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The Mesozoic Family Eremochaetidae (Diptera: Brachycera) in Burmese amber and Relationships of Archisargoidea: Brachycera in Cretaceous Amber, Part VIII

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ABSTRACT

All 16 species of the family Eremochaetidae occur from the Late Jurassic to the mid-Cretaceous of eastern and Central Asia. The first species in amber, and the latest occurrence of the family, was recently described as *Zhenia xiai*, from the mid-Cretaceous of Myanmar, ca. 100 Ma. New observations of a finely preserved specimen allow refinement of the morphological interpretations in the original description. The female of *Zhenia*, for example, has the distinctive piercing oviscap of the superfamily Archisargoidea, formed from modified cerci (not tergites 8 and 9 as originally reported). The pretarsus of *Zhenia* bears an enormous empodial pad and pair of pulvillae, but the claws are highly vestigial (contra Zhang et al., 2016). The fly was almost certainly a parasitoid. A cladistic analysis of 26 binary-state characters and six continuously variable characters, using 47 exemplar Archisargoidea species from most genera and all four families, and five outgroup Brachycera, has very poor support for most clades but confirms the position of *Zhenia* in Eremochaetidae. Evidence on the relationships of Archisargoidea to other Brachycera is reviewed, and a close relationship to the Nemestrinoidea or Muscomorpha is best supported. A catalog of the species and some higher taxa of Archisargoidea is provided.

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INTRODUCTION

The Archisargoidea is a superfamily of brachyceran flies that comprises four families, 26 genera, and 69 described species that occurred in the Late Mesozoic from the Middle Jurassic to the Late Cretaceous. They were stout bodied to gracile flies with a relatively generalized wing venation, large eyes, and in eight genera (10 species) where the female terminalia are preserved these are modified into a very distinctive aculeate, piercing structure. If the Archisargoidea is monophyletic, which the oviscapt strongly suggests (albeit incompletely surveyed), this superfamily would be the largest extinct lineage of brachyceran flies.

This paper was prompted by the senior author's discovery of a complete female specimen in mid-Cretaceous amber from northern Burma, recently described on the basis of three other females as *Zhenia xiai* (Q.-Q. Zhang et al., 2016). This species is the first Eremochaetidae found in amber, and the latest occurrence of the family. Preservation of the new AMNH specimen is so beautiful that even the original color patterns are intact, a fidelity that allows a detailed review of obscure characters, especially ones that are critical to the phylogenetic placement of this enigmatic group of flies. All other eremochaetids are lithified fossils. Preservation in shales of even the finest grain (e.g., Early Cretaceous of Yixian and Zaza formations) rarely allows one to observe minute structures such as tibial spurs, maxillary palpomeres, and a pretarsal empodium, particularly in determining whether such structures are definitely absent. The Tethepomyiidae, placed within Archisargoidea based on the aculeate oviscapt, are known only in Cretaceous amber, but the mouthparts, antennae, and wing venation of these tiny flies are too reduced to be revealing about the relationships of archisargoids to other flies.

Zhenia has features of several genera in Archisargidae and Eremochaetidae, and so it was decided that a phylogenetic analysis of Archisargoidea was needed. Indeed, the taxonomy of Archisargoidea has been assembled piecemeal, with species and genera described by 10 primary/lead authors in 32 papers, generally as new material became available. Most of the taxonomists for archisargoids have been working on extremely rich deposits within Russia and Kazakhstan (Rohdendorf, 1938; Ussatchov, 1968; Kovalev, 1986, 1989; Mostovski, 1996a, 1996b, 1997), and especially China (Hong, 1983; Ren, 1998; Ren and Guo, 1995; K.-Y. Zhang et al., 2007a, 2007b, 2008, 2009, 2010a, 2010b, 2011, 2014; J.-F. Zhang, 2010a, 2010b, 2011, 2012a, 2012b, 2014a, 2014b). Additional studies are by Oberprielar and Yeates (2012), on a Jurassic archisargid from Australia (the only Gondwanan taxon), and three reports on the family Tethepomyiidae preserved in Early Cretaceous amber from Spain (Grimaldi and Arillo, 2008), mid-Cretaceous amber from Burma (Grimaldi et al., 2011), and Late Cretaceous amber from New Jersey (Grimaldi and Cumming, 1999), and now *Zhenia* (Q.-Q. Zhang et al., 2016). The geological deposits in which Archisargoidea occur are given in appendix 1, which is a taxonomic catalog of the superfamily. Despite a great deal of generic reassignments and synonymies in Archisargoidea (i.e., J.-F. Zhang, 2012a, 2012b), these are all based on narrative. Discussions on the relationships of Archisargidae to other Brachycera are by Oberpreilar and Yeates (2012) and Nagatomi and Yang (1999), who concluded, respectively, that archisargoids are within or closely related to the Stratiomyomorpha or the Nemestrinoidea. These hypotheses are evaluated below, under Discussion.

METHODS AND MATERIALS

The new Burmese amber specimen was purchased from Scott Davies of Bangkok, Thailand. It derived from localized but prolific outcrops in the Hukawng Valley of Kachin State, northern Myanmar, from an area of Cretaceous exposure ca. 12 km² called Noiyebum. Zherikhin and Ross (2000) and Ross et al. (2010) summarized the history of use of Burmese amber; Cruikshank and Ko (2003) are the primary source on the geology of Burmese amber. These outcrops are entirely surrounded by extensive Quaternary and Tertiary exposures. Amber was recently recorded from the Magway Region, Central Myanmar, but as yet no arthropod inclusions have been reported (Sun et al., 2015). Grimaldi et al. (2002) estimated the origin of the main, Kachin deposits as Cenomanian to Turonian in age, based on the stratigraphic distributions of various Cretaceous insect families in this amber; Cruikshank and Ko (2003) reported an age of Late Albian (105–100 Ma) based on a *Mortoniceras* ammonite from the outcrop sediments. The latter age corresponds closely to the Early Cenomanian age (99 Ma) estimated by Shi et al. (2012), based on U-Pb radiometric dating of zircons of the amber sediments.

A detailed redescription of *Zhenia xiai* is provided here because some of the features in specimens studied by Zhang et al. (2016) were not observable (i.e., palp segmentation, body coloration, antennal sockets), or they are ones whose morphological interpretations we differ with (i.e., pretarsal, oviscapt, antennal structure).

The specimen was received as a small squared, polished piece of amber 10 × 13.5 mm, 4 mm. thickness, which required no further trimming and polishing; further trimming would cut into portions of the fly. Photomicrography and measurements used a Nikon SMZ1500 stereoscope with 16 MP Nikon digital camera with Nikon DIS imaging software (including z-stacking). CT scanning of the specimen was not done because all external details were observable. Compiling a data matrix for phylogenetic analysis of Archisargoidea relied upon published descriptions and diagrams of taxa from the Jurassic and Cretaceous of Eurasia, China, and Australia (citations listed above). Taxa described from Russia and Kazakhstan are based on specimens in the Paleontological Institute of the Russian Academy of Sciences, and those from China are in at least three institutions: Geological Museum, Beijing; Capital Normal University, Beijing; and the Nanjing Institute of Geology and Paleontology of the Chinese Academy of Sciences. Since borrowing specimens from or traveling to these institutions was problematic, we are assuming that the original or published revised descriptions are accurate.

