4   **A Standardized Nomenclature and Atlas of the Male Terminalia of *Drosophila melanogaster***

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32   **Abstract**

33   Animal terminalia represent some of the most diverse and rapidly evolving structures in the animal

34   kingdom, and for this reason have been a mainstay in the taxonomic description of species. The

35   terminalia of *Drosophila melanogaster*, with its wide range of experimental tools, have recently

36   become the focus of increased interest in the fields of development, evolution, and behavior.

37   However, studies from different disciplines have often used discrepant terminologies for the same

38   anatomical structures. Consequently, the terminology of genital parts has become a barrier to

39   integrating results from different fields, rendering it difficult to determine what parts are being

40   referenced. We formed a consortium of researchers studying the genitalia of *D. melanogaster* to help

41   establish a set of naming conventions. Here, we present a detailed visual anatomy of male genital

42   parts, including a list of synonymous terms, and suggest practices to avoid confusion when referring

43   to anatomical parts in future studies. The goal of this effort is to facilitate interdisciplinary

44   communication and help newcomers orient themselves within the exciting field of *Drosophila*

45   genitalia.

46

47   **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) 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.

76   Believing that the breadth and richness of the three research disciplines offers a unique

77   opportunity for integrative biology, the purpose of the current paper is to unify terminology of

78   *Drosophila* male terminalia (Figure 1). As a group of researchers working on different aspects of

79   *Drosophila* terminalia, we think that a unified system would facilitate exchanges between research

80   fields. Although some researchers highlighted the usefulness of the traditional system in providing

81   meaningful English terms rather than obscure Latin-derived names (e.g., clasper vs. surstylus), the

82   majority opted for the phylogenetic tradition which captures homology relationships between species.

83   Consequently, we provide an update of the terminalia terminology found in FlyBase. For the

84   problematic terms (parameres, paraphyses, and gonopods), we relied on Sinclair's (2000) and

85   Cumming and Wood's (2017) revisions of Diptera terminalia nomenclature to propose new terms not

86   previously used in *Drosophila* biology (namely, pregonites, postgonites, and gonocoxites). Although

87   we restricted our revision to male terminalia, we do so with the intention to address female

88   terminology later.

89   **Results and Discussion**

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

91   In much of the past literature, genital morphology was rendered by hand-drawings, and the

92   names of different parts were indicated by lines pointing to each structure. As new researchers join

93   this growing field, it can be quite difficult to grasp the exact extent of a structure based on these

94   drawings. In order to make the revised nomenclature as useful as possible, we provide here a visual

95   guide to this terminology which shows both drawings and cuticle images that outline the full extent of

96   each named part (Figures 2, 3). It is important to note that the exact size and shape of these structures,

97   such as the epandrial posterior lobe, can vary within *D. melanogaster* (Liu et al. 1996; McNeil, Bain

98   and Macdonald 2011). In Table 1, we propose a unified nomenclature of the various anatomical

99   elements containing definitions and references to previously used terms. Conversely, Table 2 provides

100   correspondence from previously used terms to the unified nomenclature. Although the current set of

101   nomenclature is centered around *D. melanogaster*, we have adopted general terms such that most

102   should also apply to other Drosophilidae species.

103   The male terminalia of *D. melanogaster* corresponds to the entire set of external structures in

104   the distal half of the male abdomen (Figures 1–3), i.e. segments 8–10. It derives from the genital disc,

105   which comprises three primordia: a reduced Abdominal segment 8 primordium, which in females

106   gives rise to most genital structures but in males gives rise only to a miniature eighth tergite (here

107   termed the epandrial anterodorsal phragma, see below); an Abdominal segment 9 primordium,

108   forming the male genitalia, and the Abdominal segment 10 primordium, making the analia (Keisman

109   et al., 2001). During development, the *D. melanogaster* male genitalia rotates 360 degrees clockwise,

110   causing the internal organs to loop around the gut; this rotation and thus the dorsal/ventral designation

111   of the genitalia varies within Diptera (Suzanne et al. 2010). We dissected and imaged adult cuticle

112   preparations of a *D. melanogaster* wild type strain (Canton S), and provide cuticle images as well as

113   drawings of the distinct parts in Figures 1–3. To maximize clarity, we present each part both in

114   isolation and in the context of intact tissue, and we indicate the outlines of each anatomical

115   component (Figures 2, 3).

