

Homology of the metapleuron of Cyclorrhapha, with discussion of the paraphyly of Syrphoidea (Diptera: Aschiza)

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Abstract

The morphology of the metathorax of brachyceran Diptera is examined, particularly the metapleuron in the superfamily Syrphoidea comprising two families Syrphidae and Pipunculidae. The homologies of the metepisternum (EPS) and metepimeron (EPM) are redefined based on the metapleural suture (PLS), which bears an internal apophysis. A new interpretation of the metathorax is provided for Syrphidae. Members of Schizophora and Pipunculidae have an articulation between EPM and the first abdominal tergite in common and the (metapleural-abdominal) articulation is indicated as a synapomorphy for them. In some species of Syrphidae the well-developed metapostnotum is articulated with the first abdominal tergite and the (metapostnotal-abdominal) articulation is diagnostic of a subgroup of the family. The articulations are evaluated and discussed with respect to abdominal flexion of Diptera.

Keywords

abdominal flexion; articulation structure; metapleural suture (PLS); metepimeral pleura (EPM); metepisternal pleura (EPS); Schizophora

Introduction

The Diptera have their hindwings reduced to small club-like organs, whereas their forewings are developed as functional flight organs. The halteres are considered the most important autapomorphy of the Diptera, which are indeed named for having only two fully developed wings. The halteres play an important role as gyroscopic organs of equilibrium and moves antiphasically to the forewing during flight (Fraenkel & Pringle 1938; Schneider 1953; Chan et al. 1998). The metathorax of flies is atrophied by the wing reduction into halteres in contrast with the mesothorax that bears the well-developed forewings and internally has large and powerful flight muscles.

The pleura of the wing-bearing (pterothoracic) segments show many minor variations in structure because of the important elements of the wing mechanism, and hence the progressive development of thoracic pleura often provides a valuable clue to resolve phylogenetic relationships among higher taxa such as orders and families

(Snodgrass 1935; Hennig 1973). The Diptera are divided into two suborders (Nematocera and Brachycera) by a feature regarding the mesopleural suture, which is associated with forewing(s) being developed as effective flight organs. The suture is bent twice at almost a right angle in members of the Brachycera, in contrast to the plesiomorphic straight suture in the Nematocera (Hennig 1973; Yeates 2002).

The Cyclorrhapha (*Muscomorpha sensu* McAlpine 1989) are one of the monophyletic clades in the suborder Brachycera, with approximately 55 000 described species (Yeates & Wiegmann 1999). The clade has traditionally been divided into two groups, Schizophora and Aschiza, based on the presence (or absence) of a ptilinal fissure. The former, Schizophora, comprises at least 80 families, over half the family-level diversity of Diptera. Monophyly of the Schizophora is strongly supported by many molecular and morphological studies (McAlpine 1989; Cumming et al. 1995; Collins & Wiegmann 2002; Yeates et al. 2007; Lambikin et al. 2013). By contrast, the latter, 'Aschiza', is currently considered paraphyletic based on morphological and molecular data (Griffiths 1972; Wada 1991; Cumming et al. 1995; Zatwarnicki 1996; Moulton & Wiegmann 2004; Wiegmann et al. 2011). In phylogenetic relationships within the 'Aschiza', the following three superfamilies or family groups are recognized by a super-tree analysis (Yeates et al. 2007): Opetiidae + Platypezidae, Phoroidea + Lonchopteridae and Syrphoidea. To date, two hypotheses concerning the sister-group of the Schizophora have been proposed from molecular and morphological research (Fig. 1). The morphological studies suggest that the Syrphoidea, comprising two families (Syrphidae and Pipunculidae), are the sister-group of the Schizophora, of which monophyly is indicated by asymmetrical structure of the male postabdominal segments (Griffiths 1972; Cumming et al. 1995; Zatwarnicki 1996). The characters uniting Syrphoidea + Schizophora are monotype ommatidia, dorsal arista and lever-like phallapodeme (Wada 1991; Cumming et al. 1995). By contrast, molecular data suggest Syrphoidea are paraphyletic and the Pipunculidae are sister to the Schizophora (Collins & Wiegmann 2002; Moulton & Wiegmann 2007; Wiegmann et al. 2011).

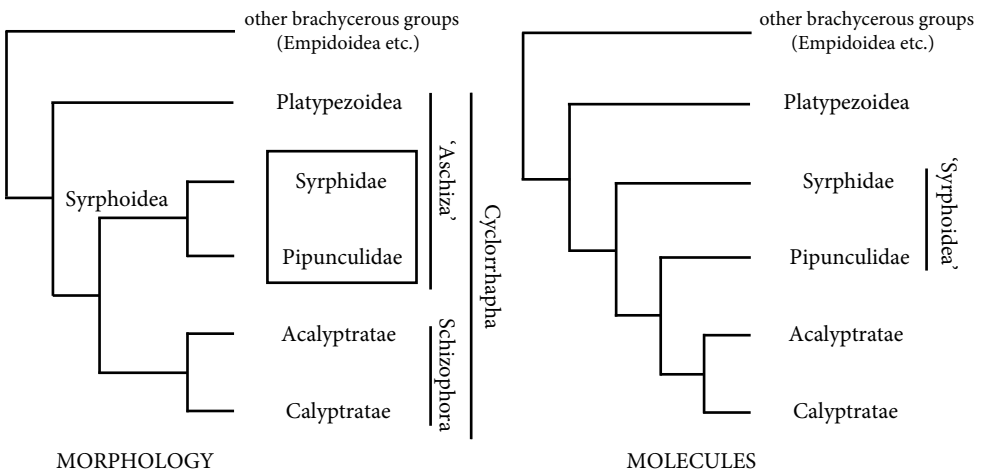


Fig. 1. Phylogenetic hypotheses of sister group of the Schizophora.

Here I investigate the characteristics of the metathorax of brachyceran Diptera, particularly the metapleuron of the Syrphoidea. The homologies of the metepisternum and metepimeron are redefined based on the metapleural suture, which bears an internal apophysis, and a new interpretation of the metathorax is provided. I evaluate a joint structure of thoracic and abdominal segments of Diptera with respect to abdominal flexion, and briefly discuss a character supporting the Syrphoidea, asymmetrical male postabdomen.

