

# **A standardized nomenclature and atlas of the male terminalia of *Drosophila melanogaster***

Gavin Rice<sup>1</sup>, Jean R. David<sup>2</sup>, Yoshitaka Kamimura<sup>3</sup>, John P. Masly<sup>4</sup>, Alistair P. McGregor<sup>5</sup>, Olga Nagy<sup>6</sup>, Stéphane Noselli<sup>7</sup>, Maria Daniela Santos Nunes<sup>5</sup>, Patrick O'Grady<sup>8</sup>, Ernesto Sánchez-Herrero<sup>9</sup>, Mark L. Siegal<sup>10</sup>, Masanori J. Toda<sup>11\*</sup>, Mark Rebeiz<sup>1\*</sup>, Virginie Courtier-Orgogozo<sup>6\*</sup>, Amir Yassin<sup>12\*</sup>

\*Corresponding authors: [hutian@lemon.plala.or.jp](mailto:hutian@lemon.plala.or.jp), [rebeiz@pitt.edu](mailto:rebeiz@pitt.edu), [virginie.courtier@ijm.fr](mailto:virginie.courtier@ijm.fr), [yassin@mnhn.fr](mailto:yassin@mnhn.fr)

<sup>1</sup> Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, United States of America; @gavinrrice, @RebeizLab

<sup>2</sup> Laboratoire Evolution, Génomes, Comportement, Ecologie (EGCE), UMR 9191, CNRS ,IRD, Univ.Paris-Sud, Université Paris-Saclay, Gif sur Yvette, 91198 cedex, France

<sup>3</sup> Department of Biology, Keio University, Hiyoshi, Yokohama 2238521, Japan

<sup>4</sup> Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019; @MaslyLab

<sup>5</sup> Department of Biological and Medical Sciences, Oxford Brookes University, Gipsy Lane, Oxford, OX3 0BP, UK; @Nunes\_lab

<sup>6</sup> CNRS UMR7592, Institut Jacques Monod, Université de Paris, Paris, France; @Biol4Ever

<sup>7</sup> Université de l'Azur, CNRS, INSERM, iBV, Nice, France

<sup>8</sup> Department of Entomology, Cornell University, Ithaca, NY

<sup>9</sup> Centro de Biología Molecular Severo Ochoa (C.S.I.C.-U.A.M.), Universidad Autónoma de Madrid, Nicolás Cabrera 1, Cantoblanco, 28049 Madrid, Spain

<sup>10</sup> Center for Genomics and Systems Biology, Department of Biology, New York University

<sup>11</sup> Hokkaido University Museum, Hokkaido University, Sapporo 060-0810, Japan

<sup>12</sup> Institut de Systématique, Evolution et Biodiversité, UMR7205, Centre National de la Recherche Scientifique, MNHN, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, 75005 Paris, France

## Abstract

Animal terminalia represent some of the most diverse and rapidly evolving structures in the animal kingdom, and for this reason have been a mainstay in the taxonomic description of species. The terminalia of *Drosophila melanogaster*, with its wide range of experimental tools, have recently become the focus of increased interest in the fields of development, evolution, and behavior. However, studies from different disciplines have often used discrepant terminologies for the same anatomical structures. Consequently, the terminology of genital parts has become a barrier to integrating results from different fields, rendering it difficult to determine what parts are being referenced. We formed a consortium of researchers studying the genitalia of *D. melanogaster* to help establish a set of naming conventions. Here, we present a detailed visual anatomy of male genital parts, including a list of synonymous terms, and suggest practices to avoid confusion when referring to anatomical parts in future studies. The goal of this effort is to facilitate interdisciplinary communication and help newcomers orient themselves within the exciting field of *Drosophila* genitalia.

**Keywords:** genitalia, terminalia, anatomy, *Drosophila melanogaster*, nomenclature

## Introduction

Insect terminalia, which usually encompass the male and female genitalia and analia, are among the most diverse and complex morphological structures (Eberhard 1985). In *Drosophila*, they have been the subjects of three research disciplines that led to different terminologies. The earliest of these is *ontogeny*, which aimed at identifying the segmental origin of the different structures and how they sexually differentiate during development from the larval genital disc in *D. melanogaster*. It is thanks to this discipline that the ‘traditional terminology’ was established (Dobzhansky 1930; Ferris 1950; Bryant 1978) and continues to be used by contemporary developmental biologists (Chatterjee et al. 2015). Most of the terms currently annotated in FlyBase ([www.flybase.org](http://www.flybase.org)) are based on the traditional system.

The second discipline was *phylogenetics*, which aimed at describing the diversity of terminalia among drosophilids in order to group species according to their similarities in these structures. The earliest comparative studies (Hsu 1949; Okada 1954) standardized the ‘traditional terminology’ in *Drosophila* systematics (e.g., Bock and Wheeler 1972). However, following the publication of McAlpine’s (1981) *Manual of Nearctic Diptera*, an effort to standardize morphological terms of putatively homologous structures across the Diptera emerged (Grimaldi 1987, 1990). Subsequently, the resulting ‘revised terminology’ was widely accepted by *Drosophila* systematists (McEvey 1990; Vilela and Bächli 1990; Zhang and Toda 1992), although some terms, such as parameres, paraphyses or gonopods, remained problematic because they sometimes refer to structures not related by clear homology in different species (Hu and Toda 2001; Bächli et al. 2004).

Recently, a third discipline, *functional morphology*, has emerged, aiming at understanding the role that each genital structure may play during copulation (Acebes et al. 2003; Kamimura 2010; Polak and Rashed 2010; Frazee and Masly 2015; LeVasseur-Viens et al. 2015; Mattei et al. 2015, Tanaka et al. 2018). With advanced techniques such as laser surgery and tomography scanning, this approach has enhanced our understanding of the functional roles of genital anatomy. However, researchers in this discipline used a mixture of traditional and revised terminologies (Kamimura and Polak 2011) that can lead to confusion as community members from different disciplines assimilate the literature.

Believing that the breadth and richness of the three research disciplines offers a unique opportunity for integrative biology, the purpose of the current paper is to unify terminology of *Drosophila* male terminalia (Figure 1). As a group of researchers working on different aspects of *Drosophila* terminalia, we think that a unified system would facilitate exchanges between research fields. Although some researchers highlighted the usefulness of the traditional system in providing meaningful English terms rather than obscure Latin-derived names (e.g., clasper vs. surstylus), the majority opted for the phylogenetic tradition which captures homology relationships between species. Consequently, we provide an update of the terminalia terminology found in FlyBase. For the problematic terms (parameres, paraphyses, and gonopods), we relied on Sinclair's (2000) and Cumming and Wood's (2017) revisions of Diptera terminalia nomenclature to propose new terms not previously used in *Drosophila* biology (namely, pregonites, postgonites, and gonocoxites). Although we restricted our revision to male terminalia, we do so with the intention to address female terminology later.

## Results and Discussion

### *A visual atlas of adult D. melanogaster male terminalia*

In much of the past literature, genital morphology was rendered by hand-drawings, and the names of different parts were indicated by lines pointing to each structure. As new researchers join this growing field, it can be quite difficult to grasp the exact extent of a structure based on these drawings. In order to make the revised nomenclature as useful as possible, we provide here a visual guide to this terminology which shows both drawings and cuticle images that outline the full extent of each named part (Figures 2, 3). It is important to note that the exact size and shape of these structures, such as the epandrial posterior lobe, can vary within *D. melanogaster* (Liu et al. 1996; McNeil, Bain and Macdonald 2011). In Table 1, we propose a unified nomenclature of the various anatomical elements containing definitions and references to previously used terms. Conversely, Table 2 provides correspondence from previously used terms to the unified nomenclature. Although the current set of nomenclature is centered around *D. melanogaster*, we have adopted general terms such that most should also apply to other Drosophilidae species.

