A COMPARATIVE STUDY OF COPULATION IN PASSALIDAE (COLEOPTERA): NEW POSITIONS FOR BEETLES[1]

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ABSTRACT

Copulation, observed in 6 species of Passalidae, occurred with one beetle up-side-down in relation to the other. In *Odontotaenius* they were end to end (known for Coleoptera only in Scolytidae); in *Passalus* they were venter to venter facing nearly the same direction (known for no other beetles and only for certain Diptera and Mecoptera among other insects).

INTRODUCTION

Little is known about mating behavior in most families of beetles. Passalidae are no exception, despite the fact that *Odontotaenius disjunctus* (formerly *Passalus cornutus* and *Popilius disjunctus*), a large beetle inhabiting rotten hardwood in the eastern U. S., is a common laboratory and classroom subject. Wojcik (1969), in his comprehensive literature survey of copulation in Coleoptera, listed no reference for Passalidae.

METHOD

For the past 8 years I have kept passalid beetles in my home to study their acoustical signals. As a result, I have occasionally observed them to mate. Usually, they were kept in large (15cm × 2cm) glass petri dishes, which afford good visibility and broadcast the sounds of stridulation throughout the house when the elytra touch the glass. They were kept in a prominent place, usually the kitchen table, to allow for more frequent observation. A fresh supply of moist rotten wood was introduced into the dishes about every 2 weeks. Various species were maintained, usually in separate dishes, 1 to 8 individuals per dish. Some individuals lived under these conditions for more than 2 years.

RESULTS

All or part of copulation was observed in 6 species of Passalidae, including members of both New World tribes. Copulation occurred between beetles that had been together from less than 1 month to as long as 11 months. In at least 1 case, partners had previously produced offspring together. In another case, a female copulated with a second male to which she was introduced after her first mate died.

Courtship often began with what appeared to be mild aggression by the male, including the production of an acoustical signal characteristic of aggressive interactions. In less than a minute, however, the pair began circling.

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This courtship behavior may continue to 12 hours, continually accompanied by a characteristic acoustical signal (Schuster & Schuster, 1971). During the circling, the male is frequently parallel and beside the female, facing in the same direction. One member (usually the male) will, at times, turn onto its back, then right itself again. Sometimes, the dorsum-up beetle (usually the female) shifts its hind legs and abdomen over the venter-up beetle resulting in the posterior halves of the bodies being venter to venter. The abdomens of both beetles are bent ventrally out of the elytra. A certain amount of rotation in the horizontal plane ensues, the degree varying among the species. In all cases, however, the tips of the abdomens are placed in close proximity, venter to venter. The tips then brush across each other a few times, finally stopping with the genital pores juxtaposed. The aedeagus is extruded and enters the female with its dark, sclerotized side (Fig. 1a, 1c) facing the female's dorsum. The courtship acoustical signal has usually ceased by this time. After a period of little or no movement, 1 or both coupled beetles begin to move their legs actively. Separation usually occurs when the female walks away, the aedeagus stretching between the beetles until it finally dislodges from her. Copulations lasted from 2 to 28 min. The male often makes a few loud sounds soon after union is broken. He is also very active, frequently pivoting on his front legs, rotating left and right. Low intensity postcopulatory acoustical signals are often produced. This general pattern varies among the species studied as follows:

Odontotaenius disjunctus (Illiger)
(4, 4, Florida, Alachua Co., Gainesville*)

This is the only species of Passalidae occurring in the eastern United States. All pairs proceeded in the same manner: the male turned on his back and the female shifted the posterior portion of her body onto his ventral surface. She then rotated until their bodies were end to end, the beetles facing in exactly opposite directions, with the tips of the abdomens still venter to venter (Fig. 2). Once in this position, the tip of the female's abdomen oscillated slightly from side to side probably stimulating the hairs around the genital pores. About 15 sec later, oscillation stopped with genital pores juxtaposed, and the aedeagus was extruded and entered the female. The 4 observed copulations lasted 28 min, 23 min, 12 min, and 10 min. Toward the end of copulation the female began to walk forward. Before union was broken, the male sometimes turned over, resulting in a 180° twist in the aedeagus. In these cases, as the aedeagus stretched between the 2 beetles, it began to untwist, so that at the time separation occurred, it was often only 90° from its original orientation. The last portion of the aedeagus to emerge from the female appeared to be a membranous, eversible sack extended from its mid-dorsal region. Orientation of the aedeagus was easily determined by its structure; the ventral surface is highly pigmented and sclerotized, while the dorsal surface is white and membranous. (See Fig. 1)

Odontotaenius striatopunctatus (Percheron)
(1, 1, MEXICO: Nuevo Leon, 12 mi. west Cola del Caballo Falls)

This is a common species ranging from northern Mexico to Costa Rica

*The first number refers to the number of copulations observed, the second to the number of different pairs observed, followed by their collection locality.

