



Contribution to the knowledge of male and female eremochaetid flies in the late Cretaceous amber of Burma (Diptera, Brachycera, Eremochaetidae)

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Abstract

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A new and a previously known species of the genus *Zhenia* Q. Zhang, 2016 (Eremochaetidae) are illustrated and described based on two males and a female in amber: *Zhenia burmensis* sp. nov. and *Z. xiai* Q. Zhang, 2016. The male *Z. xiai* is the first male of this species recorded. The relationships of Archisargoidea (including Eremochaetidae, *Zhenia*) are reassessed based on male genitalia. The superfamily is more likely related to the Stratiomyomorpha than to the Muscomorpha (including Nemestrinoidea). The components and structures of the ovipositor are re-illustrated. The results of our comparative study demonstrate that the ovipositor of *Zhenia* is similar in shape and detail to that of *Rhagoletis pomonella* (Walsh, 1867) (Tephritidae). This study concludes that the ovipositor of *Zhenia* is most likely formed from abdominal eighth and ninth segments instead of the cerci, as a previous study found.

Introduction

The Eremochaetidae is an important family of primitive, extinct flies of the lower Brachycera (Diptera) which ranged from the Late Jurassic through to the earliest Late Cretaceous (Oxfordian-Cenomanian) in Laurasia. The family includes 17 species subdivided into nine genera within two subfamilies (Ussatchov 1968; Kovalev 1986, 1989; Evenhuis 1994; Ren and Guo 1995; Mostovski 1996; Ren 1998; Zhang 2014; Zhang et al. 2014; Zhang et al. 2016). *Zhenia xiai* Q. Zhang et al., 2016 is the only eremochaetid species recovered from Late Cretaceous amber. All other eremochaetid flies are fossil impressions in shales and occur from the Late Jurassic to the Early Cretaceous. Thus, *Zhenia xiai* is the first eremochaetid tridimensionally preserved fly and the youngest spe-

cies in the geological age. Recently, several specimens of male and female *Zhenia* Q. Zhang et al., 2016 were discovered from the same locality and horizon: the Upper Cretaceous of Myanmar amber in Hukawng Valley, Kachin Province, Myanmar.

The excellent preservation of these specimens allows a detailed description and review of some taxonomic characters, especially the male terminalia, which are a key source of characters used to distinguish species of *Zhenia* and, furthermore, critical to the phylogenetic placement of the Archisargoidea. A new species, *Zhenia burmensis* sp. nov., is illustrated and described based on a male and a female specimen. *Zhenia xiai* was described based on three female flies (Zhang et al. 2016). Shortly after, Grimaldi and Barden (2016) redescribed and reviewed this species on the basis of another female fly from the same locality.

They argued that the ovipositor of *Zhenia* is formed from cerci instead of abdominal eighth and ninth segments and that the Archisargoidea (including Eremochaetidae and *Zhenia*) is closely related to the Nemestrinoidea or the Muscomorpha. On the basis of an almost complete male fly, an additional description of this species is reported here, and the systematic placement of *Zhenia* (including Eremochaetidae, Archisargoidea) is reappraised based on the characters of male genitalia. It is more likely related to the Stratiomyomorpha than to the Muscomorpha (including Nemestrinoidea). Meanwhile, the components and structures of the female ovipositor are re-illustrated and re-interpreted. Through a comparative study, we believe that, like the apple maggot fly (Tephritidae), the ovipositor of *Zhenia* is formed from the abdominal eighth and ninth segments, and the cerci (if present) form the tip of the piercing aculeus.

Materials and methods

The line drawings were produced with the aid of a camera lucida, the digital photomicrographs were taken using a stereomicroscope (Zeiss Stereo Discovery V 16), and the confocal microscopic photographs of the male terminalia were taken using a confocal scanning laser microscopy (CLSM Zeiss LSM710 with 10× objectives and a laser at 488 nm).

Wing venation terminology follows Wootton and Ennos (1989) and Shcherbakov et al. (1995). The cell traditionally named the anal cell is, in fact, considered here to be the cubital cell. The material is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Taxonomy

Order Diptera Linnaeus, 1758

Suborder Brachycera Zetterstedt, 1842

Superfamily Archisargoidea Rohdendorf, 1962

Family Eremochaetidae Ussatchov, 1968

Subfamily Eremomukhinae Mostovski, 1996

Genus *Zhenia* Q. Zhang et al., 2016

Type species. *Zhenia xiai* Q. Zhang et al., 2016.

Emended diagnosis. Closely similar to *Eremomukha* Mostovski, 1996, but smaller (body <10 mm long); cell r1 narrowly open, or closed at or just before wing margin; R4+5 simple or with a very shallow fork; M1 arising distad to end of discal cell; claw vestigial or absent; pulvillus and empodium extremely developed; male genitalia with aedeagus long, subcylindrical, gonocoxite stout, gonostylus without spine, cercus short, one-segmented, positioned behind hypoproct(?); female with ovipositor of piercing type, including swollen abdominal eighth segment, elongated, tapering eighth sternite with cloacal

opening at middle of ovipositor, aculeus (fused ninth segment + cerci?) strongly sclerotized.

Remarks. Until now, the subfamily Eremomukhinae has included eight species belonging to two genera: *Eremomukha* (*Eremocreta*) *addita* Mostovski, 1996, *Eremomukha* (*Eremocreta*) *posita* Mostovski, 1996, *Eremomukha* (*Eremocreta*) *sorosi* Mostovski, 1996, *Eremomukha* (*Eremomukha*) *angusta* J. Zhang, 2014, *Eremomukha* (*Eremomukha*) *tsokutukha* Mostovski, 1996, *Eremomukha* (*Eremomukha*) *insidiosa* Mostovski, 1996, *Eremomukha* (*Eremomukha*) *tenuissima* J. Zhang, 2014, and *Zhenia xiai*. Recently, new *Zhenia* specimens have been recovered from the Late Cretaceous amber of Myanmar. Among them, one new female and two new male flies of the genus *Zhenia* were identified. Based on these new findings, an emended diagnosis of this genus is proposed. *Zhenia* demonstrates close similarities in body structure and wing venation to *Eremomukha*, an Early Cretaceous eremochaetid genus from Mongolia and China, but *Zhenia* differs mainly from *Eremomukha* by the characterized M1, which arises distad to end of discal cell. In contrast, *Eremomukha* has M1 arising directly from the anterior margin of the discal cell.

