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Comparative Morphology of the Male Terminalia of Tephritidae and other Cyclorrhapha

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ABSTRACT

The external morphology and the musculature of the male terminalia of the Tephritidae and other Cyclorrhapha are examined and their homology is discussed. The terms surstylus and bacilliform sclerite are adopted for the ventral projection of the epandrium (apical part of the lateral surstylus of authors) and medial surstylus of the Tephritidae, respectively. The transverse bar, which connects the bases of the bacilliform sclerites (= medial surstyli) and is located at the ventral aspect of the epandrium of the Tephritidae, is a composite structure of the dorsal bridge of the hypandrium and the subepandrial sclerite of other Cyclorrhaphan Diptera.

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INTRODUCTION

Since McAlpine (1981) reviewed the morphology of adult Diptera and provided a general discussion for the male and female terminalia (postabdomen, hypopygium), various hypotheses have been advanced concerning structures of the male terminalia of the Eremoneura (Zatwarnicki, 1996; Sinclair, 2000). Among them, Wood (1991), Sinclair *et al*. (1994), and Cumming *et al*. (1995) discussed the male terminalia of Diptera and proposed a ground plan, homologies, and phylogenetic implications of these structures. They outlined the homologies of the male terminalia in the Eremoneura with inferences from ontogenetic evidence. Wood (1991) discussed the basic components of the male terminalia of Diptera and included the following parts: 1) epandrium, derived from the 9th abdominal tergite; 2) hypandrium, derived from the 9th abdominal sternite; 3) two-segmented gonopods (*sensu* Snodgrass, 1935), with proximal gonocoxite and distal gonostylus attached to the hypandrium; 4) medial tubular aedeagus (*sensu* Snodgrass, 1935), supported by the parameres (*sensu* Snodgrass, 1935); 5) paramere (*sensu* Snodgrass, 1935), separated as paired structures associated with the aedeagus (*sensu* Snodgrass, 1935); and 6) proctiger, comprising the epiproct, hypoproct, and cerci. Sinclair *et al*. (1994) proposed that the following structures of the male terminalia have been modified in the Brachycera: parameres (*sensu* Snodgrass, 1935) fused, comprising the sheath of the aedeagus (*sensu* Snodgrass, 1935) in the Stratiomyomorpha and the Muscomorpha; and epiproct lost in the Heterodactyla. Sinclair *et al*. (1994) also stressed that the subepandrial sclerite (= sternite 10 of McAlpine, 1981) is developed in the subepandrial membrane extending to the anterodorsal margin of the parameres (*sensu* Snodgrass, 1935) in the Brachycera, and a pair of the bacilliform sclerites are developed on both sides of the subepandrial sclerite. Cumming *et al*. (1995) wrote that the epandrium bears a pair of surstyli (= posterior surstylus of McAlpine, 1981) posteriorly in the Eremoneura and concluded that: (1) the surstylus is secondarily derived from the epandrium and is an apomorphic feature of the Cyclorrhapha; (2) the lateral wall of the surstylus is derived from the epandrium, and the medial wall is partly derived from the bacilliform sclerite; and (3) the surstylus is adducted by a single set of muscles attached to the bacilliform sclerite and abducted by the elasticity of the bacilliform sclerites. Sinclair *et al*. (1994) and Cumming *et al*. (1995) followed Wood's (1990) interpretation that the aedeagus (*sensu* Snodgrass, 1935) is enclosed by the parameral sheath in the Muscomorpha and called this composite structure the phallus (= aedeagus of McAlpine, 1981). Consequently, we can now see the following components in the male terminalia of the Cyclorrhapha according to Cumming *et al*. (1995): epandrium with the surstylus (*sensu* Cumming *et al*., 1995) and proctiger posteriorly and with the subepandrial sclerite bearing the bacilliform sclerite; hypandrium with a pregonite (= gonopod of McAlpine, 1981) and postgonite (= paramere of McAlpine, 1981) on each side; and phallus comprising the aedeagus and paramere (*sensu* Snodgrass, 1935).

The term surstylus has been applied to projections ventrad to the epandrium of the Tephritidae (e.g., McAlpine, 1981; Freidberg and Mathis, 1986; White, 1988; Foote *et al*., 1993; Wang, 1996; Korneyev, 1997). There are no comparative studies on the projections ventrad to the epandrium of the Tephritidae and the surstyli (*sensu* Cumming *et al*., 1995) of other families of the Cyclorrhapha except for Munro (1947). Munro (1947) made a comparative study of the male terminalia between the Tephritidae and the Calliphoridae. He claimed that the apex of the ventral projection of the epandrium of the Tephritidae is homologous with the posteroventral process of the ninth tergum (= epandrium) of the Calliphoridae which he called the outer clasper. He suggested that the transverse bar might be derived from the gonocoxite (= bacilliform sclerite *sensu* Cumming *et al*., 1995), and he also stated that it is a part of the genital ring (= hypandrium *sensu* Cumming *et al*., 1995). However, it is more relevant to compare the male terminalia of the Tephritidae with those of other families of the Tephritoidea, which are both more similar and retain plesiomorphic characters in the male terminalia, rather than with those of the Calliphoridae.

The surstylus (*sensu* White *et al*., 1999) of the Tephritidae consists of two sclerites that have been termed the inner and outer surstyli (McAlpine, 1981) and that have subsequently been renamed as medial and lateral surstyli (White *et al.,* 1999). The two medial surstyli (*sensu* White *et al*., 1999) are connected by a transverse sclerite at the base. This transverse sclerite has been variously called the transverse bar (Munro, 1947), the interparameral sclerite (Norrbom and Kim, 1988), or the subepandrial sclerite (White *et al*., 1999). The homology of the transverse sclerite, however, as found in the Tephritidae, with structures of the male terminalia in other Diptera is not well understood (White *et al*., 1999). Moreover, no studies have been published that compare the musculature of the male terminalia of the Cyclorrhapha.

In this paper I discuss the homologies of the surstylus, subepandrial sclerite, and bacilliform sclerite in the Tephritidae and other families of the Cyclorrhapha, based on observations of external structures and the musculature of the male terminalia of these groups. I also compare the Cyclorrhaphan musculature of the male terminalia and demonstrate how this character can be used in conjunction with the external morphology for determining the homologies of the above structures.

MATERIALS AND METHODS

Specimens used in this study were preserved dry and mounted on card points or pinned. Some fresh specimens were kept frozen and used for observation of the musculature. A total of 102 species from 42 Cyclorrhaphan families were examined and are listed in the Appendix. External structures and muscles were observed under a stereoscopic microscope. For observation of external structures of the terminalia, male abdomens were treated with heated 10% KOH solution for 20 minutes, stained with Chlorazol Black E, neutralized with acetic acid, washed in distilled water, and then preserved in pure glycerol in plastic microvials pinned under the mounted specimens. Frozen specimens were dissected in distilled water, fixed in pure ethanol, and then stained with eosin for observation.

I adopt here the revised epandrial hypothesis proposed by Cumming *et al*. (1995) for terminology of the male terminalia. Terminology for the musculature of the male terminalia follows Salzer (1968). Other terms in the external morphology follow McAlpine (1981) and White *et al*. (1999) except where noted otherwise.