(Reyes-Castillo, 1970). The position assumed during copulation was similar to that of *O. disjunctus* (Fig. 3a), but apparently with the male dorsum-up and the female venter-up. Near the end of copulation, as the beetles walked apart in opposite directions, the aedeagus stretched between them. The evaginated membranous area of the aedeagus was observed to stretch at least 1mm from the sclerotized portion of the female genital pore.

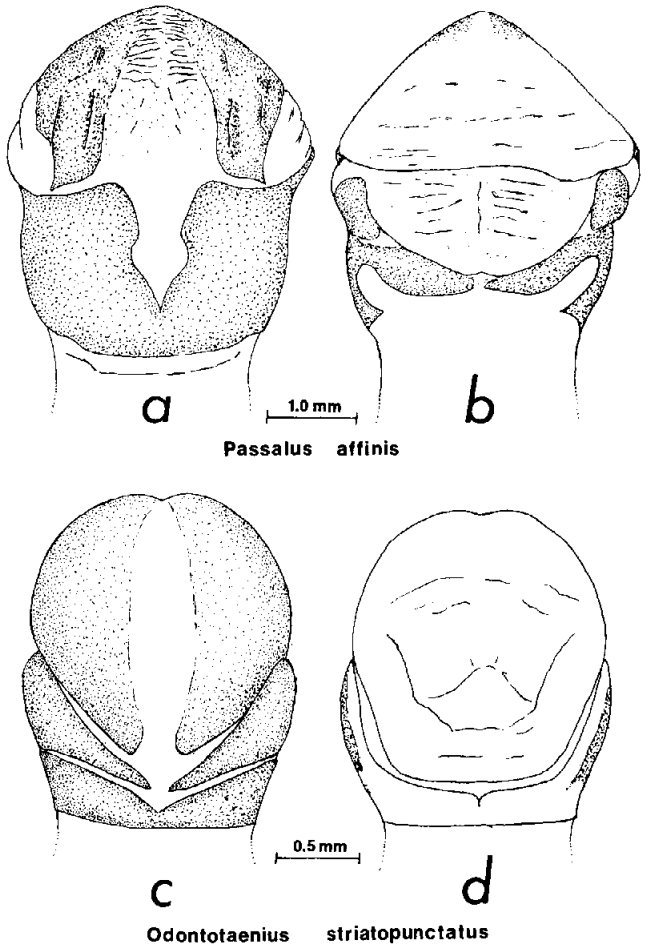

Fig. 1. Passalid aedeagi: a) *P. affinis*, ventral view; b) same, dorsal view; c) *O. striatopunctatus*, ventral view; d) same, dorsal view.

Odontotaenius zodiacus (Truqui)
(1, 1, MEXICO: Hidalgo, Zacualtipán)

This species is found in the Sierra Madre Oriental of Mexico. The position during copulation was the same as in *O. disjunctus*. The individuals were joined for at least 5 min. Toward the end of copulation, the male turned over and began walking.

Passalus (Passalus) punctiger Lepeletier et Serville
(4, 2, MEXICO: Tamaulipas, Gomez Farías; 2, 1, COSTA RICA: Osa Peninsula)

This very common species has a broad range, from northern Mexico to Argentina. Copulation of the first Mexican pair began, as in *O. disjunctus*, with the beetles facing in the same direction, the male turning on his back, and the female (still dorsum-up) shifting the posterior part of her body over the male's venter. The female did not rotate as in *O. disjunctus*. Instead, intromission occurred immediately, while the beetles were at an angle of 30° or less (Fig. 3c). Male behavior was different, too; the aedeagus, when extruded, was twisted 180° from its usual position within the male's body. The twist permitted it to enter the female in the normal manner (i.e., with the dark sclerotized portion toward the female's dorsum, in this species in which the female faces the same way as the male. In species which copulate facing in opposite directions, the aedeagus enters the female in the normal manner without being twisted). Soon after intromission, the female, in one case, superimposed her body completely venter to venter with the male. In all cases, the angle between the beetles remained at 30° or less until the initiation of separation. At this point the female rotated laterally, increasing the angle between them up to 90°, and the male turned dorsum-up. The female remained stationary and the male began walking forward. Duration of copulation was from 3 to 5.5 min.