The male terminalia of *D. melanogaster* corresponds to the entire set of external structures in the distal half of the male abdomen (Figures 1–3), i.e. segments 8–10. It derives from the genital disc, which comprises three primordia: a reduced Abdominal segment 8 primordium, which in females gives rise to most genital structures but in males gives rise only to a miniature eighth tergite (here termed the epandrial anterodorsal phragma, see below); an Abdominal segment 9 primordium, forming the male genitalia, and the Abdominal segment 10 primordium, making the analia (Keisman et al., 2001). During development, the *D. melanogaster* male genitalia rotates 360 degrees clockwise, causing the internal organs to loop around the gut; this rotation and thus the dorsal/ventral designation of the genitalia varies within Diptera (Suzanne et al. 2010). We dissected and imaged adult cuticle preparations of a *D. melanogaster* wild type strain (Canton S), and provide cuticle images as well as drawings of the distinct parts in Figures 1–3. To maximize clarity, we present each part both in isolation and in the context of intact tissue, and we indicate the outlines of each anatomical component (Figures 2, 3).

We have subdivided the terminalia into two parts, periphallic structures, which are secondarily connected to the intromittent organ (Figure 2) and the phallic structures, which comprise the intromittent organ and structures directly connected to it (Figure 3). These two classes are easily separable via dissection in the adult.

### ***Periphallic portions of the terminalia***

Periphallic structures comprise the cercus (former anal plate), the epandrium (former genital arch), the pair of surstyli (former claspers) and the subepandrial sclerite (former pons) that connects the surstyli to the other periphallic structures (Figure 1). Although periphallic structures are not directly involved in transferring sperm, several of them (cercus, surstylus, and epandrial posterior lobe) have been implicated in grasping onto the female during copulation (Robertson 1988; Eberhard and Ramirez 2004; Jagadeeshan and Singh 2006; Kamimura 2010; Kamimura and Mitsumoto 2011; Mattei et al. 2015; Frazee and Masly 2015; LeVasseur-Viens et al. 2015). Additionally, although many of these structures do not show obvious boundaries in *D. melanogaster*, they are far more complex in its close relatives, suggesting that there are natural subdivisions of these structures in some species. For example, while the ventral margin of the cercus forms a relatively flat cuticle in *D. melanogaster*, it bears a lobe-like extension in *D. bipectinata* that affects copulatory success (Polak and Rashed 2010; Kamimura and Polak 2011). Furthermore, the dorsal and ventral parts of the cercus accumulate distinct levels of *engrailed* in *D. melanogaster* (Fig. 3F in Sánchez et al. 1997).

### ***Subdivision and nomenclature of phallic parts***

During copulation, several parts of the male genitalia enter the female vagina: the aedeagus, part of the phallapodeme, the ventral and dorsal postgonites, and the aedaegal sheath (Kamimura 2010; Mattei et al. 2017). All of these structures except the phallapodeme form the intromittent organ or phallus. The aedeagus is perhaps the most complex structure of the male genitalia of *D. melanogaster*: it is covered with cuticular projections and its shape varies broadly between closely related species (see Figures 13, 14, 16, 17 of Tsacas et al. 1971; Yassin and Orgogozo 2013). The postgonites are flexible relative to the aedeagus; they move progressively during mating and have

been implicated in producing copulatory wounds in females (Kamimura 2010). The aedeagal sheath surrounds the aedeagus and the postgonites dorso-laterally. It also moves outwards during mating. The movement of the postgonites and the aedeagal sheath may be induced through the complex musculature found in the phallus (Figure 5; Kamimura 2010).

The hypandrium is a large structure that surrounds the phallus ventrally. It can be broken down into several identifiable substructures. We consider the posterior part to be fused gonocoxites (see below) and divide each gonocoxite into two parts lateral and median. The fused median gonocoxites host a pair of large bristles (Taylor 1989; Nagy et al. 2018). They connect to the phallus through via the two pregonites. Each pregonite displays two to three smaller bristles .

#### ***Justifying the separation/individuality of parts***

It is important to note that the boundary of each anatomical element is based largely on defined cuticular ridges observed in the adult. However, some key parts lack clear boundaries with other adjacent tissues. Examples include the epandrial posterior lobe, cercal ventral and dorsal lobes, and sub-parts of the hypandrium. We envision that in these cases, a careful analysis of cellular formation during development will be necessary to precisely define the boundaries of separate parts. Experiments that map the spatial expression patterns of regulatory genes such as transcription factors further support the boundaries of each anatomical element, and could motivate further refinements into smaller sub-parts (Sánchez et al. 1997; Vincent et al. 2019).

#### ***Implications of our system to the terminological debate within Diptera***

The term “surstylus” has been proposed by Crampton (1923) to refer to the clasping organs that are associated with the dorsal compartment of the genitalia (*i.e.* epandrium) in Eremoneuran (Higher) Diptera to which *Drosophila* belongs. In non-Eremoneuran (Lower) Diptera and in other related insect orders, the clasping organs consist of appendices, the gonopods, consisting of two substructures, the gonocoxites and the gonostyli, that are associated with the ventral compartment of the genitalia (*i.e.* the hypandrium). Crampton’s view, which would later be called the “surstylar concept” (Zatwarnicki 1996), postulates that the gonostyli have been lost whereas the gonocoxites

remain associated with the hypandrium in Eremoneurans. This view has a wide acceptance among Dipterologists (Yeates and Wiegmann 1999; Sinclair 2000; Cumming and Wood 2017), as well as between *Drosophila* systematists who have opted for a revised terminology (Grimaldi 1990; Hu and Toda 2001; Bächli et al. 2004). For example, the term gonopod, whereas used for different structures in *D. melanogaster* (see Tables 1 and 2), has always been applied to ventral structures associated with the phallic portions.

However, alternative hypotheses for the origin of the Eremoneuran dorsal claspers exist, *i.e.* the “gonostylar concept”, postulating that Eremoneuran dorsal claspers are homologous to the ventral gonopods (mostly to the gonostyli) of non-Eremoneuran Diptera (reviewed in Zatwarnicki 1996). Zatwarnicki (1996) further considered the subepandrial sclerite (*medandrium* in Zatwarnicki 1996) to be homologous to the gonocoxites. Although evaluating these concepts goes far beyond the scope of our paper, we believe that further research in *Drosophila* could ultimately help elucidating the origin of the Eremoneuran dorsal claspers. For example, Abd-B mutants in *D. melanogaster* genital disc transform the phallic structures, as well as a part of the surstylus (clasper), into a leg (Estrada and Sanchez-Herrero 2001). This supports the idea that the ventral parts of the Eremoneuran genitalia are of appendicular origin (as the name gonopod, *i.e.* genital leg, would suggest), but it also suggests that a part (not the whole) of the surstylus might be of appendicular origin. Further mapping of transcription factors expression in the different compartments of the male terminalia between *D. melanogaster* (e.g., Vincent et al. 2019) and other non-Eremoneuran Diptera could shed light on the deep homology between these structures. At the time being, and because our major aim is to unify terms used by *Drosophila* biologists, we have opted here for the terminology based on the “surstylar concept”, and we hope that this would prompt further research on these questions.

### ***Incorporating the new standardized terminology into diverse ongoing studies***

The revised terminology described here should facilitate cross-disciplinary synthesis of our knowledge of genital function, development, and evolution. We have worked with the FlyBase team to integrate these terms into their anatomy ontology (Costa et al. 2013; Thurmond et al. 2019).



Although we focused on the *D. melanogaster* terminalia, a standardized terminology is vital/crucial for the ease of comparing various species. Thus, it is our hope that these terms will facilitate descriptions of homologous and novel structures in other insect species. It was important for us to include as much of the community of researchers working on *Drosophila* genital morphology as possible to reach consensus in the definition and deployment of this terminology. We suggest that when publishing studies that name these structures, authors use the terms of the revised terminology, while parenthetically citing alternate synonyms such as familiar terms, e.g. surstylus (clasper). For those who would like to use familiar terms (perhaps for the purpose of continuity with previous publications), we would strongly recommend that the revised terminology is presented parenthetically, e.g. clasper (surstylus). This way, the broader scientific community can understand and integrate results with as few barriers to comprehension as possible.