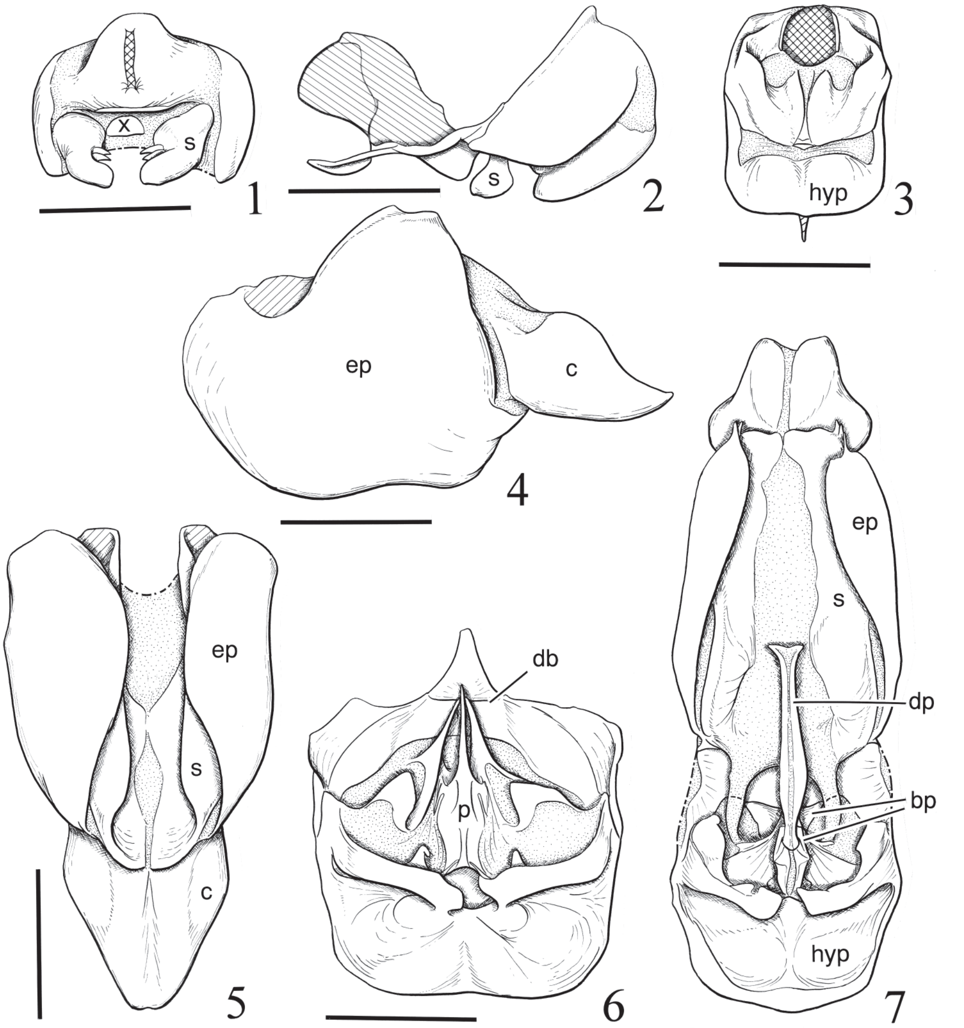
RESULTS AND DISCUSSION

Hypandrium, subepandrial sclerite, and transverse bar of the Tephritidae

According to Hennig (1976b), the dorsal bridge of the hypandrium (= Dorsalbrücke of Hennig, 1976b) connects the left and right posterior arms of the hypandrium and is articulated with the ventral plate of the epandrium (= Ventralen Epandrialsklerit of Hennig, 1976b; subepandrial sclerite of Cumming *et al*., 1995). The dorsal bridge of the hypandrium is composed of the anterodorsal margin of the paramere (*sensu* Snodgrass, 1935) (Sinclair *et al*., 1994) and makes the hypandrium an O-shaped sclerite.

I conclude that the O-shaped hypandrium, which is probably formed by fusion of the hypandrium with the dorsal bridge of the hypandrium, should perhaps be considered a part of the ground plan of the Tephritoidea. Korneyev (1999), however, stated that the hypandrium of the superfamily Tephritoidea is always C (or U) -shaped in posterior view and lacks a dorsal bridge of the hypandrium (= posterior bridge of Korneyev, 1999). The families of Korneyev's (1999) lower Tephritoidea (Richardiidae, Pallopteridae, Piophilidae, and Lonchaeidae) have an O-shaped hypandrium, including a dorsal bridge (Figs. 6, 9, 10, 16; Steyskal, 1973: Fig. 3). The family Ulidiidae, placed as a sister-group of all other families of Korneyev's (1999) higher Tephritoidea (Platystomatidae, Tephritidae, and Pyrgotidae), also has an O-shaped hypandrium (Figs. 22, 25). Korneyev (1999) treated the Tanypezidae *sensu lato* (including the Strongylophthalmyiidae) as a possible sister group of the Tephritoidea and compared its morphological characters with those of the Tephritoidea. Korneyev's (1999) own cladistic analysis, however, showed the Conopidae, not the Tanypezidae, to be a sister group of the Tephritoidea. McAlpine (1989: Figs. 116.2, 116.3) placed the Conopidae as the sister group of Tephritoidea, with the next outgroups being Nerioidea and Diopsoidea. The hypandrium of the Tanypezidae *sensu stricto* (excluding the Strongylophthalmyiidae) lacks a dorsal bridge of the hypandrium (= transandrium of Roháček, 1999: Figs. 4, 7), whereas the hypandrium of the Strongylophthalmyiidae has a distinct transverse sclerite (= epiphallus of Iwasa, 1999), which is composed of the dorsal arms of the hypandrium (Fig. 29). The hypandrium of the Conopidae has a well-developed dorsal bridge of the hypandrium (e.g., *Zodion* sp., Fig. 26; *Myopa buccata* (Linnaeus); *M. testacea* (Linnaeus); *Sicus nigricans* Kröber; and taxa examined by Steyskal, 1957), although Smith and Peterson (1987) stated that the hypandrium is Y-shaped in ventral view.

I suggest that the transverse bar of the Tephritidae and the ventral sclerite (*sensu* McAlpine, 1973) of the platystomatid and pyrgotid epandrium are homologous and are formed by fusion of the dorsal bridge of the hypandrium and the subepandrial sclerite (*sensu* Cumming *et al*., 1995). The posterior parts of the transverse bar and ventral sclerite are probably also derived from the subepandrial sclerite (*sensu* Cumming *et al*., 1995) and are fused with the dorsal bridge of the hypandrium anteriorly in the Tephritoidea, but they are lost in some species of the Platystomatidae. U or Y-shaped hypandrium, found in some species of the Lonchaeidae, Ulidiidae, Platystomatidae, Tephritidae, and Pyrgotidae (e.g., Figs. 3, 19, 33, 45, 55), are formed when the dorsal bridge of the hypandrium is separated from the hypandrium itself. These suggestions are based on the following observations. In the Pallopteridae, which have a dorsal bridge of the hypandrium (e.g., Fig. 16), a ventral plate of the epandrium (Fig. 16: x) is close to the dorsal bridge of the hypandrium and is articulated with it. The examined species of *Herina* Robineau-Desvoidy has a sclerite (Fig. 17: x) that is fused with the medial surfaces of the paired clasping organs attached to the ventral margin of the epandrium and is articulated with the posterior margin of the basiphallus but it lacks a distinctive dorsal bridge of the hypandrium. There is a single separate plate-like sclerite in the subepandrial membrane between the paired clasping organs attached to the ventral margin of the epandrium in *Dasiops* sp. (Fig. 1: x), *Rivellia basilaris* (Weidemann) (Fig. 32: vs), *Elassogaster hilgendorfi* Enderlein (Fig. 36: vs), and *Paradapsila trinotata* Chen (Fig. 56: vs), all of which have a U-shaped hypandrium. This plate-like sclerite is placed between the left and right clasping organs attached to the ventral margin of the epandrium in *Dasiops* sp. (Fig. 1) and anterior to the surstyli (*sensu* White *et al*., 1999) in *R. basilaris* (Fig. 32), *E. hilgendorfi* (Fig. 36), and



Figs. 1-7. Male terminalia of Lonchaeidae. 1-3. *Dasiops* sp. 4-6. *Lonchaea* sp. 7. *Silba excisa* (Kertesz). 1, 5. Epandrium, surstylus, and proctiger in ventral view. 2. Male terminalia in left lateral view. 3, 6. Hypandrium in ventral view. 4. Epandrium, surstylus, and proctiger in left lateral view. 7. Male terminalia in ventral view. Scale bars = 0.16 mm. Abbreviations: bp: basiphallus. c: cercus. dp: distiphallus. ep: epandrium. hyp: hypandrium. p: phallus. s: surstylus. x: sclerite. Cross or slant shading: inner surface of sclerite. All setae are abbreviated.

P. trinotata (Fig. 56). In the latter three species, this plate-like sclerite is articulated with the hypandrium anteriorly, the epandrium laterally, and the medioproximal portion of the paired clasping organs attached to the ventral margin of the epandrium posteriorly; it has been called the ventral sclerite in the Platystomatidae (McAlpine, 1973). There is a transverse sclerite that is fused with the medial surstylus (e.g., Figs. 31, 34, 35, 40: vs; 43, 48, 50, 52, 54: tb) in some species of the Platystomatidae, Tephritidae, and Pyrgotidae, although it is absent in some platystomatids (e.g., Figs. 37, 42). This transverse sclerite has been called the transverse bar (Munro, 1947) or subepandrial sclerite (White *et al*., 1999), and it generally forms a Π-shaped sclerite in the subepandrial membrane (e.g., Figs. 43, 48, 50, 52) in the Tephritidae.