With the second pair, only the termination of copulation was observed. It is noteworthy that in the 2 pairs, the males were different individuals, but the female was the same. The female was placed with the second male after her first mate died.

The copulatory position assumed by the Costa Rican beetles was an angle of about 90° (Fig. 3b) (intromission was not observed). In one case, the male was the dorsum-up beetle (duration 2 min.); in the other, the female was dorsum-up (duration more than 7 min).

Passalus (Pertinax) affinis (Percheron)
(4, 2, DOMINICAN REPUBLIC: El Seibo Prov., 8 km west of Miches)

This species is apparently the commonest of 4 species cited from the island of Hispañola (Sto. Domingo). Copulation proceeded in a manner very similar to that of *P. punctiger* of Mexico, except that the beetles remained in their original position after intromission (Fig. 3c). The female was dorsum-up. The aedeagus entered the female so that only the basal 0.5 mm of its dark sclerotized portion was visible. The 2 copulations of one pair occurred 4 months apart. Copulations lasted from 2 to 2.5 min in all cases.

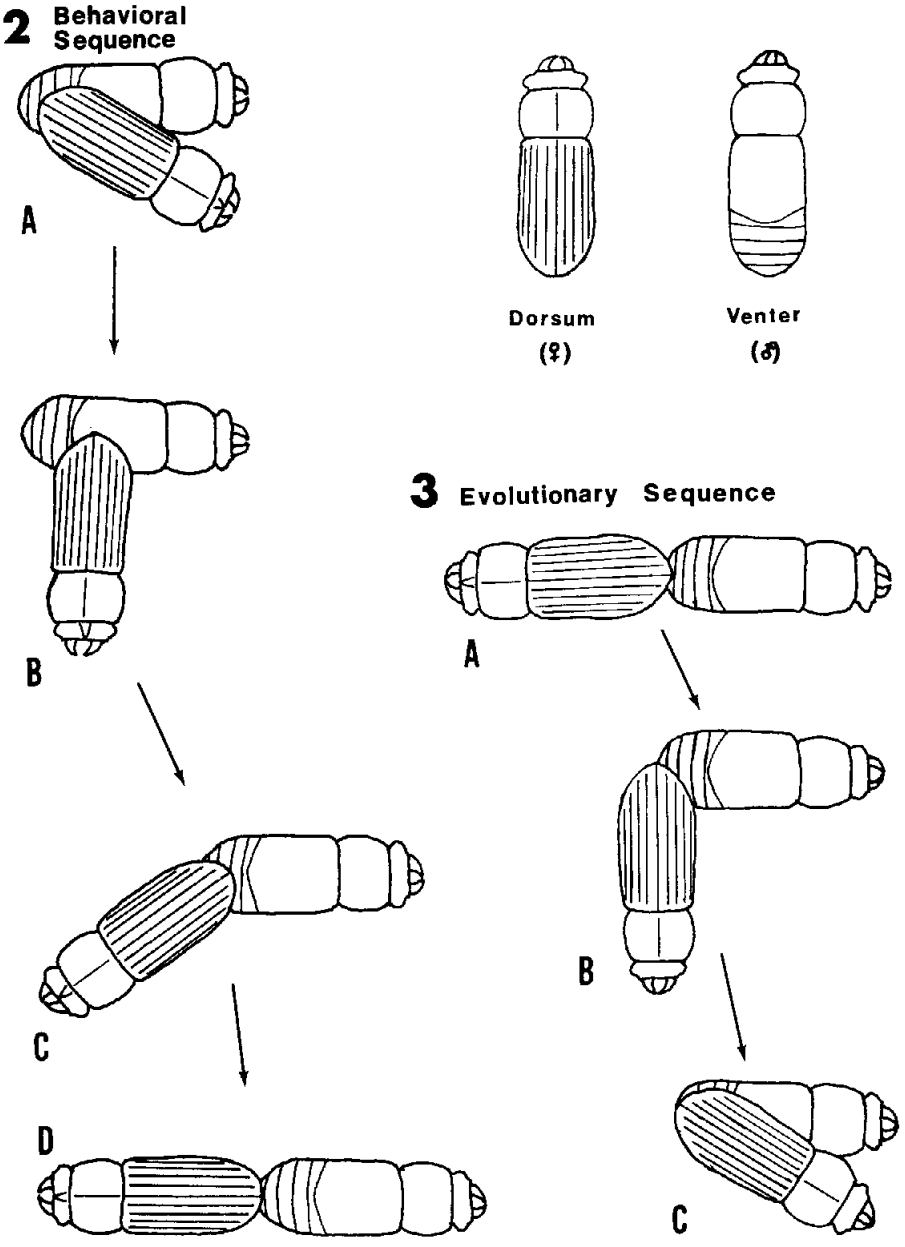

Fig. 2. Behavioral sequence of positions in *O. disjunctus* just prior to intromission. Intromissison occurs in position (D).