Studies of *Drosophila* genitalia have provided examples of large-scale differences between males and females, vital taxonomic traits to distinguish species from one another, and important factors in the reproductive incompatibility between species. Yet, the complexity of the genitalia itself presents barriers to the study of these fascinating anatomical parts. This problem has been aggravated by variability in nomenclature, which has further impeded entry into this field. The revision and visual atlas of male genital structures provided here will hopefully allow for increased communication across a range of disciplines and welcome new scientists to this growing field.

## **Materials and Methods**

A Canton S line of *Drosophila melanogaster* (Bloomington # 64349) was used for all imaging. Adult males were dissected in 100% EtOH with micro-forceps and mounted in PVA Mounting Medium (BioQuip). For Figure 1A, the sample was imaged at 500× magnification with a digital microscope VHX 2000 (Keyence) using lens VH-Z20R/W. For Figure 1B and 1C digital images were taken at different depths of focus using a Dino-Lite® Microscope Eyepiece Camera (AM7025X, AnMo Electronics Corporation) on an Olympus BX50 microscope and stacked with CombineZP 1.0 (<https://combinezp.software.informer.com/>). For Figures 2 and 3, samples were imaged at 16× magnification on a Leica M205C microscope with a Leica DFC425 camera or at 20×

227 magnification on a Leica DM 2000 with a Leica DFC540 C camera. Images from the former  
228 microscope were Z stack-compiled with the Leica Application Suite to allow for optimal focus.  
229 Images of the epandrial anterodorsal phragma, epandrial dorsal lobe, epandrial posterior lobe,  
230 epandrial ventral lobe, subepandrial sclerite, cercal dorsal lobe, cercal ventral lobe, lateral gonocoxite,  
231 median gonocoxite, transverse rod, and hypandrial phragma were modified in Adobe Photoshop via  
232 the eraser tool to isolate full parts along sutures to provide the clearest view of each part in its entirety.  
233 Photoshop was used because dissection of the various parts would be difficult.

#### 234 **Acknowledgements:**

235 We thank Clare Pilgrim and Steve Mangold for working with us to integrate our terminology into the  
236 FlyBase anatomy ontology, as well as the reviewers and Tadeusz Zatwarnicki for their useful  
237 comments.

#### 238 **Disclosure of potential conflicts of interest**

239 The authors report no conflicts of interest. The authors alone are responsible for the content and  
240 writing of the paper.

241

#### 242 **Funding**

243 Funding was provided by European Research Council (FP7/2007-2013 Grant Agreement no. 337579)  
244 to VC, by the National Institutes of Health (FP4/2014-2019 GM107387) to MR, by the Agence  
245 Nationale de la Recherche (ANR-18-CE02-0008) to AY, by the National Institutes of Health  
246 (R35GM118170) to MLS.

## References

- Acebes A, Cobb M, Ferveur JF. (2003). Species-specific effects of single sensillum ablation on mating position in *Drosophila*. *Journal of Experimental Biology*, 206: 3095-3100
- Bächli G, Vilela CR, Andersson Escher, S., & Saura, A. (2004) *The Drosophilidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica*, vol. 39, 362 pp. Brill, Leiden.
- Bock IR & Wheeler, MR (1972) *The Drosophila melanogaster Species Group*. The University of Texas Publication 7213:1-102.
- Bryant P (1978). Pattern formation in imaginal discs. In M. Ashburner and T. R. F. Wright, editors, *The Genetics and Biology of Drosophila*, volume 2c, chapter 22, pages 229--335. Academic Press, 1978.
- Bryant P and Hsei B (1977). Pattern Formation in Asymmetrical and Symmetrical Imaginal Discs of *Drosophila melanogaster*. *American Zoologist*. 17:595-611
- Chassagnard MT (1988) Esquisse phylogénétique du genre *Zaprionus* Coq. (Diptera: Drosophilidae) et description de trois nouvelles espèces afrotropicales. *Naturaliste can. (Rev. Ecol. Syst.)*, 115: 305-322.
- Chatterjee RN, Chatterjee P, Kuthe S, Acharyya-Ari M, & Chatterjee R (2015). Intersex (ix) mutations of *Drosophila melanogaster* cause nonrandom cell death in genital disc and can induce tumours in genitals in response to decapentaplegic (dppdisk) mutations. *Journal of genetics*, 94(2), 207-220.
- Costa M, Reeve S, Grumbling G & Osumi-Sutherland D (2013). The *Drosophila* anatomy ontology. *Journal of Biomedical Semantics*. 4:32
- Crampton GC (1923) *The Genitalia of Male Diptera and Mecoptera Compared with Those of Related Insects, from the Standpoint of Phylogeny*. *Transactions of the American Entomological Society* 48(3) pp. 207-225
- Cumming JM, & Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs, A. H., Sinclair, B. J., editors. *Manual of Afrotropical Diptera*. v. 1. Introductory chapters and keys to diptera families. *Suricata* 4, South African National Biodiversity Institute: Pretoria; pp. 89–133.

275 Dobzhansky T (1930) Studies on the intersexes and supersexes in *Drosophila melanogaster*. (in  
 276 Russian, with English summary). *Izvestia Biuro po evgenike* 8:91-158.  
 277 Eberhard, WG (1985). *Sexual selection and animal genitalia*. Harvard University Press.  
 278 Eberhard W, Ramirez N (2004) Functional Morphology of the Male Genitalia of Four Species of  
 279 *Drosophila*: Failure to Confirm Both Lock and Key and Male-Female Conflict Predictions. *Annals of*  
 280 *the Entomological Society of America*, 97(5) 1007–1017.  
 281 Estrada B, Sanchez-Herrero E (2001) The Hox gene Abdominal-B antagonizes appendage  
 282 development in the genital disc of *Drosophila*. *Development* 128, 331-339.  
 283 Ferris GF (1950). External morphology of the adult. In M. Demerec, editor, *Biology of Drosophila*,  
 284 chapter 5, pages 368-419. Cold Spring Harbor Laboratory Press, facsimile edition, 1994.  
 285 Frazee, SR, Masly JP, (2015) Multiple sexual selection pressures drive the rapid evolution of complex  
 286 morphology in a male secondary genital structure. *Ecology and Evolution*. 5(19):4437-4450.  
 287 Grimaldi, DA (1987) Phylogenetics and taxonomy of *Zygothrica* (Diptera: Drosophilidae). *Bulletin of*  
 288 *the American Museum of Natural History* 186:103-268.  
 289 Grimaldi, DA 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera).  
 290 *Bulletin of the American Museum of Natural History* 197:1-139.  
 291 Hsu, TC (1949) The external genital apparatus of male Drosophilidae in relation to systematics. *The*  
 292 *University of Texas Publication* 4920:80-142.  
 293 Hu, Y.-G. & Toda, MJ (2001) Polyphyly of Lordiphosa and its relationships in Drosophilinae  
 294 (Diptera: Drosophilidae). *Systematic Entomology* 26:15-31.  
 295 Jagadeeshan S, Singh RS (2006) A time-sequence functional analysis of mating behaviour and genital  
 296 coupling in *Drosophila*: role of cryptic female choice and male sex-drive in the evolution of male  
 297 genitalia. *Journal of Evolutionary Biology*, 19: 1058–1070.  
 298 Kamimura Y (2010). Copulation anatomy of *Drosophila melanogaster* (Diptera: Drosophilidae):  
 299 wound-making organs and their possible roles. *Zoomorphology*, 129(3), 163-174.  
 300 Kamimura Y & Mitsumoto H (2011) Comparative copulation anatomy of the *Drosophila*  
 301 *melanogaster* species complex (Diptera: Drosophilidae). *Entomological Science* 14: 399-410.

302 Kamimura Y, Polak M (2011) Does surgical manipulation of *Drosophila* intromittent organs affect  
 303 insemination success? *Proc. R. Soc. B* 278:815-816.

304 Keisman EL, Christiansen AE, & Baker, BS (2001). The sex determination gene *doublesex* regulates  
 305 the A/P organizer to direct sex-specific patterns of growth in the *Drosophila* genital imaginal disc.  
 306 *Dev Cell* 1(2):215-225.