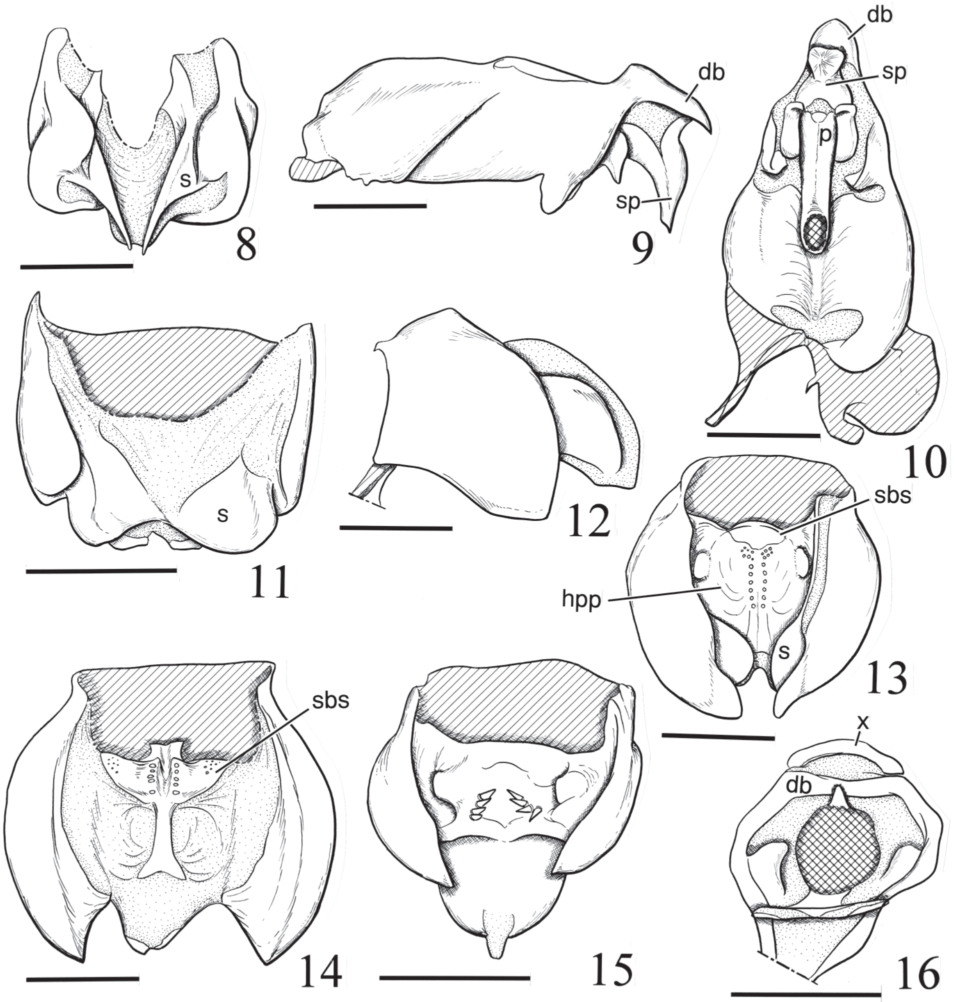
Surstylus of the Tephritidae

The finger-like or rod-like structures articulated to, or fused with, the epandrium have been considered as the surstyli (*sensu* Cumming *et al*., 1995) in the Tephritoidea. McAlpine (1989) suggested the presence of a movable surstylus (*sensu* Cumming *et al*., 1995) as a part of the ground plan of the Schizophora, and the absence of the surstylus (*sensu* Cumming *et al*., 1995) or its fusion with the epandrium as an apomorphic state within the Muscomorpha. The subepandrial membrane is completely sclerotized along its length in the Eremoneura (Cumming *et al*., 1995), and is called the subepandrial sclerite (*sensu* Cumming *et al*., 1995) (Sinclair *et al*., 1994). The two lateral processes that are derived from the base of this sclerite and extend to the surstyli (*sensu* Cumming *et al*., 1995) are the bacilliform sclerites.

I suggest that the medial surstylus (*sensu* White *et al*., 1999) is homologous with the subepandrial sclerite plus the bacilliform sclerite. In the Conopidae and families of Korneyev's (1999) lower Tephritoidea, there is an enclosed plate within the epandrium (Lonchaeidae: Figs. 5, 7), or a lobe-like process articulated to, or fused with, the epandrium (Conopidae, Piophilidae and Pallopteridae: Figs. 8, 11, 13, 27, 28), or no distinctive structures separate from the eapndrium (Pallopteridae: Figs. 14, 15). The medial and lateral surfaces of the lobe-like process are not separated in these families. When, however, the medial surfaces is separated from the lateral surface by a membrane, as in the Platystomatidae, Tephritidae, and Pyrgotidae (Figs. 31, 34, 42, 43, 48, 50, 52, 54, 56), or produced as a lobe free from the distal portion of the epandrium, as in Ulidiidae and Platystomatidae (Figs. 17, 39, 40; Kameneva, 1996: figs. 12, 13), it was called the medial surstylus (White *et al*., 1999), or inner surstylus (McAlpine, 1973; McAlpine, 1981; Hara, 1987; Kameneva, 1996). The medial surstylus extends to the basomedial portion of the lobe-like process articulated to, or fused with, the epandrium and forms the medial wall of this process (Figs. 17, 20, 23, 31, 32, 34-36, 40, 42, 43, 45, 48, 50, 52, 54, 56) in these families. The lateral wall (= lateral surstylus of White *et al*., 1999) retains an articulation with the epandrium, as in some species of Ulidiidae (Figs. 18, 21, 24), or is fused with the epandrium, as in the Platystomatidae, Tephritidae, and Pyrgotidae (Figs. 30-32, 34-38, 40-44, 47-54, 56). The medial surstyli (*sensu* White *et al*., 1999), however, generally maintain their identity as a pair of sclerites in the subepandrial membrane and are articulated with the dorsal bridge of the hypandrium or are united with the ventral sclerite of the epandrium or the transverse bar in the families of Korneyev's (1999) higher Tephritoidea (Figs. 17, 20, 23, 31, 34, 35, 37, 40, 42, 43, 48, 50, 52, 54, 56).

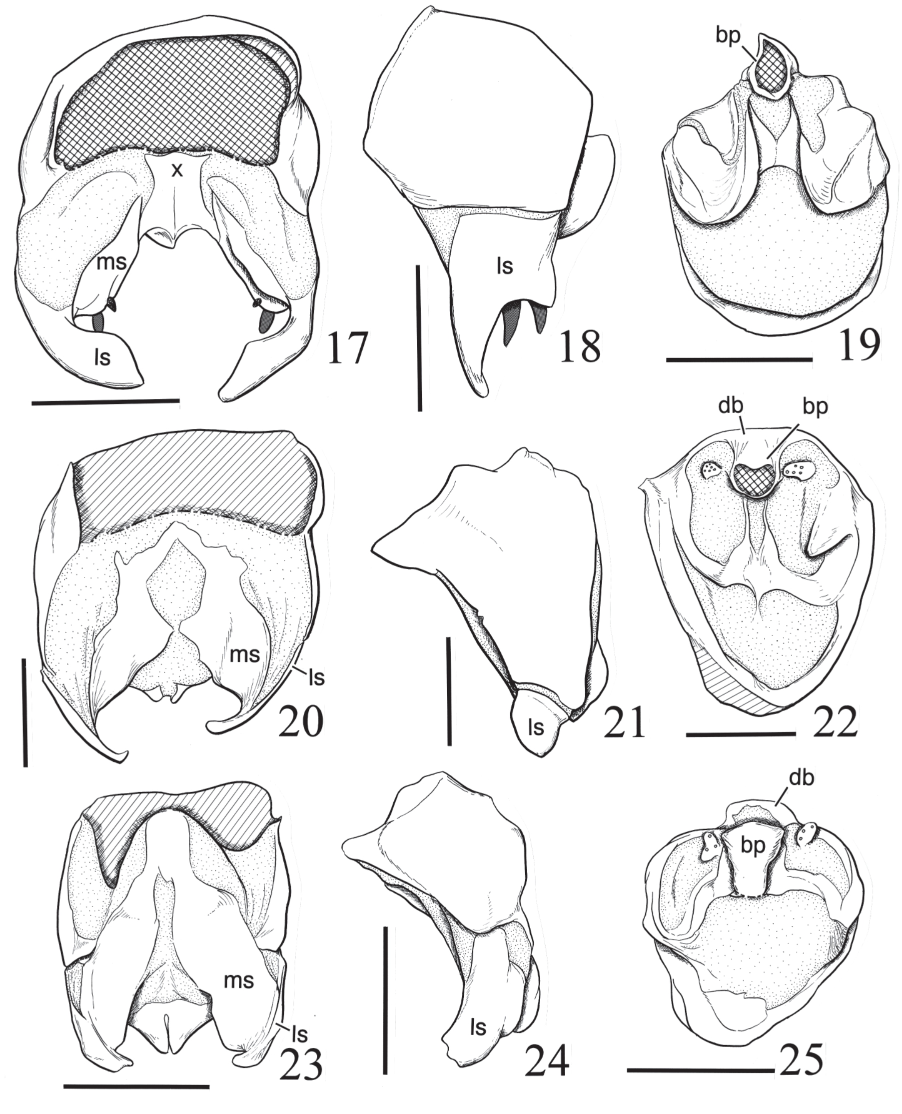
Musculature of the male terminalia

The detailed musculature of the male terminalia of several families of Cyclorrhapha has been described by many authors, and its terminology and homology are summarized in Table 1. Hanna (1938) and Valdez-Carrasco and Prado-Beltran (1990) described the musculature of *Ceratitis capitata* (Wiedemann) in the Tephritidae. The musculature of the male terminalia in all taxa examined consists of the following five groups of muscle sets. **I**) Four pairs of muscles connect the hypandrium with the phallapodeme; muscle 41 (Figs. 57, 59,63) connects the anterior part of the hypandrium with the posterior part of the phallapodeme; muscles 35 and 36