Twenty-two of the 32 characters are from the wing, and we were very deliberate to score exemplar species in which details of the head (e.g., antennae, frontal margins of eyes) and abdomen (e.g., female terminalia) were preserved, not just the wing. A total of 46 exemplar species were used for the analysis (including the new fossil), comprising 27 genera of Archisargoidea, plus five outgroup species from the orthorrhaphous Brachycera: Xylophagidae (*Rachicerus obscuripennis*), Stratiomyidae (*Beris fuscipes*), Rhagionidae (*Symphoromyia hirta*), Nemestrinidae (*Neorhynchocephalus volaticus*), and Vermileonidae (*Vermileo tibialis*). Approximately 15% of the cells were missing data. Six of the characters were continuously variable, i.e., proportions of the wing or of particular wing veins and wing-vein segments (discussed in the descriptions of characters). To accommodate these continuous characters we used the pars-

mony-based program TNT v. 1.1 (Goloboff et al., 2008). TNT allows quantitative characters scored up to three decimal places to be evaluated under maximum parsimony along with traditional discrete characters. The matrix was optimized under equal-weighted parsimony utilizing the *xmult* command employing sectorial searches, tree drifting, tree fusing, and ratchet functions until the best score was located 20 times. Node support was evaluated with bootstrap resampling (1000 pseudoreplicates). A single most-parsimonious tree was recovered with a score of 97.67. Overall support values were low, with some nodes recovered in 0% of pseudoreplicates, most likely due to missing data and homoplasy of some characters. In addition, inapplicable continuous characters must be coded as missing in TNT, which may have contributed to a lack of resampling fidelity.

SYSTEMATICS

Genus *Zhenia* Q.-Q. Zhang et al.

EMENDED DIAGNOSIS: Easily distinguished by the following combination of features: like *Calosargus* Mostovski, fusion of vein R_{2+3} with R_1 well before apex of vein R_1 ; like *Eremomukha* Mostovski and *Lepteremochaetus* Ren with very small, asymmetrical apical fork of R_{4+5} , wing base petiolate, uniquely with fusion of base of R_{4+5} to base of M_1 (rather than M_1 arising from apex of cell dm); each pretarsus with very large, long pulvillar lobes and pulvilliform empodium.

TYPE SPECIES: *Z. xiai* Q.-Q. Zhang et al.

Zhenia xiai Q.-Q. Zhang et al.

Figures 1–4, 6C

DIAGNOSIS: Same as for genus, by monotypy.

REDESCRIPTION: Features that are not mentioned in the original description (Q.-Q. Zhang et al., 2016), or that are corrected and revised here are indicated in italics.

Body slender, gracile; head large, thorax compact; legs and abdomen long and slender; *most of body light, yellowish, with dark brown markings dorsally on thorax and on abdominal tergites and sternites*. HEAD: Large, subcircular in frontal view, compressed anteroposteriad. Eyes dark, very large, occupying almost entire dorsal, ventral, and frontal surfaces of head, no genal area exposed; posterior margin of eye entire (not emarginate); eye bare, no setulae; *facets differentiated: group of ca. 50 large facets in middle of frontal surface, remaining facets $\leq 0.5 \times$ diameter of frontal facets*. Eyes holoptic in female (presumably also in male, probably more so), inner margins meeting from just above clypeus to just below antennal insertions. *Antennal sockets not separated, fused into one*. Antenna: Small, flagellum aristalike, pedicel slightly cone shaped, with apical setulae; *postpedicel with base drop shaped, finely setulose, extended apically into long, fine, bare, aristalike structure with minute apical stylus*; postpedicel base $0.2 \times$ length of entire postpedicel. Frons narrow and short, width less than distance between posterior ocelli; frons slightly longer than ocellar

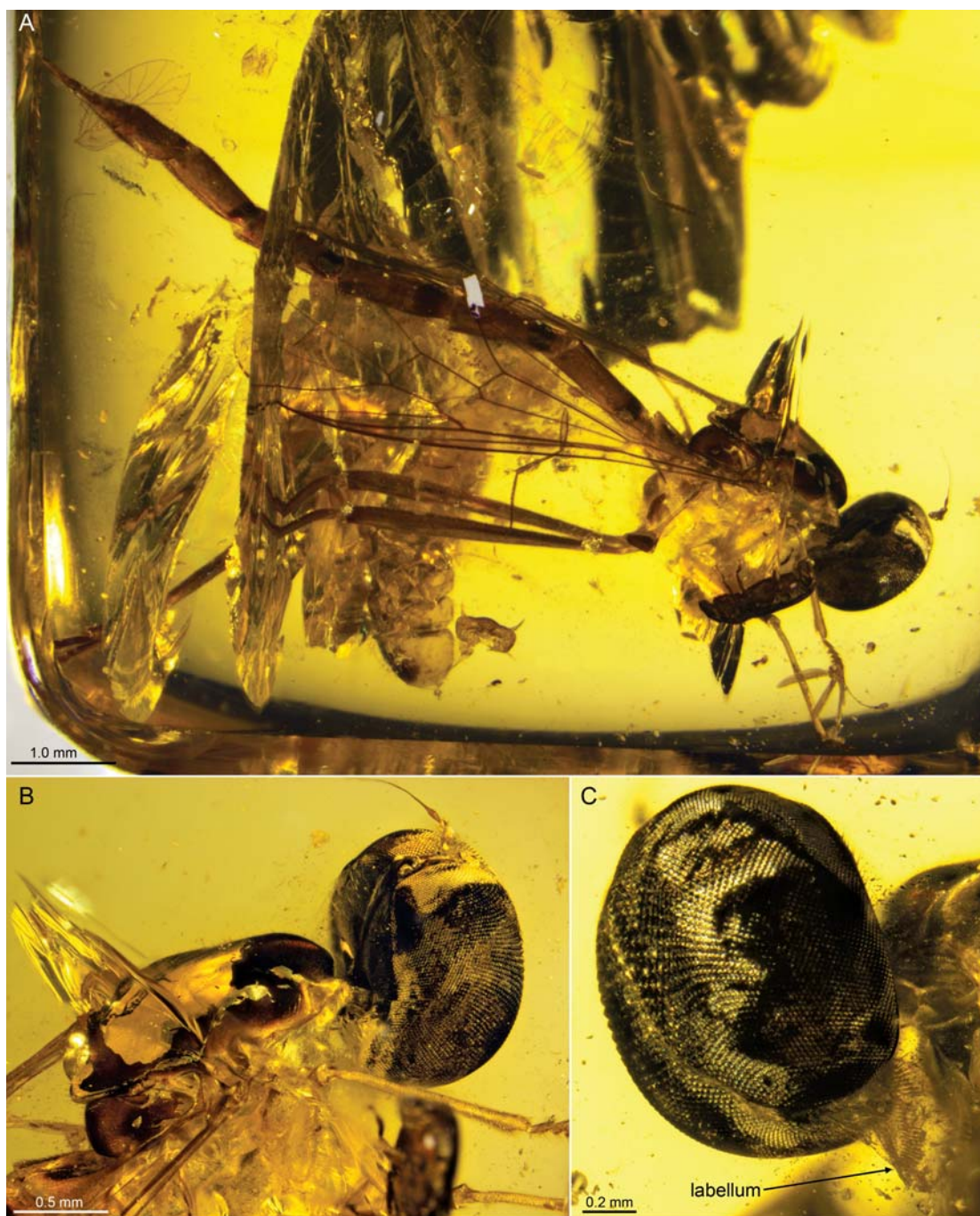


FIGURE 1. Photomicrographs of *Zhenia xiai*, AMNH BuSD-2. **A.** Right lateral habitus. **B.** Head and thorax, dorsolateral view. **C.** Head, ventrolateral view