307 Kopp AV, True JR (2002) Evolution of male sexual characters in the Oriental *Drosophila*  
 308 *melanogaster* species group. *Evolution & Development* 4:4, 278–291

309 LeVasseur-Viens H, Polak M, Moehring AJ (2015) No evidence for external genital morphology  
 310 affecting cryptic female choice and reproductive isolation in *Drosophila*. *Evolution* 69(7):1797-80

311 Liu J, Mercer JM, Stam LF, Gibson GC, Zeng ZB, and Laurie ZB (1996) Genetic analysis of a  
 312 morphological shape difference in the male genitalia of *Drosophila simulans* and *D. mauritiana*.  
 313 *Genetics* 142: 1129-1145.

314 Mattei AL, Riccio ML, Avila FW, Wolfner MF (2015) Integrated 3D view of postmating responses  
 315 by the *Drosophila melanogaster* female reproductive tract, obtained by micro-computed tomography  
 316 scanning. *Proceedings of the National Academy of Sciences* 112 (27), 8475-8480.

317 Mattei AL, Kamimura Y, Wolfner MF. (2017). Intimate intimas: positioning of copulatory organs in  
 318 mating *Drosophila*. *Mol. Repro. Devt.*, 84:1117.

319 McAlpine JF (1981) Morphology and terminology-adults. In J. F. McAlpine et al., *Manual of Nearctic*  
 320 *Diptera*, vol 1, chapter 2. Agriculture Canada Monograph No. 27. Ottawa: Minister of Supply and  
 321 Services.

322 McEvey, SF (1990) New species of *Scaptomyza* from Madagascar and Mauritius with a note on  
 323 terminology (Diptera: Drosophilidae). *Annales de la Société entomologique de France* 26(N.Ser.):51-  
 324 64.

325 McNeil C, Bain C, Macdonald S (2011) Multiple Quantitative Trait Loci Influence the Shape of a  
 326 Male-Specific Genital Structure in *Drosophila melanogaster*. *G3: Genes|Genomes|Genetics* 1(5): 343-  
 327 351.

328 Nagy O, Nuez I, Savisaar R, Peluffo AE, Yassin A, Lang M, Stern DL, Matute D, David JR, Courtier-  
 329 Orgogozo V (2018) Correlated evolution of two copulatory organs via a single cis-regulatory  
 330 nucleotide change. *Current Biology* 28 (21), 3450-3457.  
 331 Okada T (1954) Comparative morphology of the drosophilid flies. I. Phallic organs of the  
 332 melanogaster group. *Kontyu* 22:36-46.  
 333 Okada T (1956) Systematic study of Drosophilidae and allied families of Japan. Gihodo Co., Ltd.,  
 334 Tokoyo.  
 335 Okada T (1963) Cladogenetic differentiation of Drosophilidae in relation to material compensation.  
 336 *Mushi*, 37: 79-100.  
 337 Polak M, & Rashed A 2010 Microscale laser surgery reveals adaptive function of male intromittent  
 338 genitalia. *Proc. R. Soc. B* 277, 1371 – 1376.  
 339 Robertson HM, (1988) Mating asymmetries and phylogeny in the *Drosophila melanogaster* species  
 340 complex. *Pac. Sci.* 42: 72–80  
 341 Salles H (1947) Sobre a Genitalia dos Drosofilidios (Diptera): I. *Drosophila melanogaster* E. D.  
 342 *simulans*. *Summa Brasiliensis Biologiae* (15): 1-73.  
 343 z L, Casares F, Gorfinkiel N, Guerrero I (1997) The genital disc of *Drosophila melanogaster*.  
 344 II. Role of the genes *hedgehog*, *decapentaplegic* and *wingless*. *Development Genes and Evolution*  
 345 207:229–241  
 346 Sánchez L, Guerrero I (2001) The development of the *Drosophila* genital disc. *BioEssays* 23:698–  
 347 707.  
 348 Sinclair, BJ (2000) Morphology and terminology of Diptera male terminalia. In: Papp, L. and Darvas,  
 349 B. (eds), *Contributions to a Manual of Palaearctic Diptera*, Vol. 1, pp. 53-74. Science Herald,  
 350 Budapest.  
 351 Suzanne M, Petzoldt A, Spéder P, Coutelis J, Steller H, and Noselli S (2010) Coupling of apoptosis  
 352 and L/R patterning controls stepwise organ looping. *Current Biology* 20:19, 1773-1778.  
 353 Tanaka, KM, Kamimura, Y, & Takahashi, A (2018) Mechanical incompatibility caused by  
 354 modifications of multiple male genital structures using genomic introgression in *Drosophila*.  
 355 *Evolution* 72: 2406-2418.

356 Taylor, BJ (1989) Sexually Dimorphic Neurons in the Terminalia of *Drosophila Melanogaster*: I.  
 357 Development of Sensory Neurons in the Genital Disc During Metamorphosis, *Journal of*  
 358 *Neurogenetics*, 5:3, 173-192, DOI: 10.3109/01677068909066207  
 359 Thurmond J, Goodman JL, Strelets VB, Attrill H, Gramates LS, Marygold SJ, Matthews BB,  
 360 Millburn G, Antonazzo G, Trovisco V, Kaufman TC, Calvi BR, and the FlyBase Consortium. (2019)  
 361 FlyBase 2.0: the next generation. *Nucleic Acids Research* 47(D1): D759--DD765.  
 362 Tsacas L, Bocquet C, Daguzan M, & Mercier A (1971) Comparaison des genitalia males de  
 363 *Drosophila melanogaster*, de *Drosophila simulans* et de leurs hybrides (Dipt. Drosophilidae). *Annales*  
 364 *de la Société entomologique de France* 7:75-93.  
 365 Vilela, CR & Bachli, G. (1990) Taxonomic studies on Neotropical species of seven genera of  
 366 Drosophilidae (Diptera). *Mitteilungen der Schweizerische Entomologischen Gesellschaft* 63:1-332.  
 367 Vincent BJ, Rice GR, Wong GM, Glassford WJ, Downs KI, Shastay JL, Charles-Obi K, Natarajan M,  
 368 Gogol M, Zeitlinger J, Rebeiz M. (2019) An atlas of transcription factors expressed in the *Drosophila*  
 369 *melanogaster* pupal terminalia. *Biorxiv*. doi: <https://doi.org/10.1101/677260>  
 370 Wheeler MR. (1960) Sternite modification in males of the Drosophilidae (Diptera). *Annals of the*  
 371 *Entomological Society of America*, 53: 133-137.  
 372 Wheeler MR. (1987) Drosophilidae (Chap. 95). In J. F. McAlpine (ed.), *Manual of Nearctic Diptera*  
 373 2: 1011-1018. Research Branch Agriculture Canada monogr. 28. Ottawa: Minister Supply and  
 374 Services Canada.  
 375 Yassin A & Orgogozo V. (2013) Coevolution between Male and Female Genitalia in the *Drosophila*  
 376 *melanogaster* Species Subgroup. *PLoS ONE* 8:e57158.  
 377 Yeates, D.K. & Wiegmann, B.M. (1999) Congruence and controversy: toward a higher-level  
 378 phylogeny of Diptera. *Annual Review of Entomology* 44: 397–428.  
 379 Zatwarnicki T (1996) A new reconstruction of the origin of eremoneuran hypopygium and its  
 380 implications for classification (Insecta: Diptera). *Genus* 7: 103–175.

381 Zhang, W & Toda, MJ. (1992) A New Species-subgroup of the *Drosophila immigrans* Species-group  
382 (Diptera, Drosophilidae), with Description of Two New Species from China and Revision of  
383 Taxonomic Terminology. Japanese Journal of Entomology 60:839-850.



