

**AI Shatalkin** (2012) Homologies in the structure of the male genitalia of Cyclorrhapha (Diptera). *Caucasian Entomological Bulletin* 8(2): 321-7

translated by Francis Gilbert, Valeri Mutin & Anatolii Barkalov, Sep 2016

### **Brief description of the structural features of fly genitalia**

The ninth abdominal segment constitutes a major part of the male genitalia of Diptera. We can distinguish a dorsal sclerite (tergite 9, the epandrium) and a ventral sclerite (sternite 9 - the hypandrium). In many older works (Awati, 1915; Metcalf, 1921; Patton, 1932; Zumpt & Heinz, 1950; Zimin 1951) the epandrium was regarded as tergite 10 (anal tergite - Rohdendorf 1937, Graham-Smith 1938), and the hypandrium as tergo sternite 9. Accordingly, the subepandrial Y-shaped sclerite (bacilliform sclerite, processus longus (Brüel, 1897), surstylar apodeme (Vockeroth, 1969), medandrium (Zatwarnicki, 1996), which connects the base of the surstyle with the base of the aedeagus or part of the hypandrium, is considered to be sternite 10 (Metcalf, 1921; Zumpt & Heinz, 1950), or as a derivative of tergo sternite 9 (Patton & Cushing, 1934; Rohdendorf, 1937; Zimin, 1951). In the structure of the genitalia of mosquitoes and most Orthorrhaphan flies, to the two elements (epandrium and hypandrium) are added gonopods (rudiments of the abdominal extremities) which are located on the sides of the phallus and connected with its base.

We distinguish between the Dipteran phallus and the aedeagus (Snodgrass, 1935, 1957; Taxonomist's glossary ..., 1956; Sinclair et al, 1994.; Sinclair, 2000; Cumming & Wood, 2009). The phallus is composed of an axial terminal part (aedeagus = distiphallus) and the phallobase (basiphallus) which is the proximal part in the form of sclerotized leaflets, shells or a sheath (the parameral sheath), forming a basal extension (theca) and often enclosing the outside of the aedeagus. This sheath can be more or less free (as in Tabanomorpha and Xylophagomorpha), or may completely coalesce with the aedeagus (as in Stratiomyomorpha and Muscomorpha sensu Woodley 1989); it is often segregated as a pair of independent processes (the parameres). We note that the term "basiphallus" is often used as a name for the basal part of the aedeagus or the phallus when it is divided into successive morphological sections (see., e.g., Griffiths 1972, McAlpine 1981). Some authors (Cumming et al, 1995.; Sinclair, 2000) find that the phallus is characteristic of cyclorrhaphan flies. Therefore they deny the existence of parameres in representatives of this group.

In cyclorrhaphan flies there are present two apodemes associated with the phallus - the apodeme of the phallus (or of the aedeagus) and the ejaculator apodeme. It is believed (McAlpine, 1981; Sinclair, 2000) that the phallus apodeme (the phallapodeme) is a new structure, and is the result of invagination of the ventral wall of the hypandrium. As a result, there are groups where the phallapodeme is like a pocket that has functional significance. For example, in Lonchaeidae the female ovipositor is inserted into the pocket-like apodemes at copulation.

The gonopods are normally two-segmented, and, if we take the Asilidae as an example, forms a structure similar to forceps. The basal segments (gonocoxites) are wide at the base, and narrowed in the apical half; at the place where they narrow, on their inner surfaces they articulate with the gonostyli (Fig. 1, Asilid type of genitalia). During copulation the gonostyli are inserted into the vagina of the female, while the narrowed vertices of the gonocoxites hold the end of the abdomen of the female from the outside.

In cyclorrhaphan flies, the gonopods are functionally replaced by the hypandrium. Thus when copulating, male hoverflies (Syrphidae) insert the tubular hypandrium into the vagina of the female, or more precisely into a special vaginal copulatory bag made of elastic membrane (Shatalkin, 1981; Hippha, 1986; Barkalov 1992). The inside of this copulatory bag carries various folds and pockets. The hypandrial lobes are inserted into these pockets, ensuring fixation of the phallus inside the female vagina.

The epandrium and the lobes of the surstyli are usually associated with the function of retaining the end section of the female abdomen through its coverage of the rear and sides (the clasping function). According to Eberhard (2001, 2002), the grasping function of the surstyli of male sepsids (Sepsidae) was not marked either during aedeagal introduction into the vagina of the female, or afterwards. Once fixation of the aedeagus in the female genital tract had occurred, the

surstyli begin to move rhythmically, suggesting that they function as a tool for female stimulation. Narchyk (1987: 74) wrote about the shift in surstyle function in cereal flies (Chloropidae) from capturing and holding the female abdomen to a predominantly sensory [mode].

In cyclorrhaphan flies the gonopods do not occur as an independent element of the genital apparatus, but the hypandrium and epandrium carry lobes which can be correlated with the gonopods. On the issue of the origin of these processes, there are different opinions, shown in the following table [see after figures).

### **Possible scenarios for the origin of the hypopygium in cyclorrhaphan Diptera**

As mentioned, a distinctive feature of the genitalia of the Cyclorrhapha is the lack of gonopods. Several scenarios about the fate of the gonopods have been proposed in the evolution of the Orthorrhapha to the Cyclorrhapha (see Figure 1):