Zhenia xiai Q. Zhang et al., 2016

Figures 1, 2, 3b, 8C

Diagnosis. Male flies with antennal pedicel subcylindrical; Rs deviating from R clearly distal to M fork; R2+3 meeting R1 just at C (i.e. cell r1 sessile); R4+5 simple; section C between R4+5 and M1 longer than section C between M1 and M2; M1 slightly arched upwards medially, ending behind apex of wing; M3 arched downwards medially; haltere with boot-like knob; abdominal second segment longest; basitarsus of hindleg as long as, or shorter than, tarsomeres II–V combined; genitalia with gonocoxite conical, gonostylus sickle-like, aedeagus relatively short, not reaching hind margin of gonocoxite.

Description. Male. Body and legs brown (Fig. 1A, C), covered with dense short hairs (Fig. 1D). Head large, subovate. Eyes large, holoptic, occupying almost whole head (Figs 1A, C, 2A). Antenna thin and short; scape very small, spherical; pedicel elongated, subcylindrical, slightly wider apically than basally; flagellum ovate-oblong, narrower and shorter than pedicel; arista long, slightly longer than scape, pedicel and flagellum combined (Figs 1B, 2A). Mouthparts with only boot-like labellum visible (Fig. 2A).

Thorax stout, thicker and longer than head. Scutum distinctly convex; scutellum rather small, triangular. Wing narrow and long, 3.2 times longer than wide, apex of wing round (Figs 1A, 2A). Costal vein terminating at the wing apex; vein Sc short, ending nearly at level of end of distal cell; R1 long, straight; Rs deviating from R clearly distal to M fork, section of Rs stem nearly as long as section bR4 + 5; R2 + 3 almost straight, fused with R1 just at anterior margin of wing; cell r1 narrow

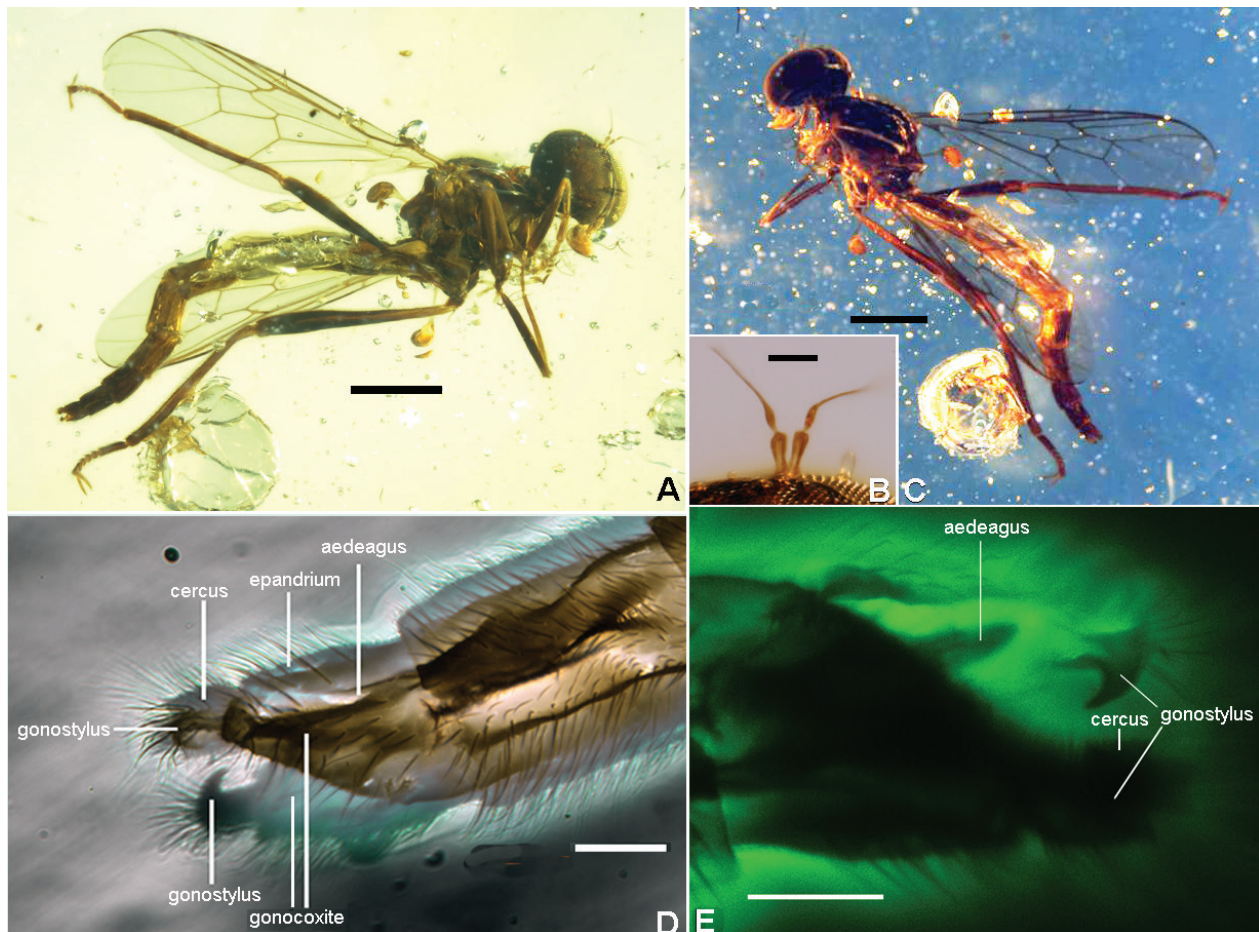


Figure 1. *Zhenia xiai* Q. Zhang et al., 2016. Photomicrographs (A–C) and Confocal microscopic photographs (D, E), topotype NIGP170824, male A habitus (right lateral view) B habitus (left lateral view) C antennae D male genitalia (right lateral view) E male genitalia (left lateral view). Scale bars: 1 mm (A, C); 0.1 mm (B, D, E).