Figures:

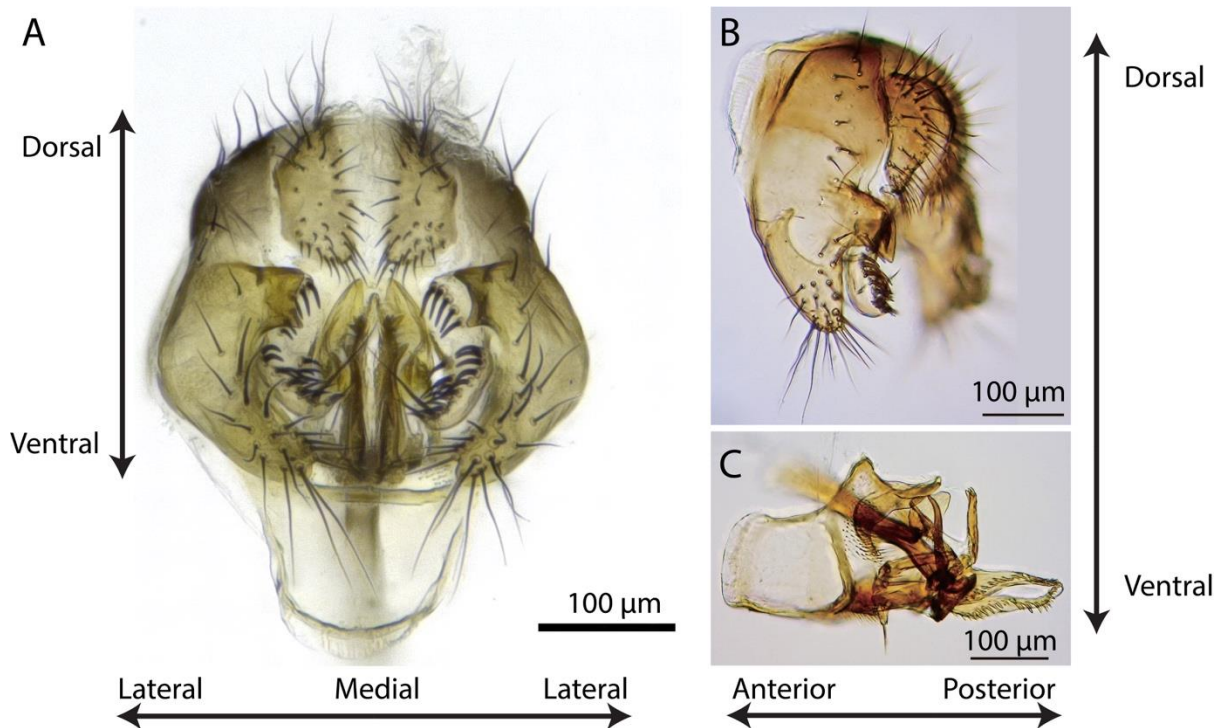


Figure 1. (A) Light microscope preparation of the entire male terminalia of *D. melanogaster* Canton S. Scale bar is 100 µm. (B) Caudolateral view of the periphallalic structures. (C) Ventrolateral view of the phallic structures. Scale bars are 100 µm. Note that the exact size and shape of terminalia structures, such as the epandrial posterior lobe, vary within *D. melanogaster* (Liu et al. 1996; McNeil, Bain and Macdonald 2011).


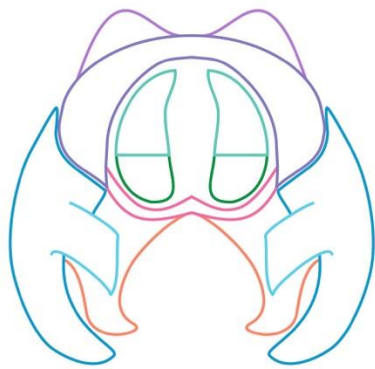






















						
Periphallic structures			Old FlyBase terminology	2019 Revised FlyBase		
 				genital arch	Epandrial anterodorsal phragma	epandrium
					Epandrial dorsal lobe	
			Posterior lobe		Epandrial posterior lobe	
			Lateral plate		Epandrial ventral lobe	
 			Pons/ Decasternum	Subepandrial sclerite		
			Clasper	Surstylus		
 				anal plate	Cercal dorsal lobe	cercus
					Cercal ventral lobe	

Figure 2. Visual atlas of periphallallic structures. Light microscopy images (Canton S strain) and diagrams representing the broad divisions and substructures of epandrium and cercus. The images are

395 oriented dorsal (top) to ventral (bottom). Previous FlyBase terms are on the left and 2019 revised  
396 terms are on the right.


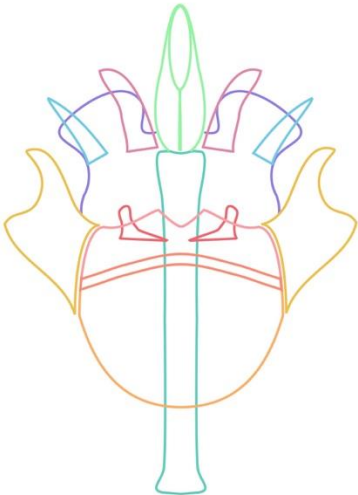























						
Phallic structures			Old FlyBase terminology	2019 Revised Flybase		
			Dorsal paramere	aedeagus	Dorsal postgonite	phallus
					Ventral postgonite	
			Penis mantle/ male gonopod		Aedeagal sheath	
			Penis		Aedeagus	
			Aedeagal apodeme		Phallapodeme	
			Ventral paramere	hypandrium	Pregonite	hypandrium
			Hypandrium		Lateral gonocoxite	
					Median gonocoxite	
					Transverse rod	
					Hypandrial phragma	

Figure 3. Visual atlas of phallic structures. Light microscopy images (Canton S strain) and diagrams representing the broad divisions and substructures of phallus and hypandrium. The images are

400 oriented posterior (top) to anterior (bottom). Previous FlyBase terms are on the left and the 2019  
401 revised terms are on the right.

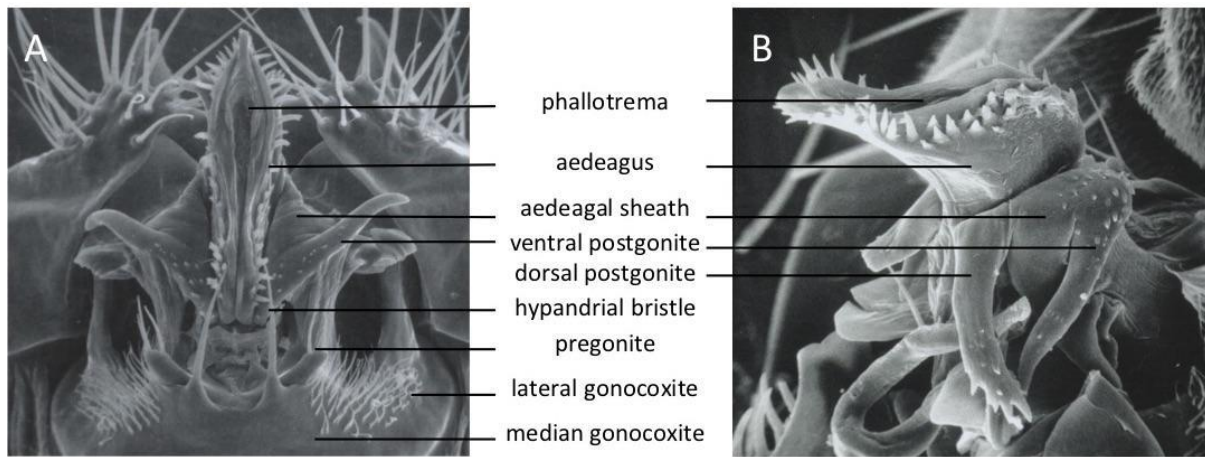


Figure 4. Scanning electron micrographs of the phallic structures in (A) ventral and (B) lateral views, from L. Tsacas' collection at the National Museum of Natural History, Paris (Courtesy of the Museum).