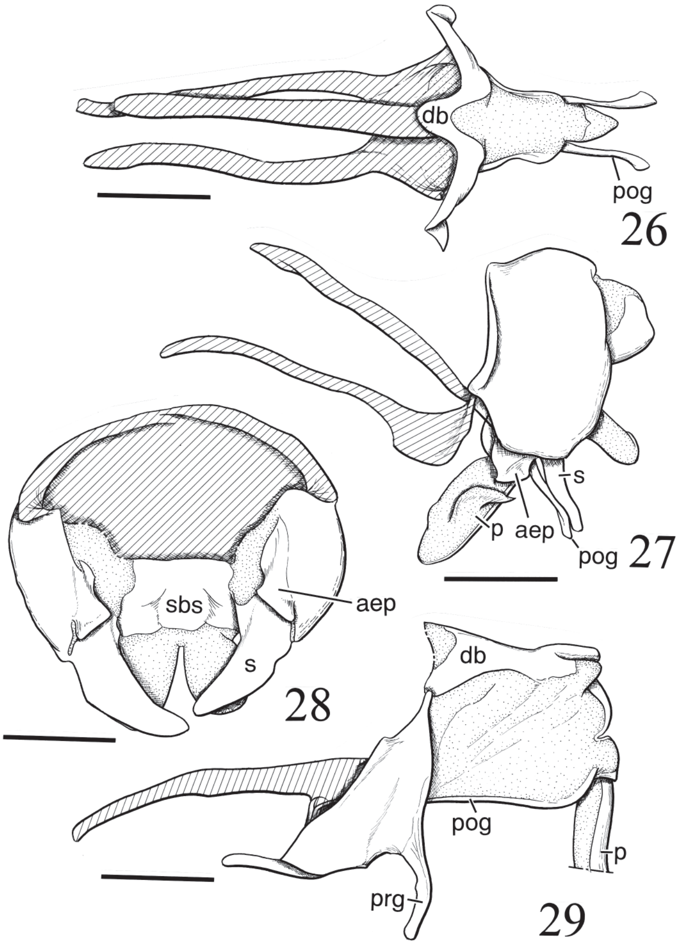
Figs. 8-16. Male terminalia of Piophilidae and Pallopteridae. 8-10. *Liopiophila varipes* (Meigen). 11. *Stearibia nigriceps* (Meigen). 12, 13. *Temnosira trichaeta* Ozerov. 14. *Gorbunia insularis* Ozerov. 15, 16. *Palloptera ustulata* Fallén. 8, 11, 13-15. Epandrium, surstylus, and proctiger in ventral view. 9. hypandrium in left lateral view. 10, 16. hypandrium in ventral view. 12. Epandrium and proctiger in left lateral view. Scale bars: 8-10, 12-16 = 0.16 mm; 11 = 0.10 mm. Abbreviations: db: dorsal bridge of hypandrium. hpp: hypoproct. p: phallus. s: surstylus. sp: spinus. sbs: subepandrial sclerite. x: transverse sclerite posterior to dorsal bridge of hypandrium. Cross or slant shading: inner surface of sclerite. All setae are abbreviated.

(Figs. 57, 59, 63) connect the dorsal projection of the phallapodeme with a transverse ligament between the posterior apex of the lateral arms of the hypandrium; muscle 37 (Figs. 57, 59, 63) connects the ventral part of the phallapodeme with the lateral or posterior part of the hypandrium. **II**) Muscle 34 (Figs. 57, 59, 61, 63) connects the lateral part of the hypandrium with the anterior margin of the epandrium. **III**) Three pairs of muscles connect the epandrium



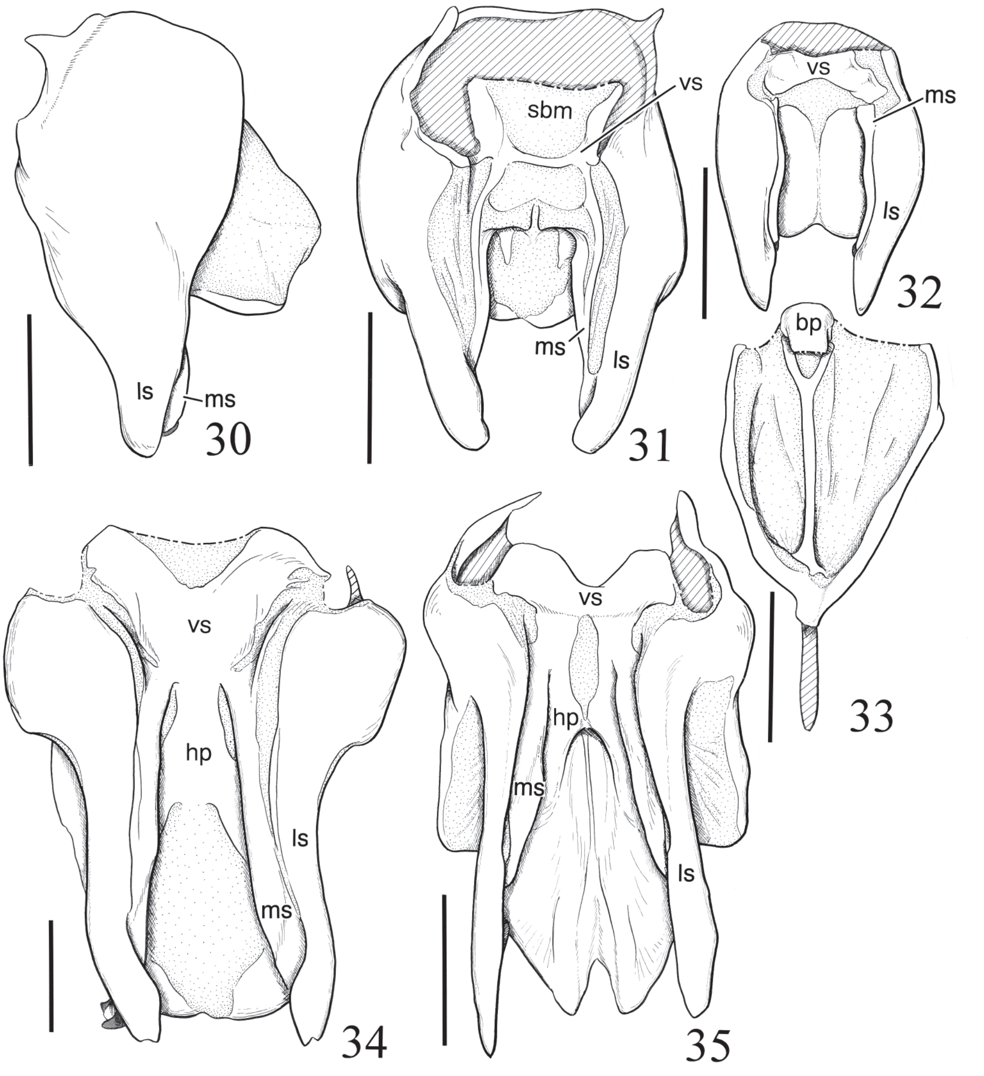
Figs. 17-25. Male terminalia of Ulidiidae. 17-19. *Herina* sp. 20-22. *Physiphora alceae* Playssler. 23-25. *Seioptera* sp. 17, 20, 23. Epandrium, surstylus, and proctiger in ventral view. 18, 21, 24. Epandrium, surstylus, and proctiger in left lateral view. 19, 22, 25. hypandrium in ventral view. Scale bars = 0.16 mm. Abbreviations: bp: basiphallus. db: dorsal bridge of hypandrium. ls: lateral surstylus. ms: medial surstylus. x: plate-like sclerite. Cross or slant shading: inner surface of sclerite; black shading: prensiseta. All setae are abbreviated.

with the bacilliform sclerite: muscles 42 and 43 (Figs. 57, 58, 60-63) connect the mediolateral part of the epandrium with the proximal angle of the surstylus (*sensu* Cumming *et al*., 1995) or bacilliform sclerite; muscle 31 (Figs. 57, 58, 61-63) connects the posterior part of the



Figs. 26-29. Male terminalia of Conopidae and Strongylophthalmyiidae. 26-28. *Zodion* sp. 29. *Strongylophthalmyia caliginosa* Iwasa. 26. Hypandrium in dorsal view. 27. Epandrium, surstylus, and proctiger in left lateral view. 28. Epandrium, surstylus, and proctiger in ventral view. 29. Hypandrium in left lateral view. Scale bars: 27 = 0.20 mm; 26, 28, 29 = 0.16 mm. Abbreviations: aep: anterior epandrial process. db: dorsal bridge of hypandrium. p: phallus. pog: postgonite. prg: pregonite. s: surstylus. sbs: subepandrial sclerite. Slant shading: inner surface of sclerite. All setae are abbreviated.