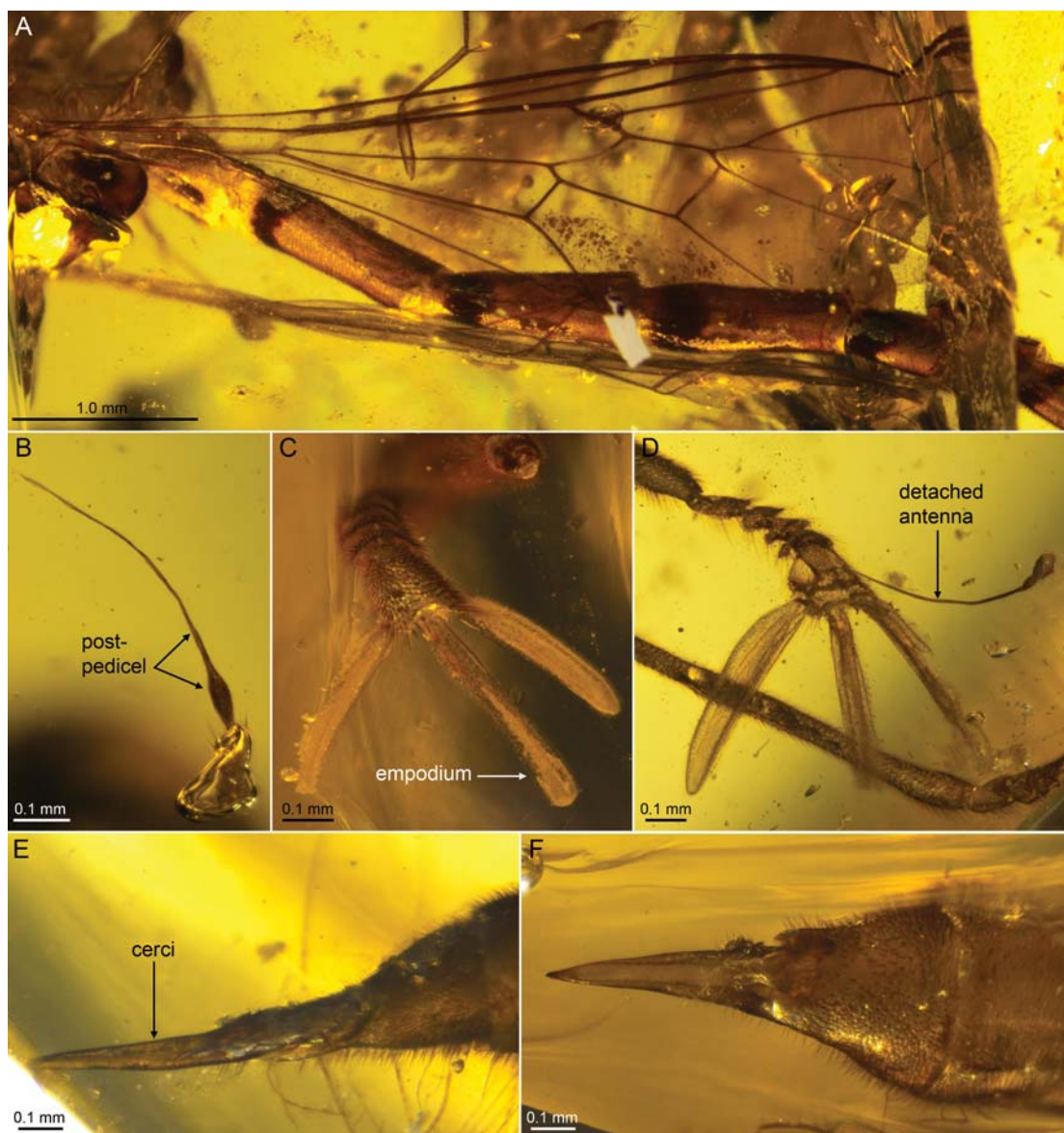


FIGURE 2. Photomicrographs of *Zhenia xiai*, AMNH Bu-SD2. **A.** Right wing. **B.** Detached antenna. **C.** Left mesotarsus. **D.** Right protarsus. **E.** Terminalia (female), dorsolateral view. **F.** Terminalia, ventral view.

triangle; ocellar triangle raised into low tubercle, darkly pigmented; ocelli well developed. Face exposed as very narrow isosceles triangle, slightly swollen near middle. Mouthparts present: labrum exposed, 0.075 mm W \times 0.25 L, slender apical margin with notch. *Maxillary palps* very small, 1-segmented, setulose, light in color. *Labellum* well developed, laterally compressed, with ≥ 25 pseudotracheae, apical margin with fringe of fine setulae. Postocciput darkly pigmented, with low median ridge between ocellar triangle and occipital foramen; protruding collar just above occipital foramen, large posterior tentorial pit on each side of occipital foramen.

