 doi:10.20944/preprints202201.0223.v2

Title

A standardized nomenclature and atlas of the female terminalia of *Drosophila melanogaster*

Authors

Eden W. McQueen[1,2], Mehrnaz Afkhami[3], Joel Atallah[4], Nicolas Gompel[5], Yael Heifetz[6], Yoshitaka Kamimura[7], Shani C. Kornhauser[6], John P. Masly[3], Patrick O'Grady[8], Julianne Peláez[9], Mark Rebeiz[1], Gavin Rice[1], Ernesto Sánchez-Herrero[10], Maria Daniela Santos Nunes[11], Augusto Santos Rampasso[8], Sandra L. Schnakenberg[12,13], Mark L. Siegal[12], Aya Takahashi[14,15], Kentaro M. Tanaka[14], Natascha Turetzek[5], Einat Zelinger[6], Virginie Courtier-Orgogozo[16]*, Masanori J. Toda[17]*, Mariana F. Wolfner[18]*, Amir Yassin[19]*

Affiliations

[1]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA
[2]Department of Molecular, Cellular, and Developmental Biology, University of Michigan, Ann Arbor, MI, USA
[3]Department of Biology, University of Oklahoma, Norman, OK, USA
[4]Department of Biological Sciences, University of New Orleans, New Orleans, LA 70148, USA
[5]Ludwig-Maximilians Universität München, Fakultät für Biologie, Biozentrum, Grosshaderner Strasse 2, 82152 Planegg-Martinsried, Germany
[6]Department of Entomology, The Hebrew University of Jerusalem, Rehovot 76100, Israel
[7]Department of Biology, Keio University, Hiyoshi, Yokohama, Japan
[8]Department of Entomology, Cornell University, 129 Garden Ave, Ithaca, NY 14850
[9]Department of Integrative Biology, University of California, Berkeley, CA, USA
[10]Centro de Biología Molecular Severo Ochoa (C.S.I.C.-U.A.M.), Universidad Autónoma de Madrid, Cantoblanco, Spain
[11]Department of Biological and Medical Sciences, Oxford Brookes University, Oxford, UK
[12]Center for Genomics and Systems Biology, Department of Biology, New York University, New York, NY, USA
[13]Sema4, Stamford, CT, 06902, USA
[14]Department of Biological Sciences, Tokyo Metropolitan University, 1-1 Minamiosawa, Hachioji 192-0397, Japan
[15]Research Center for Genomics and Bioinformatics, Tokyo Metropolitan University, 1-1 Minamiosawa, Hachioji 192-0397, Japan
[16]CNRS UMR7592, Institut Jacques Monod, Université de Paris, Paris, France
[17]Hokkaido University Museum, Hokkaido University, Sapporo, Japan
[18]Department of Molecular Biology and Genetics, Cornell University, Ithaca, NY 14853 USA
[19]Laboratoire Evolution, Génomes, Comportement, Ecologie (EGCE), UMR 9191, CNRS, IRD, Université Paris-Saclay, Gif-sur-Yvette Cedex, France

 doi:10.20944/preprints202201.0223.v2

*Corresponding authors: virginie.courtier@normalesup.org (V.C.-O.), hutian@lemon.plala.or.jp (M.J.T.); mariana.wolfner@cornell.edu (M.F.W.) yassin@egce.cnrs-gif.fr (A.Y.)

Abstract
The model organism *Drosophila melanogaster* has become a focal system for investigations of rapidly evolving genital morphology as well as the development and functions of insect reproductive structures. To follow up on a previous paper outlining unifying terminology for the structures of the male terminalia in this species, we offer here a detailed description of the female terminalia of *D. melanogaster*. Informative diagrams and micrographs are presented to provide a comprehensive overview of the external and internal reproductive structures of females. We propose a collection of terms and definitions to standardize the terminology associated with the female terminalia in *D. melanogaster* and we provide a correspondence table with the terms previously used. Unifying terminology for both males and females in this species will help to facilitate communication between various disciplines, as well as aid in synthesizing research across publications within a discipline that has historically focused principally on male features. Our efforts to refine and standardize the terminology should expand the utility of this important model system for addressing questions related to the development and evolution of animal genitalia, and morphology in general.

Keywords: Genitalia, terminalia, anatomy, Drosophila melanogaster, nomenclature

Introduction

Animal terminalia (which includes both the genitalia and analia) have a long history of being used for taxonomic and phylogenetic purposes, as well as being studied in the context of functional morphology and morphological evolution. This is because these structures possess a remarkable level of anatomical diversity, making them excellent morphological features for distinguishing species as well as understanding mechanisms of rapid morphological change (Eberhard, 1985; Hosken and Stockley, 2004; Simmons, 2014). Past investigations mostly focused on male terminalia, and female terminalia were generally considered to be relatively invariable (Eberhard, 1985; Eberhard, 2010). In the last several decades however, there has been a burgeoning interest in improving our understanding of female genital diversity (Méndez and Córdoba-Aguilar, 2004; Ah-King, Barron, and Herberstein, 2014; Yassin, 2016; Sloan and Simmons, 2019; Craddock et al., 2018; Green et al., 2019; Crava et al., 2020). This interest has been motivated by the realization that some evolutionary hypotheses, for instance with respect to coevolution of genitalia, are best addressed by studying both male and female genital morphology simultaneously (Brennan et al., 2007; Kuntner, Coddington, and Schneider, 2009; Simmons, 2014; Brennan and Prum, 2015; Yassin, 2016; Yassin and Orgogozo, 2013). In addition, the female terminalia can evolve in response to ecological factors, such as the properties of egg-laying substrates (Craddock et al., 2018). Furthermore, as morphological adaptations in female genitalia are central to the ability of many pest species to damage crops when laying their eggs into plants (Childers, 1997; Dreves, Walton, and Fisher, 2009; Seraj, 2000; Atallah et al., 2014; Omoloye et al., 2016), studying female genitalia can potentially lead to practical applications.

In recent years, the genitalia of species in the *Drosophila* genus have become an important study system to address research questions in ecology, behavior, evolution, development and taxonomy. A survey of the egg-laying apparatus of Hawaiian drosophilids for example revealed that ovipositor form, and especially length and patterns of sensory structures, differ between species and strongly correlate with adaptations to different oviposition substrates (Craddock et al., 2018). Similar observations were made for *Drosophila suzukii*, which has evolved an elongated ovipositor with derived sensory structures, enabling piercing through the skin of still ripening fruits, which allows this species to access a new ecological niche and simultaneously makes it a pest causing massive agricultural damage (Atallah et al., 2014; Green et al., 2019).

Cross-disciplinary communication among researchers investigating different aspects of *Drosophila* female terminalia has often been impeded by two important challenges. First, many important features are internal, mostly composed of folded soft tissues, which can make it more difficult to identify, delimit and rigorously quantify variation in shape between individuals or species. For example, commonly used terms such as vulva, vagina and uterus have no clear delineations and have been applied to variable portions of the genitalia in different publications (see **Table 1**). Imaging and dissecting technology developed in recent years has greatly mitigated this technical limitation (Ah-King, Barron, and Herberstein, 2014). For instance, micro-computed tomography (micro CT) scanning can now provide detailed images of internal structures (Mattei et al., 2015). The second challenge has been that individual structures have often been referred to by several different names. This is most obvious in the long list of synonyms that have been applied to the egg-laying sclerites laterally surrounding the gonopore (e.g., ovipositor, vaginal plates, oviscapt, gonopod, etc. See **Table 1**).

In a previous paper, we delineated the structures of the male terminalia of *D. melanogaster* and proposed a standard set of terms for these parts (Rice et al., 2019). Following a discussion with the members of the consortium, we opted to designate terms that can be homologized across the Diptera, but we recommended that authors also indicate common terms, whenever possible, in their manuscripts in order to guarantee maximum understanding among disciplines. In this paper, we follow the same approach and collectively propose a collection of terms and definitions to unify the terminology associated with the female terminalia in *D. melanogaster* (**Table 1**). In contrast to our previous paper, which was limited to the external male terminalia, we also include here a comprehensive overview of the internal reproductive structures of females. Many of these structures make contact with intromittent parts of the male genitalia during mating and may therefore be of interest in studies of genital evolution and coevolution (e.g., Kamimura, 2012; Yassin and Orgogozo, 2013; Mattei et. al., 2015).

Distinguishing between the various parts of the female genitalia can be challenging, especially where clear boundaries (e.g., sutures, joints) do not exist. To achieve maximum clarity in our visual depictions, we have used a combination of bright field images of dissected cuticle (Canton S wild type strain) and line drawings.

Results and Discussion

A visual atlas of adult *D. melanogaster* female terminalia

We provide below a unified nomenclature of the anatomical parts of the female terminalia of *D. melanogaster,* together with images to visualize the various structures with as much clarity as possible. We hope that this effort will facilitate the study of female terminalia in *D. melanogaster* and related species by providing both a common language for cross-reference and delimitations for features of interest.

The female terminalia of *D. melanogaster* is composed of anatomical structures arising from a fusion of abdominal primordia 8-10 (Schüpbach, Wieschaus, and Nöthiger, 1978; Epper, 1983). In females, the abdominal segment 8 primordium of the genital disc develops into the majority of the internal and external female genital structures (Keisman, Christiansen, and Baker, 2001; Sánchez and Guerrero, 2001). The abdominal segment 9 primordium is reduced in females, giving rise to the internal structure of the female accessory gland and the dorsal surface of the uterus (Keisman et al., 2001; Estrada, Casares, and Sánchez-Herrero, 2003). In females, as in males, the abdominal segment 10 primordium of the genital disc develops to become the analia (Nöthiger, Dübendorfer, and Epper, 1977). We divide our descriptions of the terminalia into two regions, internal and external. The external terminalia have prominent roles in oviposition and copulation, while the internal terminalia have roles in ovulation and sperm storage. We use the junction of the oviprovector (external) and vulva (internal) as the division between these two regions. **Table 1** details our proposed unified nomenclature. Each proposed term is listed along with a description of the structure, previously used alternate names, and references. For ease of conversion, **Table 2** provides the reverse search functionality; previously used terms are listed in the first column, with the corresponding unified nomenclature term we propose here given in the second column. Instances where the same term has been used elsewhere for more than one distinct structure are indicated with an asterisk.

External structures of the female terminalia

The external structures of the female terminalia (**Figures 1-3**) consist of the female analia and external genitalia, both of which harbor sensilla (bristles). In females, the analia are subdivided into a dorsal plate (the epiproct), and a ventral plate (the hypoproct). The analia are surrounded by the genital tissue of the epigynium (formerly female abdominal tergite 8). The epigynial ventral lobe connects to the paired valves (left and right) of the hypogynium via the perineal membrane. We further subdivide the hypogynium into several parts. The hypogynial posterior lobe and hypogynial anterior lobe are the posterior and anterior parts of each valve of the hypogynium. The ventral side of both valves is connected by the hypogynial anteroventral bridge (**Figure 2**, **panel b**). The hypogynial mid-dorsal incision is an indentation on the outside of each hypogynial valve. The posterior and anterior hypogynial lobes are delimited by an imaginary line connecting the hypogynial mid-dorsal incision with the hypogynial long sensillum. During copulation, the male surstylus contacts the hypogynium near this incision (Kamimura and Mitsumoto, 2011). The hypogynial posterodorsal pouch is a depression positioned at the apical end of each hypogynial valve (**Figure 2**, **panel a**), which contacts the male epandrial posterior lobe early in copulation (Jagadeeshan and Sing, 2006; Yassin and Orgogozo, 2013). The two hypogynial valves are connected medially by the oviprovector, an eversible membrane whose ventral surface bears the oviprovector scales (**Figure 2**, panel c; **Figure 3, d**), which likely act to prevent bidirectional movement of eggs (Austin and Browning, 1981).
The setation of the external female terminalia has several readily identifiable components (**Figures 2 and 3**). Sensilla on the epiproct and the hypoproct are referred to as epiproctal sensilla and hypoproctal sensilla, respectively (**Figure 2**, panel a). On the genitalia, both the epigynium (epigynial sensilla) and hypogynium (hypogynial sensilla) have characteristic setation. The hypogynial sensilla are subdivided into three types (**Figure 3**). Hypogynial short sensilla (previously gonopod sensillum trichodeum; **Figure 3c**, blue) are small apical bristles at the dorsal tip of the hypogynial posterior lobe. The hypogynial posterior lobe of each valve also possesses a single hypogynial long sensillum (previously gonopod long

 doi:10.20944/preprints202201.0223.v2

bristle; **Figure 3b**,**c**, green) at the apical end. Finally, each valve of the hypogynium possesses a row of stout hypogynial teeth (previously gonopod thorn bristles or vaginal teeth; **Figure 3b**,**c**, red).

Internal female genital and reproductive structures

The upper reproductive tract consists of the ovaries and oviducts, which transfer mature eggs to the lower reproductive tract (**Figures 4, 5**). The lower reproductive tract is composed of the genital chamber, female accessory glands, seminal receptacle and spermathecae. The seminal receptacle and spermathecae store sperm after mating, while the female accessory glands and the spermathecal secretory glandular cells that surround the spermatheca capsule serve as secretory organs. The genital chamber is subdivided into the uterus (or bursa; anterior) and vagina (posterior) (**Figure 4**). It is in the uterus that fertilization of eggs takes place (Nonidez, 1920). The posterior opening of the lower reproductive tract consists of the vagina through which sperm is transferred to the female and the vulva, a name which has also previously been used for the oviprovector, and where copulation occurs and where the egg exits the reproductive tract (e.g., Tsacas and David, 1975; Bryant, 1978).

Delineation of structures

Some parts of the female genitalia that we outline in this work do not have clear boundaries, such as ridges or clefts. We justify the demarcation of these structures in several ways. In some cases, we note the structure separately because the feature appears to have functional significance. For instance, the hypogynial mid-dorsal incision (**Figure 2**) does not have clear boundaries with surrounding tissue, but there is evidence to suggest that this depression is a site that makes contact with the male surstylus during copulation (Kamimura and Mitsumoto, 2011). Delimitation of anatomical features can also be aided by considering the distribution of important developmental molecules (e.g., transcription factors), the patterning of which may indicate regions that harbor developmental or evolutionary independence (Sánchez and Guerrero, 2001; Christiansen et al., 2002; Estrada, Casares, and Sánchez-Herrero, 2003). Lastly, some identified features are quite subtle in *D. melanogaster* but are more exaggerated in closely related species, providing reasoning for their designation as notable structures of the female genitalia in this group. For example, the hypogynial posterodorsal pouch is relatively shallow in *D. melanogaster* but is unambiguous in *D. simulans* (Yassin and Orgogozo, 2013), a closely related species which diverged about 2 million years ago (Li, Satta, and Takahata, 1999). Future work investigating the development and function of these structures will further aid in structural demarcation.