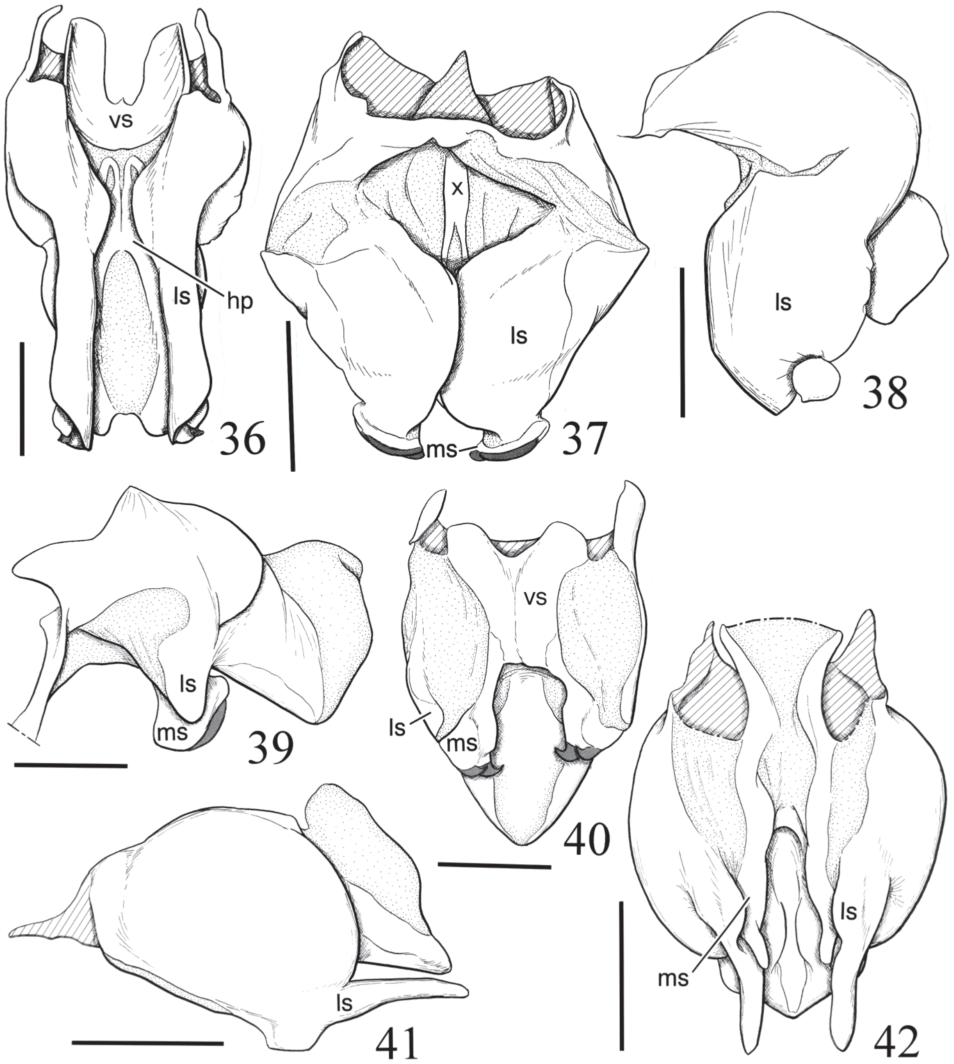
bacilliform sclerite with the cercus. **IV**) A muscle connects the subepandrial sclerite with the cerci. **V**) Muscle 44 (Figs. 57, 58, 62, 63) connects the lateral posterior margin of the epandrium with the anterior margin of the hypoproct (or posterior margin of subepandrial sclerite of Cumming *et al*., 1995). Zatwarnicki (1996) proposed a ground plan for the musculature of the male terminalia of the Cyclorrhapha and the "hinge hypothesis" for the homology of the male terminalia structures of Diptera. I suggest that muscles "f" and "g" of his hypothesis correspond with my group **I**, muscles "d" and "e" correspond with my group **II**, muscle "b" corresponds with my group **III**, and muscle "a" corresponds with my groups **III** and **V**. Although muscle "c"



Figs. 30-35. Male terminalia of Platystomatidae. 30, 31. *Agadasys hexablepharis* Whittington. 32, 33. *Rivellia basilaris* (Wiedemann). 34. *Lamprophthalma japonica* Frey. 35. *Lamprogaster nigrihirta* McAlpine. 30. Epandrium, surstylus, and proctiger in left lateral view. 31, 32, 34, 35. Epandrium, surstylus, and proctiger in ventral view. 33. Hypandrium in ventral view. Scale bars: 30-33 = 0.16 mm, 34 = 0.20 mm, 35 = 0.40 mm. Abbreviations: bp: basiphallus. hp: hypoproct. ls: lateral surstylus. ms: medial surstylus. sbm: subepandrial membrane. vs: ventral sclerite of epandrium. Slant shading: inner surface of sclerite; black shading: prensiseta. All setae are abbreviated.

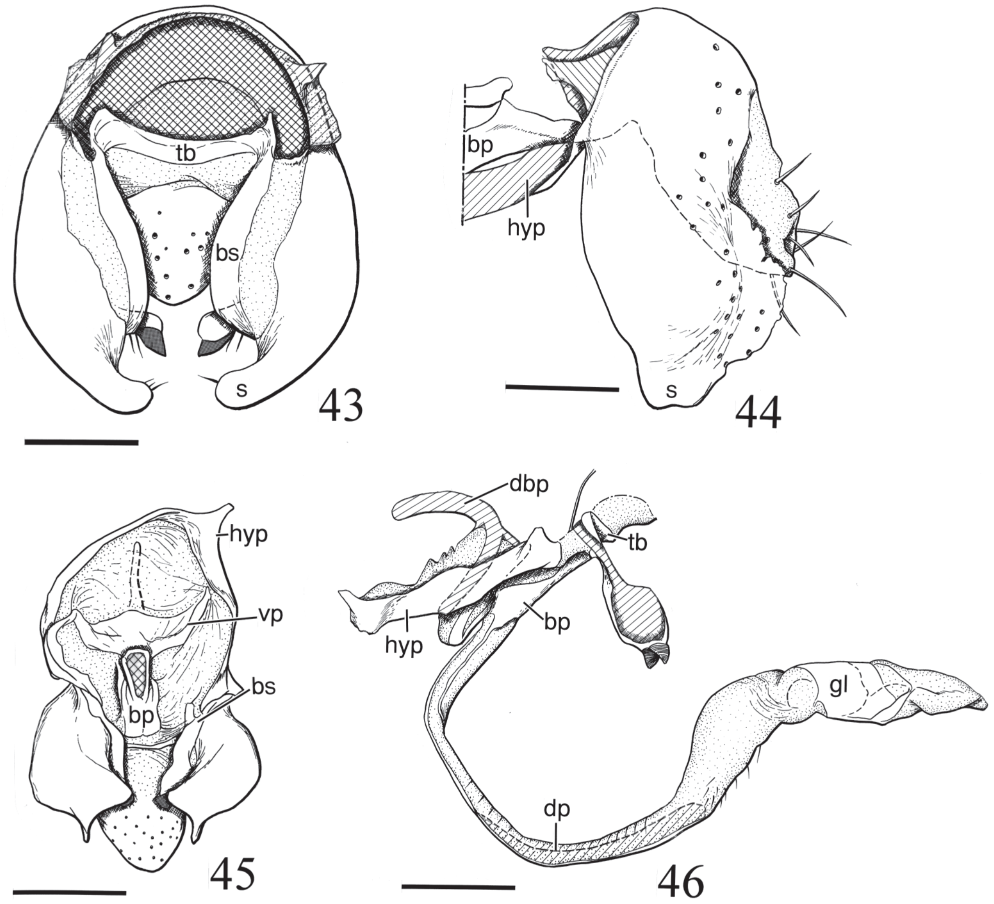
of Zatwarnicki (1996) is the adductor muscle of the surstylus (= gonostylus of Zatwarnicki, 1996) this muscle was not observed in the present study.

