Arthropod Structure & Development xxx (2017) 1–15

Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd

Haltere morphology and campaniform sensilla arrangement across Diptera

Sweta Agrawal [a], David Grimaldi [b], Jessica L. Fox [c, *]

[a] Department of Physiology and Biophysics, University of Washington, Seattle, WA, 98195, USA
[b] Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, 10024-5192, USA
[c] Department of Biology, Case Western Reserve University, Cleveland, OH, 44106-7080, USA

ARTICLE INFO

Article history:
Received 9 August 2016
Accepted 30 January 2017
Available online xxx

Keywords:
Diptera
Halteres
Sensilla
Hicks papillae
Mechanoreceptors
Campaniform sensilla

ABSTRACT

One of the primary specializations of true flies (order Diptera) is the modification of the hind wings into club-shaped halteres. Halteres are complex mechanosensory structures that provide sensory feedback essential for stable flight control via an array of campaniform sensilla at the haltere base. The morphology of these sensilla has previously been described in a small number of dipteran species, but little is known about how they vary across fly taxa. Using a synoptic set of specimens representing 42 families from all of the major infraorders of Diptera, we used scanning electron microscopy to map the gross and fine structures of halteres, including sensillum shape and arrangement. We found that several features of haltere morphology correspond with dipteran phylogeny: Schizophora generally have smaller halteres with stereotyped and highly organized sensilla compared to nematoceran flies. We also found a previously undocumented high variation of haltere sensillum shape in nematoceran dipterans, as well as the absence of a dorsal sensillum field in multiple families. Overall, variation in haltere sensillar morphology across the dipteran phylogeny provides insight into the evolution of a highly specialized proprioceptive organ and a basis for future studies on haltere sensory function.

1. Introduction

Dipteran insects, the “true flies,” include species that are amongst the most maneuverable of all flying animals. Much of this aerial agility is due to the modification of their hind wings into small, club-shaped mechanosensory organs that are entirely unattached to the forewings. These structures, the halteres, are a major defining characteristic of the order Diptera (“two wings”). Although the halteres do not generate lift, they experience multiple inertial forces during flight, and a sophisticated array of mechanosensory cells at the haltere base detects the cuticular deformations caused by these forces (Pringle, 1948; Keil, 1997). This sensory information is sent to motor neurons that steer the wings (Chan and Dickinson, 1996; Fayyazuddin and Dickinson, 1996) and stabilize the fly's gaze (Hengstenberg, 1991; Huston and Krapp, 2009). If the halteres are removed, flies are unable to maintain stable flight (Derham, 1714).

The halteres are imbued with hundreds of mechanosensory cells, the vast majority of which are in campaniform sensilla (Chapman, 1982; Gnatzy et al., 1987). Although significant strides have been made in understanding how halteres influence flight behavior in flies (Dickinson, 1999; Sherman and Dickinson, 2003; Bender and Dickinson, 2006; Mureli and Fox, 2015), less is known about how the arrangement of the haltere campaniform sensilla influences their function, and which forces they may detect. Furthermore, it is not known how the arrays of campaniform sensilla may differ among fly species. Diptera is the second-largest order of insects after Coleoptera (Grimaldi and Engel, 2005), and contains species that exhibit a broad range of flight behaviors (Brodsky, 1994). Previous work has discussed haltere campaniform shape and arrangement for two highly-derived fly species: *Calliphora* (Calliphoridae: Pflugstaedt, 1912; Gnatzy et al., 1987), and *Drosophila* (Drosophilidae: Cole and Palka, 1982). These studies reported similar fields of campaniform sensilla and named them according to their relative locations (Fig. 1A). Are these fields conserved across the entire order? How might they vary in shape,

Abbreviations: SEM, scanning electron micrograph; dSP, dorsal scapal plate; dBP, dorsal basal plate; dHP, dorsal Hicks papillae; dFS, dorsal flanking sensilla/sensillum; vHP, ventral Hicks papillae; vSP, ventral scapal plate.

* Corresponding author.
E-mail addresses: sagrawal@u.washington.edu (S. Agrawal), grimaldi@amnh.org (D. Grimaldi), jlf88@case.edu (J.L. Fox).

