid particular attention to frames of the videotape in which one or both of the animals was blurred. Those frames portrayed the animals' most rapid movements and thus served as indicators of particularly forceful movements (blows, twists, etc., Figure 2). It was sometimes difficult to distinguish cause and effect when one animal's movements resulted in displacement of the other, but the slightly earlier initiation of movement by the aggressor (often a single frame of the video tape, 0.03 s), and occasionally his more solid and unvarying leg positions, usually allowed us to distinguish attacker from defender in each interaction.

All figures of behavior were traced from video images. Our descriptions are largely qualitative, and they concentrate on distinctive, repeated patterns. We have avoided presenting extensive quantitative analyses because we believe they would be misleading. Details of behavior, especially in male-male aggression, clearly varied intraspecifically according to the responses of opponents, as did the intensities of interactions. The length of time of observations and the numbers of specimens observed also differed between species.

Although there are pitfalls in any attempt to apply discrete and subjective labels to behavior, it seemed important and unavoidable to attempt to discriminate levels of intensity of aggressive interactions. The following examples of extremes illustrate how we distinguished levels of intensity. Some behavior, such as tapping an opponent with the antennae, was brief, differed little from preinteraction behavior, and was of little apparent consequence to the other individual. Interactions with these characteristics were termed low-level interactions. Other behavior, such as pinching another male with the cerci and turning him upside down, or throwing him across the petri

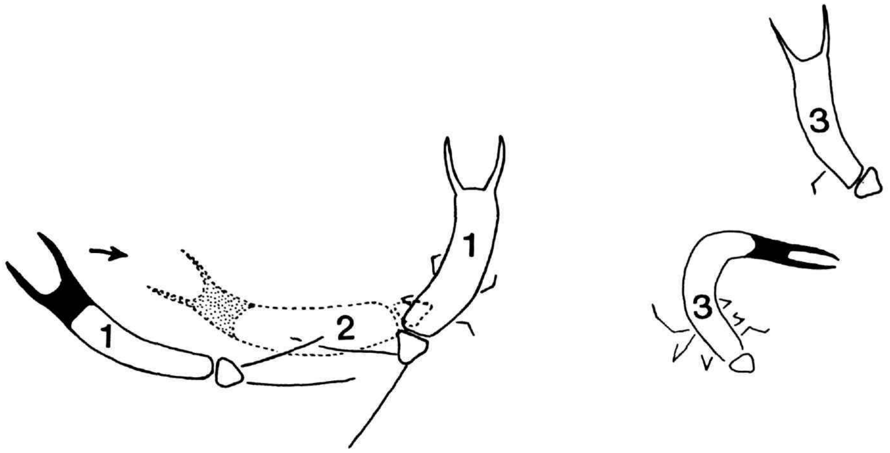

FIGURE 2. An aggressive male *Vostox quadripunctatus* (black) ran toward another male (1,2) and turned to deliver a strong lateral slam that ended with his abdomen twisted about 45° (3). Time between drawings: 1-2, 0.27 s; 2-3, 0.1 s.

dish, involved more substantial modifications of previous behavior and had much greater consequences for the other individual. Interactions including this type of behavior were termed high-level interactions. High-level interactions often involved especially quick, forceful movements (as judged by blurring in video images).

Although classification of extremes was relatively straightforward, intermediate behavior was not always as easily typified. Usually, however, we had a clear, although admittedly subjective impression of the levels of different behaviors. We probably were dealing with what is commonly termed levels of "motivation," but we have avoided the term because it implies knowledge of the animals' internal states that we did not have. Because our main objective is to correlate morphology and behavior, distinctions of levels of behavior are, in any case, of secondary importance.

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Results

A. MALE-MALE AGGRESSION: SHARED BEHAVIOR PATTERNS

Some behavior patterns occurred in most or all of the species examined. The most widely distributed aggressive patterns were at the extremes of very high and very low levels of interaction. They are listed in order of ascending level of aggression.

1. ANTENNATE.—The animal tapped and waved its antennae in the area just in front of its head while moving forward. Even in the well-illuminated observation chambers, antennae apparently were more important in sensing the presence of another individual than was sight. Thus, males sometimes immediately attacked others following first antennal contact, after previously repeatedly failing to respond even though they had passed within 1/4 body length of each other. This reliance on tactile stimuli is not surprising, given the generally nocturnal habits and dark, enclosed habitats of many earwigs. In some species, males performed apparent low-level threats by sustained rapid antennal tapping or lashing.

2. CURVE ABDOMEN TOWARD OPPONENT.—After touching or being touched by another animal, the earwig curved his abdomen laterally and/or dorsally so that the cerci projected toward the other individual. Low-level curving behavior was not followed by attacking movements. We call this behavior "presenting" in the descriptions below.

3. TURN 180° AND MOVE BACKWARD.—An earwig's first aggressive response to another animal in front of it usually was to turn 180° to direct its cerci toward the other individual. Usually the cerci were spread during such a turn. Movement backward toward the other individual often followed a turn, and in some cases it occurred during the turn itself. In some cases the male moved backward by taking several running steps. The speed of a turn also varied, especially in aggressive interactions, with low-level behavior being executed more slowly.

4. STRIKE AND SLAM.—The posterior part of the body was launched rapidly backward (strike) or to the side or dorsoventrally (slam). These movements often were produced by turning

most or all of the body (Figure 3) or by moving directly backward (Figure 4). Even large species moved so fast in strikes that the video image (0.03 s in duration) was very blurred. In some cases the cerci closed during a strike or a slam in an apparent attempt to pinch the opponent (Figure 5-2). In others, the cerci stayed open in an apparent attempt to strike a blow with either the pygidial area (Figure 6) or with the side of one cercus (Figure 3).

5. PINCH.—The cerci were closed forcefully. If there was an object between them (e.g., another earwig's body), they held

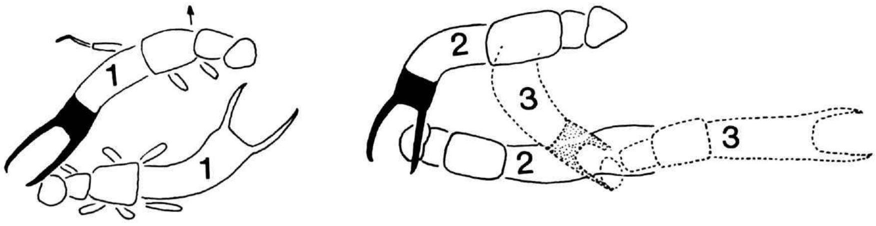


FIGURE 3.—An aggressive *Vostox quadripunctatus* male (black) slammed laterally at his opponent (2,3), driving him backward a full body length. Time between drawings: 1-2, 0.03 s; 2-3, 0.07 s.

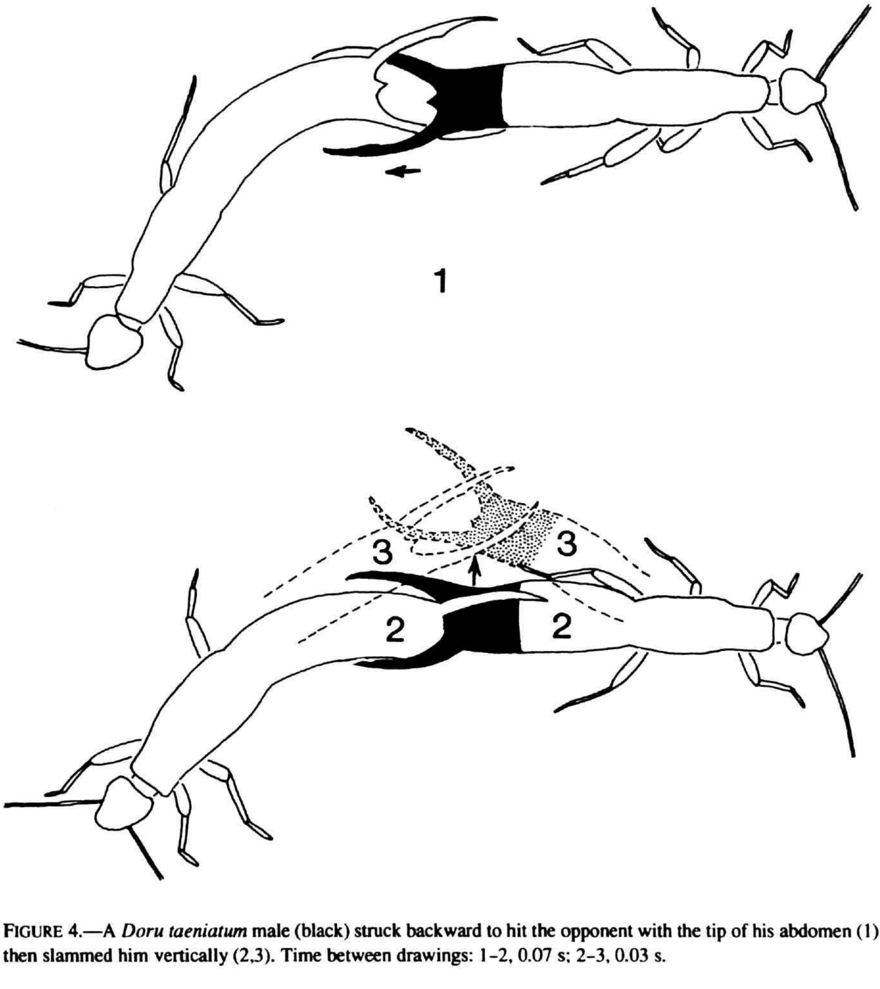


FIGURE 4.—A *Doru taeniatum* male (black) struck backward to hit the opponent with the tip of his abdomen (1), then slammed him vertically (2,3). Time between drawings: 1-2, 0.07 s; 2-3, 0.03 s.

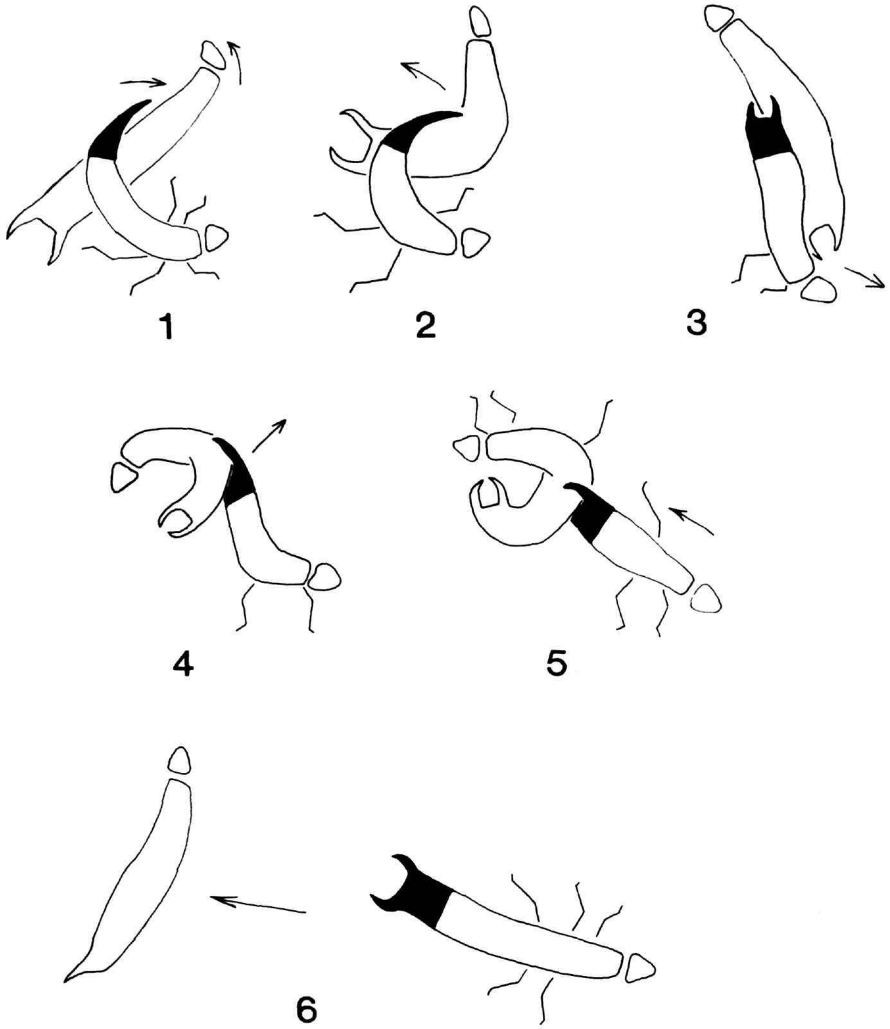


FIGURE 5.—An aggressive male *Anisolabis maritima* (black) struck rapidly backward (1), seized the abdomen of the other (2), and lifted him so that he lost contact with the substrate (3). The attacking male then moved rapidly backward, shook his opponent (4,5), and then threw him (6). Time between drawings: 1-2, 0.03 s; 2-3, 0.18 s; 3-4, 0.27 s; 4-5, 0.07 s; 5-6, 0.03 s.

on tightly at least momentarily. In mutual pinches both animals pinched each other simultaneously. It was very difficult to distinguish short-duration pinches during some extended close-range struggles; we were generally unable to distinguish pinches lasting less than 0.1 s. Some short-duration pinches were detected when the pinch by one animal displaced the other's body at least slightly. On rare occasions (seen only in two species) a pinch resulted in physical injury.

B. MALE-MALE AGGRESSION: SPECIES DESCRIPTIONS

The species descriptions below are arranged taxonomically according to Reichardt (1968a,b, 1970, 1971a,b): *Doru, Skalistes, Metrasura,* and *Ancistrogaster* are in Forficulidae (each in a different subfamily); *Sparatta, Vostox, Paralabella,* and *Pseudomarava* are in Labiidae; *Anisolabis* and *Carcinophora* are in Carcinophoridae; and *Pyragra* is in Pygidicranidae. In each species, high-level aggression is described first, followed by lower levels of aggression. Sample sizes are given in terms of pairs of males videotaped.

1. *Doru taeniatum* (Dohrn)

This species was common on corn plants and was active day and night. The earwigs were most common in the leaf sheath, which envelopes the stalk, where they took refuge, mated, and

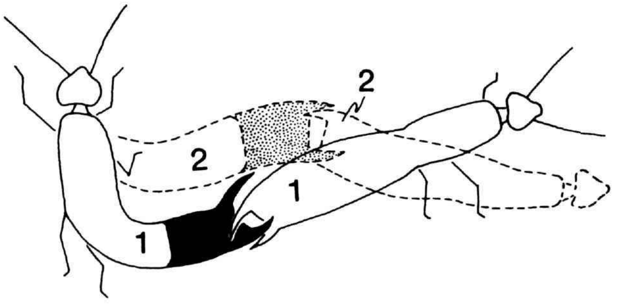


FIGURE 6.—A *Paralabella dorsalis* male (black) pushed backward by extending his abdomen, struck the opponent, and pushed him with his pygidium. Time between drawings: 0.07 s.

laid eggs (Briceño and Schuch, 1988). They were observed on several occasions in small refuges made by biting through the sheath in order to enter the space between the sheath and the stalk. On several occasions in the field, males were observed fighting over refuges containing females. The resident male blocked the entrance with his cerci. If the intruder persisted in attempting to enter, the resident backed out onto the stalk, and they fought using behavior generally similar to that seen in captivity.

The males of this species differ from females in having longer, curved cerci with a single large tooth on the inner edge, a series of smaller teeth nearer the base of the cerci, and a sharply pointed pygidium (Figure 7).

We taped 7 high-level and 25 lower-level aggressive

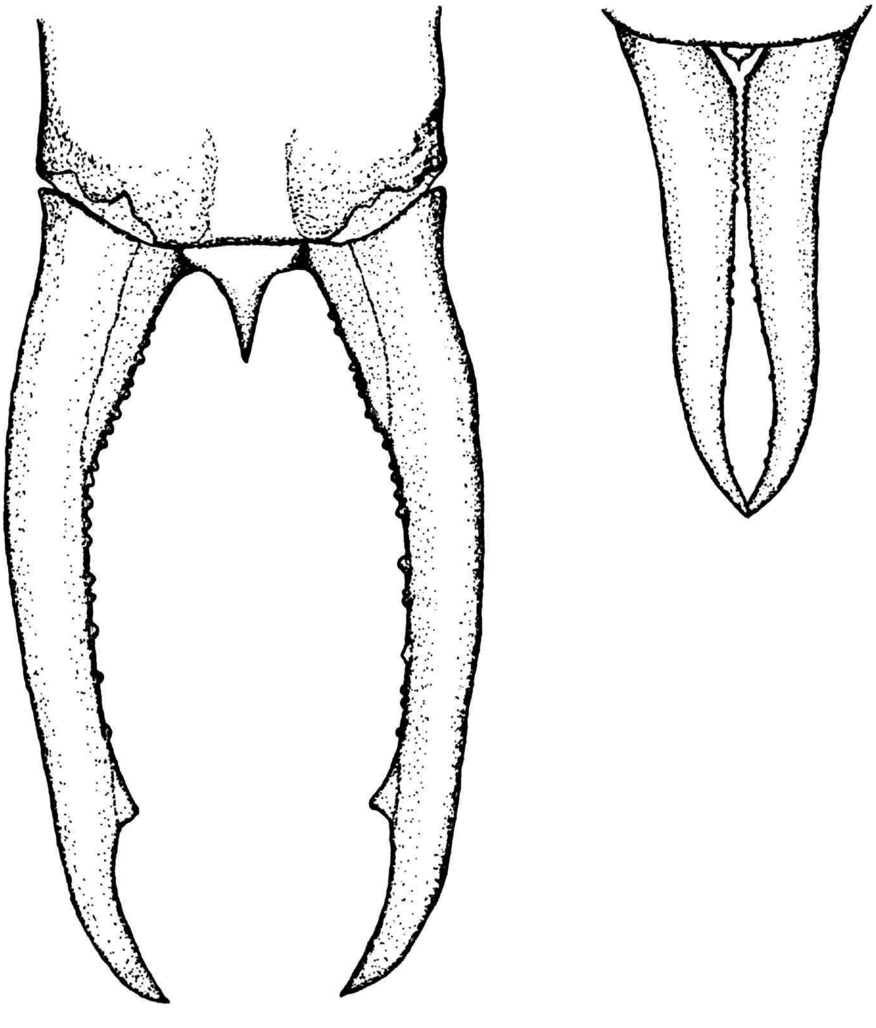


FIGURE 7.—Posterior portions of male (left) and female (right) *Doru taeniatum*.

interactions in captivity. Pygidium-pygidium tests of strength with rapid backward pushes and dorsally directed slamming movements were especially important. These sequences always began with a series of cercus-cercus taps in which one or both males used his cerci to strike the other's cerci with one or more small, sometimes brisk blows. Occasionally one male retreated after only this tapping and hitting, but usually the two came together so that their cerci interlocked and the pygidium of at least one touched the other (Figure 4). In some cases, males made lateral or ventral slamming movements while interlocked (Figure 4), but the most common energetic moves were backward strikes, sometimes produced by extending the abdomen and rocking back on the legs and other times by taking one or more steps backward. Strikes often were combined with or immediately followed by a dorsally directed slamming movement. Probably, though we could not always be sure, they also were accompanied by a brief pinch using the entire length of the cercus (Figure 8-1,2); it was clear that cerci often were brought together as a backward strike was launched. Usually the pygidium contacted the opponent during a backward strike (Figure 4), and frequently a slam ended with a twist of the abdomen that sometimes displaced the opponent (Figure 9). If his cerci lost contact with the opponent, an aggressive male swung his abdomen laterally and also dorsoventrally in apparent attempts to reestablish contact.

The result of a successful attack with a backward strike and dorsal slam was to push the opponent's abdomen upward so his hind legs were stretched or lifted off the substrate (Figures 9, 10) and to displace his body anteriorly. Five battles ended when one male fled after his opponent had just attacked with a backward strike and dorsal slam.

Subtle forceful lateral and twisting movements undoubtedly also occurred during pygidium-pygidium interactions. Occasionally an apparently minor movement of one male resulted in a rapid displacement of the other, suggesting that strong force had been applied (e.g., Figures 11, 12) or that a forceful movement of the opponent had been deflected (Figure 8). These forceful movements were probably brief; prolonged twisting interactions, such as those of *Skalistes inopinata* (below), were never seen.

Males moved their abdomens actively in both lateral and dorsoventral directions while interlocked. In contrast to the sustained periods of strong backward pushing in the pygidium-pygidium pushing battles of *Vostox quadripunctatus* (below),

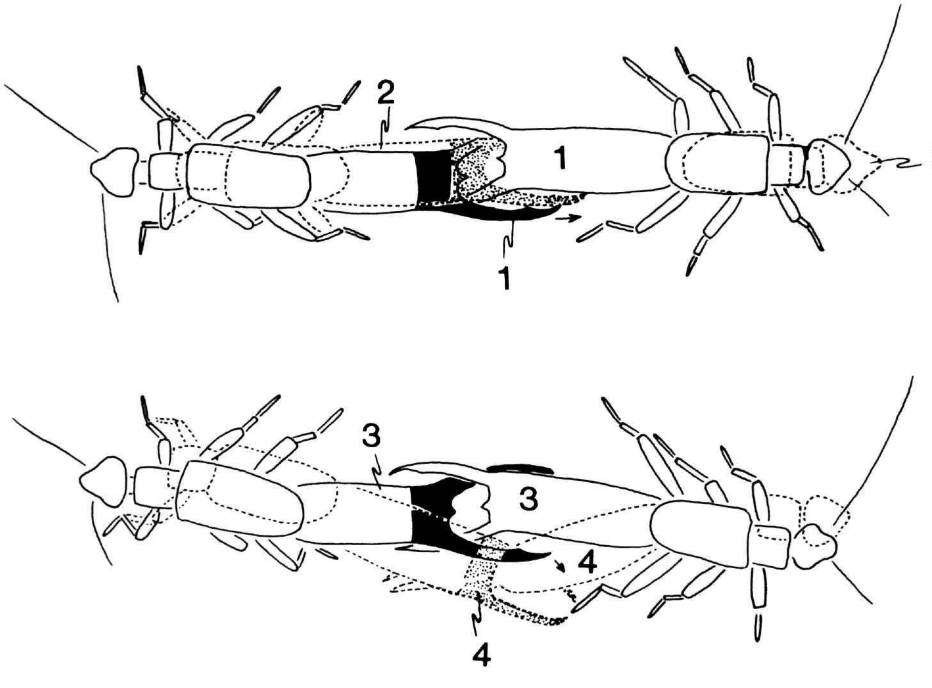


FIGURE 8.—A *Doru taeniatum* male (black) rocked backward on his legs to strike at another male (1,2), closing his cerci on the other male's abdomen (2). He then made a second backward strike, rocked on his legs again (3,4), but this time the other male deflected the strike to the side, avoiding both being pinched and being pushed forward. Time between drawings: 1-2, 0.1 s; 2-3, 0.09 s; 3-4, 0.13 s.

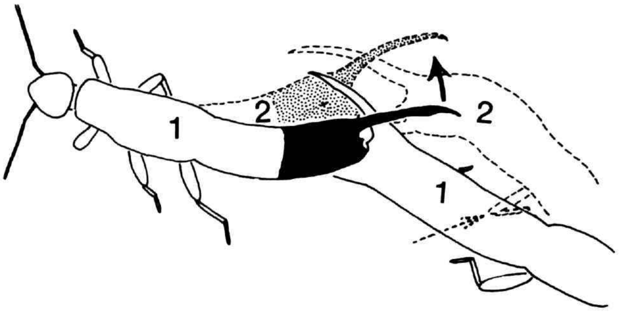


FIGURE 9.—Following a dorsal slam (not shown), a *Doru taeniatum* male (black) slammed laterally and simultaneously twisted his abdomen, which caused the right rear leg (dotted arrow) of the other male to lose its foothold. Time between drawings: 0.97 s.

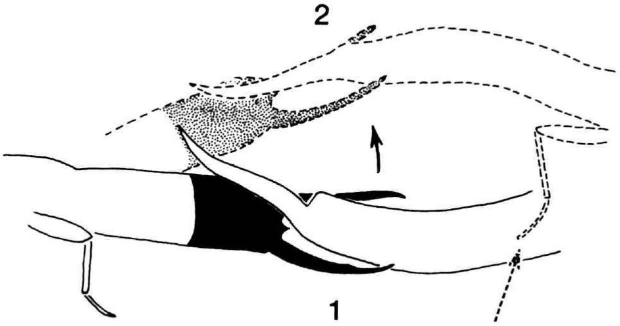


FIGURE 10.—A dorsal slam followed by a twist by a male *Doru taeniatum* (black) momentarily lifted the other male's near hind leg off the substrate (dotted arrow at bottom). Time between drawings: 1-2, 0.1 s; 2-3, 0.03 s.

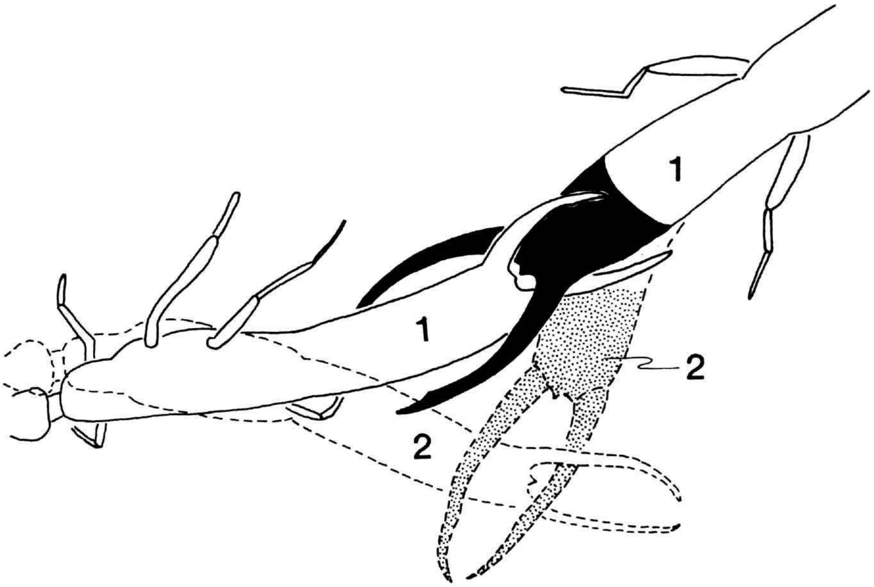


FIGURE 11.—Immediately following a backward strike (not shown), a *Doru taeniatum* male (black) made a lateral upward slam and twist. The left cercus of the attacking male snapped across the lateral margin on his opponent's abdomen, indicating that strong force had been applied. Time between drawings: 0.07 s.

males of *Doru* usually appeared to give only brief, intense pushes. In addition, their backward strikes were more consistently associated with dorsal slams.

An apparently defensive behavior involved lowering the tips of the cerci to rest on the substrate. This behavior occurred in some tapping interactions, and it may function to prevent the opponent from getting a lower, advantageous position.

On two occasions a fight ended when one male gave a long pinch to the other and caused him to flee, pulling the pinching male behind. In at least one case the pinch may have been mutual, at least during part of the time, as both males seemed to pull and twist to escape. Pulling was so strong in this interaction that the abdomens of both males were perceptibly extended.

The tapping preceding and during pygidium contact involved the cerci and not the pygidia. They did not consistently involve any particular behavior patterns. Different portions of the cerci tapped against different parts of the opponent's cerci

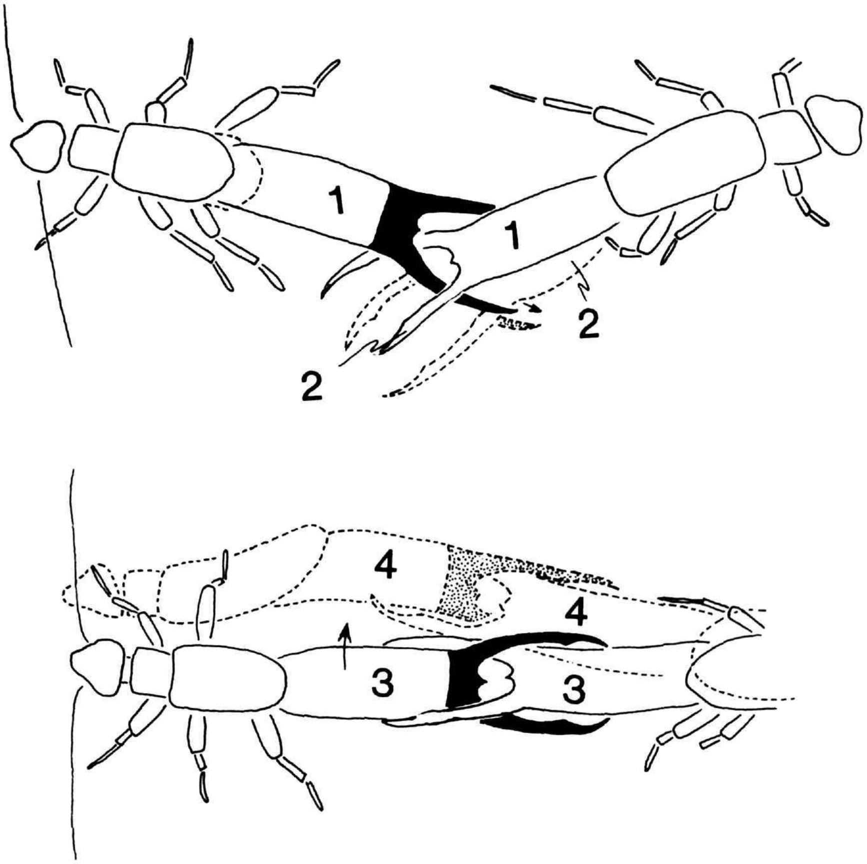


FIGURE 12.—A male *Doru taeniatum* struck backward (1,2), but his entire body then was displaced laterally by a swing of the other male's abdomen (3,4). Time between drawings: 1-2, 0.07 s; 2-3, 0.18 s; 3-4, 0.07 s.

and the posterior portion of his abdomen. These movements were probably at least partly exploratory, as each individual usually moved his abdomen more or less continually.

Lower-level interactions involved antennal lashing, lateral and dorsoventral swinging of the abdomen after loss of contact with an opponent or after first being contacted (some swings in this context were quite energetic and formed a continuum with slams), running toward the opponent, mouthing the opponent (especially on his cerci), and presenting the cerci. Forceful attacks (slams, strikes) usually were not launched immediately following first contact; however, there were exceptions. In one case, a male struck and attempted to pinch the posterior portion of his opponent's abdomen following a series of cercal taps but without ever having interlocked cerci with his opponent.

Apparent homosexual courtship, with one male tapping the other with his cerci, was observed nine times. In seven cases, the male also quivered as do courting males when they produce substrate vibrations (Briceño and Schuch, 1988).

2. *Skalistes inopinata* (Burr)

During the day, this species was found in forks of large branches, on trunks of trees up to 5 m above the ground, and in a house; at night it was found on rotting *Anona* sp. fruit and on rotten wood.

Male cerci differ from those of females and nymphs in being longer and more crescent-shape. In addition, they have a horn-like triangular process that projects dorsally near the base (Figure 13). Male cerci have only a few teeth on the inner margin near the base (Figure 13).