I suggested above that the transverse bar of Tephritidae was formed by fusion of the subepandrial sclerite and the dorsal bridge of the hypandrium. This suggestion is based on



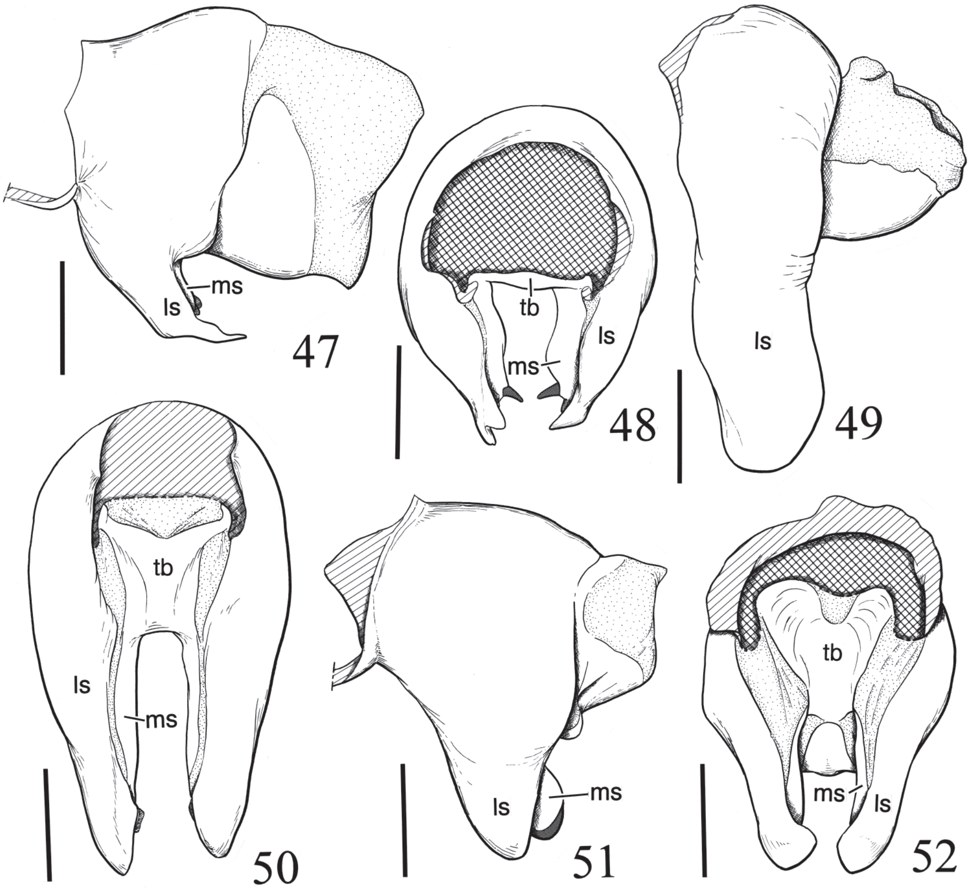
Figs. 36-42. Epandrium, surstylus, and proctiger of Platystomatidae. 36. *Elassogaster hilgendorfi* Enderlein. 37, 38. *Euthyplatystoma sauteri* Hendel. 39, 40. *Prosthiochaeta flavihirta* Hara. 41, 42. *Scholastes* sp. 36, 37, 40, 42. Ventral view. 38, 39, 41. Left lateral view. Scale bars: 36, 39, 40 = 0.20 mm; 37, 38 = 0.16 mm; 41, 42 = 0.40 mm. Abbreviations: hp: hypoproct. ls: lateral surstylus. ms: medial surstylus. vs: ventral sclerite of epandrium. x: proximal portion of medial surstylus. Slant shading: inner surface of sclerite; black shading: prensiseta. All setae are abbreviated.

external structures and is also supported by the presence of the following two pairs of muscles attached to the transverse bar: one pair of muscles connects the transverse bar with the posterior margin of the epandrium (Fig. 57: muscle 31), and the other pair connects the transverse bar with the phallapodeme (Fig. 57: muscle 35-37).



Figs. 43-46. Male terminalia of *Campiglossa hirayamae* (Matsumura) (Tephritidae). 43. Epandrium and proctiger in ventral view. 44. Epandrium and proctiger in left lateral view. 45. Male terminalia in ventral view (excluding distiphallus). 46. Male terminalia in left lateral view (excluding epandrium and proctiger). Scale bars: 43, 44 = 0.10 mm; 45, 46 = 0.16 mm. Abbreviations: bp: basiphallus. bs: bacilliform sclerite (= medial surstylus). dbp: dorsal bar of phallapodeme. dp: distiphallus. gl: glans of distiphallus. hyp: hypandrium. s: surstylus. tb: transverse bar. vp: vane of phallapodeme. Cross or slant shading: inner surface of sclerite; black shading: prensiseta.

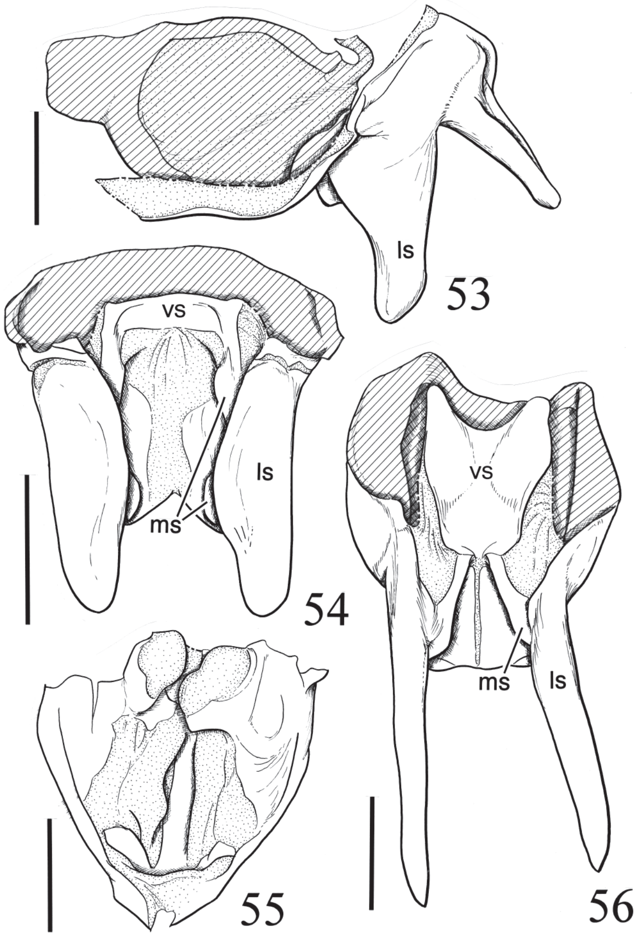
Muscle 178 of Valdez-Carrasco and Prado-Beltran (1990), connecting the bacilliform sclerite with the epandrium, is homologous with muscles 31 of Hennig (1976b) and Salzer (1968), and M3 of Ovchinnikova (1989, 1994). In tephritid species examined by me and in *Ceratitis capitata* (Valdez-Carrasco and Prado-Beltran, 1990), a pair of muscles connecting the lateral end of the transverse bar and the posterior margin of the epandrium was observed (Figs. 57, 58: muscle 31; muscle 178 of Valdez-Carrasco and Prado-Beltran, 1990). In *Temnosira trichaeta* Ozerov and *Rivellia basilaris*, this muscle connects the posterior margin of the epandrium with the anterior margin of the subepandrial sclerite (Figs. 62, 63: muscle 31) or the ventral sclerite (Fig. 61: muscle 31). Ovchinnikova (1989) also described muscle M4 of



Figs. 47-52. Epandrium, surstylus, and proctiger of Tephritidae. – 47, 48. *Ceratitis capitata* Wiedemann. 49, 50. *Acanthonevra pteropleuralis* Hendel. 51, 52. *Ortalotrypeta isshikii* Shiraki. 47, 49, 51. Left lateral view. 48, 50, 52. Ventral view. Scale bars: 47-50 = 0.16 mm; 51, 52 = 0.20 mm. Abbreviations: ls: lateral surstylus. ms: medial surstylus. tb: transverse bar. Cross or slant shading: inner surface of sclerite; black shading: prensiseta.