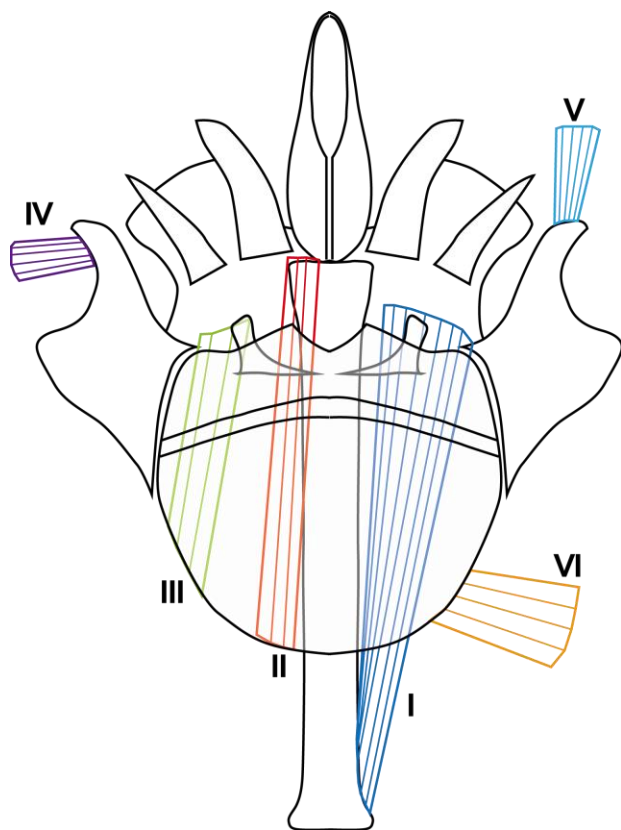


Figure 5. Musculature of the phallic structures. Same diagram of cuticular parts as in Fig. 3 (ventral view). Muscles are indicated in distinct colors and numbered I to VI (Kamimura 2010). These muscles are bilateral. For sake of clarity, muscles are shown either on the left or on the right side of the diagram. See Table 1 for muscles description.

416 **Tables**

417

418 Table 1. Definition of the terms in the standardized nomenclature.

419

<b>Parts</b>
<p><b>Male analia</b> (FBbt:00004825).  Definition: The entire set of external structures in the distal half of the male abdomen, i.e. segment 10, that makes up the anal apparatus (<i>cerci</i> and anus). It develops from the male genital disc.</p>
<p><b>Male genitalia</b> (FBbt:00004828).  Definition: Set of internal and external structures originating from segments 8--9, that makes up the genital apparatus. It develops from the male genital disc.</p>
<p><b>Male terminalia</b> (FBbt:00004835).  Definition: The entire set of external structures in the distal half of the male abdomen, i.e. segments 8--10, that makes up the <i>male genitalia</i> and <i>male analia</i>. It develops from the male genital disc.</p>
<b>Sclerites</b>
<p><b>Aedeagal sheath</b> (FBbt:00004845)  FlyBase synonyms: male gonopod, male paramere, penis mantle.  Definition: A membranous process that dorsally connects to the two posterior sides of the <i>hypandrium</i>, embracing the <i>aedeagus</i> and both pairs of <i>postgonites</i>.  Synonyms: phallus envelope (Tsacas et al. 1971), penis mantle (Salles 1947, Bryant and Hsei 1977), gonopod (Hu and Toda 2001, Kamimura 2010), posterior paramere (Okada 1954, Bock and Wheeler 1972), dorsal arch (Bächli et al. 2004).</p>
<p><b>Aedeagus</b> (FBbt:00004852)  FlyBase synonyms: penis.  Definition: A tubular organ with a single external opening called <i>phallotreme</i>. The aedeagus is entirely membranous and laterally covered with fringe-like, irregular rows of long and blunt scales.  Synonyms: penis (Salles 1947, Ferris 1950, Bryant and Hsei 1977), phallus (Tsacas et al. 1971).</p>
<p><b>Cercal dorsal lobe</b> (FBbt:00048379)  FlyBase synonyms: New term.  Definition: Dorsal portion of the cercus bearing long thin <i>cercal dorsal bristles</i>.</p>
<p><b>Cercal ventral lobe</b> (FBbt:00048380)  FlyBase synonyms: New term.  Definition: Ventral portion of the cercus bearing short rigid <i>cercal ventral bristles</i>.  Synonyms: secondary clasper (Hsu 1949).</p>
<p><b>Cercus</b> (FBbt:00004844)  FlyBase synonyms: anal plate.  Definition: Paired tergite that lies immediately lateral to the anus in males. There are two of these in a male individual.  Synonyms: abdominal tergite 10 (Salles 1947); anal plate (Salles 1947, Hsu 1949, Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977), cercus (Hu and Toda 2001, Bächli et al. 2004).</p>
<p><b>Dorsal postgonite</b> (FBbt:00048381)  FlyBase synonyms: New term.  Definition: Dorsal branch of the postgonite, covered with tiny scales.  Synonyms: dorsal branch of basal process (Kamimura 2010), dorsal paramere (Bryant and Hsei 1977).</p>
<p><b>Epandrial anterodorsal phragma</b> (FBbt:00048382)  FlyBase synonyms: New term.  Definition: thin sclerite connecting the <i>epandrium</i> to abdominal tergites 6 and 7.  Synonyms: abdominal tergite 8 (Salles 1947), phragma (Hsu 1949, Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977).</p>



**Epandrial dorsal lobe** (FBbt:00048383)

FlyBase synonyms: New term.

Definition: Dorsal portion of the *epandrium* above the *epandrial posterior lobe*. The two dorsal lobes are fused into a single sclerite. It contains about 8 long thin bristles.

**Epandrial posterior lobe** (FBbt:00004841)

FlyBase synonyms: posterior lobe.

Definition: Lobe on the posterior region of the *epandrium*. It is posterior to the *epandrial ventral lobe* and mostly covers the *surstylus*.

Synonyms: posterior process (Salles 1947, Hsu 1949), posterior lobe (Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977), dorsal branch of the ventral epandrial lobe (Bächli et al. 2004), lateral lobe (Sánchez and Guerrero 2001), ventral lobe (Eberhard and Ramirez 2004), ventral process (Eberhard and Ramirez 2004).

**Epandrial ventral lobe** (FBbt:00004842)

FlyBase synonyms: lateral plate.

Definition: Lobe ventral to the *epandrial dorsal lobe* and anterior to the *epandrial posterior lobe*. It contains about 22 long thin bristles.

Synonyms: lateral plate (Bryant and Hsei 1977), pouch (Salles 1947), toe (Hsu 1949), epandrial ventral lobe (Bächli et al. 2004).

**Epandrium** (FBbt:00004839)

FlyBase synonyms: genital arch, abdominal tergite 9.

Definition: Horseshoe-shaped tergite which, dorsally, surrounds the male cerci. It contains about 30 *epandrial bristles* on each side. The left and right sides of the epandrium are connected by the *subepandrial sclerite*. The ventral part of each side of the epandrium is divided into an *epandrial ventral lobe* and an *epandrial posterior lobe*.

Synonyms: abdominal tergite 9 (Salles 1947), genital arch (Salles 1947, Hsu 1949, Ferris 1950, Tsacas et al. 1971), epandrium (Tsacas et al. 1971, Hu and Toda 2001, Bächli et al. 2004).

**Gonocoxite** (FBbt:00048384)

FlyBase synonyms: New term.

Definition: Part of the *hypandrium* posterior to the *hypandrial transverse rod*. It is posteriorly protruded into the *lateral gonocoxite* and the *median gonocoxite*.

Synonyms: abdominal sternite 9 (Ferris 1950), novasternum (Okada 1954, Tsacas et al. 1971), gonopod (Bächli et al. 2004).

**Hypandrial phragma** (FBbt:00048385)

FlyBase synonyms: New term.

Definition: Part of the *hypandrium* anterior to the *hypandrial transverse rod*.

Synonyms: intersegmental phragma (Ferris 1950), ventral fragma (Okada 1954), ventral phragma (Tsacas et al. 1971), hypandrium (Bächli et al. 2004), hypandrial apodeme (Kamimura 2010).

