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# Male Foretibial Plates and Mating in *Crabro cribrellifer* (Packard) (Hymenoptera: Sphecidae), with a Survey of Expanded Male Forelegs in Apoidea

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**ABSTRACT** In *Crabro cribrellifer* (Packard), the outer edge of the male foretibia is greatly expanded into a thin, flexible plate or shield. Observations on the mating behavior of these unusual wasps describe the use of modified forelegs during mating. A male places his forelegs over the female's eyes, strokes her antennae with his antennae, and then tries to copulate. Males in a flight cage frequently disrupted mating pairs by dislodging the resident males, showing that the plates are not effective "claspers," contrary to a hypothesis proposed by Darwin. Photographs of *Crabro* male foretibial plates show intra- and interspecific variation in patterns of light transmitted through the male plates. A tabulation of taxa (Apoidea, including Sphecoidea) with species having expanded forelegs is provided for comparative purposes. Information on emergence phenologies and secondary sex ratios over a 3-yr period is also presented.

**KEY WORDS** Insecta, Sphecidae, *Crabro*, mating

THE FORELEGS of numerous female wasps and bees (Hymenoptera: Apoidea) are structurally modified for digging in the soil or collecting food (e.g., Radović & Krunic 1979; Thorp 1979), and less frequently the forelegs of males are modified, but there are few ethological observations to determine their function (Anzenberger 1977, Batra 1978). About 75% of the 85 named species of digger wasps in the mostly Holarctic genus *Crabro* are sexually dimorphic (Bohart 1976). In many species, the outer and lower edge of the male foretibia is greatly expanded in the form of a strikingly beautiful "plate" (Bohart & Menke 1976). There are species-specific differences in size and shape, and in color patterns seen in both reflected (Bohart 1976) and transmitted light. Among free-flying males, at least in some species including *C. cribrellifer* (Packard), the plates on the male forelegs "sparkle in the sun, much like diamonds" (H. E. Evans, personal communication concerning *C. latipes* Smith). Darwin (1871) illustrated this dimorphism in *C. cribrarius* (L.), where he discussed male structures that evolved for clasping a female to prevent separation during mating (see also Richards [1927] and Bohart [1976]). Bohart (in Bohart & Menke [1976]) noted that a clasping function would not explain the great diversity in forms and colors of the foretibial plates. He hypothesized they have a

display function for females, although it is also plausible that they function in displays to other males. Matthews et al. (1979) observed that caged male *C. argusinus* Bohart place their foretibial plates over females' eyes before intromission. Given this fact, West-Eberhard (1984) also illustrated this dimorphism and suggested that the tibial plates signal information to the female during courtship.

Little is known about these much-discussed wasps, so this note describes brief observations on the mating biology of *Crabro cribrellifer*, including interactions between males, and between males and females. In addition, it summarizes known information on foreleg expansions in Apoidea.

## Materials and Methods

Observations were made from 1981 to 1984. Females nested in an aggregation (2 by 65 m) on a seldom-used sandy two-track road running through second-growth forest at the University of Michigan Biological Station (Cheboygan County, Mich.). Details of the site are given in Wcislo et al. (1985).

Emerging males and females were captured in twenty traps (30 by 30 cm), and in three larger sections of netting (each about 1 by 3 m) with the edges buried in the sand. Traps were checked daily and the numbers of males and females recorded. Wasps were then individually marked on the thorax with enamel paints and transferred to a large ( $\approx 2$  by 4 by 2.5 m) flight cage adjacent to

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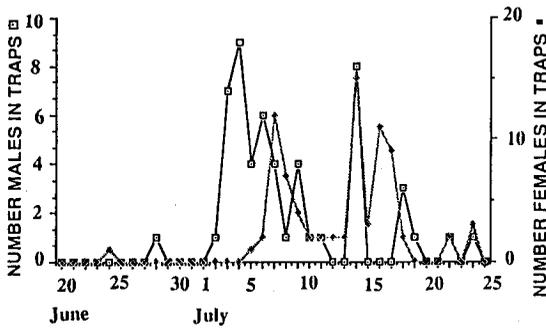


Fig. 1. Emergence phenologies into traps for male and female *C. cribrellifer* from 1981 to 1983.

the nesting site ( $n = 16$  males and  $n = 15$  females introduced over several days). Bracken fern and other understory vegetation growing at the nesting site also grew in the cage, and sugar-water was provided ad libitum via sponges. Excluding the majority of time when wasps were inactive in the flight cage, male and female behaviors were observed for 345 min. Observations were recorded with a tape recorder, and timed with a stopwatch to the nearest second. Body lengths (head to tip of extended abdomen) were measured (in mm) with calipers. Means are given with variances.