and long, fusiform, with no petiole; section of R4 + 5 + M1 separating from anterior margin of cell d nearly at its end, forked distinctly distad to level of the apex of the discal cell, about 10 times longer than section bm2; M1 slightly arched medially, terminating clearly behind wing apex. M2 more or less arched downwards apically; M3 clearly arched downwards apically, M4 absent; cell d hexagonal, nearly 2.7 times longer than wide; m-m long, straight; bm3 short; m-cu long, nearly three times longer than bm3; cell br obviously longer than, but nearly as wide as, cell bm; cell cu (traditionally anal cell) closed with short petiole (Figs 1A, 2A). Haltere thin and long, knob relatively large, boot-like (Fig. 2A). Forelegs and midlegs relatively thin and short but with pulvillus and empodium extremely elongated, which are very closely similar in length and in shape to those of hindleg; hindlegs relatively stout and long; coxa stout, obtuse-triangular; femur clavate, nearly as long as half of abdominal length; tibia subcylindrical, slightly shorter and obviously narrower than femur; tarsus very short, nearly one-third of length of tibia, basitarsus shorter than, or nearly as long as, tarsomeres II–V combined, ratio of tarsomeres 1.0:0.24:0.21:0.33:0.55, empodium

similar in length and shape to pulvillus, narrowly phylliform in lateral view, less than one-half of length of tarsus (Fig. 2A, C).

Abdomen thin and long, subcylindrical, nearly two times longer than head and thorax combined; eight segments visible; first very short, second longest, remainder gradually reduced in length terminally; ratio of segments 1.0:2.2:2.1:1.5:1.5:1.0:0.9:0.8; ninth segment forming male genitalia, nearly as long as eighth (Figs 1A, B, 2A). Genitalia covered with thin and long hairs; gonocoxite stout and long, subconical, basally thicker than apically; gonostylus with dense hairs on outer margin but glabrous on inner margin, relatively small, sickle-like, sharp apically, strongly curved inwards; aedeagus (phallus) relatively short, not reaching hind margin of gonocoxite, simple (not forked apically), rounded apically (Figs 1D, E, 2B).

Dimensions. Topotype NIGP170824, body length ca 7.8 mm; head length 1.0 mm; thorax length 1.5 mm; wing length 4.4 mm, width 1.4 mm; hindleg length 5.9 mm (coxa 0.5 mm, trochanter 0.2 mm, femur 2.3 mm, tibia 2.1 mm, tarsus 0.8 mm); abdomen length 5.3 mm.

Distribution. Myanmar amber, Late Cretaceous (Cenomanian); Hukawng Valley, Kachin Province, Myanmar.

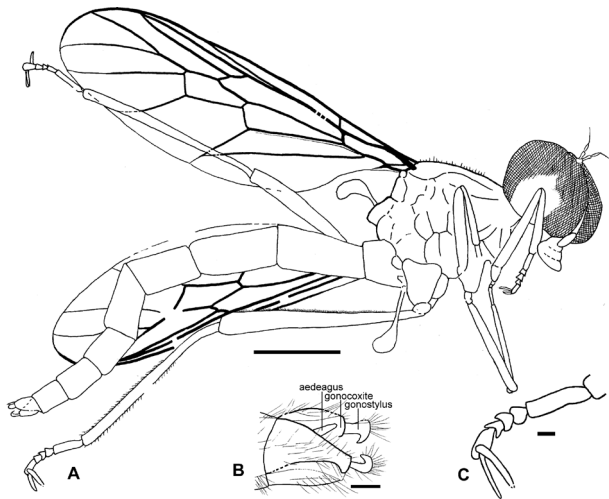


Figure 2. *Zhenia xiai* Q. Zhang et al., 2016. Line drawings, to-potype NIGP170824 **A** habitus (right lateral view) **B** male genitalia (left lateral view) **C** tarsus of hindleg. Scale bar 1 mm (**A**); 0.1 mm (**B, C**).

Remarks. *Zhenia xiai* was erected based on three female flies from Myanmar amber: the holotype BA02-15001 and two paratypes NIGP163430 and BA02-15003 (Q. Zhang et al. 2016). The new male specimen from the same locality demonstrates many close similarities in body structures and wing venation to those of *Z. xiai* and is assigned to this species. The following characters are shared by the male and females: antennal pedicel elongate, subcylindrical, wider apically than basally; the second abdominal segment longest; basitarsus of hindleg shorter than (or nearly as long as) tarsomeres II–V combined; in wing venation, Rs deviating from R clearly distal to M fork; section C between R4+5 and M1 longer than section C between M1 and M2; M1 arched upwards medially, ending behind apex of wing; M3 arched downwards medially (vs *Z. burmensis* sp. nov. described below). The male differs from those females in that: cell r1 is sessile (vs with short petiole in female); and R4+5 is simple (vs forked apically in female). These differences might be sexually dimorphic or individual variation.

