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A Standardized Nomenclature and Atlas of The Male Terminalia of *Drosophila melanogaster*

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

*Corresponding authors: hutian@lemon.plala.or.jp (M.J.T.); rebeiz@pitt.edu (M.R.), virginie.courtier@ijm.fr (V.C.-O,), yassin@mnhn.fr (A.Y.)

[1] Department of Evolution and Ecology, University of California–Davis, Davis, California, United States of America; grr24@pitt.edu

[2] Laboratoire Evolution, Génomes, Comportement, Ecologie (EGCE), UMR 9191, CNRS ,IRD, Univ.Paris-Sud, Université Paris-Saclay, Gif sur Yvette, 91198 cedex, France; Jean.David@egce.cnrs-gif.fr

[3] Department of Biology, Keio University, Hiyoshi, Yokohama 2238521, Japan; kamimura@fbc.keio.ac.jp

[4] Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019; masly@ou.edu

[5] Department of Biological and Medical Sciences, Oxford Brookes University, Gipsy Lane, Oxford, OX3 0BP, UK; p0032455@brookes.ac.uk (A.P.M); p0076379@brookes.ac.uk (M.D.S.N.);

[6] CNRS UMR7592, Institut Jacques Monod, Université de Paris, Paris, France; olga.nagy@ijm.fr

[7] Université Côte d'Azur, CNRS, INSERM, iBV, Nice, France; Stephane.NOSELLI@unice.fr

[8] Department of Entomology, Cornell University, Ithaca, NY; ogrady@drosophilaevolution.com

[9] Centro de Biología Molecular Severo Ochoa (C.S.I.C.-U.A.M.), Universidad Autónoma de Madrid, Nicolás Cabrera 1, Cantoblanco, 28049 Madrid, Spain; esherrero@cbm.csic.es

[10] Center for Genomics and Systems Biology, Department of Biology, New York University; mark.siegal@nyu.edu

[11] Hokkaido University Museum, Hokkaido University, Sapporo 060-0810, Japan

[12] 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

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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

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Introduction

Insect terminalia, which usually encompass the male and female genitalia, 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) 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; Frazee and Masly 2015; Hurtado-Gonzales et al. 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) revision 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.

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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* (McNeil, Bain and Macdonald 2011; Liu et al. 1996). In Table 1, we propose a unified nomenclature of the various anatomical elements as well as their correspondences with previously used terms. Correspondence with previously used terms is presented in Table 2. 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).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 connect 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 Sanchez 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). All of these structures except the phallapodeme form the intromittent organ or phallus. The

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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 movement of these parts may be induced through the complex musculature found in the phallus (Figure 5; Kamimura 2010).

The aedeagus is surrounded dorso-laterally by the aedeagal sheath and ventrally by the hypandrium. The hypandrium is a large structure that can be broken down into several identifiable substructures. The posterior end of the hypandrium, named the median gonocoxite hosts a pair of large bristles whereas each pregonite displays two to three smaller bristles (Taylor 1989; Nagy et al. 2018).

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, pregonites 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 (Sánchez et al. 1997) may also better justify the exact boundaries of each anatomical element, and could motivate further refinements into smaller sub-parts.

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. Although we focused on the *D. melanogaster* terminalia, a standardized terminology will be vital for clarity in studies of *Drosophila* species and their comparisons. 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 500x magnification with a digital microscope VHX 2000 (Keyence) using lens VH-Z20R/W. For Figure 1B and 1C digital

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images were taken at different depths of focus using a Dino-Lite® Microscope Eyepiece Camera (AM7025X, AnMo Electronics Corporation) on a Olympus BX50 microscope and stacked with CombineZP 1.0 (https://combinezp.software.informer.com/). For Figures 2 and 3, samples were imaged at 16X magnification on a Leica M205C microscope with a Leica DFC425 camera or at 20X magnification on a Leica DM 2000 with a Leica DFC540 C camera. Images from the former microscope were Z stack-compiled with the Leica Application Suite to allow for optimal focus. Images of the epandrial anterodorsal phragma, epandrial dorsal lobe, epandrial posterior lobe, epandrial ventral lobe, subepandrial sclerite, cercal dorsal lobe, cercal ventral lobe, lateral gonocoxite, median gonocoxite, transverse rod, and hypandrial phragma were modified in Adobe Photoshop via the eraser tool to isolate full parts along sutures to provide the clearest view of each part in its entirety. Photoshop was used because dissection of the various parts would be difficult.