116   We have subdivided the terminalia into two parts, periphallic structures, which are secondarily

117   connected to the intromittent organ (Figure 2) and the phallic structures, which comprise the

118   intromittent organ and structures directly connected to it (Figure 3). These two classes are easily

119   separable via dissection in the adult.

120

121   *Periphallic portions of the terminalia*

122   Periphallic structures comprise the cercus (former anal plate), the epandrium (former genital

123   arch), the pair of surstyli (former claspers) and the subepandrial sclerite (former pons) that connects

124   the surstyli to the other periphallic structures (Figure 1). Although periphallic structures are not

125   directly involved in transferring sperm, several of them (cercus, surstylus, and epandrial posterior

126   lobe) have been implicated in grasping onto the female during copulation (Robertson 1988; Eberhard

127   and Ramirez 2004; Jagadeeshan and Singh 2006; Kamimura 2010; Kamimura and Mitsumoto 2011;

128   Mattei et al. 2015; Frazee and Masly 2015; LeVasseur-Viens et al. 2015). Additionally, although

129   many of these structures do not show obvious boundaries in *D. melanogaster*, they are far more

130   complex in its close relatives, suggesting that there are natural subdivisions of these structures in

131   some species. For example, while the ventral margin of the cercus forms a relatively flat cuticle in *D.*

132   *melanogaster,* it bears a lobe-like extension in *D. bipectinata* that affects copulatory success (Polak

133   and Rashed 2010; Kamimura and Polak 2011). Furthermore, the dorsal and ventral parts of the cercus

134   accumulate distinct levels of *engrailed* in *D. melanogaster* (Fig. 3F in Sánchez et al. 1997).

135

136   *Subdivision and nomenclature of phallic parts*

137   During copulation, several parts of the male genitalia enter the female vagina: the aedeagus,

138   part of the phallapodeme, the ventral and dorsal postgonites, and the aedaegal sheath (Kamimura

139   2010; Mattei et al. 2017). All of these structures except the phallapodeme form the intromittent organ

140   or phallus. The aedeagus is perhaps the most complex structure of the male genitalia of *D.*

141   *melanogaster:* it is covered with cuticular projections and its shape varies broadly between closely

142   related species (see Figures 13, 14, 16, 17 of Tsacas et al. 1971; Yassin and Orgogozo 2013). The

143   postgonites are flexible relative to the aedeagus; they move progressively during mating and have

144   been implicated in producing copulatory wounds in females (Kamimura 2010). The aedeagal sheath

145   surrounds the aedeagus and the postgonites dorso-laterally. It also moves outwards during mating.

146   The movement of the postgonites and the aedeagal sheath may be induced through the complex

147   musculature found in the phallus (Figure 5; Kamimura 2010).

148   The hypandrium is a large structure that surrounds the phallus ventrally. It can be broken

149   down into several identifiable substructures. We consider the posterior part to be fused gonocoxites

150   (see below) and divide each gonocoxite into two parts lateral and median. The fused median

151   gonocoxites host a pair of large bristles (Taylor 1989; Nagy et al. 2018). They connect to the phallus

152   through via the two pregonites. Each pregonite displays two to three smaller bristles.

153

154   *Justifying the separation/individuality of parts*

155   It is important to note that the boundary of each anatomical element is based largely on

156   defined cuticular ridges observed in the adult. However, some key parts lack clear boundaries with

157   other adjacent tissues. Examples include the epandrial posterior lobe, cercal ventral and dorsal lobes,

158   and sub-parts of the hypandrium. We envision that in these cases, a careful analysis of cellular

159   formation during development will be necessary to precisely define the boundaries of separate parts.

160   Experiments that map the spatial expression patterns of regulatory genes such as transcription factors

161   further support the boundaries of each anatomical element, and could motivate further refinements

162   into smaller sub-parts (Sánchez et al. 1997; Vincent et al. 2019).