Grimaldi and Barden (2016) described another female fly (AMNH BuSD-2) from the same locality that was assigned to *Z. xiai*. Indeed, it demonstrates close similarities in body structures and wing venation to those of *Z. xiai* but differs from the holotype of (BA02-15001) and the paratype (NIGP163430) of this species in that: antennal pedicel is conical, basally clearly thicker than apically (vs subcylindrical, apically thicker than basally); body is covered with dark brown markings dorsally on thorax and on abdominal tergites and sternites (vs no dark brown markings dorsally on thorax and on abdominal tergites and sternites except for the paratype BA02-15003); and the abdominal second to sixth segments are almost equal in length, with the third longest (vs the second longest); ovipositor is fringed with dense hairs ventrally (vs almost glabrous), and relatively shorter and stouter than that of the

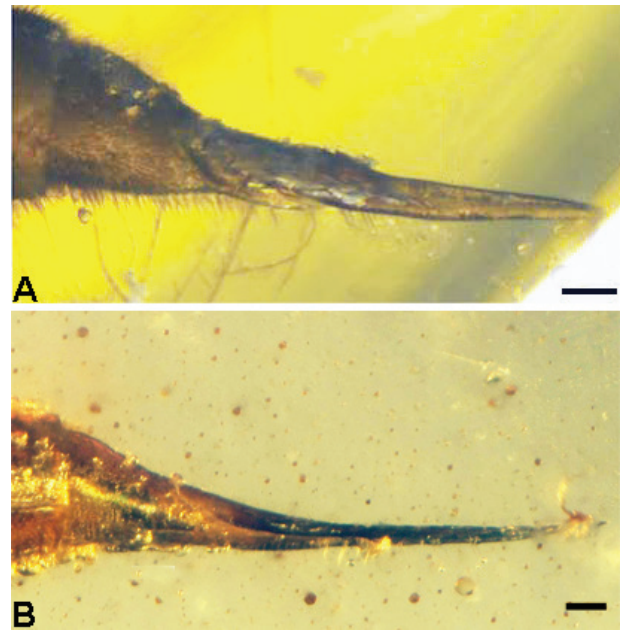


Figure 3. Difference and similarity between two sets of ovipositors. Photomicrographs (lateral view), **A** *Zhenia xiai* Q. Zhang et al., 2016 (after Grimaldi and Barden 2016, AMNH BuSD-2) **B** *Zhenia xiai* Q. Zhang et al., 2016 (after Q. Zhang et al. 2016, holotype BA02-15001). Scale bars: 0.1 mm (**A, B**).

holotype (Fig. 3). Grimaldi and Barden's (2016) specimen is very closely similar to the female *Z. burmensis* sp. nov. (Figs 6E, 7C; see descriptions below). These differences indicate that this fly (AMNH BuSD-2) may not be a member of *Z. xiai* and is most likely related to *Z. burmensis* sp. nov. Owing to the same markings on abdominal tergites and sternites, and the almost equal abdominal second to sixth segments in length (Q. Zhang et al. 2016: 3, fig. 1C), the paratype (BA02-15003) may be closely related to the specimen AMNH BuSD-2 rather than to *Z. xiai* (BA02-15001 and NIGP163430). Unfortunately, it is a poorly preserved specimen, and many taxonomic characteristics are indistinct. Therefore, the placement of the female specimens BA02-15003 and AMNH BuSD-2 is debatable.

Zhenia burmensis sp. nov.

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Figures 4–7, 8D

Diagnosis. Rs deviating from R just at level of M fork; R2+3 meeting R1 before C (i.e. cell r1 closed with short petiole); R4+5 simple; section C between R4+5 and M1 slightly shorter than section C between M1 and M2; M1 straight, ending at apex of wing; M3 straight; haltere with globose knob; abdominal fourth segment longest; basitarsus of hindleg longer than tarsomeres II–V combined; male genitalia with subovate gonocoxite, straight and clavate gonostylus, aedeagus long, obviously reaching beyond hind margin of gonocoxite; female ovipositor relatively short and stout.