Choice of terms

 doi:10.20944/preprints202201.0223.v2

The term hypogynium was first proposed by Crampton (1920) to refer to the abdominal sternite below the genital apparatus of the female, which in the case of Diptera corresponds to sternite 8. In the same paper, Crampton (1920) defined the term hypandrium as the abdominal sternite below the genital apparatus of the male, *i.e.*, sternite 9 in Diptera. Whereas the term hypandrium has been used in *Drosophila* systematics and developmental biology as early as the 1940s (e.g., Salles, 1947; Hildreth, 1965), "hypogynium" has never been applied to *Drosophila*. Instead, a variety of non-anatomical terms such as "egg-guide" and "ovipositor" have been applied to the female egg-laying external structures. In entomology, the ovipositor is usually formed from the appendices of the genital segment (Snodgrass, 1935), and indeed Ferris (1950) called the external egg-laying structure (in *D. melanogaster*) the 'female gonopod'. However, it has been suggested that Diptera females lack an ovipositor, in the proper entomological sense (Snodgrass, 1935). Indeed, in *D. melanogaster* the homeotic gene *Abdominal-B* represses all leg-development genes in female A8, confirming the sternal nature of the hypogynium (Estrada and Sánchez-Herrero, 2001). Crampton (1942) suggested that specific terms, such as oviscapt, would be more appropriate. Grimaldi (1990) has introduced this term in *Drosophila* systematics, and since then it has been used in multiple systematic and functional morphology studies (Hu and Toda, 2001; Bächli et al., 2004; Kamimura, 2010; Kamimura and Mitsumuto, 2011; Yassin and Orgogozo, 2013). However, given our conservation of the terms hypandrium and epandrium for the sternite and tergite of abdominal segment 9 in our paper on male terminalia anatomy (Rice et al., 2019), we prefer here for consistency the usage of the terms hypogynium and epigynium for the sternite and tergite of female abdominal segment 8. As the anatomical term hypogonium is not commonly used in the literature, it would be preferable to cite it alongside the more common functional term "ovipositor" in publications, e.g., hypogynium (ovipositor) or ovipositor (hypogynium).

The terminalia have formerly been called the proctiger and consequently the sternite and tergite surrounding the anus were called the hypoproct and the epiproct, respectively (Grimaldi, 1990; Vilela and Bächli, 1990; Zhang and Toda, 1992; Hu and Toda, 2001; Bächli et al., 2004; Kamimura and Mitsumuto, 2011). However, in some Dipteran species, two additional lateral plates, called the cerci, also surround the anus. Remarkably, there are no hypo- and epiprocts in males and no cerci in females of *D. melanogaster*. Nonetheless, it has been observed that in *doublesex*, *transformer-2*, *hermaphrodite,* or *intersex* mutant females, the hypoproct is reduced and the epiproct shifts laterally, resembling the male cerci, but still usually fused on the dorsal side (Belote and Baker, 1982; Li and Baker, 1998; Garrett-Engele et al., 2002; Siegal and Baker, 2005). This suggests that the female epiproct may have the same developmental origin as both male cerci. Females of the subfamily Steganinae have a pair of lateral plates identified as cerci posteriorly to the epiproct (Grimaldi, 1990). In the subfamily Drosophilinae, however, these cerci have been lost or possibly fused to the epiproct. In addition, we note that in some insect groups (such as odonates) the terms hypoproct, epiproct, and paraproct describe terminal structures that

are not functionally homologous to the structures named here for *D. melanogaster* and could very well derive from different segment primordia during terminalia development (Snodgrass, 1952; Boudinot, 2018).
Considering the internal structures, we propose here a term in *Drosophila*, the furca (**Figure 6**). In non-Cyclorrhaphan Diptera, the furca is an internalized sclerite on the dorsal surface of the genital chamber derived from sternite 9 (Cumming and Wood, 2017), and it was believed to be absent or unrecognizable in most Cyclorrhapha. Interestingly, developmental studies showed that the dorsal wall of the genital chamber in *D. melanogaster* derives from the A9 primordium (Keisman, Christiansen, and Baker, 2001), suggesting the furca to be present in this species though far less sclerotized. The furca has several folds that we choose to define more precisely here, motivated by evidence that some of these may interact with male intromittent organs. For example, the vaginal furcal dorsolateral fold (**Figure 6**, **b**) is the location of one type of copulatory wound described by Kamimura and Mitsumuto (2011).

Incorporation of our standardized terminology across areas of research and species
A primary goal of this article is to facilitate the flow of information across disciplines and research areas. We understand that there may be good reasons for individual authors to continue using the terminology that they are accustomed to in their own work. In such cases, our suggestion would be to parenthetically reference the unified terminology that we outline here, e.g., parovaria (female accessory glands). In this manner, there will be greater ease in translating across works that employ different terminology for the same feature.
Our work here focused on the terminalia of *Drosophila melanogaster* females. However, despite the great morphological diversity of the female genitalia in the Drosophilidae, the general ground plan of these structures is fairly well conserved. Therefore, most of the terms we define are easily extensible to other species, facilitating comparison across studies outside *D. melanogaster*. In cases where structures have been lost in *D. melanogaster* (and thus are not named here), we hope that this set of unified terms will mitigate potential confusion by giving common references for surrounding structures. We briefly illustrate below two exciting research areas for which our unified terminology may prove useful in facilitating fruitful comparisons across species or in different species groups.

Evolution of genitalia in response to ecological factors
Evolution of the female genitalia has frequently taken place in response to changing oviposition substrates. Adaptations usually involve changes in size and shape of the hypogynium as well as in the number, disposition and shape of the hypogynial sensilla (Craddock et al., 2018; Atallah et al., 2014). For example, species laying eggs on solid substrates, such as *D. suzukii* or leaf and bark-breeding Hawaiian drosophilids (O'Grady et al., 2011), often have large and elongate hypogynium with numerous, large teeth-like

 doi:10.20944/preprints202201.0223.v2

sensilla. On the other hand, species laying eggs in decaying or soft tissues, such as *D. melanogaster*, often have short and roundish hypogynium with fewer and less sharp sensilla. In some cases, female genital evolution in *Drosophila* has important consequences for agriculture. For example, the evolution of a serrated ovipositor in *D. suzukii* and closely related species (e.g., *D. subpulchrella*) has allowed these flies to oviposit in ripening fruit, making them crop-damaging pests, while closely related species such as *D. biarmipes*, where the ovipositor retains the basal shape and setation, are benign (Atallah et al., 2014). A common language with respect to anatomical structures will ensure that studies conducted in disparate systems come together to inform our collective understanding of the forces and mechanisms driving such changes in response to ecological factors.

Coevolution of the sexes

The rapid evolution of animal genitalia is a longstanding area of research interest (Eberhard, 1985; Hosken and Stockley, 2004; Simmons, 2014). While early work focused specifically on male structures, added emphasis has recently been placed on understanding the evolution of female structures (Ah-King, Barron, and Herberstein, 2014; Sloan and Simmons, 2019), and how coevolution of male and female genitalia might contribute to the rapid evolution of these structures in both sexes (Brennan and Prum, 2015; Yassin, 2016). Adaptations of male genitalia to rapidly evolving female genitalia (Muto et al., 2018), or vice versa, usually involve changes concerning specific genital features, such as the shape and size of the hypogynial posterodorsal pouch in the *melanogaster* species complex and the sclerification of some internal walls of the oviprovector (e.g., in *D. teissieri*), the vulva (e.g., in *D. orena*) and the vagina (e.g., in *D. erecta*) (Kamimura and Mitsumoto, 2012; Yassin and Orgogozo, 2013; Kamimura, 2016). Some internal sperm-storage organs, such as the seminal receptacle, have co-evolved with the size of the male sperm (Pitnick, Marrow, and Spicer, 1999; Joly and Schiffer, 2010). We hope that the common set of terms we outline here to reference the various parts of the female genitalia, in combination with the previous work outlining terms for the male genital structure (Rice et al., 2019), will aid in the synthesis of empirical studies of genital evolution and coevolution across Drosophilid species.

Methods

Scanning electron microscopy

Scanning electron micrographs from **Figure 1,b** and **Figure 3,d** were graciously provided by Dr. John M. Belote, Syracuse University. The exact strain of *D. melanogaster*, and exact methods used to collect these images are no longer known, as these images were collected about 40 years ago.

The scanning electron micrograph in **Figure 3,c** was collected as follows: Adult female *D. melanogaster* were fixed in 2% glutaraldehyde in 0.1M sodium cacodylate, stained with osmium tetroxide, dried through an ethanol series (35-100%) and the ethanol dried with a

Tousimis AutoSamdri 815 critical point dryer. The terminalia were then dissected from the abdomen, mounted on stubs, and coated with gold-palladium using a Tousimis sputter coater. Specimens were visualized with a Hitachi SM-5000 scanning electron microscope. The scanning electron micrograph in **Figure 6**, **A** was collected by fixing a female sample from the Oregon-R strain in ice-cold ethanol, followed by a t-butanol wash, and drying by sublimation. The samples were then gold-coated and observed under a scanning electron microscope (Hitachi S-510).
The scanning electron micrographs in **Figure 6, B and C**, are from L. Tsacas' collection at the National Museum of Natural History, Paris (Courtesy of the Museum).

Bright Field Cuticle imaging

For cuticle images in **Figure 2 (except Figure 2, panel c)**, a Canton S line of *Drosophila melanogaster* (Bloomington # 64349) was used. Adult females were dissected in 100% EtOH with micro-forceps and mounted in PVA Mounting Medium (BioQuip). Samples were imaged at 10x and 20× magnification on a Leica DM 2000 with a Leica DFC540 C camera. Images were Z stack-compiled with the Leica Application Suite to allow for optimal focus. For cuticle image in **Figure 2**,**c** and the image of the spermatheca in **Figure 4 (inset),** female specimens from a culture strain of Canton S were used. The distal portion of abdomen after the segment 7 including the spermatheca therein was detached from the main body in 70% EtOH, treated with 10% KOH solution at 80–90°C for about 5 min, and mounted in a droplet of glycerin on a cavity slide. After removing the tergite and sternite 7 within glycerin, the dissected and cleaned terminalia and spermatheca were microphotographed at different depths of focus using a DinoLite® Digital Eyepiece Camera attached to an Olympus BX50 microscope. The photos were stacked into an all-in-focus composite using the software CombineZP (Hadley, 2010). The confocal images were edited using Adobe Photoshop CS6 and Adobe Illustrator CS6.
For **Figure 3a** cuticle image, a female from the Canton S strain was used. The sample was mounted in 50:50 Hoyer's medium and lactic acid. The sample was imaged at 20x magnification using a Zeiss Axioplan with a Manta G609C camera (Alited Vision Technologies). Focus stacking was performed with the software Picolay (www.picolay.de, version 2020-08-13).

Visualization of the upper and lower RT

Reproductive tracts were dissected in Schneider's Drosophila medium (Sigma) on ice and processed for electron microscopy as described in Kapelnikov et al. (2008a). Briefly, tracts were flat-embedded between two sheets of Aclar (Electron Microscopy Sciences), which allowed us to image the entire tract at the light microscopic level prior to sectioning. Sections were cut on a Reichart Ultracut microtome. One-μm thick sections were stained with 1% toluidine blue and viewed with a Zeiss Axoplan microscope.

Immunocytochemistry

Reproductive tracts were dissected in Yamamoto's Ringer, fixed in 4% paraphormaldehyde in PBS and incubated in blocking solution and stain with Alexa Fluor 594-phalloidin (1:200) and DAPI (Molecular Probes) as described in Kapelnikov et al. (2008a). Reproductive tracts of the different treatments were mounted with Antifade media (Giloh and Sedat, 1982**)** on a multi-well glass slide.

Reporter constructs

The image in Fig 5L shows the pattern of *DsRed* expression (magenta) for an enhancer-reporter construct containing 301 bp of sequence between the transcription start site of *CG32833* and a distal transcription start site of *twist* (coordinates 2,2985,299 - 2,2985,599 in *D. melanogaster* genome v6.42). Note that this intergenic sequence is also upstream of the transcription start site of *miR-4939* (transcribed in the same direction as *CG32833*) and of the transcription start site of long non-coding RNA gene *CR42742* (transcribed in the same direction as *twist*). It is not known to which gene's expression pattern the reporter corresponds. The 301-bp fragment was amplified by PCR with primers respectively containing a KpnI site and an XhoI site, for cloning into the KpnI and XhoI sites in the polylinker of pRed H-Stinger (Barolo, Castro, and Posakony, 2004). The construct was inserted into strain w^{1118} by *P*-element-mediated transformation, and the reproductive tract of a female from the resulting strain was dissected and imaged as done previously (Schnakenberg et. al. 2011).

Confocal microscopy

Reproductive tracts were imaged in a Leica TCS SP8 multiphoton (MP) laser scanning confocal microscope operated by the LAS X software. Fluorescence was detected by using argon excitation lasers of 488 nm captured by a conventional photomultiplier (PMT). Image processing was done using Fiji and Imaris 8.4 (Bitplane).

Micro Computed Tomography (Micro-CT)

Reproductive tracts were stained with a mixed contrasting dye [1% crystalline I2 (Merck 376558) and 1% Tannic acid (Merck 1401-55-4) in 200 proof ethanol] for 24-48 hours at 40°C. Before imaging, the samples were washed two times for ten minutes each in fresh 200 proof ethanol. Micro-CT was done with a Zeiss Xradia micro XCT-400 at X20 magnification and data processing was done using AVIzO and Fiji (Zelinger E, Brumfeld V, Rechav K, Heifetz Y, in prep).