Materials and methods

Homologies in thoracic pleuron are defined by the position of the pleural suture (Snodgrass 1935; Matsuda 1970). The pleural suture is easily distinguished by having an internal apophysis dividing the pleuron into presutural and postsutural plates. The former is generally termed the episternum and the latter the epimeron. In this study I confirmed the placement of the internal apophysis on the pleural suture in relation to the determination of homologous sclerites.

The whole body was used in this study. It was treated with a 10% solution of potassium hydroxide, neutralized with a 3–5% solution of acetic acid for approximately 10 min, and then washed with distilled water. After the treatment, the characters of the thoracic pleura were examined in glycerol or 70–80% ethanol. Drawings were made with an ocular grid set to a Leica M205C stereoscopic microscope.

Taxa used in this study (more than 40 species belonging to 30 families) are listed in the Appendix. They were selected from the Cyclorhapha (Cumming et al. 1995; Muscomorpha *sensu* McAlpine 1989) of the Brachycera to investigate the sister group of Schizophora (either Syrphoidea or Pipunculidae). The classification of Syrphidae and Pipunculidae follows Vockeroth & Thompson (1987) and Rafael & De Meyer (1992), respectively.

Results

In brachyceran flies (Figs. 2–11), the metapleural suture (PIS) is nearly straight from the base of the halter to the hind coxa. The metapleuron is differentiated into the presutural metepisternum (EPS) and postsutural metepimeron (EPM) by the metapleural suture. The metascutum (Sct) and metascutellum (Scl) are usually located at the base of the halter. The metapostnotum is greatly reduced in the examined taxa and is connected to the first abdominal tergite (or first and second abdominal syntergite) by a transverse membranous portion. The metathoracic features of each group are described as follows.

Schizophora (Figs. 2–4)

The EPS is roughly square or rectangular below the metathoracic spiracle. The EPM is similar to the EPS in shape (Figs. 2–3), and it has usually an extended posterior (upper) arm (Fig. 2). The tip of the posterior arm articulates with the lateral side of the first

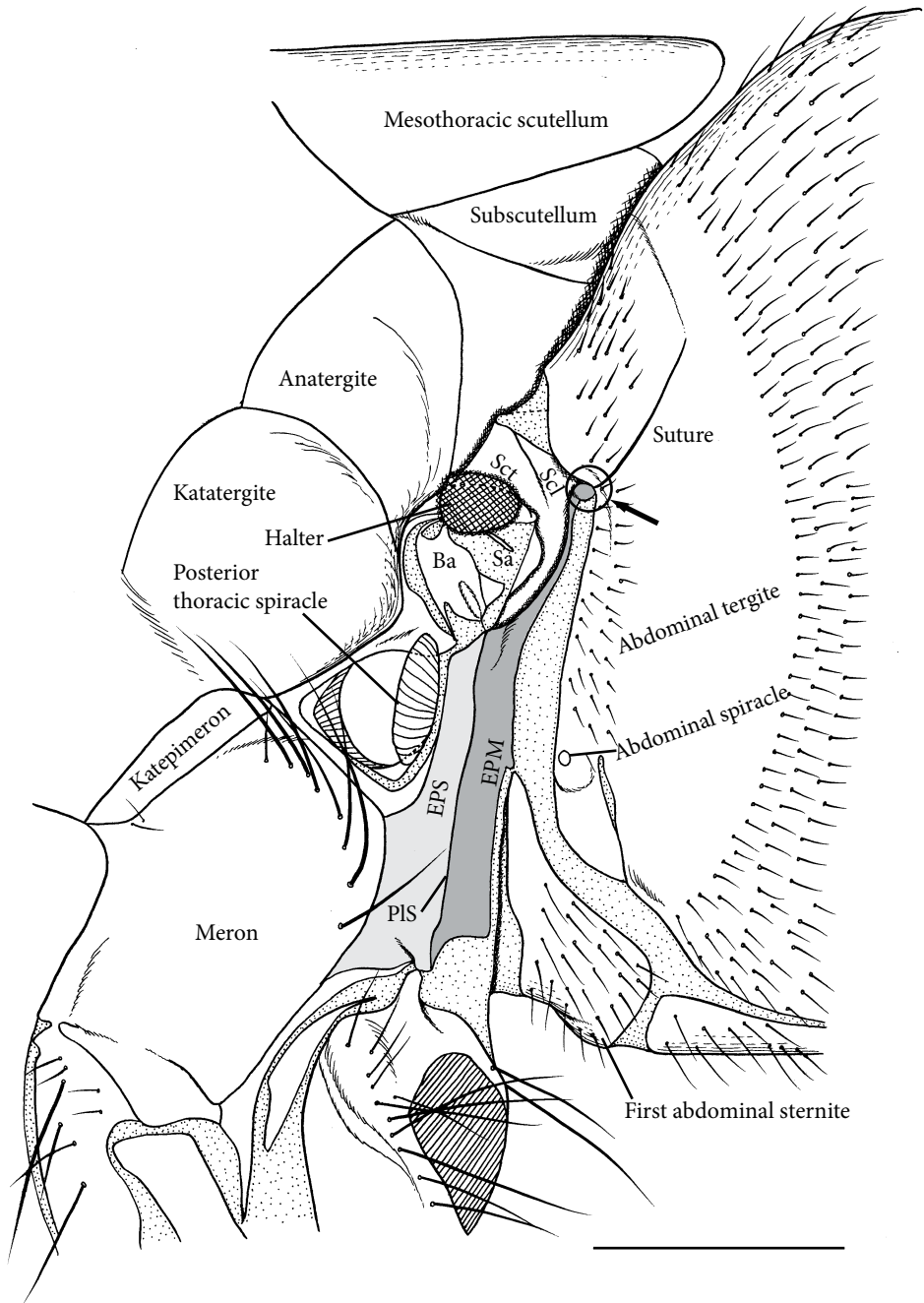
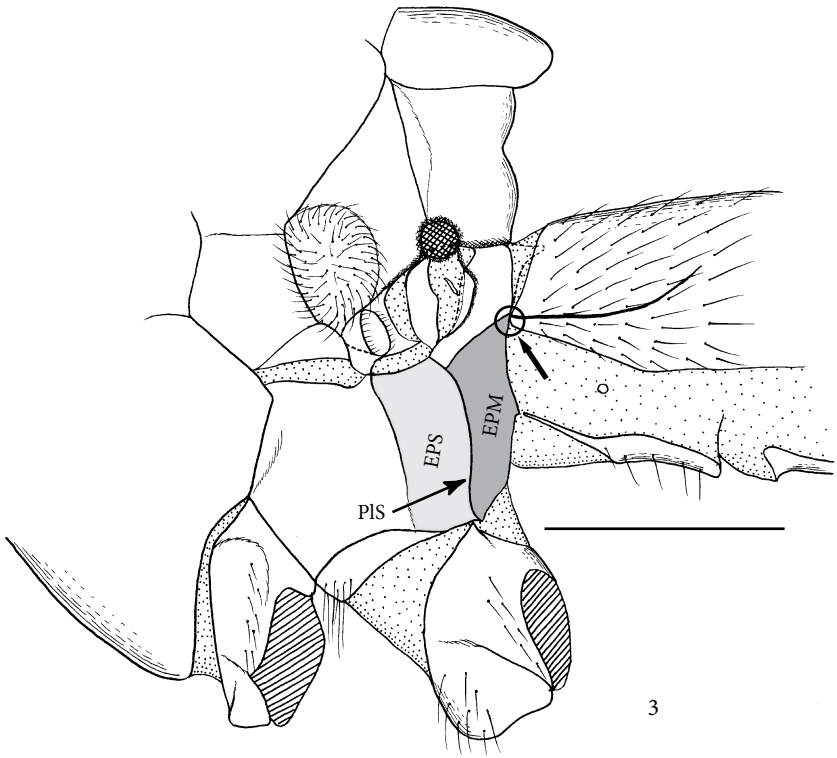
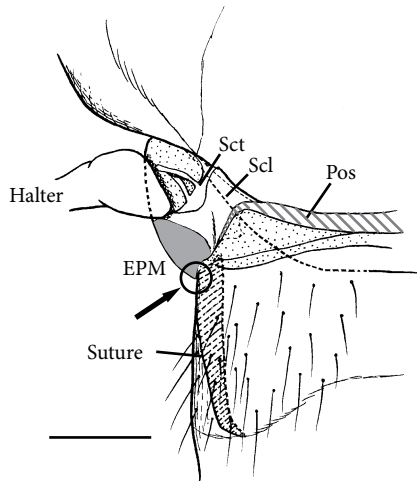


