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SEX COMB IN *Drosophila* FLIES: A SECONDARY SEXUAL CHARACTER THAT RENDERS REPRODUCTIVE SIGNIFICANCE

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ABSTRACT

Certain structure may originate suddenly in a particular group of animal and evolve during its phylogenic journey, most reasonably due to its significance to the group. Such structures therefore, become of taxonomic importance. While scrutinizing animal features, one can enumerate group specific characters to classify it into its different taxonomic categories. Sex comb in some species of genus *Drosophila* is such a secondary sexual character that it has also undergone morphological variation in its different species. This structure is found only in its male flies and hence is one of the features that assist in sexual dimorphism. The fore legs, i.e., prothoracic legs of males possess a bunch of melanin rich bristles in the form of a comb confined in its upper tarsus segment/s. Sex comb are believed to play a significant role in courtship and mating behavior. The sex comb in *Drosophila* is an essential male-specific trait that serves several important functions related to mating behavior, sexual selection, and intra-sexual competition. It helps males to hold onto females during copulation and plays a role in evolutionary processes that influence male reproductive success. The structure is regulated by genes such as sex combs reduced (Scr), highlighting its genetic and developmental significance.

KEYWORDS: Sex comb, *Drosophila* Species, Secondary Sexual Character, Sexual Dimorphism, Courtship and Mating

Drosophila flies have special status in the field of biological research (Meigen 1830; Kohler 1994). Initially, it was mainly utilized to decipher various aspects of genetics owing to the availability of its several phenotypic mutants, presence of polytene chromosomes that assisted in cytological studies but later, it became important to study various facets of biology like taxonomy, evolution, development, disease biology, molecular biology etc. Scientists across the globe chose different species of *Drosophila* to scrutinize their research perspectives. The genus *Drosophila* is represented by a paraphyletic subgenus *Sophophora* (Sturtevant 1939). Male flies of this group are characterized to possess sex comb in the terminal segment (tarsus) of prothoracic legs (first pair of legs). The sex comb consists of several bristles arranged in a linear pattern, primarily found on the first tarsal segment of the foreleg in the males of *Drosophila* (Wang, *et al.* 2023). Wang and his coworkers (Wang, *et al.* (2023) performed comparative analysis between multiple *Drosophila* species examining the evolutionary divergence in their sex comb and elaborated on how this structure varies across species and the selective pressures that have shaped its evolution. Ravi and Murugan (2023) explored how environmental factors, such as temperature and nutrition, influence the morphology of the sex comb in *D. melanogaster*, and how these variations affect mating success and reproductive fitness.

With regard to its implication, it plays an important role in mating behavior, particularly during courtship and copulation. During mating, the male *Drosophila* uses its sex comb to grasp and hold onto the female, particularly during the copulatory courtship (a sequence of behaviors that precedes actual mating). The sex comb bristles may help to secure the male to the female, providing better control during mating. Smith and O'Connor (2022) performed quantitative behavioral assays to test the hypothesis that the sex comb is an adaptation for improving male mating success in *Drosophila*. It provides evidence that males with larger sex combs are more successful in mating trials.

The sex comb is often used in sexual selection. Males with more pronounced or better-formed sex combs may be more successful in securing mates. Thus, the sex comb may be involved in the male's ability to attract and mate with females, which could have evolutionary implications. Research has shown that the size and structure of the sex comb can vary between different strains or populations of *Drosophila*. This variation can potentially influence mating success and is under sexual selection pressures, where females may prefer males with larger or more symmetrical sex combs (Gonzalez and Mateos 2021; Ravi and Murugan 2023; Tiefer and Smeets 2024). Gonzalez and Mateos (2021) integrated genomic analysis and morphological data to trace the evolutionary history of the sex comb in *Drosophila*. Their study

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provides new insights into how genetic variation contributes to the diversification of this sexually selected trait. In one of the reviews on sex comb related aspects, Tiefer and Smeets (2024) provided a comprehensive report on the developmental origins and evolutionary significance of the sex comb in *Drosophila*. It discusses how this structure, which is primarily used in mating behaviors, has evolved in different species of *Drosophila*. The sex comb may also be involved in intrasexual competition, particularly between males. Males may use their sex combs to help hold onto females during mating attempts or dislodge rivals in competitive mating scenarios. This function contributes to sperm competition and increases the male's reproductive success. The presence of the sex comb in *Drosophila* provides evolutionary insights into the development of sexually dimorphic traits and how physical features evolve in response to mating and reproductive behaviors. The sex comb is an example of how physical traits can evolve to improve reproductive success, in this case through better mate acquisition or retention.