Acknowledgements:

We thank Clare Pilgrim and Steven Marygold from FlyBase for working with us to integrate our terminology into the FlyBase terms and John Belote for providing the SEM images for Figures 1 and 3. We also thank Patricia Rivlin and Anat Kapelnikov for images used in

Figure 5D, E and G, and Zohar Nir-Amitin for the female reproductive tract drawing in Figure 5A.
Funding: This work was supported by funding from the National Institutes of Health (R35GM14196 and GM112758 to M.R.), from the Louisiana Board of Regents (LEQSF(2017-20)-RD-A-26 to J.A.), from the Japan Society for the Promotion of Science (19H03276 to Y.K., and A. T.), from the Agence Nationale de la Recherche (ANR-18-CE02-0008) to AY, M.F.W. acknowledges support from R37-HD038921 and R03-HD101732, as well as from R01-HD059060 to M.F.W. and A.G. Clark. V. C.-O. acknowledges support from the CNRS as part of the MITI interdisciplinary action "Défi Adaptation du vivant à son environnement" 2020. M.L.S. acknowledges support from R35GM118170. Project BFU2017-86244-P funded by MICIN/AEI/10.13039/50110001033/ and ERDF A way of making Europe to E.S. Y.H. acknowledges support from Israel Science Foundation (ISF-2041/17 and ISF-2470/21).
The authors have no potential competing interests to report.

Data availability statement:
Data sharing is not applicable to this article as no new data were created or analyzed in this study.

References

Adams EM, Wolfner MF. (2007). Seminal proteins but not sperm induce morphological changes in the *Drosophila melanogaster* female reproductive tract during sperm storage. *Journal of Insect Physiology*. Apr;53(4):319-31. doi: 10.1016/j.jinsphys.2006.12.003. Epub 2006 Dec 29. PMID: 17276455; PMCID: PMC2144743.

Ah-King, M., Barron, A. B., & Herberstein, M. E. (2014). Genital evolution: why are females still understudied? *PLoS biology*, 12(5), e1001851.

Allen, A. K., and A. C. Spradling. (2008), The Sf1-related nuclear hormone receptor Hr39 regulates *Drosophila* female reproductive tract development and function. *Development*, 135 (2): 311–321. doi: https://doi.org/10.1242/dev.015156

Al Sayad, S. and Yassin, A. (2019), Quantifying the extent of morphological homoplasy: A phylogenetic analysis of 490 characters in *Drosophila*. *Evolution Letters*, 3: 286-298. https://doi.org/10.1002/evl3.115

Anderson R. C. (1945). A Study of the Factors Affecting Fertility of Lozenge Females of *Drosophila melanogaster*. *Genetics*, 30(3), 280–296. https://doi.org/10.1093/genetics/30.3.280

Atallah, J., Teixeira, L., Salazar, R., Zaragoza, G., and Kopp, A. (2014). The making of a pest: the evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. *Proceedings of the Royal Society B*. 281, 20132840. http://dx.doi.org/10.1098/rspb.2013.2840.

Austin, A. D. and Browning, T. O. (1981). A mechanism for movement of eggs along insect ovipositors. *International Journal of Insect Morphology and Embryology,* 10, 93–108.

Avila F.W., Sánchez-López J.A., McGlaughon J.L., Raman S., Wolfner M.F., Heifetz Y. (2016) Nature and Functions of Glands and Ducts in the *Drosophila* Reproductive Tract. In: Cohen E., Moussian B. (eds) *Extracellular Composite Matrices in Arthropods*. Springer, Cham. https://doi.org/10.1007/978-3-319-40740-1_11

Bächli G, Vilela CR, Escher AS, Saura A (2004) The Drosophilidae (Diptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, Vol. 39. Brill, Leiden 362 pp.

Baker BS, and Ridge KA (1980) Sex and the single cell. I. On the action of major loci affecting sex determination in *Drosophila*. *Genetics*, 94:383-423.

Belote, JM, and B S Baker. (1982). Sex determination in *Drosophila melanogaster*: analysis of transformer-2, a sex-transforming locus. *Proceedings of the National Academy of Sciences*, 79 (5) 1568-1572; DOI: 10.1073/pnas.79.5.1568

Bloch Qazi M.C., Heifetz Y., and M.F. Wolfner (2003) The developments between gametogenesis and fertilization: ovulation and female sperm storage in *Drosophila melanogaster*. *Developmental Biology*, 256:195-211.

Bock, I. R., and Wheeler, M. R. 1972. The *Drosophila melanogaster* species group. Univ. Texas Publ. 7213: 1–102.

Bodenstein, D. (1950). The postembryonic development of *Drosophila*. In: Demerec, M. (ed). "The Biology of *Drosophila*." pp. 275-367.

Barolo, S., Castro, B., & Posakony, J. W. (2004). New *Drosophila* transgenic reporters: insulated *P*-element vectors expressing fast-maturing RFP. *Biotechniques*, 36(3), 436-442.

Boudinot, B. E. (2018). A general theory of genital homologies for the Hexapoda (Pancrustacea) derived from skeletomuscular correspondences, with emphasis on the Endopterygota. *Arthropod Structure & Development*, 47(6), 563-613.

Brennan, P. L., & Prum, R. O. (2015). Mechanisms and evidence of genital coevolution: the roles of natural selection, mate choice, and sexual conflict. *Cold Spring Harbor Perspectives in Biology*, 7(7), a017749.

Brennan, P. L., Prum, R. O., McCracken, K. G., Sorenson, M. D., Wilson, R. E., & Birkhead, T. R. (2007). Coevolution of male and female genital morphology in waterfowl. *PLoS one*, 2(5), e418.

Bryant PJ (1978) Pattern formation in imaginal discs. In: Ashburner M, Wright TRF (eds). "The genetics and biology of *Drosophila*." Academic Press, New York and London, pp 229–335

Casares, F., Sánchez, L., Guerrero, I., and Sánchez-Herrero, E. (1997). The genital disc of *Drosophila melanogaster*. *Development genes and evolution*, 207(4), 216-228.

Chen, E. H., and Baker, B. S. (1997). Compartmental organization of the Drosophila genital imaginal discs. *Development*, 124(1), 205-218.

Childers, C. C. (1997). Feeding and oviposition injuries to plants. In T. Lewis [ed.], Thrips as Crop Pests. CAB International, New York, pp. 505-537.

Christiansen, A. E., Keisman, E. L., Ahmad, S. M., and Baker, B. S. (2002). Sex comes in from the cold: the integration of sex and pattern. *Trends in genetics*, 18(10), 510-516.

Craddock, E.M., Kambysellis, M.P., Franchi, L., Francisco, P., Grey, M., Hutchinson, A., Nanhoo, S., and Antar, S. (2018). Ultrastructural variation and adaptive evolution of the ovipositor in the endemic Hawaiian Drosophilidae. *Journal of Morphology*, 279, 1725–1752.

Crampton GC (1920) V. The Terminal Abdominal Structures of the Primitive Australian Termite, Mastotermes darwinensis Froggalt. *Transactions of the Royal Entomological Society of London,* 68: 137-145.

Crampton (1942) The external morphology of the Diptera. In guide to the insects of Connecticut. Part VI. *Connecticut Geological and Natural History Survey Bulletin,* 64, 76.

Crava, M.C., Zanini, D., Amati, S., Sollai, G., Crnjar, R., Paoli, M., Valerio Rossi-Stacconi, M., Rota-Stabelli, O., Tait, G., Haase, A., et al. (2020). Structural and transcriptional evidence of mechanotransduction in the *Drosophila suzukii* ovipositor. *Journal of Insect Physiology*, 104088.

Cumming JM, and Wood DM. Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ, editors. Manual of afrotropical diptera. v. 1. Introductory chapters and keys to diptera families. Suricata 4. Pretoria: South African National Biodiversity Institute; 2017. p. 89–133.

Dobzhansky, T. and Pavan, C. (1943). Studies on Brazilian species of *Drosophila*. Boletim da Faculdade de Filosofia, Ciências e Letras. Universidade de São Paulo 36(Biol. Geral, 4): 7-72, pl. 1-7.

Dreves, A. J., Walton, V, M. and G. C. Fisher. (2009). "A new pest attacking healthy ripening fruit in Oregon: spotted wing Drosophila: *Drosophila suzukii* (Matsumura)." https://ir.library.oregonstate.edu/concern/open_educational_resources/st74cq71x

Eberhard WG. 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge, Massachusetts, USA.

Eberhard, W. G. (2010). Evolution of genitalia: theories, evidence, and new directions. *Genetica*, 138(1), 5-18.

Epper, F., and Sánchez, L. (1983). Effects of engrailed in the genital disc of *Drosophila melanogaster*. *Developmental biology*, 100(2), 387-398.

Epper, F. (1983). Three-dimensional fate map of the female genital disc of *Drosophila melanogaster*. *Wilhelm Roux's archives of developmental biology*, 192(5), 270-274.

Estrada, B., Casares, F., & Sánchez-Herrero, E. (2003). Development of the genitalia in *Drosophila melanogaster*. *Differentiation*, 71(6), 299-310.

Estrada, B., and Sánchez-Herrero, E. (2001). The Hox gene Abdominal-B antagonizes appendage development in the genital disc of Drosophila. *Development*, 128(3), 331-339.

Ferris GF (1950) External morphology of the adult. In: M Demerec (ed.) Biology of *Drosophila*, pp 368– 419. Hafner, New York.

Fung, S. T. C., and Gowen, J. W. (1957). The developmental effect of a sex-limited gene in *Drosophila melanogaster*. *Journal of Experimental Zoology*, 134(3), 515-532.

Gao, J. Watabe, H. Toda, M. J., Zhang, Y., and T. Aotsuka (2003). "The *Drosophila obscura* Species-group (Diptera, Drosophilidae) from Yunnan Province, Southern China," *Zoological Science*, 20(6), 773-782.

Garrett-Engele, C. M., Siegal, M. L., Manoli, D. S., Williams, B. C., Li, H., and Baker, B. S. (2002). intersex, a gene required for female sexual development in *Drosophila*, is expressed in both sexes and functions together with doublesex to regulate terminal differentiation. *Development*, 129:4661-4675.

Giloh H, Sedat JW (1982) Fluorescence microscopy: reduced photobleaching of rhodamine and fluorescein protein conjugates by n-propyl gallate. *Science*, 217:1252-1255.

Gleichauf, R. (1936) Anatomie und variabilitat des geschlechtapparates von *Drosophila melanogaster* (Meigen). *Zeitschrift für wissenschaftliche Zoologie*, 148, 1–66.

Gorfinkiel, N., Sánchez, L, and I. Guerrero. (1999). "*Drosophila* terminalia as an appendage-like structure." *Mechanisms of development* 86.1-2, 113-123.

Gorfinkiel, N., Sánchez, L., and I. Guerrero. (2003). "Development of the *Drosophila* genital disc requires interactions between its segmental primordia." Development, 130(2):295-305.

Green, J.E., Cavey, M., Médina Caturegli, E., Aigouy, B., Gompel, N., and Prud'homme, B. (2019). Evolution of Ovipositor Length in *Drosophila suzukii* Is Driven by Enhanced Cell Size Expansion and Anisotropic Tissue Reorganization. *Current Biology,* 29, 2075-2082.e6.

Grimaldi, D. A. (1987). Phylogenetics and taxonomy of Zygothrica (Diptera: Drosophilidae). Filogenia y taxonomía de Zygothrica (Diptera: Drosophilidae). *Bulletin of the American Museum of Natural History*, 186, 104-268.

Grimaldi, D. A. (1990). A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bulletin of the American Museum of Natural History*, (197), 1-139.

Hadley, A. (2010) Combine ZP software, new version, [WWW document]. Available from: http://www.hadleyweb.pwp.blueyonder.co.uk/CZP/News.htm

Hardy, D. E. (1965). Diptera: Cyclorrhapha II, Series Schizophora. Section Acalypteratae I. Family Drosophilidae. In: Zimmerman, E. C. (ed.). Insects of Hawaii. The University Press of Hawaii, Honolulu 12, vii + 814 pp.

Heifetz, Y., Lindner, M., Garini, Y., and Wolfner, M. F. (2014). Mating regulates neuromodulator ensembles at nerve termini innervating the *Drosophila* reproductive tract. *Current Biology*, 24(7), 731-737.

Heifetz, Y., Lung, O., Frongillo Jr, E. A., and Wolfner, M. F. (2000). The *Drosophila* seminal fluid protein Acp26Aa stimulates release of oocytes by the ovary. *Current Biology*, 10(2), 99-102.

Heifetz Y, Rivlin PK (2010) Beyond the mouse model: using *Drosophila* as a model for sperm interaction with the female reproductive tract. *Theriogenology*, 73:723-739.

Hildreth, P. E. (1965). Doublesex, a recessive gene that transforms both males and females of *Drosophila* into intersexes. *Genetics*, 51(4), 659.

Hosken, D. J., & Stockley, P. (2004). Sexual selection and genital evolution. *Trends in ecology and evolution*, 19(2), 87-93.

Hu, Y. G., and Toda, M. J. (2001). Polyphyly of Lordiphosa and its relationships in Drosophilinae (Diptera: Drosophilidae). *Systematic Entomology*, 26(1), 15-31.

Jagadeeshan, S., and Singh, R. S. (2006). A time-sequence functional analysis of mating behaviour and genital coupling in *Drosophila*: role of cryptic female choice and male sex-drive in the evolution of male genitalia. *Journal of Evolutionary Biology*, 19(4), 1058-1070.

Joly, D., and M. Schiffer. (2010). Coevolution of male and female reproductive structures in *Drosophila*. *Genetica*, 138(1), 105-118.

Kamimura, Y. and Mitsumoto, H. (2011). Comparative copulation anatomy of the *Drosophila melanogaster* species complex (Diptera: Drosophilidae). *Entomological Science*, 14(4), 399-410.

Kamimura, Y. (2010). Copulation anatomy of *Drosophila melanogaster* (Diptera: Drosophilidae): wound-making organs and their possible roles. *Zoomorphology*, 129(3), 163-174.

Kamimura, Y. (2012). Correlated evolutionary changes in *Drosophila* female genitalia reduce the possible infection risk caused by male copulatory wounding. *Behavioral Ecology and Sociobiology*, 66(8), 1107-1114.

Kamimura, Y. (2016) Significance of constraints in genital coevolution: why does female *Drosophila* appear to cooperate males by accepting harmful traumatic matings? *Evolution,* 70(7): 1674-1683.

Kamimura, Y. and H. Mitsumoto. (2012) Lock-and-key structural isolation between sibling *Drosophila* species. *Entomological Science,* 15: 197-201.

Kapelnikov A, Rivlin PK, Hoy RR, Heifetz Y (2008) Tissue remodeling: a mating-induced differentiation program for the *Drosophila* oviduct. *BMC Developmental Biology*, 8:114.