Fig. 2. Thoracic and abdominal segments of Calypttratae (Tachinidae: *Carcelia rasa* (Macquart)) in lateral view. Circle indicates articulation between metepimeron and first and second abdominal synergite. Scale = 0.5 mm. Abbreviations: Ba, basalare; EPM (dark gray), metepimeron; EPS (light gray), metepisternum; PLS, metapleural suture; Sa, subablare; Sct, metascutum; Scl, metascutellum.



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Figs. 3–4. Metathoracic and abdominal segments of Acalypratae (Micropezidae: *Compsobata japonica* Hennig) in lateral (3) and in dorsal (4) views. Circles indicate articulation between metepimeron and first abdominal tergite. Scales = 0.5 mm (3), 0.2 mm (4). Abbreviations: EPM (dark gray), metepimeron; EPS (light gray), metepimeron; PLS, metapleural suture; Sct, metascutum; Scl, metascutellum; Pos (hatched area), metapostnotum.

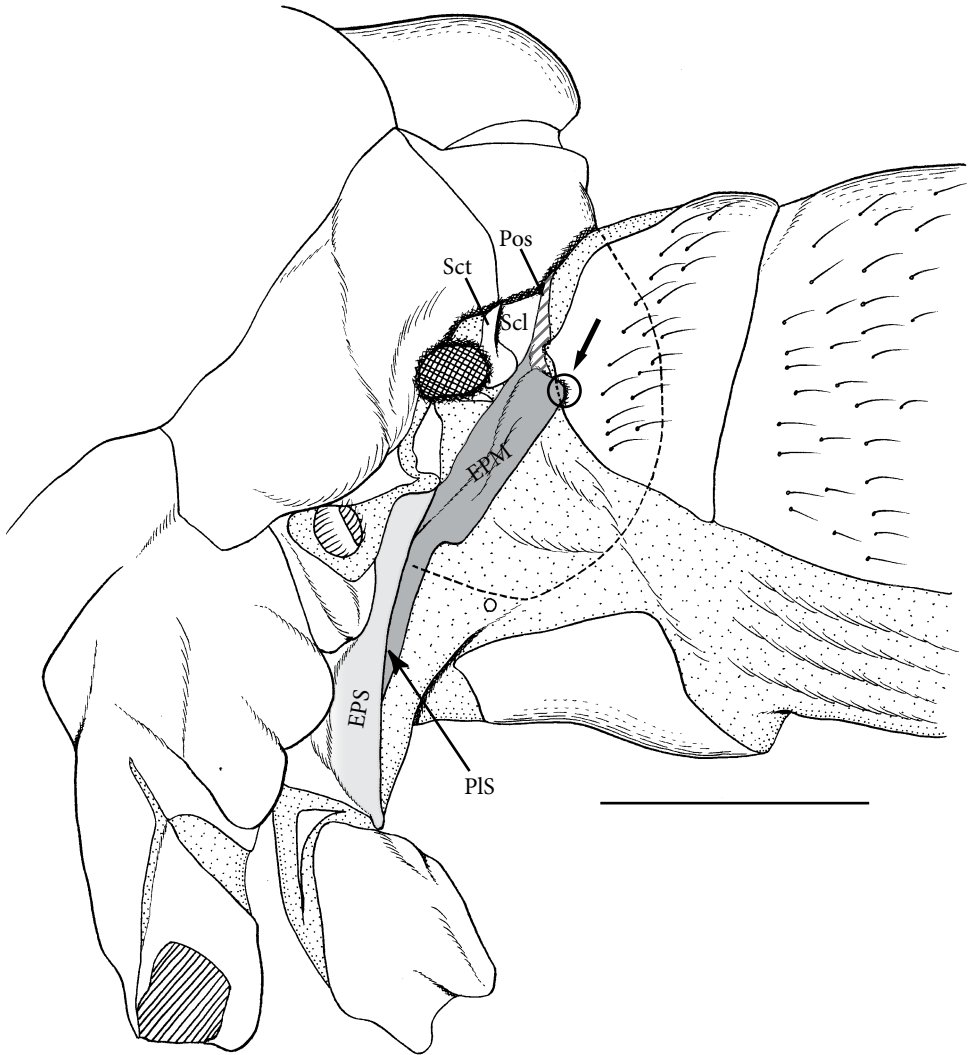


Fig. 5. Metathoracic and abdominal segments of *Aschiza* (Pipunculidae: *Pipunculus* sp.) in lateral view. Circle indicates articulation between metepimeron and first abdominal tergite. Scale = 0.5 mm. Abbreviations: EPM (dark gray), metepimeron; EPS (light gray), metepisternum; PIS, metapleural suture; Sct, metascutum; Scl, metascutellum; Pos (hatched area), metapostnotum.