163

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

165   The term "surstylus" has been proposed by Crampton (1923) to refer to the clasping organs

166   that are associated with the dorsal compartment of the genitalia (*i.e.* epandrium) in Eremoneuran

167   (Higher) Diptera to which *Drosophila* belongs. In non-Eremoneuran (Lower) Diptera and in other

168   related insect orders, the clasping organs consist of appendices, the gonopods, consisting of two

169   substructures, the gonocoxites and the gonostyli, that are associated with the ventral compartment of

170   the genitalia (*i.e.* the hypandrium). Crampton's view, which would later be called the "surstylar

171   concept" (Zatwarnicki 1996), postulates that the gonostyli have been lost whereas the gonocoxites

172   remain associated with the hypandrium in Eremoneurans. This view has a wide acceptance among

173   Dipterologists (Yeates and Wiegmann 1999; Sinclair 2000; Cumming and Wood 2017), as well as

174   between Drosophila systematists who have opted for a revised terminology (Grimaldi 1990; Hu and

175   Toda 2001; Bächli et al. 2004). For example, the term gonopod, whereas used for different structures

176   in *D. melanogaster* (see Tables 1 and 2), has always been applied to ventral structures associated with

177   the phallic portions.

178   However, alternative hypotheses for the origin of the Eremoneuran dorsal claspers exist, *i.e.*

179   the "gonostylar concept", postulating that Eremoneuran dorsal claspers are homologous to the ventral

180   gonopods (mostly to the gonostyli) of non-Eremoneuran Diptera (reviewed in Zatwarnicki 1996).

181   Zatwarnicki (1996) further considered the subepandrial sclerite (*medandrium* in Zatwarnicki 1996)

182   to be homologous to the gonocoxites. Although evaluating these concepts goes far beyond the scope

183   of our paper, we believe that further research in *Drosophila* could ultimately help elucidating the

184   origin of the Eremoneuran dorsal claspers. For example, Abd-B mutants in *D. melanogaster* genital

185   disc transform the phallic structures, as well as a part of the surstylus (clasper), into a leg (Estrada and

186   Sanchez-Herrero 2001). This supports the idea that the ventral parts of the Eremoneuran genitalia are

187   of appendicular origin (as the name gonopod, *i.e.* genital leg, would suggest), but it also suggests that

188   a part (not the whole) of the surstylus might be of appendicular origin. Further mapping of

189   transcription factors expression in the different compartments of the male terminalia between *D.*

190   *melanogaster* (e.g., Vincent et al. 2019) and other non-Eremoneuran Diptera could shed light on the

191   deep homology between these structures. At the time being, and because our major aim is to unify

192   terms used by *Drosophila* biologists, we have opted here for the terminology based on the "surstylar

193   concept", and we hope that this would prompt further research on these questions.

194

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

196   The revised terminology described here should facilitate cross-disciplinary synthesis of our

197   knowledge of genital function, development, and evolution. We have worked with the FlyBase team

198   to integrate these terms into their anatomy ontology (Costa et al. 2013; Thurmond et al. 2019).

199   Although we focused on the *D. melanogaster* terminalia, a standardized terminology is vital/crucial

200   for the ease of comparing various species. Thus, it is our hope that these terms will facilitate

201   descriptions of homologous and novel structures in other insect species. It was important for us to

202   include as much of the community of researchers working on *Drosophila* genital morphology as

203   possible to reach consensus in the definition and deployment of this terminology. We suggest that

204   when publishing studies that name these structures, authors use the terms of the revised terminology,

205   while parenthetically citing alternate synonyms such as familiar terms, e.g. surstylus (clasper). For

206   those who would like to use familiar terms (perhaps for the purpose of continuity with previous

207   publications), we would strongly recommend that the revised terminology is presented

208   parenthetically, e.g. clasper (surstylus). This way, the broader scientific community can understand

209   and integrate results with as few barriers to comprehension as possible.