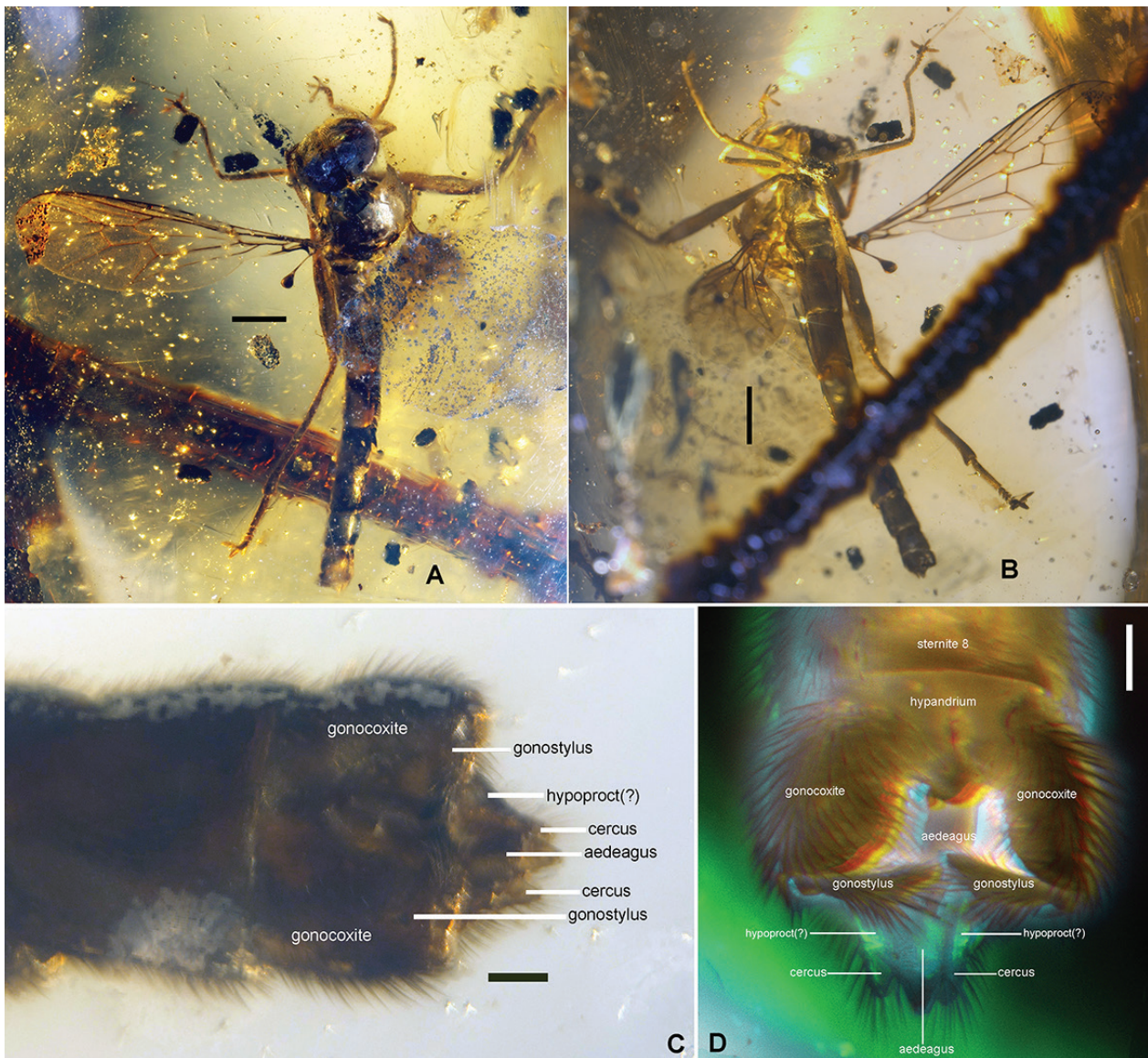


Figure 4. *Zhenia burmensis* sp. nov. Photomicrographs (A–C) and Confocal microscopic photograph (D), holotype NIGP170825, male **A** habitus (dorsal view) **B** habitus (ventral view) **C** male genitalia (ventral view) **D** male genitalia (ventral view). Scale bars: 1 mm (A, B); 0.1 mm (C, D).

Description. Male. Body and legs brown (Fig. 4A, B), covered with dense short hairs (Fig. 4C, D). Head large, subovate. Eyes large, holoptic, occupying almost the entire head (Figs 4A, 5A).

Thorax relatively small, nearly globose, almost as wide as but slightly longer than head. Scutellum rather shorter but relatively wide, over three times wider than long (Figs 4A, 5A). Wing narrow and long, 3.3 times longer than wide, apex of wing round (Fig. 5A). Costal vein terminating at the wing apex; vein Sc short, ending nearly at level of middle of distal cell; Rs deviating from R just at level of M fork, section of Rs stem nearly as long as section bR4 + 5; R2 + 3 slightly arched apically, running slightly convergent to R1, fused with R1 just before anterior margin of wing; cell r1 narrow and long, fusiform, with short petiole; section of R4 + 5 + M1 separating from

anterior margin of cell d nearly at its end, forked distinctly distal to the level of the apex of the discal cell, about 1.5 times longer than section bM2; M1 straight, terminating nearly at wing apex. M2 and M3 almost straight; M4 absent; cell d hexagonal, nearly 2.7 times longer than wide; m-m long, straight; bM3 short; m-cu long, twice longer than bM3; cell br obviously longer than, but nearly as wide as, cell bm; cell cu (traditionally anal cell) closed with short petiole (Fig. 5A). Haltere thin and long, club relatively small, subglobose (Fig. 5A). Forelegs and midlegs relatively thin and short but with pulvillus and empodium extremely elongate, very similar in length and in shape to the hindleg; hindlegs relatively stout and long; femur clavate, less than half of abdominal length; tibia subcylindrical, longer and obviously narrower than femur; tarsus very short, less than one-half of length of

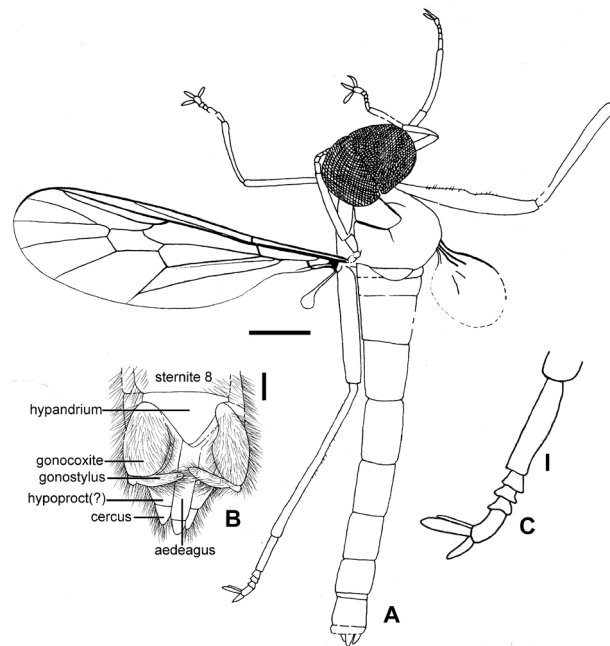


Figure 5. *Zhenia burmensis* sp. nov. Line drawings, holotype NIGP170825, **A** habitus (dorsal view) **B** male genitalia (ventral view) **C** tarsus of hindleg. Scale bar: 1mm (A); 0.1 mm (B, C).

tibia, basitarsus longer than tarsomeres II–V combined, ratio of tarsomeres 1.0:0.16:0.11:0.11:0.36, empodium longer than pulvillus, narrowly phylliform in lateral view, less than one-third of length of tarsus (Fig. 5C).

Abdomen thin and long, subcylindrical, nearly 2.4 times longer than head and thorax combined; eight segments visible; first very short, fourth longest, ratio of segments 1.0:2.9:3.6:4.0:3.1:2.9:2.1:1.7; ninth segment forming male genitalia, clearly shorter than eighth (Figs 4A, B, 5A). Genitalia covered with thin and long hairs; hypandrium large, triangular, 1.7 times wider than long, separated from epandrium, and articulated horizontally with gonocoxite; gonocoxite stout and long, subovate, distinctly narrowed basally; gonostylus relatively small, straight, clavate, slightly thickened medially, rounded apically, and articulated horizontally on gonocoxite; aedeagus (phallus) stout and long, cylindrical, distinctly extending beyond hind margin of gonocoxite, simple (not forked apically), rounded apically; cercus one-segmented, short and wide, subtriangular, slightly longer than wide, not reaching apex of aedeagus (Figs 4D, 5B).