1. *Complete reduction of the gonopods.* The epandrium and hypandrium in this case are derived from tergite 9 and sternum 9, respectively. Therefore in this scenario the hypandrial lobe appendages must represent new developments (Crampton, 1942; Hennig, 1976a). The same conclusion was reached by Ovchinnikova (1989, 2000) while studying the muscles of the genitalia. The gonopods of lower flies are associated with specific muscles. But when the muscles are absent in cyclorrhaphan flies, then how should we relate the gonopods to the hypandrial lobes? Due to uncertainty of this issue, many authors use neutral terms - such as the pregonites and postgonites proposed by Crampton (see Emden & Hennig 1956).
2. *The gonopods are involved in the formation of the epandrium.* There are several possible options, two of which are shown in Fig. 1.
  - 2.1. The gonocoxites merge by their gonopods dorsally to the aedeagus, and completely replace tergite 9; the surstyli are derived gonostyles (the periandrial hypothesis of Griffiths 1972, 1994, 1996).
  - 2.2. The gonopods merge with the epandrium; the surstyli are derived gonocoxites or gonostyles (merger hypothesis). In pure form this idea came from Ulrich (1972, 1975) analyzing the structure of the genitalia of representatives of the Orthogenya. He considered the epandrium a composite structure formed by the merger of the ninth tergite and the gonocoxites; thus the surstyli are derived gonostyles. This view differs from Griffiths' periandrial hypothesis as follows. Griffiths based his conclusion on a single assumption - a possible merger of the gonopods at the base. In this case, there is no need for any additional assumptions about the origin of the "surstyles"; it is clear that they represent gonostyli. The merger hypothesis does not address the issue as to which appendages the "surstyli" are - gonopods, tergite 9 or shared. Although Ulrich (1972, Abb. 19) calls them gonostyli, their dorsal position is more consistent with them being a component of a tergal part of a composite epandrium.

Avati (1915), and later Lindner (1925: 21-76) and Hendel (1928) were in favour of a gonopodal origin of the surstyles, including being derivatives of the gonostyles; according to these authors, the gonocoxites have disappeared. Later this view with some of the changes was adopted by Rohdendorf (1937), who linked the surstyles (as coxites) with tergosternite 9 (ie, the hypandrium - author's note), and Hennig (1936), who identified the surstyles (as basal gonopodial segments) with the tenth segment. McAlpine (1981: 54) believed that the surstyles are derivatives of tergite 10, while the subepandrial sclerite is a derivative of sternite 10, but according to this author the epandrium belongs to tergite 9.

In post-war work, based on an analysis of the Lauxaniidae, Hennig (1948, cf. Emden & Hennig, 1956) recognized the surstyli as the distal segments (dististylus) of the gonopods. "The basal segment (basistylus) of all cyclorrhaphan flies is firmly fused to the ninth abdominal

segment" (Hennig, 1948: 408). Later, he (Hennig, 1976b) talked about a merger between the gonopods, the 9th tergite and the 10th segment.

3. The hypothesis of Zatwarnitski (1996). *The gonopods are involved in the formation of the transandrium* (the dorsal bridge of other authors) *and the medandrium* (Fig. 1). The gonocoxites merge at the base and form an internal Y-shaped sclerite (the medandrium); the surstyli are derived from the gonostyles; a gonocoxite apodeme forms the back wall of the hypandrium - the transandrium.
4. *The gonopods are involved in the formation of the hypandrium* (Fig. 1). The surstyli are derived from the epandrium (epandrial hypothesis). This hypothesis is usually associated with the work of Crampton (1936), but Zatwarnitski (1996) noted that the key idea was in circulation before (see., eg, Lowne 1895: 744). Crampton (1936: 146) formulated the epandrial hypothesis as follows: "the surstyli of higher Diptera are appendages of tergite 9 and should not be homologized with the coxites and styles of lower Diptera, as claimed by Awati (1915), Hendel (1928), Patton (1932) and other experts in the higher Diptera. Not surstyli, but rather the anterior and posterior gonapophyses (i.e. hypandrial lobes - author's note) in the higher Diptera are segments of the genital forceps, the coxites and styles of lower Diptera ... ". Two variants of the epandrial hypotheses are related to the understanding of the parameres:
  - 4.1. McAlpine (1981) considered that the parameres in cyclorrhaphan flies, if present, are represented by a pair of sclerites located on either side of the aedeagus and correspond to the postgonites in dipteran terminology. The subepandrial sclerites are the surstyli derived from segment 10 (see also Ovchinnikova 1994, 2000; Narchyk 2003).
  - 4.2. Other authors (Sinclair et al 1994, Cumming et al 1995, Sinclair 2000, Cumming & Wood 2009) believe that the intromittant organ in cyclorrhaphan flies represents the phallus, and therefore these flies do not have independent parameres.

### **The two-stage process of evolution of the genitalia of lower groups to the cyclorrhaphan flies**

Fig. 1 gives a simplified scheme since it does not reflect an important step in the changes in the genitalia, which occurred in the evolution of Orthorrhapha to Cyclorrhapha. Griffiths (1972) drew attention to an important difference between the genitalia of cyclorrhaphan flies - a special type of truncated phallus (aedeagus) oriented ventrally (Fig. 1, cyclorrhaphan type). In Orthorrhaphan flies the phallus is massive and has a dorsal orientation (Fig. 1, asilid type). The change in the orientation of the phallus and its shortening proceeded independently in initial families, and in some cases has resulted in the differentiation of the parameres and the transformation of the phallus into the aedeagus. The families Platypezidae, Pipunculidae and Syrphidae present both types of phallic structures: the "dorsal" phallus is typical for representatives of subfamilies Platypezinae, Chalarinae and Microdontinae (Fig. 2).

The transition to genitalia lacking free gonopods from representatives of the Cyclorrhapha therefore occurred in two stages (Fig 2). First there was a complete reduction of the gonopods or their merger with sternite 9. Then the surstyli and subepandrial sclerite appeared, the ventral edge of which articulates with the base of the aedeagus. As a result, this created a powerful lever mechanism of the aedeagus in the caudal direction. The second stage was the transformation of the phallus from dorsal to ventral with a sharp decrease in its size. The hypandrium closed dorsally in a ring, and in lower groups into a tubular structure, thereby forming a stable platform for ventral movements of the phallus in the dorsoventral plane. There was a need to develop hypandrial lobes, including the parameres, that provide the delicate locking of the aedeagus in the vagina. We suggest that the conversion of the genitalia in the Schizophora was carried out in two stages. The reason for this judgment was the finding of the relict South African genus *Belobackenbardia* Shatalkin 2001, which is characterized by the asilid-type aedeagus. At first (Shatalkin, 2001) we thought that the genus is related to the family Psilidae, but most likely it is a plesiomorphic form in the evolution of

the superfamily Diopsoidea, and possibly a larger number of groups.