**Hypandrial transverse rod** (FBbt:00048386)

FlyBase synonyms: New term.

Definition: Sclerotized line extended transversally from left to right that separates the *hypandrium* into the *gonocoxite* and the *hypandrial phragma*.

Synonyms: transversal thickening of the hypandrium (Salles 1947), sclerotized rod (Tsacas et al. 1971).

**Hypandrium** (FBbt:00004847)

FlyBase synonyms: abdominal sternite 9.

Definition: The male ninth abdominal sternum which extends beneath the phallus. Its posterior ends are dorsally connected to the *aedeagal sheath*. The hypandrium is composed of the *gonocoxite* posteriorly, the *hypandrial phragma* anteriorly and the *hypandrial transverse rod* in between.

Synonyms: novasternum (Wheeler 1960, Okada 1963), hypandrium (Salles 1947, Tsacas et al. 1971, Zhang and Toda 1992, Hu and Toda 2001).

**Lateral gonocoxite** (FBbt:00004849)

FlyBase synonyms: hypandrial process.

Definition: Lateral part of the *gonocoxite*. It comprises a sclerotized pocket into which the female ovipositor inserts during copulation. It is connected with *epandrium* (*epandrial ventral lobe* and *epandrial posterior lobe*) via two pairs of muscle bundles (*male genital muscles IV* and *male genital muscles V*).

Synonyms: outer process (Salles 1947), lateral process (Okada 1954), lateral expansion (Tsacas et al. 1971), paramere (Wheeler 1987, Grimaldi 1990).

**Median gonocoxite** (FBbt:00048387)

FlyBase synonyms: New term.

<p>Definition: Medial part of the <i>gonocoxite</i>, which bears the <i>hypandrial bristle</i>. The two gonocoxites are medially fused into a single sclerite bearing the two hypandrial bristles.</p>
<p><b>Periphallic sclerite</b> (FBbt:00048388)  FlyBase synonyms: New term.  Definition: Sclerites that are used during mating to grasp the female oviscapt from the outside. They include the <i>epandrium</i>, the <i>surstyli</i> and the <i>cerci</i>.</p>
<p><b>Phallapodeme</b> (FBbt:00003524)  FlyBase synonyms: aedeagal apodeme, basal apodeme of penis.  Definition: Long, slender apodeme extending from the base of the <i>phallus</i> into the body.  Synonyms: aedeagal apodeme (Hu and Toda 2001; Bächli et al. 2004)), basal apodeme of penis (Ferris 1950, Okada 1954), penis apodeme (Salles 1947, Bryant and Hsei 1977), phallapodeme (Tsacas et al. 1971)</p>
<p><b>Phallotreme</b> (FBbt:00048389)  FlyBase synonyms: New term.  Definition: External opening of the aedeagus.  Synonyms: gonopore (Grimaldi 1987, Chassagnard 1988, Zhang and Toda 1992, Bächli et al. 2004), phallotreme (Eberhard and Ramirez 2004), secondary gonopore (Sinclair 2000).</p>
<p><b>Phallic sclerites</b> (FBbt:00048390)  FlyBase synonyms: New term.  Definition: Sclerites that are used during mating to penetrate or facilitate penetrating the female vagina. They include the <i>phallus</i>, the <i>phallapodeme</i> and the <i>hypandrium</i>.  Synonyms: penis apparatus (Bryant and Hsei 1977).</p>
<p><b>Phallus</b> (FBbt:00004850)  FlyBase synonyms: aedeagus.  Definition: The main part of the <i>male genitalia</i> used for intromission. The distal portion, through which the male ejaculates, is the <i>aedeagus</i>. The basal portion consists of a pair of bifurcate processes called <i>postgonites</i> and the <i>aedeagal sheath</i>.  Synonyms: aedeagus. Note that the aedeagus corresponds to another anatomical part in the new nomenclature.</p>
<p><b>Postgonite</b> (FBbt:00004854)  FlyBase synonyms: dorsal paramere.  Definition: Bifurcate process on the basal portion of the <i>phallus</i>. The <i>dorsal postgonite</i> is covered with tiny scales, whereas the <i>ventral postgonite</i> has a texture similar to gooseflesh. The dorsal and ventral postgonites are parallel to the aedeagus at rest and spread laterally during erection.  Synonyms: posterior paramere (Okada 1954, Tsacas et al. 1971), dorsal gonapophysis (Salles 1947), basal process (Hu and Toda 2001), inner paraphysis (Bächli et al. 2004).</p>
<p><b>Pregonite</b> (FBbt:00004855)  FlyBase synonyms: ventral paramere.  Definition: A pair of lobes arising from and attached to the <i>hypandrium</i>, anterior to the phallus. They bear small <i>pregonal bristles</i>.  Synonyms: hypandrial process (Bryant and Hsei 1977), paramere (Hu and Toda 2001), paraphysis (Grimaldi 1990), anterior paramere (Okada 1954, Bock and Wheeler 1972), ventral gonapophysis (Salles 1947).</p>
<p><b>Subepandrial sclerite</b> (FBbt:00004840)  FlyBase synonyms: pons, decasternum.  Definition: A bridge-like sclerite that internally connects the two sides of the <i>epandrium</i> beneath the anus.  Synonyms: abdominal sternite 10 (Salles 1947), decasternum (Okada 1956; Bächli et al. 2004), bridge (Salles 1947, Tsacas et al. 1971), pons (Bryant and Hsei 1977).</p>
<p><b>Surstylus</b> (FBbt:00004843)  FlyBase synonyms: clasper.  Definition: Paired hook-shaped sclerotized lobe that extends ventrally from the <i>subepandrial sclerite</i> and surrounds the phallus. It contains 25 thorn-like bristles (<i>surstylar teeth</i>) in a curved band and one <i>long surstylar bristle</i> at the end.  Synonyms: inner lobe of tergite 9 (Ferris 1950), coxopodite (Ferris 1950), clasper (Salles 1947), primary clasper (Hsu 1949), forceps (Tsacas et al. 1971), surstylus (Hu and Toda 2001, Bächli et al. 2004).</p>
<p><b>Ventral postgonite</b> (FBbt:00048391)  FlyBase synonyms: New term.  Definition: Ventral branch of the postgonite, covered with tiny scales.  Synonyms: ventral branch of basal process (Kamimura 2010), ventral paramere (Bryant and Hsei 1977).</p>

<b>Setation</b>
<p><b>Cercal bristle</b> (FBbt:00048392)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>cercus</i>. There are nearly 40 of these.</p>
<p><b>Cercal dorsal lobe bristle</b> (FBbt:00048393)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>cercal dorsal lobe</i>. They are longer and less rigid than the <i>cercal ventral lobe bristle</i>.</p>
<p><b>Cercal ventral lobe bristle</b> (FBbt:00048394)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>cercal ventral lobe</i>. They are shorter and more rigid than the <i>cercal dorsal lobe bristle</i>.</p>
<p><b>Epandrial bristle</b> (FBbt:00048395)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>epandrium</i>. There are 30 of these.</p>
<p><b>Epandrial dorsal lobe bristle</b> (FBbt:00048396)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>epandrial dorsal lobe</i>. There are 8 of these.</p>
<p><b>Epandrial ventral lobe bristle</b> (FBbt:00048397)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>epandrial ventral lobe</i>. There are 22 of these on each lobe.</p>
<p><b>Hypandrial bristle</b> (FBbt:00004472)  Definition: Long bristle located on the <i>median gonocoxite</i>. There are two of these on the <i>hypandrium</i>.</p>
<p><b>Hypandrial hair</b> (FBbt:00004473)  Definition: Fine hair on the <i>median gonocoxite</i>. There is a group of these.</p>
<p><b>Male terminalia sensillum</b> (FBbt:00004469)  Definition: Any sensillum that is part of some <i>male terminalia</i>.</p>
<p><b>Pregonal bristle</b> (FBbt:00048398)  FlyBase synonyms: New term.  Definition: Any bristle that is part of the <i>pregonite</i>. They are 3 of these.</p>
<p><b>Surstylar long bristle</b> (FBbt:00004471)  FlyBase synonyms: clasper long bristle.  Definition: Single long bristle at the end of the <i>surstylus</i>. Sometimes there is more than one long bristle per surstylus.</p>
<p><b>Surstylar teeth</b> (FBbt:00004470)  FlyBase synonyms: clasper tooth.  Definition: Thorn-like bristles of the <i>surstylus</i>. There are 25 of these arranged in a curved band.  Synonyms: clasper teeth (Kopp and True 2002), prenisetae (Grimaldi 1990).</p>
<b>Musculature</b>
<p><b>Male genital muscle I</b> (FBbt:00003552)  FlyBase synonyms: penis protractor muscle.  Definition: A pair of large muscle bundles connecting the anterior end of the <i>phallapodeme</i> and the base of <i>aedeagal sheath + lateral gonocoxite</i>, which works as the protractor muscles of the <i>phallus</i> and its associated structures.  Synonyms: aedeagus protractor muscle, muscles i (Kamimura 2010).</p>
<p><b>Male genital muscle II</b> (FBbt:00110926)  FlyBase synonyms: penis retractor muscle.  Definition: A pair of muscle bundles connecting the base of <i>phallus</i> and the <i>hypandrial phragma</i> which works as the retractor muscles of the <i>phallus</i> and its associated structures.  Synonyms: aedeagus retractor muscle, muscles ii (Kamimura 2010).</p>