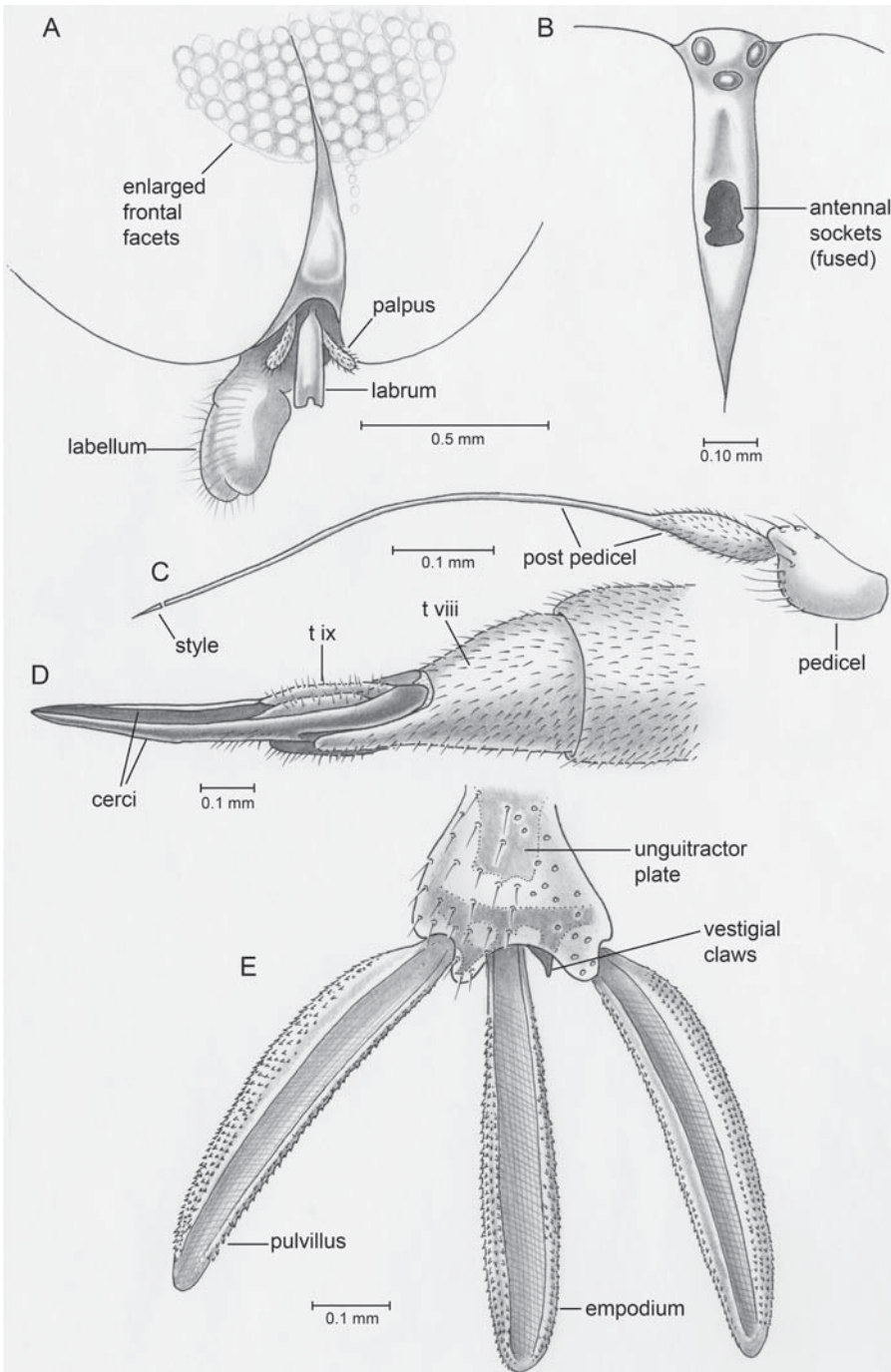


FIGURE 3. Illustrations of important details of *Zhenia xiai*, based directly on AMNH Bu-SD2. **A.** Front of head, showing enlarged frontal facets, face and mouthparts. **B.** Frons, showing fused antennal sockets. **C.** Detached antenna, with minute apical style. **D.** Female terminalia; the cerci are modified into a piercing structure. **E.** Pretarsus, showing the enormous development of the empodium and pulvillae, and the minute claws.



FIGURE 4. Reconstructed habitus of *Zhenia xiai*. The posture with its abdomen curled under is conjectural, based on the habits of various living flies with similar piercing oviscaps. Color patterns are entirely as preserved.

THORAX: Short, compact, $0.16\times$ body length, with *well-preserved color pattern: most of scutum, all of scutellum and mediotergite dark brown; scutum with broad, median, lighter stripe; mediotergite with darker central and lateral spots; posterior surface of metacoxa and most of halter knob dark brown; all other portions of thorax (pleura, legs, etc.) light, yellowish. Pleural sclerites as illustrated (fig. 4).*

WING: Slender, petiolate, veins dark brown, but membrane with no pigmentation, and entirely covered with fine, dense microtrichia. Vein C tapered toward apex, ends at wing tip just before tip of M_{1+2} . Short, incomplete crossvein h slightly distal to level of arcus; *faint sc-r₁ crossvein present*. Sc complete, long, $0.65\times$ length of entire wing. R_1 with *setulae on upper surface*; Rs stem very short, situated in middle of R_1 ; apex of R_{2+3} fused to R_1 well before apex of R_1 . Stem of R_{4+5} fused to base of M_{1+2} ; apical fork of R_{4+5} very small, asymmetrical (R_4 ca. $0.5\times$ length of R_5). Apices of R_{4+5} and M_1 nearly encompassing wing tip; M_3 lacking. Cell dm with 6 irregular sides, *veins forming proximal and distal sides weak in middle (probably a line of flexion through middle of cell dm)*. Stem of M between cells br and bm well formed; cell br slightly longer than bm. No m cell present. CuA_2 fused to A_1 just before wing margin (cup cell closed). Anal lobe essentially absent, alula absent; *vein A₂ present but short and incomplete, within petiole of wing*; wing with narrow base, petiolate. LEGS: Long and slender, without spines or macrosetae; tibiae without apical spurs. Coxae: procoxa slender, meso and metacoxa ca. $0.6\times$ length of procoxa; trochanters well developed, slender. Metafemur $1.8\times$ length of profemur; metatibia $1.8\times$ length of protibia; metatarsus $1.5\times$ length of protarsus; length of metabasitarsomere equal to combined length of distal four metatarsomeres; length of probasitarsomere $0.35\times$ combined length of four distal protarsomeres. *All distitarsomeres dorsally with apical notch and pair of smaller lateral notches. Pretarsus with minute, short, highly vestigial claws (largely hidden under distitarsomere); pulvilli and empodium developed into extremely long pads, 0.5 mm L \times 0.1 mm W (propretarsus), 0.4 mm L \times 0.1 mm W (metapretarsus). Empodium and pulvillar pads with fine, dense scales laterally, striations medially.*

ABDOMEN: Long and slender, cylindrical, comprising 0.75 length of entire body, greatest thickness of abdomen 0.45 mm (segment VII). *Abdomen mostly yellowish, with dark brown, short transverse bands on tergites and sternites of segments I–VI near anterior margin of each sclerite (segments VII and VIII entirely yellowish); band on tergite and sternite of each segment contiguous.* Lengths of abdominal segments (relative to VIII, the shortest segment): I 1.2 : II 1.9 : III 2.0 : IV 1.9 : V 1.6 : VI 1.6 : VII 1.1 : VIII 1.0. No macrosetae present, only dense, fine, decumbent setulae. Each tergite overlapping dorsal margins of corresponding sternite. Spiracle positions (in membrane/sclerite) not observed. Tergite 8 with posterior margin produced into ventrolateral lobes. *Terminus* produced into sclerotized, glabrous, aculeate oviscapt 0.70 mm length, with dorsal and ventral grooves (paired valves), *which are the cerci*; dorsal to the oviscapt is a small, setulose sclerite (or pair). Male terminalia unknown.

MATERIAL EXAMINED: Female, AMNH Bu-SD2, Department of Invertebrate Zoology, AMNH. Specimen in 99 myo amber (Late Albion–Early Cenomanian) from Kachin Province,

northern Myanmar, outcrops ca. 20 km SW of the village of Tanai. Preservation of fly is excellent, with color patterns beautifully preserved. The only portions missing are metatarsi and right mesotarsus; antenna detached but lying close to fly (one antenna is above fly's head, other under the right pretarsus, both floating free).