210   Studies of *Drosophila* genitalia have provided examples of large-scale differences between

211   males and females, vital taxonomic traits to distinguish species from one another, and important

212   factors in the reproductive incompatibility between species. Yet, the complexity of the genitalia itself

213   presents barriers to the study of these fascinating anatomical parts. This problem has been aggravated

214   by variability in nomenclature, which has further impeded entry into this field. The revision and visual

215   atlas of male genital structures provided here will hopefully allow for increased communication across

216   a range of disciplines and welcome new scientists to this growing field.

217

218   **Materials and Methods**

219   A Canton S line of *Drosophila melanogaster* (Bloomington # 64349) was used for all

220   imaging. Adult males were dissected in 100% EtOH with micro-forceps and mounted in PVA

221   Mounting Medium (BioQuip). For Figure 1A, the sample was imaged at 500× magnification with a

222   digital microscope VHX 2000 (Keyence) using lens VH-Z20R/W. For Figure 1B and 1C digital

223   images were taken at different depths of focus using a Dino-Lite® Microscope Eyepiece Camera

224   (AM7025X, AnMo Electronics Corporation) on an Olympus BX50 microscope and stacked with

225   CombineZP 1.0 (https://combinezp.software.informer.com/). For Figures 2 and 3, samples were

226   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.

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

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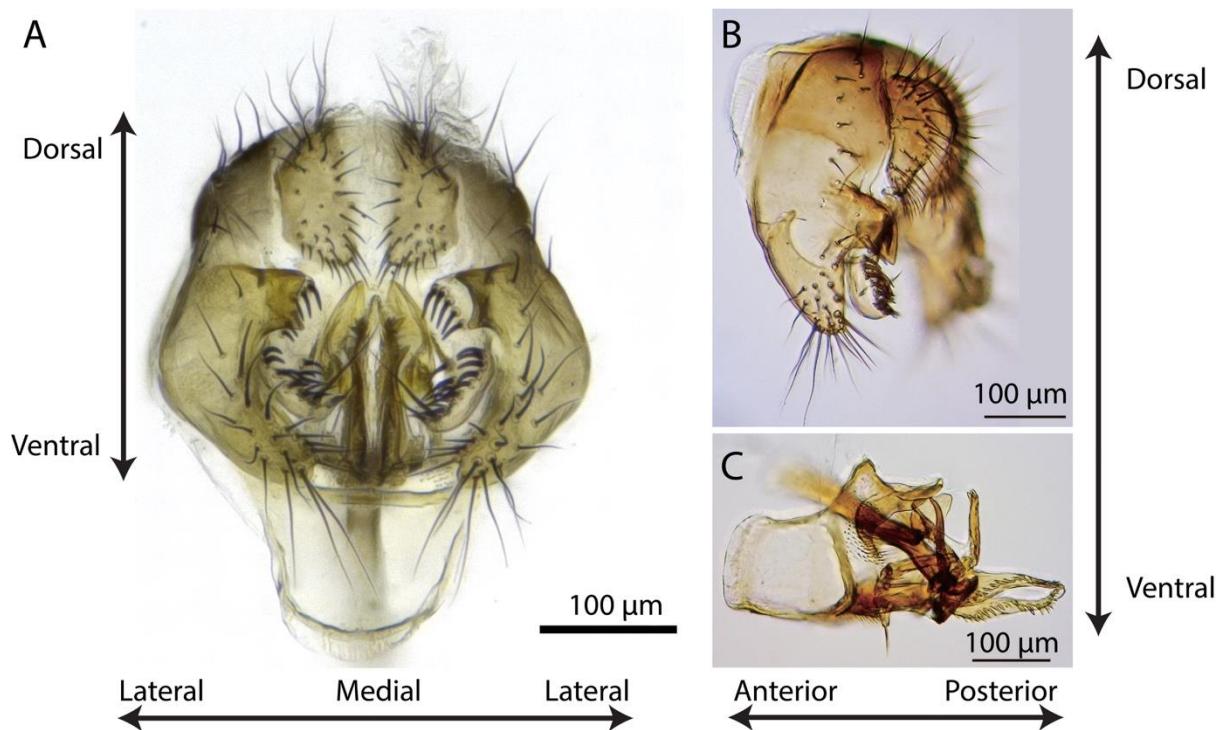
384 **Figures:**