Kapelnikov A, Zelinger E, Gottlieb Y, Rhrissorrakrai K, Gunsalus KC, and Y. Heifetz (2008). Mating induces an immune response and developmental switch in the *Drosophila* oviduct. *Proceedings of the National Academy of Sciences of the United States of America*, 105:13912-13917.

Keisman, E.L., Baker, B.S. (2001). The *Drosophila* sex determination hierarchy modulates wingless and decapentaplegic signaling to deploy dachshund sex-specifically in the genital imaginal disc. *Development,* 128(9): 1643--1656.

Keisman, E. L., Christiansen, A. E., & Baker, B. S. (2001). The sex determination gene doublesex regulates the A/P organizer to direct sex-specific patterns of growth in the *Drosophila* genital imaginal disc. *Developmental cell,* 1(2), 215-225.

Kikkawa, H. (1938). THE “SUMP” METHOD FOR *DROSOPHILA* MORPHOLOGY*. Journal of Heredity*, 29(10), 395-397.

 doi:10.20944/preprints202201.0223.v2

Knight, G. R. (1990). Chromosome number and morphology of *Drosophila silvestris* Basden — With a descriptive note on the internal genitalia of the adults. *Zeitschrift für indukt. Abstammllngs- und Vorerbungslehre,* 87:430-442.

Kuntner, M., Coddington, J. A., & Schneider, J. M. (2009). Intersexual arms race? Genital coevolution in nephilid spiders (Araneae, Nephilidae). Evolution: *International Journal of Organic Evolution*, 63(6), 1451-1463.

Li, H. and B.S. Baker. (1998). Hermaphrodite and Doublesex Function Both Dependently and Independently to Control Various Aspects of Sexual Differentiation in *Drosophila*. *Development.* 125(14):2641-51.

Li, Y. J., Satta, Y., and Takahata, N. (1999). Paleo-demography of the *Drosophila melanogaster* subgroup: application of the maximum likelihood method. *Genes and genetic systems*, 74(4), 117-127.

Mather, W. B. (1955). The genus *Drosophila* in eastern Queensland I. Taxonomy. *Australian Journal of Zoology*, 3: 545-582.

Mattei, A. L., Riccio, M. L., Avila, F. W., and Wolfner, M. F. (2015). Integrated 3D view of postmating responses by the *Drosophila melanogaster* female reproductive tract, obtained by micro-computed tomography scanning. *Proceedings of the National Academy of Sciences*, 112(27), 8475-8480.

Mayhew, M. L., and Merritt, D. J. (2013). The morphogenesis of spermathecae and spermathecal glands in *Drosophila melanogaster*. *Arthropod structure and development*, 42(5), 385-393.

Miller, A. (1950). The internal anatomy and histology of the imago of *Drosophila melanogaster*. In Biology of *Drosophila*, In: M. Demerec, ed. (New York, Wiley), pp. 420–534.

Méndez, Vivian, and Alex Córdoba-Aguilar. (2004). Sexual selection and animal genitalia. *Trends in ecology and evolution*, 19.5, pp. 224-225.

Muto, L., Kamimura, Y., Tanaka, K. M., and Takahashi, A. (2018). An innovative ovipositor for niche exploitation impacts genital coevolution between sexes in a fruit-damaging *Drosophila*. *Proceedings of the Royal Society B: Biological Sciences*, 285(1887), 20181635.

Nonidez, J.F. (1920). The Internal Phenomena of Reproduction in *Drosophila*. Biological Bulletin, Oct. 1920, Vol. 39, No. 4, pp. 207-230 Published by: The University of Chicago Press in association with the Marine Biological Laboratory Stable URL: https://www.jstor.org/stable/1536488

Nöthiger, R., Dübendorfer, A., & Epper, F. (1977). Gynandromorphs reveal two separate primordia for male and female genitalia in *Drosophila melanogaster*. *Wilhelm Roux's archives of developmental biology*, 181(4), 367-373.

O'Grady, P. M., Lapoint, R. T., Bonacum, J., Lasola, J., Owen, E., Wu, Y., & DeSalle, R. (2011). Phylogenetic and ecological relationships of the Hawaiian *Drosophila* inferred by mitochondrial DNA analysis. *Molecular Phylogenetics and Evolution*, 58(2), 244-256.

Okada, T. (1956). Systematic study of Drosophilidae and allied families of Japan. Tokyo: Gihodo Co.

Okada, T. (1963). Cladogenetic differentiation of Drosophilidae in relation to material compensation. *Mushi*, 37: 79-100.

Omoloye, A. A., Oladapo, O. G., Ibitoye, O., & Alabi, O. Y. (2016). Effects of field attack by Ceratitis capitata Wiedemann (Diptera: Tephritidae) on the morphology and nutritional quality fresh fruit of Citrus sinensis L. *African Journal of Agricultural Research,* 11(11), 967-973.

Pascini TV, Martins GF. (2017). The insect spermatheca: an overview. *Zoology*, 121:56–71.

Patterson, J. T. and Stone, W. S. (1952). Evolution in the genus *Drosophila*. 610 pp. New York.

Pitnick, S., Marrow, T., and Spicer, G. S. (1999). Evolution of multiple kinds of female sperm-storage organs in *Drosophila*. *Evolution*, 53(6), 1804-1822.

Polidori, C., and Wurdack, M. (2019). Mg-enriched ovipositors as a possible adaptation to hard-skinned fruit oviposition in *Drosophila suzukii* and *D. subpulchrella*. *Arthropod-Plant Interactions,* 13, 551–560. https://doi-org.proxy.lib.umich.edu/10.1007/s11829-018-9641-x

Rice G, David JR, Kamimura Y, Masly JP, Mcgregor AP, Nagy O, Noselli S, Nunes MDS, O'Grady P, Sánchez-Herrero E, Siegal ML, Toda MJ, Rebeiz M, Courtier-Orgogozo V, Yassin A. A standardized nomenclature and atlas of the male terminalia of *Drosophila melanogaster*. *Fly* (Austin). (2019) Mar-Dec;13(1-4):51-64. doi: 10.1080/19336934.2019.1653733. Epub 2019 Aug 19. PMID: 31401934; PMCID: PMC6988887.

Robertson HM (1988) Mating asymmetries and phylogeny in the *Drosophila melanogaster* species complex. *Pacific Science,* 42, 72–80.

Salles H. (1947) Sobre a Genitalia dos Drosofilidios (Diptera): I. *Drosophila melanogaster* E. *D. simulans*. *Summa Brasiliensis Biologiae,* Vol 1, 15:1–73.

Sánchez, L., Casares, F., Gorfinkiel, N., & Guerrero, I. (1997). The genital disc of *Drosophila melanogaster*. *Development genes and evolution*, 207(4), 229-241.

Sánchez, L., & Guerrero, I. (2001). The development of the *Drosophila* genital disc. *Bioessays*, 23(8), 698-707.

Schnakenberg, S. L., Matias, W. R., and Siegal, M. L. (2011). Sperm-storage defects and live birth in *Drosophila* females lacking spermathecal secretory cells. *PLoS biology*, 9(11), e1001192.

Schüpbach, T., Wieschaus, E., & Nöthiger, R. (1978). The embryonic organization of the genital disc studied in genetic mosaics of *Drosophila melanogaster*. *Wilhelm Roux's archives of developmental biology*, 185(3), 249-270.

Seraj, A. A. (2000). "Comparison of Plant Species as Host for Cabbage Leaf Miner in Khuzestan Province." *Journal of Agricultural Science and Technology,* 2.2, 127-135.

Siegal, M. L., & Baker, B. S. (2005). Functional conservation and divergence of intersex, a gene required for female differentiation in *Drosophila melanogaster*. *Development genes and evolution*, 215(1), 1-12.

Simmons, L. W. (2014). Sexual selection and genital evolution. *Austral Entomology*, 53(1), 1-17.

Sloan, N. S., & Simmons, L. W. (2019). The evolution of female genitalia. *Journal of evolutionary biology*, 32(9), 882-899.

Snodgrass, R. E. (1903). The terminal abdominal segments of female Tipulidae. *Journal of the New York Entomological Society,* 11: 177-183.

Snodgrass, R. E. (1935). The abdominal mechanisms of a grasshopper. Smithsonian Miscellaneous Collections.

Snodgrass, R. E. (1952). A textbook of arthropod anatomy. Ithaca, N. Y.: Comstock Pub.; Cornell University Press, pp. 363

Spieth, H. T. (1975). The behavior and biology of the Hawaiian *Drosophila anomalipes* species group. *Annals of the Entomological Society of America*, 68(3), 506-510.

Sturtevant, A. H. (1921). The North American species of *Drosophila* (No. 301). Carnegie institution of Washington.

Sturtevant, A.H. (1942). The classification of the genus *Drosophila*, with descriptions of nine new species. University of Texas Publishing, 4213:5-51.

 doi:10.20944/preprints202201.0223.v2

Sturtevant, A. H. (1939). On the subdivision of the genus *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America,* 25: 137-141.

Throckmorton, L.H., (1962). The problem of phylogeny in the genus *Drosophila*. University of Texas Publishing 6205, 207–343.

Tsacas, L., and David, J. (1975). Les Drosophilidae (Diptera) de la Réunion et de l'Ile Maurice. II. Trois nouvelles espèces des genres *Drosophila* et *Zaprionus*. *Publications de la Société Linnéenne de Lyon*, 44(10), 373-380.

Van Emden, F. and Hennig, W. (1970). Diptera. pp. 130–140 in Tuxen, S. L. (Ed.). Taxonomist's glossary of genitalia in insects. —2nd edition, 395 pp. Copenhagen, Munksgaard.

Vaz, S. C., Vilela, C. R., Krsticevic, F. J. and Carvalho, A. B. (2014). Developmental sites of Neotropical Drosophilidae (Diptera): V. Inflorescences of Calathea cylindrica and Calathea monophylla (Zingiberales: Marantaceae). *Annals of the Entomological Society of America,* 107:607-620.

Vilela, C. R., and Bächli, G. (1990). Taxonomic studies on Neotropical species of seven genera of Drosophilidae (Diptera). *Mitteilungen der schweizerischen entomologischen Gesellschaft*, 63

Vilela, C. R., and Prieto, D. (2018). A new Costa Rican species of *Drosophila* visiting inflorescences of the hemi-epiphytic climber Monstera lentii (Araceae). *Revista Brasileira de Entomologia*, 62, 225-231.

Wheeler, M. R. 1954. V. Taxonomic studies on American Drosophilidae. The University of Texas Publishing, 5422: 47-64,

Yassin, A. (2008). Molecular and morphometrical revision of the Zaprionus tuberculatus species subgroup (Diptera: Drosophilidae), with descriptions of two cryptic species. *Annals of the Entomological Society of America,* 101: 978-988.

Yassin, A. (2016). Unresolved questions in genitalia coevolution: bridging taxonomy, speciation, and developmental genetics. *Organisms Diversity and Evolution*, 16(4), 681-688.

Yassin, A., and Orgogozo, V. (2013). Coevolution between male and female genitalia in the *Drosophila melanogaster* species subgroup. *PloS one*, 8(2), e57158.

Zhang, W. X., and Toda, M. J. (1992). A new species-subgroup of the *Drosophila immigrans* species-group (Diptera, Drosophilidae), with description of two new species from China and revision of taxonomic terminology. *Japanese Journal of Entomology*, 60(4), 839-850.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

Figures

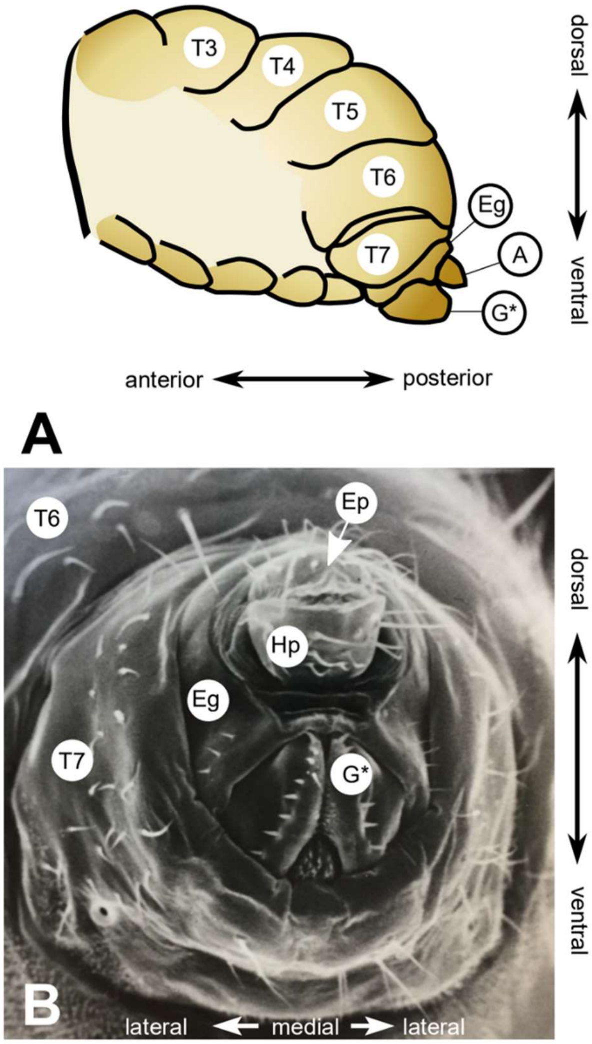

Figure 1. The terminalia of female *D. melanogaster.* (a) Model diagram of posterior female abdomen of *D. melanogaster,* lateral view. (b) Scanning electron micrograph of *D. melanogaster* female terminalia, posterior view, kindly provided by Dr. John M. Belote, Syracuse University. **T3-T7** = female abdominal tergites 3-7. **G*** = female genitalia, **A** = female analia, **Eg** = Epigynium (T8), **Hp** = hypoproct, **Ep** = Epiproct. The hypoproct and the epiproct together form the female analia. *Note that the female genitalia includes the epigynium, which is indicated separately in this figure.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