Female. Body dark brown, legs brown (Fig. 6A). Head large, subovate; antennal first flagellomere conical, basally distinctly wider than apically; arista rather thin and long. Eyes large, occupying almost whole head in lateral view (Figs 6B, 7A, B).

Thorax relatively large, nearly globose, clearly longer than head. Scutellum rather shorter (Figs 6A, 7A). Wing narrow and long, 2.8 times longer than wide, apex of wing round (Fig. 7A). Costal vein terminating at the wing apex; vein Sc short, ending nearly at level of middle

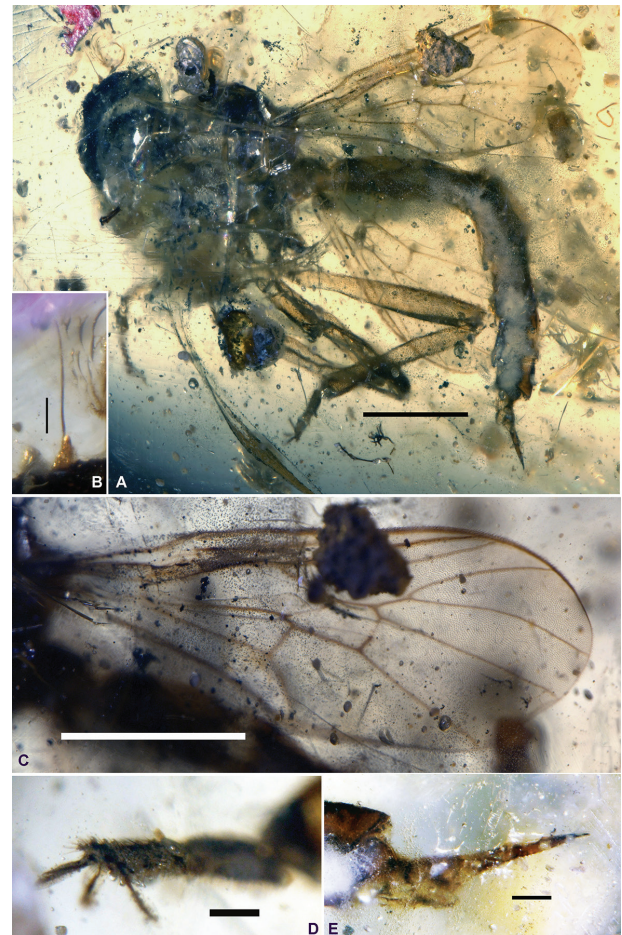


Figure 6. *Zhenia burmensis* sp. nov. Photomicrographs, paratype NIGP170826, female **A** habitus (lateral view) **B** antenna **C** wing **D** tarsus of hindleg **E** ovipositor (lateral view). Scale bars: 1mm (A, C); 0.1 mm (B, D, E).

of distal cell; Rs deviating from R just at level of M fork, section of Rs stem nearly as long as section bR4 + 5; R2 + 3 nearly straight, running slightly convergent to R1, but not coalesced with R1; cell r1 narrow and long, narrowly open apically; section of R4 + 5 + M1 separating from anterior margin of cell d nearly at its end, forked distinctly distad to level of d's end, about twice longer than section bM2; M1 smoothly arched, terminating nearly at wing apex. M2 and M3 almost straight; M4 absent; cell d hexagonal, nearly twice longer than wide; m-m long, straight; bM3 short; m-cu long, about three times longer than bM3; cell br obviously longer and wider than cell bm; cell cu (traditionally anal cell) closed nearly at hind margin (Fig. 7A). Hindlegs relatively stout and long; femur clavate, about half of abdominal length; tibia subcylindrical, slightly shorter and narrower than femur; tarsus very short, about one-third of length of tibia, basitarsus slightly longer than tarsomeres II–V combined, empodium and pulvillus narrowly phylliform, about one-third of length of tarsus (Figs 6D, 7A).

Abdomen thin and long, subcylindrical, nearly 1.8 times longer than head and thorax combined; eight seg-

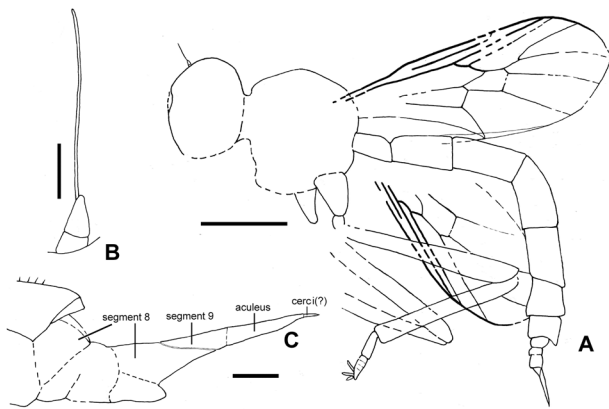


Figure 7. *Zhenia burmensis* sp. nov. Line drawings, paratype NIGP170826, female **A** habitus (lateral view) **B** antenna **C** ovipositor (lateral view). Scale bar: 1mm (A); 0.1 mm (B, C).

ments visible; first very short, third, and fourth longest, ratio of segments 1.0:1.6:1.8:1.8:1.5:1.0:0.5:0.9; ovipositor formed from modified eighth and ninth segments: eighth elongated, separated in two or three sections, its sternite only moderately (not extremely) elongate, ninth forming sclerotised aculeus, cerci (if present) located at apex of aculeus (Figs 6E, 7C, 8D).