abdominal tergite. Some species of Acalyptratae (e.g., Micropezidae) lack the upper extension but the EPM still articulates with the first abdominal tergite at the postero-dorsal corner (Fig. 3). At the articulation point, a suture is always found on the abdominal tergite and is accompanied by an internal apophysis (Fig. 4). The metapostnotum (Pos) is a narrow and transverse sclerotized plate connecting the two apices of the metascutellum. It is usually concealed beneath the base of the first abdominal tergite.

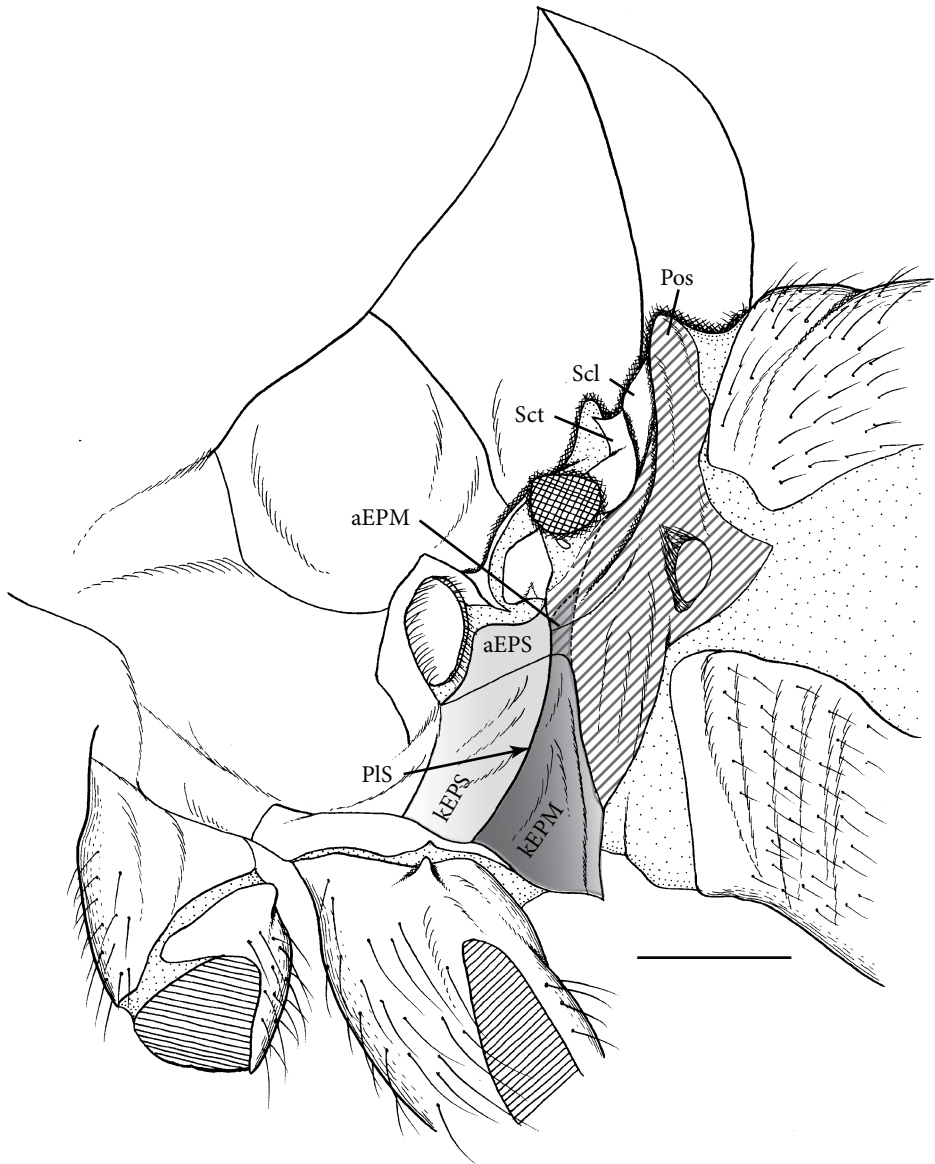


Fig. 6. Metathoracic and abdominal segments of *Aschiza* (Syrphidae: *Microdon japonicus* Yano) in lateral view. Scale = 0.5 mm. Abbreviations: aEPM (dark gray), metanepimeron; aEPS (light gray), metanepisternum; kEPM (dark gray), metakatepimeron; kEPS (light gray), metakatepisternum; PIS, metapleural suture; Sct, metascutum; Scl, metascutellum; Pos (hatched area), metapostnotum.



Fig. 7. Metathoracic and abdominal segments of *Aschiza* (Syrphidae: *Microdon japonicus* Yano) in inner view. Scale = 0.5 mm. Abbreviations: aEPM (dark gray), metanepimeron; aEPS (light gray), metanepisternum; kEPM (dark gray), metakatepimeron; kEPS (light gray), metakatepisternum; PIS, metapleural suture; Pos (hatched area), metapostnotum.