COMMENTS: *Zhenia* has myriad specialized features; the ones shared with other families of Brachycera that seem important for discerning relationships are discussed below (Discussion). Here we review the autapomorphic features of *Zhenia*.

The very dorsal attachment of the antennae near the ocelli appears to be a synapomorphy for Archisargoidea. Because the antennae of the AMNH specimen are detached, the antennal attachment sites are exposed, revealing that the sockets are entirely fused into one. Antennal sockets can be contiguous in some orthorrhaphans, and even partially fused, but no fly to our knowledge possesses a single, fully fused socket as in *Zhenia*. The antennal flagellum of the fossil is also distinctive, being single-articled and styluslike, with a microscopic stylus at the tip. The only orthorrhaphan group with a single-articled flagellum is Acroceridae. Large eyes that are holoptic or nearly so in both sexes is another archisargoid feature. The enlarged frontal facets is an unusual feature found, for example, in some Asilidae, particularly forest-dwelling genera. This feature strongly suggests that *Zhenia* had excellent frontal resolution, likely used for spotting hosts.

The most distinctive aspects regard the pretarsus: extremely vestigial claws and very large, elongate pretarsal lobes. The pulvillae of *Zhenia* were originally interpreted as enlarged pretarsal claws (Q.-Q. Zhang et al., 2016), but the fine structure of the pulvillae and empodium (also called the mediolobus) are identical, leaving no doubt about the identity of the paired structures. The pretarsal claws are, in fact, minute structures not extending beyond the distal margin of the distitarsomere. Vestigial pretarsal claws of *Zhenia* appear to be an autapomorphy within the Archisargoidea since well-developed claws have been reported in at least 12 other genera of archisargoids (Grimaldi and Cumming, 1999; Grimaldi and Arillo, 2008; Grimaldi et al., 2011; Mostovski, 1996a; Nartshuk, 1996; Ren and Guo, 1995; Ren, 1998; J.-F. Zhang, 2012a, 2014a; K.-Y. Zhang et al., 2010a). Virtual loss of the claws is probably related to the enormous development of the pulvilli and empodium. Large to very large empodia (none the size in *Zhenia*) are found in some Recent families of flies, such as many Asilidae, most Pipunculidae, and *Stylogaster* (Conopidae). These taxa are either predators or they are parasitoids that inject eggs into their hosts.

A pointed, piercing oviscapt is functionally convergent in various Brachycera that oviposit either by piercing plants (various Tephritoidea and Nerioidea), or piercing arthropod hosts (Pipunculidae, *Stylogaster*, some Phoridae [e.g., *Apocephalus*], Pyrgotidae, and some Tachinidae). Given the structure of the eyes and pretarsi, it is most likely that *Zhenia* used its oviscapt as a parasitoid, as was previously concluded (Q.-Q. Zhang et al., 2016).

RELATIONSHIPS IN ARCHISARGOIDEA

In the character descriptions below those states indicated by a "0" are plesiomorphic (based on comparison to various outgroup orthorrhaphans); states "1" or higher are derived.

CHARACTERS AND DESCRIPTIONS

BODY FORM

1. Thorax compact, short but deep; abdomen long, slender, and cylindrical in both sexes, abdomen comprising $\geq 0.60\times$ combined length of thorax of abdomen (figs. 1A, 4). These two features were not separated because they seem to always co-occur in Diptera, in various nematocerans and assorted Brachycera (e.g., leptogastrine Asilidae, systropine Bombyliidae, Evocoidae, Vermileonidae, etc.). The abdomen is sexually slightly dimorphic in Tethepomyiidae, with the one known female having a somewhat shorter, stouter abdomen (e.g., Grimaldi et al., 2011: *Tethepomyia zigrasi*). Based on a few other archisargoids where both sexes are known (e.g., *Alleremonomus xingi* [J.-F. Zhang, 2014a: fig. 4]) there otherwise doesn't seem to be dimorphism in body shape.

HEAD

2. Shape: spherical or subspherical, with eyes large and occupying much of head surface (fig. 1B, C) (vs. hemispherical, or slightly dorsoventrally flattened, with eyes occupying largely just lateral surfaces of head capsule).

3. Head hemispherical, with eyes in both sexes occupying virtually all of lateral and much of dorsal surfaces (and replacing most of occiput in males).

4. Eyes with facial margins very close or medially contiguous (e.g., figs. 1C, 3A); at least the male is holoptic (e.g., Tethepomyiidae) and sometimes both sexes (e.g., *Alleremonomus xingi* [J.-F. Zhang, 2014]).

5. Position of antennal articulation: situated distinctly dorsally, and close to the ocellar triangle (e.g., figs. 1B, 3B) (vs. frontally near anterior margin of frons, or ventrally above clypeus). This is one of the defining features of Archisargoidea, fortunately well preserved in various lithified genera. The antennae in Tethepomyiidae are not dorsally situated.

6. Antennal size and shape: small, with postpedicel having a drop-shaped base and produced apically into a slender, style- or aristalike projection (figs. 2B, D, 3C). The excellent preservation of *Zhenia* reveals at $400\times$ that there is a minute apical article on the postpedicel (fig. 3C), which corresponds to the true stylus. The pedicel is a typical cone-shaped segment in Archisargoidea. The postpedicel in the Tethepomyiidae is unique (char. 7).

7. Structure of postpedicel: reduced to a U-shaped or crescentic article. Found only in Tethepomyiidae. It is possible that a minute style or terminal antennal article is nestled within the postpedicel cavity, but this has not been observable.

8. Mouthparts: vestigial, with theca and labellum either lost or so vestigial as to be unobservable. Found in those Tethepomyiidae where the mouth region is observable; at least in *Tethepomyia thauma* Grimaldi and Cumming (in New Jersey amber) the palpi are present (and 1-segmented), though very small, and the other mouthparts appear absent or highly vestigial.

WING

9. General shape: width to length ratio (i.e., thickness of wing blade), a continuously quantitative character. Wings vary from long and slender (0.21) (e.g., fig. 5A) to short and broad (0.42) (e.g., fig. 6D).

10. Venation highly reduced: longitudinal veins apically incomplete/evanescent (complete in *Tethepomima*); veins R_1 and R_s are thick and sclerotized, but simple (unbranched) in *Tethepomymia* and 2-branched in *Tethepomima*.

11. R veins crowded (parallel and very close for most of their length), especially R_1 and R_{2+3} , a condition found in Kovalevisargidae (fig. 5C).

12. Relative length of stem R_s measured as a proportion of the total length of R_s . A continuously quantitative character varying from a very short stem (0.05, in *Mesosolva zhangi* [not coded in matrix]) to one approximately one-third the total length of R_s (0.33, in *Daohugosargus eximius*).

13. R_{2+3} fused with anterior border of cell d , arising from cell d (*Lepteremochaetus*, *Dissup*: fig. 6B, D) or even basal to it (*Alleremonomus*).

14. Tip of R_{2+3} upturned and converging very close to tip of R_1 or actually meeting it, found in *Archisargus* spp. (fig. 5A), as well as in some beridine and other Stratiomyidae.