Ovchinnikova (1989, 2000) showed that the cyclorrhaphan hypandrial muscles were not the same as those of the gonopods of the Orthorrhapha. She concluded that “there are no real gonostyles in studied representatives of the Cyclorrhapha” (Ovchinnikova 2000: 36). In her opinion, “in the course of evolution the cyclorrhaphan gonostyles were lost, and then in the various groups there were parallel evolutionary searches for compensatory structures to complement the functions of the surstyles” (Ovchinnikova 2000). A similar opinion was expressed by Hennig (1976a: LI): “the muscle connections of the phallopodeme exclude the possibility of homology with the pre- or postgonites (or both) to the telomeres [=distal segment of the paramere]”. This conclusion agrees with our data on a two-phase transformation sequence of the aschizan genitalia. First the gonopods merged with sternite 9 (or disappeared), and since the gonostyles were not expressed, the need for their muscles was eliminated. Then the hypandrium lobe differentiated which in the absence of adequate muscles was hardly worth association with the gonostylus. But if these structures are new developments, they can either arise fused to the base of sternite 9, or to the base of the gonopods. In the latter case it is justified to talk about the possible gonopodal origin of the hypandrial lobes.

### Examples of hypandrial disintegration in sternite 9 and the gonopodium

We believe that once the merger took place of the gonopods, presumably either with the epandrium or the hypandrium, then successive Cyclorrhapha could realize a reverse process, where the merged structure decayed to [re]form the source elements. We found a few examples of such disintegration, evidence that a merger had indeed taken place between sternite 9 and the gonopods (Fig. 3).

The clearest proof of this is the structure of the genitalia of the genus *Psila* Meigen, 1803 (s. str.) and *Chamaepsila* Hendel, 1917 (Psilidae). Instead of a single hypandrium, here we see three sclerites. The unpaired ventral sclerite is sternite 9. The two dorsolateral sclerites can be homologized only with derivatives of the gonopods. They cannot relate to the bacilliform sclerite. In this genus there are no surstyles. Therefore, this sclerite underwent a reduction, and its remains are recognizable as a pair of small sclerites lying between the epandrium and the hypandrium (Fig. 3).

We see a similar example in the structure of the genitalia of a strongylophthalmid (*Strongylophthalmyia* Heller, 1902) and a syringogastrid. In a recent revision of the genus *Syringogaster* Cresson 1912, Marshall et al. (2009) designate what we call the gonopods as the “anterior hypandrial arm” (Fig 3); our parameres they designate by the term “posterior hypandrial arm”; and lobes associated with the latter [the posterior hypandrial arm] they call the pregonites. The name “hypandrial arms” is, I must say, unfortunate, because other authors have used this term to characterize sclerites of a “hypandrial bridge” associated with the bacilliform sclerite (e.g. Cumming & Wood 2009).

### The hypandrial lobes

Theoretically, these lobes can have three sources - they can come from sternite 9, the gonopods or the parameres. Therefore the question of their homology cannot have a unique solution (Ovchinnikova 1994).

The pre- and postgonites are usually identified with the gonopods and parameres respectively. Both characterize the hypandrial lobes of the fungus flies (subfamily Platyppezinae, in part). In hoverflies (Syrphidae) there is a single pair of lobes (the ‘superior lobes’ of Metcalf 1921) correlated with the parameres (Vockeroth & Thompson 1987), gonostylus (Cumming et al. 1995) or the postgonites (Zatwarnicki 1996). We believe that the parameres of hoverflies do not differentiate as lateral sclerites and the form of the chitin capsule (chitinous box - Berlese 1909, Metcalf 1921), or the parameral sheath of the aedeagus (Cumming et al 1995) (Fig. 2, *Epistrophe*). In this case, “parameres” (sensu Vockeroth & Thompson 1987) and “postgonites” (sensu Zatwarnicki 1996) correspond to a derivative of the gonopods (Fig. 2, *Epistrophe*, gonopodial lobe).

The two pairs of hypandrial lobes in many schizophoran taxa are parameres (Fig. 3, highlighted in black) and the so-called parameral arms (Shatalkin 1995). The latter correspond to

the anterior parameres or pregonites of different authors. The anterior and posterior parameres are considered to be the result of splitting of single parameres (Zumt & Heinz 1950: 212).

We offer another scenario of the origin of the parameral arms. In the structure of the genitalia of *Psila* and *Chamaepsila*, the parameres are connected to the gonopods via narrow unsclerotized bands (parameral arms). When the aedeagus is bent, it can be lengthened by an extension of the basal section. The parameres are located at the junction of the basal and apical sections. Therefore when the aedeagus elongates, they would lose contact with the hypandrium. The development of the parameral arms provides this link. In advanced groups, the parameres and parameral arms may look like two pairs of hypandrial lobes, which because of their ontogenetic unity were called the anterior and posterior parameres (see Table 1: Zumt & Heinz 1950).

Finally, in some cases, the hypandrial lobes are derived from the 9th sternite: for example, the unpaired lingula in representatives of the family Syrphidae (Fig. 2, *Epistrophe*) and the paired lobes of the hypandrium of male *Polypathomyia stackelbergi* Krivosheina 1979 (Pseudopomyzidae) (McAlpine & Shatalkin 1998: 160, fig. 13-14).

We can conclude that in Aschizan flies, particularly in the families Platypezidae and Syrphidae, a central role in fixing the aedeagus in the female genital tract is taken by lobe derivatives of the gonopods. In derived groups mainly in families of schizophorans the gonopods were functionally substituted by the parameres and their derivatives.