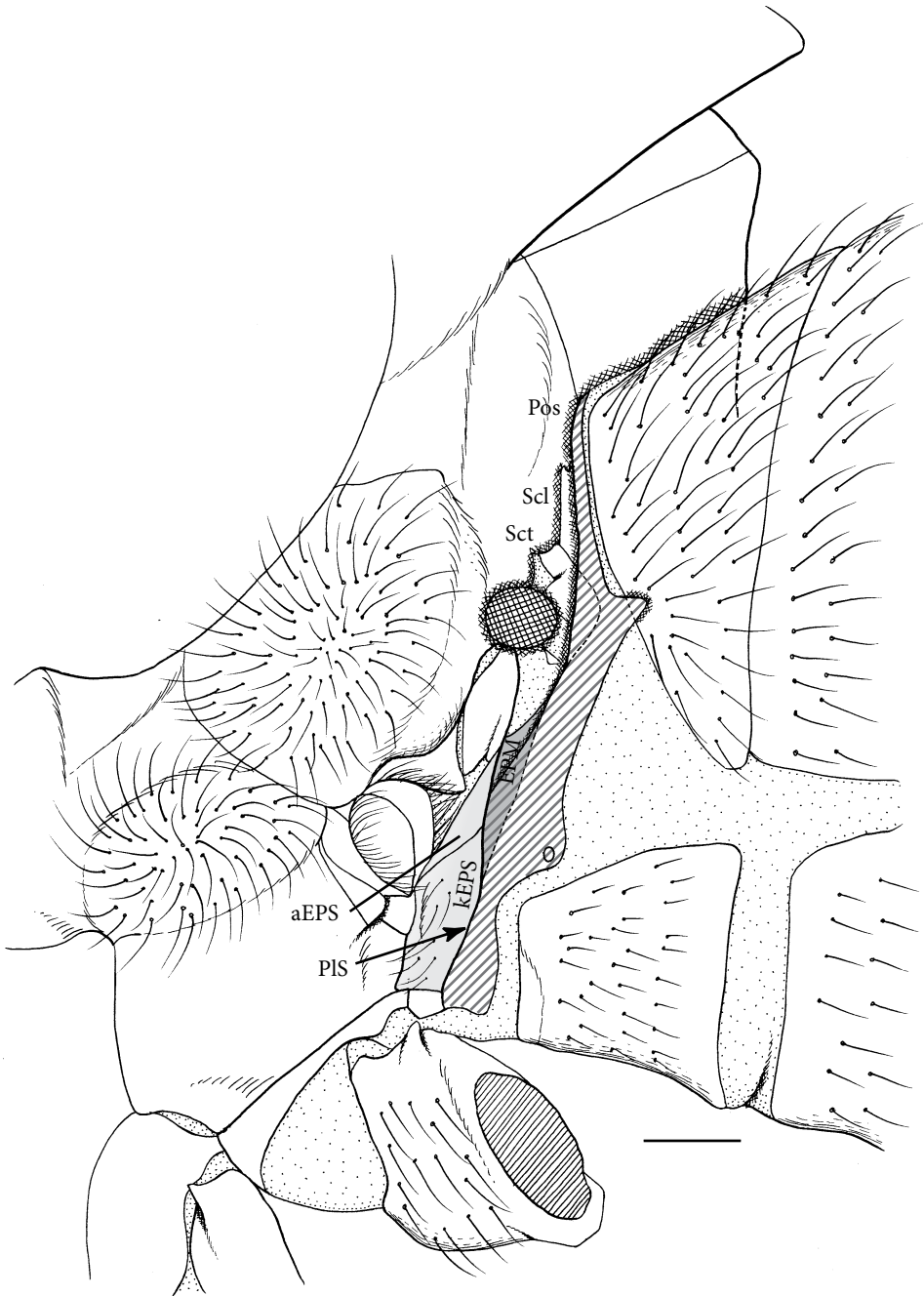


Fig. 8. Metathoracic and abdominal segments of *Aschiza* (Syrphidae: *Episyrphus* sp.) in lateral view. Circles indicate articulation between metapostnotum and first abdominal tergite. Scale = 0.5 mm. Abbreviations: aEPS (light gray), metanepisternum; EPM (dark gray), metepimeron; kEPS (light gray), metakatepisternum; PIS, metapleural suture; Sct, metascutum; Scl, metascutellum; Pos (hatched area), metapostnotum.