Disclosure of potential conflicts of interest

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

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Figures:

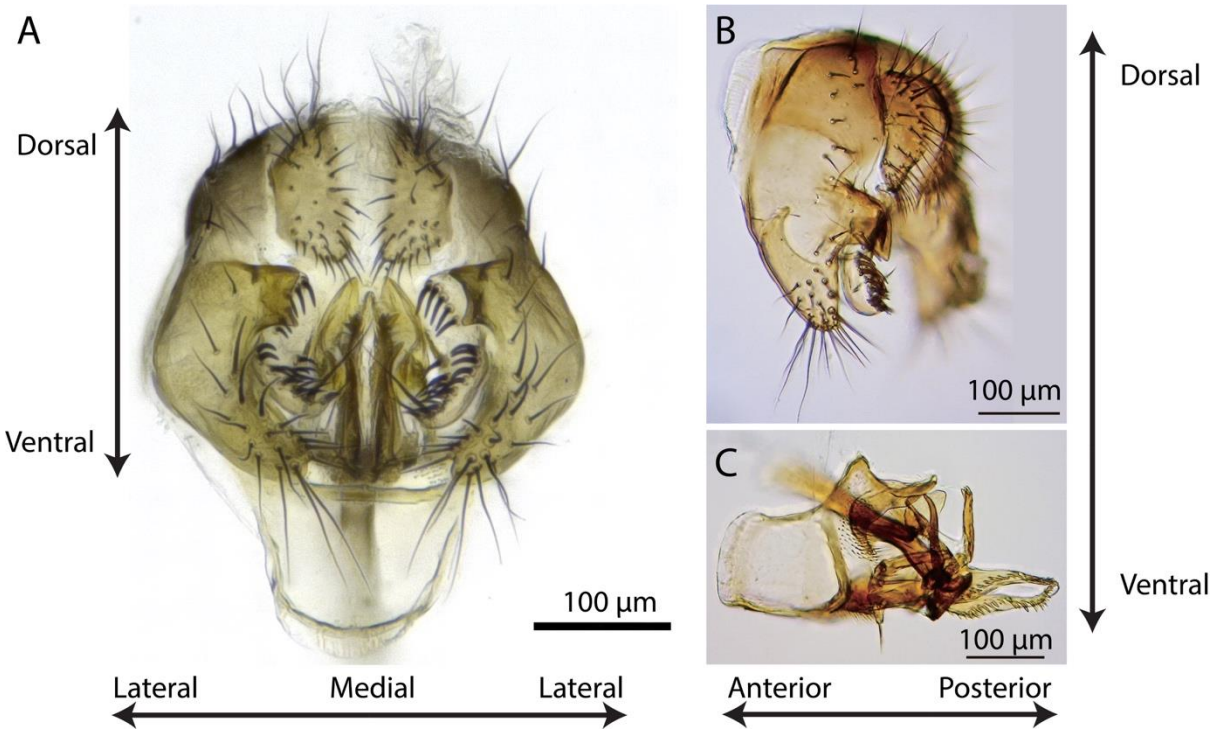

Figure 1. (A) Light microscope preparation of the entire male terminalia of *D. melanogaste*r Canton S. Scale bar is 100 µm. (B) Caudolateral view of the periphallic structures. (C) Ventrolateral view of the phallic structures. Scale bars are 100 µm. Note that the exact size and shape of terminalia structures,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