#### Acknowledgements

The author expresses his sincere gratitude for assistance from EP Narchyk (ZIN), OG Ovchinnikova (ZIN), IV Shamshevo (VIZR RAAS), J.M. Cumming (Biological Resources Division, Agriculture Canada, Ottawa) and T. Zatwarnicki (University of Agriculture, Wrocław, Poland).

#### Literature

- Awati PR (1915) Studies in flies. II. Contribution to the study of specific differences in the genus *Musca*. 1. Genitalia. Indian Journal of Medical Research 3: 510-529.
- Barkalov AV (1992) Functional morphology of the structure of the genitalia in *Temnostoma* Lep. et Serv. (Diptera, Syrphidae). in *Systematics, zoogeography and karyology of Diptera (Insecta: Diptera)* (EP Narchyk ed.). SPb: Zoological Institute of the Russian Academy of Sciences: 9-15.
- Berlese A. 1909. Tipulid, syrphid, and muscid genitalia. Gli Insetti. Milano: Societa Editrice Libreria: 326-328.
- Böttcher G. 1912. Die männlichen Begattungswerkzeuge bei dem Genus *Sarcophaga* Meig. und ihre Bedeutung für die Abgrenzung der Arten. Deutsche Entomologische Zeitschrift. 6: 525-544; 705-776.
- Brüel L. 1897. Anatomie und Entwicklungsgeschichte der Geschlechtsausführwege samt Annexen von *Calliphora erythrocephala*. Zoologische Jahrbücher, Abteilung für Anatomie. 10: 511-618.
- Chandler P.J. 2001. The flat-footed flies (Diptera: Opetiidae, Platypezidae) of Europe. Fauna Entomologica Scandinavica. Vol. 36. Leiden - Boston - Köln: E.J. Brill. 276 p.
- Cole F.R. 1927. A study of the terminal abdominal structures of male Diptera (two-winged flies). Proceedings of the California Academy of Sciences. Ser. 4. 16 (14): 397-499.
- Crampton G.C. 1936. Suggestions for a new interpretation of the postabdomen in male Cyclorrhaphous Diptera. Bulletin of the Brooklyn Entomological Society. 31: 141-148.
- Crampton G.C. 1941. The terminal abdominal structures of male Diptera. Psyche. 48: 79-94.
- Crampton G.C. 1942. The external morphology of the Diptera. Guide to the Insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. 1st fascicle. Connecticut State Geological and Natural History Survey. Bulletin. 64: 10-165.
- Cumming J.M., Sinclair B.J., Wood D.M. 1995. Homology and phylogenetic implications of male genitalia in Diptera-Eremoneura. Entomologica Scandinavica. 26: 120-151.
- Cumming J.M., Wood D.M. 2009. Adult morphology and terminology. pp. 9-50 in *Manual of Central American Diptera* (B.V. Brown, A. Borkent, J.M. Cumming, D.M. Wood, N.E. Woodley, and M. Zumbado eds.). Vol. 1. Ottawa: NRC Research Press. 714 p.
- Eberhard W.G. 2001. Species-specific genitalic copulatory courtship in sepsid flies (Diptera, Sepsidae, *Microsepsis*). Evolution. 55: 93-102.
- Eberhard W.G. 2002. Female resistance or screening? Male force vs. selective female cooperation in intromission in sepsid flies and other insects. Revista de Biología Tropical. 50: 485-505.
- Emden F. van, Hennig W. 1956. Diptera. *Taxonomist's glossary of genitalia in Insects* (S.L. Tuxen ed.). Kopenhagen: Munksgaard: 111-122.
- Graham-Smith G.S. 1938. The generative organs of the blow-fly *Calliphora erythrocephala* L., with special reference to their musculature and movements. Parasitology. 30: 441-476.
- Griffiths G.C.D. 1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. Series Entomologica. Vol. 8. The Hague: Dr. W. Junk N.V. Publishers. 340 p.
- Griffiths G.C.D. 1994. Relationships among the major subgroups of Brachycera (Diptera): a critical review. The Canadian Entomologist. 126: 861-880.