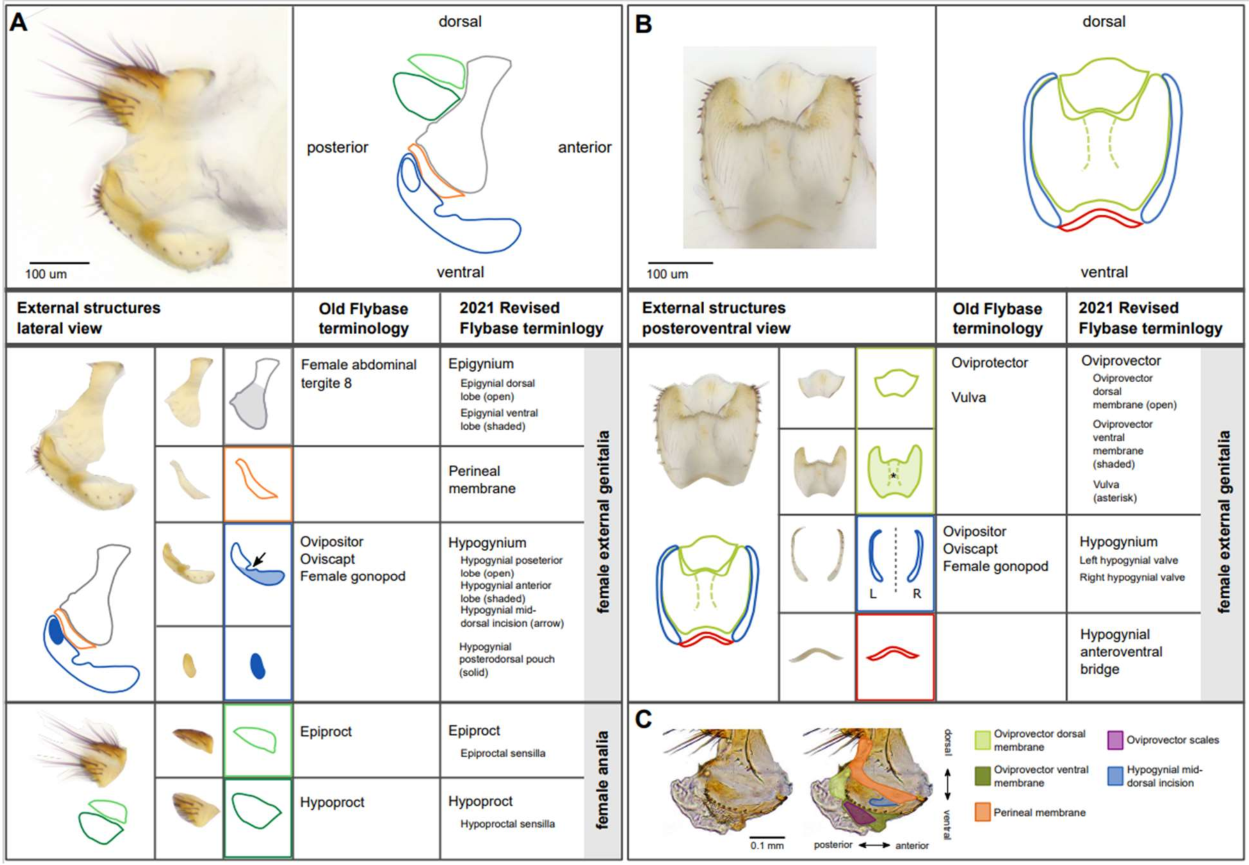

Figure 2. Visual atlas of the external female terminalia. Light microscopy images showing the whole external terminalia in lateral view (**panel a**) and the genitalia in posteroventral view (**panel b**). Individual structures are highlighted below each image, with line drawings to aid identification. Previous FlyBase terms are listed in the left column and 2021 revised terms are given in the right column. **Panel c** is a detail of a lateral view with internal structures extruded (as during egg laying), to highlight interior membranous structures.

 doi:10.20944/preprints202201.0223.v2

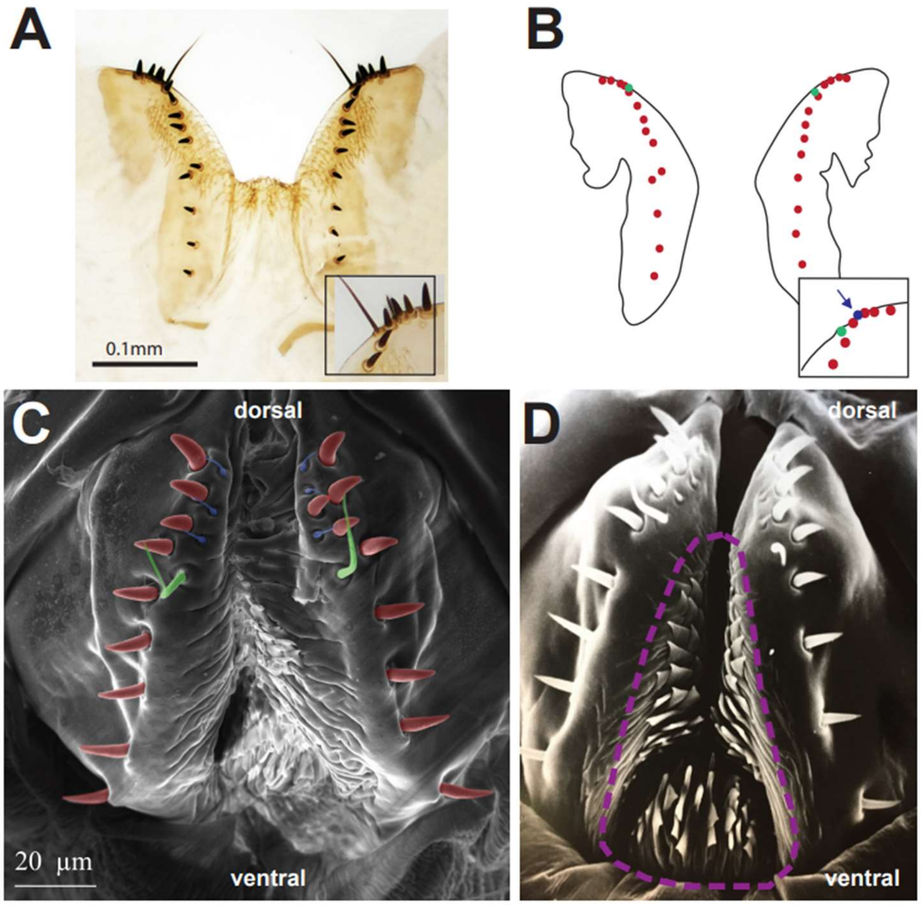

Figure 3. Hypogynial sensilla. (a) Light microscopy image of hypogynial lobes. Inset is a closeup of the posterior tip of one lobe. **(b)** Line tracing of **(a)**, showing locations of bristle types. Hypogynial short sensilla are barely visible from this angle, but one is shown in the inset (arrow). **(c)** Scanning electron micrograph of female genitalia, posterior view. Color-coding of sensilla types is as follows: Red, Hypogynial tooth; Green, Hypogynial long sensillum; Blue, hypogynial short sensillum. **(d)**. Scanning electron micrograph of female genitalia, posterior view. The region covered with oviprovector scales is indicated with a dashed purple line.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

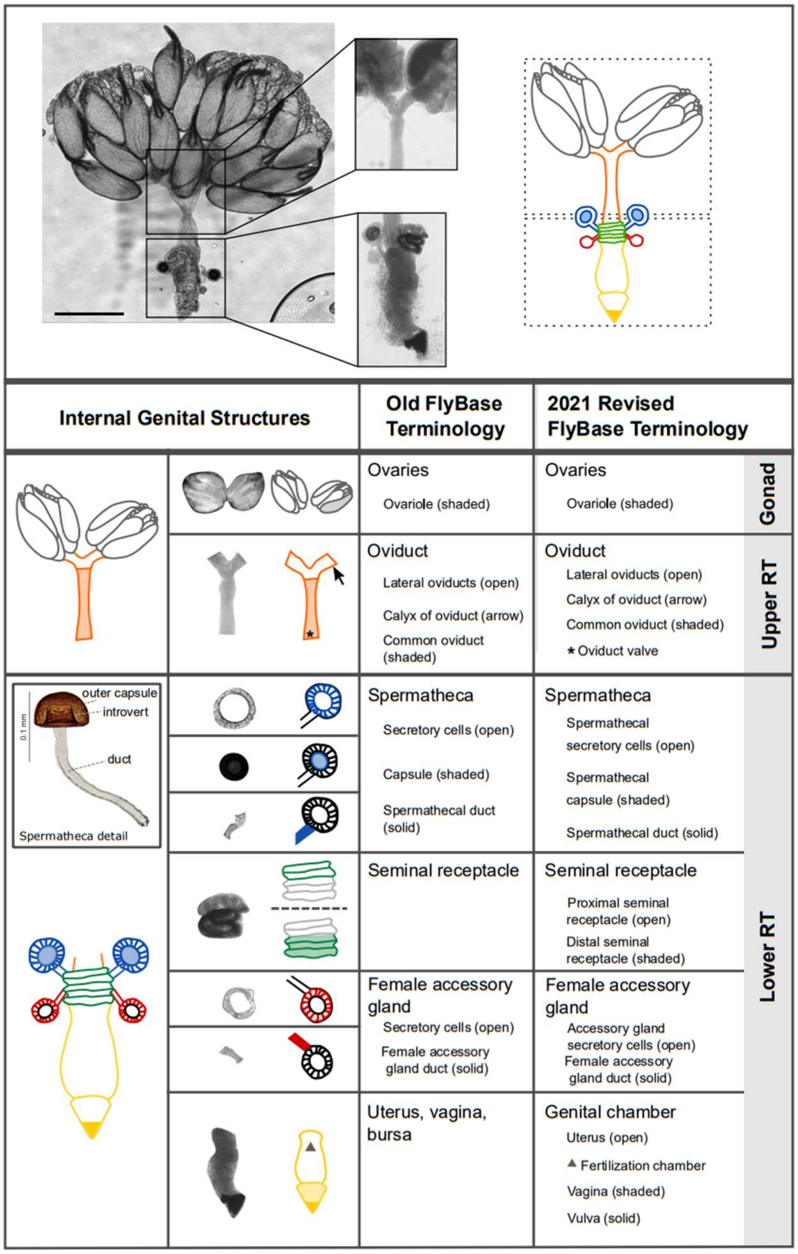

Figure 4. Visual atlas of internal female genitalia and reproductive structures. Confocal bright-field images and schematic of *Drosophila melanogaster* female (Canton S strain) reproductive system. Scale bar is 500µm. The upper box shows the upper reproductive tract (upper RT) and the ovaries, the lower box is the lower reproductive tract (Lower RT). The lower panel displays individual structures with line drawings to aid identification. The internal structures and substructures include the gonad (ovaries), the upper RT (oviduct) and the lower RT (seminal receptacle, spermatheca, female accessory glands, genital chamber). Inset is a detail of the spermatheca to highlight substructures. Previous FlyBase terms are on the left and 2021 revised terms are on the right.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

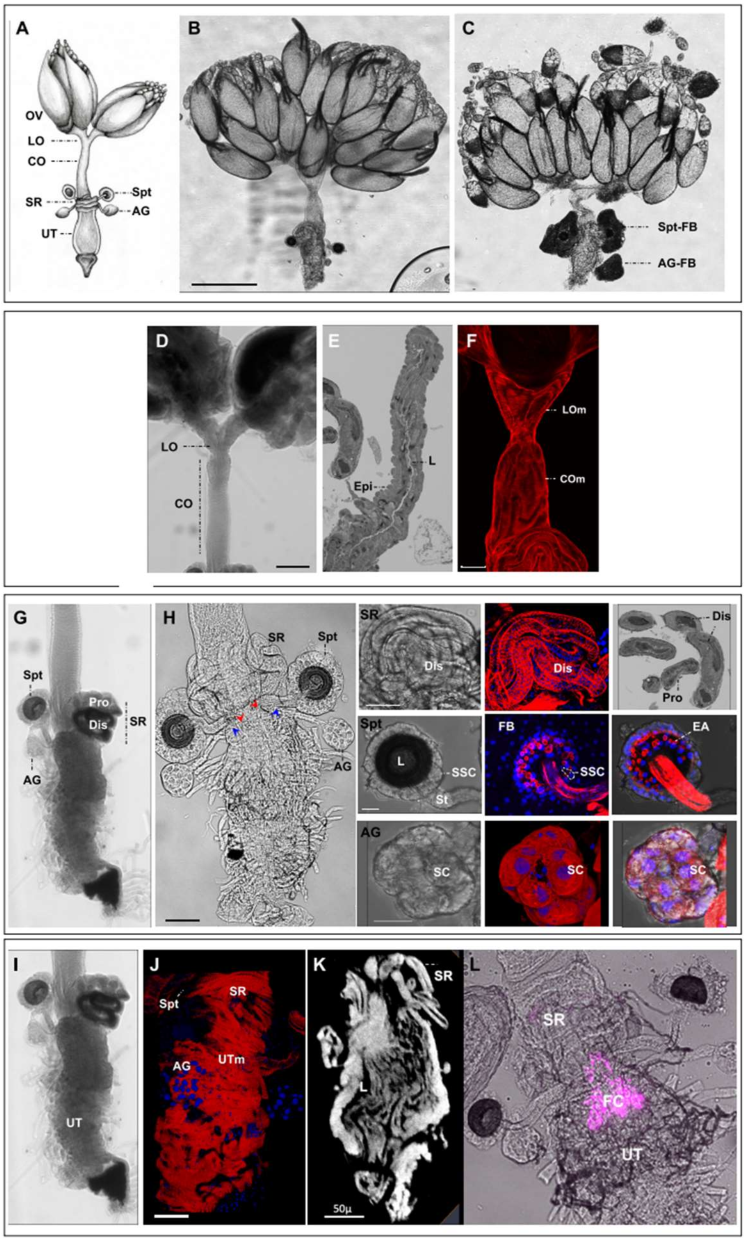

Figure 5. Internal genital structures of the female reproductive tract. [A] The *Drosophila* female reproductive tract consists of a pair of ovaries (OV) connected to a median common oviduct (CO) by two lateral oviducts (LO), and a uterus (UT) that leads to the vagina, which opens to the exterior through the vulva. The reproductive tract also includes specialized organs: a pair of spermathecae (Spt), seminal receptacle (SR), and a pair of female accessory glands (AG); drawing by Zohar Nir-Amitin. **[B, C]** The whole system with fat body **[C]** or without the fat body **[B]** that covers the spermatheca (Spt-FB) and the female accessory glands (AG-FB) (scale bar is 500µm). **[D-F]** Upper RT that includes the lateral and common oviducts (scale bar is 100µm), **[D].** Toluidine blue stained 1µm thick section of the oviduct that highlight the lumenal space (L) and the epithelia cells (Epi) **[E].** Upper RT stained with Alexa Fluor 594-phalloidin (red) showing the muscle fibers in different regions

 doi:10.20944/preprints202201.0223.v2

of oviduct (scale bar is 50µm), **[F]**. **[G, H]** Lower reproductive tract, including the spermatheca (Spt), seminal receptacle (SR), and female accessory glands (AG). note the red and blue arrowheads that mark the connection of the Spt and AG stalks to the uterus (scale bar is 50µm). The panel also presents bright-field, phalloidin and DAPI images of the: SR showing the proximal (Pro) and distal (Dis) regions and the surrounding layer of visceral muscle (scale bar is 50µm); Spt showing the spermathecal secretory cells (SSC), the lumen where sperm is stored (L), the stalks (St) (scale bar is 20µm), and the fat body (FB, stained with DAPI) that surrounds the Spt and female accessory glands (AG) showing the secretory cells (scale bar is 20µm). **[I-L]** Zoom-in image of the uterus: **[J]** layers of circular muscle fibers (UTm) (scale bar is 50µm), **[K]** micro-CT of the uterus highlighting the structure of the uterine lumen (L) (scale bar is 50µm), **[L]** DsRed expression (magenta) showing the location of the fertilization chamber (FC), a structure to which the stalks of the SR, Spt and AG enter.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