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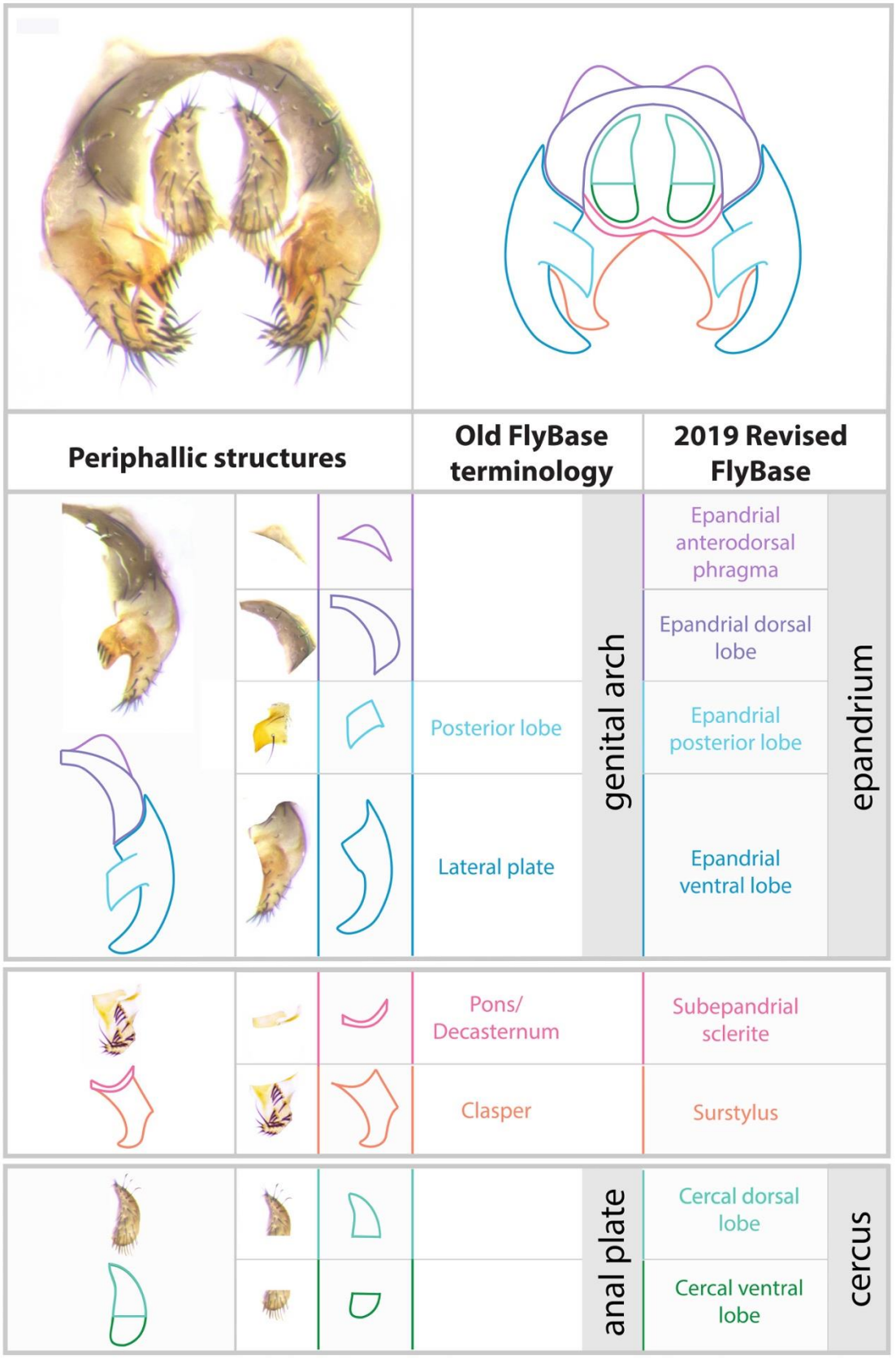

Figure 2. Visual atlas of periphallic structures. Light microscopy images (Canton S strain) and diagrams representing the broad divisions and substructures of epandrium and cercus. The images are oriented dorsal (top) to ventral (bottom). Previous FlyBase terms are on the left and 2019 revised terms are on the right.