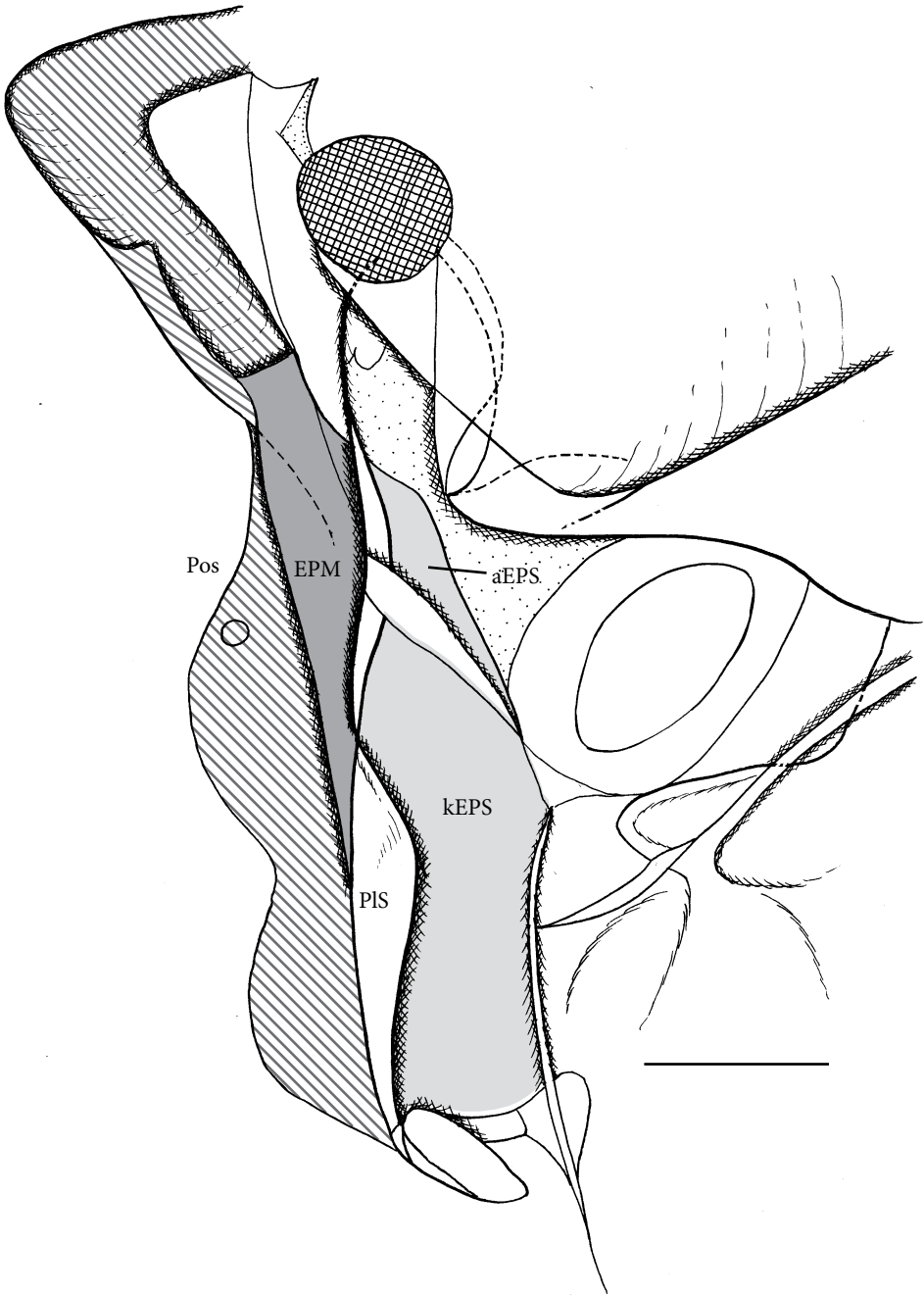


Fig. 9. Metathoracic and abdominal segments of *Aschiza* (Syrphidae: *Episyrphus* sp.) in inner view. Scale = 0.2 mm. Abbreviations: aEPS (light gray), metanepisternum; EPM (dark gray), metepimeron; kEPS (light gray), metakatepisternum; PIS, metapleural suture; Sct, metascutum; Scl, metascutellum; Pos (hatched area), metapostnotum.

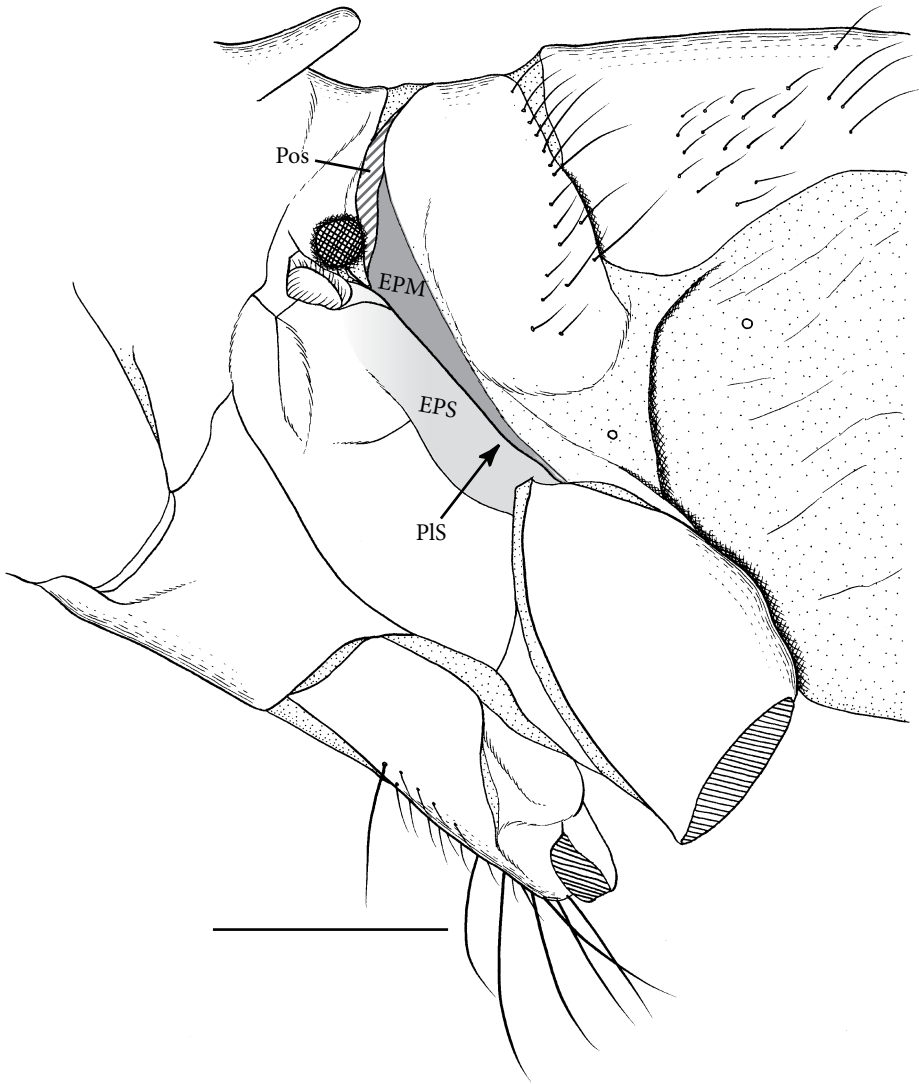


Fig. 10. Metathoracic and abdominal segments of *Aschiza* (Phoridae: *Hypocera anularia* Nakayama & Shima) in lateral view. Scale = 0.5 mm. Abbreviations: EPM (dark gray), metepimeron; EPS (light gray), metepisternum; PIS, metapleural suture; Pos (hatched area), metapostnotum.

Pipunculidae (Fig. 5)

The EPS and EPM are both longitudinal sclerites. The EPM articulates with the first abdominal tergite at the posterodorsal corner. Unlike members of the Schizophora, a suture is not found on the tergite. The metapostnotum is a narrow and transverse sclerite continuous to the EPM.



Fig. 11. Metathoracic and abdominal segments of Brachycera (Empididae: *Empis* sp.) in lateral view. Scale = 0.5 mm. Abbreviations: EPM (dark gray), metepimeron; EPS (light gray), metepisternum; PIS, metapleural suture; Pos (hatched area), metapostnotum.

Syrphidae (Figs. 6–9)

All members of the *Syrphidae* examined have a nearly square or triangular EPS. The metapostnotum is strongly developed and extended to the lateral sides. The first abdominal spiracle is placed on or close to the metapostnotum. The EPM is varied in size and sometimes reduced in some species (e.g., *Allobaccha apicalis* (Loew), *Baccha maculata* Walker and *Sphegina* sp.). A part of the EPM is often covered by the expanded metapostnotum.

In the genus *Microdon* (Figs. 6–7: *M. japonica*) of the subfamily Microdontinae, the EPM is divided into metanepimeron (Figs. 6–7: aEPM) and metakatepimeron (Figs. 6–7: kEPM). The metanepimeron is always covered by the well-developed metapostnotum and the metakatepimeron is nearly triangular and located below the metapostnotum.