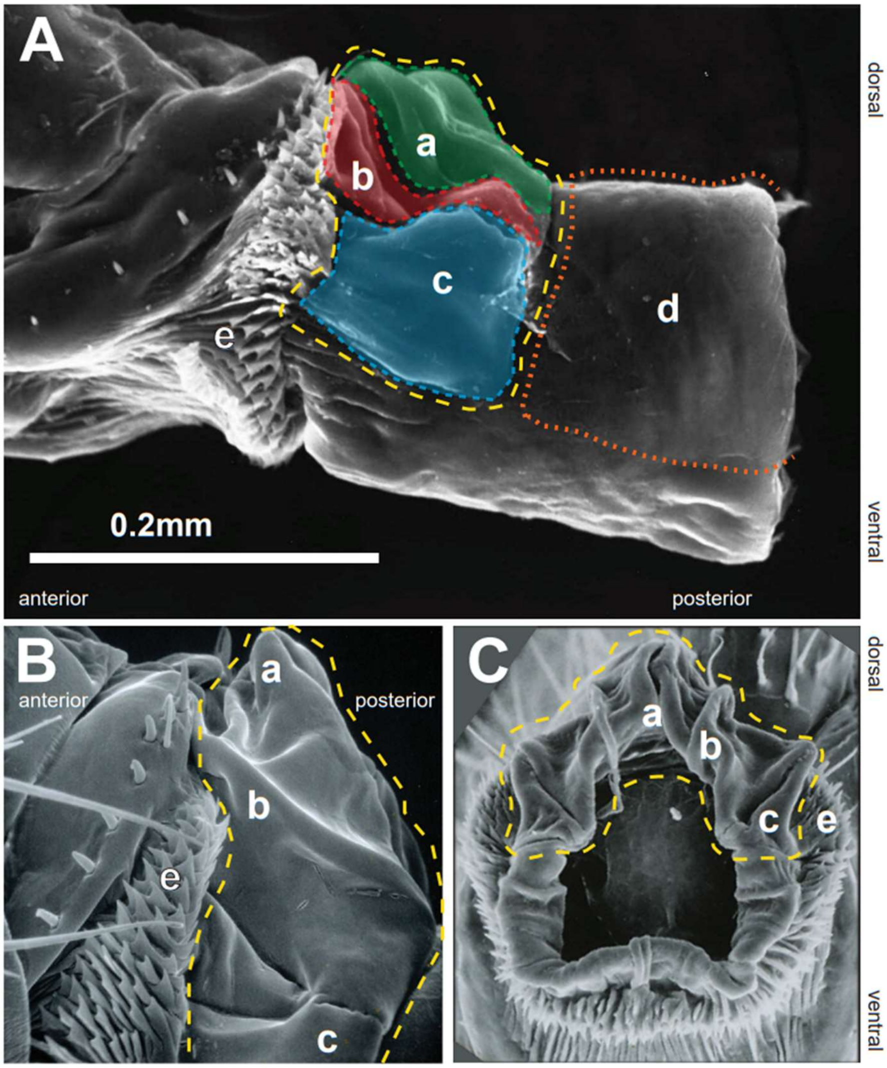

Figure 6. Scanning electron micrographs of the furca and furcal folds. **A.** Lateral view with internal structures extruded. **B.** lateral view, unextended. **C.** posterior view. In each image, the vaginal furca is indicated by the yellow dashed line. **a.** vaginal furcal dorsal fold, **b.** vaginal furcal dorsolateral fold, **c.** vaginal furcal lateral fold, **d.** uterine furca. Not shown in the figure is the portion of the uterine furca that extends internally until the entry point of the spermathecal and accessory gland ducts into the genital chamber. **e.** oviprovector scales.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

Tables

Table 1. Definition of the terms in the standardized nomenclature.
Parts
Female terminalia Flybase ID: FBbt:00004830. Definition: The entire set of internal and external structures in the distal half of the female abdomen that are derived from segments 8-10. Makes up the *female genitalia* and *female analia*. It develops from the female genital disc.
Female genitalia Flybase ID: FBbt:00004827. Definition: Set of internal and external structures originating from segments 8-9, that makes up the genital apparatus. It develops from the female genital-primordium part of the genital disc.
Female analia Flybase ID: FBbt:00004824. Definition: Set of external structures originating from segment 10, that makes up the anal apparatus. It develops from the female genital disc. Synonyms: female proctiger (Ferris, 1950; Jagadeeshan and Singh, 2006).
Sclerites
Epigynium FlyBase synonyms: female abdominal tergite 8 (FBbt:00110704). Definition: Horseshoe-shaped tergite which, dorsally, surrounds the female analia. It is chitinized, and each side (left and right) is divided into the epigynial dorsal lobe and the epigynial ventral lobe. Synonyms: female abdominal tergite 8 (Ferris, 1950; Epper, 1983; Epper and Sánchez, 1983; Grimaldi, 1990; Vilela and Bächli, 1990; Casares et al., 1997; Sánchez et al., 1997), female abdominal tergite 9 (Robertson, 1988; Jagadeeshan and Singh, 2006).
Epigynial dorsal lobe FlyBase synonyms: New term. Definition: Dorsal portion of the epigynium above the epigynial ventral lobe. The two dorsal lobes (left and right) are fused dorsally into a single sclerite. It does not normally harbor sensilla (bristles). Synonyms: dorsal part of the female abdominal tergite 8 (Epper and Sánchez, 1983).
Epigynial ventral lobe FlyBase synonyms: New term. Definition: Ventral portion of the epigynium below the epigynial dorsal lobe. There are two of these, one on each side. Each lobe (left and right) normally harbors four or five small, unpigmented sensilla (bristles). Synonyms: ventral part of the female abdominal tergite 8 (Epper and Sánchez, 1983).
Epiproct FlyBase ID: FBbt:00004833. Definition: The plate dorsally surrounding the anus in females. It has an average of 18 sensilla of which two are large. It arises from segment 10 primordium in the female genital disc (Grimaldi, 1990; Vilela and Bächli, 1990; Zhang and Toda, 1992; Hu and Toda, 2001; Bächli et al., 2004; Kamimura and Mitsumuto, 2011). Synonyms: abdominal tergite 9 (Ferris, 1950), abdominal tergite 10 (Cumming and Wood, 2017), dorsal anal plate (Sturtevant, 1921; Epper, 1983; Chen and Baker, 1997; Gorfinkiel, Sánchez, and Guerrero, 1999; Casares et al., 1997; Sánchez et al., 1997), upper anal plate (Salles, 1947), supraanal plate (Miller, 1950).
Female accessory gland FlyBase ID: FBbt:00004914. Definition: Small, bilaterally paired gland that lies caudal to the spermathecae and is connected to the uterus by a duct. The gland wall consists of a single layer of secretory cells, each with a large vacuole and a minute acidophilic granule towards the gland lumen. It arises from segment 9 primordium in the female genital disc.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

Synonyms: appendicular gland (Cumming and Wood, 2017), colleterial gland (Cumming and Wood, 2017), parovarium (Okada, 1956; Fung and Gowen, 1957; Bock and Wheeler, 1972; Epper, 1983; Chen and Baker, 1997; Keisman and Baker, 2001; Cumming and Wood, 2017)

Female accessory gland duct

FlyBase ID: FBbt:00004915.

Definition: A duct connecting the female accessory gland to the uterus, opening just caudal to the spermathecal ducts. It consists of a tube of thin epithelium lined with a thin chitinous intima, irregularly ringed with sharp ridges that project into the lumen.

Female accessory gland fat body

FlyBase synonyms: New term.

Definition: Adipose tissue surrounding the female accessory gland. This tissue may be attached to the fat body surrounding the spermatheca. The female accessory gland fat body is in close contact with the rectum (Bodenstein, 1950).

Furca

FlyBase synonyms: New term.

Definition: The dorsal wall of the genital chamber that developmentally arises from segment 9 primordium in the female genital disc. It extends from the female accessory gland ducts anteriorly to the vulva posteriorly (**Figure 6**). It is divided into a uterine furca, in which the female accessory gland duct open and which has an inner posterior thickness called papillate elevation, and a vaginal furca which extrudes from the vulva during oviposition.

Synonyms: female sternite 9 (Cumming and Wood, 2017), genital fork (Cumming and Wood, 2017), vaginal apodeme (Cumming and Wood, 2017).

Genital chamber

FlyBase synonyms: vagina (FBbt:00004925), uterus (FBbt:00004924).

Definition: An elongate muscular pouch, the anterior part of which is the uterus, where eggs are fertilized, and the posterior part of which is the vagina, where insemination takes place during copulation. It opens posteriorly through the vulva.

Synonyms: uterus (Hildreth, 1965; Chen and Baker, 1997; Keisman and Baker, 2001).

Hypogynium

FlyBase synonyms: female gonopod (FBbt:00004832).

Definition: Female abdominal sternite 8 modified for oviposition. It consists of paired chitinous valves (left and right) that are anteriorly connected through the hypogynial anteroventral bridge and posteriorly surrounds the vulva. The ventral margin of each valve is strongly sclerotized and contiguous with the hypogynial anteroventral bridge. Each valve carries 11-16 marginal and apical teeth on its outer wall and four trichoid apical sensilla on its inner wall, the ventral most of which is the hypogynial long sensillum. The dorsal margin of each valve harbors a mid-dorsal incision. An imaginary line connecting the hypogynial long sensillum to the hypogynial mid-dorsal incision delimits the borders between the posterior and anterior lobes of each valve. The posterior lobe of each valve carries a posterodorsal pouch. The anterior lobes of the hypogynial valves are internally connected by the oviprovector. (Snodgrass, 1903; van Emden and Hennig, 1970)

Synonyms: egg-guide (Okada, 1956; Bock and Wheeler, 1972), female gonopod (Ferris, 1950), female abdominal sternite 8 (Cumming and Wood, 2017), ovipositor (Sturtevant, 1921; Salles, 1947; Tsacas and David, 1975; Vilela and Bächli, 1990), oviscape (Grimaldi, 1987; Jagadeeshan and Singh, 2006; Kamimura, 2010; Kamimura and Mitsumoto, 2011), oviscapt (Grimaldi, 1990; Zhang and Toda, 1992; Hu and Toda, 2001; Bächli et al., 2004; Kamimura, 2010; Kamimura and Mitsumoto, 2011; Yassin and Orgogozo, 2013; Vilela and Prieto, 2018; Al Sayad and Yassin, 2019), vaginal plates (Kikkawa, 1938; Hildreth, 1965; Epper, 1983; Casares et al., 1997; Chen and Baker, 1997; Gorfinkiel, Sánchez, and Guerrero, 1999; Keisman and Baker, 2001).

Hypogynial anteroventral bridge

FlyBase synonyms: New term.

 doi:10.20944/preprints202201.0223.v2

Definition: A transverse, strongly sclerotized rod connecting the anterior tips of the hypogynial valves beneath the oviprovector and the vagina.

Synonyms: basal isthmus (Okada, 1956; Bock and Wheeler, 1972), heavily sclerotized bar (Ferris, 1950).

Hypogynial posterior lobe

FlyBase synonyms: New term.

Definition: The posterior portion of each hypogynial valve, posterior to an imaginary line connecting the hypogynial long sensillum and the hypogynial mid-dorsal incision. It is double-walled and carries on the outer wall a series of sensilla that are larger and less interspaced than those carried by the anterior lobe. On the inner wall, there are three terminal, minute sensilla trichoidea and one subterminal, long sensillum. The outer wall is sclerotized, lobate, and harbors the posterodorsal pouch.

Synonyms: upper margin of the egg-guide lobe (Okada, 1956), mesal surface of the oviscapt (Hu and Toda, 2001), distal part of the oviscapt valve (Bächli et al., 2004), dorsal vaginal plate (Epper and Sánchez, 1983; Gorfinkiel, Sánchez, and Guerrero, 1999, 2003; Sánchez et al., 1997).

Hypogynial mid-dorsal incision

FlyBase synonyms: New term.

Definition: A mid-dorsal incision on the dorsal margin of each hypogynial valve.

Synonyms: submedian incision of the egg-guide lobe (Okada, 1956).

Hypogynial posterodorsal pouch

FlyBase synonyms: New term.

Definition: A posterodorsal depression on the outer wall of the hypogynial posterior lobe of each hypogynial valve.

Synonyms: dorsodistal depression (Bächli et al., 2004), oviscapt pouch (Yassin and Orgogozo, 2013).

Hypogynial anterior lobe

FlyBase synonyms: New term.

Definition: The anterior portion of each hypogynial valve, anterior to an imaginary line connecting the hypogynial long sensillum to the hypogynial mid-dorsal incision. It is double walled, slightly rounded and carries a series of teeth that are smaller and more interspaced than those carried by the hypogynial posterior lobe.

Synonyms: lower margin of the egg-guide lobe (Okada, 1956), ventral vaginal plate (Epper and Sánchez, 1983; Gorfinkiel, Sánchez, and Guerrero, 1999, 2003; Sánchez et al., 1997).

Hypoproct

FlyBase synonyms: Hypoproct (FBbt:00004834)

Definition: The plate ventrally surrounding the anus in females (Grimaldi, 1990; Vilela and Bächli, 1990; Zhang and Toda, 1992; Hu and Toda, 2001; Bächli et al., 2004; Kamimura and Mitsumuto, 2011). It has an average of 19 sensilla of which four are large. It arises from segment 10 primordium in the female genital disc.