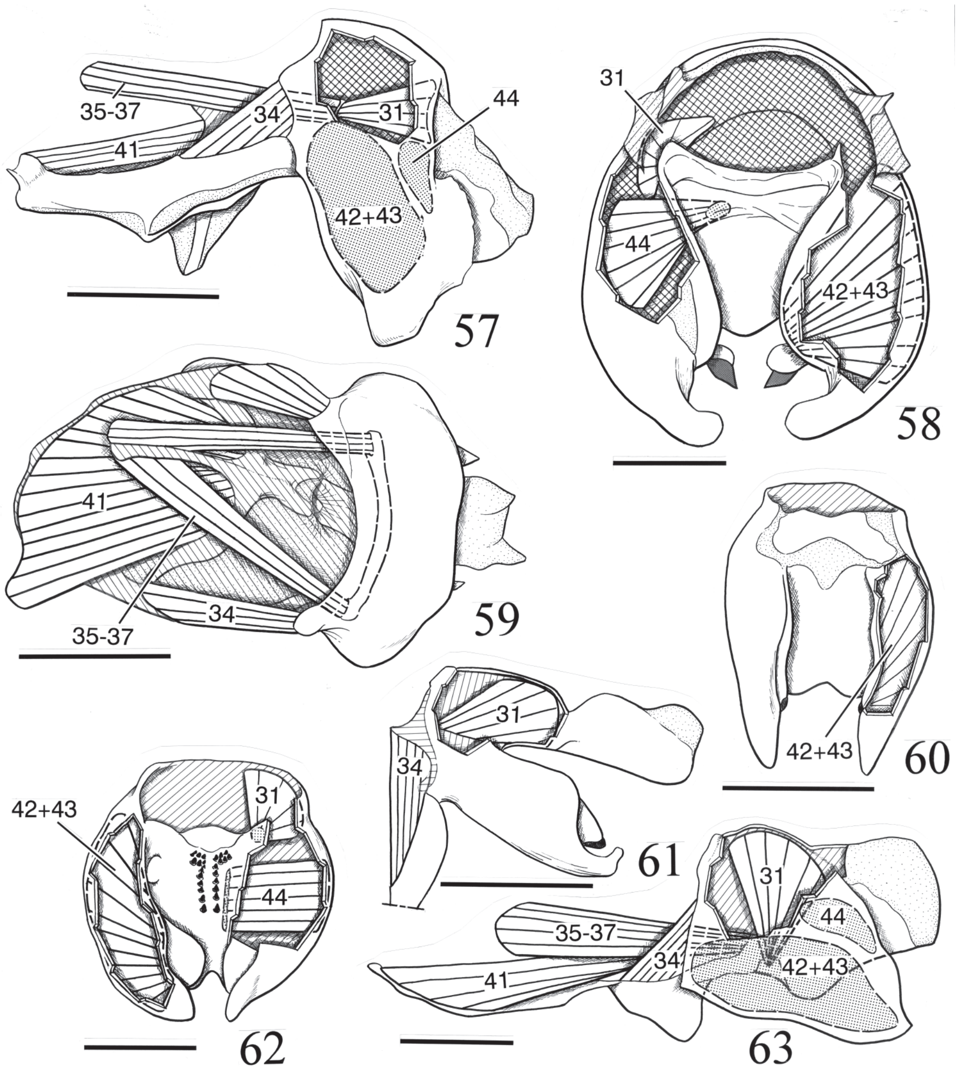
Eristalis nemorum (Linnaeus) and muscle M21 of *Lipara lucens* Meigen and *Dryomyza anilis* Fallén, as originating from the posterior margin of the epandrium and inserted on the subepandrial sclerite.

Muscle M2 of Ovchinnikova, connecting the bacilliform sclerite with the phallapodeme, is suggested to be homologous with muscle 37 of Salzer (1968). Muscles 35 and 36, found in *Fucellia* Robineau-Desvoidy, *Delia* Robineau-Desvoidy, and *Calliphora*, probably are split from muscle M2 of Ovchinnikova (1989, 1994) and shifted from the hypandrium to the transverse ligament between the lateral arms of the hypandrium in the Anthomyiidae and Calliphoridae. Muscle 174 of Valdez-Carrasco and Prado-Beltran (1990) is also suggested to be homologous with muscles 35-37 of Salzer (1968) as found in *Fucellia*, *Delia*, and *Calliphora*, and has probably shifted its attachment from the hypandrium to the transverse bar (*sensu*



Figs. 53-56. Male terminalia of Pyrgotidae. 53-55. *Eupyrgota luteola* (Coquillett). 56. *Paradapsila trinotata* Chen. 53. Epandrium, surstylus, and proctiger in left lateral view. 54, 56. Epandrium, surstylus, and proctiger in ventral view. 55. Hypandrium in ventral view. Scale bars: 53, 55, 56 = 0.50 mm; 54 = 1.00 mm. Abbreviations: ls: lateral surstylus. ms: medial surstylus. vs: ventral sclerite of epandrium. Slant shading: inner surface of sclerite. All setae are abbreviated.

Munro, 1947) in the Tephritidae (Figs. 57, 59: muscle 35-37) in connection with the separation of the dorsal bridge of the hypandrium from the hypandrium itself. These assumptions are based on the following observations. Many authors have described a pair of muscles (e.g., M2 of Ovchinnikova, 1989) connecting the phallapodeme and the lateral or dorsal arms of the hypandrium in some families of the Cyclorrhapha (Table 1). In *Temnosira trichaeta*, which has an O-shaped hypandrium, this muscle is attached to the lateral arm of the hypandrium (Fig. 63: muscle 35-37). However, *Ceratitis capitata* has a pair of muscles connecting the lateral end of the phallapodeme and the transverse bar but not the hypandrium (muscle 174 of Valdez-Carrasco and Prado-Beltran, 1990), and I found similar muscles in other tephritid species (Fig. 59: muscle 35-37).



Figs. 57-63. Hypopygial musculature of Tephritoidea. 57-59. *Campiglossa hirayamae* (Matsumura). 60-61. *Rivellia basilaris* (Wiedemann). 62-63. *Temnosira trichaeta* Ozerov. 57, 61, 63. Male terminalia in left lateral view (phallus omitted). 58, 60, 62. Epandrium and proctiger in ventral view. 59. Male terminalia in dorsal view. Scale bars: 57 = 0.10 mm, 58-63 = 0.16 mm. Number of musculature follows Salzer (1968). Cross or slant shading: inner surface of sclerite; sparse black shading: attached point of muscle; dense black shading: prensiseta. All setae are abbreviated.

Observations of the musculature of the male terminalia also provide evidence for the homology of the medial surstylus (*sensu* White et al., 1999) and the bacilliform sclerite and the identity of the lateral surstylus (*sensu* White et al., 1999) of the Tephritidae. The term surstylus (*sensu* Cumming *et al*., 1995) should be applied to the apex of the ventral projection of the epandrium or at least to a finger-like structure beyond the area of the epandrium to which

Table 1
Hypopygial musculature in Cyclorrhapha

		hypandrium-phallapodeme		epandrium-hypandrium	epandrium-bacilliform sclerite		cerci-subepandrial sclerite	epandrium-hypoproct	
Eristalis nemorum (Linnaeus)	1	M1	M2	M5	M3	M4	M7 (=M29)	-	
Sphaerophoria indiana Bigot	2	14	13	9	10, 12	11	-	-	
Lonchoptera lutea Panzer	3	M41?	M37-39	M34	-	M31+42+43	MC	-	
Ceratitis capitata (Wiedemann)	4	175	174	176	178	180	181/182	179	
Ceratitis capitata	5	Mus.1	Mus.2	-	-	-	-	-	
Rachispoda hoplites (Spuler)	6	-	-	A	-	B	-	-	
Dryomyza anilis Fallén	7	M1	M2	M51	M52	M21	M3, M4	M29	-
Lipara lucens Meigen	8	M1	M2	M51	M52	M21	M4	M29	-
Scathophaga stercoraria (Linnaeus)	9	M1	M2	M52	M51	M25	M3	-	-
Fucellia tergina (Zetterstedt)	10	41	35-37	34	31	42/43	-	44	
Delia platura (Meigen)	11	41	35-37	34	31	42/43	-	44	
*Calliphora erythrocephala (*Meigen)	12	k	f	e	a	-	a/b	-	d
Calliphora erythrocephala	13	41	35/37	34	31	42/43	-	44	
Musca domestica Linnaeus	14	M1	M2	M5	-	M4	-	M26	
Nycteribia latreillii Leach	15	e.m.p.	-	-	-	-	-		
Hippobosca longipennis Fabricius	16	r.a.	p.a.	p.g.d.	-	-	-	-	

References. 1, 7-9, 14: Ovchinnikova, 1989. 2: Zaka-ur-Rab, 1979. 3: Hennig, 1976a. 4: Valdez-Carrasco and Prado-Beltran, 1990. 5: Hanna, 1938. 6: Wheeler, 1995. 10-11: Hennig, 1976b. 12: Graham-Smith, 1938. 13: Salzer, 1968. 15: Theodor, 1954. 16: Theodor and Oldroyd, 1964 muscle 42-43 is attached in the Tephritidae, based on the following suggestion. This application of the terminology is almost the same as that of Munro (1947), who compared the external structures of the male terminalia between the Tephritidae and Calliphoridae. My suggestion, however, is based on the observation of the musculature of the male terminalia in addition to the external structures of the male terminalia of 42 Cyclorrhaphan families, including the Tephritidae. A proximal part of the lateral surstylus actually consists of the lateral wall of the epandrium, because a muscle inserted onto the medial surstylus is attached to the lateral surstylus of the Tephritidae. The contention above, that the medial surstylus of the Tephritidae is the bacilliform sclerite, is also supported by this musclature as discussed below. No muscles connecting the lateral and medial walls of the surstylus (*sensu* Cumming *et al*., 1995) have yet been described in the literature (see references listed in Table 1).