- Griffiths G.C.D. 1996. Review of the papers on the male genitalia of Diptera by D.M.Wood and associates. *Studia Dipterologica*. 3 (1): 107-123.
- Hendel F. 1928. Zweiflügler oder Diptera. II: Allgemeiner Teil. *Die Tierwelt Deutschlands*. 11. Teil. Jena: Verlag von Gustav Fischer. 135 S.
- Hennig W. 1936. Beiträge zur Kenntnis des Kopulationsapparates der cyclorrhaphen Dipteren. *Zeitschrift für Morphologie und Ökologie der Tiere*. 31 (2): 328-370.
- Hennig W. 1948. Beiträge zur Kenntnis des Kopulationsapparates und der Systematik der Acalyptraten. IV. Lonchaeidae und Lauxaniidae. *Acta Zoologica Lilloana*. 6: 333-429.
- Hennig W. 1976a. Anthomyiidae. *Die Fliegen der Palaearktischen Region* (E. Lindner ed.). Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung. Lfg. 306. Bd. VII / I (1): A1-A131.
- Hennig W. 1976b. Das Hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). *Stuttgarter Beiträge zur Naturkunde*. 283: 1-63.
- Hippa H. 1986. Morphology and taxonomic value of the female external genitalia of Syrphidae and some other Diptera by new methodology. *Acta Zoologica Fennica*. 23: 307-320.
- Kessel E.L. 1987. Platypezidae. *Manual of the Nearctic Diptera* (J.F. McAlpine et al. eds.). Ottawa: Research Branch Agriculture. Vol. 2. Monograph 28: 681-688.
- Lindner E. 1925. Handbuch. Geschichte der Dipterologie und Literatur, Morphologie und Terminologie, Anatomie, Sinnesorgane, Metamorphose (Ei, Larve, Puppe, Parthenogenese), Biologie (Parasitismus, Pflanzenschädlinge, Blutsauger, Krankheitsüberträger), Stammbaum, systematische Einteilung. *Die Fliegen der Palaearktischen Region*. Band I. XII. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung. 422 S.
- Lowne B.T. 1895. The anatomy, physiology, morphology and development of the blow fly (*Calliphora erythrocephala*). Vol. 2. London: R.H. Porter: 351-778.
- Marshall S.A., Buck M., Skevington J.H., Grimaldi D. 2009. A revision of the family Syringogastridae (Diptera: Diopsoidea). *Zootaxa*. 1996: 1-80.
- McAlpine J.F. 1981. Morphology and terminology - Adults. *Manual of Nearctic Diptera* (J.F. McAlpine et al. Eds.). Ottawa: Research Branch Agriculture. Vol. 1. Monograph 27: 9-64.
- McAlpine D.K., Shatalkin A.I. 1998. Pseudopomyzidae. *Contributions to a Manual of Palaearctic Diptera* (L. Papp, B. Darvas eds.). Vol. 3. Budapest: Science Herald: 155-163.
- Metcalf C.R. 1921. The genitalia of male Syrphidae: Their morphology, with especial reference to its taxonomic significance. *Annals of the Entomological Society of America*. 14: 169-214.
- Narchyk EP (1987) Cereal flies (Diptera: Chloropoidea), their systematics, evolution and connection with plants. *Proceedings of the Zoological Institute*. 136: 1-278. L: Nauka.
- Narchyk EP (2003) Key to the families of flies (Insecta, Diptera) of Russia and adjacent countries (with a brief overview of the world fauna). *Proceedings of the Zoological Institute* 294: 1-251. SPb: ZIN.
- Newstead R. 1911. On the genital armature of the males of *Glossina medicorum*, Austen, and *Glossina tabaniformis*, Westwood. *Bulletin of Entomological Research*. 2: 107-110.
- Ovchinnikov OG (1989) The muscles of the male genitalia of Diptera Brachycera-Orthorrhapha (Diptera). *Proceedings of the Zoological Institute* 190: 1-166.
- Ovchinnikova O.G. 1994. On the homology of male genital sclerites of Diptera Brachycera and Cyclorrhapha based on musculature. *Dipterological Research*. 5 (4): 263-269.
- Ovchinnikov OG (2000) The muscles of the male genitalia of the family Syrphidae (Diptera). *Papers in memory of ON Cholodkovskii* 52(2): 1-69.
- Patton W.S. 1932. Studies on the higher Diptera of medical and veterinary importance. A revision of the species of *Musca* based upon a comparative study of the male terminalia. I. The natural grouping of the species and their relationship to each other. *Annals of Tropical Medicine and Parasitology*. 26: 347-405.
- Patton W.S., Cushing E.C. 1934. Studies on the higher Diptera of medical and veterinary importance. A revision of the genera of the subfamily Calliphorinae based on a comparative study of the male and female terminalia. The genus *Calliphora* Robineau-Desvoidy (sens. Lat.). *Annals of Tropical Medicine & Parasitology*. 28: 205-216.
- Rohdendorf BB (1937) Family Sarcophagidae. Part 1. *Fauna of the USSR*. Insects: Diptera 19(1). M-L: Publishing House of the USSR. 261 (New Series №12).
- Schlein Y., Theodor O. 1971. On the genitalia of the Pupipara and their homologies with those of *Calliphora* and *Glossina*. *Parasitology*. 63: 331-342.
- Schröder T. 1927. Das Hypopygium 'circumversum' von *Calliphora erythrocephala*. Ein Beitrag zur Kenntnis des Kopulationsapparates der Dipteren. *Zeitschrift für Morphologie und Ökologie der Tiere*. 8: 1-44.
- Shatalkin AI (1981) Towards a morphological and functional characterization of the genitalia of hoverflies (Diptera, Syrphidae). *Proceedings of the Zoological Museum of Moscow State University* 19: 98-116.
- Shatalkin AI (1985) Review of mushroom flies (Diptera, Platypezidae) in the fauna of the USSR. *Proceedings of the Zoological Museum of Moscow State University* 23: 69-136.
- Shatalkin A.I. 1995. Palaearctic species of Pseudopomyzidae (Diptera). *Russian Entomological Journal*. 1994. 3: 129-145.
- Shatalkin A.I. 2001. Afrotropical Psilidae (Diptera). 1. Genera *Belobackenbardia* gen.n. and *Psila* Meigen, 1803. *Russian Entomological Journal*. 10 (4): 417-424.
- Sinclair B.J. 2000. 1.2. Morphology and terminology of Diptera male terminalia. *Contributions to a Manual of Palaearctic Diptera*. General and Applied Dipterology (L. Papp, B. Darvas eds.). Vol. 1. Budapest: Science Herald: 53-74.