Dimensions. Holotype (male) NIGP170825, body length ca 8.6 mm; head length 1.2 mm; thorax length 1.5 mm; wing length 5.5 mm, width 1.7 mm; hindleg length ca 6.8 mm (femur 2.4 mm, tibia 2.9 mm, tarsus 1.5 mm); abdomen length 6.3 mm. Paratype (female) NIGP170826, body length approximately 7.1 mm; head length 0.8 mm; thorax length 1.5 mm; wing length 3.2 mm, width 1.3 mm; hindleg length ca 4.4 mm (femur 2.0 mm, tibia 1.8 mm, tarsus 0.6 mm); abdomen length (excluding ovipositor) 4.0 mm, ovipositor length 0.8 mm.

Distribution. Myanmar amber, Late Cretaceous (Cenomanian); Hukawng Valley, Kachin Province, Myanmar.

Remarks. Based on the following characters, male *Z. burmensis* sp. nov. can be distinguished from male *Z. xiai*: knob of haltere is globose; third and fourth abdominal segments are longest; basitarsus of hindleg is longer than combined tarsomeres II–V; genitalia has ovate gonocoxite, straight and clavate gonostylus, and longer aedeagus, which obviously reaches beyond the hind margin of the gonocoxite.

On the other hand, the wing venation, ratio of abdominal segments and ratio of tarsi of hindleg of this female specimen resemble closely that of male *Z. burmensis* sp. nov., and, thus, it can be provisionally regarded as a member of *Z. burmensis* sp. nov. Female *Z. burmensis* sp. nov. can also be separated from female *Z. xiai* in that: the first flagellomere of the antenna becomes conical instead of subcylindrical; cell r1 runs open apically, R4+5 is simple (not forked apically); tarsus of hindleg is relatively short and stout; and ovipositor is relatively short and stout.

Nevertheless, owing to the clearly smaller size than that of male *Z. burmensis* sp. nov., the female described here may represent another, as yet, undescribed species.

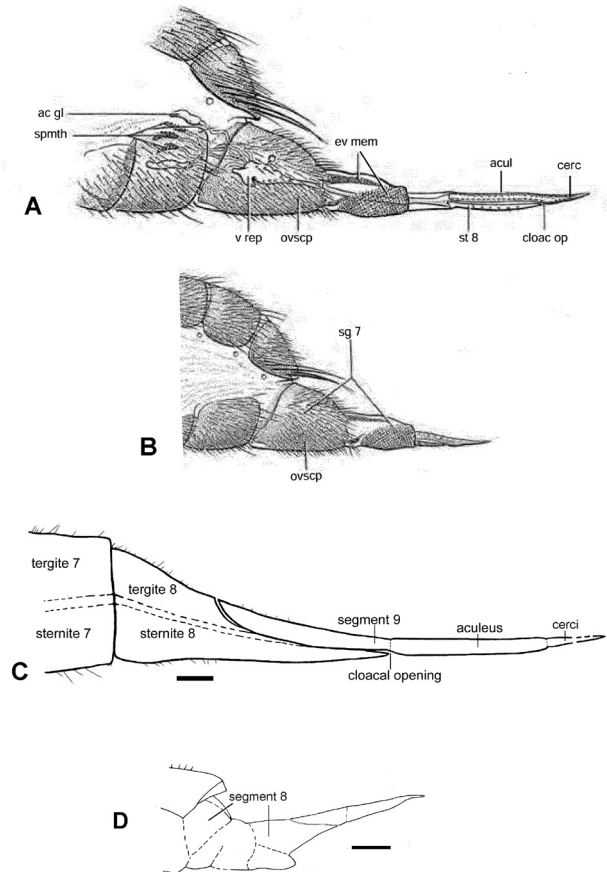


Figure 8. Difference and similarity between four sets of ovipositors. Line drawings (lateral view), **A** *Rhagoletis pomonella* (Walsh, 1867) (ovipositor extended, after Cumming and Wood 2009) **B** *Rhagoletis pomonella* (Walsh, 1867) (ovipositor not extended, after Norrbom 2010) **C** *Zhenia xiai* Q. Zhang et al., 2016 **D** *Zhenia burmensis* sp. nov. Scale bars: 1mm (C, D). **ac gl** – accessory gland; **acul** – aculeus; **cerc** – cercus; **cloac op** – cloacal opening; **ev mem** – eversible membrane; **ovscp** – oviscape; **sg** – segment; **spmth** – spermatheca; **st** – sternite; **tg** – tergite; **v rep** – ventral receptacle.

Discussion

Male terminalia in Diptera demonstrate the most extreme diversity and greatest variability in structure. This is especially significant when comparing the lower Diptera to cyclorrhaphans. In addition, male terminalia are a key morphological source of characters used to distinguish species in the vast majority of dipteran families (Sinclair et al. 2013). To date, however, only seven specimens of male eremochaetid flies have been discovered. All are impression fossils and were found in shales from the Callovian-Oxfordian Karabastau Formation in Kazakhstan (Ussatchov 1968), the Lower Cretaceous Gurvan-Eren Formation in Mongolia (Kovalev 1986), and the Lower Cretaceous Yixian Formation in China (Ren and Guo 1995; Zhang et al. 2014; Zhang 2014). Among them, the characteristics of the male genitalia have been described only in three species: *Eremomukha* (*Eremomukha*) *an-*

gusta, *E. (E.) tenuissima* and *Lepteremochaetus elegans* (Zhang 2014).

Here we describe male eremochaetid flies from amber for the first time. The male genitalia of *Zhenia* reveal that this genus is very similar to the Early Cretaceous genus *Eremomukha* (*Zhenia xiai* and *Z. burmensis* sp. nov. vs *Eremomukha* (*Eremomukha*) *angusta* and *E. (E.) tenuissima*). They share the extremely swollen gonocoxites, the relatively thin and short gonostyli, and the elongate, subcylindrical aedeagi that are indistinguishably fused to the parameral sheath. Additionally, they are also closely similar in their body structures and wing venation: very large head, small thorax, very thin and long abdomen, the long and straight R2+3, the narrow and elongated cell r1 which is closed with very short petiole or just at C, and the characterized R4+5, which is simple, or forked very shallowly. All these morphological similarities indicate that *Zhenia* is closely related to *Eremomukha*.