15. Tip of R_{2+3} meeting and fused with R_1 well before tip of R_1 ; found only in *Calosargus* spp. and *Zhenia* (see also character 16) (fig. 6C, E).

16. R_{2+3} very short, meeting R_1 well before tip of R_1 (for a length \geq length of R_{2+3}): found in *Alleremonomus*, *Dissup*, and *Lepteremochaetus* (fig. 6B, D).

17. Stem of R_{4+5} connected to apex of cell dm , as found, e.g., in *Alleremonomus*, *Dissup*, *Eremochaetus*, *Eremomukha*, and *Lepteremochaetus* (fig. 6).

18. Fork of R_{4+5} : small, branches asymmetrical, with anterior branch significantly shorter (fig. 6A–D) (vs. fork longer, symmetrical or nearly so, with tips encompassing tip of wing). A strongly asymmetrical fork occurs in beridine and many higher stratiomyids, but the fork is not particularly short or small. A longer, symmetrical fork in most other archisargoids suggests that the asymmetry in archisargoids and stratiomyids is convergent.

19. Fork of R_{4+5} absent or lost, found only in Kovalevisargidae among the taxa that were studied here (fig. 5C).

20. Width of cell dm in proportion to its length (i.e., thickness). A continuously quantitative character varying from stout (width $0.54\times$ the length—*Eremomukha addita*) to long and slender (width $0.13\times$ the length—*Orientisargus illecebrosus*, *Kerosargus argus*).

21. Length of cell bm relative to that of cell br . A continuously quantitative character varying from cell bm significantly shorter than br (0.69, in *Daohugosargus eximius*) to longer than cell br (1.29, in *Kerosargus argus*).

22. Position of $r-m$ crossvein relative to length of cell dm . A continuously quantitative character varying from very close to the base of cell dm (0.05, in *Orientisargus illecebrosus*) to three-quarters the length of cell dm (0.77, in *Origoasilus pingquanensis*).

23. Cell m_3 is closed before the wing margin (M_4 is joined to M_3) (figs. 5D, E; 6D) (vs. cell open, these M veins not joined before the wing margin). In Archisargoidea cell m_3 occurs in

Alleremonomus, *Archisargus strigatus*, *Dissup*, *Mesosolva* (including species formerly placed in *Brevisolva* and *Prosolva*), *Orientisargus*, *Origoasilus*, and *Parvisargus malus*. In other Brachycera cell m_3 also occurs in some Acroceridae, Apioceridae, many Asilidae, Nemestrinidae, some Therevidae and Xylophagidae, Xylomyidae, and in Vermileonidae.

24. Apical branches of vein M: 2 (M_3 is lost) (fig. 5B) (vs. 3 branches). Found in *Calosargus* (except *C. thanasymus* Mostovski), *Eremomukha tsokotukha*, *Flagellisargus*, and *Sharasargus*.

25. Vein M: simple, unbranched in all Tethepomyiidae.

26. Cell cup is closed (i.e., CuA_2 and A_1 meet before the wing margin) (figs. 5A; 6A, C, D), vs. open.

27. Cell br with longitudinal spurious vein (e.g., fig. 5D). This vein was mentioned by Ren and Guo (1995) and K.-Y. Zhang et al. (2007a), but not reported in descriptions by J.-F. Zhang (though indicated in some drawings, e.g., *Tabanisargus*, *Archirhagio mostovskii*). There are some discrepancies among descriptions and images, e.g., *Mesosolva sinensis* has a spurious vein according to J.-F. Zhang (2010) but not according to the original description by K.-Y. Zhang et al. (2010a). A spurious vein is not reported in *Mesosolva huabaiensis* (Hong) by J.-F. Zhang (2015) but is visible in the photo in that paper.

28. Vein CuA or CuA_2+A_1 (originally interpreted as $CuA-CuP$ [Grimaldi and Cumming, 1999]): apically forked in *Tethepomima holomma* Grimaldi and Arillo, *Tethepomyia buruhandi* Grimaldi and Arillo, and *Tethepomyia zigrasi* Grimaldi and Arillo (not visible for *T. thauma*).

29. Anal lobe is lost or highly reduced, measured as the width of the anal lobe as a proportion of the overall width of the wing, a continuously quantitative character. This feature is found in most Archisargoidea, where it is preserved (the anal lobe margin was not preserved in 13 lithified species). *Tethepomyia zigrasi* has a reduced anal lobe, although the other three species of tethepomyiids have a well-developed anal lobe.

30. Base of wing: petiolate, long, and slender (fig. 6A–C). To some extent this is correlated with the character above (anal lobe highly reduced), but not entirely the same. Found in *Eremomukha*, *Lepteremochaetus*, and *Zhenia*.

ABDOMEN AND TERMINALIA

31. Abdomen extremely long, slender, and cylindrical; abdomen is $\geq 0.80 \times$ combined length of thorax + abdomen (cf. char. 1) (figs. 1A, 4).

32. Oviscapt: Three conditions are scored: 1. Formed from elongate cerci. In Recent orthorrhaphans this condition is found in several genera of Nemestrinidae (*Hirmoneura*, *Neorhynchocephalus*, *Trichopsidea*), but the cerci are not pointed at the tips nor are they rigid and heavily sclerotized. 2. The base of the oviscapt 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*) (figs. 2E, F, 3D), exceptions being *Orientisargus illecebrosus* and *Uranorhagio* (J.-F. Zhang, 2012a). 3. Oviscapt base not particularly bulbous, and the oviscapt (which includes at least the cerci) is curved ventrad. This condition (3) occurs in