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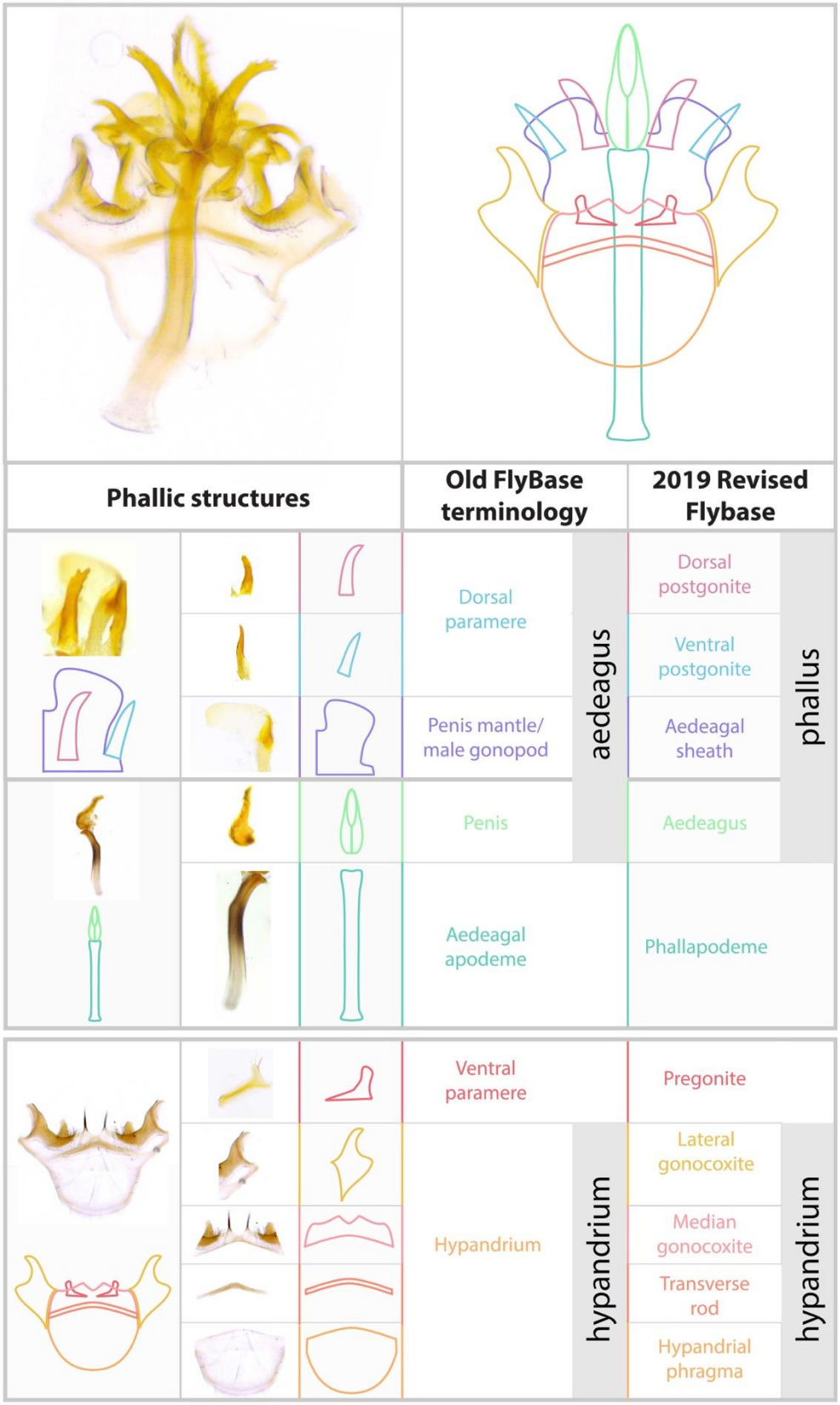

Figure 3.
Visual atlas of phallic structures. Light microscopy images (Canton S strain) and diagrams representing the broad divisions and substructures of phallus and hypandrium. The images are oriented posterior (top) to anterior (bottom). Previous FlyBase terms are on the left and the 2019 revised terms are on the right.