Synonyms: abdominal sternite 9 (Ferris, 1950), subanal plate (Miller, 1950), ventral anal plate (Sturtevant, 1921; Epper, 1983; Casares et al., 1997; Chen and Baker, 1997; Gorfinkiel et al., 1997; Sánchez et al., 1997), lower anal plate (Salles, 1947).

Oviduct

FlyBase synonyms: oviduct (FBbt:00004911)

Definition: Duct of the female reproductive tract that connects the ovaries to the uterus (Hildreth, 1965; Epper, 1983; Chen and Baker, 1997). Oviducts are divided into two lateral oviducts (each connected to an ovary) and one common oviduct, to which the lateral oviducts connect, and which itself connects to the uterus.

Oviduct, calyx of

FlyBase synonyms: calyx of oviduct (FBbt:00004918)

Definition: The anterior-most, cup-shaped region of the lateral oviduct (Bloch Qazi, Heifetz, and Wolfner, 2003; Kapelnikov et al., 2008a). Formed by the joining together of the individual pedicels (small tubes coming from the base of each ovariole).

Oviduct, common

FlyBase synonyms: common oviduct (FBbt:00004913)

Definition: Epithelial tube that connects the lateral oviducts to the uterus (Bryant, 1978; Heifetz et al., 2000; Adams and Wolfner, 2007; Kapelnikov et al., 2008a; Kapelnikov et al., 2008b; Heifetz et al., 2014; Avila et al., 2016). It is lined with a chitinous intima and surrounded by circular muscles.

Oviduct dorsal ridge

FlyBase synonyms: New term.

Definition: A ridge in the oviduct dorsal wall that is a part of the oviduct valve (See Figures 1A, 1B, and Figure 2, Stage 7, in Adams and Wolfner 2007, marked by an asterisk).

Oviducts, lateral

FlyBase synonyms: lateral oviduct (FBbt:00004912)

Definition: Epithelial tubes that connect the ovary to the common oviduct. They are lined with a chitinous intima and surrounded by muscle. There are two lateral oviducts (one per ovary) in *D. melanogaster*. They usually have a loop near the base of the ovary in unmated females; the loop relaxes after mating to allow egg transit. (Bryant, 1978; Kapelnikov et al., 2008a).

Oviduct valve

FlyBase synonyms: New term.

Definition: The opening of the common oviduct into the uterine posterodorsal pouch. It consists of the oviduct valve flap and the oviduct dorsal ridge (Adams and Wolfner, 2007).

Oviduct valve flap

FlyBase synonyms: New term.

Definition: A chitinous flap that presses against the oviduct dorsal ridge, potentially blocking passage of substances between the uterus and the oviduct (See Figures 1A, 1B, and Figure 2, Stage 6 and Stage 7, in Adams and Wolfner 2007).

Oviprovector

FlyBase synonyms: oviprotector [sic] (FBbt:00004831), vulva (FBbt:00004926).

Definition: Eversible membrane between the hypogynial valves that surrounds the vagina and the vulva (Grimaldi, 1987, 1990; Bächli et al., 2004).

Synonyms: dented membrane (Tsacas, 1975), vagina (Gleichauf, 1936), vulva (Tsacas, 1975; Bryant, 1978; Epper, 1983; Casares et al., 1997; Chen and Baker, 1997; Gorfinkiel, Sánchez, and Guerrero, 1999).

Oviprovector dorsal membrane

FlyBase synonyms: New term.

Definition: Dorsal membrane of the oviprovector connecting the hypogynial valves dorsally and surrounding the vulva dorsally. It bears no scales.

Synonyms: dorsal vulva (Epper, 1983; Chen and Baker, 1997).

Oviprovector ventral membrane

FlyBase synonyms: New term.

Definition: Ventral membrane of the oviprovector connecting the hypogynial valves ventrally and the vulva laterally and ventrally. It bears oviprovector scales in serrated rows.

Synonyms: ventral vulva (Epper, 1983; Chen and Baker, 1997).

Perineal membrane (perineum)

FlyBase synonyms: New term.

Definition: Intersegmental membrane connecting the female genitalia with the female analia. It extends from the posterior margin of tergite 7 to the ventral margin of the hypoproct. It is the place of type B copulatory wounds caused by the male epandrial posterior lobes during copulation.

Synonyms: female abdominal tergites 8/9 intersegmental membrane (Robertson, 1988; Jagadeeshan and Singh, 2006), female abdominal tergites 7/8 intersegmental membrane (Kamimura and Mitsumuto, 2011), perineal plate (Bächli et al., 2004).

Seminal receptacle

FlyBase synonyms: seminal receptacle (FBbt:00004922)

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

Definition: A compactly coiled epithelial tube connected to the anterior end of the uterus. The tube is long (1.7-2.7 mm) and slender, consisting of a proximal duct around 22 micrometers wide with a narrow lumen (2.5 - 4.5 micrometers) and a wider distal half (around 28 micrometers) with a larger lumen (12-19 micrometers). It is lined with a thin chitinous intima and surrounded by a nucleated sheath. The coil is surrounded by a sparsely nucleated peritoneal envelope. After copulation, the lumen of this tube is filled with spermatozoa. Sperm are stored in this structure after mating (Heifetz and Rivlin, 2010).

Synonyms: tubular receptacle (Anderson, 1945), ventral receptacle (Sturtevant, 1939; Sturtevant, 1942; Dobzhansky and Pavan, 1943; Patterson and Stone, 1952; Wheeler, 1954; Mather, 1955; Okada, 1956; Throckmorton, 1962; Okada, 1963; Hardy, 1965; Bock and Wheeler, 1972; Spieth, 1975; Grimaldi, 1990; Knight, 1990; Zhang and Toda, 1992; Bachli et al., 2004; Yassin, 2008; Vaz et al., 2014).

Spermatheca

FlyBase synonyms: spermathecum [sic] (FBbt:00004921)

Definition: A mushroom-shaped organ consisting of a capsule (end apparatus) connected to the uterus by a slender duct. Sperm is stored in this organ after mating (Sturtevant, 1921; Salles, 1947; Okada, 1956; Fung and Gowen, 1957; Throckmorton, 1962; Hildreth, 1965; Bock and Wheeler, 1972; Epper, 1983; Chen and Baker, 1997; Keisman and Baker, 2001; Heifetz and Rivilin, 2010). The capsule is an inverted, double-walled bowl, i.e., outer capsule and basal introvert consisting of schlerotized intima (Pitnick et al., 1999; Mayhew and Merritt, 2013). The intima is secreted by a layer of cuboidal epithelium, called the spermathecal secretory cells, which cover the outer wall (Miller, 1950). After copulation, the lumen of the capsule is filled with spermatozoa. *D. melanogaster* typically has two spermathecae, but there is variation in spermatheca number within Drosophilidae (Pascini and Martins, 2017).

Spermathecal duct

FlyBase synonyms: spermathecal duct (FBbt:00004923)

Definition: Duct connecting the capsule of the spermatheca to the uterus. It opens into the uterine posterodorsal pouch, just posterior to the opening of the oviduct and close to the openings of the female accessory gland ducts.

Spermathecal fat body

FlyBase synonyms: New term.

Definition: A small and delicate mass of fat body that surrounds each of the spermatheca and is in close contact with the rectum (Bodenstein, 1950).

Spermathecal secretory cells

FlyBase synonyms: New term.

Definition: A layer of cuboidal epithelium that surrounding the spermathecal capsule and secretes the sclerotized intima of the capsule (Miller, 1950; Schnakenberg, Matias, and Siegal, 2011).

Synonyms: gland cells (Allen and Spradling, 2008).

Uterus

FlyBase synonyms: Revised term (see genital chamber)

Definition: Anterior part of the genital chamber. It is an ectodermal invagination that is the site of egg fertilization. It is connected to the common oviduct anterodorsally and the vagina posteriorly. It is surrounded by muscles (Epper, 1983; Adams and Wolfner, 2007).

Synonyms: Bursa (Cumming and Wood, 2017)

Uterine anterior projection

FlyBase synonyms: New term.

Definition: Inner elevation of the anterior wall of the uterus separating the uterine anterodorsal pouch and the uterine anteroventral pouch.

Synonyms: anterior uterus projection (See Figure 1B in Adams and Wolfner 2007).

Uterine anterodorsal pouch

FlyBase synonyms: New term.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

Definition: Anterodorsal invagination of the uterus holding the openings of the common oviduct, the spermathecal ducts and the female accessory gland ducts. It is separated from the uterine dome by the uterine anterior projection.

Synonyms: pre-oviduct space (See Figure 1B, and Figure 2, Stage 7 and Stage 10, in Adams and Wolfner 2007).

Uterine anteroventral pouch

FlyBase synonyms: New term.

Definition: Anteroventral invagination of the uterus holding the opening of the seminal receptacle. It is separated from the uterine anterodorsal pouch by the uterine anterior projection.

Synonyms: vaginal pouch (Patterson and Stone, 1952), uterine dome (See Figure 1B and Figure 2, Stage 7, in Adams and Wolfner 2007).

Uterine furca

FlyBase synonyms: New term.

Definition: The dorsal wall of the anterior part of the genital chamber (**Figure 6, d**).

Uterine furcal papillate elevation

FlyBase synonyms: New term.

Definition: A thickened tissue of the uterine furca that forms the dorsal wall of the uterine anterodorsal pouch.

Synonyms: papillate elevation (Miller, 1950; Adams and Wolfner, 2007).

Uterine posteroventral intima

FlyBase synonyms: New term.

Definition: The ductal region between the base of the uterus and the exterior. The intima is thin in this region.

Synonyms: specialized vaginal intima (Miller, 1950; Adams and Wolfner, 2007, Figures 1A and 1B).

Vagina

FlyBase synonyms: Revised term (see genital chamber).

Definition: Posterior part of the genital chamber. It is an ectodermal invagination where insemination takes place. It extends from the posterior edge of the uterine specialized intima anteriorly to the vulva posteriorly (Epper, 1983; Adams and Wolfner, 2007).

Vaginal furca

FlyBase synonyms: New term.

Definition: The dorsal wall of the posterior part of the genital chamber.

Vaginal furcal folds

FlyBase synonyms: New term.

Definition: Folds in the inner membrane of the vaginal furca that can be recognized when the furca is extruded during oviposition (**Figure 6, a-c**). It consists of a dorsal long fold, a pair of dorsolateral folds and a pair of lateral folds, which contact during copulation the male aedeagus, dorsal postgonites and ventral postgonites, respectively. The dorsolateral folds are the place of type A copulatory wounds (Kamimura and Mitsumoto, 2011).

Vaginal furcal dorsal fold

FlyBase synonyms: New term.

Definition: Dorsal fold of the vaginal furca that contacts the male aedeagus during copulation (**Figure 6, a**).

Synonyms: uterine shield (Yassin and Orgogozo, 2013), vaginal shield (Kamimura, 2016).

Vaginal furcal dorsolateral fold

FlyBase synonyms: New term.

Definition: Dorsolateral fold of the vaginal furca that contacts the male dorsal postgonite during copulation (**Figure 6, b**). It is the site of type A copulatory wounds (Kamimura, 2012; Mattei et. al., 2015). There are two of these.

Synonyms: lateral folds (Kamimura and Mitsumuto, 2011), membranous pouch (Kamimura, 2016).

Vaginal furcal lateral fold

 doi:10.20944/preprints202201.0223.v2

FlyBase synonyms: New term.

Definition: Lateral fold of the vaginal furca (**Figure 6, c**). There are two of these.

Vulva

FlyBase synonyms: Revised term (see oviprovector).

Definition: External opening of the vagina located medially between the posterior apices of the hypogynial valves. It is dorso-laterally surrounded by the oviprovector dorsal membrane and ventrally by the oviprovector ventral membrane. It is the copulatory orifice and site of exit for eggs.

Synonyms: genital opening (Cumming and Wood, 2017), secondary gonopore (Cumming and Wood, 2017).

Setation

Epigynial sensilla

FlyBase synonyms: female abdominal tergite 8 bristle (FBbt:00110706).

Definition: Small unpigmented sensilla on the ventral margin of the epigynial ventral lobe. There are 4 to 5 of these on each side.

Epiproctal sensillum

FlyBase synonyms: New term.

Definition: Any sensillum on the epiproct. There are on average 18 of these sensilla, of which two are large.

Hypogynial sensilla

FlyBase synonyms: New term.

Definition: Any bristle on the outer or inner surface of a hypogynial valve. They are divided into 11-16 peg-like hypogynial teeth or thorns on the outer surface of a hypogynial valve, and 3 short and one long hypogynial trichoid sensilla on the inner surface of the hypogynial posterior lobe on each side.

Synonyms: vaginal teeth (Baker and Ridge, 1980; Li and Baker, 1998), ovisensilla (Craddock et al., 2018)

Hypogynial short sensillum

FlyBase synonyms: gonopod sensillum trichodeum (FBbt:00004468)

Definition: One of three, minute, apical sensilla on the inner surface of each hypogynial posterior lobe.

Synonyms: microbristle (Hildreth, 1965), sensillum trichodeum (Tsacas, 1975; Epper, 1983; Chen and Baker, 1997; Sánchez et al., 1997), ovisensillum trichoideum (Grimaldi, 1987; Hu and Toda, 2001), apical ovisensillum trichoideum (Zhang and Toda, 1992), inner ovisensillum (Bächli et al., 2004), trichoid sensillum (Crava et al., 2020).

Hypogynial long sensillum

FlyBase synonyms: gonopod long bristle (FBbt:00004467)

Definition: One long sub-apical sensillum on the inner surface of each hypogynial posterior lobe, ventral to the three hypogynial short sensilla.

Synonyms: long bristle (Sturtevant, 1921; Hildreth, 1965; Tsacas, 1975; Epper, 1983; Chen and Baker, 1997; Sánchez et al., 1997), subapical bristle (Salles, 1947; Okada, 1956), subterminal hair (Bock and Wheeler, 1972), subapical ovisensillum trichoideum (Zhang and Toda, 1992), inner ovisensillum (Bächli et al., 2004), subapical sensillum (Craddock et al., 2018), chaetic sensillum (Crava et al, 2020), subterminal inner ovisensilla (Vilela and Prieto, 2018), subterminal trichoid seta (Gao et al., 2003).