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386

387   Figure 1. (A) Light microscope preparation of the entire male terminalia of *D. melanogaste*r Canton

388   S. Scale bar is 100 μm. (B) Caudolateral view of the periphallic structures. (C) Ventrolateral view of

389   the phallic structures. Scale bars are 100 μm. Note that the exact size and shape of terminalia

390   structures, such as the epandrial posterior lobe, vary within *D. melanogaster* (Liu et al. 1996; McNeil,

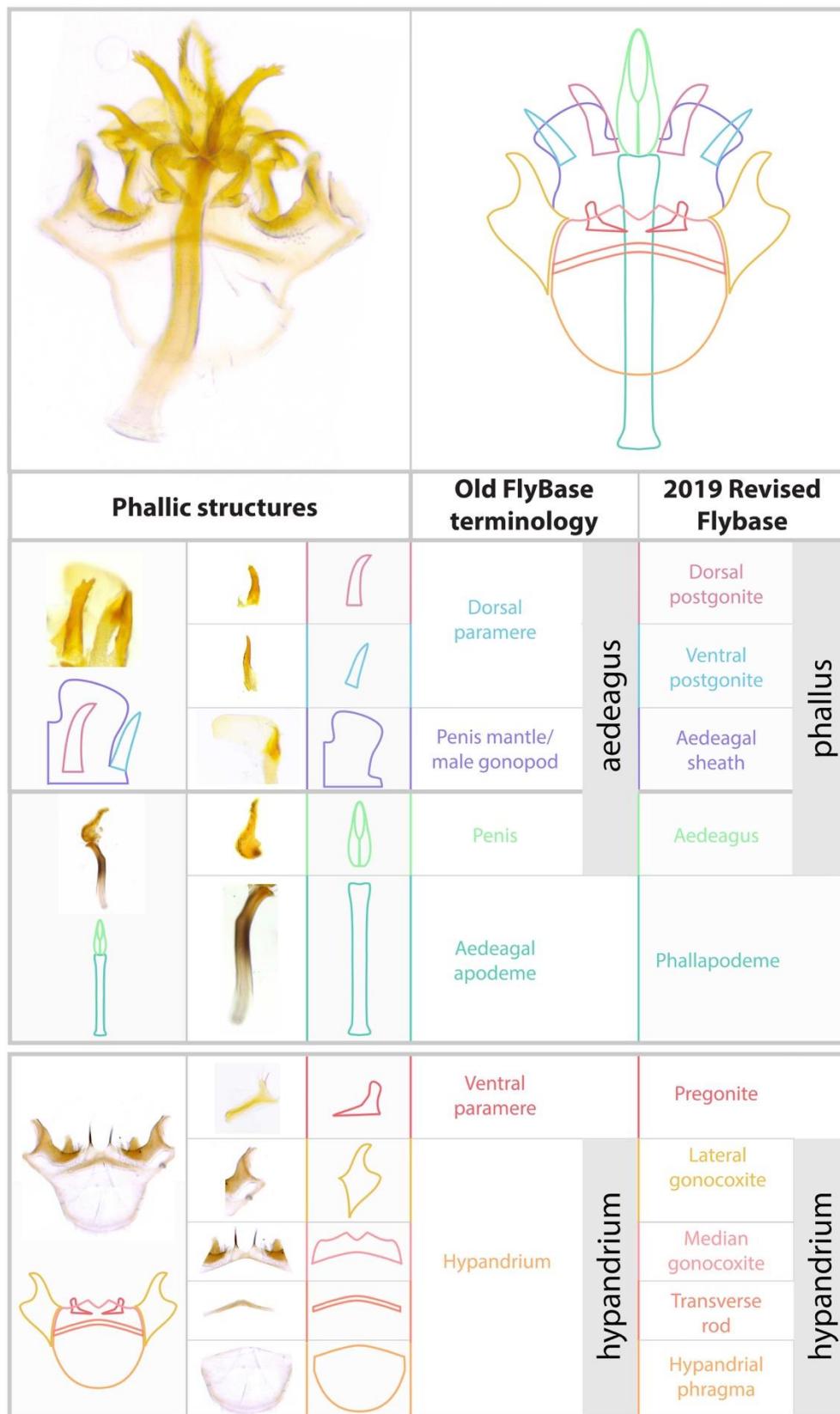
391   Bain and Macdonald 2011).