- Sinclair B.J., Chandler P.J. 2007. A new species of *Microsania* Zetterstedt from Fiji (Diptera: Platypezidae). Bishop Museum Occasional Papers. 91: 29-32.
- Sinclair B.J., Cumming J.M. 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa*. 1180: 1-172.
- Sinclair B.J., Cumming J.M., Wood D.M. 1994. Homology and phylogenetic implications of male genitalia in Diptera - Lower Brachycera. *Entomologica Scandinavica*. 1993. 24 (4): 407-432.
- Snodgrass R.E. 1935. *Principles of Insect Morphology*. New York - London: McGraw-Hill. 667 p.
- Snodgrass R.E. 1957. A revised interpretation of the external reproductive organs of male insects. *Smithsonian Miscellaneous Collections*. 135: 1-60.
- Taxonomist's glossary of genitalia in Insects* (S.L. Tuxen ed.). 1956. Copenhagen: Munksgaard. 284 p.
- Ulrich H. 1972. Zur Anatomie des Empididen-Hypopygiums (Diptera). *Veröffentlichungen der Zoologischen Staatssammlung*. 16: 1-28.
- Ulrich H. 1975. Das Hypopygium von *Chelifera precabunda* Collin (Diptera, Empididae). *Bonner zoologische Beiträge*. 26: 264-275.
- Vockeroth J.R. 1969. A revision of the genera of the Syrphini (Diptera: Syrphidae). *Memoirs of the Entomological Society of Canada*. 62: 1-176.
- Vockeroth J.R., Thompson F.C. 1987. Syrphidae. *Manual of the Nearctic Diptera* (J.F. McAlpine et al. Eds.). Ottawa: Research Branch Agriculture. Vol. 2. Monograph 28: 713-743.
- Wesché W. 1906. The genitalia of both sexes of the Diptera and their relation to the armature of the mouth. *Transactions of the Linnean Society of London*. 9: 339-386.
- Woodley N.E. 1989. Phylogeny and classification of the "Orthorrhaphous" Brachycera. *Manual of the Nearctic Diptera* (J.F. McAlpine et al. eds.). Ottawa: Research Branch Agriculture. Vol. 3. Monograph 32: 1371-1395.
- Zatwarnicki T. 1996. A new reconstruction of the origin of the eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus*. 3: 103-175.
- Zimin LS (1951) Fam. Muscidae. True flies (tribe Muscini, Stomoxydini). in 'Fauna of the USSR. Insects: Diptera' 18(4). M-L: Publishing House of the USSR. 286. (New Series №45).
- Zumt F., Heinz H.J. 1950. Studies in the sexual armature of Diptera. II. A contribution to the study of the morphology and homology of the male terminalia of *Calliphora* and *Sarcophaga* (Dipt., Calliphoridae). *Entomologist's Monthly Magazine*. 86: 207-216.

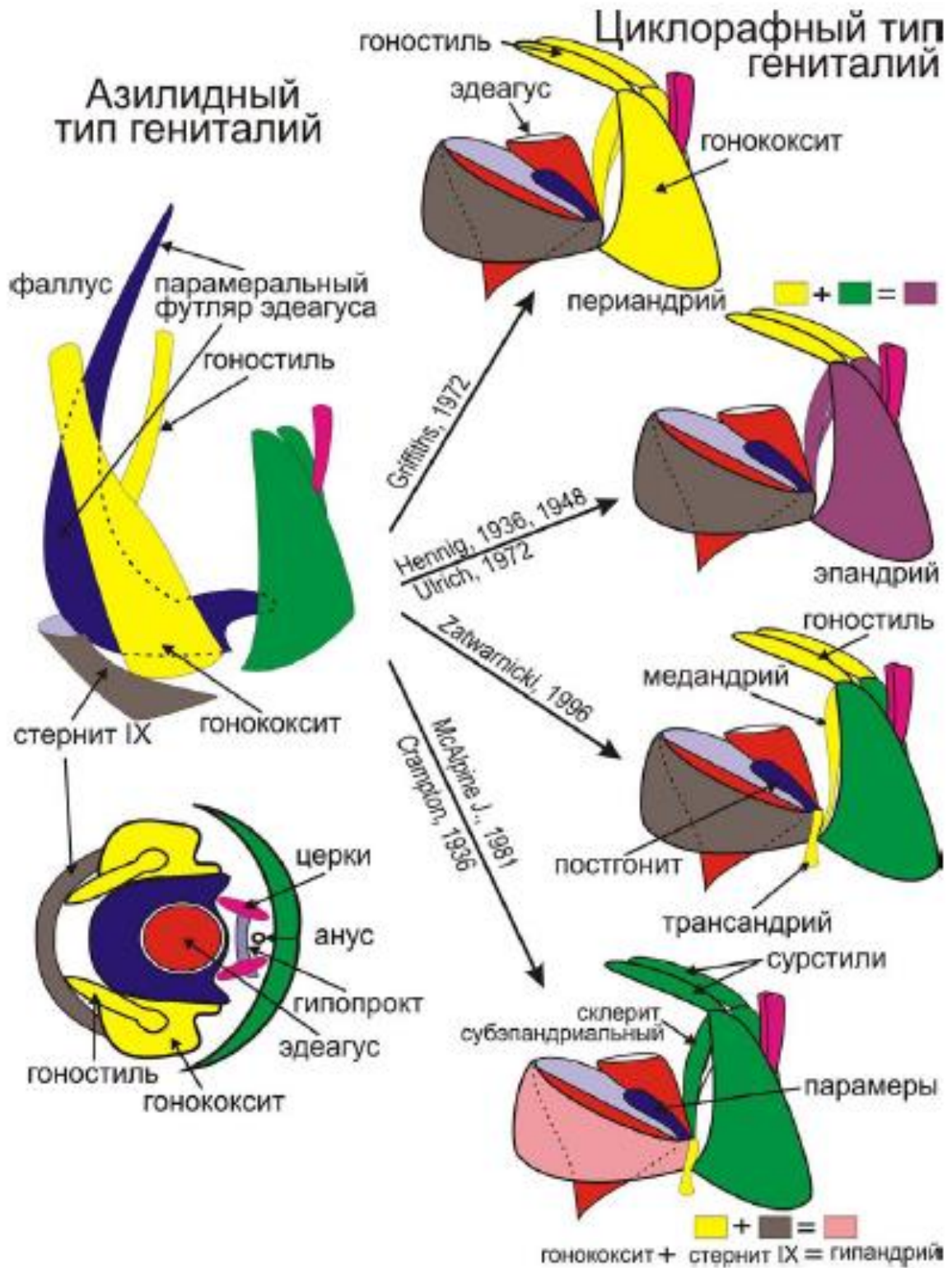


Fig. 1. Suggested scenarios of transformation of male genitalia in evolution from Orthorrhapha to Cyclorrhapha.