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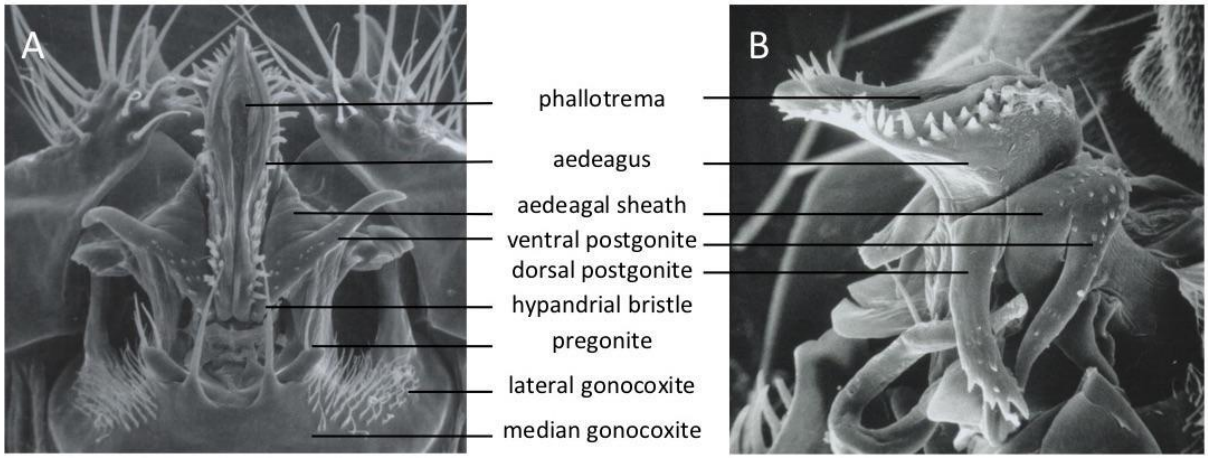

Figure 4. Scanning electron micrographs of the phallic structures in (A) ventral and (B) lateral views, from L. Tsacas' collection at the National Museum of Natural History, Paris (Courtesy of the Museum).

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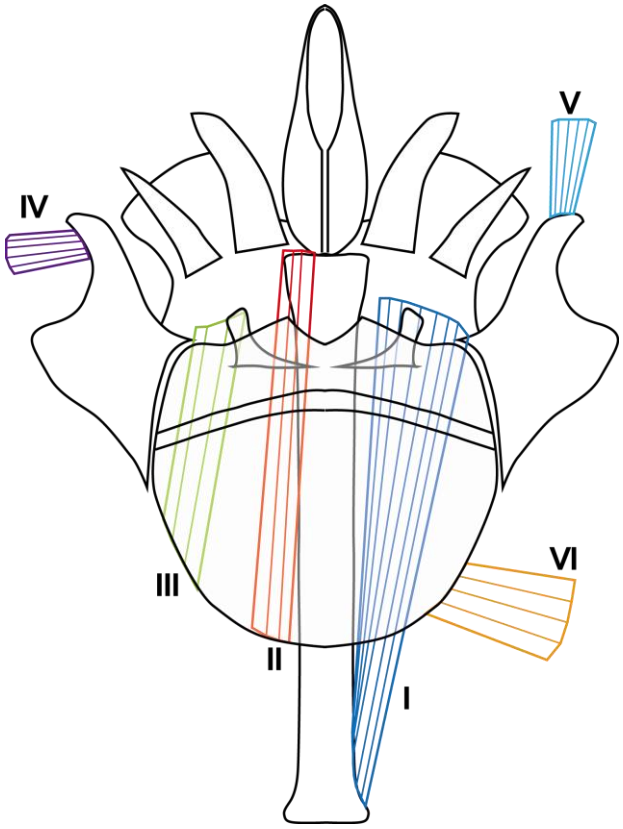