392

393   Figure 2. Visual atlas of periphallic structures. Light microscopy images (Canton S strain) and

394   diagrams representing the broad divisions and substructures of epandrium and cercus. The images are

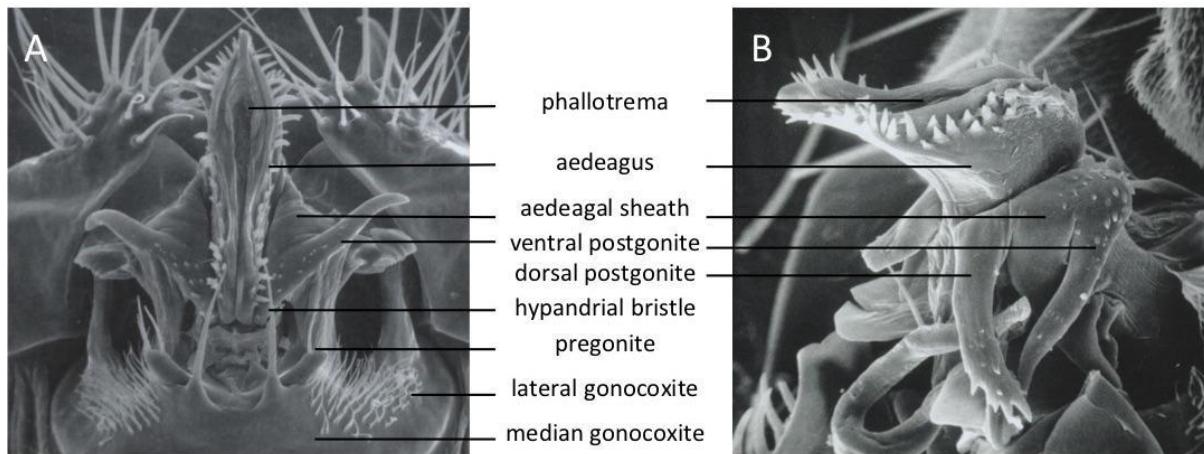
395   oriented dorsal (top) to ventral (bottom). Previous FlyBase terms are on the left and 2019 revised

396   terms are on the right.

397

398   Figure 3. Visual atlas of phallic structures. Light microscopy images (Canton S strain) and diagrams

399   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.

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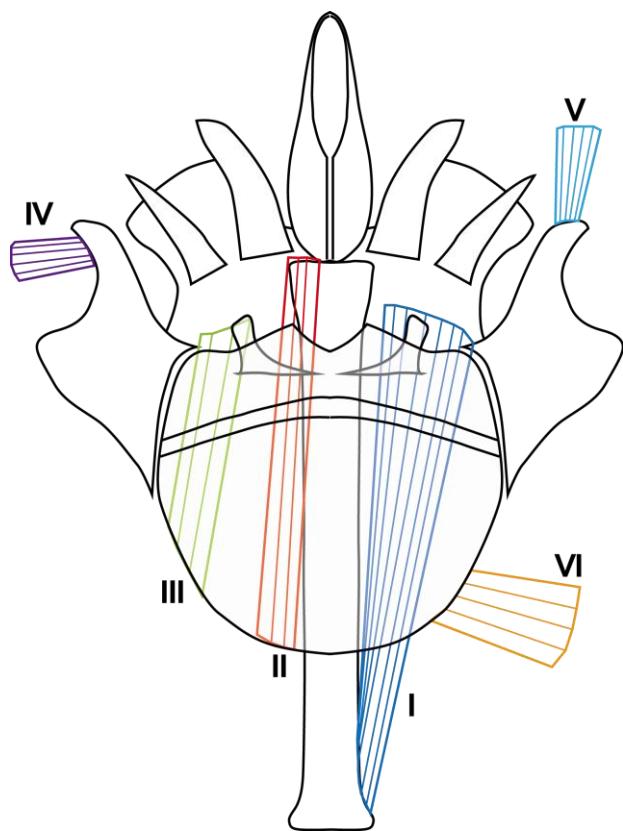
404   Figure 4. Scanning electron micrographs of the phallic structures in (A) ventral and (B) lateral views,