The placement of Archisargoidea (including Eremochaetidae) is currently disputed. It is assigned either within Stratiomyomorpha (Oberprieler and Yeates 2012) or (more probably) as an extinct sister group to the Muscomorpha (Grimaldi and Barden 2016). Fortunately, some male genitalic structures of *Zhenia* can be distinguished using confocal scanning laser microscopy: the aedeagus completely encircled by and indistinguishably fused with the parameral sheath reveals that, like the Archisargidae (Zhang 2017), the Eremochaetidae (including *Zhenia*) can be placed into the Stratiomyomorpha + Muscomorpha (sensu Woodley 1989; Sinclair et al. 1993, 2013; Cumming and Wood 2009). Furthermore, its gonostyli are directed medially and articulated, moving only in a horizontal plane in opposition to each other (Figs 1D, E, 4D, 5B). This arrangement undoubtedly represents the plesiomorphic condition in Stratiomyomorpha (as well as in Xylophagomorpha and Tanbanomorpha). In contrast, the gonostyli of Muscomorpha move obliquely or in a dorso-ventral direction, which is considered a synapomorphic character (Sinclair et al. 2013). Thus, on the basis of the male genitalia of *Zhenia*, the Archisargoidea (including Eremochaetidae) is most likely related to Stratiomyomorpha and not to Muscomorpha. These flies belong to an extinct, primitive group within the lower Brachycera and lived in the Jurassic to the Cretaceous (ca 160–100 Ma).

As for the female *Zhenia*, we contend that the ovipositor is formed from the abdominal eighth and ninth segments, “eighth segment forming base of ovipositor, with its sternite clearly longer than tergite” (Zhang et al. 2016: 4). However, Grimaldi and Barden (2016: 1) argued that the ovipositor is “formed from modified cerci (not tergites 8 and 9 as originally reported)”, albeit with the disclaimer (Grimaldi and Barden 2016: 18) that “the base of the oviscapit is bulbous and the sharp tips of the cerci (aculeus) point posteriad, which is seen in most archisargoid females whose terminalia are preserved (including *Zhenia*)”. Due to having different explanations, we consider a further discussion of the ovipositor of *Zhenia* is required. The female terminalia include the genital and anal segments of the abdomen posterior to the preabdo-

men that are modified for oviposition and copulation. The segments involved vary depending on the group, but generally consist of the eighth to tenth segments (including proctiger) in lower Brachycera (i.e. orthorrhaphous Brachycera) (Cumming and Wood 2009). The eighth segment of *Zhenia* is beyond doubt the base of the ovipositor (Zhang et al. 2016: 4; Grimaldi and Barden 2016: 18). The base of aculeus of *Zhenia* arises directly from the hind margin of the eighth segment (Figs 3, 8C, D). This state is inconsistent with the conjecture previously proposed that the aculeus is formed from cerci (Grimaldi and Barden 2016). As a ground plan of Diptera, cerci are one of a pair of terminal appendages on either side of the anus derived from the proctiger, which is, in a strict sense, the anus-bearing region posterior to, or arising from, the tenth segment, but generally used for all associated structures behind the ninth segment (cerci) in male dipterans and in females of at least Cyclorrhapha (Cumming and Wood 2009). Thus, it is a reasonable deduction that the aculeus arises from the eighth segment and is formed from the ninth segment.

An aculeate ovipositor has evolved a number of times in Diptera. It occurs in various groups, including a few Tipulidae, Phoridae, Pipunculidae, some Conopidae, Tephritoidea, Cryptochaetidae and Tachinidae (Pritchard 1983; Feener and Brown 1997; Skevington and Dang 2002; Stireman 2006; Grimaldi et al. 2011; Zhang et al. 2016; Grimaldi and Barden 2016; Zhang 2017). In various groups, the ovipositor involves different segments and structures (Cumming and Wood 2009). Compared with these groups, the ovipositor of female *Z. xiai* and *Z. burmensis* sp. nov. demonstrates close similarities in shape and detail to of the ovipositor in female *Rhagolepis pomonella* (Walsh, 1867) (Tephritidae, Tephritoidea, Cyclorrhapha), the apple maggot fly. They share some similar characters (Fig. 8): the base of ovipositor is bulbous and formed respectively from either the eighth (in the two former species) or the seventh (in the latter species) segment; the following posterior one (the ninth and the eighth, respectively) forms the piercing part of the ovipositor, the aculeus; the cloacal opening is well developed, and positioned at the tip of the eighth sternite (in the two former species), or between the divided sclerites of the eighth sternite (in the latter species); and the cerci (if present) are, as the terminal part of aculeus, located at the tip of the ovipositor. It should be noted that in Tephritidae the aculeus consists of an elongate tergite and sternite and is formed from the eighth segment (Cumming and Wood 2009; Norrbom 2010). For this reason, we propose that the aculeus of *Zhenia* is formed most likely from the ninth segment (or ninth+tenth segments) instead of cerci as proposed by Grimaldi and Barden (2016). In addition, there is no indication of extinct or extant brachycerans with a piercing aculeus formed from an extremely elongate cercus. But, like those of female Archisargidae (Zhang 2017), the similarities of ovipositor in shape and structures of Eremochaetidae (including *Zhenia*) and Tephritidae are considered to be the result of convergent evolution, and do not represent evidence of close relationships.

Prior to this study, the genus *Zhenia* was regarded as including endoparasitoid flies having larvae that feeding on other arthropods (Zhang et al. 2016), and this conjecture was also accepted by other authors (Grimaldi and Barden 2016). However, given the characterized structures of the pretarsi (unsclerotized and phylloid pulvilli and empodia, as well as vestigial claws) and the location of the cloacal opening (distant from the tip of ovipositor), it is most likely that, like various Tephritoidea, *Zhenia* oviposits by piercing plants (e.g. fruits or rotten wood) instead of arthropod hosts. In particular, the pretarsi can only adhere to the surface of inactive hosts and cannot hold onto active hosts, such as arthropods.

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