Specimens for scanning electron microscopy were prepared using standard techniques (courtesy of S. Reyes), and transmitted light photographs were taken through a Wild microscope fitted with a Polaroid camera. Voucher specimens of male and female *C. cribrellifer* are deposited in the Snow Entomological Museum, University of Kansas; other *Crabro* species were borrowed from the same museum, and are in that collection.

## Results

**Natural History.** Males and females began emerging in late June and early July; the population is mildly protandrous (Fig. 1). The secondary sex ratio was female-biased in 1982 (13 ♂♂: 39 ♀♀) ( $\chi^2 = 13.0$ ,  $df = 1$ ,  $P < 0.001$ ), but not in 1981 (6 ♂♂: 5 ♀♀) or 1983 (34 ♂♂: 32 ♀♀) (both years,  $\chi^2 = 0.1$ ,  $df = 1$ ,  $P > 0.5$ ). Females are slightly longer than males (Females: mean,  $14.3 \pm 1.0$ ; range, 11.0–17.1;  $n = 39$ . Males: mean,  $10.5 \pm 2.8$ ; range, 8.1–13.0;  $n = 13$ ).

*C. cribrellifer* males were never seen patrolling at the nesting site and were never seen flying near vegetation or flowers in the vicinity of the nesting site. Female wasps leave the nest site to visit flowers for nectar, and to hunt robber flies (Diptera: Asilidae), which were frequently observed flying, perching, or mating within 2 m of the ground. One anecdotal observation suggests that *C. cribrellifer* mate at or above tree-top level

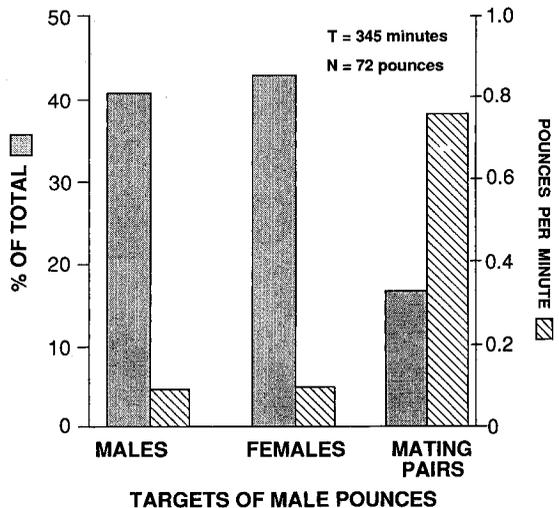
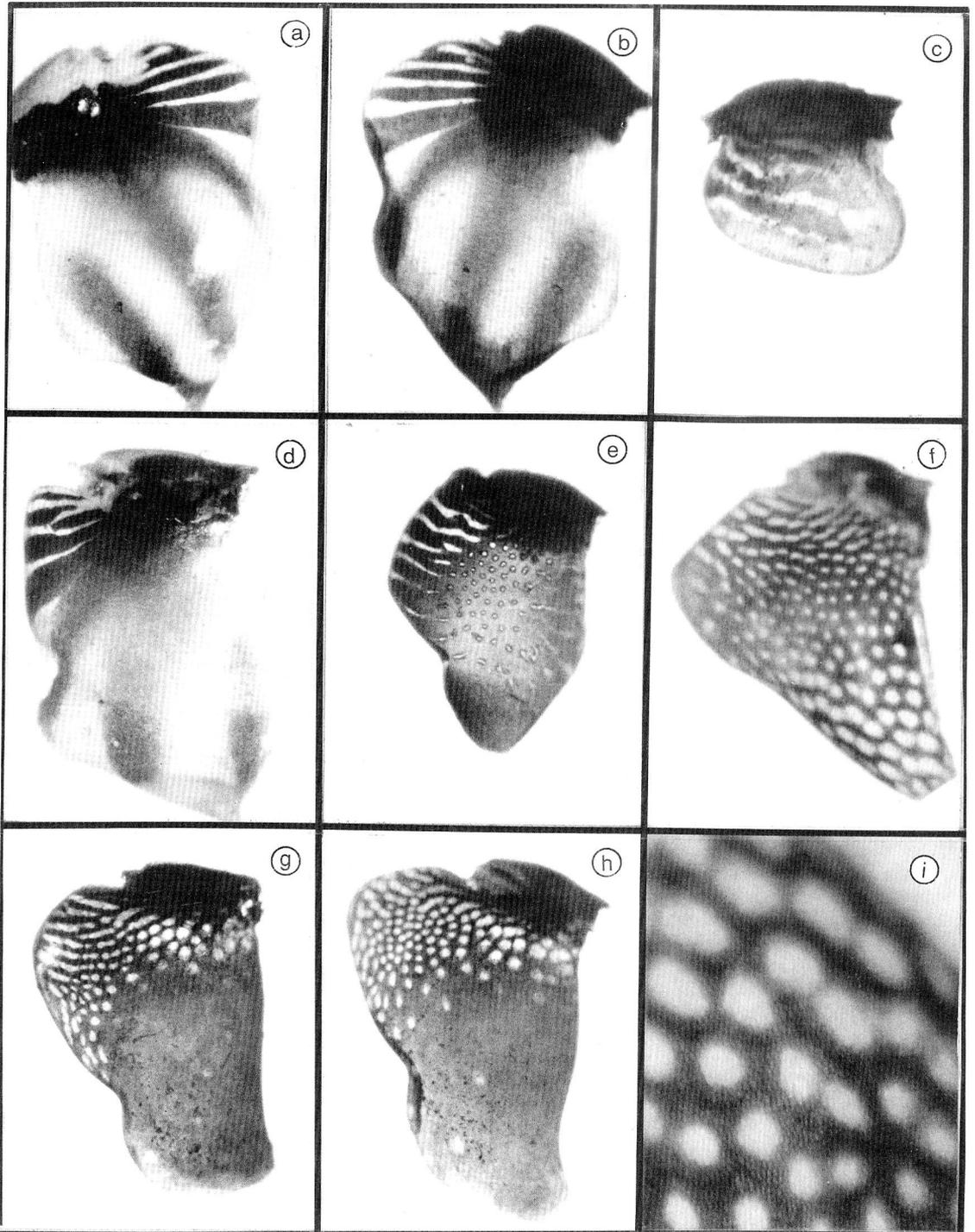