In some species (e.g., *Episyrphyrus* sp.: Figs. 8–9) of the other two subfamilies (*Syrphinae* and *Milesiinae*) the EPM is strongly reduced and is covered partially or completely by the metapostnotum (Fig. 9). The metapostnotum sometimes articulates with first abdominal tergite laterally (Fig. 8). A postcoxal bridge is often formed by the fusion of the developed metapostnotum and postcoxal sclerite behind the hind coxa in some genera such as *Sphegina*.

Platypezoidea (*Phoridae*, *Lonchopteridae* and *Platypezidae*), other families (*Empididae* etc.) of *Brachycera* (Figs. 10–11) and *Nematocera*

The EPS and EPM are both nearly rectangular, and the former is generally smaller than the latter. For all species examined in this study the metapostnotum is continuous with the dorsal portion of the EPM. These taxa have no peculiar articulation between the EPM and first abdominal tergite. Ulrich (1971, 1984) indicated the homology of the metapleuron of *Empidoidea*, and he considered the EPS has two components or sclerites (dorsal and ventral sclerites) in many taxa (Sinclair & Cumming, 2006). In this study I regarded the dorsal and ventral sclerites of Ulrich as the EPS and coxopleurite, respectively.

Discussion

Phylogenetic implications of attachment of thoracic and abdominal segments

Abdominal flexion plays an important role in functional morphology and phylogenetics. In the Hymenoptera, the integrated structures of the mesosoma (thoracic and first abdominal segments) and metasoma (the remaining abdominal segments) in the Apocrita have been investigated because of the valuable characters for phylogenetic implications (Telenga 1969; Hashimoto 1996; Vilhelmsen 2001; Vilhelmsen et al. 2010). However, there is no discussion on the thoracic-abdominal articulation in the Diptera. In this study I investigated the morphology of the metapleuron in the abdominal flexion of the Diptera, particularly of *Syrphoidea*. There are three types of connection in between the metathorax and abdomen in the Diptera. One is a membranous connection in the *Nematocera* and lower *Brachycera* (e.g., Fig. 11: *Empis*

sp. (Empididae)). In some families (e.g., Fig. 10: Phoridae and Asilidae) the membranous connection lies between the first and second abdominal tergites due to the fusion of the EPM and first abdominal tergite. The others are an articulation in the metathorax and abdomen, as seen in the Schizophora and Pipunculidae (Figs. 2, 3, 5), and as Syrphidae (Fig. 8). According to Snodgrass (1935), the possible movement at a joint depends on the extent of the membrane. The motion of the membranous connection in the Nematocera and lower Brachycera would be limited because its movable area is rather small. On the other hand, the metathorax-abdominal articulation is much more flexible than the membranous connection since its attachment is articulated at each lateral side of the abdominal tergite. Accordingly, the articulation of metathorax and abdomen is a distinct apomorphic condition in relation to abdominal flexion. However, the articulation in the Schizophora and Pipunculidae is distinctly different from that in the Syrphidae. Members of the Schizophora and Pipunculidae have the structure composed of the EPM and abdominal tergite (Figs. 2, 3, 5). The posterior part of the EPM is jointed with the anterolateral portion of the first abdominal tergite (or first and second abdominal syntergite). In particular, it is generally extending rod-like to form a firm structure articulated with the abdominal tergite in most species of the Schizophora (Fig. 2). By contrast, the Syrphidae have the tergite articulated with the well-developed metapostnotum (Figs. 8, 9). The articulation of the Schizophora and Pipunculidae is non-homologous with that of the Syrphidae, though similar in the movement of the flexion. Consequently, it is interpreted as a synapomorphy for members of Schizophora and Pipunculidae, and this result is consistent with the hypothesis inferred by molecular data (Fig. 1). The homology of the metathoracic pleura in the Syrphidae is discussed below. A structural difference between Pipunculidae and Schizophora is the absence or presence of the suture on the abdominal tergite. Young (1921) indicated that members of the Schizophora have a suture on the first abdominal tergite, although the classification of the higher categories was slightly different from the present one (Aldrich 1905). This character state is currently treated as one of the autapomorphies of the Schizophora (Griffiths 1972; Lambkin et al. 2013). From my observations, the suture is always accompanied by an internal apophysis (Fig. 4) because it probably reinforces the articulated structures of the metathoracic and abdominal segments.

As mentioned in the Introduction, asymmetrical structure of male postabdominal segments is also important for Dipteran phylogeny. In the traditional morphological hypotheses, the sister group of the Schizophora is the Syrphoidea comprising two families, Syrphidae and Pipunculidae (Griffiths 1972; Cumming et al. 1995). In both families the male terminalia are flexed or deflexed forward to the right side of the abdomen (asymmetric position below tergite 4 or 5) and involve an asymmetric configuration of segments 6–8 (Vockeroth & Thompson 1987; Cumming et al. 1995; Huber et al. 2007: review). The asymmetries of the male pregenital and genital segments have been so far considered a synapomorphy of members of Syrphoidea (Griffiths 1972; Cumming et al. 1995; Zatwarnicki 1996). Griffiths (1972) treated the tergal and sternal sclerites of the male abdominal segments 6–8 as a single character despite the fact that they are often reduced and fused into a syntergosternite (McAlpine 1981). It may be problematic to code the character state as a single character in respect to