I suggest that a bundle of muscles attached to the bacilliform sclerite and the epandrium is homologous with muscles 42 + 43 of Salzer (1968) and muscle M4 of Ovchinnikova (1989; 1994). Cumming *et al*. (1995) considered that the surstylus is adducted by a single set of muscles. This adductor muscle is inserted directly onto the base of the surstylus (Cumming *et al*., 1995) or onto the posterior half of the bacilliform sclerite (Cumming *et al*., 1995). According to descriptions of the musculature of the male terminalia in many families of the Cyclorrhapha (Table 1) and my own observations, there is a muscle originating from the lateral wall of the epandrium and extending to the bacilliform sclerite (in the subepandrial membrane) or to the inner basal portion of the surstylus (*sensu* Cumming *et al*., 1995) (Figs. 58, 60, 62). This muscle is actually an adductor muscle of the surstylus (*sensu* Cumming *et al*., 1995) and connects the epandrium and the medial basal part of the surstylus (*sensu* Cumming *et al*., 1995) in *Eristalis* Latreille, *Lipara* Meigen, and *Musca* Linnaeus (Ovchinnikova, 1994). This muscle corresponds with muscle M4 of Ovchinnikova (1989, 1994) and it connects the mediodorsal part of the epandrium and the anterior epandrial process (*sensu* Steyskal and Knutson, 1978), anterior surstylus (Steyskal, 1957; McAlpine, 1981), or lateral lobe of the surstylus (Ovchinnikova, 1989, 1994) in *Dryomyza* Fallén. Muscle M4 of Ovchinnikova (1989; 1994) may also be split into two muscle pairs of the group III (muscles 42 and 43) connecting the epandrium and bacilliform sclerite in the Calliphoridae and Anthomyiidae. Valdez-Carrasco and Prado-Beltran (1990) reported that a bundle of muscles (muscle 180) originates from the broad basal region of the lateral surstylus (*sensu* White *et al*., 1999) in *Ceratitis capitata*, and showed that this muscle is connected to the medial surstylus (*sensu* White *et al*., 1999). I found a similar muscle in the male terminalia of *Campiglossa hirayamae* (Matsumura) (Fig. 48: muscle 42 + 43), *Xyphosia punctigera* Coquillett, *Acanthonevra speciosa* (Hendel), and *Bactrocera scutellata* (Hendel). This muscle is usually connected with the lateral portion of the epandrium, which is sometimes called the lateral surstylus by authors.

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APPENDIX

Species of Cyclorrhapha examined for this study

The family order and classification follows McAlpine (1989), and the species are arranged alphabetically. An asterisk denotes species also examined for the hypopygial musculature.

ASCHIZA
Lonchopteridae: *Lonchoptera stackelbergi* (Czerny), **Lon. japonica* Matsumura, *Lon. platytarsis* (Okada); **Platypezidae**: *Paraplatypeza* sp., *Callomyia* sp., *Opetia alticola* Saigusa, *Microsania* sp.; **Syrphidae**: **Eristalis tenax* (Linnaeus), **Sphaerophoria macrogaster* (Thompson), *Syrphus torvus* Osten-Sacken, *Syrphus vitripennis* Meigen, *Temnostoma apiforme* (Fabricius), *Volucella pellucens tabanoides* Motschulsky, *Rhingia laevigata* Loew, *Ferdinandea cuprea* (Scopoli), *Pipiza* sp.; **Pipunclidae**: *Eudorylas* sp.

SCHIZOPHORA
ACALYPTRATA. Micropezidae: *Calobata rufithorax* (Hennig), *Mimegralla albimana* (Doleschell); **Neriidae**: *Stypocladius appendiculatus* (Hendel); **Cypselosomatidae**: *Cypselosoma* sp., *Formicosepsis hamata* (Enderlein); **Strongylophthalmyiidae**: *Strongylophthalmyia caliginosa* Iwasa, *St. japonica* Iwasa; **Psilidae**: *Chyliza flavifrons* Iwasa, *Loxocera maculipennis* Hendel, *Psila nigripalpis* Shatalkin; **Megamerinidae**: **Textra compressa* Walker; **Diopsidae**: *Megarabops* sp.; **Conopidae**: *Conops* (*Asiconops*) sp., *Myopa buccata* (Linnaeus), *My. testacea* (Linnaeus), **Sicus nigricans* Krober, *Zodion* sp.; **Lonchaeidae**: *Dasiops* sp., *Lonchaea* sp., **Silba excisa* (Kertesz); **Ulidiidae**: *Herina* sp. (undescribed), *Physiphora alceae* Playssler, *Seioptera* sp.; **Platystomatidae**: *Agadasys hexablepharis* Whittington, *Elassogaster hilgendorfi* Enderlein, *Euprosopia grahami* Malloch, *Euthyplatystoma sauteri* Hendel, *Lamprogaster nigrihirta* McAlpine, *Lamprophthalma japonica* Frey, *Plagiostenopterina aenea* (Wiedemann), *Prosthiochaeta flavihirta* Hara, **Rivellia basilaris* (Wiedemann), *Rivellia mandschurica* Henning, *Scholastes* sp.; **Pyrgotidae**: *Campylocera* sp., *Eupyrgota luteola* (Coquillett), *Paradapsila trinotata* Chen; **Tephritidae**: *Acanthonevra pteropleuralis* Hendel, **Ac. speciosa* (Hendel), **Campiglossa hirayamae* (Matsumura), *Ceratitis capitata* Wiedemann, *Ortalotrypeta isshikii* Shiraki, **Xyphosia punctigera* Coquillett; **Pallopteridae**: *Gorbunia insularis* Ozerov, *Palloptera ustulata* Fallén, *Temnosira czurniki* Ozerov, **Temnosira trichaeta* Ozerov; **Piophilidae**: *Liopiophila varipes* (Meigen), *Protopiophila contecta* (Walker), *Stearibia nigriceps* (Meigen); **Lauxaniidae**: *Homoneura euaresta* (Coquillett), **Hom. hirayamae* (Matsumura), *Minettia nigriventris* (Czerny); **Celyphidae**: *Spaniocelyphus phillippinus* Frey; **Chamaemyidae**: *Leucopis pallidolineata* Tanasijtshuk; **Coelopidae**: **Coelopa frigida* (Fabricius); **Dryomyzidae**: *Helcomyza ustulata* Curtis, *Heterocheila buccata* (Fallén), *Dryomyza ecalcarata* Kurahashi, **D. formosa* (Wiedemann), **Paradryomyza spinigera* Ozerov; **Sciomyzidae**: *Limnia japonica* Yano, *Pherbellia cinerella* (Fallén), **Sepedon aenescens* Wiedemann, *Tetanocera elata* (Fabricius); **Sepsidae**: *Sepsis monostigma* Thomson; **Clusiidae**: *Heteromeringia* sp.; **Agromyzidae**: *Agromyza* sp.; **Opomyzidae**: **Geomyza advena* Frey; **Milichiidae**: *Aldrichiomyza flaviventris* Iwasa; **Cryptochetidae**: *Cryptocheta smaragdinum* Séguy; **Chloropidae**: *Chlorops (Sclerophallus) varsoviensis* Becker; **Lipara japonica* Kanmiya; **Heleomyzidae**: **Suillia gorodkovi* Okadome; **Sphaeroceridae**: *Sphaerocera cervipes* Latreille; **Drosophilidae**: *Drosophila* (*Sophophora*) *suzukii* (Matsumura); **Ephydridae**: *Ochtera mantis* (de Geer). **CALYPTRATA. Hippoboscidae**: **Stenepterix hirundinis* (Linnaeus); **Scathophagidae**: *Norellisoma agrion* Séguy, **Scathophaga stercoraria* (Linnaeus); **Anthomyiidae**: **Fucellia apicalis* Kertész; **Muscidae**: **Musca domestica* Linnaeus; **Calliphoridae**: **Calliphora nigribarbis* Vollenhoven; **Sarcophagidae**: *Sarcophaga* sp.; **Tachinidae**: *Exorista japonica* (Townsend), *Phasia hemiptera* (Fabricius).