

Some Sexually Dimorphic Characters in the Mediterranean Fruit Fly *Ceratitis capitata* (Wiedemann) and their Variations¹

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ABSTRACT

Sexually dimorphic traits in the Mediterranean fruit fly *Ceratitis capitata* are described. The significance of these sexual differences to genetical and behavioral research is discussed.

There has been interest in the biology of the Mediterranean fruit fly, *Ceratitis capitata* (Wied.) since its first appearance in fruit growing areas of the Mediterranean region approximately 2 hundred years ago. As the species spread throughout the subtropical and subtemperate zones of the world this interest has increased, based on the hope that scientific knowledge would lead to new and better techniques for preventing the millions of dollars of damage to fruit crops caused by this pest species. One area of research that has only begun to develop recently is that of genetic methods of control, e.g., use of translocations, conditional lethal genes, and meiotic drive loci. In order to pursue this line of research we need much basic genetic, ecological, and behavioral information, and, as noted by Rössler and Koltin (1976), "the development of such sophisticated methods necessitates a basic knowledge of the genetics of the Mediterranean fruit fly, which at present is virtually unknown."

The program of genetic research in our laboratory required us to carefully screen thousands of flies for visible and biochemical variation. In the course of this work we noted a number of morphological differences between male and female flies. When we consulted the literature on *Ceratitis capitata* we found that a few of these differences had been described before, but no author, or combination of authors, listed all of the differences we observed. In addition we found that these characters are subject to phenotypic and/or genetic variation and this too had not been systematically described.

Describing these sexual dimorphisms and their variations is the main purpose of this paper, as well as commenting on the significance of these differences to genetical and behavioral research. For example, we noticed that of the dimorphic characters observed, all except for the genitalia, are located on the anterior parts of the fly's body. All are visible from the front of the fly, and since behavioral interactions in *C. capitata* begin primarily in a head-to-head position, these characters may play an important role in aggressive and courtship displays.

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Sexually Dimorphic Characters

The differences described below were consistently observed in flies of Hawaiian origin. Laboratory stocks and stocks founded from wild flies (usually examined as F3 to F10 generation) were used in this study.

One or more of the first four secondary sexual characters have been described by several workers (Bodenheimer 1951, Back and Pemberton 1918, quoting Froggatt 1908, Silvestri 1914, Hardy & Delfinado 1980) and are used regularly when sorting flies as to sex.

1) Male "head bristle" character. (Figs 1A, 1B.) Males possess a pair of modified anterior superior fronto-orbital (S.F.O.) bristles each with a shiny black, finely striated, spatulate appendage. Occasionally a small additional bristle is found near these male spatulate bristles either bilaterally or unilaterally. The frequency of these additional small bristles in the population is low, but responds to selection, and true breeding lines can be established in which both males and females have an extra pair of bristles. Less frequently this additional bristle takes the form of a second (unilateral or bilateral) spatulate bristle. Rössler and Koltin (1976) selected a line of flies which bred true for "double chaetae" and demonstrated the genetic basis for this character.

2) Color of frons. (Figs 1B, 2B.) The frons color is variable, tending towards yellow in flies reared from certain field-collected fruits, to white in laboratory reared flies. Still, there is a distinct non-overlapping difference between males and females; white male frons versus the grey female frons is one of the most easily observed "sexing" characters. We did not observe any genetic variation in this character, all differences seem to depend on larval diet.

3) Mesopleural bristles. (Figs 1C, 2C.) Both males and females possess 3 large black bristles in a roughly triangular arrangement on the sides of the thorax. One is on the sternopleural, one on the pteropleural, and the third on the mesopleural plate. In males a tuft of smaller surrounding setae (densest on the mesopleura) are black; in females the setae are white. We have observed limited variation in size and depth of pigmentation of the larger and smaller bristles, but no overlap between males and females, and no variation responding to selection or true breeding.