homology. The sclerites (tergites and/or sternites) are highly variable in each species of *Cyclorhapha* from my observation and literature data. For example, in *Compsobata japonica* Hennig (Micropezidae) tergite 7 is reduced and fused with sternite 7, and syntergosternite 8 is present (e.g., Steyskal 1987a (p. 764: *C. mimia* (Hennig)), whereas in *Homoneura hirayamae* (Matsumura) (Lauxaniidae) and *Limnia japonica* Yano (Sciomyzidae) syntergosternite 7 + 8 and syntergosternite 6 + 7 are present, respectively. The segments 6–8 should be therefore coded as each sclerite (tergite or sternite), not a single character, for homology. The asymmetrical position of the male genital segments (genitalia) is also indicated to be important for Syrphoidea (Cumming et al. 1995: character 29). The male genitalia of Syrphoidea are situated on the right side of the abdomen, as compared to that of Schizophora where the genitalia is nearly medial in most species (Griffiths 1972; Cumming et al. 1995). However, the data of the genital position appears not to be useful for family-level phylogeny of Diptera. It is because the asymmetrical position is observed in Syrphoidea and some families (Coleopidae, Platystomatidae, Sphaeroceridae, Tephritidae etc) of Acalypttratae in examined taxa, though there is a difference in the degree. I consider that the difference is based on the size and shape of the sclerites in the pregenital (abdominal) segments 6–8. It is known that the asymmetry of the sclerites (tergites and/or sternites) of the male abdominal segments 6–8 is often found in many families (e.g., Peterson 1987: Lonchopteridae; Steyskal 1987b: Neriidae) of *Cyclorhapha* (Griffiths 1972; McAlpine 1989). Moreover, the tergites and sternites have a wide range of character states in size and shape according to taxa (e.g., Steyskal 1987c,d: Platystomatidae (p. 811), Dryomyzidae (p. 925); Knutson 1987: Sciomyzidae (p. 932)). In particular, the sternites 6 and 7 of Syrphoidea are usually broader than those of Schizophora. These data may suggest that the asymmetric position of the male genital segments is caused by the character states of pregenital segments 6–8. Since this subject is beyond the scope of this paper, the homology and character coding of the male abdominal segments 6–8 should be discussed in further studies.

Homology of metapleuron in Syrphidae

The thoracic pleura are defined by the placement of the pleural suture that has an internal apophysis (Snodgrass 1935; Matsuda 1970). However, Speight (1987) probably determined the homology of the thoracic pleura without examining an internal pleural suture of the metathorax. Therefore, the metapostnotum (Pos) was interpreted as the metaepimeron (EPM). The homologous interpretation of the metathorax has been widely accepted for syrphid researchers in description of species and phylogenetic inferences (e.g., Doczkal & Pape 2009). From the results of this study I redefine the homology of the metapleuron based on the internal apophysis in the family Syrphidae (Figs. 6–9). The metepimeron (EPM) is rather reduced and the metapostnotum (Pos) is strongly developed in comparison with that of other flies. The placement of the first abdominal spiracle appears to be caused by the extension of the metapostnotum. The character state of the developed metapostnotum is an autapomorphy of Syrphidae.

Many members of the Syrphidae have been proposed to be Batesian mimics of bees

and wasps, although this is imperfect in some species (Penney et al. 2012). As far as I have examined, most species of the two subfamilies Syrphinae and Eristalinae have an articulation between the metapostnotum and first abdominal tergite at the lateral portion (Fig. 8); this articulation is incomplete in members of the subfamily Microdontinae (Fig. 6). Species of former two subfamilies often move their abdomen using this articulation when resting (Tachi, personal observation). This kind of abdominal movement seems to enhance the resemblance to stinging Hymenoptera already brought about by the color patterns displayed by these flies.

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Appendix:

Table A1. Taxa observed in metathoracic plura.

	Family	Subfamily	Species
Nematocera	Tipulomorpha		<i>Trichocera</i> sp.
	Bibionomorpha		<i>Bibio</i> sp.
Brachycera	Tabanomorpha	Chrysopsinae	<i>Chrysops suavis</i> Loew
Orthorrhapha		Tabaninae	<i>Tabanus chrysurus</i> Loew
	Asiloidea	Apocleinae	<i>Promachus</i> sp.
		Laphriinae	<i>Laphria</i> sp.
		Leptogasterinae	<i>Leptogaster</i> sp.
	Empidoidea	Empidinae	<i>Empis</i> sp.
		Hybotinae	<i>Hybos</i> sp.
Cyclorrhapha	Platypezoidea	Metopininae	<i>Lonchoptera</i> sp.
Aschiza			<i>Gymnophora</i> sp.
			<i>Megaselia</i> sp.
		Phorinae	<i>Hypocera anularia</i> Nakayama & Shima
			<i>Stichilus</i> sp.
			<i>Lindneuromyia</i> sp.
		Milesiinae	<i>Ferdinandea nigrifrons</i> (Egger)
			<i>Rbingia laevigata</i> Loew
			<i>Eristalinus aeneus</i> (Scopoli)
		Syrphinae	<i>Allobaccha apicalis</i> (Loew)
			<i>Baccha maculata</i> Walker
			<i>Episyrphus</i> sp.
			<i>Eumerus</i> sp.
			<i>Merodon equestris</i> (Fabricius)
			<i>Sphagina</i> sp.
		Microdontinae	<i>Microdon bifasciatus</i> Matsumura
			<i>M. japonicus</i> Yano
			<i>M. yokohamai</i> Hironaga & Maruyama

(Continued)

Table A1. (Cont.)

	Family	Subfamily	Species
Schizophora	Acalyptratae	Pipunculidae	<i>Chalarus</i> sp. <i>Nephrocerus</i> sp. <i>Pipunculus</i> sp. <i>Cyrtotopsis</i> sp. <i>Crumomyia nipponica</i> (Richards) <i>Compsobata japonica</i> Hennig <i>Stycoladinus appendiculatus</i> Hendel <i>Rivellia apicalis</i> Hendel <i>Bacrocera cucurbitae</i> (Coquillett) <i>Homoneura hiryamae</i> (Matsumura) <i>Coelopa frigida</i> (Fabricius) <i>Myopa buccata</i> (Linnaeus) <i>Dryomyza formosa</i> (Wiedemann) <i>Tephroclanis japonica</i> Okadome <i>Limnia japonica</i> Yano <i>Ochthera mantis</i> (De Geer) <i>Drosophila suzukii</i> (Matsumura) <i>Scatophaga stercoraria</i> (Linnaeus) <i>Musca domestica</i> Linnaeus <i>Calliphora nigribarbis</i> Vollenhoven <i>Stomobina obsleta</i> (Wiedemann) <i>Sarcophaga</i> sp. <i>Carcelia rasa</i> (Macquart)
			Diopsideae
			Sphaeroceridae
		Nerioidea	Micropezidae
			Neriidae
		Tephritoidea	Platystomatidae
			Tephritidae
			Lauxaniidae
			Coelopidae
			Conopidae
			Dryomyzidae
			Heleomyzidae
	Sciomyzidae		
	Ephydriidae		
Calypttratae	Ephydroidea	Drosophilidae	
		Scatophagidae	
	Muscidae		
Oestroidea	Calliphoridae	Calliphoridae	
		Rhiniidae	
	Sarcophagidae		
	Tachinidae		