Fig. 2. Pounces by males of *C. cribrellifer* in a flight cage directed toward other males, females, or mating pairs. Pounce rates are also expressed on the per minute availability of males, females, and mating pairs (based on 345 min of activity).

near the nesting site: a pair in copula literally fell from the sky, landing in front of W.T.W. Males of *C. latipes* patrol in open, sunny places or near vegetation (H. E. Evans, personal communication), and on occasion are not more than 1–2 m above the ground (field notes of J. Gelhaus, Academy of Natural Sciences of Philadelphia); males of a Costa Rican species patrolled near the upper third of a flowering bignoniaceous tree (W.T.W., personal observation).

**Flight Cage.** Several days after they were introduced to the flight cage, males began flying circuits around its perimeter, like the flights of males of other species patrolling vegetation (e.g., Evans & O'Neill 1988).

Males frequently pounced on females, other males, and pairs of wasps (Fig. 2). In 21 cases, males pounced on females and were rejected before they mounted the females; in 10 cases (32%), pounces were followed by further courtship and copulation, as described below. After contacting a receptive female, a male immediately placed his foretibial plates over her eyes. He then stroked her antennae with his antennae, alternating with his left and right antenna at a rate of  $\approx 1$  stroke per second ( $n = 4$  pairs). The parts of the male antennae that contact the female antennae also are modified: flagellomeres 2 and 3 have long hairs, and the basal flagellomeres are flattened (for other species, see Bohart [1976]). The male then everted his genitalia and used them to stroke the female metasoma (abdomen), from front to back, again at  $\approx 1$  stroke per second. After intromission, no other male movements were discernible.



**Fig. 3.** Interspecific and intraspecific variation in transmission light patterns through the foretibial plates of male *Crabro*. O, outer view, as the plate is viewed when is flying or at rest; I, inner view, as seen if a plate is placed over a female's left eye. (a) *C. cognatus* Fox, O; (b) *C. cognatus*, I; (c) *C. alticola* Cameron, I; (d) *C. latipes* Smith, I; (e) *C. tenuis* Fox, I; (f) *C. argusinus* Bohart, I; (g) *C. cribrellifer* (Packard) specimen #8213a, I. Note the continuous lines, upper left. (h) *C. cribrellifer* specimen #8214d, I. Note the dots, upper left. (i) *C. argusinus* 8 $\times$ , I.