4) Femoral bristles. (Figs 1D, 2D.) The femora of the first pair of legs of both males and females are golden, red-brown in color. The bristles on the femora of the male are the same color and do not stand out distinctly. The female also has bristles of this same color, fewer in number than the male. However, the female also possesses a row of approximately 7-9 large, dark brown to black bristles on the anteroventral surface of the femur which stand out distinctly from the other bristles. These dark bristles taper in size from the proximal to distal portion of the femur, finally merging in size with the smaller setae, so that the exact number of these bristles is hard to count, but is approximately 7-9. There is some variation in color of the female anteroventral bristles in different populations, ranging from black to dark brown. However, these bristles are always darker than the other bristles on the female femur and all the bristles on the male femur. There was no response to selection for darker or lighter bristle color.

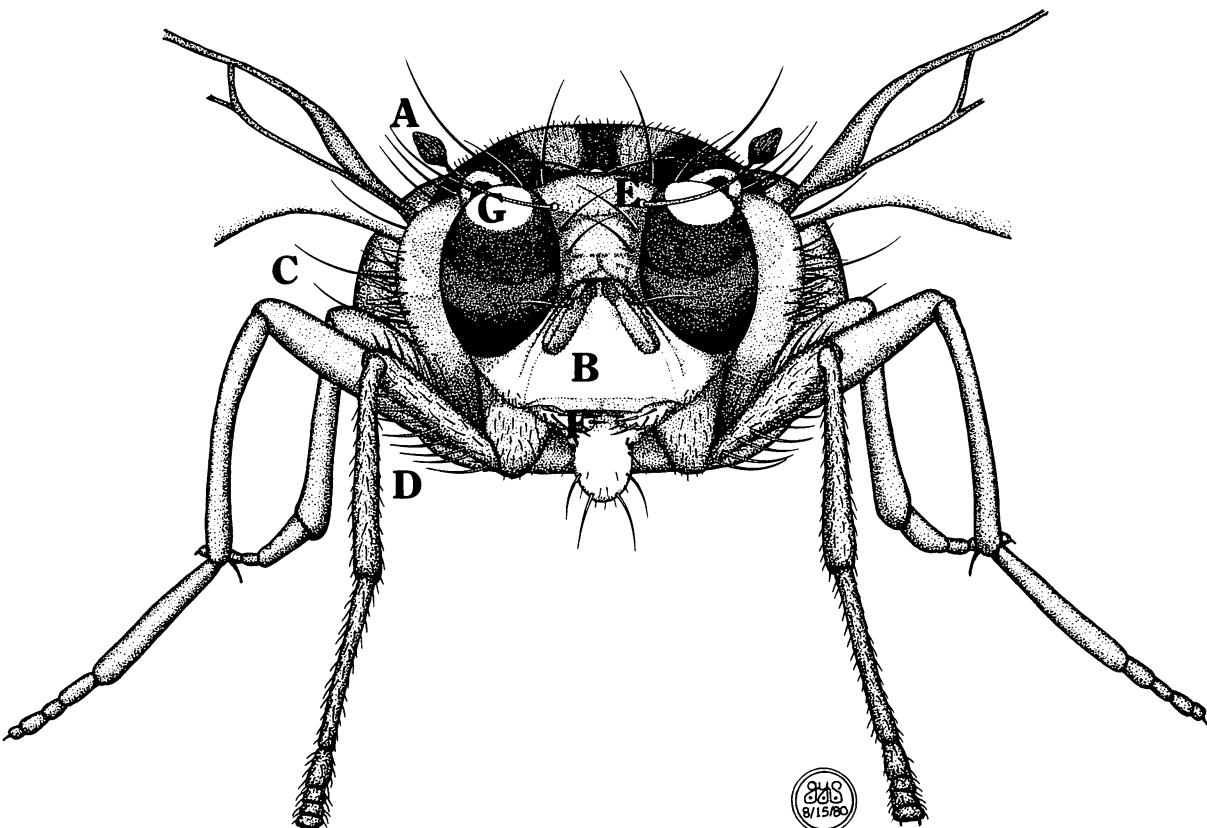


FIGURE 1. Male of *Ceratitis capitata*. Artist's drawing of head-on view. For lettering see text.