**Male genital muscle III** (FBbt:00048399)  
 FlyBase synonyms: New term.  
 Definition: A pair of muscle bundles connecting the base of *aedeagal sheath*, the *lateral gonocoxite* and the *hypandrial phragma*.  
 Synonyms: muscles iii (Kamimura 2010).

**Male genital muscle IV** (FBbt:00048400)  
 FlyBase synonyms: New term.  
 Definition: A pair of muscle bundles connecting the *lateral gonocoxite* and the *epandrial ventral lobe*.  
 Synonyms: muscles iv (Kamimura 2010).

**Male genital muscle V** (FBbt:00048401)  
 FlyBase synonyms: New term.  
 Definition: A pair of muscle bundles connecting the *lateral gonocoxite* below the *epandrial posterior lobe*.  
 Synonyms: muscles v (Kamimura 2010).

**Male genital muscle VI** (FBbt:00048402)  
 FlyBase synonyms: New term.  
 Definition: A pair of muscle bundles connecting the *hypandrial phragma* and the abdominal sternite 6.  
 Synonyms: muscles vi (Kamimura 2010).

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
abdominal sternite 10	Subepandrial sclerite	Salles 1947
abdominal sternite 9*	Gonocoxite	Ferris 1950
abdominal sternite 9*	Hypandrium	old FlyBase terminology
abdominal tergite 10	Cercus	Salles 1947
abdominal tergite 8	Epandrial anterodorsal phragma	Salles 1947
abdominal tergite 9	Epandrium	Salles 1947
aedeagal apodeme	Phallapodeme	Hu and Toda 2001, Bächli et al. 2004
anal plate	Cercus	Salles 1947, Hsu 1949, Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977
anterior paramere	Pregonite	Okada 1954, Bock and Wheeler 1972
basal apodeme of penis	Phallapodeme	Ferris 1950, Okada 1954
basal process	Postgonite	Hu and Toda 2001
bridge	Subepandrial sclerite	Salles 1947, Tsacas et al. 1971
cercus	Cercus	Hu and Toda 2001, Bächli et al. 2004
clasper	Surstylus	Salles 1947
clasper teeth	Surstylar teeth	Kopp and True 2002
coxopodite	Surstylus	Ferris 1950
decasternum	Subepandrial sclerite	Okada 1956; Bächli et al. 2004
dorsal arch	Aedeagal sheath	Bächli et al. 2004
dorsal branch of basal process	Dorsal postgonite	Kamimura 2010

dorsal branch of the ventral epandrial lobe	Epandrial posterior lobe	Bächli et al. 2004
dorsal gonapophysis	Postgonite	Salles 1947
dorsal paramere*	Dorsal postgonite	Bryant and Hsei 1977
dorsal paramere*	Postgonite	old FlyBase terminology
epandrial ventral lobe	Epandrial ventral lobe	Bächli et al. 2004
forceps	Surstylus	Tsacas et al. 1971
genital arch	Epandrium	Salles 1947, Hsu 1949, Ferris 1950, Tsacas et al. 1971
gonopod*	Gonocoxite	Bächli et al 2004
gonopod*	Aedeagal sheath	Hu and Toda 2001, Kamimura 2010
gonopore	Phallotrema	Grimaldi 1987, Chassagnard 1988, Zhang and Toda 1992, Bächli et al. 2004
hypandrial apodeme	Hypandrial phragma	Kamimura 2010
hypandrial process	Pregonite	Bryant and Hsei 1977
hypandrium	Hypandrial phragma	Bächli et al. 2004
inner lobe of tergite 9	Surstylus	Ferris 1950
inner paraphysis	Postgonite	Bächli et al. 2004
intersegmental phragma	Hypandrial phragma	Ferris 1950
lateral expansion	Lateral gonocoxite	Tsacas et al. 1971
lateral lobe	Epandrial posterior lobe	Sánchez and Guerrero 2001
lateral plate	Epandrial ventral lobe	Bryant and Hsei 1977
lateral process	Lateral gonocoxite	Okada 1954
male paramere	Aedeagal sheath	old FlyBase terminology
novasternum*	Gonocoxite	Okada 1954, Tsacas et al. 1971
novasternum*	Hypandrium	Wheeler 1960, Okada 1963
outer process	Lateral gonocoxite	Salles 1947
paramere*	Lateral gonocoxite	Wheeler 1987, Grimaldi 1990
paramere*	Pregonite	Hu and Toda 2001
paraphysis	Pregonite	Grimaldi 1990
penis	Aedeagus	Salles 1947, Ferris 1950, Bryant and Hsei 1977
penis apodeme	Phallapodeme	Salles 1947, Bryant and Hsei 1977
penis apparatus	Phallic sclerites	Bryant and Hsei 1977
penis mantle	Aedeagal sheath	Salles 1947, Bryant and Hsei 1977
phallotreme	phallotrema	Eberhard and Ramirez 2004
phallus	Aedeagus	Tsacas et al. 1971

phallus envelope	Aedeagal sheath	Tsacas et al. 1971
phragma	Epandrial anterodorsal phragma	Hsu 1949, Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977
pons	Subepandrial sclerite	Bryant and Hsei 1977
posterior lobe	Epandrial posterior lobe	Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977
posterior paramere*	Postgonite	Okada 1954, Tsacas et al. 1971, Bock and Wheeler 1972
posterior paramere*	Aedeagal sheath	Okada 1954
posterior process	Epandrial posterior lobe	Salles 1947, Hsu 1949
pouch	Epandrial ventral lobe	Salles 1947
prensisetae	Surstylar teeth	Grimaldi 1990
primary clasper	Surstylus	Hsu 1949
sclerotized rod	Hypandrial transverse rod	Tsacas et al. 1971
secondary clasper	Cercal ventral lobe	Hsu 1949
secondary gonopore	Phallotrema	Sinclair 2000
toe	Epandrial ventral lobe	Hsu 1949
transversal thickening of the hypandrium	Hypandrial transverse rod	Salles 1947
ventral branch of basal process	Ventral postgonite	Kamimura 2010
ventral fragma	Hypandrial phragma	Okada 1954
ventral gonapophysis	Pregonite	Salles 1947
ventral lobe	Epandrial posterior lobe	Eberhard and Ramirez 2004
ventral paramere*	Pregonite	old FlyBase terminology
ventral paramere*	Ventral postgonite	Bryant and Hsei 1977
ventral phragma	Hypandrial phragma	Tsacas et al. 1971
ventral process	Epandrial posterior lobe	Eberhard and Ramirez 2004
<b>* Note that these previously used terms correspond to multiple anatomical parts in the new nomenclature.</b>		