405   from L. Tsacas' collection at the National Museum of Natural History, Paris (Courtesy of the

406   Museum).

407

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409

410   Figure 5. Musculature of the phallic structures. Same diagram of cuticular parts as in Fig. 3 (ventral

411   view). Muscles are indicated in distinct colors and numbered I to VI (Kamimura 2010). These

412   muscles are bilateral. For sake of clarity, muscles are shown either on the left or on the right side of

413   the diagram. See Table 1 for muscles description.

414

415

416   **Tables**

417

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

419

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 (FBbt:00004845) FlyBase synonyms: male gonopod, male paramere, penis mantle. 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 (FBbt:00004852) FlyBase synonyms: penis. 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), phallus (Tsacas et al. 1971).
Cercal dorsal lobe (FBbt:00048379) FlyBase synonyms: New term. Definition: Dorsal portion of the cercus bearing long thin *cercal dorsal bristles*.
Cercal ventral lobe (FBbt:00048380) FlyBase synonyms: New term. Definition: Ventral portion of the cercus bearing short rigid *cercal ventral bristles*. Synonyms: secondary clasper (Hsu 1949).
Cercus (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).
Dorsal postgonite (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).
Epandrial anterodorsal phragma (FBbt:00048382) FlyBase synonyms: New term. Definition: thin sclerite connecting the *epandrium* 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).

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), scleoritzed 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.

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 sclerite (FBbt:00048388)
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 (FBbt:00003524)
FlyBase synonyms: aedeagal apodeme, basal apodeme of penis.
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 (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).

Phallic sclerites (FBbt:00048390)
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 (FBbt:00004850)
FlyBase synonyms: aedeagus.
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 (FBbt:00004854)
FlyBase synonyms: dorsal paramere.
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 (FBbt:00004855)
FlyBase synonyms: ventral paramere.
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 (FBbt:00004840)
FlyBase synonyms: pons, decasternum.
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 (FBbt:00004843)
FlyBase synonyms: clasper.
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 (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).

Setation

Cercal bristle (FBbt:00048392)
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *cercus*. There are nearly 40 of these.

Cercal dorsal lobe bristle (FBbt:00048393)
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 bristle*.

Cercal ventral lobe bristle (FBbt:00048394)
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 bristle*.

Epandrial bristle (FBbt:00048395)
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *epandrium*. There are 30 of these.

Epandrial dorsal lobe bristle (FBbt:00048396)
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *epandrial dorsal lobe*. There are 8 of these.

Epandrial ventral lobe bristle (FBbt:00048397)
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 (FBbt:00004472)
Definition: Long bristle located on the *median gonocoxite*. There are two of these on the *hypandrium*.

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

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

Pregonal bristle (FBbt:00048398)
FlyBase synonyms: New term.
Definition: Any bristle that is part of the *pregonite*. They are 3 of these.

Surstylar long bristle (FBbt:00004471)
FlyBase synonyms: clasper long bristle.
Definition: Single long bristle at the end of the *surstylus*. Sometimes there is more than one long bristle per surstylus.

Surstylar teeth (FBbt:00004470)
FlyBase synonyms: clasper tooth.
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 (FBbt:00003552)
FlyBase synonyms: penis protractor muscle.
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 (FBbt:00110926)
FlyBase synonyms: penis retractor muscle.
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 (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).

420
421
422
423   Table 2. Table of correspondence between terms previously used in publications and term of the
424   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
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
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
* Note that these previously used terms correspond to multiple anatomical parts in the new nomenclature.		

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