We taped 7 high-level and 8 lower-level aggressive interactions. High-intensity aggression involved pinching. Most pinches were unilateral; in only 2 of 18 pinches did males seize each other simultaneously. Unilateral pinches usually were short in duration, lasting an average of 7.9 ± 19.5 s (N = 17, median = 0.7, range = 0.1–71.1). The pinching male usually released the other spontaneously rather than

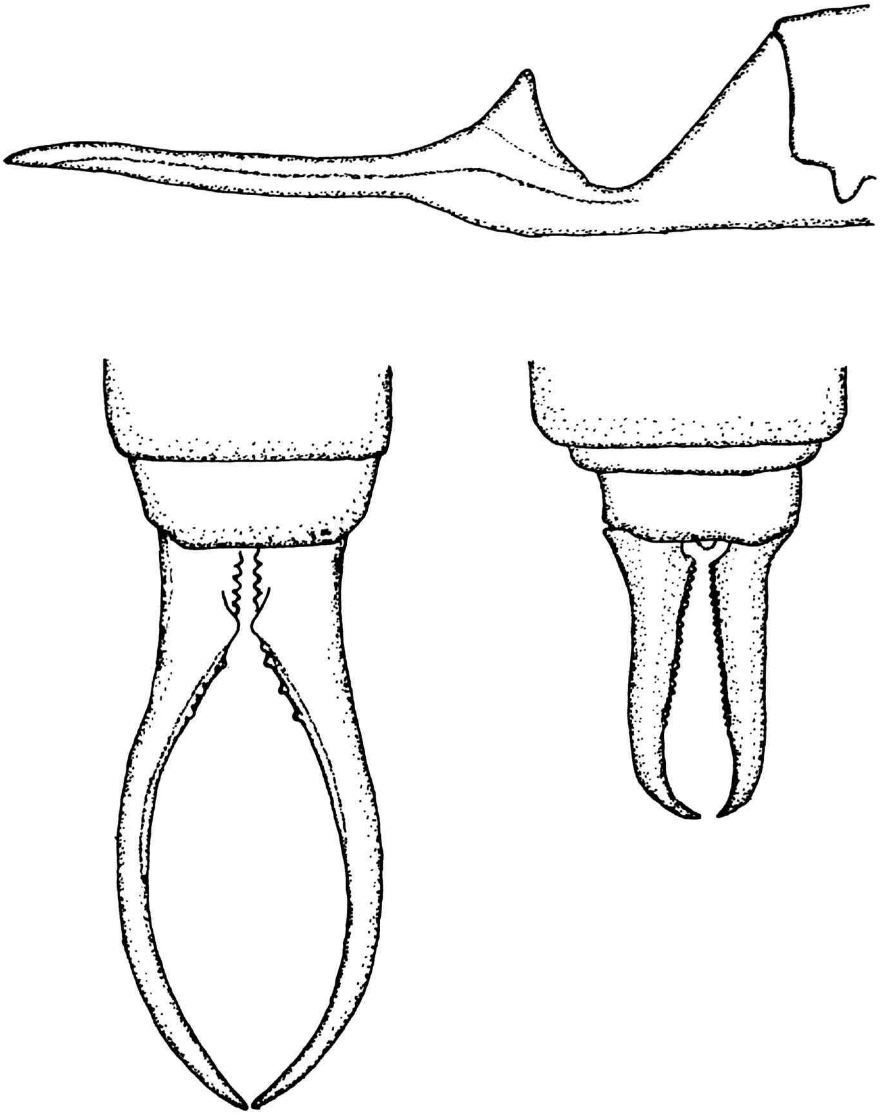


FIGURE 13.—Posterior portions of male (left and top) and female (right) *Skalistes inopinata*.

being forced to do so.

Some pinches were on the cerci or at the posterior tip of the opponent's abdomen, and they were released relatively quickly. In six cases, the opponent was seized farther forward, with the distal, tong-like portion of the cerci (Figure 14). The pinching animal almost immediately twisted his abdomen so as to lift the opponent off the substrate and turn him upside down (Figure 14-3). Sometimes the pinching male then turned him back so the other male was right-side up again; in other cases the second male struggled and twisted to bring his tarsi back into contact with the substrate. In one mutual pinch one male was turned upside down, but he regained his footing, twisted his own abdomen, and turned the first male upside down twice in succession.

In general, forceful movements, such as strikes and slams, were relatively rare in this species as compared, for example, with *Doru taeniatum*, or with *Carcinophora* spp. and *Vostox quadripunctatus* (below). In some cases, however, one male swung his abdomen vigorously in an apparent attempt to slam against the other. In most of these swings (17 of 29), the male's

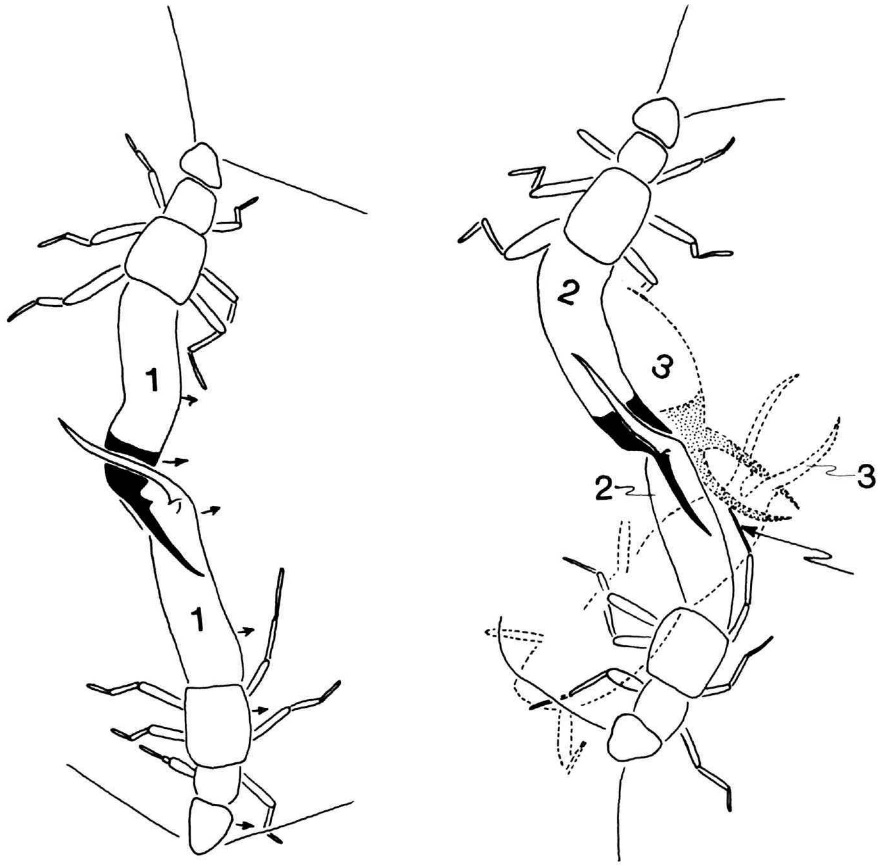


FIGURE 14.—A male *Skalistes inopinata* (black) pushed another male laterally while they were locked together (1). The lateral displacement of the entire body of the opponent (arrows at left) indicates that he was tensing his body; probably each male was pressing hard against the other. The opponent's foothold then began to slip (2, arrow indicates left hind leg that had started to slip), and then the attacking male turned the other upside down with a quick twist of his abdomen (3). Time between drawings: 1-2, 0.17 s; 2-3, 0.07 s.

abdomen was twisted so that the dorsal surfaces of his cerci (including the triangular processes) would hit the opponent; in nine other cases the male hit his opponent with the ventral surfaces of his cerci. It was not always easy to distinguish between vigorous tapping and weak slamming movements, especially because some apparent "slams" ended just as they reached the site where the other animal was, or had been when the slam was initiated. Some males made one or more apparent slamming movements while pinching the other male; in six of seven such cases the slams were directed dorsally. The quickest, most energetic movements were *withdrawals* from contact and twisting movements of the abdomen during pinches.

Lower-level aggression was much more common and included presentations in which the abdomen was bent forward and also twisted 90° so that one cercus was above the other, and the dorsal triangular structures were on the side closest to the opponent (or at least where the opponent had been when the maneuver began) (106 cases). Sometimes the aggressor's cerci touched the opponent on the abdomen or cerci (Figure 14), and sometimes they were held immobile in this position. More often (71%) the posterior end of the abdomen was swung in an apparently exploratory fashion, especially in a dorsoventral direction (which, because of the abdomen's turned and twisted position, gave the cerci an anteroposterior movement). Other presentations involved touching the opponent one or more times with the dorsal surfaces of the cerci. Usually swinging movements were relatively slow and short, and the quickest movements were short withdrawals when the cerci had made brief contact with the opponent. This pattern of movement reinforces the impression that the swings generally had an exploratory function.

A puzzling behavior seen in several pairs of males was apparent homosexual courtship (behavior indistinguishable from courtship directed toward females; see below) and repeated copulation attempts. In some cases, the male being "courted" responded aggressively, presenting and tapping as described above, or even pinching. The "courting" male usually continued his courtship unless the aggressive response of the other became forceful. In other cases, the courted male responded by twisting the tip of his abdomen 90° as would a receptive female, and the two males spent extended periods (up to 50 s) actively rubbing their genital areas against each other as if attempting intromission. On at least 14 occasions, it was clear, when males pulled apart momentarily, that one had at least partially everted his genitalia (Figure 15). In some cases, both males everted their genitalia during such interactions. Four apparent homosexual copulation attempts either immediately preceded or followed aggressive movements, such as presentation or a soft slam, by the same male (behavior patterns never seen in males courting females), so it was not clear whether homosexual courting represents cases of mistaken identity or fighting behavior in which primary male genitalia are used (an unusual if not unique phenomenon; Eberhard, 1985).

Another common, slightly lower-level aggressive behavior was to run toward the opponent, often hitting him one or more times (if he fled) with the head (especially the mouthparts). Such running attacks, which were unusual in that the abdomen was not bent farther toward the opponent than it was at the start of the attack, were seen 31 times. This type of interaction sometimes was associated with touching the other repeatedly with the mouthparts ("mouthing"), which occurred on 17 occasions. Usually the mouthparts contacted the cerci and/or posterior portion of the other male's abdomen.

3. *Metrasura ruficeps* Burmeister

This species was found during the day in bromeliads, under accumulations of leaf litter, and under other decaying vegetable matter. At night individuals were found in exposed sites, such as flowers and leaf surfaces, in both woody and herbaceous vegetation up to 3 m above the ground.

Male-specific cercus characters include much greater length, a pair of teeth on the inner margin about 1/3 of the distance from the tip, and a wider, less pointed pygidium (Figure 16).

We taped 2 high-level and 31 lower-level aggressive interactions. High-intensity interactions involved pinches as well as pygidium-pygidium contact accompanied by apparent blows, twisting, and prying movements with the cerci. Pinches usually were unilateral and brief. They almost never occurred as a part of a strike; instead they followed extensive cercus-cercus and/or pygidium-pygidium contact.

FIGURE 15.—Eversion of genitalia (arrow) by a male *Skalistes inopinata* (black) during homosexual "courtship." The entire genital structure was retracted 0.07 s later. In some cases, the everted genitalia of one male contacted the other near his genital opening.

Many pinches were accompanied by apparent attempts to break the opponent's hold on the substrate and/or to fling him (Figures 17–19, 22). In one case, a male was seized on the thorax (apparently by surprise) and was thrown several body lengths with such force that he crashed into the side of the petri dish and bounced back more than one body width (Figure 19). The throwing movement in this and one other throwing sequence was clear: rather than involving a dorsal-ventral or a lateral movement of the abdomen and cerci as one might expect, it was mostly a very quick twisting movement (note abdominal twist and lack of dorsal "follow-through" in Figure 19). Presumably the twisting movement caused the opponent to lose his foothold.

In five cases, a pinching male shook his opponent back and forth (up to four times in 1.3 s; the most rapid shake was three times in 0.8 s), either by repeatedly twisting his abdomen or by moving back and forth in a dorsal-ventral direction in apparent attempts to loosen the opponent's hold on the substrate or to keep him from regaining his footing. In at least some cases, the pinching individual twisted his abdomen with each shake in a way appropriate to break the other's foothold on the substrate.

The portion of the cerci used to pinch the other individual varied greatly. In some cases only the distal half was used (Figure 18); in some only the basal portion was used (Figure 17); and in others (probably the majority) more or less the entire length of the cercus was used to grasp the opponent (Figure 20).

During prying movements, in contrast, the tips of the cerci contacted the opponent (Figure 21). The great length of the cerci aided in making prying effective because the tips of the cerci were near the opponent's legs (Figure 21). The fulcrum of a prying movement apparently was the pygidium of the other male where it contacted the pygidium of the attacker (Figure 21).

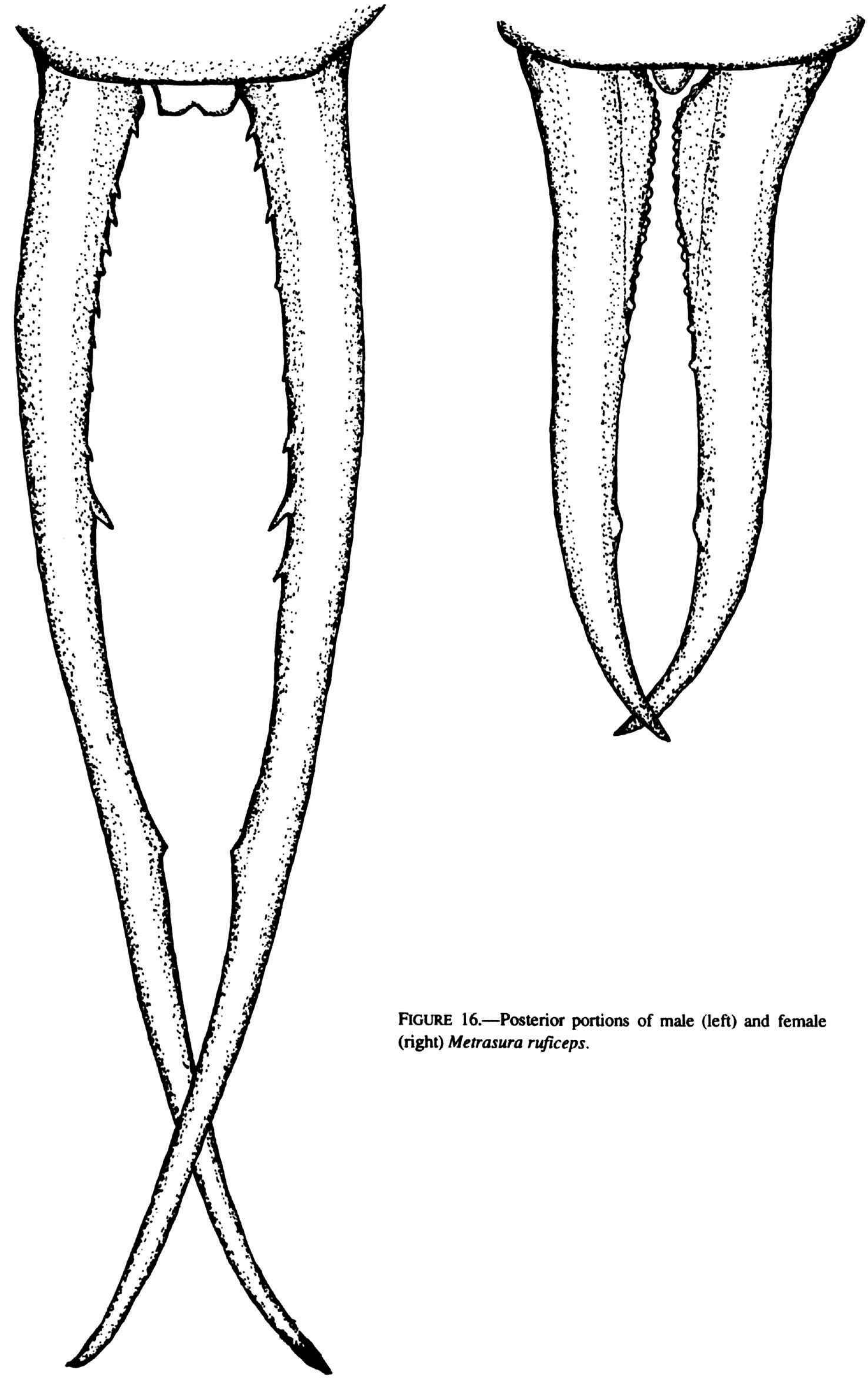


FIGURE 16.—Posterior portions of male (left) and female (right) *Metrasura ruficeps*.

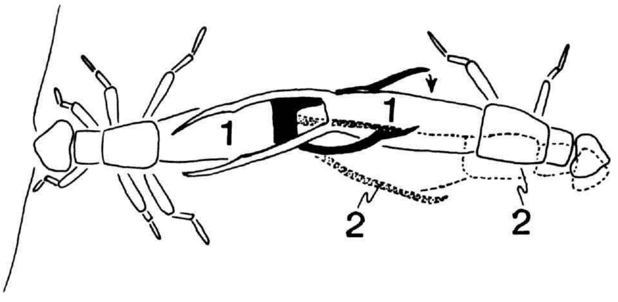


FIGURE 17.—A male *Metrasura ruficeps* (black) pried another male's entire body laterally (2) by pinching with the basal portion of his cerci as he swung his abdomen ventrally and laterally. His right cercus also pried against the side of the other male's abdomen. Time between drawings: 0.1 s.

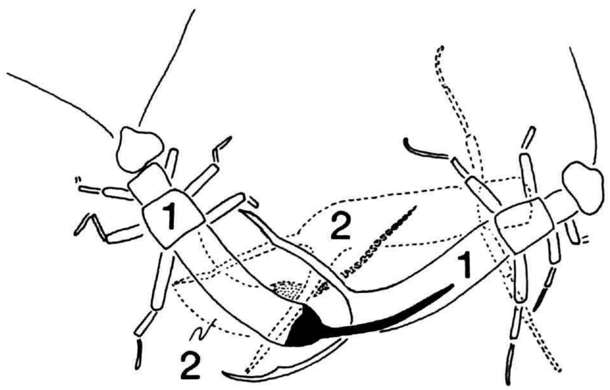


FIGURE 18.—An aggressive *Metrasura ruficeps* male (black) seized another male, pried him laterally, and pulled him nearer (2). The attacking male's cerci apparently gripped the other's body with the tooth on the inner surface (note point of rotation). Note also the braced and powerful positions of the legs of the attacking male and the spread-eagle, weak positions of the other male's legs (2). Time between drawings: 0.17 s.

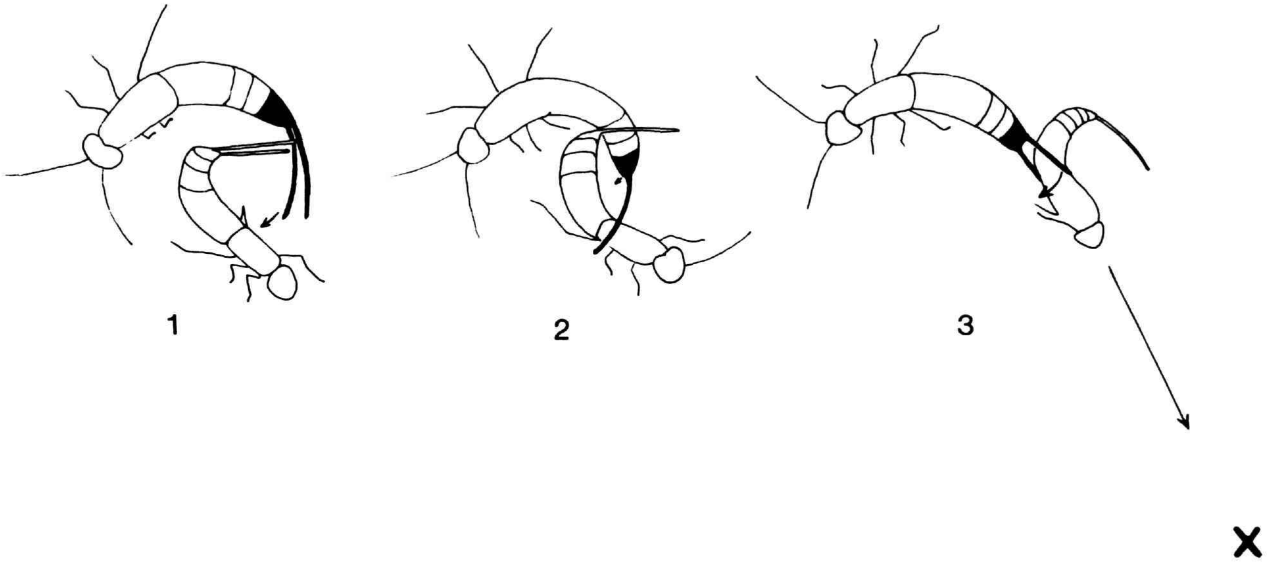


FIGURE 19.—A male *Metrasura ruficeps* (black) seized a passing male (1,2) and then flung him across the petri dish with a short but powerful flick of his abdomen (3) (he hit the wall at X). The attacking male's swing was arrested at approximately the position in (3), and then he twisted back (arrow). Time between drawings: 1-2, 0.2 s; 2-3, 0.2 s.

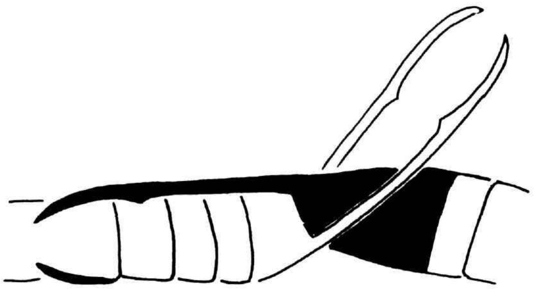


FIGURE 20.—A male *Metrasura ruficeps* (black) pinched another male that attempted to pull away. The entire length of the cerci appeared to pinch the opponent's abdomen.

As illustrated in Figures 22 and 23, some displacements followed a whip-like dorsal-ventral blow in which the cerci or the tip of the abdomen struck the abdomen of the opponent. In some cases, the cerci were twisted following a blow (Figure 23); when successful, this caused the opponent, whose hold on the substrate probably had been somewhat loosened by the blow, to be displaced. Twisting movements sometimes turned the opponent onto his side or upside down. On several occasions a male apparently attempted one of these maneuvers, which caused the opponent's abdomen to bend and/or his legs to strain in position, but failed to dislodge him.

The most powerful movements seemed to occur when a male straightened his abdomen from a curved position (e.g., Figure 22). Some "footwork" of some males during fights probably represented attempts to put themselves into such curved positions so as to increase their ability to launch forceful attacks. In some cases, one of the males, after having made cercus-to-cercus contact, walked partially around his opponent to face in the same direction, curved his abdomen so as to maintain cercus contact, and thereby positioned himself so that he could produce a lateral displacement of his opponent by straightening his abdomen.

High-intensity fights involved extended struggles in which pygidium-pygidium contact was nearly continual and the cerci repeatedly contacted the sides of the opponent's abdomen. Each male's abdomen and cerci usually were in nearly continuous motion, and occasionally one male made a strong dorsal or ventral slamming movement. Many of these had no apparent effect on the other animal. It seems likely that during these interchanges each male was attempting to position himself in relation to his opponent so that he could deliver an effective displacement attack, but at the same time to avoid being attacked successfully himself. Because males moved their abdomens and cerci quite rapidly, and usually were positioned rear end to rear end with their antennae out of contact with the opponent, probably a certain amount of their behavior was slightly misdirected. In addition, some slamming movements appeared to hit their mark but failed to dislodge the opponent. Perhaps due to a combination of these complicating factors, generally it was impossible to understand in functional terms most of the many movements during pygidium-pygidium struggles. It is also possible that some of the pygidial and/or cercal contact constituted threat behavior.

Males of *M. ruficeps* clearly differed from those of many other species in that they almost never launched rapid movements, such as strikes or slams, immediately after an initial contact, even in high intensity interactions. Instead, their strong, forceful movements were made at close quarters after cercus and often pygidium contact had occurred. When a male contacted another individual, he curved his abdomen forward, either laterally or sometimes dorsally, or turned 180° and then moved relatively slowly toward the opponent (seldom producing a blurred image on the video). Often the male swung his abdomen from side to side in apparent exploratory movements

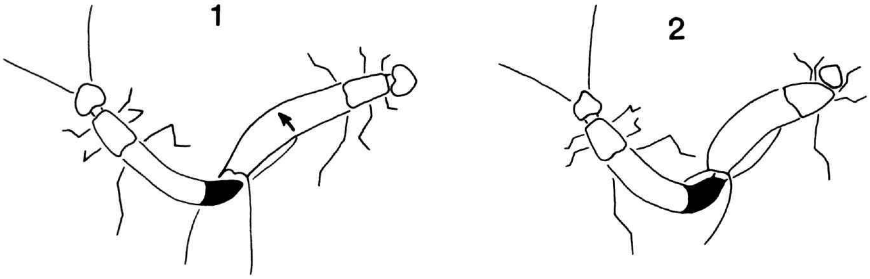


FIGURE 21.—A male *Metrasura ruficeps* (black) used his long cerci to pry an opponent by flexing his abdomen dorsally and possibly twisting it (1), which caused the other male to momentarily lose his footing (2) with most of his legs. Time between drawings 0.03 s.

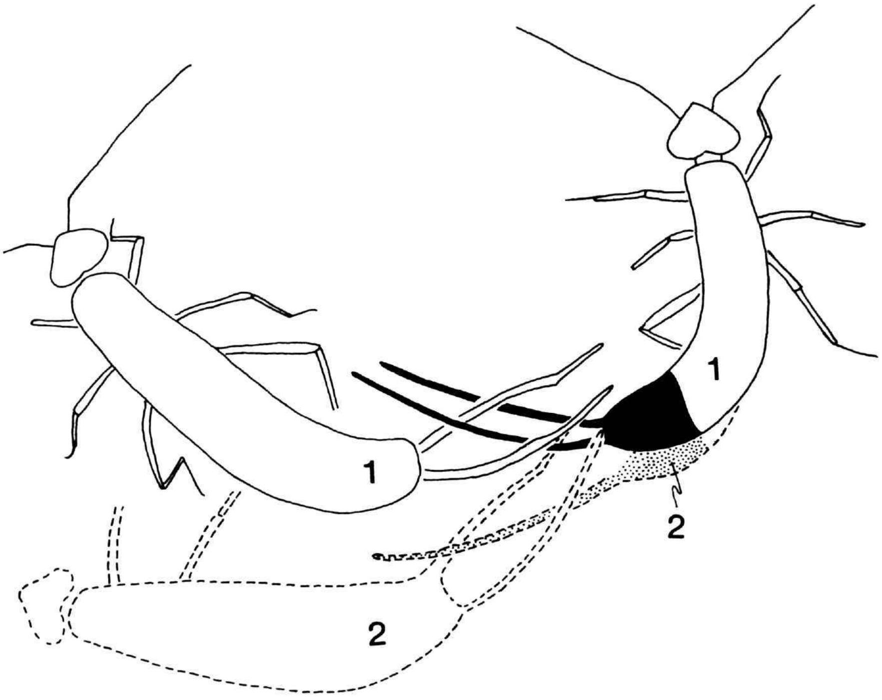


FIGURE 22.—A short slam (flick) by a male *Metrasura ruficeps* (black) resulted in the opponent being displaced laterally about two body widths. Time between drawings: 0.1 s.

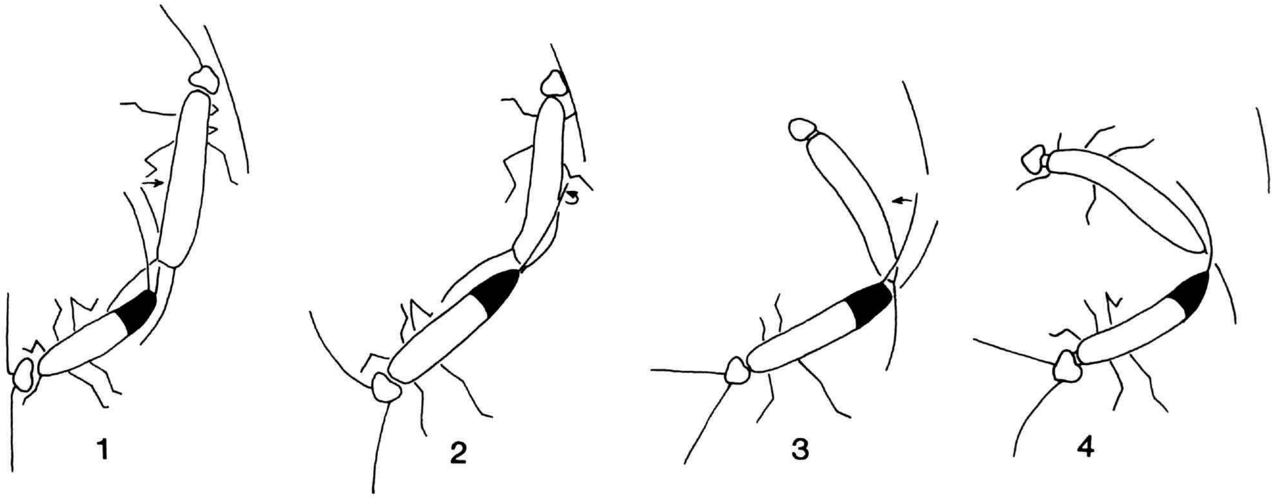


FIGURE 23.—An aggressive *Metrasura ruficeps* male (black) made a ventral slam (1,2), followed by a twist (2), and then a dorsal slam (3,4). The ventral slam displaced his opponent's abdomen laterally, which caused the abdomen to curve and his head to collide with the side of the petri dish (curved line in 2). The twist by the aggressor then caused the opponent's anterior end to be displaced to the left (3), and the dorsolateral slam that followed displaced him even more (4). Time between drawings: 1–2, 0.23 s; 2–3, 0.1 s; 3–4, 0.07 s.

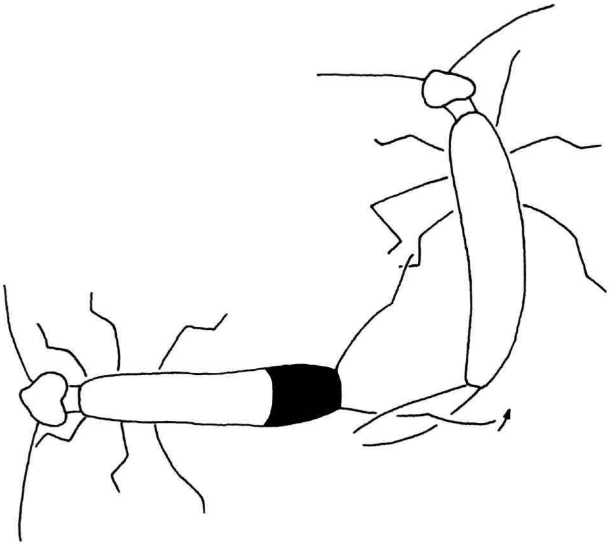


FIGURE 24.—An aggressive *Metrasura ruficeps* male (black) opened his left cercus and moved his abdomen to the left, apparently using his cercus as an antenna to locate the other male.

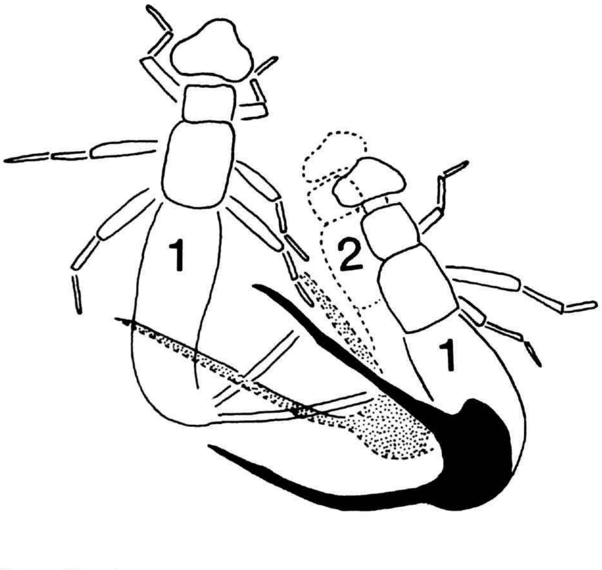


FIGURE 25.—An aggressive *Metrasura ruficeps* male (black) stabbed at, but failed to hit, another male with his open cerci. Time between drawings: 0.1 s.

as he moved backward. In some cases, the cerci were opened much wider than necessary to grasp the opponent (Figure 24), and they may have been used as sensory organs to locate (and perhaps threaten) the other male.

Lower-level aggression consisted of dorsal or lateral presentations of cerci and repeated touching or tapping of cerci against each other, often with one male backing toward the other while the other moved away. Often the cerci were not simply curved forward, but rather they were moved forward and backward repeatedly in a sort of "pawing" or "stabbing" movement (Figure 25). In no case did the cerci actually stab forcefully against the opponent's body.

Another low-level behavior was antennal lashing, in which one or both individuals swung the antennae in unusually wide arcs at unusually high velocities. The high speed and frequent reversal of direction resulted in the antennae often being bent in videotape images. Antennal lashing was not performed in higher-level interactions, even though males frequently touched one another with their antennae.