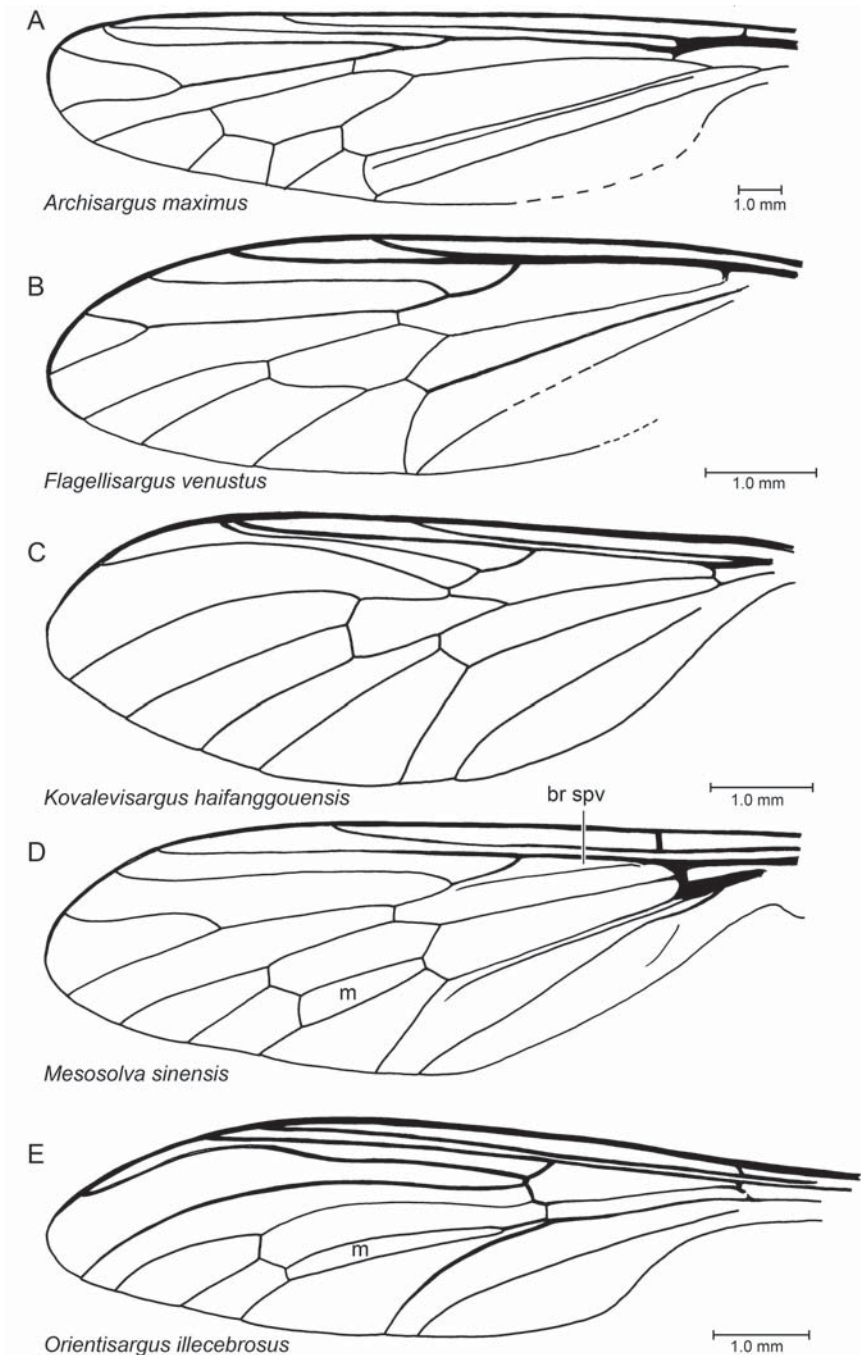


FIGURE 5. Wings of exemplar Archisargoidea, redrawn from original sources. Not to scale.

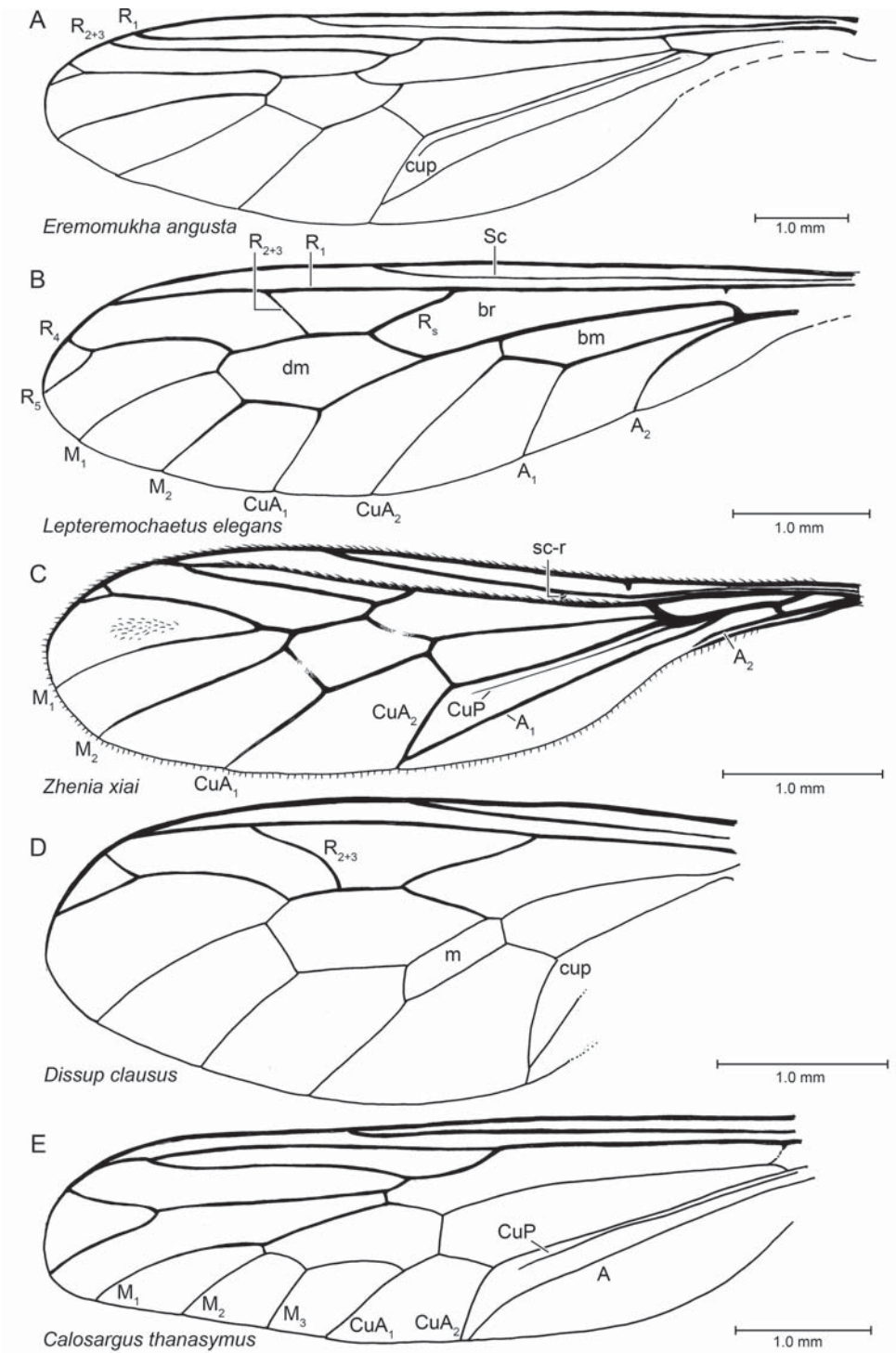


FIGURE 6. Wings of exemplar Archisargoidea, redrawn from original sources. Not to scale.