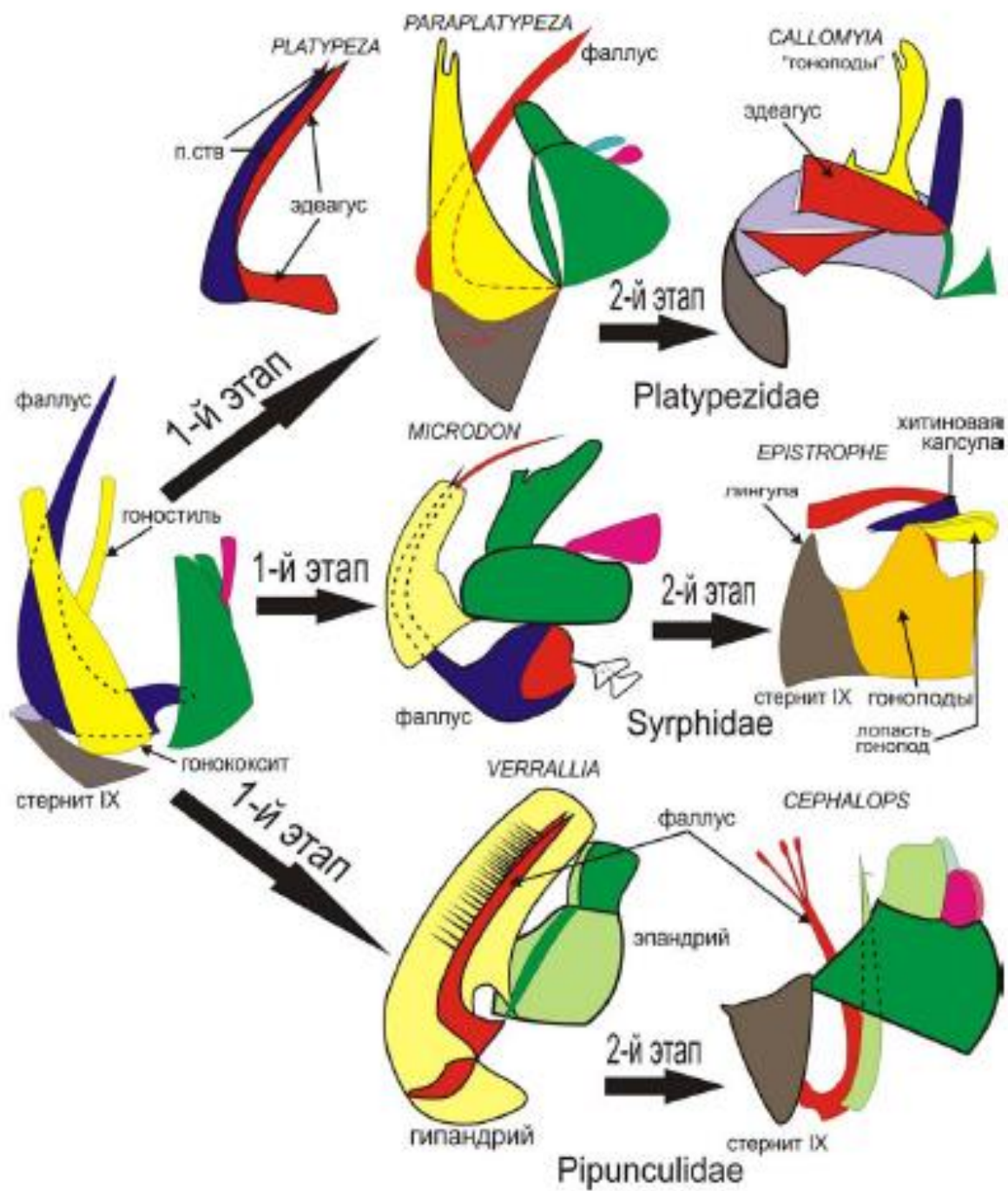


Fig. 2. Two-stage process of transformation of genitalia in Cyclorrhapha. Only the hypandrium is pictured for *Callomyia* and *Epistrophe*; п. ств – parameral sheath.