On seven occasions, one male tapped the other with the ventral surfaces of his cerci in a pattern similar to courtship. Some courting movements were associated with apparently aggressive acts, so, as with *Skalistes*, it is not certain whether or not this "homosexual courtship" resulted from mistaken identity.

4. *Ancistrogaster scabilosa* Steinmann

This species was found during the day in bromeliads at elevations of approximately 2000 m and under boards and decaying vegetation on the ground at 1300 m near San José.

Male cerci are widely separated at the base, long, mostly smooth, and strongly curved, with expanded tips that have a pair of prominent teeth. Those of the female are shorter, smooth, nearly straight, and sharp (Figure 26). In addition, several of the male's posterior abdominal tergites have lateral extensions (Figure 27).

We taped 7 high-level and 51 lower-level aggressive interactions. High-intensity combats in this species did not appear to involve tests of strength, as in, for example *Doru*, *Metrasura*, and *Vostox*, and instead were more ritualized. All battles began with a series of short blows with various portions of the cerci and abdomen on the head, thorax, abdomen, or cerci of the opponent (Figures 28, 29). In some cases, the males met cercus-to-cercus and struck each other on their dorsal surfaces with their cerci (Figure 28). As the intensity of the blows they gave each other increased, they both raised their abdomens until they were nearly perpendicular with the surface on which they walked (Figure 30-3,4). They continued to touch each other with the ventral surfaces of their cerci for short intervals, alternating with small, brief, rapid flexions of the abdomen forward and backward. At times the cerci slipped to one side (Figure 30-6), probably as a result of mutual pushing, and their abdomens rubbed against each other. We were not able to

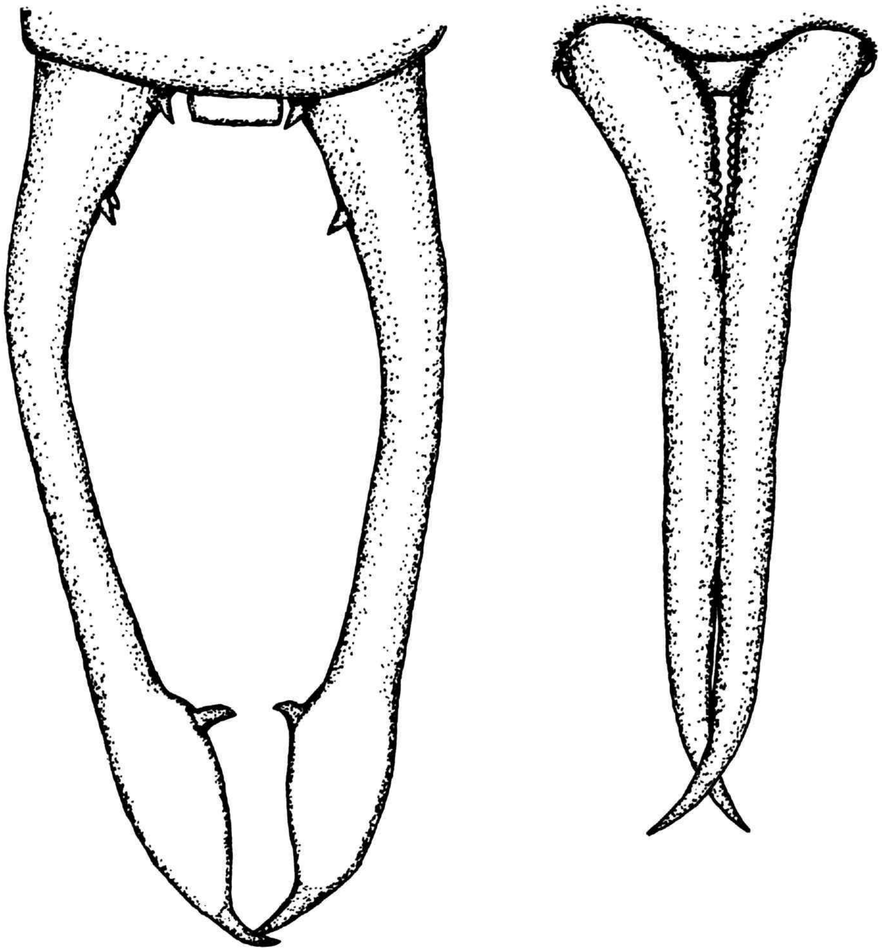


FIGURE 26.—Posterior portions of male (left) and female (right) *Ancistrogaster scabilosa*.

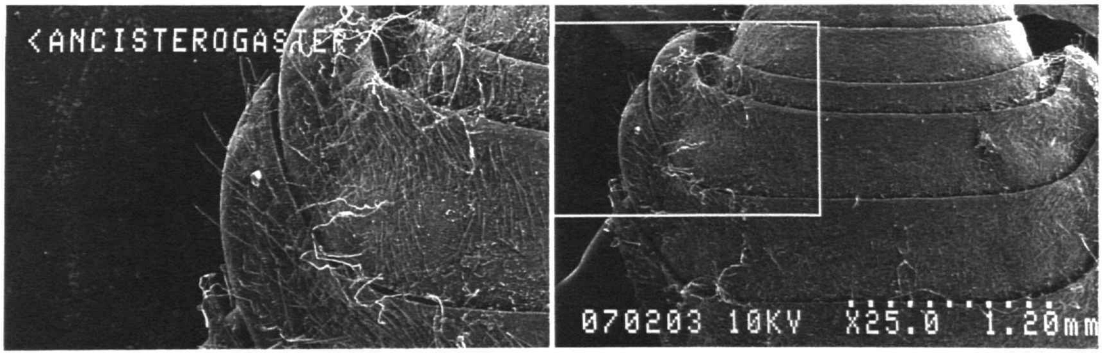


FIGURE 27.—Scanning electron micrographs of lateral extensions of posterior segments of the abdomen of a male *Ancistrogaster scabilosa*.

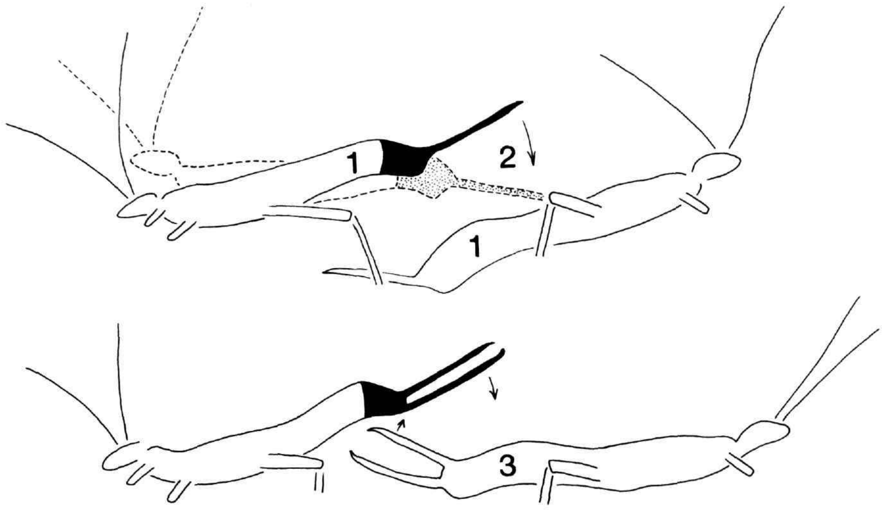


FIGURE 28.—An aggressive *Ancistrogaster scabilosa* male (black) hit his opponent rapidly and repeatedly with the distal portion of his cerci (1,2). The opponent responded by raising his abdomen slightly, with the cerci open (3). Time between drawings: 1-2, 0.07 s; 2-3, 0.09 s.

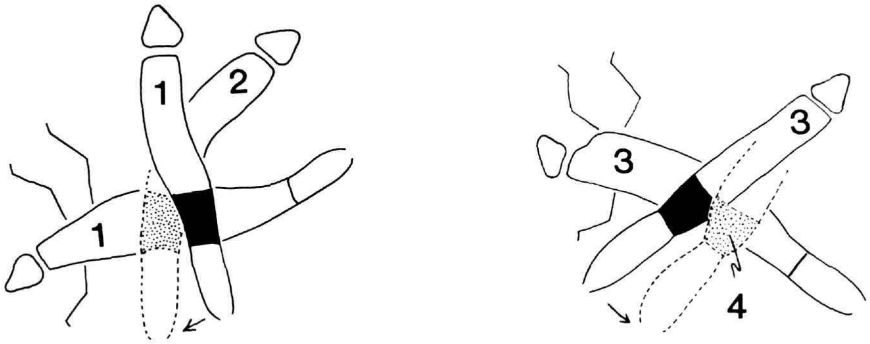


FIGURE 29.—An aggressive *Ancistrogaster scabilosa* male (black) lifted his abdomen and rubbed the dorsal surface of the abdomen of the other (1,2). One or both twisted their abdomens slightly during the rubbing so that probably the lateral abdominal extensions made repeated contact with each other (3,4). Time between drawings: 1-2, 0.1 s; 2-3, 0.07 s; 3-4, 0.1 s.

determine whether the lateral extensions of their tergites touched, partly because the movements were rapid, and also because the animals often circled one another rapidly during these interactions. Nevertheless, the intense rubbing in the general area of the extensions suggests that they were brought into contact.

The longest interaction involving this type of behavior lasted 12 min. The interactions continued until one of the males opened his cerci and moved rapidly backward to pinch the opponent in the thorax or the middle of the abdomen with the distal portion of his cerci (Figure 31). Usually the pinches were unilateral and short in duration, and the pinched individual fled after freeing himself.

5. *Sparatta bolivari* de Bormans

Males, females, and nymphs of this dorsoventrally flattened species were found under the bark of a tree whose bark still adhered tightly to the trunk in places.

Both male and female cerci are elongate, but those of the male differ in having more teeth on the inner edge. In addition, males have a trilobed pygidium (Figure 32).

We taped four high-level and one lower-level aggressive interactions in this species. Contact generally was established when one or both earwigs struck rapidly with his cerci or one individual mouthed the other. The cerci consistently were held wide open while slamming backward or laterally against the

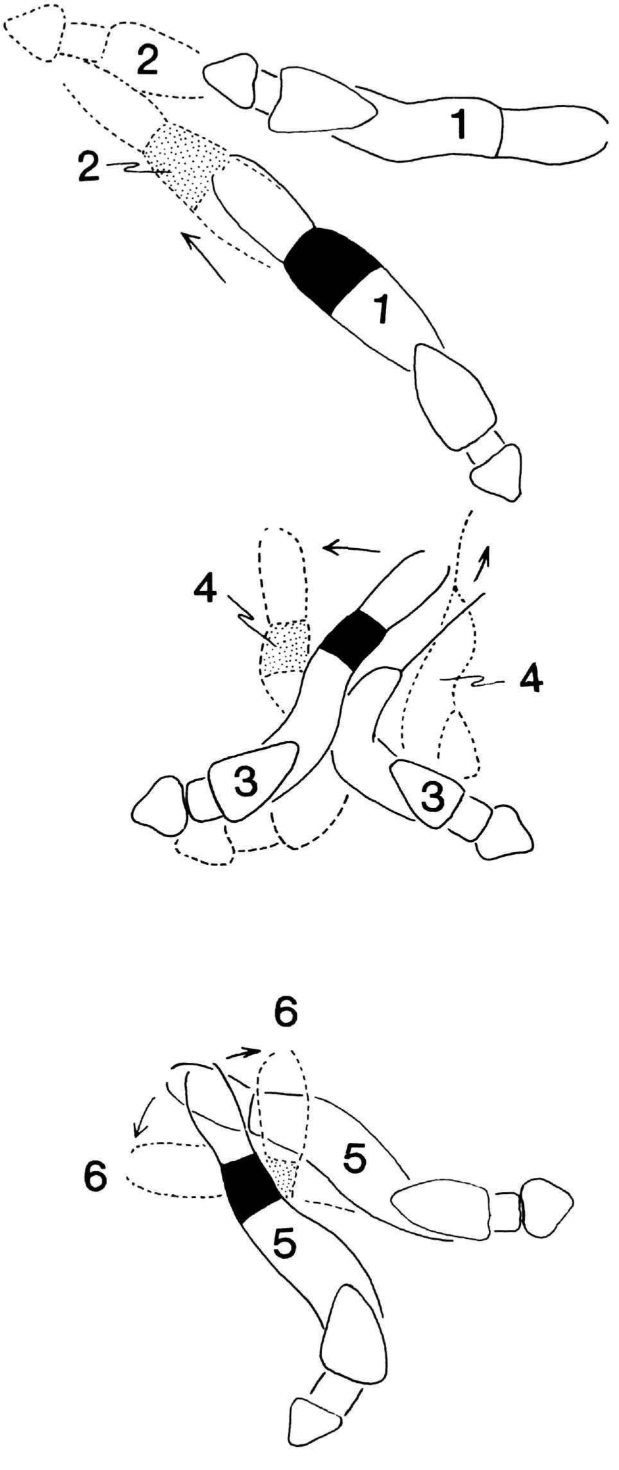


FIGURE 30.—An aggressive *Ancistrogaster scabilosa* male (black) moved rapidly backward with his cerci closed and slightly raised (1,2). Both males then bent their abdomens upward (3,4). They stayed in contact with their abdomens upward for 0.15 s until an apparent slip occurred (5,6), suggesting that they were pushing against each other. Time between drawings: 1-2, 0.07 s; 2-3, 3.0 s; 3-4, 0.18 s; 4-5, 0.27 s; 5-6, 0.15 s.

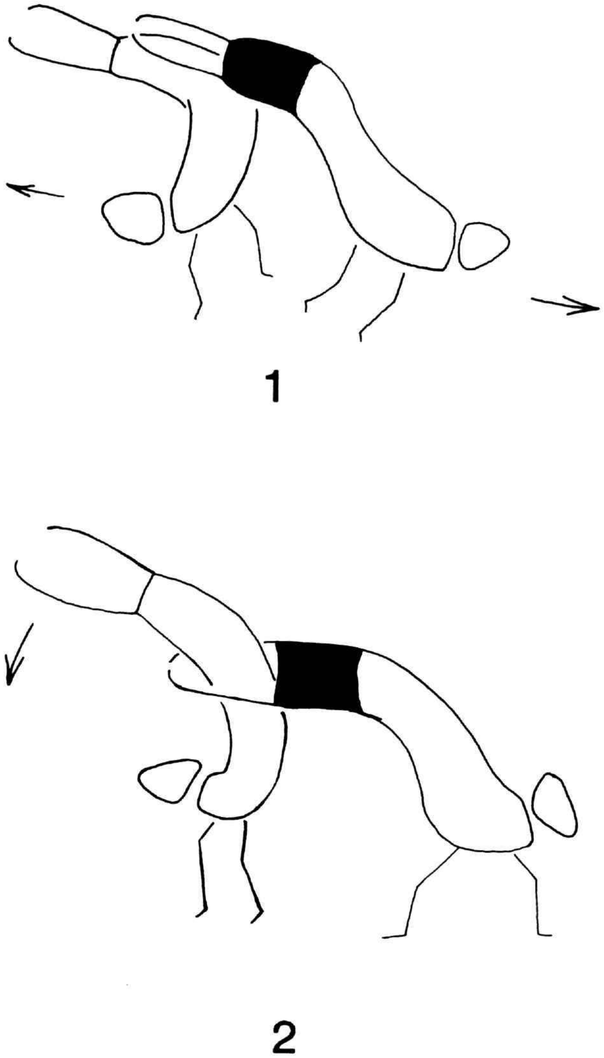


FIGURE 31.—Two fighting male *Ancistrogaster scabilosa* raised their curved abdomens and repeatedly, rapidly tapped cercus-on-abdomen and cercus-on-cercus (1). One of the two (black) then moved rapidly backward and pinched the abdomen of the other; the male being pinched succeeded in freeing himself by curving his abdomen anteriorly (2). Time between drawings: 0.3 s.

opponent (Figure 33). Most strikes resulted in cercus-cercus contact, but some brought the attacker's cerci into contact with the anterior portions of the opponent's body (Figure 33). In these cases, the attacker kept his cerci spread and generally did not pinch despite apparent opportunities to do so. The pygidium probably struck the opponent forcefully during some backward strikes in which the cerci were open. Males never combined strikes with abdomen twisting or with dorsal flips as seen in other species such as *Doru, Vostox,* and *Metrasura.* Occasionally an aggressive male reached dorsally with his front and middle legs on one side in an apparent attempt to turn

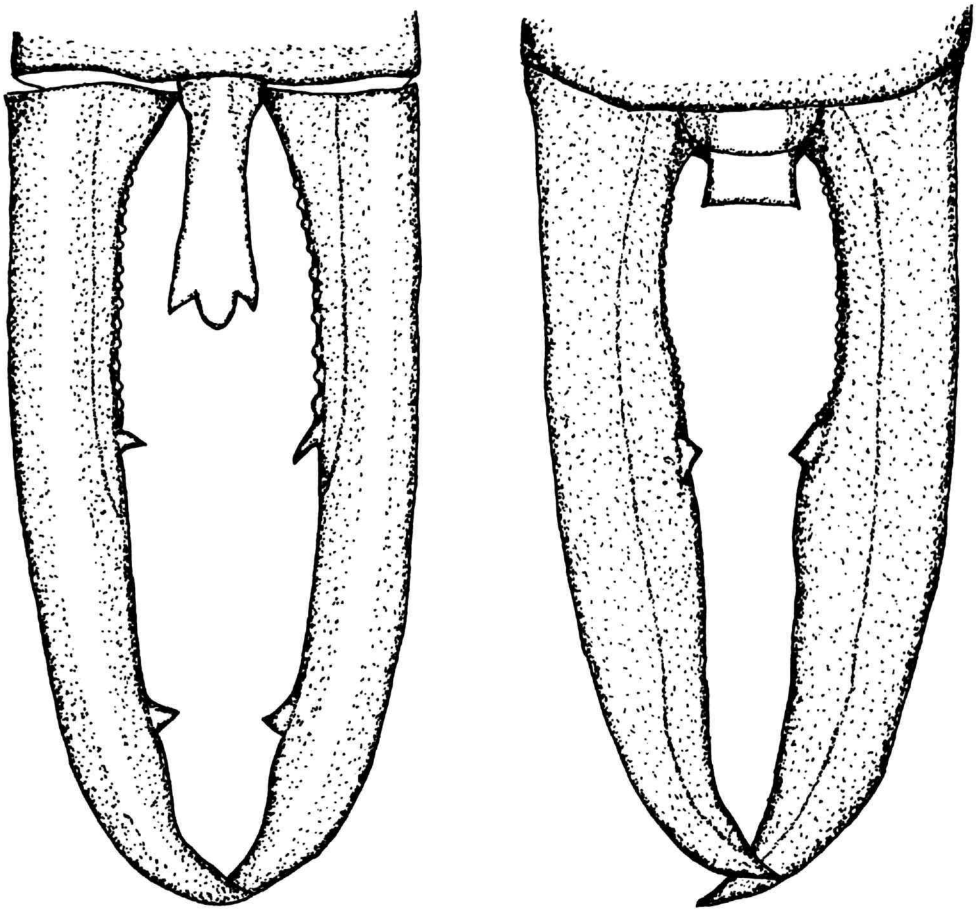


FIGURE 32.—Posterior portions of male (left) and female (right) *Sparatta bolivari*.

himself upside down (these attempts were not successful in our glass-topped observation chambers; they were recognizable as turning attempts by their resemblance to the male turning behavior that preceded copulation; e.g., Figure 85).

One especially intense interaction included repeated backward strikes, several short pinches on the cerci or tip of the opponent's abdomen, and finally a long, apparently mutual pinch in which the males were aligned end to end (Figure 34). It appeared that this was a test of strength; the winning male flexed his abdomen laterally and displaced the loser.

Many short pinches were on one or both of the opponent's cerci. In at least some of these pinches, it was clear that the opponent's cercus was held between the pygidium and the inner edge of one cercus (Figure 35).

In several cases, the males' pygidia came into contact and meshed (Figure 36). The functional significance of such contacts was not clear. In one battle, two brief contacts of this sort were each followed by short withdrawals and then high-level aggression. A third contact lasted about 12 s (Figure 36) and ended when each male moved away without any sign of further aggression. There was no indication that the males pushed against each other during pygidium-pygidium contact.

Males commonly mouthed or bit one another, and such contact often was associated with subsequent middle-level aggression (Figures 37, 38). In no case did a male seize another with his mouthparts for an extended period of time.

Apparent homosexual courtship was also common, especially rubbing movements with the ventral surfaces of the abdomen and cerci. In one case, a male attempted to turn himself over after "courting" another, as is typical just before intromission.

Low-level aggression consisted mainly of turning to present the cerci toward the other male and tapping movements with the cerci (Figure 39).

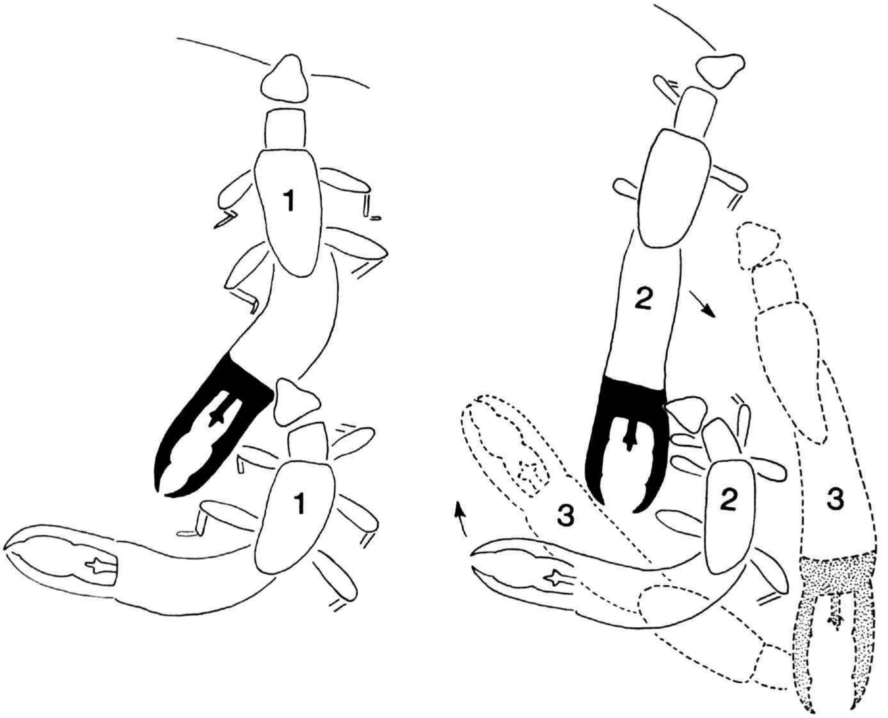


FIGURE 33.—A male *Sparatta bolivari* (black) responded to the contact of another male's mouth on the side of his abdomen (1) by straightening his abdomen and moving his entire body to strike laterally and backward (2,3) with open cerci. The other male moved backward rapidly, thereby avoiding the strike. Time between drawings: 1-2, 0.4 s; 2-3, 0.3 s.

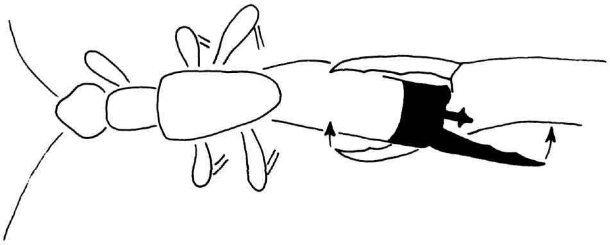


FIGURE 34.—A pair of *Sparatta bolivari* males begin a mutual pinch (arrows).

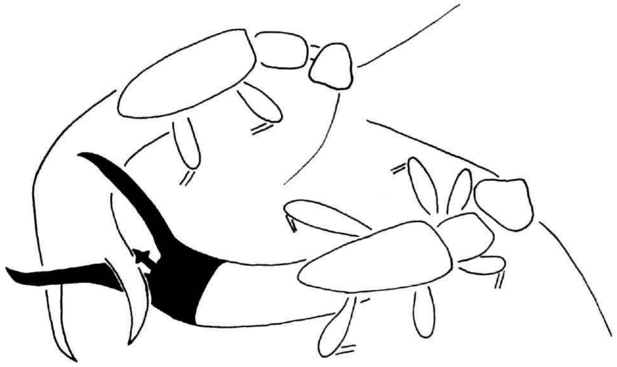


FIGURE 35.—One *Sparatta bolivari* male (black) pinched the cercus of another using his pygidium. The pinched male, which had just finished pinching the other, retreated, pulling the other after him.

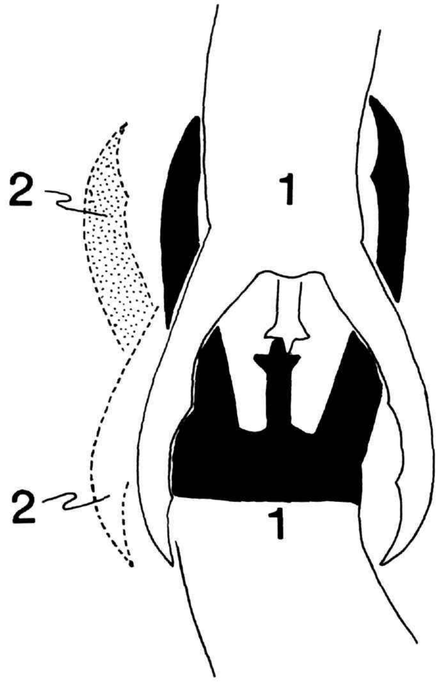
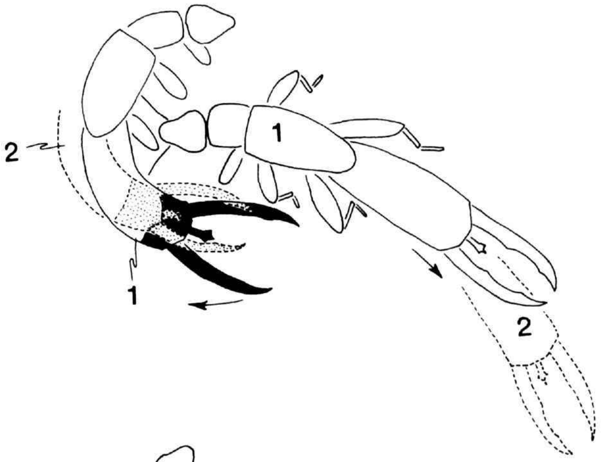


FIGURE 36.—A pair of male *Sparatta bolivari* made prolonged pygidium-pygidium contact in a low-level interaction. They held the position indicated by solid lines for 4.2 s until each opened one cercus (dotted lines) while their pygidia remained meshed. They held this second position for 7.3 s more, then both opened their cerci and held this position with the pygidia still meshed. After a further 19.2 s, both pulled away slightly and remained immobile.



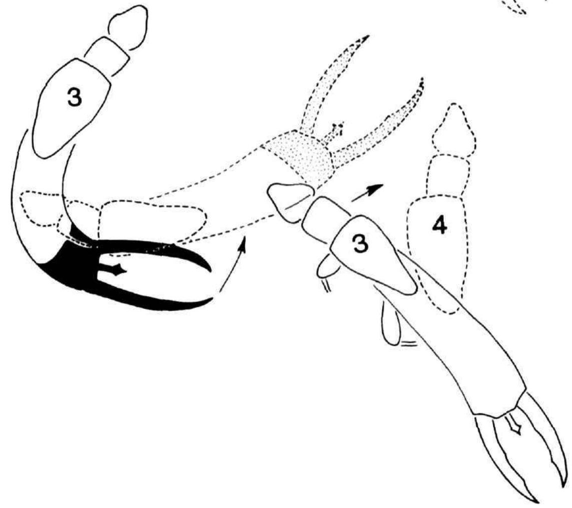


FIGURE 37 (top right).—An aggressive male *Sparatta bolivari* (black) apparently was bitten on the hind leg by another male (1), which had moved foward 0.1 s previously. He pulled his abdomen back as the other male retreated (2). The bitten male then struck backward rapidly with open cerci as the other male barely succeeded in bending his head and thorax out of the way (3,4). Time between drawings: 1-2, 0.1 s; 2-3, 0.03 s; 3-4, 0.07 s.

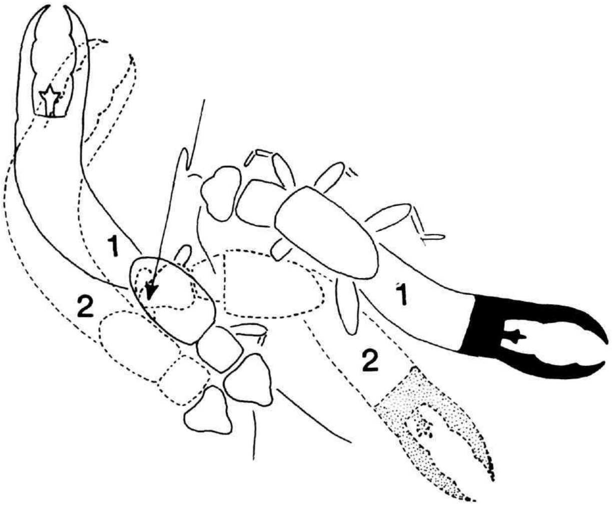


FIGURE 38 (bottom right).—An aggressive *Sparatta bolivari* male (black) moved rapidly to the side and probably bit the leg of another male (2). The bitten male bent his cerci toward the other male (2), but he did not move away until after 0.37 s of contact by the biter. The biting male moved forward with him and kept his mouth in contact with him. Time between drawings: 0.07 s.

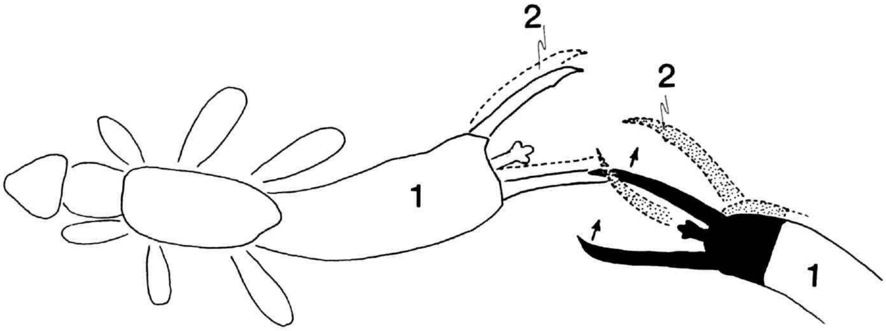


FIGURE 39.—An aggressive male *Sparatta bolivari* (black) tapped laterally against the cerci of another male, displacing his circi laterally. In this low-level interaction, the tapping male moved backward, held his cerci in contact with the cerci and abdomen of the other for about 10 s, then walked away. Time between drawings: 0.1 s.

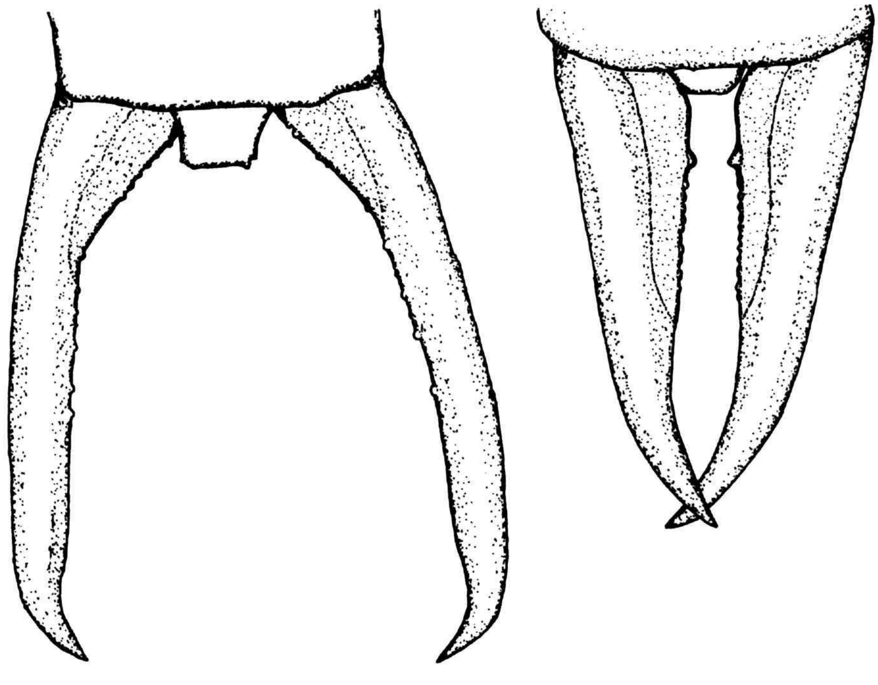


FIGURE 40.—Posterior portions of male (left, in open position) and female (right, in closed postion) *Vostox quadripunctatus*.