Table 1. Genera of Apoidea with expanded male forelegs; in each taxon, at least one species displays the sexual dimorphism

Taxon	Foreleg modification			Reference
	Femur	Tibia	Tarsus	
Spheciformes				
<i>Crabro</i>		X	X	Bohart 1976
<i>Ectemnius</i>	X			Bohart & Menke 1976
<i>Crossocerus</i>			X	Bohart & Menke 1976
<i>Lestica</i>			X	Bohart & Menke 1976
<i>Didineis</i>		X	X	Bohart & Menke 1976
<i>Bembix</i> (Australian species)			X	Evans & Matthews 1973
Apiformes				
<i>Xylocopa tenuiscapa</i> Westwood		X		R. L. Minckley, pers. comm.
<i>X. magnifica</i> (Cockerell)		X		R. L. Minckley, pers. comm. W.T.W., pers. obs.
<i>Nomada hesperia</i> Cockerell	X			B. Alexander, pers. comm.
<i>Nomada</i>	X			
7 spp of <i>armata</i> group				B. Alexander, pers. comm.
3 spp of <i>furva</i> group				B. Alexander, pers. comm.
<i>Megachile</i> (various subgenera: e.g., <i>Eumegachile</i> , <i>Pseudocentro</i> , <i>Chelostomoides</i> , <i>Austromegachile</i> )		X	X	Mitchell 1979
<i>Chalicodoma</i>		X	X	Mitchell 1979, Batra 1978
<i>Fidelia</i>			X	W.T.W., pers. obs., J. Rozen, Jr., pers. comm.
<i>Stictonomia</i>		X		(Batra 1970)
<i>Ptyumoides</i> (♀)			X	Bohart & Menke, 1976: 410

Males are probably attracted to females initially by visual cues, because they contacted males and females with equal frequency (Fig. 2). Males pounced more frequently on mating pairs than on either males or females (Fig. 2). In 11 of 12 cases (92%), males were successful in dislodging the resident male.

The patterns of light transmitted through the male plates are species-specific (Fig. 3), confirming what has been known informally by hymenopterists for some time. Additionally, there is considerable intraspecific variation, as seen for *C. cribrellifer* (Fig. 3 g,h). The foretibial plates of males from a series of *C. cribrellifer* and eight other *Crabro* species were examined under ultraviolet light, and there were no observable ultraviolet patterns.

### Discussion

A male *C. cribrellifer* covers his mate's compound eyes with elongate foretibial plates after he mounts her, as does *C. argusinus* (Matthews et al. 1979). Darwin's hypothesis that the male plates are claspers is wrong for *C. cribrellifer*, and is probably wrong for *Crabro* in general. In some smaller *Crabro* species, the plates are rather rigid, but they are somewhat pliable in larger species even for dried, pinned specimens. In several living *C. cribrellifer*, they are flexible. Structurally, they make poor claspers. Comparative information also supports this conjecture. Plate-like expansions of different segments of the male foreleg are modified independently in various genera of Apoidea (Table 1; genera with enlarged spines were not included). In leafcutter bees (*Megachile*), for example, the expansions consist partly of long fringes of hairs, whereas in

a few carpenter bees (*Xylocopa*), the expansions seem far too small to seize and clasp the robust females. On structural bases, the modifications generally seem unlikely to function as effective claspers: they are either too small or too flexible.

Behavioral observations that males usually dislodge other males from females support the view that the plates do not function as claspers. The real function of these plates is unknown. Possible functions include stimulation of females with light displays in the contexts of sexual selection or species recognition, or for use in contests with other males. The male might use his plates to reduce light intensity (analogous to draping a cloth over a bird cage) while he provides other tactile stimulation. (Females hunt fast-flying asilids and presumably have acute vision, yet are also active underground in darkness.)

Two distantly related bee species with modified male legs were observed during mating, and both authors (Anzenberger 1977, Batra 1978) suggested that the male behavior calms the female. A male mason bee (*Chalicodoma*) places his expanded hairy foretarsi over the upper part of the female compound eyes during mating. If the female moved, then the male "rubbed her eyes with these tarsal brushes, which calmed her" (Batra 1978: 554). A carpenter bee male, *Xylocopa torrida* (Westwood), has expansions on the tarsal segments of the midleg, which are placed over the eyes of females during mating flights (Anzenberger 1977). The pair fly together (male on top, powered by male flight), and Anzenberger suggests that male leg structures reduce optical stimuli that might produce interfering flight responses from the female (which otherwise glides).

In contrast to *C. cribrellifer*, many bees and sphecids wasps mate only briefly, usually without any obvious courtship (Alcock et al. 1978). Generally, male structures used for contact courtship are divergent at the species level as discussed by Eberhard (1985, 1991), who shows that certain patterns of morphological diversification are consistent with predictions based on sexual selection. In *Crabro*, other structures such as antennae also are used by males during mating, and have species-specific modifications (see Bohart 1976). Antennae are used in courtship in various aculeate Hymenoptera (partial review in Eberhard [1991]). Similarly, in other groups, males use their metasoma to stroke (Cowan 1986), caress (Genise 1982), or tap (Batra 1978, Wcislo et al. unpublished data) the female metasoma before or after mating.

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