Fig. 3. Position at intromission in (A) *Odontotaenius* spp., and (B & C) *Passalus* spp. Arrows indicate possible evolutionary sequence.

Passalus (Pertinax) convexus Dalman
(1, 1, PERU: Huánuco Dept., Tingo María)

In this common South American species, the position during copulation was 90° (Fig. 3b), with the female dorsum-up. Near the end of copulation the position shifted to 180°, the male subsequently turning over. The female started walking, pulling the male after her until the aedeagus finally dislodged.

DISCUSSION AND CONCLUSIONS

In the cases where the initiation of copulation was observed (*O. disjunctus*, *P. punctiger*, and *P. affinis*), the beetles remained quiescent in approximately the intromission position until separation began. Thus, in situations where the initiation of copulation wasn't observed, but the beetles were found quiescent *in copula*, it may be inferred that this position was that in which intromission occurred. Therefore, it appears that in *Passalus*, intromission occurs with the beetle's longitudinal axes oriented at 90° or less, the pair partially or totally venter to venter, whereas, in *Odontotaenius* intromission takes place with the beetles end to end, up-side-down in relation to each other.

The only beetles previously known to have this inverted end to end copulation are scolytids: *Dendroctonus spp.* (Yu and Tsao, 1967; Cerezke, 1964; Reid, 1958) and *Pityogenes* (Reid, 1958). These also live in tunnels in wood. For example, in *D. monticolae* Hopk., the male, after contacting the female's posterior with the anterior section of his body, backs down the tunnel to a wider area, where he turns around. He then backs up the tunnel again and contacts the female end to end, the position in which copulation ensues (Reid, 1958). No previous cases are known for beetles using the venter to venter position (Wojcik, 1969 and pers. comm., 1974) as in *Passalus*. For insects in general, inverted end to end mating as in *Odontotaenius* occurs in a few Diptera, Homoptera, Hemiptera, Tettigonioidea (Alexander, 1964), Blattodea (Alexander and Otte, 1967), Dermaptera (Fulton, 1924), and the scolytids mentioned above. Among insects, only certain Diptera (Alexander, 1964) and *Bittacus* (Mecoptera) (Thornhill, 1974) are known to mate venter to venter facing the same way. In other Arthropoda, inverted end to end mating occurs in some Acarina, whereas venter to venter mating facing the same way occurs in Crustacea, Diplopoda (Alexander, 1964) and some Acarina (Radinovsky, 1965).

Fig. 3 suggests an evolutionary sequence of intromission positions in the Passalidae. I speculate that the sequence was from "a" (end to end) to "c" (almost superimposed). In all species, during the courtship dance just prior to copulation, the male and the female are usually side by side, facing in the same direction. Usually the male then turns over and the female moves her body over onto his, both beetles still facing in nearly the same direction. From this position, a female of *O. disjunctus* rotates through a series of angles, corresponding to intromission positions in *Passalus*, and finally arrives at the end to end position (Fig. 2), where intromission occurs with the aedeagus untwisted. As the male developed better ability to twist the aedeagus, intromission could occur earlier in the rotational sequence. This should be a selective advantage because it would decrease the time until intromission and minimize the likelihood of loss of contact between the sexes. Contact was, in fact, often broken as the *O. disjunctus* female rotated. If contact were renewed, courtship

began again with the dance, and time was consumed passing through the whole sequence once again. Also, if intromission occurs at an angle of 30° or less, the beetles remain in antennal contact, and thus other avenues for stimulation and communication are available. The advantages of retaining the end to end position in *Odontotaenius*, however, are as yet unclear. Reading the sequence in reverse (i.e., from "c" to "a", would require the evolution of the initial aedeagal twist and subsequently its loss again in *Odontotaenius*). This is rejected because it is not the simplest interpretation in the light of the present evidence. Thus, I postulate that copulation in Passalidae evolved from an end to end position, with untwisted aedeagus (as illustrated by *Odontotaenius*) to an almost superimposed position with twisted aedeagus (as in *Passalus*).

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