6. *Vostox quadripunctatus* Brindle

This species was found during the day under the loose bark of a fallen *Croton* sp. tree near San José. At night, individuals were on the surface of the tree and also under the bark.

Male cerci are longer and more widely separated at the base than those of females. Males also differ in having slightly larger teeth on the inner edges of the cerci and a slightly larger, nearly rectangular pygidium (Figure 40).

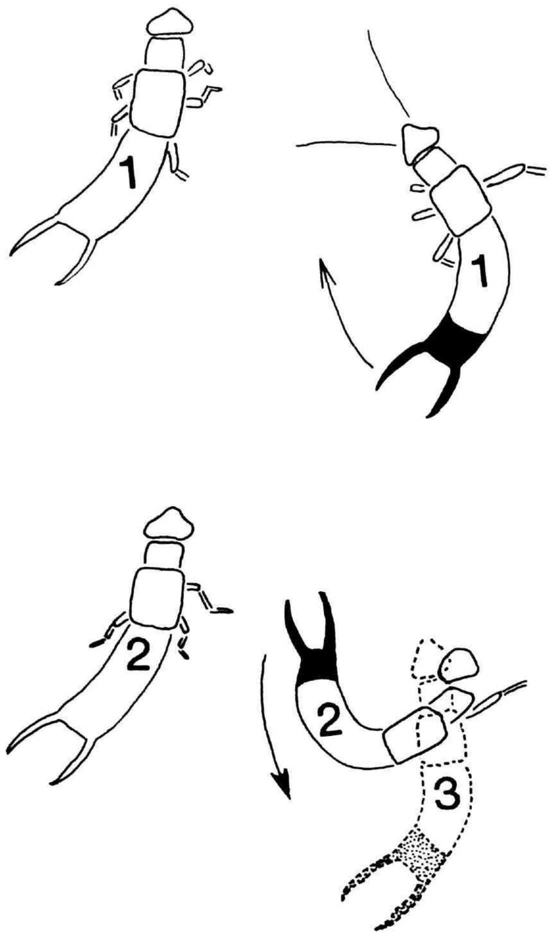


FIGURE 41.—After having contacted another male, a *Vostox quadripunctatus* male (black) turned (1) and slammed his abdomen rapidly from side to side (2,3). Time between drawings: 1-2, 0.03 s; 2-3, 0.03 s.

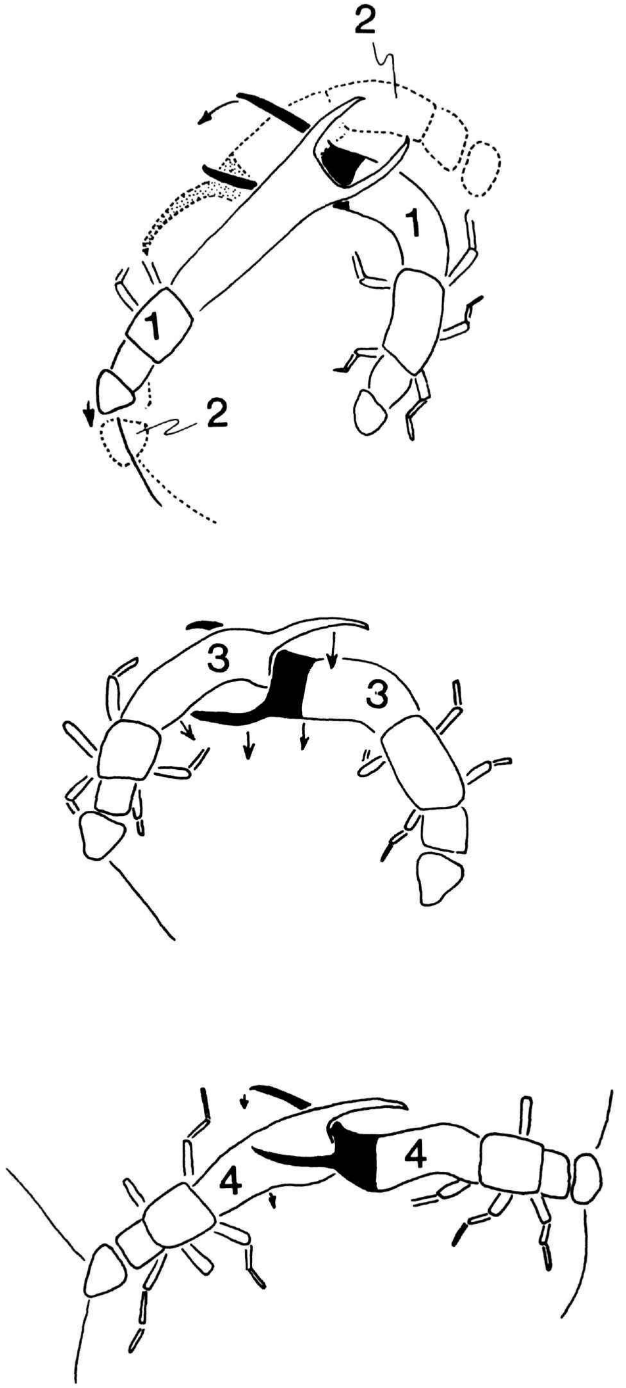


FIGURE 42.—An aggressive male *Vostox quadripunctatus* (black) slammed backward and laterally (1,2). The other male responded with a dorsal slam and then a lateral slam while their pygidia were in contact (3). A pushing battle ensued (4) (note distortion of abdomen of male on the right). The pushing battle lasted for 0.1 s before the male on the right pinched the other, which caused him to walk away with the male on the right still pinching him. Time between drawings: 1-2, 0.6 s; 2-3, 0.3 s; 3-4, 0.1 s.

Fights were observed in petri dishes and also in grooves carved in enclosed spaces, such as wood and in sponges covered with glass. We taped 46 high-level and 47 lower-level aggressive interactions. Brief aggressive interactions similar to low- and intermediate-level interactions seen in petri dishes were observed on the open surface of a log during brief observations in nature.

Pushing and slamming rather than pinching were the most common high-level fighting tactics in open spaces, and they often involved pygidium-pygidium contact. In petri dishes, such interactions usually began when one or both males made energetic lateral slamming movements and backed toward the opponent (Figures 2, 3, 41). Pygidium-pygidium contact occurred with each male usually having one cercus above and the other below the tip of the opponent's abdomen (Figure 42).

Violent slamming movements continued in this position, but they were less common. Instead, males usually made smaller, quick movements that appeared to represent adjustments to one another as each attempted to push (Figure 42) and perhaps to twist the opponent's abdomen. They seemed to exert substantial backward force, as their abdomens often became arched and bent (Figure 42). In many fights both of the males' abdomens briefly became directed more or less dorsally. Some quick movements appeared to result from shifts when one individual changed his position so that the backward force applied by the opponent made a new angle with his body axis. The most energetic pushing movements usually were occasional backward thrusts that resulted from the straightening and extension of a curved abdomen, or, less commonly, when one male walked backward. Fights usually ended when one male succeeded in pushing the other forward. The losing male then continued forward, and the winner generally backed after him, often delivering one or more lateral slams. On two occasions, a retreat was produced when one male pinched the other, with the loser dragging the winner for a short distance before being released.

Both high- and middle-level aggression involved the use of lateral slams delivered by rapid lateral swings of the abdomen to hit the opponent with the lateral or dorsal surfaces of the cerci. Upon first touching an opponent with his antennae, an aggressive individual usually swung his abdomen very rapidly laterally and forward, and turned his body at the same time so that the lateral or dorsal surfaces of the cerci struck the opponent (or where he had been when the slam was launched) (Figure 43). Often this movement was followed immediately by an equally rapid swing back in the opposite direction (Figure 43) or a strike rearward. In some lateral slams, the male lifted his abdomen in the last half of the swing so that the blow he delivered was both lateral and dorsal (Figure 43); in others, the abdomen's movement was nearly strictly lateral. When a blow of this sort landed on the opponent, the opponent sometimes was knocked one or more body lengths away (Figures 3, 44). On a tree trunk, a solid hit probably would knock the opponent off the trunk. It appeared that the cerci remained open during lateral slams, and in no case was the opponent pinched as a result of a slam. Thus, slamming movements probably represented attempts to deliver blows rather than pinches.

In many cases, one male consistently retreated from the other (Figure 45), and, in these cases, the aggressive male often ran quickly toward the opponent after initial antennal contact for up to a body length or more before launching a slam. When a male lost contact with an opponent, after either hitting or missing with a slam, or after the opponent retreated following cercus-to-cercus contact, the male usually swung his abdomen from side to side in apparent exploratory movements that were occasionally as rapid as slams.

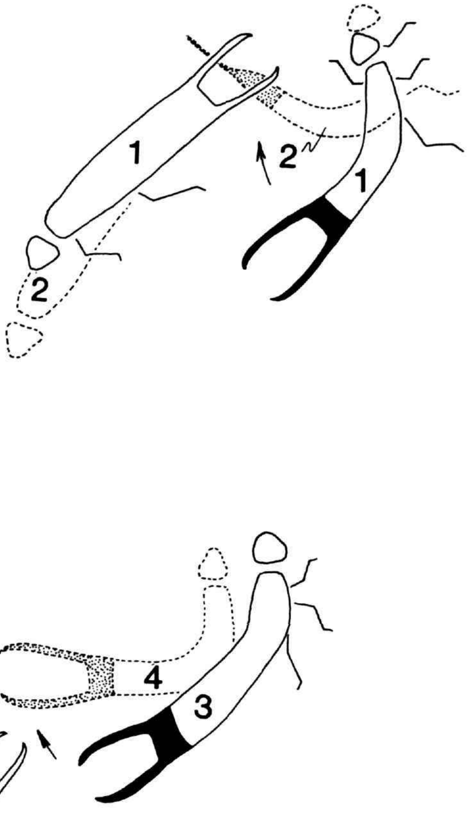


FIGURE 43.—An aggressive *Vostox quadripunctatus* male (black) swung his abdomen laterally and twisted it 90° (1,2), then he swung it again laterally without twisting it as his opponent fled (3,4). Time between drawings: 1–2, 0.07 s; 2–3, 0.07 s; 3–4, 0.18 s.

Low-level aggression in petri dishes included turning to present cerci when another individual was encountered and raising or waving the cerci and not moving away.

Fights in tunnels were similar to those in dishes in that pushing was the most common tactic, but they differed in that slamming behavior was nearly completely absent (males made occasional abortive attempts to slam laterally or ventrally). Pygidium-pygidium pushing contests often were quite pro-

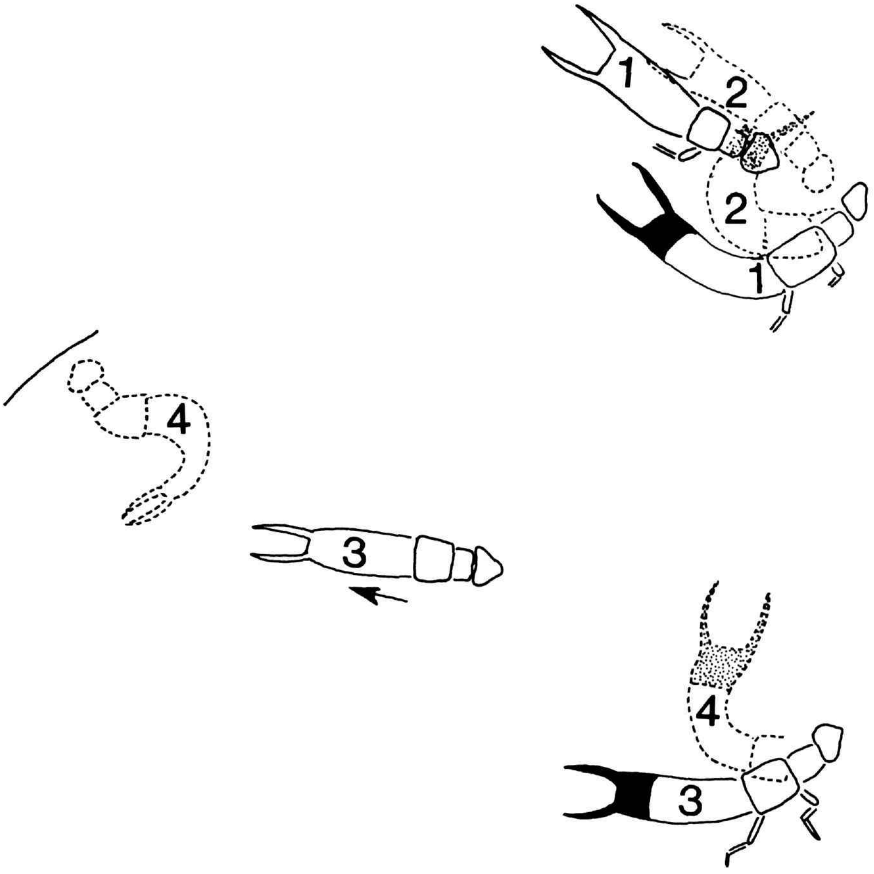


FIGURE 44.—A male *Vostox quadripunctatus* (black) struck another male with his pygidium (1,2), knocking him about one body width laterally (2). He then struck him with a small flick of his abdomen (2,3), knocking him several body lengths backward, where he crashed against the wall of the petri dish (curved line in 4). The attacking male swung his abdomen laterally again (4) as the other male flew toward the petri wall. Time between drawings: 1-2, 0.17 s; 2-3, 0.07 s; 3-4, 0.07 s.

longed, as a male apparently was difficult to dislodge when he curved his body so as to brace himself against the tunnel's wall (Figure 46). Both males often remained immobile for several seconds between bouts of pushing. Closeup observations of contacts between the cerci and pygidia of opposing males in pushing battles revealed that most commonly the two pygidia pushed against each other; the precise area of contact varied, and a male's abdomen sometimes moved so far laterally that the pygidium pushed against the base of the opponent's cercus (Figure 46). As the males struggled to push each other in this position, the most common movements were pushing by straightening the abdomen from a curved position, twisting the tip of the abdomen so as to twist the other's abdomen, and opening and closing the cerci as if to obtain a new grip. On three occasions a male gave a short series of quick pinching movements, and, in one case, the opponent responded by retreating. The tips of the cerci seldom appeared to pinch the opponent's body.

Less-aggressive males often did not flee from opponents in tunnels. Instead, they turned to present their cerci and stood their ground. Because moderately aggressve males tended not to move backward for appreciable distances in tunnels, low-level interactions often consisted of the more active male encountering another, turning 180° so his cerci fell just short of contacting the other, and then, after a brief period with little or no contact, walking away, apparently having lost interest.

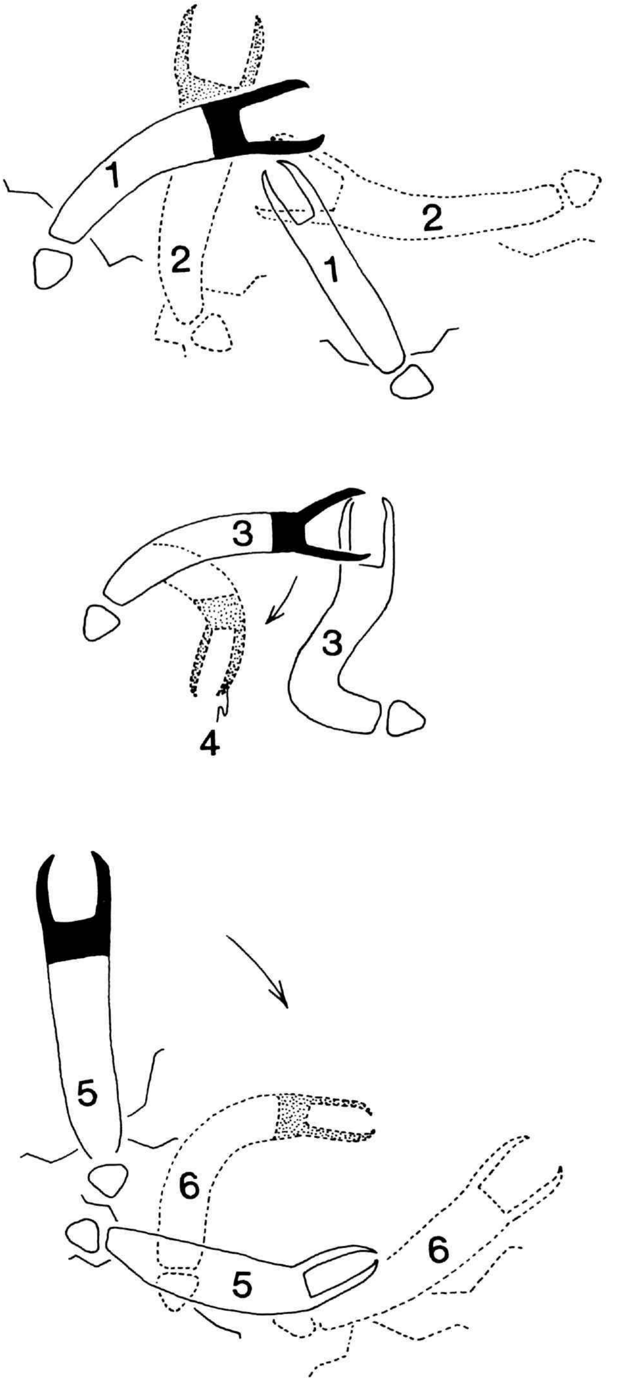


FIGURE 45.—An aggressive *Vostox quadripunctatus* male (black) withdrew his abdomen as an opponent approached (1,2), then he launched a strong lateral swing (3,4). The other male fled after further strikes (5,6).

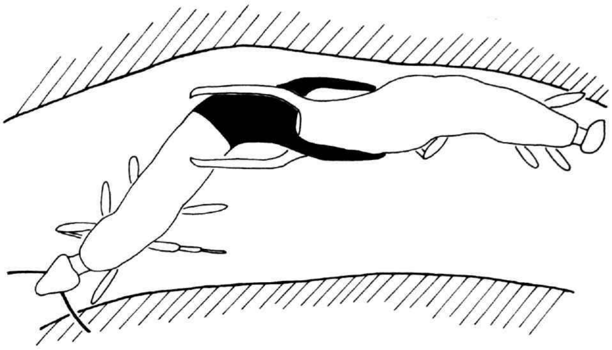


FIGURE 46.—An aggressive *Vostox quadripunctatus* male (black) braced himself against a tunnel wall as he pushed backward. His pygidium contacted the opponent near the base of one of his cerci.

7. *Paralabella dorsalis* Burmeister

This species is moderately flattened dorsoventrally. It was common deep in rotting trunks (actually, overlapping leaf sheaths) of fallen plantain plants, where individuals moved in the flat spaces between sheaths of vegetative material.

Male cerci are approximately the same length as those of the female, but they are thicker in the distal portion and more crescent-shape (Figure 47). Males also differ in having a small blunt tooth on the interior surface of the cercus and a broader and more rounded pygidium.

We taped 7 high-level and 12 lower-level aggressive interactions. In the open spaces of petri dishes, the high-level aggressive behavior of this small, rapid species involved a series of quick strikes and counter-strikes in apparent attempts to pinch, push, or throw the opponent. Much of the time the pygidia were in contact, each male having one cercus above and one below the tip of his opponent's abdomen (Figure 6). Males in this position delivered repeated pinches to the bases of the cerci and/or to the tip of the opponent's abdomen, but these pinches seemed to have little effect on the opponent (never causing him to retire as did pinches farther forward on the abdomen; see below). Pinches often were of short duration. Often a male pushed his opponent vigorously with his cerci and/or pygidium while in this position, sometimes he pushed directly backward (Figures 6, 48), and sometimes to the side. In one case, a male delivered a blow with his pygidium and/or cerci that knocked his opponent completely over the attacker's head; lateral blows also sometimes displaced opponents. Some pairs appeared to engage in tests of strength in which each pushed backward or laterally against the other's pygidium and/or cerci. This behavior was especially common in tunnels. Occasionally one of the male's cerci pinched so that its tooth may have been in contact with the other's cercus. These

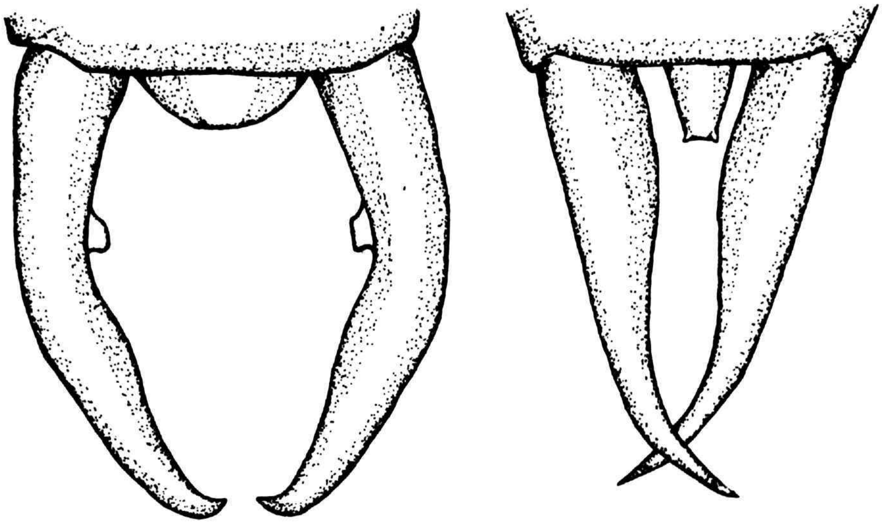


FIGURE 47.—Posterior portions of male (left) and female (right) *Paralabella dorsalis*.

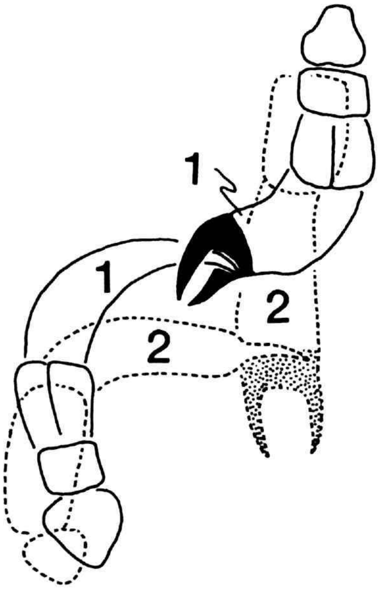


FIGURE 48.—A male *Paralabella dorsalis* (black) straightened his abdomen to strike backward at another male, but the other male used his pygidium to deflect the strike to the side (2). Time between drawings: 0.07 s.

pinches did not confer any obvious mechanical advantage, were not terminated any less quickly than others, and no special attacks were launched from these grips; it thus appears unlikely that the teeth are functionally important in this context.

High-level fights in tunnels commonly involved pushing. In one prolonged pygidium-pygidium battle, each male attempted to reach dorsally with his legs and twist to turn himself upside down; on three occasions, one male succeeded in this maneuver, and the other quickly followed suit. In one case, both males made complete 360° turns within about 4 s.

Both in tunnels and in the open, it appeared that males also used pygidium-pygidium contact to defend themselves by limiting the opponent's pinching attacks to the cerci and abdominal tip and by deflecting the other's strikes (Figure 48). The most effective attacks occurred when a male freed himself from the pygidium-pygidum position and pinched the opponent farther forward on his body (Figure 49). The pinched male always stopped fighting and walked away, dragging the pinching male with him.

In lower-level aggression, males executed quick runs toward the opponent (as in *Skalistes*) and sometimes followed with a lateral slam (Figure 50); the opponent often responded very rapidly by either fighting or fleeing (Figure 50). Cerci were held open during presentations and usually were oriented so that the posterior rather than dorsal or ventral surface of the pygidium was directed toward the opponent.

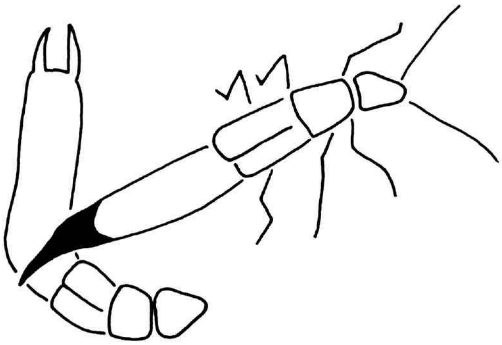


FIGURE 49.—A male *Paralabella dorsalis* (black) struck backward by straightening his abdomen and then pinched another male in the anterior portion of his abdomen. This action occurred just after the other male failed in a backward strike.

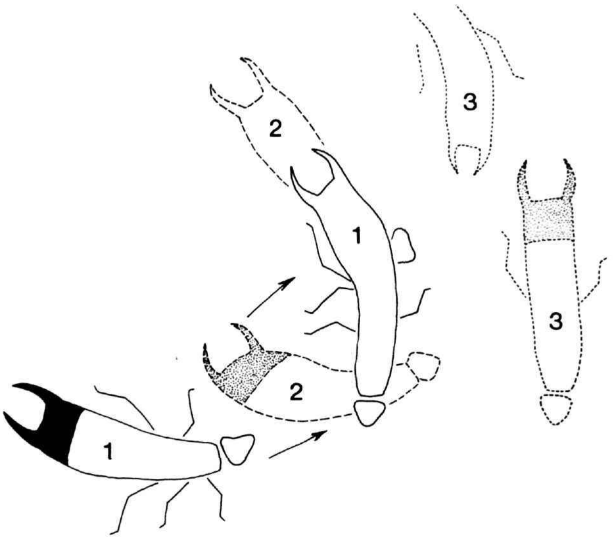


FIGURE 50.—An aggressive male *Paralabella dorsalis* struck forward with his head (2) and then slammed laterally as the opponent beat a hasty retreat (3). Time between drawings: 1-2, 0.06 s; 2-3, 0.09 s.

8. *Pseudomarava prominensis*

This small species was found in rotting plantain trunks.

Male cerci are short, smooth, crescent-shape, and set far apart at the base. Female cerci are straighter, closer together at the base, and also smooth and pointed (Figure 51). The male pygidium is broader and less prominent.

We taped 5 high-level and 38 lower-level aggressive interactions. This species differed from all others in a number of respects. Fights began when males bit each other, rather than after turning to orient their cerci toward each other. One male seized an antenna or leg of the other with his mouthparts and simultaneously curved his abdomen forward dorsally and/or laterally while attempting to grab his opponent with his cerci (Figures 52-54). When a male had his antenna or foot bitten by another, he usually attempted to pull away (Figure 52). Occasionally, the second male responded aggressively by curving his abdomen toward the first (Figures 53, 54), and they usually both struck each other repeatedly with their cerci. In intense fights, one of the males eventually succeeded in pinching the posterior portion of the abdomen or another part of the body of the other (Figures 53, 55). The pinched animal

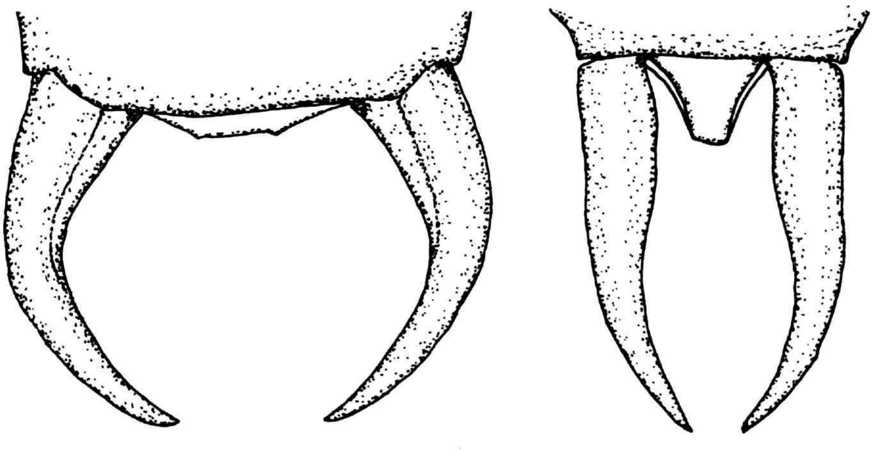


FIGURE 51.—Posterior portions of male (left) and female (right) *Pseudomarava prominensis*.

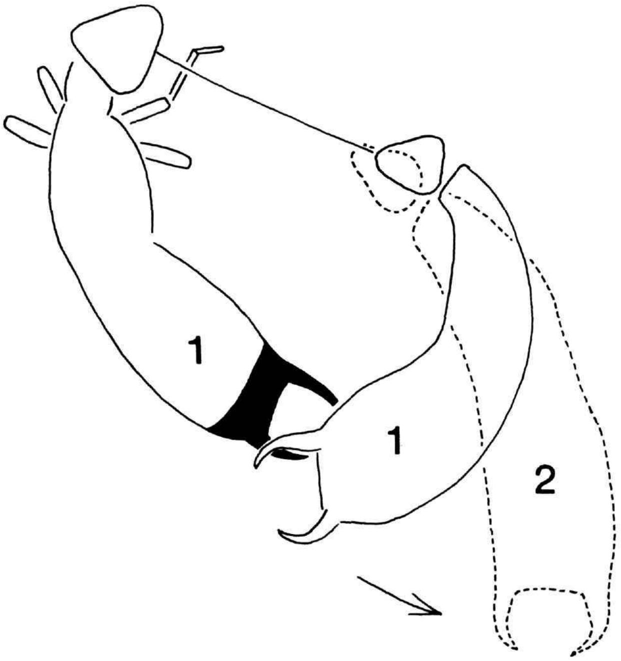


FIGURE 52.—An aggressive *Pseudomarava prominensis* male (black) grasped the antenna of his opponent in his mouthparts. The other pulled away and also swung his abdomen away in an apparent attempt to avoid being pinched. Time between drawings: 1.6 s.

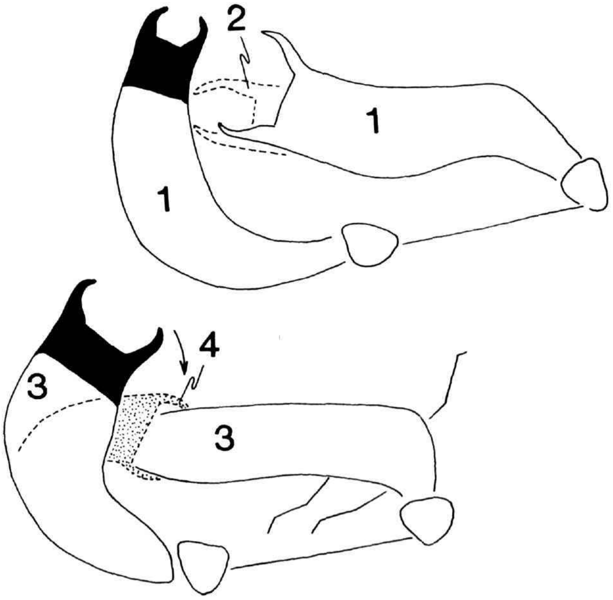


FIGURE 53.—A *Pseudomarava prominensis* male held the antenna of an opponent (black) in his mouthparts and moved backward as if to pinch him (2). The opponent responded by bending his abdomen laterally and pinching (3,4). Time between drawings: 1-2, 0.33 s; 2-3, 0.18 s; 3-4, 0.18 s.