5) Superior fronto-orbital bristles. (Figs 1E, 2E.) The female fly bears 3 pairs of long reclinate bristles along the outer margins of the vertical calli. The males possess only the anterior and posterior pairs. There is much variation in the superior fronto-orbital bristles in laboratory populations and in stocks founded from wild flies. We observed many cases of missing and additional bristles either unilaterally, or less commonly, bilaterally. By selecting flies with extra bristles we could produce lines where the frequency of the variants increased. We obtained a true breeding population with 4 pairs of evenly spaced superior fronto-orbital bristles in females and an extra pair of bristles next to the anterior S.F.O. bristles in males. In contrast to this case we could not obtain a true breeding line with fewer than normal bristles, even though individuals with missing bristles appeared from time to time in our stocks.

6) Labial palp bristles. (Figs 1F, 2F.) The palpi bear approximately 10 short, thick bristles on their anterior surfaces. In the males these bristles are white, in the female, they are dark black. This trait was clearcut, with no overlap. We did not observe any variation in the expression of this trait.

7) Eye color. (Figs 1G, 2G.) This is a subtle difference, often overlooked because of the complex pattern in the *C. capitata* eye and because it is not apparent except in live flies. When once pointed out to an observer, however, one can sort flies as to sex quickly and accurately using this feature alone. The fly is best viewed from a consistent angle or the multicolored, iridescent pattern of the eye will seem to be constantly changing and may confuse the observer. If a live fly is observed from the front either "head-on," or from slightly above, the male will be seen to possess a round, dark blue-violet, iridescent "spot" in each eye. The female eye appears reddish blue with no reflectance from this angle. In low light levels the male eye spots are striking — appearing like deep blue-violet "headlights". This trait clearly distinguishes the sexes, in laboratory and wild populations, even in those eye color mutants that we were able to isolate in true breeding lines. While the basic eye color may be altered the male always retains a brighter area corresponding to the eye spot. The white eye mutant (Sharp and Chambers 1973) which we have not observed may be an exception to this statement.

Significance to Behavioral Research

Male flies can be observed to show aggressive behavior towards males, females, and other insects. They consistently orient to the other organism in a "head-to-head" position. At some time the encounter changes to courtship, also head-to-head, (Bach and Pemberton 1918, p. 66), remains aggressive, or breaks off. These behavioral patterns in males and females are partially expressed using the structures described in this paper and so these dimorphic differences should be important objects of study in behavioral research.

Under natural light cycles, courtship and sexual activity starts at the beginning of the photophase under low light conditions (Cavalloro 1977). If we place ourselves, as best as possible, in the position of the fly we find that the shiny black spatulate S.F.O. bristles, the fluorescent "eye spot," bright frons, etc, of the male are all prominent under low light conditions. It seems reasonable to assume