GENETIC BASIS

Yuan, and Pitnick, (2003) discussed the role of genetic manipulation to show that males lacking sex combs have reduced mating success, highlighting their functional role. They opined immense importance of sex combs for male mating success in *D. melan*ogaster. Studies have been conducted to explores the evolutionary forces shaping sex comb morphology, linking it to sexual selection and genetic variation (Chippindale, and Rice, 2001). Frankel and his coworker (Frankel, and Pruneda, 2000) wrote a comprehensive review on the genetic control of sex comb development, emphasizing its role in evolutionary change. Ho, *et al.* (2018) investigated the cellular and mechanical processes underlying sex comb development, particularly the rotation of the structure. They suggested that rotation of sex combs in *Drosophila melanogaster* requires precise and coordinated spatio-temporal dynamics from forces generated by epithelial cells.

The sex comb is controlled by the Sex combs reduced (Scr) gene, which is part of the homeotic gene cluster in *Drosophila*. This gene is crucial for the development of the sex comb and other leg structures (Struhl, 1982). The gene plays a role in the regulation of segment identity and the patterning of the legs in male flies. Mutations in the Scr gene can lead to the loss or alteration of the sex comb, illustrating its genetic basis and significance in male morphology. Thompson, *et al.* (2023) described the molecular basis of sex comb formation in *Drosophila* analyzing CRISPR-Cas9 gene editing and transcriptomic profiling to dissect the principal pathways involved in the development of the sex comb. Through this study they focused on key genes and signaling pathways that regulate this sexually dimorphic trait. Salahuddin *et al.* (2022) published a paper pertaining to sex comb gene expression in Drosophila dealing the interactions with hormonal pathways and their evolutionary implications. They in fact investigated the gene expression patterns of sex combs, under the influence of hormonal signals, particularly those involving juvenile hormone and ecdysone that regulate the formation of sex combs in *D. melanogaster* and related species.

(A) (B) (C) (D) (E)

Figure 1: Male pro-thoracic leg of five species of *Drosophila* showing their sex comb patterns in upper portion of tarsus segment (*D. melanogaster* (A), *D. ananassae* (B), *D. melarkotliana* (C), *D. bipectinata* (D) and *D. biarmipes* (E)

OBSERVATION IN SOME SPECIES COMMONLY FOUND IN INDIA

In figure-1, sex combs of five species of *Drosophila* are depicted. All these five species belong to subgenus- Sophophora, which is characterized for this specific trait. One can see the confinement of sex combs in proximal portion of the tarsus segment of the pro-thoracic leg. In *D. melanogaster*, one of the ubiquitously represented species, a single comb laced with 10 to 11 stout bristles, is clustered in the first sub-segment of tarsus whereas, in another cosmopolitan species, like *D. ananassae*, this structure is arranged in several rows spread along the first and second subtarsal segments. Two closely related species of *bipectinata* species complex, *D. melarkotliana* and *D. bipectinata* (Bock 1978; Singh *et al.* 2016; Singh and Singh 2020; 2021; 2022a; 2022b; 2023; 2024; Singh *et al.* 2022) also differ in their sex comb morphology (Gupta 1973). In *D. melarkotliana*, the pattern of sex comb bristles follows 1, 3-4 in first sub-segment and 1, 2-3 in second sub-segment of tarsus whereas, in *D. bipectinata*, it is marked as 5-8 and 6-9 in first sub-segment of tarsus and 1 to 2 in the second sub-segment of tarsus. The fifth species shown in the figure, i.e., *D. biarmipes* also shows conspicuous differences from the other four in which this structure is in the form of two distinct combs. More interestingly, it has also been recorded that in some of the possible inter-species crosses, the hybrid males are characterized by the presence of mixed pattern of sex comb of their parental species. This can be witnessed in the hybrids availed by making a cross between females of *D. bipectinata* and males of *D. melarkotliana* (or if their reciprocal cross is performed). Male hybrids of such cross possess sex comb that partially match to both the species (Gupta 1973).

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