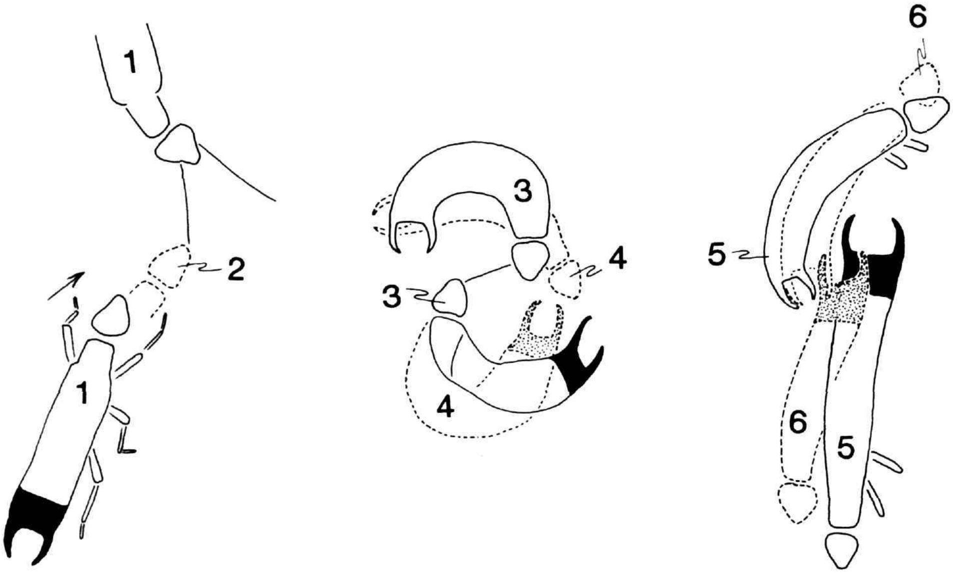


FIGURE 54.—An aggressive *Pseudomarava prominensis* male (black) moved forward rapidly to seize the antenna of an opponent in his mouthparts (1,2). The males turned to direct their cerci toward each other (3,4) and to push and give short pinches with their cerci after the first male released his hold on the other's antenna (5,6). Time between drawings: 1-2, 0.07 s; 2-3, 0.09 s; 3-4, 0.07 s; 4-5, 0.18 s; 5-6, 0.63 s.

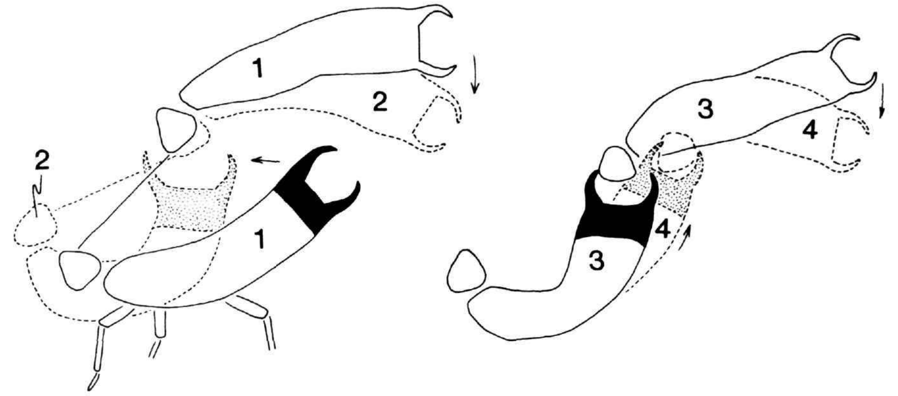


FIGURE 55.—An aggressive *Pseudomarava prominensis* male (black) held the antenna of an opponent in his mouthparts, and, at the same time, he bent his abdomen laterally so his cerci were directed toward the opponent's head (2). He then moved rapidly backward, pinching the opponent's head (4). Time between drawings: 1-2, 0.07 s; 2-3, 0.1 s; 3-4, 0.8 s.

immediately attempted to walk away, but he was held for several seconds, in some cases he pulled his attacker along behind. Sometimes after contacting another male, a male withdrew slightly and rapidly vibrated his entire body backward and forward, then moved about one head length forward again to seize his opponent. In some fights, males bumped each other repeatedly with their heads without biting. Other fighting pairs were oriented cercus to cercus, and one moved rapidly backward with his cerci open and grasped the abdomen of his opponent.

In less-intense interactions, one male often responded to being touched by another by folding his antennae rearward in an apparently defensive posture.

9. *Anisolabis maritima* Borelli

This species was found under rocks and logs that were in advanced stages of decomposition and in drains from houses where organic debris had accumulated.

The cerci of males and females are similar. Male cerci are somewhat more curved than those of the female, and the male pygidium is slightly wider (Figure 56).

We taped 12 high-level and 6 lower-level aggressive interactions. High-intensity interactions often occurred immediately following first contact. In open sites (petri dishes), antennal contact was followed by turning and striking or by curving the abdomen forward and then striking; only occasion-

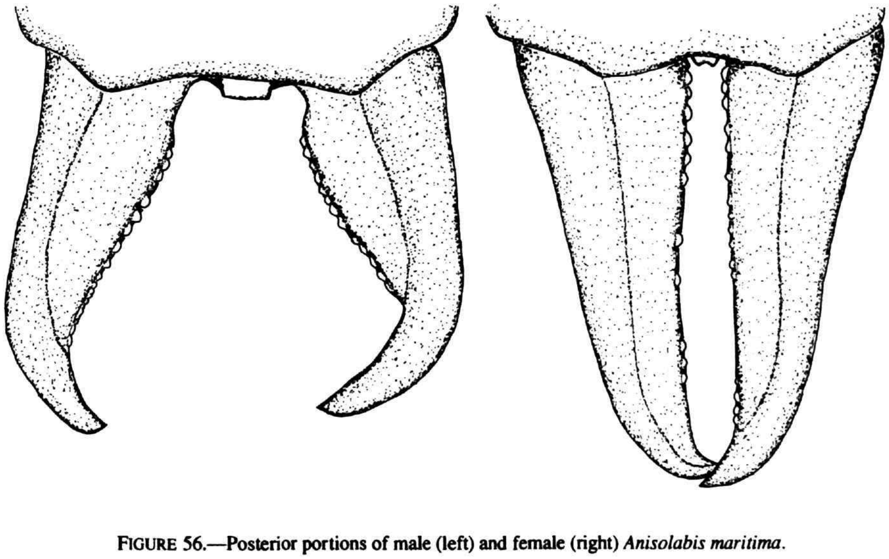


FIGURE 56.—Posterior portions of male (left) and female (right) *Anisolabis maritima*.

ally did a male strike directly backward. In contrast, in tunnels, where the animals were less mobile, males struck by first turning 180° and then moving directly backward.

Pinches were frequent in both situations. They lasted longer in tunnels than in the open. Pinches in the open usually occurred on the posterior portion of the abdomen (Figure 57), whereas those in tunnels occurred often on both the abdomen (Figure 58) and the thorax. Simultaneous pinches were rare. In three cases a male in the open lifted and shook a pinched opponent; in one case he then threw him against the wall of the dish (Figure 5). In some cases one male struck another with a lateral or a backward slam and knocked him some distance (Figures 59, 60).

When pinched, the opponent struggled to free himself by

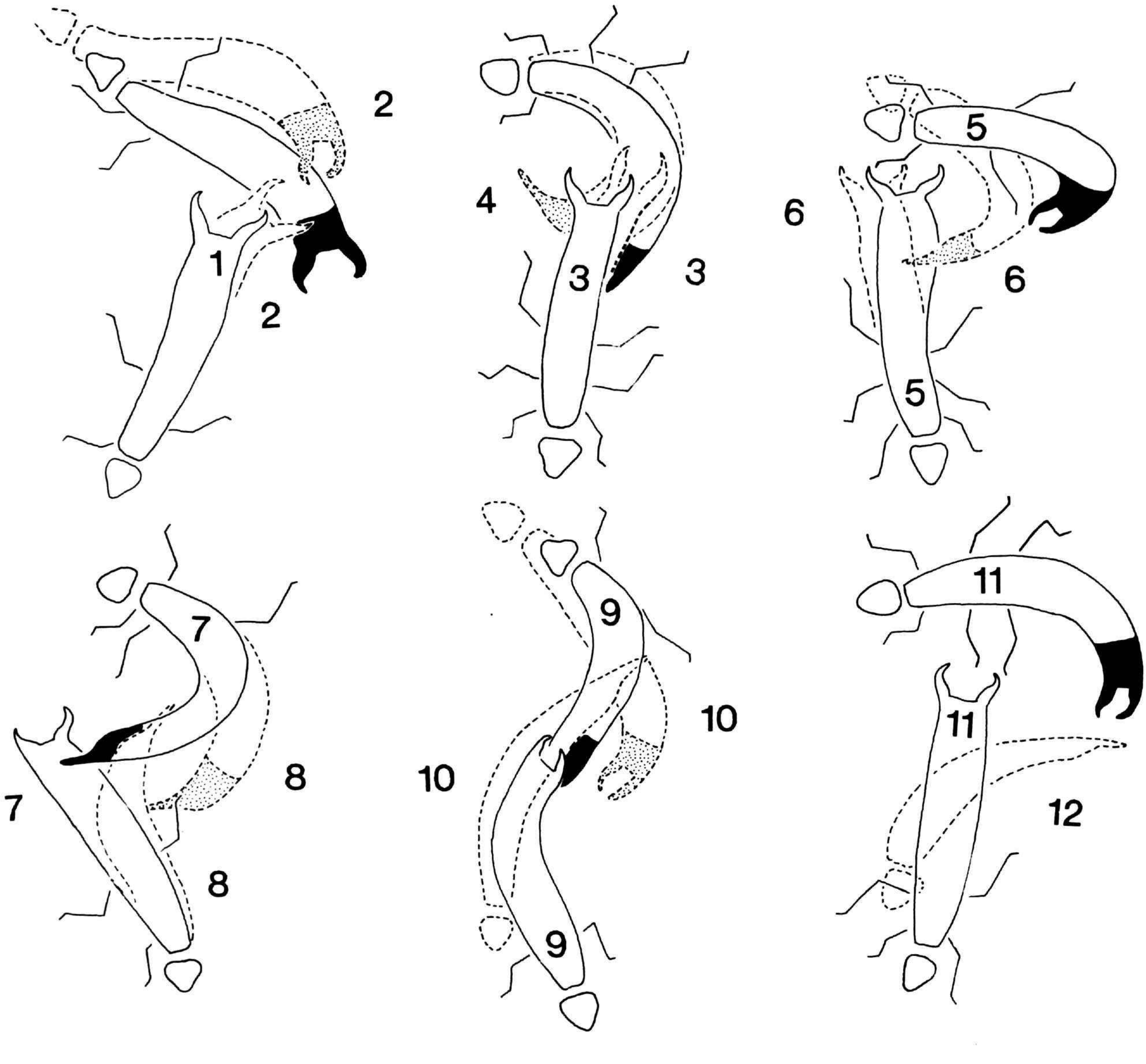


FIGURE 57.—An aggressive male *Anisolabis maritima* (black) pinched his opponent briefly (6–8) as the two struck and dodged each other. Time between drawings: 1–2, 0.45 s; 2–3, 0.3 s; 3–4, 0.27 s; 4–5, 0.27 s; 5–6, 0.18 s; 6–7, 0.24 s; 7–8, 0.24 s; 8–9, 0.27 s; 9–10, 0.27 s; 10–11, 0.24 s; 11–12, 0.18 s.

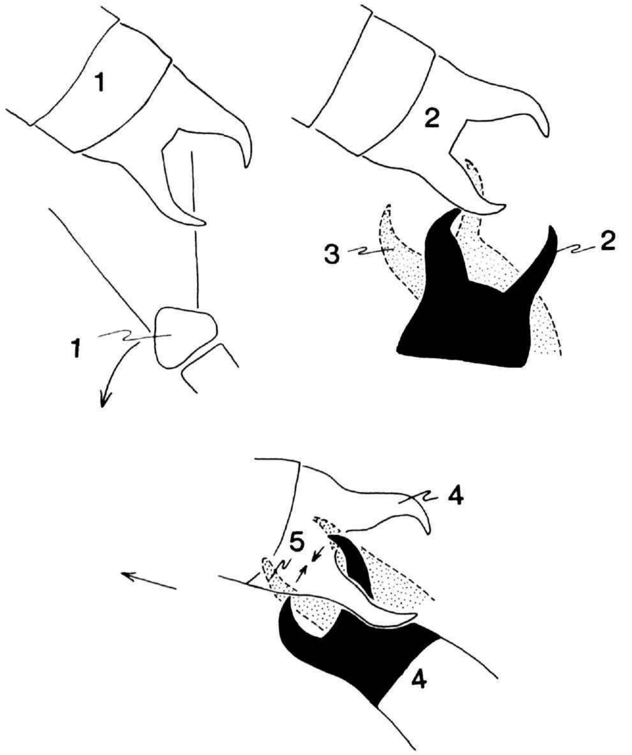


FIGURE 58.—After an aggressive male *Anisolabis maritima* (black) touched another in a tunnel with his antennae (1), he turned 180°, tapped his opponent with his cerci (2,3), and then pinched one of his opponent's cerci, which caused the opponent to move forward (4,5). Time between drawings: 1-2, 1.1 s; 2-3, 0.1 s; 3-4, 0.13 s.

pulling, twisting his abdomen, returning the pinch, or biting the other male. Another tactic with which males freed themselves on several occasions was for the pinched male to turn and move forward under the abdomen of the other male, thus twisting the pinching male's abdomen sharply (Figure 61).

Low-intensity battles both in the open and in tunnels included presentations and short pushes with the cerci. Opponents were struck with the tip of the abdomen with the cerci spread. Winners of interactions in the open often swung their abdomens strongly from side to side after the opponent withdrew. Losers in tunnels were less likely to withdraw, rather they simply remained more or less immobile with their cerci toward the opponent.

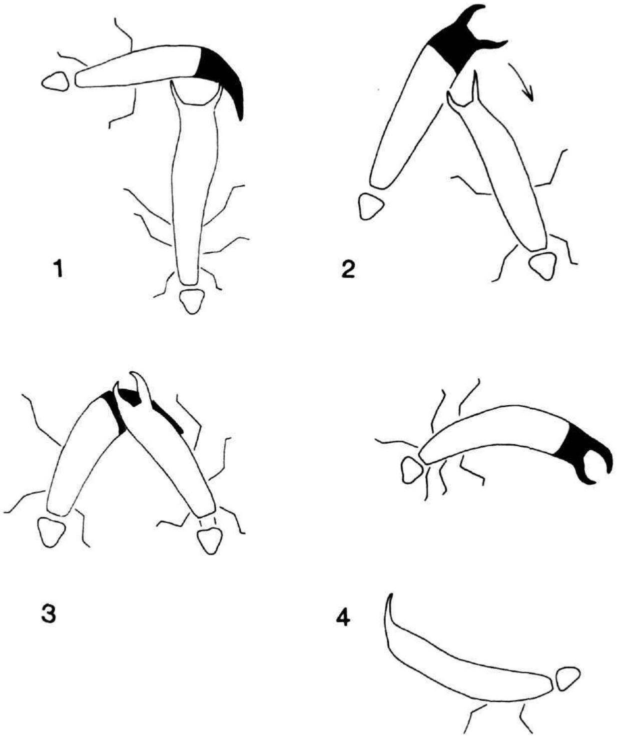


FIGURE 59.—An aggressive male *Anisolabis maritima* (black) swung his abdomen laterally (1,2), struck the ventral surface of his opponent's abdomen (3), and threw him against the wall of the petri dish (4). Time between drawings: 1-2, 0.07 s; 2-3, 0.03 s; 3-4, 0.03 s.

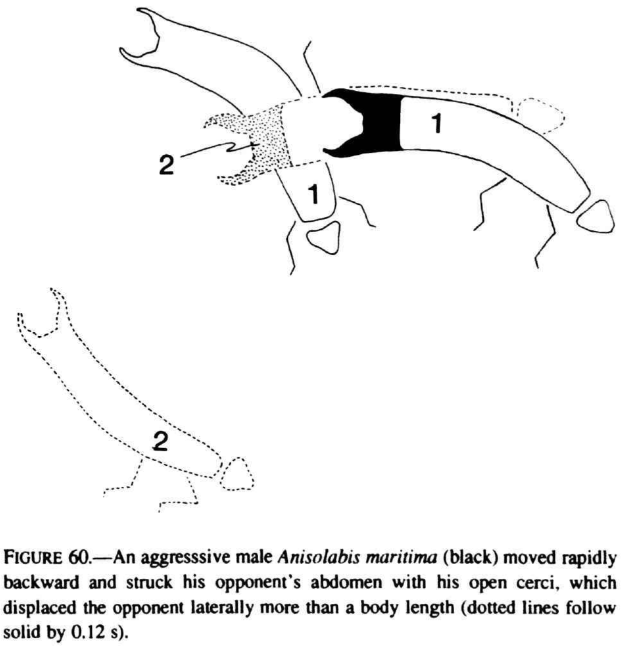


FIGURE 60.—An aggresssive male *Anisolabis maritima* (black) moved rapidly backward and struck his opponent's abdomen with his open cerci, which displaced the opponent laterally more than a body length (dotted lines follow solid by 0.12 s).

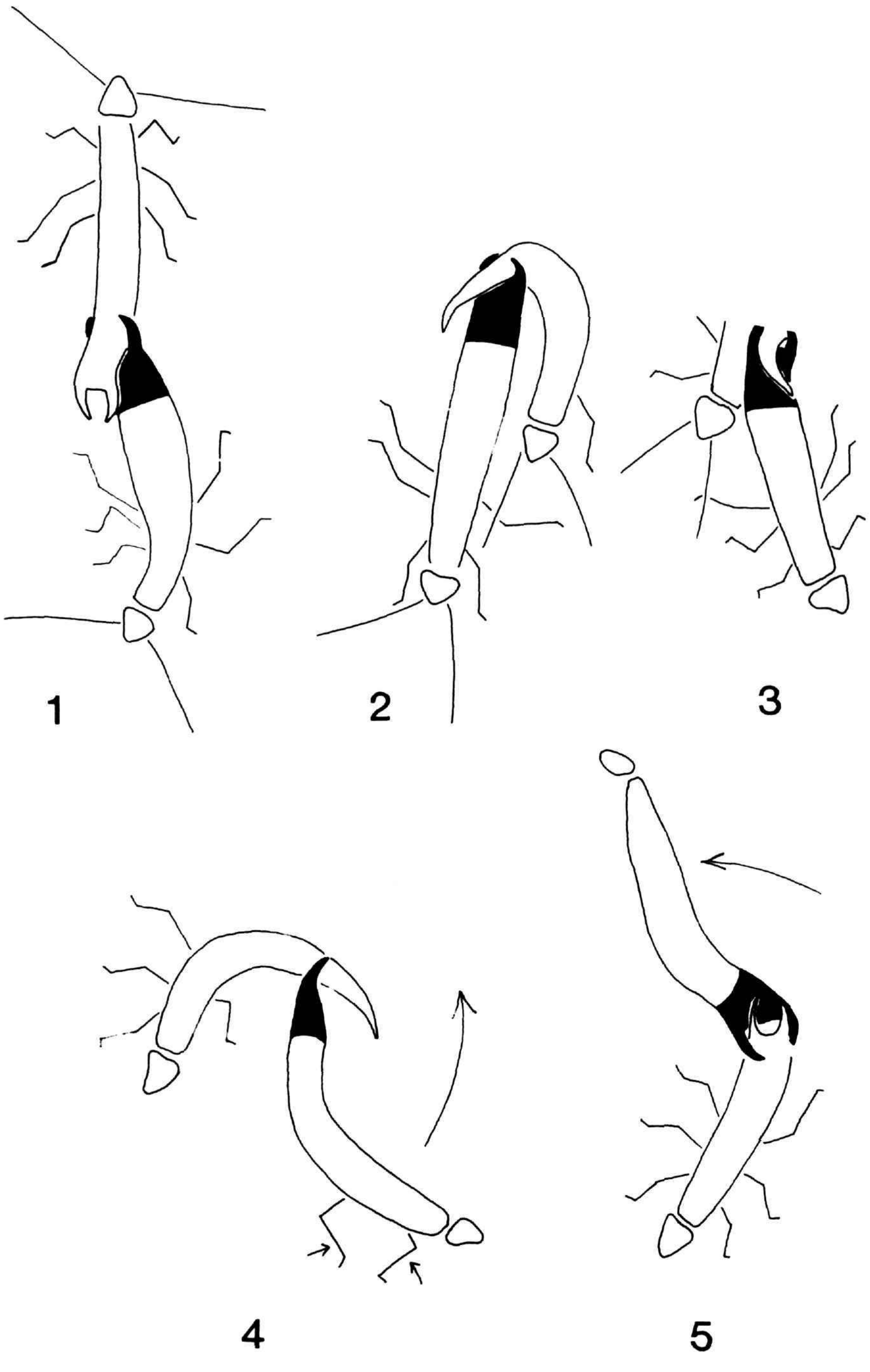


FIGURE 61.—An aggressive male *Anisolabis maritimus* (black) pinched his opponent (1), and the opponent retaliated by turning to pass under the first male's abdomen (2,3). This apparently loosened the aggressive male's grip on the substrate (arrows to legs in 4), which allowed the opponent to swing him nearly 180° (5). Time between drawings: 1-2, 0.3 s; 2-3, 0.2 s; 3-4, 0.3 s; 4-5, 0.1 s.

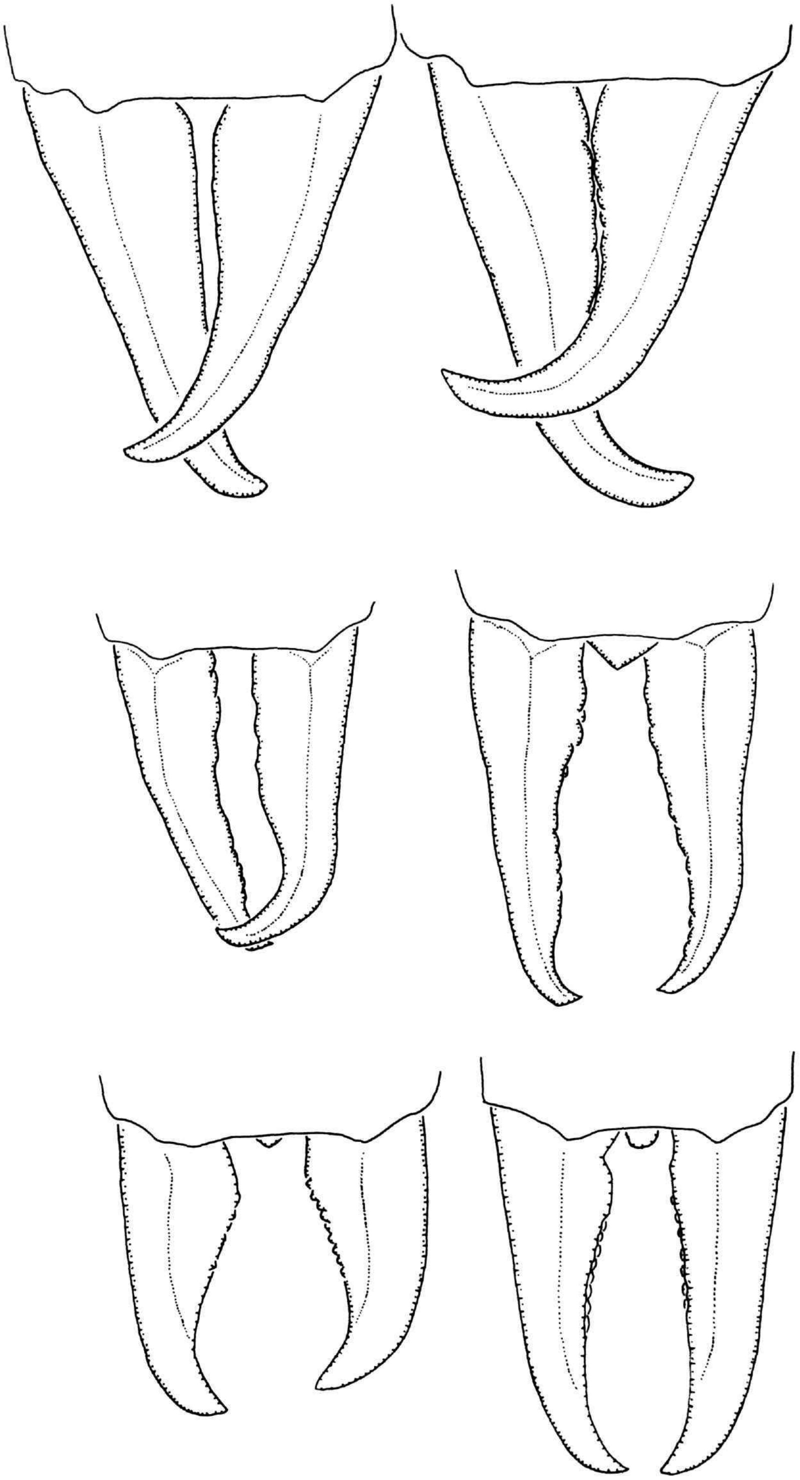


FIGURE 62.—Posterior portions of male (left) and female (right) *Carcinophora robusta* (top), *C. rosenbergi* (middle), and *C. americana* (bottom).

10–12. *Carcinophora rosenbergi* Burr, *C. americana* Beauvois, and *C. robusta* Scudder

These species were found in and under rotten logs and rotting plantain trunks and also under stones.

In all three species male cerci are asymmetrical to varying degrees, and male cercus morphology is very similar to that of females (Figure 62 on page 37). We taped 7 high-level and 3 lower-level interactions in *C. rosenbergi*, 3 high- and 3 low-level interactions in *C. americana*, and 13 high- and 8 lower-level interactions in *C. robusta*. We were unable to discern differences in fighting behavior of males of these species, and thus we describe them together.

Most strikes in high-level interactions occurred immediately following first contact. Usually they occurred from a curved-abdomen position or as the animal turned (Figure 63). Pinches usually lasted several seconds and generally were on the opponent's abdomen (Figure 64) or, less often, farther forward (Figure 65). Sustained simultaneous pinches did not occur. Slams occasionally resulted in the opponent being knocked off his feet momentarily (Figure 63), but probably most slams included an attempt to pinch. On some occasions, the pinching animal eventually released his grip spontaneously. In others, the opponent seemed to break free by pulling, by slamming with his abdomen, by giving a return pinch with his cerci, or by twisting under the other male's body (Figure 64). In one case, a male *C. robusta* punctured his opponent's abdomen with a pinch, causing him to lose hemolymph.

Often strikes missed, apparently due to evasive movements by the opponent (Figure 66), and attackers sometimes responded to evasive actions by moving rapidly backward (Figure 67). Cerci also were held open during the strong side-to-side or dorsal swings of the abdomen that often followed a missed strike. Some of these swinging movements brought the cerci into contact with the other individual and were immediately followed by further attacks, suggesting that at least some swings were searching movements designed to reestablish contact with the opponent. Winners often chased losers with their cerci directed more or less anteriorly, a position from which further attacks were launched (Figure 67).

Some mid-level interactions involved hitting the opponent with the tip of the abdomen between the cerci while the cerci were held open. Missed strikes often were followed by strong side-to-side swings of the abdomen.

Low-level interactions involved presentation of cerci or, on one occasion, a series of mutual cercal taps while the cerci were held open.

13. *Pyragra nigrescens* Brindle

This species was collected under loose bark. The male cerci are very similar to those of the females (Figure 68).

We taped 13 high-level and 26 low-level aggressive interactions. Because cercus morphology was virtually identical in males and females, some battles may have involved females that we could not distinguish. Intense interactions began when antennal contact was followed by a very rapid 90° or 180° turn and a lateral slam or series of slams (Figure 69). On several occasions the tips or lateral surfaces of the cerci struck

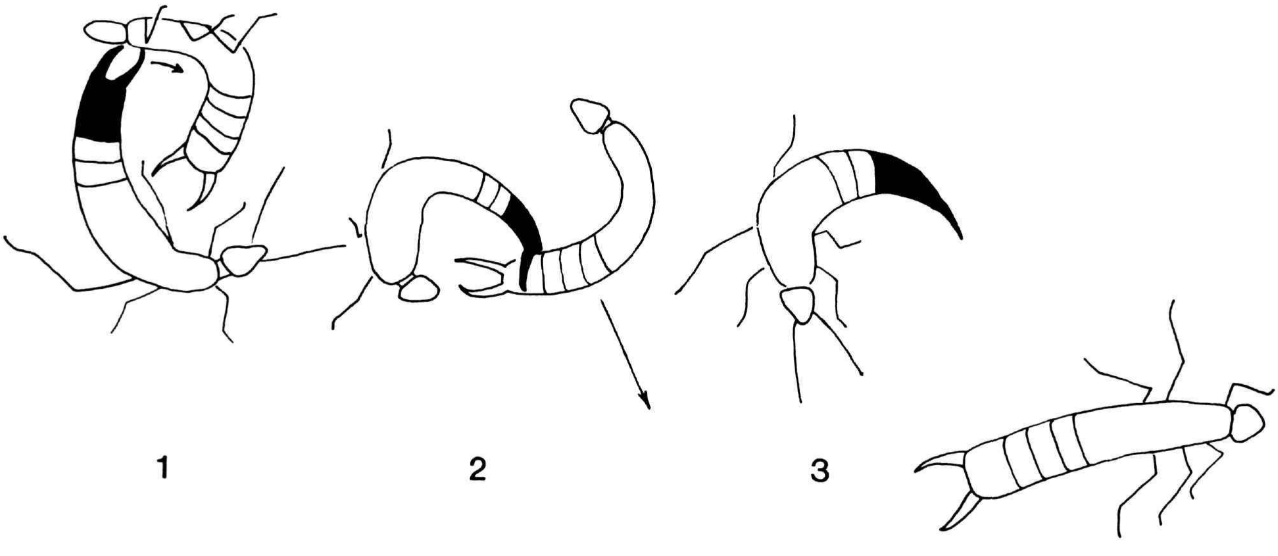


FIGURE 63.—A male *Carcinophora robusta* (black) slammed his pygidium against the abdomen of his opponent (2) and displaced the other with the blow (3). Time between drawings: 1-2, 0.1 s; 2-3, 0.1 s.

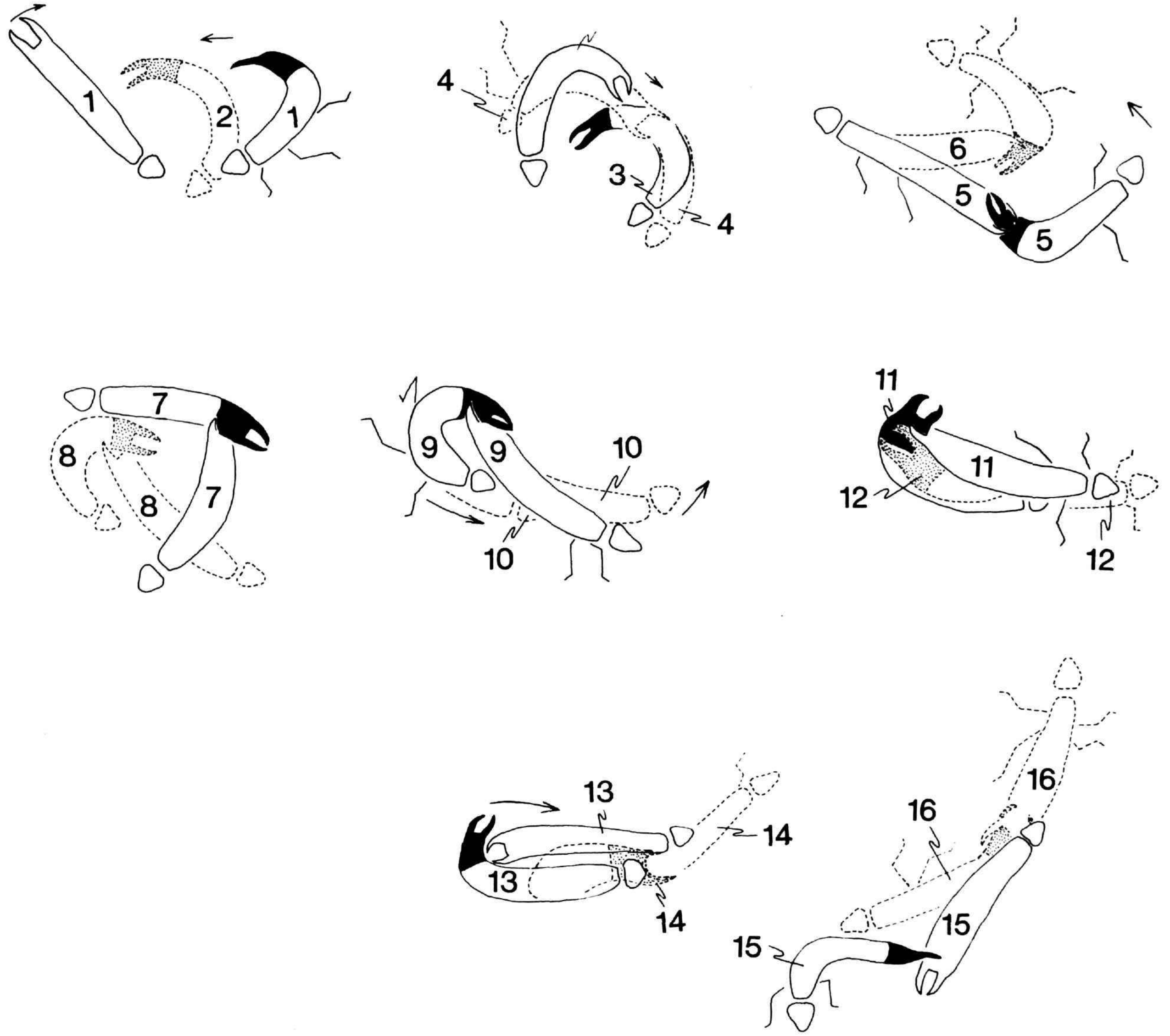


FIGURE 64.—An aggressive *Carcinophora rosenbergi* male (black) struck at his opponent by swinging his abdomen laterally (1,2). When this attack failed, the opponent struck laterally and pinched the first male's abdomen (3,4). The first male pulled his opponent (5) and turned sharply so his body went below that of the opponent (6–12). He also twisted his abdomen and succeeded in freeing himself (13). He then immediately struck forward with his abdomen (14) and pinched the second male near the base of his cerci (15, 16). Time between drawings: 1–2, 0.45 s; 2–3, 0.13 s; 3–4, 0.27 s; 4–5, 0.45 s; 5–6, 1.10 s; 6–7, 1.62 s; 7–8, 1.3 s; 8–9, 0.36 s; 9–10, 1.6 s; 10–11, 0.72 s; 11–12, 1.8 s; 12–13, 1.62 s; 13–14, 0.24 s; 14–15, 0.36 s; 15–16, 0.63 s.

the opponent as this turn was executed, and, on two occasions, the opponent was displaced by such an impact (Figure 70).