http://dx.doi.org/10.1016/j.asd.2017.01.005
1467-8039/

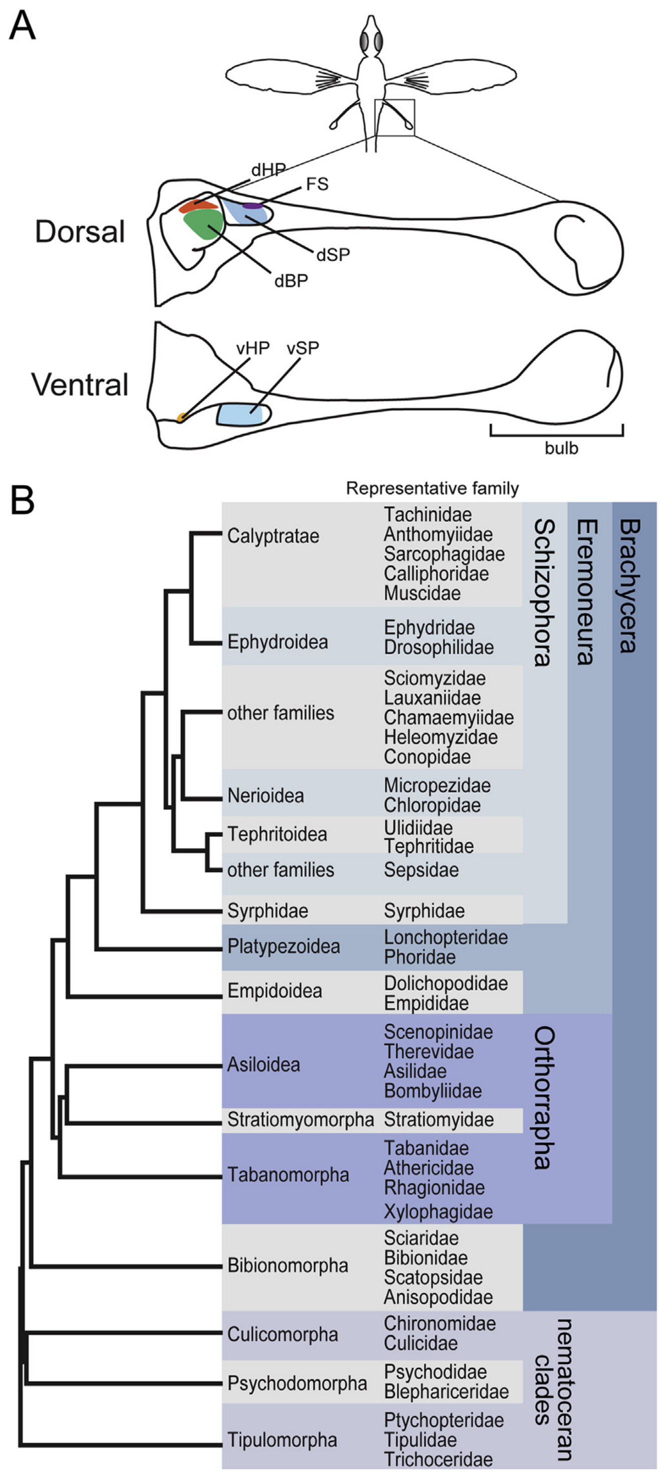

Fig. 1. Haltere morphology and sensilla were examined in 42 families spanning the dipteran order. (A) Schematic of the haltere and its major sensilla fields. Halteres are the modified hind wings of dipterans. Sensilla are clustered into four fields on the dorsal side: dorsal Hicks papillae (dHP), dorsal basal plate sensilla (dBP), dorsal scapal plate sensilla (dSP), and the flanking sensilla (FS). On the ventral side, they are clustered in either the ventral Hicks papillae (vHP) or the ventral scapal plate sensilla (vSP). (B) Phylogenetic tree (adapted from Wiegmann et al., 2011) showing the families we studied along with their clade. 1–9 specimens were studied per family, not necessarily all from the same species.

size, or placement? Because campaniform sensilla function by coupling deformation of a flexible cuticular dome to mechanical strain detected by an underlying mechanosensitive neuron, surface morphology and location will greatly impact the forces detectable by these structures. As a result, any variation we see in sensillar morphology or arrangement between fly species likely affects haltere function.

To better understand how the campaniform sensilla may detect inertial forces during flight in different species, we used scanning electron microscopy (SEM) to map and compare the arrays of campaniform sensilla of 150 flies from over 40 families across fly phylogeny, from the nematocera-type flies (the clades Tipulomorpha, Psychodomorpha, and Culicimorpha) to the calyptrates (Fig. 1B). We find distinct phylogenetic patterns of gross haltere morphology and sensillum arrangements, revealing a greater diversity of haltere morphology than previously documented and providing insight into the evolution and function of a complex, highly specialized organ.

2. Methods

2.1. Sample collection

Flies were collected from northeastern Ohio, New York City, and New Jersey. Other samples were taken from museum collections at the American Museum of Natural History and the Cleveland Museum of Natural History. All specimens were identified to family level, and a subset to genus and species levels (noted in Table S1). Up to nine specimens were studied per family.

2.2. SEM methods

The halteres of all specimens were dissected from the body by cutting through the pleural sclerites in a ring around the base and then immersed in 95% ethanol overnight and allowed to air-dry. Halteres were mounted on SEM stubs (Ted Pella Inc., Redding, CA), coated with gold-palladium, and examined using either a Hitachi S4700 SEM (at the American Museum of Natural History) or a Helios Nanolab 650 SEM (at Case Western Reserve University).

2.3. Gross measurements

Gross measurements of halteres (e.g., haltere and bulb length) were made either from SEM images or with a Zeiss stereoscope outfitted with a digital stage micrometer. Bulb length of the haltere was defined as the length from the tip of the haltere to the point where the haltere expands from the stalk. In many of these specimens, it was not possible to accurately measure body length due to deformations upon drying.

2.4. Quantifying row arrangements

We digitized the position of the centroid of each campaniform sensillum using custom software written in Matlab (The Mathworks, Natick, MA). To estimate the linearity of the rows of sensilla that we observed, we sorted the sensilla into rows and measured the distance between adjacent sensilla. The total distance for the row of sensilla was divided by the straight-line distance between the first and last sensilla. Using this calculation, a row of campaniform sensilla that were aligned in a perfectly straight row would have a score of 1, the minimum possible score, and a row with less alignment would have a higher score.

2.5. Phylogenetic analysis

We used a family-level chronogram from Wiegmann et al. (2011) to account for phylogenetic relationships. The tree was pruned to include only the taxa for which we had morphological

Please cite this article in press as: Agrawal, S., et al., Haltere morphology and campaniform sensilla arrangement across Diptera, Arthropod Structure & Development (2017), http://dx.doi.org/10.1016/j.asd.2017.01.005