Figure 5. Musculature of the phallic structures. Same diagram of cuticular parts as in Fig. 3 (ventral view). Muscles are indicated in distinct colors and numbered I to VI (Kamimura 2010). These muscles are bilateral. For sake of clarity, muscles are shown either on the left or on the right side of the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

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Tables

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

Parts
Male analia (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 (*cerci* and anus). It develops from the male genital disc.
Male genitalia (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.
Male terminalia (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 *male genitalia* and *male analia*. It develops from the male genital disc.
Sclerites
Aedeagal sheath FlyBase synonyms: male gonopod, male paramere (FBbt:00004845), penis mantle (FBbt:00004853). Definition: A membranous process that dorsally connects to the two posterior sides of the *hypandrium*, embracing the *aedeagus* and both pairs of *postgonites*. 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).
Aedeagus FlyBase synonyms: penis (FBbt:00004852). Definition: A tubular organ with a single external opening called *phallotrema*. 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), aedeagus (Okada 1954, Hu and Toda 2001, Bächli et al. 2004), phallus (Tsacas et al. 1971).
Cercal dorsal lobe FlyBase synonyms: New term. Definition: Dorsal portion of the cercus bearing long thin *cercal dorsal bristles*.
Cercal ventral lobe FlyBase synonyms: New term. Definition: Ventral portion of the cercus bearing short rigid *cercal ventral bristles*. Synonyms: secondary clasper (Hsu 1949).
Cercus FlyBase synonyms: anal plate (FBbt:00004844). 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).
Dorsal postgonite 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).
Epandrial anterodorsal phragma FlyBase synonyms: New term. Definition: thin sclerite connecting the *epandrium* to abdominal tergites 6 and 7.

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Synonyms: abdominal tergite 8 (Salles 1947), phragma (Hsu 1949, Ferris 1950, Tsacas et al. 1971, Bryant and Hsei 1977).

Epandrial dorsal lobe
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
FlyBase synonyms: posterior lobe (FBbt:00004841).
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
FlyBase synonyms: lateral plate (FBbt:00004842).
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
FlyBase synonyms: genital arch, abdominal tergite 9 (FBbt:00004839)
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. 2001).

Gonocoxite
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
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
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), scleoritzed rod (Tsacas et al. 1971).

Hypandrium
FlyBase synonyms: hypandrium, abdominal sternite 9 (FBbt:00004847).
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, Zhang and Toda 1992), hypandrium (Salles 1947, Tsacas et al. 1971, Hu and Toda 2001).

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Lateral gonocoxite
FlyBase synonyms: hypandrial process (FBbt:00004849)
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
FlyBase synonyms: New term.
Definition: Medial part of the *gonocoxite*, which bears the *hypandrial bristle*. The two gonocoxites are medially fused into a single sclerite bearing the two hypandrial bristles.

Periphallic sclerites
FlyBase synonyms: New term.
Definition: Sclerites that are used during mating to grasp the female oviscapt from the outside. They include the *epandrium*, the *surstyli* and the *cerci*.

Phallapodeme
FlyBase synonyms: aedeagal apodeme (FBbt:00003523), basal apodeme of penis (FBbt:00003524).
Definition: Long, slender apodeme extending from the base of the *phallus* 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)

Phallotrema
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).

Phallic sclerites
FlyBase synonyms: New term.
Definition: Sclerites that are used during mating to penetrate or facilitate penetrating the female vagina. They include the *phallus*, the *phallapodeme* and the *hypandrium*.
Synonyms: penis apparatus (Bryant and Hsei 1977).

Phallus
FlyBase synonyms: aedeagus (FBbt:00004850).
Definition: The main part of the *male genitalia* used for intromission. The distal portion, through which the male ejaculates, is the *aedeagus*. The basal portion consists of a pair of bifurcate processes called *postgonites* and the *aedeagal sheath*.
Synonyms: aedeagus. Note that the aedeagus corresponds to another anatomical part in the new nomenclature.