Some slams involved twisting the abdomen, and, in some cases, a strike resulted in a pinch of the opponent's abdomen (Figure 71-4,5). On five occasions, one individual pinched the opponent and then lifted it in the air and shook it briefly (Figure 72). One pinched individual apparently wrenched itself free by twisting the other's abdomen (Figure 71) as in *Anisolabis* and *Carcinophora*. Sustained simultaneous pinches did not occur.

Mutually aggressive individuals both turned, each backed

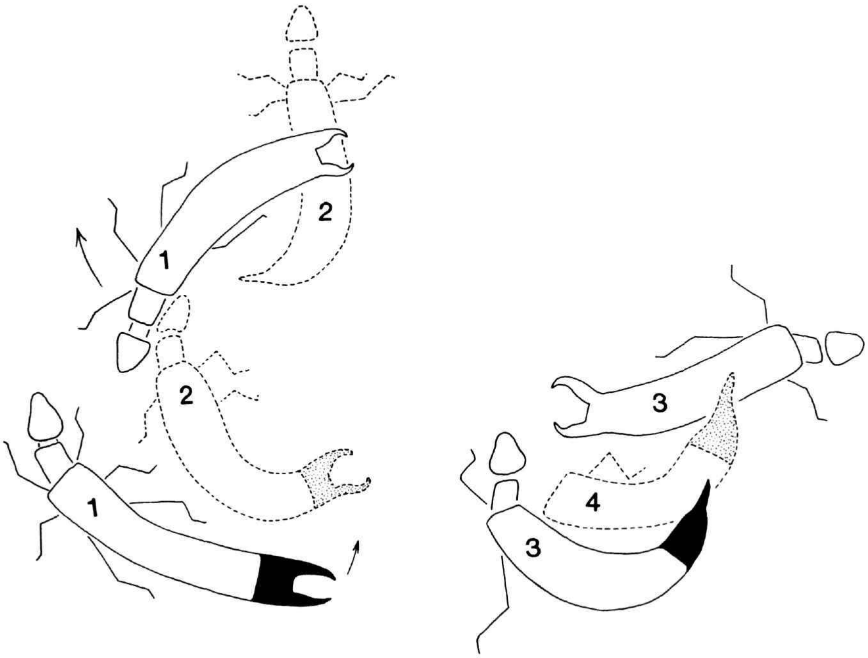


FIGURE 65.—An aggressive *Carcinophora rosenbergi* male (black) moved rapidly sideways toward his opponent (1,2). The opponent turned and retreated, but he was not in time to avoid being pinched on the thorax (4). Time between drawings: 1–2, 0.51 s; 2–3, 0.36 s; 3–4, 0.15 s.

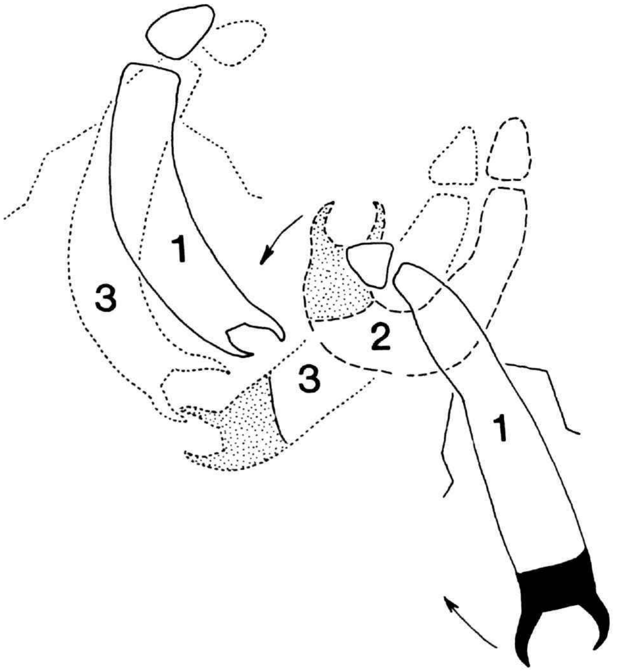


FIGURE 66 (left).—An aggressive male *Carcinophora rosenbergi* (black) swung his abdomen forward rapidly, but his opponent dodged the blow by moving forward (2). The attacking male then swung his abdomen back (dotted lines) and struck the cercus of the other male with the base of his cerci (3). Time between drawings: 1–2, 0.03 s; 2–3, 0.36 s.

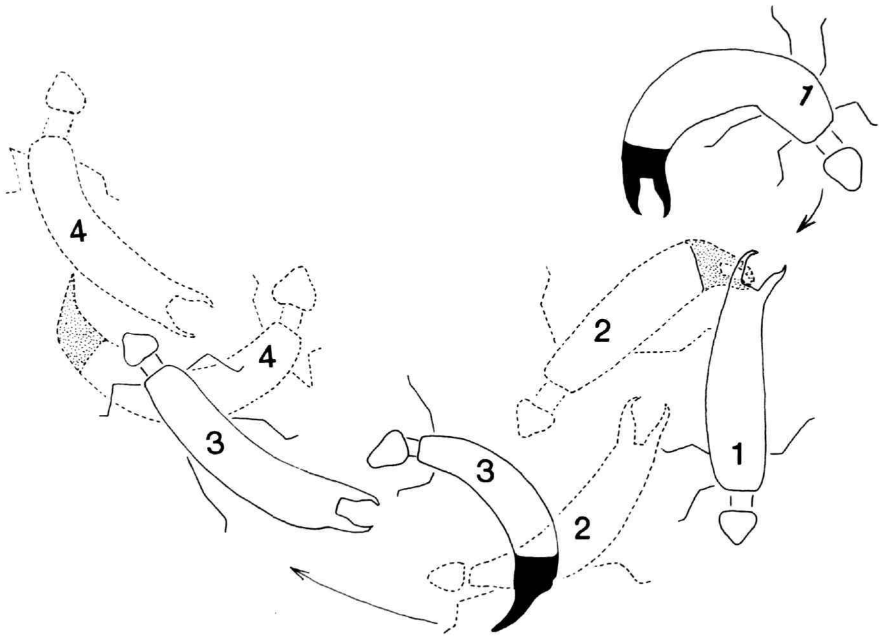


FIGURE 67.—An aggressive *Carcinophora rosenbergi* male (black) turned, moved forward, and changed sides with his abdomen as he chased an opponent (1,2). He then swung his abdomen forward toward the still-retreating opponent (3,4). Time between drawings: 1-2, 0.27 s; 2-3, 0.24 s; 3-4, 1.3 s.

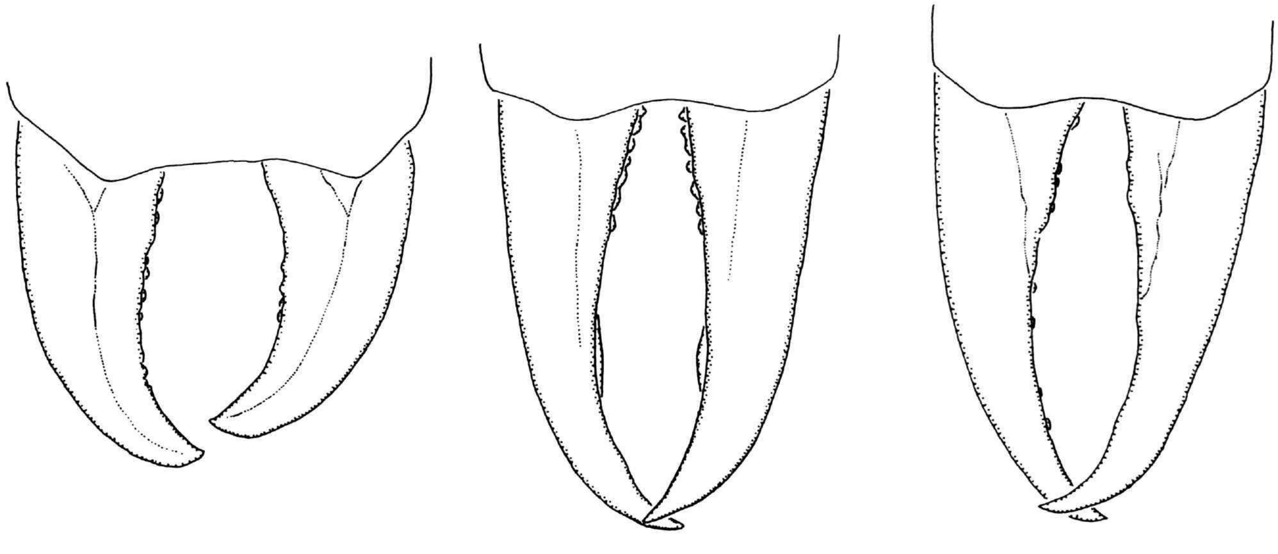


FIGURE 68.—Cerci of a male (left, center) and female (right) *Pyragra nigrescens*.

rapidly toward the other, their cerci interlaced, and each gave brief pinches to the other on the distal and middle portions of the other's abdomen (Figure 73-1). Often they also pushed briefly and slammed laterally; the points and lateral margins of the cerci contacted the opponent as they struggled (Figure 73-5,6,7). In one case in which confounding stimuli from other

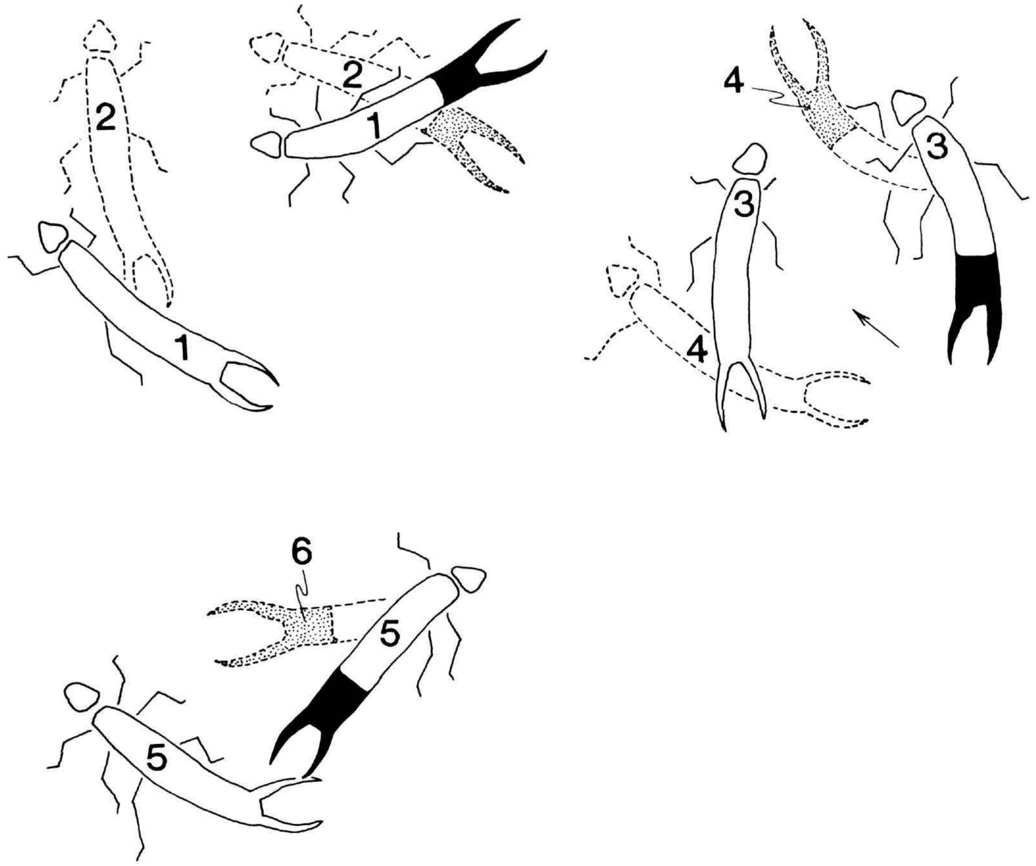


FIGURE 69.—Apparently after having located the opponent with taps of its antenna (1,2), an aggressive *Pyragra nigrescens* (black) struck laterally with an 180° swing of his body (3,4); following a swing back to its original position (5), it made a second, weaker swing (6). Time between drawings: 1-2, 0.63 s; 2-3, 0.18 s; 3-4, 0.03 s; 4-5, 0.15 s; 5-6, 0.03 s.

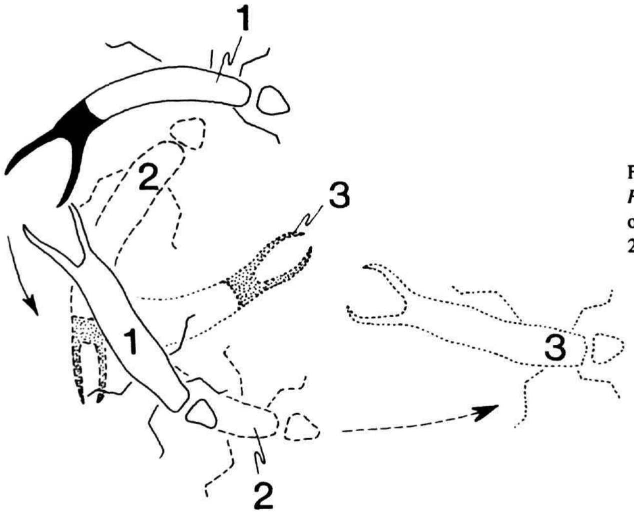


FIGURE 70 (left).—With a rapid turn, an aggressive individual (black) of *Pyragra nigrescens* struck with the sides of its cerci (1,2), which displaced the opponent about one body length (3). Time between drawings: 1-2, 0.18 s; 2-3, 0.07 s.

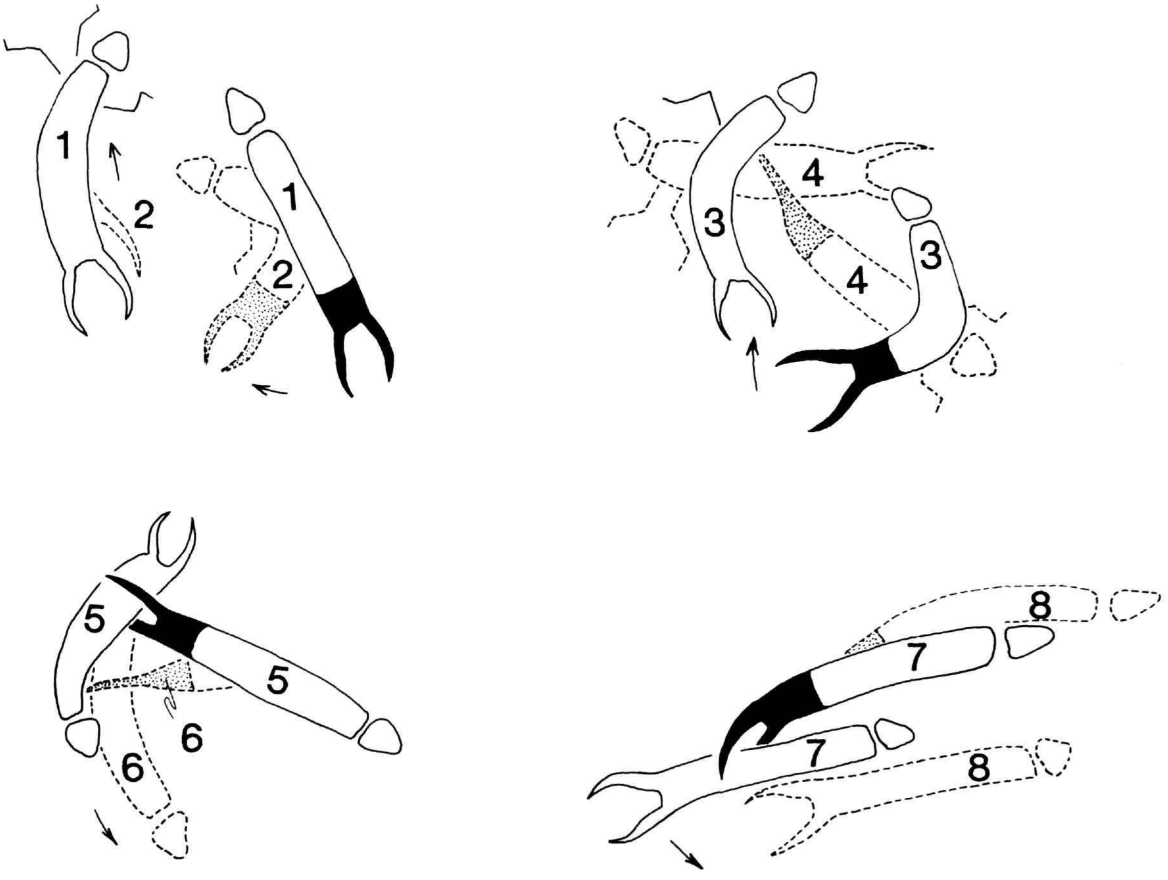


FIGURE 71.—An aggressive *Pyragra nigrescens* (black) struck tentatively (2), then struck again (3,4) to pinch its opponent on the abdomen. The opponent turned and moved forward (6,7), thereby freeing itself from the grip of its opponent (8). Time between drawings: 1-2, 0.07 s; 2-3, 0.18 s; 3-4, 0.07 s; 4-5, 1.35 s; 5-6, 0.07 s; 6-7, 0.18 s; 7-8, 0.03 s.

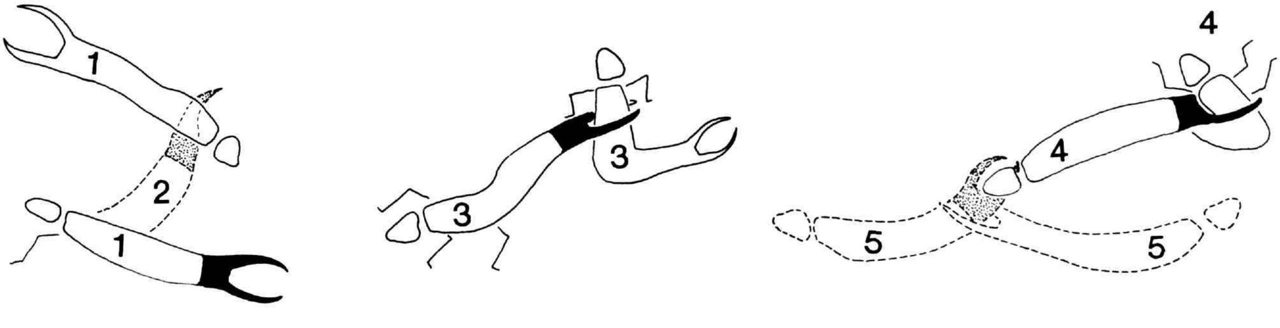


FIGURE 72.—An aggressive *Pyragra nigrescens* pinched its opponent (2) and lifted and shook it (3). The opponent succeeded in returning the pinch (4), which apparently caused the first to release its hold (5). Time between drawings: 1-2, 0.07 s; 2-3, 0.18 s; 3-4, 0.4 s; 4-5, 0.15 s.

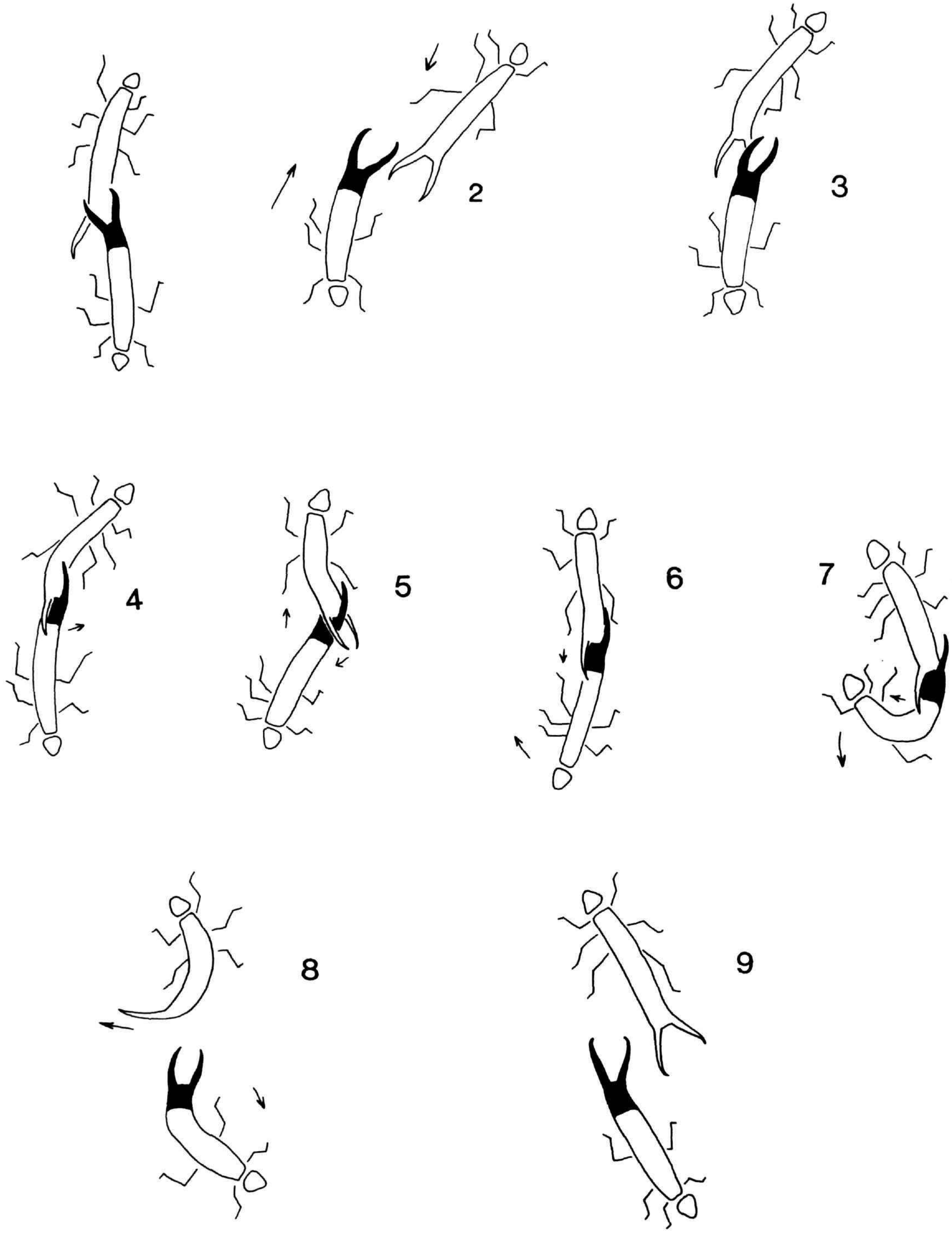


FIGURE 73.—An aggressive *Pyragra nigrescens* (black) gave a quick pinch (1) and then released its opponent. The cerci then meshed (4), and the two animals apparently pushed each other, as indicated by the curvature of their bodies (5–7). The animal that originally was pinched then made a lateral slam (8), which had little effect on the opponent. Time between drawings: 1–2, 1.0 s; 2–3, 0.27 s; 3–4, 0.72 s; 4–5, 3.24 s; 5–6, 3.35 s; 6–7, 3.06 s; 7–8, 3.87 s; 8–9, 0.12 s.

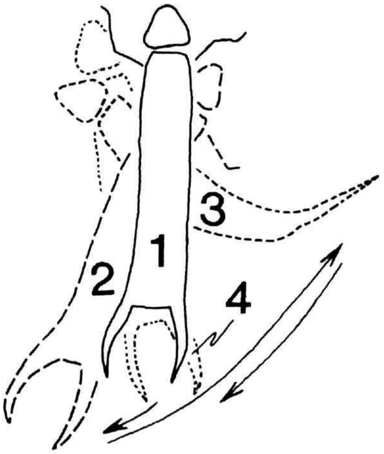


FIGURE 74.—Study of a strike made by a *Pyragra nigrescens* that had interacted very aggressively with other individuals, but which was not in contact with them at that moment. Just before striking, the body moved slightly toward the side opposite the strike and slightly rearward (1,2). During the strike (3), the animal turned its body 45°, then it returned to its original position (4). Time between drawings: 1-2, 0.07 s; 2-3, 0.07 s; 3-4, 0.07 s.

individuals were not present, it appeared that an individual "wound up" to deliver a forceful lateral slam by bending its abdomen slightly in one direction before slamming in the other (Figure 74).

When one individual had won a battle, it often chased the loser, striking at it with its cerci (Figure 75). Occasionally strong rapid vibrations of the body were seen in aggressive contexts while the two individuals were out of contact.

C. COURTSHIP AND COPULATION

1. *Doru taeniatum*

We taped five courtships and three copulations and observed five other complete copulations. Courtship times varied between 1 and about 45 min. Receptive females usually were passive throughout the courtship. An unreceptive female repeatedly moved away from the male or lowered her abdomen to the substrate thus making intromission impossible.

In a typical courtship, the male first approached the female from the rear and touched her with his antennae. He turned and moved backward toward her, moving his abdomen slowly from side to side until he touched her cerci with his. He then often brushed the dorsal surface of the female's abdomen repeatedly with the ventral surfaces of his cerci. Intermittently the male paused to attempt to copulate, twisting the posterior part of his abdomen about 180° and inserting his cerci between the female's abdomen and the substrate. The male sometimes responded to a female that had lowered her abdomen by standing nearby and rapidly vibrating his entire body, thus producing substrate vibrations (Briceño and Schuch, 1988).

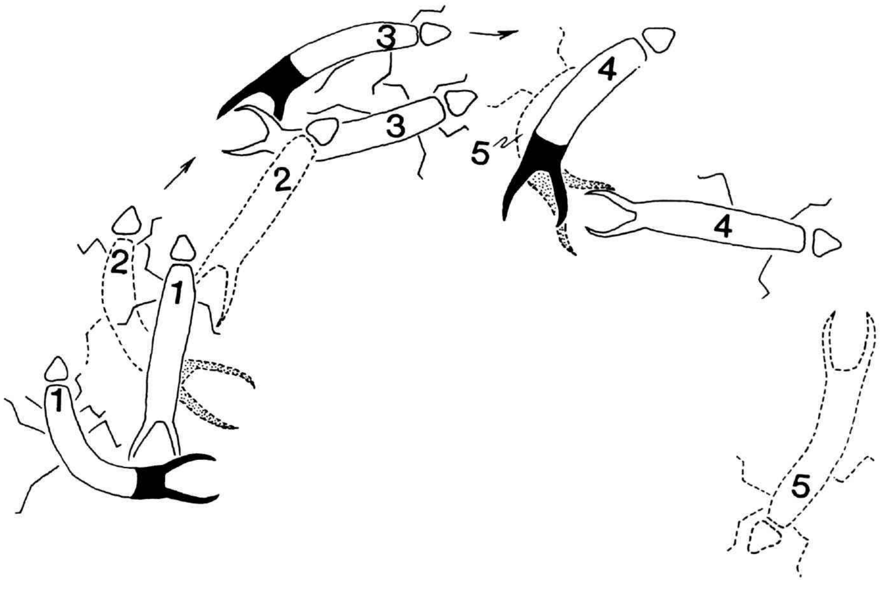


FIGURE 75.—An aggressive *Pyragra nigrescens* swung its body laterally (2) and ran forward (2,3) in pursuit of an opponent. It then swung its body laterally again (4,5) as the opponent continued to flee. Time between drawings: 1-2, 1.62 s; 2-3, 0.09 s; 3-4, 0.1 s; 4-5, 0.24 s.

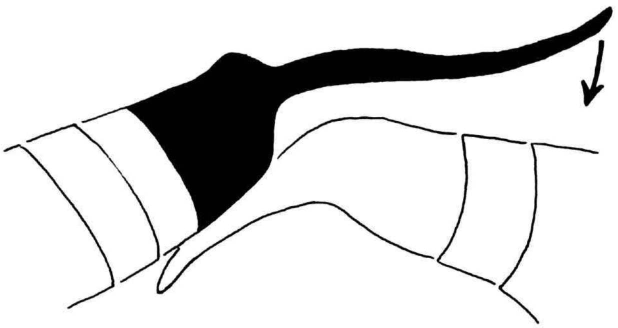


FIGURE 76.—A male *Doru taeniatum* tapped a female gently with his cerci during copulation. The frequency of taps was about 1.2 per s.

Occasionally a receptive female gently pinched the male's cerci with hers.

The female acceded to a male's courtship by lifting and twisting the tip of her abdomen slightly. This allowed the male, with his abdomen twisted in the opposite direction, to establish genitalic contact. Usually during copulation the male gently tapped the female's abdomen rhythmically with the ventral surfaces of his cerci (Figure 76). Often females appeared to attempt to terminate copulation with gentle pulls, by placing their cerci on the male's abdomen, or by pulling him around violently. Copulations lasted an average of 10±3.89 min (N = 8), and often a pair remated after separating. On several occasions a second male interrupted a copulation by inserting his cerci between the genitalia of the pair and tapping the male with his cerci, or by pinching the male's abdomen with his cerci.

2. *Skalistes inopinata*

We taped five courtships and one copulation. Courting males performed gentle forward-backward vibrations of the abdomen. They also tapped the female's head, thorax, and abdomen repeatedly with their cerci, mostly with the ventral surfaces of the basal or middle portions of the cerci. The male tapped with both cerci at once, sometimes by rocking his body backward, sometimes by moving his cerci ventrally, or a combination of the two. Sometimes the male tilted his abdomen from side to side as he tapped. At no time did the dorsal "horns" at the bases of the male's cerci touch the female. Acceptance was signaled when the female raised and twisted her abdomen slightly, and the male twisted and inserted his abdomen ventral to hers to copulate (Figures 77, 78).

During copulation the male sometimes gave single, brief dorsal flicks or jerks of his abdomen lasting only about 0.03 s (Figure 77), perhaps in response to movements by the female. In most cases, it seemed that his movement did not result in a new contact with the female, rather it pulled and/or twisted the genital union. Early in one copulation the male made eight flicks in the space of 50 s. Males also tapped and rubbed females gently with the bases of their cerci during copulation (Figure 78).

Two copulations were preceded by almost no courtship other than the male raising his abdomen and attempting to keep its tip directly toward the female. In one pair, the female repeatedly pursued the male, antennating him several times and bringing her abdomen around to press its ventral surface against that of the male's until the male successfully achieved intromission.