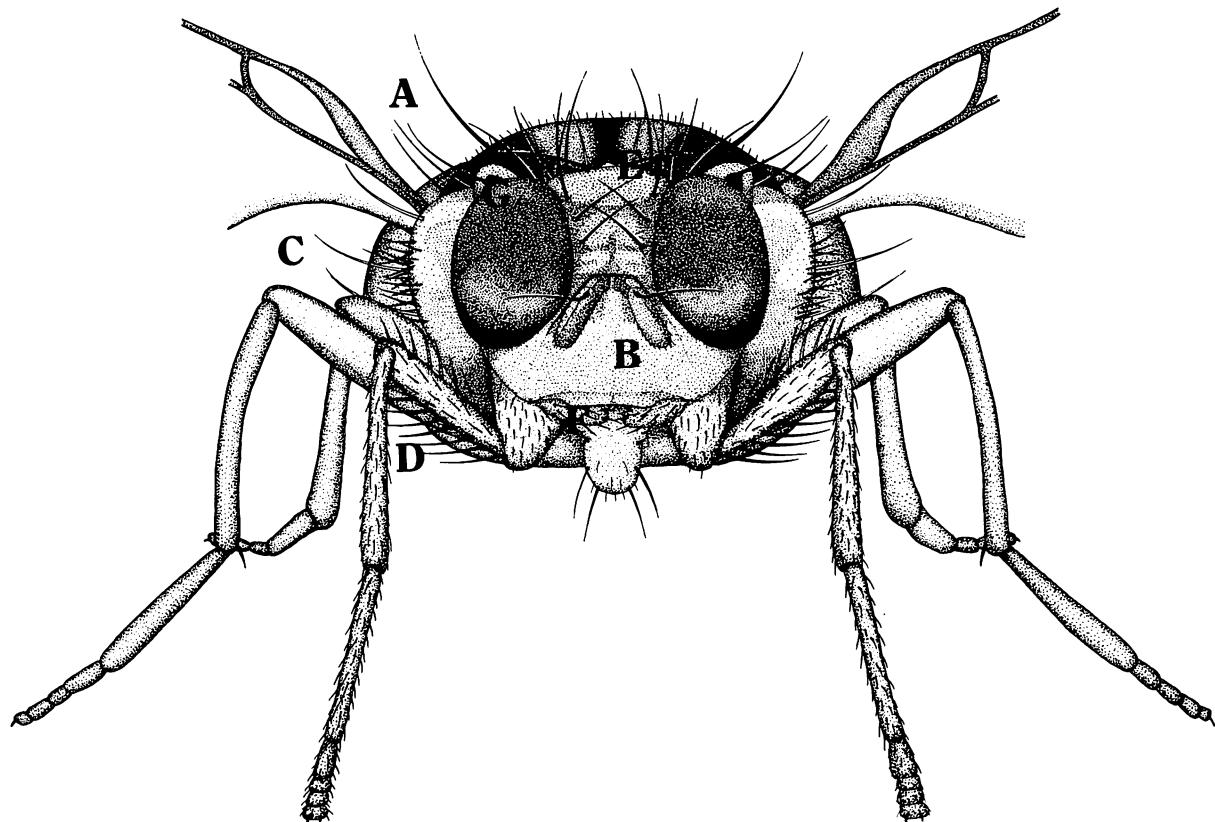


FIGURE 2. Female of *Ceratitis capitata*. Artist's drawing of head-on view. For lettering see text.

these traits have some connection with species and sex recognition. Not all sensory information is visual, of course, and vibrational and chemical signals are undoubtedly important, but it seems warranted to predict that future experimental work in mating behavior will, at least, comment on these sexually dimorphic characters and their role in courtship and aggressive behavior. As simple examples one could amputate the spatulate bristle of the male, or "paint" the frons and observe the alteration in behavioral interaction and species recognition.

Significance to genetic research

The first, and most obvious use of this work in genetics is to enable workers to recognize within sex, from between sex, variation. One cannot begin to identify eye or bristle mutants without knowing how males and females differ.

Less obvious, but just as important are the clues given to us for understanding species biology by the variation observed in different characters.

From work done in our laboratory we have found that there are characters in *C. capitata* which: are sexually dimorphic and respond to selection (like increased S.F.O. bristle numbers); are sexually dimorphic and do not respond to selection (like "eye spot"); are sexually monomorphic and respond to selection (like wing vein variation); are sexually monomorphic and do not respond to selection (like thoracic bristle number). In addition there are characters like decreased S.F.O. bristle number and number of "bent" scutellar bristles which respond to artificial selection with increasing sterility and lowered population fitness. We can hypothesize that fixed dimorphic differences, like "eye spot" are under strong selection for sex recognition and/or mating behavior. The traits like "bent" scutellars probably are linked to genetic elements which are important to individual mating fitness since artificial selection for increased expression leads to decreased fitness. On the other hand, variable traits that respond to selection, like increased S.F.O. bristle number may be the "raw material" on which sexual selection can act.

The observations and hypotheses presented in this paper are meant to be useful in generating further hypotheses and suggesting future experiments in areas of genetics and behavior of the Mediterranean fruit fly.

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