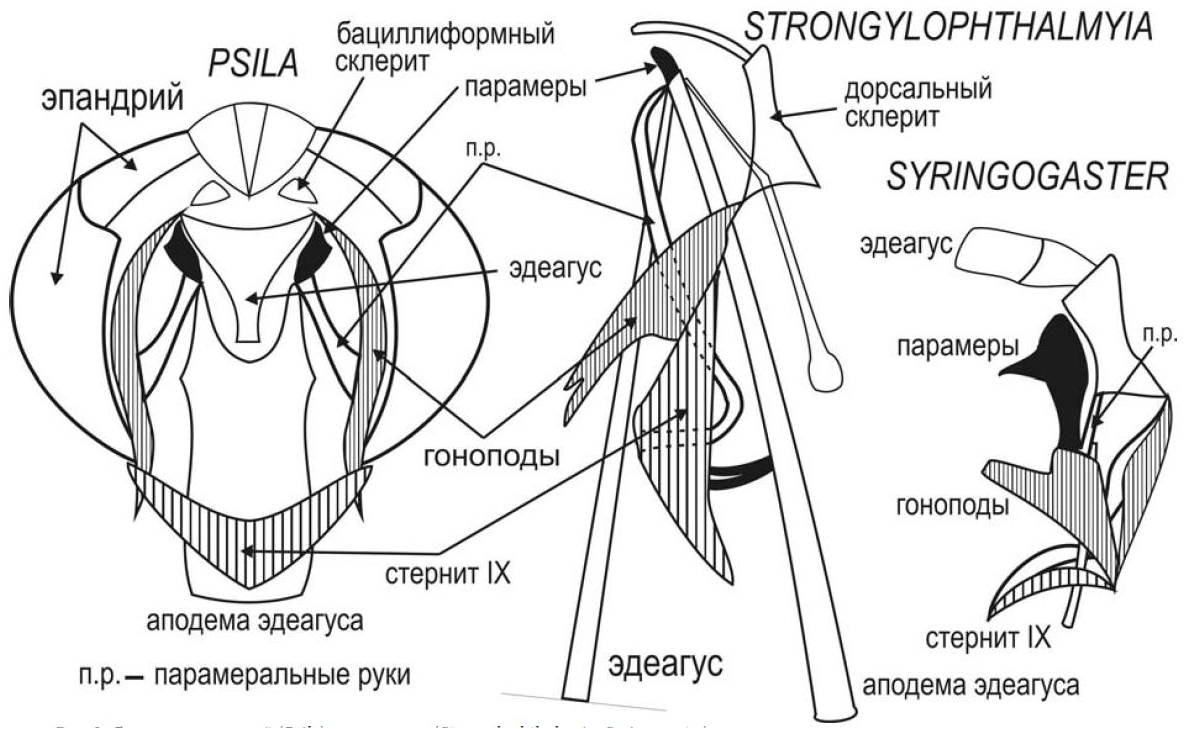


Fig. 3. Structure of genitalia in *Psila* and of hypandrium in *Strongylophthalmyia* and *Syringogaster*.

| Epandrium                                | Hypandrium                             |                                      | Taxon  | Source  |
|--|--|--------------------------------------|--|---|
| valvulse externae                        | anterior gonapophyses (=gonopods)      | posterior gonapophyses               | Calliphoridae  | Lowne 1895  |
| styli, gonopods                          | distal gonapophyses                    | proximal gonapophyses                | Schizophora  | Hendel 1928                                       |
| gonopods (dististyli)                    | anterior gonapophyses                  | posterior gonapophyses               | Lauxaniidae  | Hennig 1948                                       |
| forcipes inferiores                      | palpi genitalium                       | forcipes interiores                  | Sarcophagidae  | Wesché 1906                                       |
| adjacent lobes (gonopods)                | anterior hooks                         | posterior hooks                      | Sarcophaga   | Böttcher 1912; Lindner 1925                       |
| surstyli                                 | palpi genitalium                       | forcipes interiores (paraphalli)     | Schizophora  | Cole 1927   |
| surstyli                                 | pregonites (=gonocoxites)              | postgonites (=gonostyli)             | Cyclorrhapha   | Crampton 1936                                     |
| surstyli                                 | basimere (basistyli) 1st parameres     | distimere (dististyli) 2nd parameres | Syrphidae, Muscidae                                    | Crampton 1941, 1942                               |
| gonopods (valvules lateralis)            | hook processes                         | parameres                            | Cyclorrhapha   | Schröder 1927; Hennig 1936                        |
| gonostyli                                | pregonites (=paraphyses)               | postgonites (=paraphyses)            | Cyclorrhapha   | Griffiths 1972                                    |
| coxites of 9th tergosternum              | anterior parameres                     | posterior parameres                  | Calliphoridae  | Patton & Cushing 1934                             |
| coxites of 9th tergosternum (hypandrium) | anterior parameres                     | posterior parameres                  | Sarcophagidae, Muscidae                                | Rodendorf 1937, Zimin 1951                        |
| paralobi (sternite 10)                   | anterior parameres                     | posterior parameres                  | Calliphoridae, Muscidae                                | Zumt & Heinz 1950                                 |
| surstyli                                 | pregonites                             | postgonites                          | Cyclorrhapha   | Emden & Hennig 1956                               |
| surstyli                                 | gonopods                               | parameres                            | Calliphoridae  | McAlpine 1981                                     |
| surstyli                                 | pregonites                             | gonostyli                            | Tachinidae   | Cumming et al 1995                                |
| surstyli                                 | hypandrial lobes                       | parameres                            | Platypezidae   | Shatalkin 1985                                    |
| surstyli                                 | gonopods                               | parameres                            | Platypezidae   | Kessel 1987, Chandler 2001                        |
| surstyli                                 | hypandrial lobes                       | postgonites                          | Platypezidae ( <i>Agathomyia</i> , <i>Microsania</i> ) | Sinclair & Cumming 2006, Sinclair & Chandler 2007 |
| gonostyli                                | pregonites (lingula, hypandrial lobes) | postgonites (=paraphyses)            | Syrphidae ( <i>Syrphus</i> )                           | Zatwarnicki 1996                                  |
| surstyli                                 | pregonites (hypandrial lobes)          | parameres                            | Scathophagidae   | Ovchinnikova 2000                                 |
| surstyli                                 | pregonites                             | (no)                                 | <i>Glossina</i>  | Schlein & Theodor 1971                            |
| surstyli                                 | gonopods or hypandrial lobes           | parameral arms & parameres           | Pseudopomyzidae  | McAlpine & Shatalkin 1998                         |
| superior claspers                        | inferior claspers                      |                                      | <i>Glossina</i>  | Newstead 1911                                     |
| gonopods                                 | parameres                              |                                      | other families   | Bruel 1897, Patton 1932                           |
| styli                                    | superior lobes                         |                                      | Syrphidae  | Metcalf 1921                                      |
| styli                                    | dististyli(?)                          |                                      | Platypezidae ( <i>Platypeza</i> )                      | Cole 1927   |
| styli                                    | paraphalli (parameres)                 |                                      | Syrphidae ( <i>Eristalis</i> )                         | Cole 1927   |
| styli                                    | inferior forceps                       |                                      | Syrphidae ( <i>Melanostoma</i> )                       | Cole 1927   |
| surstyli                                 | gonostyli                              |                                      | Syrphidae  | Cumming et al 1995                                |
| surstyli                                 | parameres                              |                                      | Syrphidae  | Ovchinnikova 2000                                 |