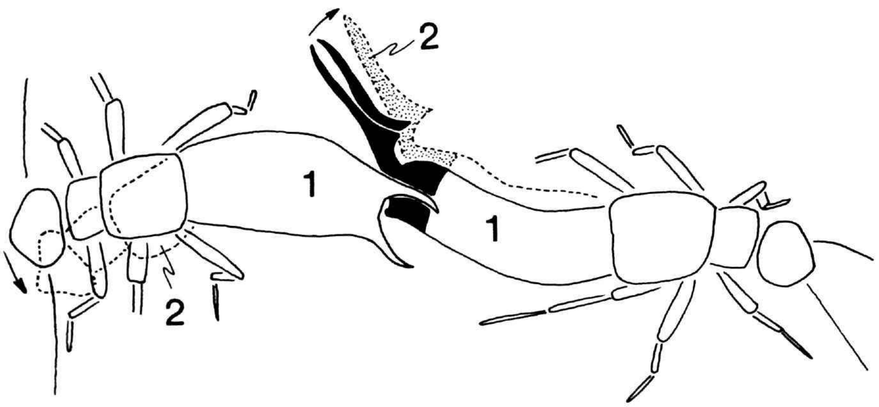


FIGURE 77.—A copulating male *Skalistes inopinata* (black) jerked dorsally and to the side, pulling the female with his genitalia as she began to walk in the opposite direction. Time between drawings: 0.03 s.

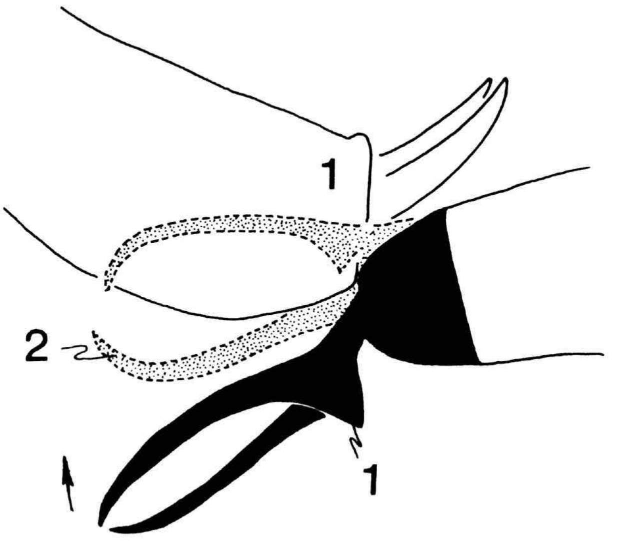


FIGURE 78.—A male *Skalistes* (black) tapped a female during copulation with a ventral movement of his cerci. Time between drawings: 0.1 s.

3. *Metrasura ruficeps*

We taped 12 courtships and 4 copulations. Receptive females were passive and remained immobile or cleaned themselves. After contacting a female with his antennae, the male bent his abdomen to orient his cerci toward her, and then he turned to face away. He then gently tapped the dorsal surface of the female's abdomen, head, and/or thorax with the middle and distal portions of his cerci (Figure 79). Taps occurred in pairs or singly; sometimes they alternated with twists of the abdomen that apparently first brought one cercus into contact with the female and then the other. Side-to-side movements of the male abdomen also occurred. The frequency of taps during one series of eight single taps averaged about 1 every 1.2 s. In some cases it was clear that the large teeth on the internal surfaces of the male's cerci contacted the female during a tap; more often, however, contact was with the more ventral basal portions of the male's cerci.

Courting males usually were behind the female or at her side. If the male lost contact with the female, he moved backward as he tapped with his cerci, then turned and walked forward using his antennae in an apparent attempt to relocate her. The male eventually positioned himself at the female's rear, twisting his abdomen while he continued to tap her, and attempted to copulate by placing his cerci to one side of the ventral surface of the female's abdomen. A receptive female responded by twisting her abdomen. Unreceptive females moved away and/or lowered their abdomens. As in *Doru,* males tapped females gently with the basal and middle portions of their cerci during copulation.

4. *Ancistrogaster scabilosa*

We taped 17 courtships and 2 copulations. A courting male curved the tip of his abdomen slightly dorsally and moved backward toward the female to tap her repeatedly on her cerci, abdomen, thorax, or head. Usually he tapped her with the tips

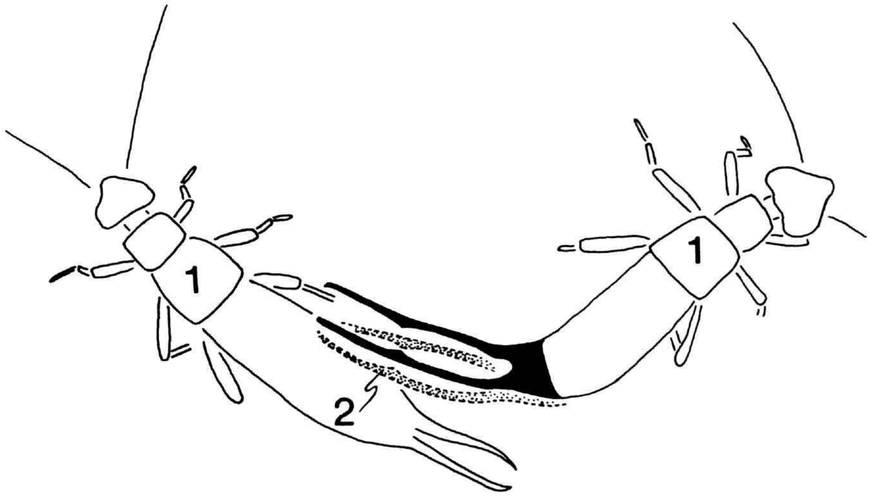


FIGURE 79.—A courting *Metrasura ruficeps* male (black) tapped the dorsal surface of the female's abdomen with a lateral and ventral swing of his cerci, thereby touching her with their ventral surfaces. Time between drawings: 0.17 s.

of his cerci (Figure 80). If the female did not move, the male placed his cerci at the side of her abodmen, twisted the distal portion of his abdomen about 90°, and attempted to make genital contact. Receptive females did not move away; instead they twisted their abdomens, which allowed intromission. The lateral projections of the male's abdomen did not come into play during courtship, nor did the male tap the female during copulation as in *Doru taeniatum, Skalistes inopinata,* and *Metrasura ruficeps.*

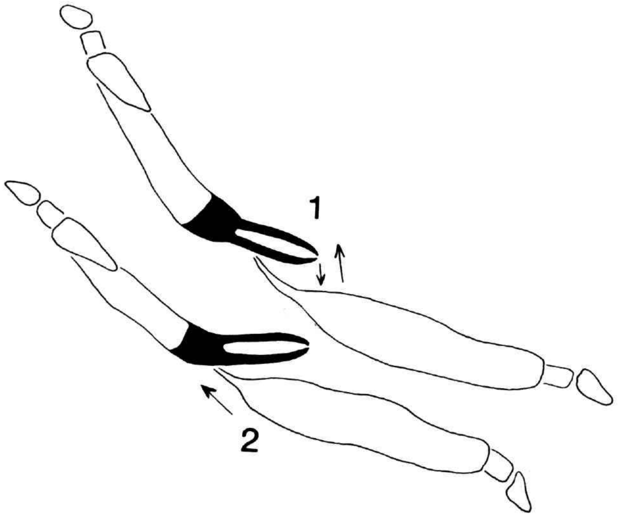


FIGURE 80.—A courting *Ancistrogaster scabilosa* male (black) repeatedly tapped on the dorsal surface of the female (1). The female was receptive, and she moved toward the male, allowing him to move toward her and place his genital opening opposite hers (2).

5. *Sparatta bolivari*

We taped two courtships and one copulation. A courting male occasionally mouthed the female briefly and used the tips of his cerci to nip the cerci or legs of the female (Figure 81). On some occasions, the male made quick lateral taps on the female cerci with his cerci (Figure 82). Eventually the male began energetic rubbing with the ventral surfaces of his cerci and abdomen on the dorsal surface of the female, using short, rapid forward and backward, or side to side movements (Figure 83). Frequently the male's body was directly behind that of the female as he rubbed her dorsal surface (Figure 84). In some cases, he may have rubbed her with his pygidium (we could not

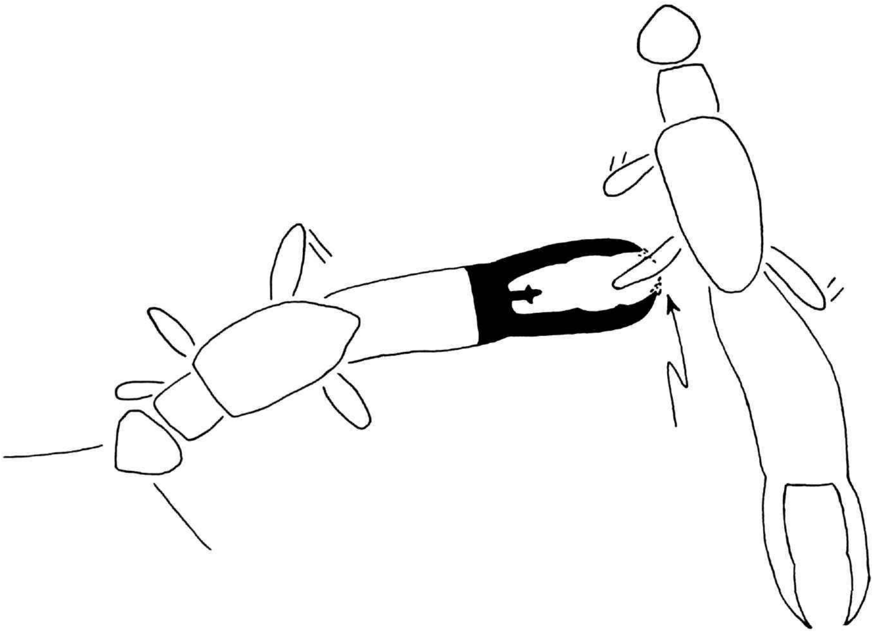


FIGURE 81.—A courting male *Sparatta bolivari* (black) nipped a female on her leg (arrow) by closing his cerci. Time between drawings: 0.1 s.

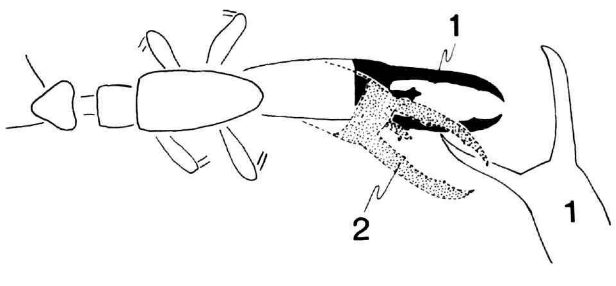


FIGURE 82.—A courting male *Sparatta bolivari* (black) tapped laterally against the cerci of a female. Time between drawings: 0.07 s.

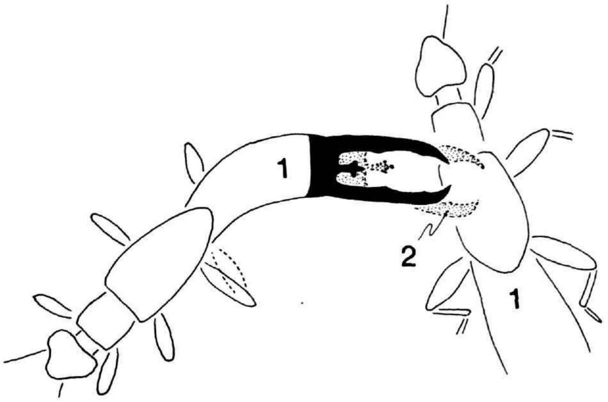


FIGURE 83.—A male *Sparatta bolivari* (black) rocked backward to rub a female's elytra with the ventral surfaces of his cerci. Note that the male's pygidium did not contact the female. Time between drawings: 0.33 s.

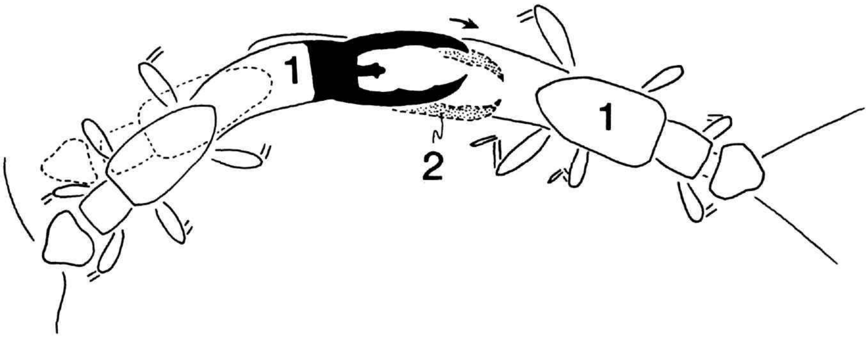


FIGURE 84.—A courting male *Sparatta bolivari* (black) aligned his abdomen on the dorsal surface of that of the female. He then moved backward and presumably rubbed his ventral surface against her dorsal surface. Time between drawings: 0.7 s.

be sure). After rubbing, the male often attempted to turn upside down. This was not possible in our glass-topped observation chambers, but in a narrow tunnel with one glass side a courting male succeeded in turning upside down, and he immediately moved backward to place the ventral surface of his cerci against the ventral side of the female's abdomen and copulate.

6. *Vostox quadripunctatus*

We taped only a single, successful courtship. Copulation lasted 94 s. Both before and after copulation the male apparently was aggressive toward the female, hitting her repeatedly with strong lateral slams of his cerci (Figure 85). The female repeatedly twitched her abdomen dorsally, a behavior not seen in any other occasion or in any other species. Each twitch was brief (≤0.03 s) and appeared to consist of a quick dorsal flexion of variable magnitude followed by a lateral displacement, also of variable magnitude. In one span of 5 s the female twitched 12 times. Twitches were performed both in front of and behind the male. At least some of the times the female rocked her entire body slightly backward during a twitch. To copulate, the male twisted his abdomen sharply while the female lifted and twisted hers slightly (Figure 86). During copulation the male occasionally appeared to contract his abdomen (or perhaps twisted it) and to tap the female's side with his cerci.

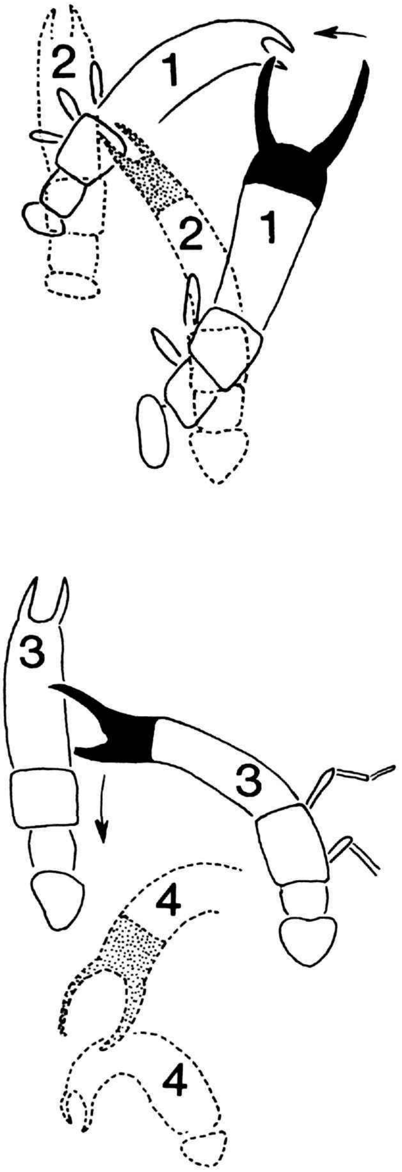


FIGURE 85.—A male *Vostox quadripunctatus* (black) "courted" a female by slamming her laterally (1,2) and then throwing her about one body length across the petri dish where she landed on her side (4). The female responded by immediately performing strong twitches typical of a receptive female, which finally led to copulation. Time between drawings: 1-2, 0.13 s; 2-3, 0.1 s; 3-4, 0.1 s.

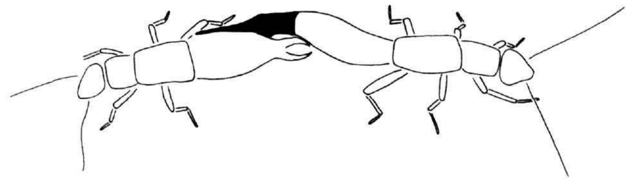


FIGURE 86.—A copulating male *Vostox quadripunctatus* (right) twisted his abdomen more than 90° while the female lifted and slightly twisted her abdomen.

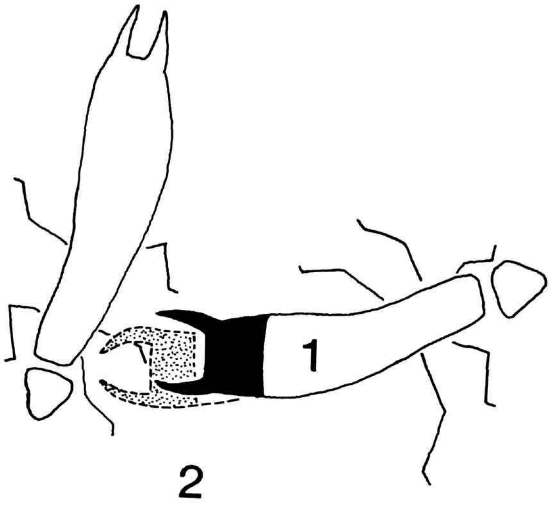


FIGURE 87.—A courting male *Paralabella dorsalis* (black) pushed on the leg of a female. Time between drawings: 0.09 s.

7. *Paralabella dorsalis*

We taped 38 courtships and 5 copulations. A courting male oriented his cerci toward the female and moved backward with their cerci tilted slightly downward. Once a male made contact, he rocked forward and backward with his cerci held downward so that his cerci pushed gently on the female's legs or head (Figure 87). Sometimes the female moved away, and the male backed after her, apparently attempting to keep his cerci in contact with her. To copulate, the male kept his cerci pointed downward as he twisted the tip of his abdomen approximately 90°; then, by raising his cerci, he attempted to induce the female to raise the tip of her abdomen or cerci (Figure 88). If the female's abdomen was raised, the male grasped the base of her cerci with his (Figure 89), and they copulated. During copulation the male made slight movements of his abdomen.

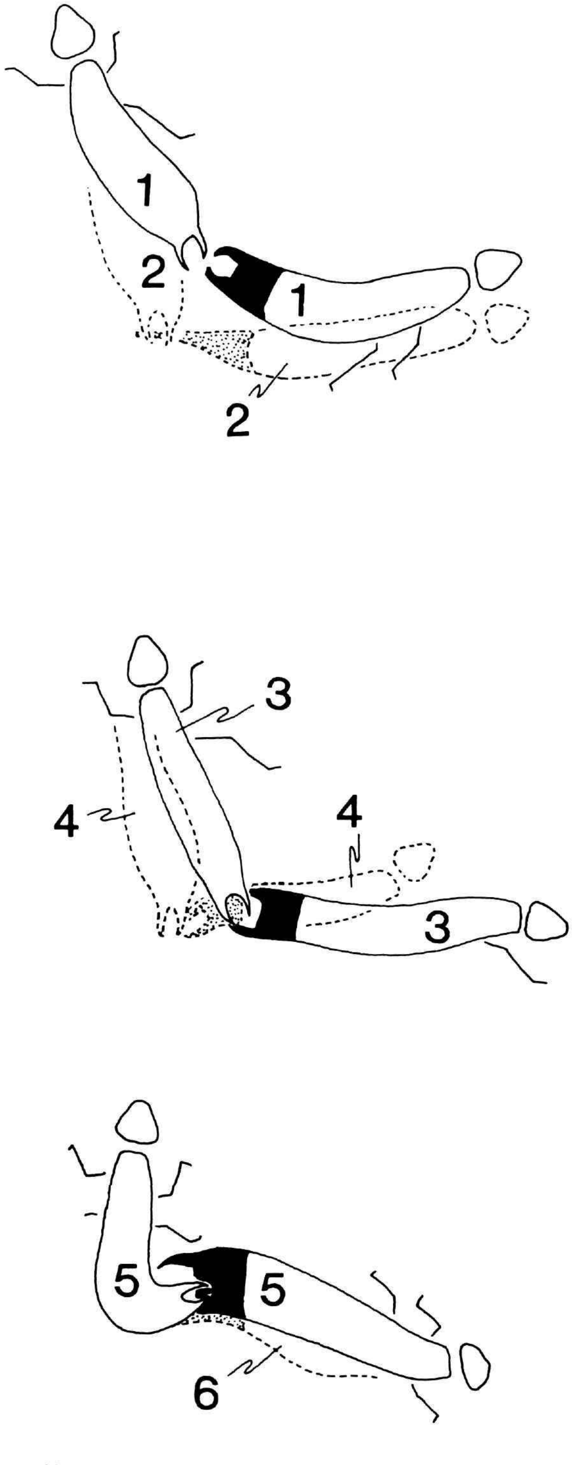


FIGURE 88.—A *Paralabella dorsalis* male (black) twisted his abdomen 90°, and the female moved hers laterally and slightly dorsally (1). Once the male's cerci were below those of the female, he pushed rearward and upward, apparently trying to grasp her with his cerci (2). Repeated attempts of this sort failed (3–6). Time between drawings: 1–2, 0.36 s; 2–3, 0.27 s; 3–4, 0.33 s; 4–5, 2.90 s; 5–6, 0.24 s.

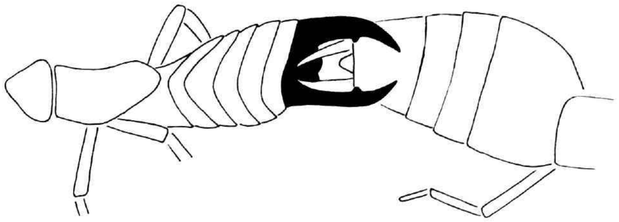


FIGURE 89.—A male *Paralabella dorsalis* (black) clasped the base of the cerci of a female that had raised her abdomen prior to copulating. The teeth on the inner edges of the male cerci meshed with the cerci of the female.

8. *Pseudomarava prominensis*

We taped seven courtships and six copulations. One copulation lasted 64 s. A male initiated copulation attempts by grabbing and holding a leg or an antenna of the female with his mouthparts (Figure 90). A female caught this way responded defensively, pulling away and curving her abdomen dorsally or laterally in an apparent attempt to pinch the male. The male responded by attempting to grasp the female's abdomen at the base of her cerci with his curved cerci (Figure 90). If he succeeded, he released his hold with his mouthparts and apparently immediately introduced his genitalia into hers, while maintaining his hold on her with his cerci. Once intromission had occurred, the male released the hold with his cerci. The female usually pulled him about for many seconds before both became quiet except for cleaning movements.

On several occasions a second male interrupted a copulation by pinching the copulating male on his abdomen while biting his leg or antenna. The copulating male withdrew from the female to defend himself.

9. *Anisolabis maritima*

We taped seven courtships and three copulations. Females were aggressive toward males in the preliminary stages of courtship, hitting them frequently with their cerci. In contrast to *Carcinophora* (below), males responded aggressively and frequently pinched females. A receptive female became gradually less aggressive, and the male oriented his cerci toward her and tapped her gently on the tip of her abdomen with the ventral surfaces of his cerci, also giving her brief pinches with the tips of his cerci (Figure 91). The male attempted intromission by twisting the tip of his abdomen 180° and pushing gently until their genitalia were in contact (Figure 91). Some courtships were short, with only a few taps by the male's cerci before intromission. During copulation the male moved his cerci gently from side to side and occasionally vibrated his antennae.

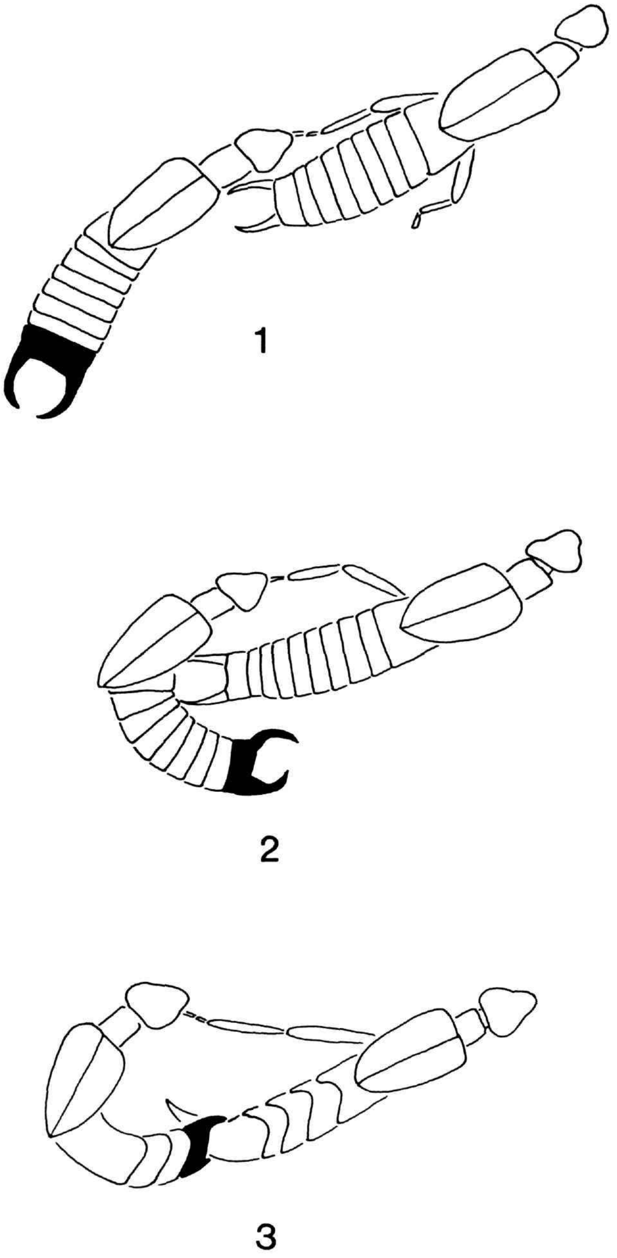


FIGURE 90.—A *Pseudomarava prominensis* male (black) seized a female's hind leg (1), bent his abdomen toward her as she held her abdomen near him defensively (2), and then seized the tip of her abdomen with his cerci (3). The male then released his hold on the female's leg and copulated. Time between drawings: 1–2, 0.54 s; 2–3, 3.0 s.

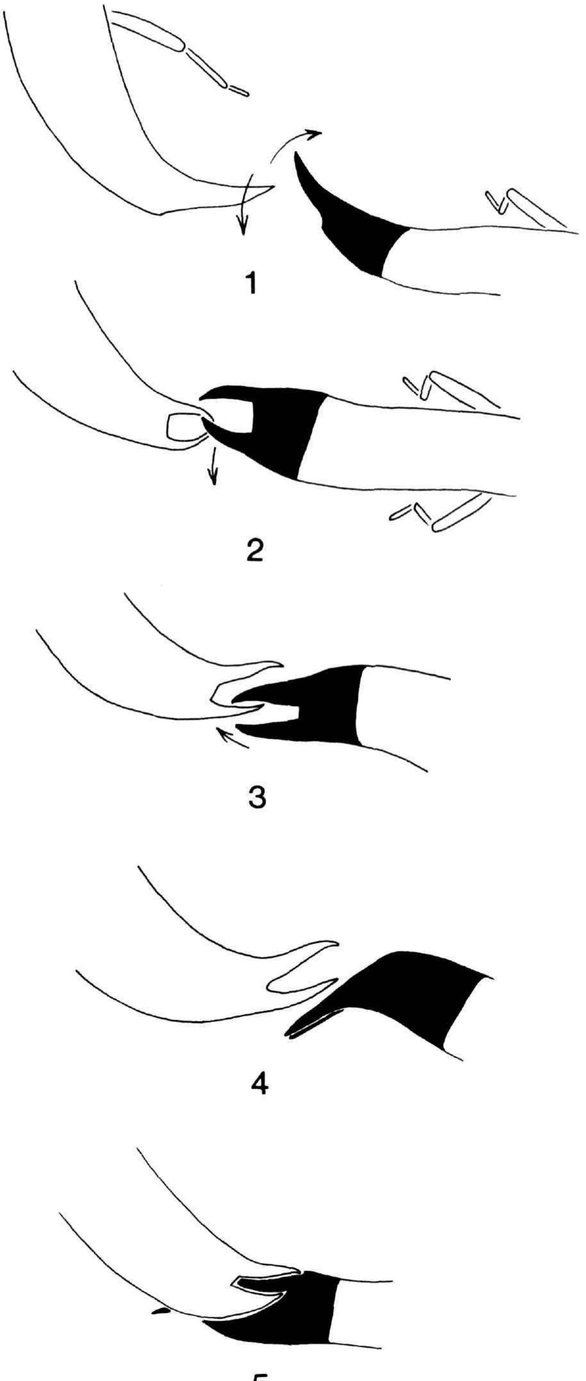


FIGURE 91.—A male *Anisolabis maritima* (black) twisted his cerci about 90° (1), touched the female (2), and then gripped the ventral part of the female's cercus (3). Similar taps were repeated until the male encountered the genital aperture of the female. The female made several movements, which culminated with a twist of her abdomen that allowed the male to press his genital opening to hers (4,5). Time between drawings: 1–2, 0.54 s; 2–3, 0.45 s; 3–4, 0.18 s; 4–5, 1.3 s.

10, 11. *Carcinophora robusta* and *C. americana*

We taped 14 and 3 courtships, and 7 and 1 copulations respectively. No differences were noted between the species. Females pinched courting males on various occasions, but, when receptive, they became less aggressive and sometimes later in the interaction nibbled at the cerci of the male as he opened and closed them. The male did not respond aggressively to attacks from females, rather he repeatedly twisted the tip of his abdomen and gently tapped and rubbed against the female's abdomen and cerci with the ventral surfaces of the tip of his abdomen and the basal portions of his cerci (Figure 92). The male attempted to copulate by rubbing and pushing repeatedly with the ventral surface of his cerci against the genitalia of the female (Figure 93).

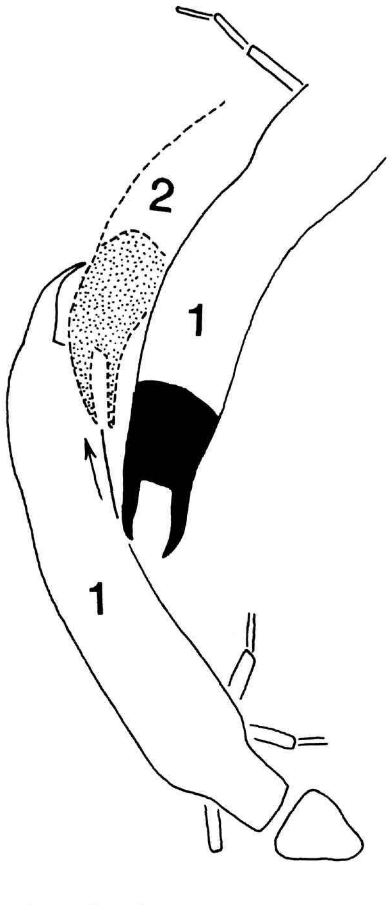


FIGURE 92.—A courting *Carcinophora americana* male (black) moved forward and backward, rubbing gently on the abdomen of the motionless female prior to copulation. Time between drawings: 0.24 s.

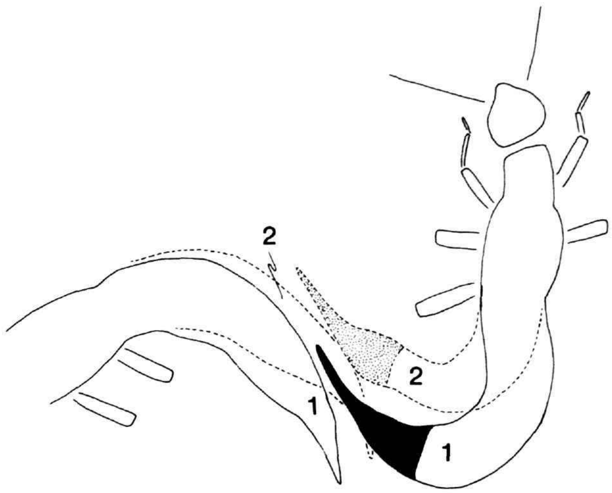


FIGURE 93.—Just prior to copulation a male *Carcinophora americana* rubbed the base of his cerci against that of the female in an apparent attempt to locate her genital aperture. Time between drawings: 1.0 s.