Postgonite
FlyBase synonyms: dorsal paramere (FBbt:00004854).
Definition: Bifurcate process on the basal portion of the *phallus*. The *dorsal postgonite* is covered with tiny scales, whereas the *ventral postogonite* 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).

Pregonite
FlyBase synonyms: ventral paramere (FBbt:00004855).
Definition: A pair of lobes arising from and attached to the *hypandrium*, anterior to the phallus. They bear small *pregonal bristles*.
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).

Subepandrial sclerite
FlyBase synonyms: decasternum (FBbt:00004848), pons (FBbt:00004840).

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Definition: A bridge-like sclerite that internally connects the two sides of the *epandrium* 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).

Surstylus
FlyBase synonyms: clasper (FBbt:00004843).
Definition: Paired hook-shaped sclerotized lobe that extends ventrally from the *subepandrial sclerite* and surrounds the phallus. It contains 25 thorn-like bristles (*surstylar teeth*) in a curved band and one *long surstylar bristle* 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).

Ventral postgonite
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).

Setation

Cercal bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *cercus*. There are nearly 40 of these.

Cercal dorsal lobe bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *cercal dorsal lobe*. They are longer and less rigid than the c*ercal ventral lobe bristles*.

Cercal ventral lobe bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *cercal ventral lobe*. They are shorter and more rigid than the *cercal dorsal lobe bristles*.

Epandrial bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *epandrium*. There are 30 of these.

Epandrial dorsal lobe bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *epandrial dorsal lobe*. There are 8 of these.

Epandrial ventral lobe bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *epandrial ventral lobe*. There are 22 of these on each lobe.

Hypandrial bristle
FlyBase synonyms: hypandrial bristle (FBbt:00004472).
Definition: Long bristle located on the *median gonocoxite*. There are two of these on the *hypandrium*.

Hypandrial hair
FlyBase synonyms: hypandrial hair (FBbt:00004473).
Definition: Fine hair on the *median gonocoxite*. There is a group of these.

Male terminalia sensillum
FlyBase synonyms: male terminalia sensillum (FBbt:00004469).
Definition: Any sensillum that is part of some *male terminalia*.

Pregonal bristles
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *pregonite*. They are 3 of these.

Surstylar long bristle

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FlyBase synonyms: clasper long bristle (FBbt:00004471). Definition: Single long bristle at the end of the *surstylus*. Sometimes there is more than one long bristle per surstylus.
Surstylar teeth FlyBase synonyms: clasper tooth (FBbt:00004470). Definition: Thorn-like bristles of the *surstylus*. There are 25 of these arranged in a curved band. Synonyms: clasper teeth (Kopp and True 2002), prensisetae (Grimaldi 1990).
Musculature
Male genital muscle I FlyBase synonyms: penis protractor muscle (FBbt:00003552). Definition: A pair of large muscle bundles connecting the anterior end of the *phallapodeme* and the base of *aedeagal sheath + lateral gonocoxite*, which works as the protractor muscles of the *phallus* and its associated structures. Synonyms: aedeagus protractor muscle, muscles i (Kamimura 2010).
Male genital muscle II FlyBase synonyms: penis retractor muscle (FBbt:00110926). Definition: A pair of muscle bundles connecting the base of *phallus* and the *hypandrial phragma* which works as the retractor muscles of the *phallus* and its associated structures. Synonyms: aedeagus retractor muscle, muscles ii (Kamimura 2010).
Male genital muscle III 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 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 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 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

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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 goncoxite	Tsacas et al. 1971
lateral lobe	Epandrial posterior lobe	Sánchez and Guerrero 2001
lateral plate	Epandrial ventral lobe	Bryant and Hsei 1977

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lateral process	Lateral goncoxite	Okada 1954
male paramere	Aedeagal sheath	old FlyBase terminology
novasternum	Gonocoxite	Okada 1954, Tsacas et al. 1971
novasternum	Hypandrium	Wheeler 1960, Okada 1963, Zhang and Toda 1992
outer process	Lateral goncoxite	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
scleoritzed 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

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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