Hypogynial tooth

FlyBase synonyms: gonopod thorn bristle (FBbt:00004466)

Definition: Any peg-like tooth on the outer surface of a hypogynial valve. There are 11-17 teeth of these on each side (Natascha Turetzek, personal communication).

Synonyms: peg-like bristle (Sturtevant, 1921), tooth (Salles, 1947; Okada, 1956; Bock and Wheeler, 1972; Estrada and Sánchez-Herrero, 2001), spine bristle (Hildreth, 1965; Tsacas, 1975), thorn bristle (Epper, 1983; Chen and Baker, 1997; Sánchez et al., 1997), peg ovisensillum (Grimaldi, 1987), peg (Zhang and Toda, 1992; Crava et al., 2020), peg-like ovisensillum (Hu and Toda, 2001), outer ovisensillum (Bächli et al., 2004), conical peg (Crava et al., 2020), hairlike sensillum (Craddock et al., 2018), peg-like sensillum (Craddock et al., 2018), peg sensillum (Craddock et al., 2018), small proximal bristle (Polidori and Wurdack, 2019), large distal bristle (Polidori and Wurdack, 2019), vaginal tooth (Li and Baker, 1998).

Hypoproctal sensillum

FlyBase synonyms: New term.

Definition: Any sensillum on the hypoproct. There are on average 19 of these sensilla, of which four are large.

Oviprovector scales

FlyBase synonyms: New term.

Definition: Scale-like projections on the surface of the ventral oviprovector membrane. These structures may act as ratchets to prevent bidirectional movement of an egg (Austin and Browning, 1981).

Synonyms: Ovipositor scales (Austin and Browning, 1981)

Musculature

Abdominal 7 female sternal muscle 144

FlyBase synonyms: FBbt:00003510.

Definition: Muscle of the adult female abdominal segment 7 that extends to the uterine posteroventral intima (Miller, 1950).

Abdominal 8 female dorsal muscle 145

FlyBase synonyms: FBbt:00003469.

Definition: Muscle of the adult female abdominal segment 8 that extends posteriorly along the epigynium to the epiproct. It is the most dorsal of the abdominal 8 female dorsal muscles (Miller, 1950).

Abdominal 8 female dorsal muscle 146

FlyBase synonyms: FBbt:00003470.

Definition: Muscle of the adult female abdominal segment 8 that extends posteriorly from the epigynium to the hypoproct. It is ventral to the female dorsal muscle 147 (Miller, 1950).

Abdominal 8 female dorsal muscle 147

FlyBase synonyms: FBbt:00003471.

Definition: Muscle of the adult female abdominal segment 8 that extends posteriorly from the epigynium to the uterus. It is dorsal to the female dorsal muscle 146 (Miller, 1950).

Abdominal 8 female dorsal muscle 148

FlyBase synonyms: FBbt:00003472.

Definition: Muscle of the adult female abdominal segment 8 that extends dorsoventrally from the epigynium to the hypogynium. It is posterior to the female dorsal muscle 147 (Miller, 1950).

Abdominal 8 female ventral muscle 149

FlyBase synonyms: FBbt:00003486.

Definition: Muscle of the adult female abdominal segment 8 that extends ventrally from the hypogynium to the uterus (Miller, 1950).

Abdominal 8 female lateral ventral muscle 150

FlyBase synonyms: FBbt:00003511.

Definition: Muscle of the adult female abdominal segment 8 that extends along the lateral wall of the hypogynium from anterior to posterior (Miller, 1950).

Abdominal 8 female transverse ventral muscle 151

FlyBase synonyms: FBbt:00003512.

 doi:10.20944/preprints202201.0223.v2

Definition: Muscle of the adult female abdominal segment 8 that extends dorsoposteriorly from the hypogynium (Miller, 1950).

Common oviduct circular muscle

FlyBase synonyms: FBbt:00003553.

Definition: A striated array of circular muscle fibers forming an almost continuous sheet around the common oviduct (Miller, 1950).

Lateral oviduct circular muscle

FlyBase synonyms: FBbt:00007338.

Definition: A striated array of circular muscle fibers forming an almost continuous sheet around the common oviduct (Miller, 1950).

Uterine circular muscle

FlyBase synonyms: FBbt:00003554.

Definition: Circular muscle that surrounds the adult female uterus (Miller, 1950).

Table 2. Table of correspondence between terms previously used in publications and term of the standardized nomenclature

Previous terminology	Synonym in the new nomenclature	Reference(s)
abdominal sternite 9	hypoproct	Ferris, 1950
abdominal tergite 10	epiproct	Cumming and Wood, 2017
abdominal tergite 9	epiproct	Ferris, 1950
anterior uterus projection	uterine anterior projection	Adams and Wolfner, 2007
apical ovisensillum trichodeum	hypogynial short sensillum	Zhang and Toda, 1992
appendicular gland	female accessory gland	Cumming and Wood, 2017
basal isthmus	hypogynial anteroventral bridge	Okada, 1956; Bock and Wheeler, 1972
bursa	uterus	Cumming and Wood, 2017
chaetic sensillum	hypogynial long sensillum	Crava et al., 2020
colleterial gland	female accessory gland	Cumming and Wood, 2017
conical peg	hypogynial tooth	Crava et al., 2020
dented membrane	oviprovector	Tsacas and David, 1975
distal part of the oviscapt valve	hypogynial posterior lobe	Bächli et al., 2004

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

dorsal anal plate	epiproct	Epper and Sanchez, 1983; Gorfinkiel, Sánchez, and Guerrero, 1999, 2003; Sanchez et al., 1997
dorsal part of the female abdominal tergite 8	epigynial dorsal lobe	Epper and Sanchez, 1983
dorsal vaginal plate	hypogynial posterior lobe	Epper and Sanchez, 1983; Gorfinkiel et al., 1999, 2003; Sanchez et al., 1997
dorsal vulva	oviprovector dorsal membrane	Epper, 1983; Chen and Baker, 1997
dorsodistal depression	hypogynial posterodorsal pouch	Bächli et al., 2004
egg guide	hypogynium	Okada, 1956, Bock and Wheeler, 1972
female abdominal sternite 8	hypogynium	Cumming and Wood, 2017
female abdominal tergite 8	epigynium	Ferris, 1950, Epper, 1983, Epper and Sanchez, 1983, Grimaldi, 1990, Vilela and Bächli, 1990, Casares et al., 1997, Sanchez et al., 1997
female abdominal tergite 9	epigynium	Robertson, 1988; Jagadeeshan and Singh, 2006
female abdominal tergites 7/8 intersegmental membrane	perineal membrane	Kamimura and Mitsumuto, 2011
female abdominal tergites 8/9 intersegmental membrane	perineal membrane	Robertson, 1988; Jagadeeshan and Singh, 2006
female abdominal tergite 8 bristle	epigynial sensillum	FlyBase term
female gonopod	hypogynium	Ferris, 1950
female proctiger	female analia	Ferris, 1950; Jagadeeshan and Singh, 2006
female sternite 9	furca	Cumming and Wood, 2017
genital fork	furca	Cumming and Wood, 2017
genital opening	vulva	Cumming and Wood, 2017
gonopod long bristle	hypogynial long sensillum	FlyBase
gonopod sensillum trichodeum	hypogynial short sensillum	FlyBase
gonopod thorn bristle	hypogynial tooth	FlyBase
gland cells	spermathecal secretory cells	Allen and Spradling, 2008
hairlike sensillum	hypogynial tooth	Craddock et al., 2018
heavily sclerotized bar	hypogynial anteroventral bridge	Ferris, 1950
inner ovisensillum*	hypogynial long sensillum	Bächli et al., 2004

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

inner ovisensillum*	hypogynial short sensillum	Bächli et al., 2004
large distal bristle	hypogynial tooth	Polidori and Wurdack, 2018
lateral folds	vaginal furcal dorsolateral fold	Kamimura and Mitsumuto, 2011
long bristle	hypogynial long sensillum	Sturtevant, 1921; Hildreth, 1965; Tsacas and David, 1975; Epper, 1983; Chen and Baker, 1997; Sanchez et al., 1997
lower anal plate	hypoproct	Salles, 1947
lower margin of the egg-guide lobe	hypogynial anterior lobe	Okada, 1956
membranous pouch	vaginal furcal dorsolateral fold	Kamimura, 2016
mesal surface of the oviscapt	hypogynial posterior lobe	Hu and Toda, 2001
microbristle	hypogynial short sensillum	Hildreth, 1965
outer ovisensillum	hypogynial tooth	Bächli et al., 2004
ovipositor	hypogynium	Sturtevant, 1921; Salles, 1947; Tsacas and David, 1975; Vilela and Bächli, 1990
ovipositor scales	oviprovector scales	Austin and Browning, 1981
oviprotector	oviprovector	FlyBase
oviscape	hypogynium	Grimaldi, 1987; Jagadeeshan and Singh, 2006; Kamimura, 2010; Kamimura and Mitsumoto, 2011
oviscapt	hypogynium	Grimaldi, 1990; Zhang and Toda, 1992; Hu and Toda, 2001; Bächli et al., 2004; Kamimura, 2010; Kamimura and Mitsumoto, 2011; Yassin and Orgogozo, 2013; Vilela and Prieto, 2018; Al Sayad and Yassin, 2019
oviscapt pouch	hypogynial posterodorsal pouch	Yassin and Orgogozo, 2013
ovisensillum	hypogynial sensillum	Craddock et al., 2018
ovisensillum trichodeum	hypogynial short sensillum	Grimaldi, 1987; Hu and Toda, 2001
papillate elevation	uterine furcal papillate elevation	Miller, 1950; Adams and Wolfner, 2007
parovarium	female accessory gland	Okada, 1956; Fung and Gowen, 1957; Bock and Wheeler, 1972; Epper, 1983; Chen and Baker, 1997; Keisman and Baker, 2001; Cumming and Wood, 2017
peg	hypogynial tooth	Zhang and Toda, 1992; Crava et al., 2020
peg ovisensillum	hypogynial tooth	Grimaldi, 1987
peg sensillum	hypogynial tooth	Craddock et al., 2018

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 27 January 2022 doi:10.20944/preprints202201.0223.v2

peg-like bristle	hypogynial tooth	Sturtevant, 1921
peg-like ovisensillum	hypogynial tooth	Hu and Toda, 2001
peg-like sensillum	hypogynial tooth	Craddock et al., 2018
perineal plate	perineal membrane	Bächli et al., 2004
pre-oviduct space	uterine anterodorsal pouch	Adams and Wolfner, 2007
secondary gonopore	vulva	Cumming and Wood, 2017
sensillum trichodeum	hypogynial short sensillum	Tsacas and David, 1975; Epper, 1983; Chen and Baker, 1997; Sanchez et al., 1997
small proximal bristle	hypogynial tooth	Polidori and Wurdack, 2018
specialized vaginal intima	uterine posteroventral intima	Milner, 1950; Adams and Wolfner, 2007
spermathecum	spermatheca	FlyBase
spine bristle	hypogynial tooth	Hildreth, 1965; Tsacas and David, 1975
subanal plate	hypoproct	Miller, 1950
subapical bristle	hypogynial long sensillum	Salles, 1947; Okada, 1956
subapical ovisensillum trichoideum	hypogynial long sensillum	Zhang and Toda, 1992
subapical sensillum	hypogynial long sensillum	Craddock et al., 2018
submedian incision of the egg-guide lobe	hypogynial mid-dorsal incision	Okada, 1956
subterminal hair	hypogynial long sensillum	Bock and Wheeler, 1972
subterminal inner ovisensilla	hypogynial long sensillum	Vilela and Prieto, 2018
subterminal trichoid seta	hypogynial long sensillum	Gao et al., 2003
supraanal plate	epiproct	Miller, 1950
thorn bristle	hypogynial tooth	Epper, 1983; Chen and Baker, 1997; Sanchez et al., 1997
tooth	hypogynial tooth	Salles, 1947; Okada, 1956; Bock and Wheeler, 1972; Estrada and Sanchez-Herrero, 2001
trichoid sensillum	hypogynial short sensillum	Crava et al., 2020
tubular receptacle	seminal receptacle	Anderson, 1945
upper anal plate	epiproct	Salles, 1947

 doi:10.20944/preprints202201.0223.v2

upper margin of the egg-guide lobe	hypogynial posterior lobe	Okada, 1956
uterine dome	uterine anteroventral pouch	Adams and Wolfner, 2007
uterine shield	vaginal furcal dorsal fold	Yassin and Orgogozo, 2013
uterus	genital chamber	Hildreth, 1965; Chen and Baker, 1997; Keisman and Baker, 2001
vagina*	genital chamber	FlyBase
vagina*	oviprovector	Gleichauf, 1936
vaginal apodeme	furca	Cumming and Wood, 2017
vaginal plates	hypogynium	Kikkawa, 1938; Hildreth, 1965; Epper, 1983; Casares et al., 1997; Chen and Baker, 1997; Gorfinkiel, Sánchez, and Guerrero, 1999; Keisman and Baker, 2001
vaginal pouch	uterine anteroventral pouch	Patterson and Stone, 1952
vaginal shield	vaginal furcal dorsal fold	Kamimura, 2016
vaginal teeth	hypogynial sensillum	Baker and Ridge, 1980; Li and Baker, 1998
vaginal tooth	hypogynial tooth	Li and Baker, 1998
ventral anal plate	hypoproct	Sturtevant, 1921; Epper, 1983; Casares et al., 1997; Chen and Baker, 1997; Gorfinkiel, Sánchez, and Guerrero, 1999; Sanchez et al., 1997
ventral part of the female abdominal tergite 8	epigynial ventral lobe	Epper and Sanchez, 1983
ventral receptacle	seminal receptacle	Sturtevant, 1939; Sturtevant, 1942; Dobzhansky and Pavan, 1943; Patterson and Stone, 1952; Wheeler, 1954; Mather, 1955; Okada, 1956; Throckmorton, 1962; Okada, 1963; Hardy, 1965; Bock and Wheeler, 1972; Spieth, 1975; Grimaldi, 1990; Knight, 1990; Zhang and Toda, 1992; Bachli et al., 2004; Yassin, 2008; Vaz et al., 2014
ventral vaginal plate	hypogynial anterior lobe	Epper and Sanchez, 1983; Gorfinkiel et al., 1999, 2003; Sanchez et al., 1997
ventral vulva	oviprovector ventral membrane	Epper, 1983; Chen and Baker, 1997
vulva	oviprovector	Tsacas and David, 1975

* Note that these previously used terms correspond to multiple anatomical parts in the new nomenclature