12. *Carcinophora rosenbergi*

We taped six courtships and three copulations. Females of this species also were aggressive in the first stages of courtship, and they repeatedly pinched and struck the male. This species differed from its congeners in that the male vibrated his body rapidly forward and backward two or three times while about 1-2 cm from the female (Figure 94). Later, the male turned to orient his cerci toward the female and then tapped and rubbed her as described above for *C. robusta* and *C. americana*. If the female was receptive she eventually moved her abdomen to one side and forward, and the male twisted the tip of his abdomen and rubbed and pushed with the ventral surface of the tip of his abdomen against the ventral surface of the tip of hers to establish genital contact (Figure 95). In some cases, a receptive female gently nipped the male's cerci with hers (Figure 95). The female sometimes twisted her abdomen repeatedly during the first stages of copulation.

13. *Pyragra nigrescens*

We taped five courtships, none of which led to copulation. In at least two interactions an apparent male rubbed with the basal portion of his cerci or the sides of his cerci on the abdomen of the other individual (Figure 96). Prior to and during rubbing, the apparent male sometimes also vibrated his body and antennae rapidly in apparent courtship movements.

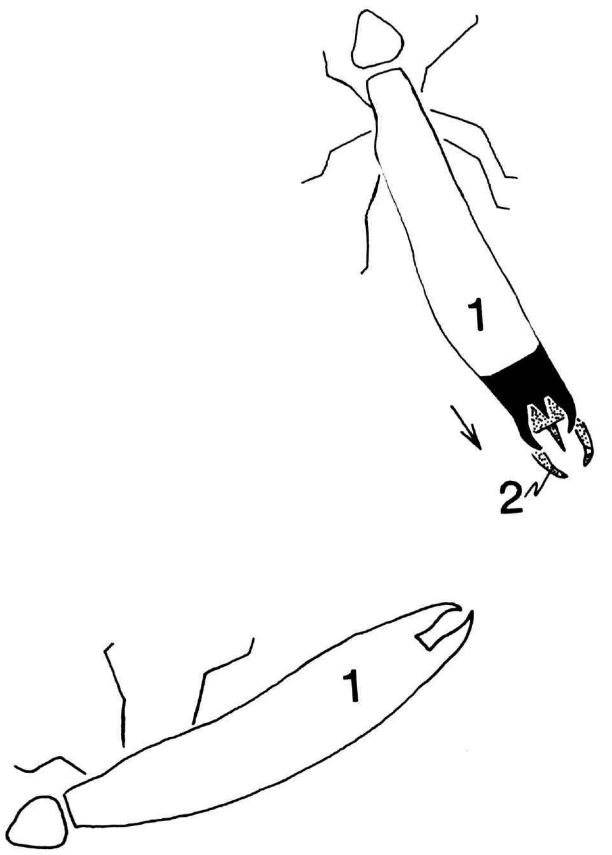


FIGURE 94 (left).—A male *Carcinophora rosenbergi* (black), with his genitalia protruding, shook his body rapidly forward and backward. After shaking several times, he turned, touched the female with his antennae, then turned to resume his original position and shook his body again. Time between drawings of male: 0.07 s.

Discussion

A. FUNCTIONAL MORPHOLOGY OF MALE CERCI AND PYGIDIA

Animals generally failed to respond to each other until they made physical contact, suggesting that visual stimuli are of little importance in either aggression or courtship. The generally claustral and/or nocturnal habits of most species reinforce this conclusion. We will therefore attempt to deduce possible functions of cerci and associated structures on the basis of the ways in which they contacted other earwigs during our observations.

Before beginning a detailed discussion of possible functions, it should be noted that in only two species (*Doru taeniatum* and *Vostox quadripunctatus)* was male-male aggression observed in the field, and only in *Doru* was courtship seen in the field. Our observations thus give neither the biological context of fights (e.g., near females, food, or a refuge) nor the physical sites where fights and courtship occur (e.g., in closed tunnels, small chambers, open sites, or on vertical trunks). The kinds of behavior used in fights clearly were influenced by the physical setting (tunnels vs. open petri dishes) in those species in which we made observations in both settings (*Doru, Vostox,*

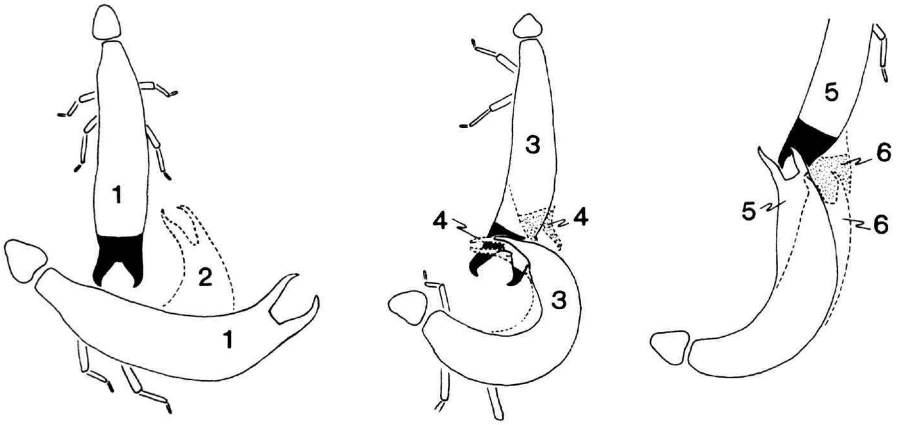


FIGURE 95.—A female *Carcinophora rosenbergi* curved her abdomen toward the male (black) (2) and pinched him gently on his cerci (3) before turning her abdomen dorsally as the male twisted his to bring his genital aperture into contact with hers (6). Time between drawings: 1-2, 0.33 s; 2-3, 0.63 s; 3-4, 0.63 s; 4-5, 2.61 s; 5-6, 1.0 s.

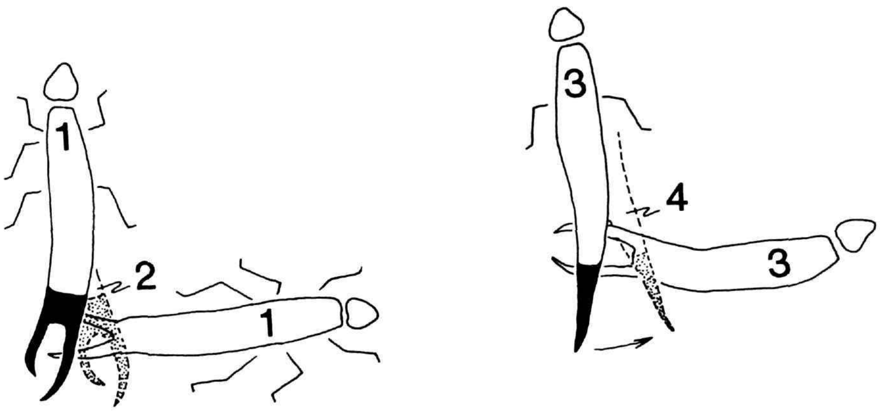


FIGURE 96.—A courting male *Pyragra nigrescens* (black) rubbed the posterior portion of the female's abdomen first with both cerci above her (1,2) and then with one of his cerci above her and the other below (3,4) (the male had one deformed, shorter cercus). While he stroked the female, the male's body vibrated rapidly, as did his antennae.

Paralabella, Anisolabis). In order to permit interpretations of probable functions, we made the assumption that the behavior patterns of males in our observation chambers are similar enough to those that occur in nature. Although this assumption is justified in the one species we observed in detail in nature (*Doru*), further studies are needed on other species.

This limitation is less severe in the species found in relatively flat, enclosed spaces (*Sparatta, Paralabella,* to a lesser extent *Vostox*). In *Sparatta,* the flattened body design, the lack of abdomen twisting or dorsal flexion associated with slams and strikes, and the attempts of males to turn themselves upside down both when fighting and when courting lead us to believe that individuals of this species normally interact in spaces that are dorsoventrally compressed. The same is probably true of *Paralabella,* in which the body also is relatively compressed dorsoventrally. The acceptance posture of females of this species, however, is only feasible where there is some space dorsally. On the other hand, both the morphology and behavior of *Metrasura, Skalistes,* and *Ancistrogaster* suggest that they must fight in relatively open spaces. Our field observations are in accord with this, as all three were found in open sites at night.

Some general preliminary statements can be made regarding the functional significance of the forms of some structures. The males of many species have cerci whose internal margins have teeth and other irregularities, especially near the base of the cercus. Males of all species pinch opponents with their cerci at least occasionally. It seems probable that the teeth serve to increase the friction against the surface of the opponent and/or to produce discomfort. The small teeth of *Doru* are highly corrugated (Figure 97), probably facilitating the proposed

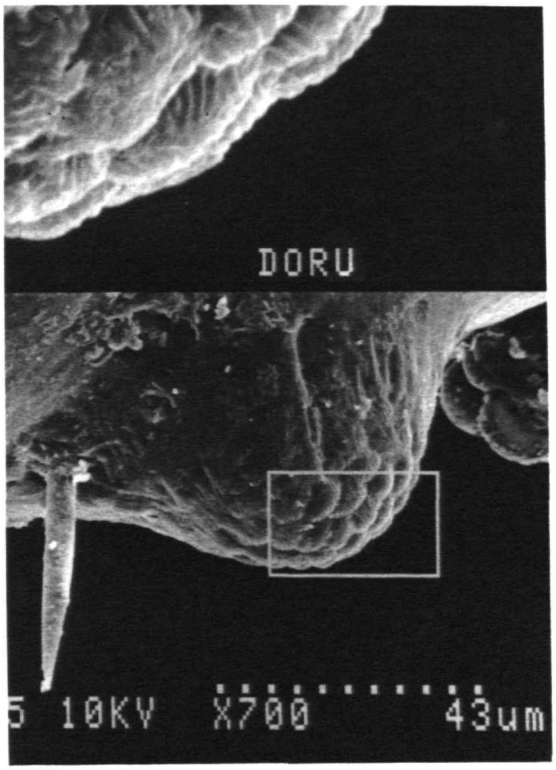


FIGURE 97.—Scanning electron micrograph of a tooth on the inner margin of the cercus of a male *Doru taeniatum*, showing the corrugated surface and the nearby seta.

friction function. There is a seta on the posterior side of each small tooth of *Doru* (Figure 97). These setae probably are deflected when the cercal tooth touches another object, and they may play an important role in sensing contact with opponents during cercal tapping and squeezing. Only in *Paralabella dorsalis* did courtship behavior clearly suggest that a prominence on the inner margin of the cerci was used in interactions with females.

The largest cercal teeth usually occur near the middle of the cercus, as in *Metrasura*, *Sparatta*, and *Ancistrogaster*, or near the tip, as in *Doru*. The reasons for these differences are not clear. Larger teeth probably allow the male to give more forceful pinches to their opponents than they can with the tips of the cerci, because the teeth reduce the effective length of the cercus.

Table 1 summarizes the possible functional significance of different male-specific cercus and pygidium morphologies. Species-by-species discussions follow that explain how we reached the conclusions in the table.

1. *Doru taeniatum*

In high-level interactions, opponents usually were defeated by pushing and lifting movements. Thus, details of male-

TABLE 1.—Possible functions of male-specific morphological characters on the cerci and associated structures in 12 earwig species (justifications for proposing these functions and reasons for doubts are discussed in the text).

Species and characters	Interaction with			
	Other males		Females	
	Threat	Weapon	Court	Hold
1. *Doru taeniatum*				
Teeth on inner surface of cerci	?	yes?	no?	no
Greater length of cerci	?	yes?	no?	no
Sharp pygidium	?	no?	no	no
2. *Skalistes inopinata*				
Dorsal projection on cerci	yes	no	no	no
Cerci long, crescent-shape	no?	yes	no	no
3. *Metrasura ruficeps*				
Greater length of cerci	?	yes	no	no
Large teeth on inner surface of cerci	?	yes?	no	no
Wider pygidium	?	yes?	no	no
Notched pygidium	?	yes?	no	no
4. *Ancistrogaster scabilosa*				
Lateral abdominal processes	yes	no	no	no
Teeth at tips of cerci	?	yes?	no	no
Cerci widely separated at base	?	yes?	no	no
5. *Sparatta bolivari*				
Tridentate pygidium	?	?	?	no
Teeth on inner surface of cerci	?	?	no?	no
6. *Vostox quadripunctatus*				
Longer and straighter cerci	?	yes	?	no
Cerci widely separated at base	?	yes	no?	no
Cerci curved at base	?	yes	no?	no
Cerci curved at tip	?	yes	no?	no
7. *Paralabella dorsalis*				
Tooth at base of inner edge of cercus	no	no	yes	no
Greater thickness of cerci	?	?	no	no
Pygidium wider, curved	no?	yes	no	no
8. *Pseudomarava prominensis*				
Cerci with wide curve	?	yes?	no	yes
9. *Anisolabis maritima*				
One cercus shorter, with sharper curve at tip	?	yes?	no	no
10–12. *Carcinophora americana, C. robusta, C. rosenbergi*				
One cercus shorter, with sharper curve at tip	?	yes?	no	no

specific cercus and pygidium morphology seem not to be especially useful. Occasionally movements associated with a pinch were used; in at least some pinches the tooth on the inner edge of the cercus probably served to grip the opponent (Figure 12). In others, the length of the cercus may have provided increased mechanical effectiveness of the male's lifting or slamming attack (e.g., Figures 10, 12). On the other hand, many (most) slams did not involve pinches, and the force on the opponent apparently was exerted by the pygidium (e.g., Figure 9), so there were many fights in which male-specific cercus morphology did not seem to confer mechanical advantages.

The pointed pygidium probably does not function as an effective penetrating weapon. It undoubtedly struck the opponent in many backward strikes, but the posterior portion of the male abdomen is heavily sclerotized, and there are no pits or grooves into which an opponent's pygidium could fit so as to produce a tighter mesh with the opponent. Perhaps the point functions as a mechanism for increasing contact in dorsal slams or to intensify the stimuli associated with backward strikes, and thus it functions as a threat device.

Tapping behavior always occurred before and usually during the time cerci were meshed. Although tapping was probably partly exploratory in function, it also may serve as threat behavior. Some interactions ended with one male fleeing after being tapped. During tapping, cercal length, cercal teeth, and the pygidium presumably could all have been sensed by the opponent as they touched him. Thus, these male-specific characters may function as threat devices.

Possible courtship functions for some male-specific cercal characters also are possible. Although males usually tapped females with only the ventral, proximal portions of their cerci, females sometimes mouthed male cerci and sometimes pinched them with their own cerci. Female pinching of male cerci probably, however, was a signal to the male that the female was ready to copulate, as it usually was followed immediately by tilting of the abdomen by the female to facilitate intromission. The male pygidium was not contacted by females and played no apparent role in male-female interactions.

In sum, we cannot confidently assign functions to several male-specific characters; at least some may function as threat devices.

2. *Skalistes inopinata*

Two male-specific characters that seem to be involved in male-male aggression rather than courtship are the dorsal triangular projections at the bases of the cerci and the strongly curved, smooth, tong-like distal portions of the cerci. The dorsal projections appear to be used in threat displays, and the tongs probably serve as weapons in fights. The male abdomen usually is turned and moved so that the dorsal projections tap on the opponent during low- and moderate-level male-male aggression. The general lack of hard, dorsally directed slamming movements, the rarity of forceful movements in which the projections were brought to bear on the opponent's body, and the lack of any other mechanical contact or meshing of the projections during pinching movements all indicate that the projections are not weapons used to gain physical advantage.

The tong-like form of the distal portion of the cercus probably allows the cerci to fit snugly around the opponent's body so that he can be turned upside down when the attacker's abdomen is twisted.

Most courtship is performed by tapping with the ventral, basal portions of the cerci. The female is not in position to sense either of these male-specific characters during such taps.

3. *Metrasura ruficeps*

The cerci of male *Metrasura* appear to be used as weapons in fights in a number of different ways. Opponents were thrown after being pinched (Figure 19), and they also were twisted or pried away from the substrate (e.g., Figures 21, 22). Both twisting and shaking often were combined with prying movements (in various combinations, e.g., Figures 22, 23) in apparent attempts to weaken or break the opponent's foothold. The extreme length of the cerci in this species probably increases the effectiveness of these fighting tactics.

In contrast to species like *Carcinophora* spp., pinches per se played little role in the fights of *Metrasura* males. Pinches were rare, and those that occurred usually were short and combined with prying and/or twisting. Presumably the tooth on the inner margin of the male cerci serves to increase the male's ability to hold opponents when they are seized and pried (Figure 18) and when they are thrown (Figure 19).

Thus, the extreme length of the male cerci in this species seems to serve to make the cerci more effective as levers. The cerci are used in combination with blows from the abdomen to dislodge the opponent or even fling him. The male cerci have thus largely lost the primitive function of delivering forceful pinches, a function for which their great length makes them unsuited.

It also is possible that the extensive cercus-cercus and cercus-abdomen contact that always occurred while males were in intense pygidium-to-pygidium fights functions as threat behavior. If this is true (we see no compelling reason to either accept or reject the possibility), then the extreme length of male cerci, which repeatedly touch the opponent during such interactions, also could function to increase the effectiveness of the threats.

In contrast to these uses in male-male aggression, the basal and ventral rather than the distal portions of the male cerci generally were used to tap on females during courtship, so the long length of the cerci, the teeth on their inner surfaces, and pygidium characteristics are unlikely to be important in courtship.

4. *Ancistrogaster scabilosa*

The lateral extensions of the male's posterior abdominal tergites did not come into contact with the female during courtship, but they apparently did make contact with the extensions of other males during middle-level fights in which both males raised their abdomens (Figures 30, 31). Because the extensions gave no obvious mechanical advantage, we suspect that they are threat or assessment devices, analogous to the lateral prolongations of the heads of some flies (e.g., McAlpine, 1979; Dodson, 1989).

The greater length of male cerci and their wider separation at the base may aid in fights by permitting the male to pinch at a greater distance and more forcefully. The presence of a large tooth near the tip of the cercus is in accord with the idea that the cerci are used to pinch in this way (see discussion of teeth above). Both of these characters also could function as threat devices. Neither appeared to be involved in courtship, as only more basal portions of the male's cerci touched the female.

5. *Sparatta bolivari*

Understanding the significance of male-specific characters on the cerci and pygidium of this species is difficult, perhaps due to the small number of high-intensity fights we observed. Possibly the lateral prongs of the longer male pygidium function to make it easier for males to pinch the cerci of opponents (an otherwise unusual behavior that was common in this species; Figure 35), but such pinches did not seem to influence the outcomes of battles. The pygidia of fighting males sometimes meshed (Figure 36), but again the significance for the outcomes was unclear. It also was unclear whether the form of the male pygidium could be sensed by the female during courtship (Figure 84). Perhaps the pygidium and the somewhat longer cerci of males both function as threat devices.

6. *Vostox quadripunctatus*

The only male-female interaction that led to copulation resembled mid-level male-male aggression, so it is not possible to distinguish between the possible effects of courtship and aggression on male cercus morphology. The marked difference with the courtship behavior of *V. apicedentatus*, in which the male taps, rubs, and presses the female with his cerci (Moore and Wilson, 1993), suggests that our observations may have been of aberrant behavior.

Cerci and pygidia were used in three different ways in male-male fights: to deliver hard lateral and sometimes partially dorsal slams that could knock the opponent off his feet; to push with the pygidium against the opponent's pygidium or the base of one of his cerci so as to push him away (pushing of this sort seemed to determine winners in many pairings); and, more rarely, to pinch him with the entire length of the cercus.

The wide space between the bases of male cerci, the outward curve of the cercus at the base, and the prominent pygidium may all function to bring a male's pygidial area to bear on his opponent in pushing contests. Assuming that fights in tunnels were typical with respect to body parts that are brought together in pushing attempts in other contexts, the exact site on the pygidium that contacted the opponent during battles varied, as did the site on the opponent where contact was made. Thus, there appears to be no precise mesh during pushing battles; the function of the rectangular form of the pygidium is not clear.

We can offer only even more tentative speculations on the functional significance of secondary sexual differences in other details of male cercus morphology. The inward curve at the tip and the point on the tip may serve to make pinches more painful and/or less likely to slip on the opponent's body. The straight middle portion and its relatively thick diameter may increase the effectiveness of the cercus as a rod with which to deliver slamming blows and/or to pry or hold the opponent's abdomen so that backward pushes will be more effective. Any or all of these characteristics could be sensed by opposing males during pushing fights or the preceding interactions, and thus they also could serve as threat devices.

The aggressive behavior of a second species of *Vostox*, *V. apicedentatus*, is quite different (Moore and Wilson, 1993) (their terms are denoted parenthetically). Pushing contests apparently do not occur, whereas pinching (pinch and grab) is more common. Slams (bats) involve lifting the abdomen dorsally and then striking ventrally with the cerci, rather than swinging them laterally. We did not observe several types of behavior seen in *V. apicedentatus:* pressing down on the opponent with the cerci (press); prying the opponent up with the cerci (lift); and biting the opponent with the mouthparts (bite). Several of the differences involve greater use of dorsoventral movements by *V. apicedentatus*. This pattern may be related to the habitat of this species (in and around large rotting cacti), which is probably less dorsoventrally compressed than that of *V. quadripunctatus* (under loose bark).

7. *Paralabella dorsalis*

The blunt teeth near the bases of male cerci were not consistently brought into play during male-male fights. Their design did not seem appropriate to aid males mechanically in any of the contexts observed in male battles. On the other hand, the proximal edges of the teeth appeared to mesh with the dorsal surfaces of the female's cerci, forming a clamp when the male seized the female just prior to intromission. Thus, these teeth seem likely to function in interactions with females rather than with males. Because the male seizes the female with his cerci only after an extended courtship, and after the female has raised her abdomen to an otherwise unusual acceptance position, it is unlikely that the teeth function as devices with which the male physically forces the female to copulate. Instead, they probably are analogous to the nongenitalic holding and clasping devices of the males of many other animals (Eberhard, 1985), which probably function as contact courtship devices.

Male pygidia made extensive contact with opponents in battles. The breadth of the pygidium could increase its effectiveness as a defensive shield against the opponent's pinching attacks (Figure 48), but this interpretation is speculative. The greater inward curvature of male cerci probably is related to the wide separation at their bases associated with the wide pygidium. Greater curvature allows the cerci to grasp and squeeze forcefully on the body of an opponent during fights (Figure 49) despite their wide basal separation. We are unable to explain why male pygidia have their particular rounded form.

8. *Pseudomarava prominensis*

The wide, flattened pygidium and the wide curve of the smooth male cerci make it possible for the male to grasp and hold another individual's abdomen. Other individuals' abdomens are squeezed in this way just prior to copulation (Figure 90) and during male-male fights (Figure 53). In contrast to *Paralabella dorsalis*, the female often was seized while apparently resisting the male. Thus, the male design may function to force the female to copulate, rather than to court her as in *P. dorsalis*. We cannot determine if the design to grasp another individual arose in the context of male-male fights and was incidentally useful in male-female interactions, or vice versa.

The clearest use of cerci in fights between males was to pinch, and the sharp points of male cerci may make pinches more painful and/or more tenacious.

9–12. *Anisolabis maritima* and *Carcinophora* spp.

The short length and inward curvature of one cercus make the cerci mechanically strong and able to produce strong pressure when they pinch. The behavior of these species supports the idea that these male features evolved as weapons. Males often began fights by immediately striking and attempting to pinch. These were the only genera in which fights were seen that resulted in physical damage to males (one puncture wound in each genus). Male courtship behavior involved tapping with the ventral surfaces of the cerci, not pinching or clamping.

13. *Pyragra nigrescens*

The lack of clear sexual dimorphism in the cerci of this species is associated with relatively simple fighting behavior, which included quick pinches and slams.

B. EVOLUTION OF AGGRESSIVE BEHAVIOR

Male-male aggressive behavior generally varied more between species than did courtship. In all species, however, intense interactions included pinches. Females and nymphs generally use their cerci to pinch defensively (see "Introduction"). Their relatively simple cercus designs resemble more closely the cerci of fossil Dermaptera (Carpenter, 1992) and other orthopteroid insects. Thus, pinching in male-male battles probably represents the retention of a primitive trait.

We documented a number of additional, probably derived aggressive behavior patterns. Some of these probably have their evolutionary origins in behavior designed for other purposes. For instance, both turning to direct the cerci toward a disturbing stimulus and swinging the abdomen from side to side in an exploratory fashion while backing up are widespread and probably ancient behaviors. The strong lateral slams, which were especially frequent in *Vostox, Sparatta,* and *Pyragra,* and the strong pushes, such as those of *Doru* and *Paralabella,* probably derive from these behavior patterns. Because they are executed so rapidly and energetically, they acquire the added function of inflicting unpleasant stimuli on an opposing male. Prying the opponent *(Metrasura)*, flipping him over *(Skalistes)*, and raising the abdomen to tap him *(Ancistrogaster)* may represent further modifications of pushing behavior. Only in *Pseudomarava* and perhaps *Sparatta* were the male's other obvious potential weapons, his mouthparts, used in aggression.

Males of *Pseudomarava* employed aggressive behavior in an additional, presumably derived context. By biting the legs and antennae of females, they manipulated them into situations in which they could bring their genitalia into position for copulation. When the female bent her cerci toward a male to defend herself against the bite, the male seized her abdomen with his tong-shape cerci (Figure 90) and thus achieved intromission.

Homosexual courtship was observed several times in each of three forficulid species and in one labiid. The males' lack of contact with other earwigs for at least one week before our observations may have caused them to make an increased number of behavioral mistakes. However, in at least two species (*Skalistes* and *Metrasura*) the male's behavior immediately before or after he "courted" another male was sometimes clearly aggressive, suggesting the possibility that homosexual courtship may actually be an aggressive display. Apparently aggressive use of male courtship behavior (or the opposite, i.e., use of aggresive behavior as courtship) occurs frequently in natural situations in a long-horned orthopteran (Field and Sandlant, 1983). Homosexual courtship also is known in captive orthopterans (Alexander, 1964; Steinberg and Willey, 1983) and (in the presence of female odor) in bees (O'Neill and Bjostad, 1987). The possibility that males of *Skalistes* use their genitalia as weapons in intraspecific battles, a very unusual trait (Eberhard, 1985), merits further study.

C. GENERAL COMMENTS

Of the seven male-specific morphological characters to which we have assigned functions with relative confidence, three are weapons in male-male battles, two are threat devices in these battles, one is a courtship device, and one is a device to force copulations on females. Of the 14 assignments with somewhat less confidence ("yes?" in Table 1), all are weapons. The predominant pattern seems to be for these features to function as weapons, as do horns in beetles (Eberhard, 1979). This conclusion must be tentative, however, even for the species described here, because more subtle uses, such as threat devices, are very difficult to document. There are many other designs of earwig cerci (Figure 1) that were not included in our sample, and future studies may find different trends.

Similarly, our level of comparison was not fine enough to attempt explanations of more subtle differences in cercus and pygidium design in closely related species. For instance, we can hardly even speculate on the reasons for the differences in relative pygidium length and bluntness or the minor differences in patterns of teeth on the inner edges of cerci or cercus shape commonly seen in different species of a genus (e.g., *Doru;* Figure 98).

Although it is possible that hardened cerci first evolved in

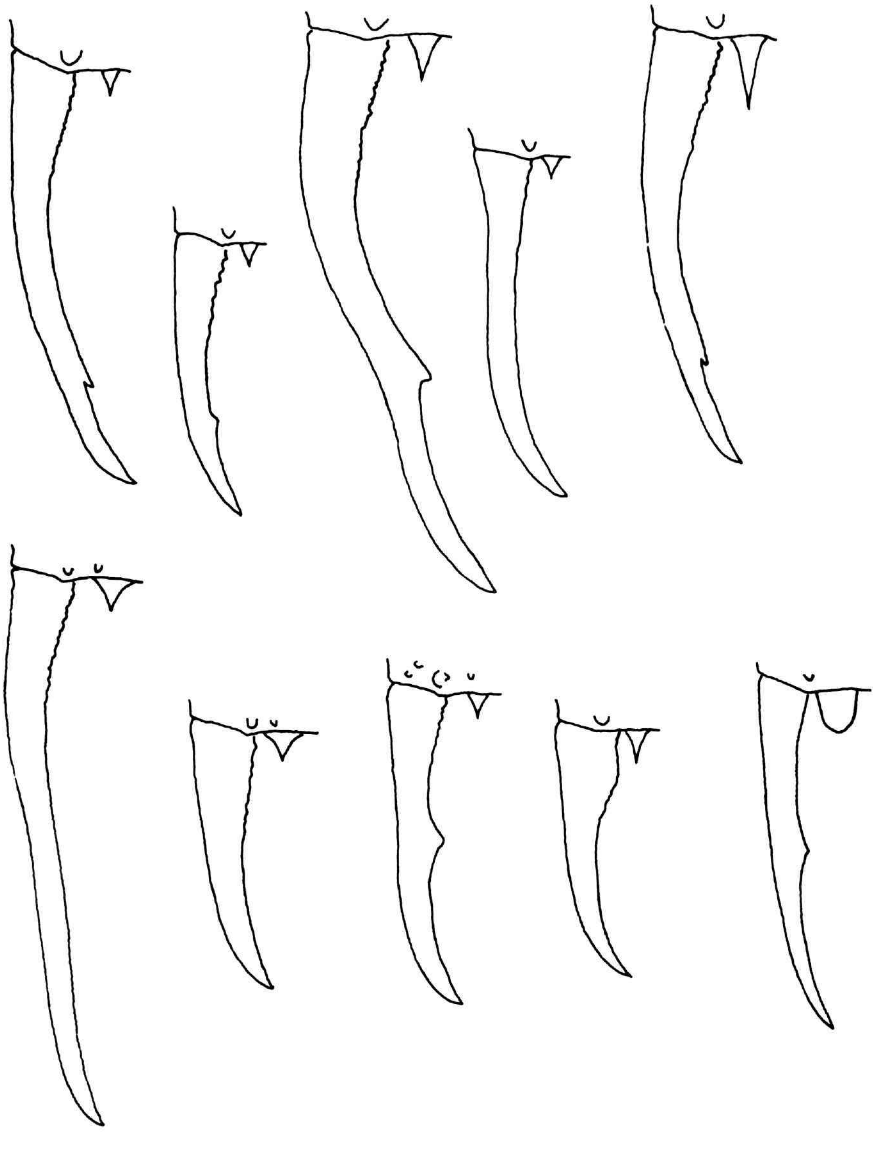


FIGURE 98.—The left cercus and the pygidium of the males of 10 species of *Doru*, showing differences between species (after Brindle, 1971).

Dermaptera when they were used by males to function in sexual contexts, and were only later acquired by females and immatures for defense, we suspect that the opposite sequence occurred. Probably hardened cerci and the ability to close them forcefully originally arose in earwigs as a defense against predators, because males, females, and nymphs of all the species we observed, as well as many others (see "Introduction"), pinch with their cerci when disturbed. Presumably early male cerci were similar in form and size to those of females and nymphs (e.g., females in Figures 7, 16, 26, 40, 51, 57, 63). Probably males began to use their cerci in different contexts associated with competition for sexual access to females. Given that, as we have observed, cerci can inflict wounds and combat can result in dislodgement, there would have been selection on males to judge the fighting capacities of opponents before entering into serious combat. This situation would create selection favoring signalling devices best able to intimidate rivals, and it could produce rapid evolution in the signalling characteristics (West-Eberhard, 1983), involving both the cerci themselves (for instance, the horns of *Skalistes* and possibly the extreme elongation of *Metrasura*) and other parts of the body (such as, lateral abdominal projections in *Ancistrogaster* and the vibrations of the entire body in *Pseudomarava*). In addition, battles using cerci would create selection favoring cercal structures improving the male's ability to fight (for instance, the teeth on the inner margins of several species). Some or all weapons also may function as signalling devices (e.g., the teeth of *Doru* could function during cercal tapping as do the knobs on the claws of male fiddler crabs, Crane, 1975), but our level of analysis was not adequate to demonstrate this.

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