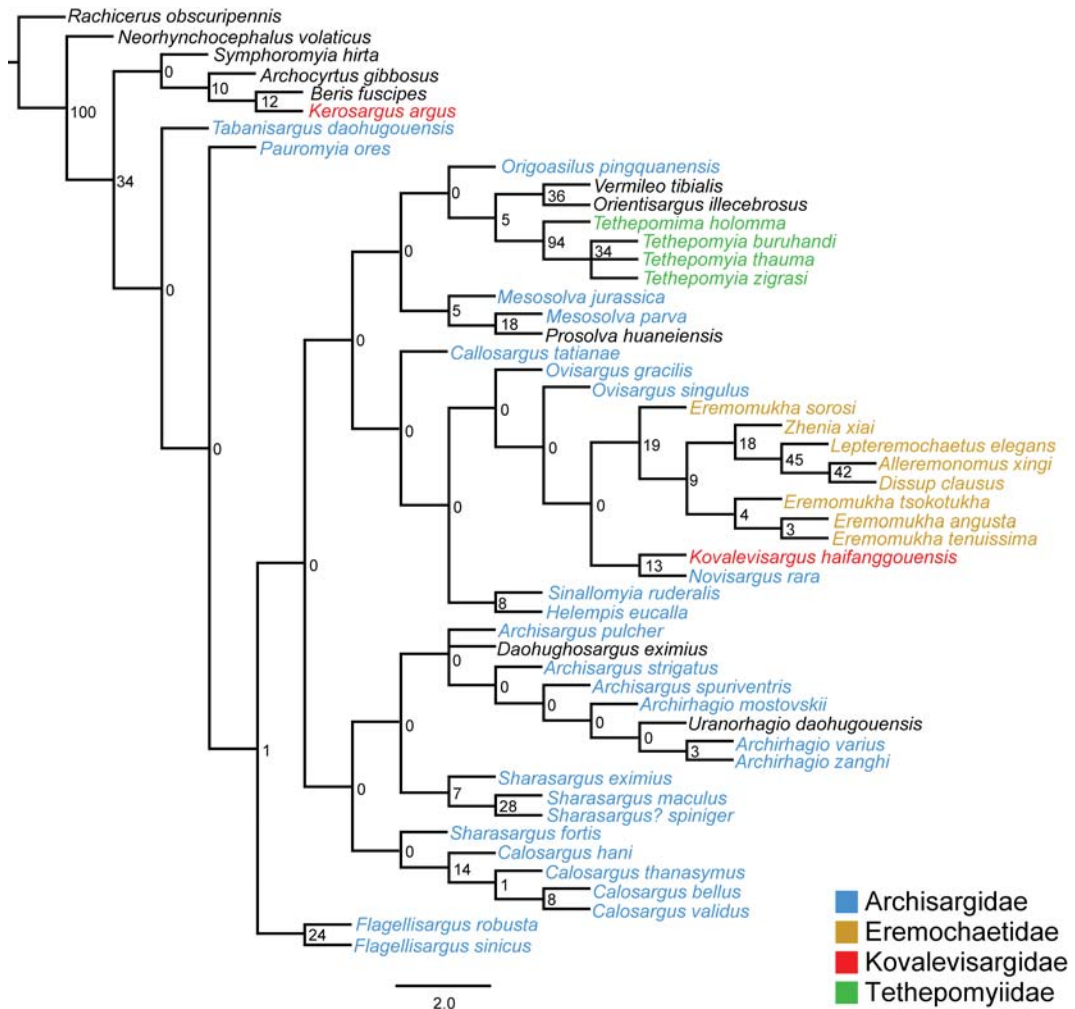


FIGURE 7. Most parsimonious cladogram of the Archisargoidea, based on 32 morphological characters (22 from the wings, six of these being continuously variable), for 46 exemplar in-group species and five out-group taxa. Most clades are very poorly supported, due to missing and homoplasious characters; *Zhenia* is within the Eremochaetidae. Color coding refers to current classification (see appendix 1): pink, Kovalevisargidae; blue, Archisargidae; green, Tethepomyiidae; yellow, Eremochaetidae. *Daohugosargus*, *Orientisargus*, and *Uranorhagio* are removed from Archisargoidea.

Tethepomyia zigrasi, the only species of tethepomyiid whose female is known. It needs to be noted that a similar, ventrally hooked structure was reported in the compression fossil *Kovalevisargus haifanggouensis*, but which was interpreted as male genitalia (J.-F. Zhang, 2014a). Kovalev (1986) indicated that the aculeate female terminalia define the Eremochaetidae, but this distinctive character has been found since then to be more widespread among Archisargoidea. Mostovski (1997) mentioned an undescribed species/specimen of Archocyrtidae with a “needlelike ovipositor,” which if verified would place this family also within the Archisargoidea.

DISCUSSION

RELATIONSHIPS WITHIN ARCHISARGOIDEA: The single most-parsimonious tree (fig. 7) from the cladistic analysis is very poorly supported, with many nodes recovered in 0% of pseudoreplicates. As mentioned above, this is most likely due to a combination of factors: many fragmentary, lithified taxa (plus the fact that inapplicable characters that are continuously variable need to be scored as absent in TNT) and the homoplasy of some characters. Thus, most of the relationships in figure 7 must be regarded as tentative, particularly of basal nodes, with the exception of a few that are reasonably supported by direct morphological evidence. The better-supported groupings are *Calosargus*, Eremochaetidae, *Flagellisargus*, and Tethepomyiidae. It is interesting, in fact, that three genera of archisargoids that possess the plesiomorphic condition of unmodified (nonaculeate) female terminalia are not basal to Archisargoidea in this analysis: *Daohugosargus*, *Orientosargus*, and *Uranorhagio*. However, for the sake of archisargoid monophyly and direct morphological evidence these three genera should be removed from the superfamily. *Flagellisargus* has a plesiomorphic, nonstylate type of antenna and may also lie outside the Archisargoidea sensu stricto, but this would need to be confirmed with female specimens (only males presently are known). It is likely that the family Archisargidae is paraphyletic with respect to Eremochaetidae, as the analysis suggests.

On first appearance *Zhenia* seems to belong to *Calosargus* (Archisargidae), since R_{2+3} is virtually parallel to and ends in R_1 before the wing margin. However, as the cladistic analysis supports, and as was concluded previously (Q.-Q. Zhang et al., 2016), *Zhenia* is in the Eremochaetidae: the wing apex is broadly rounded; the wing base is petiolate; R_4 - R_5 is a very small asymmetrical fork (apparently absent in *Eremochaetus incompleta*); and a closed cup cell is present (common in *Dissup*, *Eremomukha*, and *Lepteremochaetus*). In *Calosargus* the wing is more linear, the apex not so rounded, the anal lobe is reduced but the wing base not petiolate, the R_4 - R_5 fork is larger and nearly symmetrical; and cell cup is open. Thus, the fusion of the tip of R_{2+3} with R_1 in *Zhenia* and *Calosargus* is convergence. In some Eremochaetidae (e.g., *Eremomukha*) R_{2+3} lies close and parallel to R_1 and apically converges toward (though not meeting) R_1 . In other eremochaetids R_{2+3} is short and joined to R_1 near its midpoint. Venation of Eremochaetidae shows a predisposition to the type of radial vein fusion seen in *Calosargus*. *Zhenia* uniquely has the base of vein M_1 fused to the base of R_{4+5} instead of to cell dm.

RELATIONSHIPS OF ARCHISARGOIDEA TO OTHER BRACHYCERA: The exquisite preservation of *Zhenia* affords a unique opportunity to assess the relationships of Archisargoidea sensu stricto (i.e., aculeate taxa) to other orthorrhaphan flies.

Several authors have suggested that certain archisargoids are closely related to the small, Recent, and phylogenetically isolated family Vermileonidae (Hennig, 1973; Stuckenberg, 1996). This is understandable since both groups have a nearly spherical head, short compact thorax; a long, slender abdomen and legs; and a petiolate wing with similar venation. However, this gracile body form has evolved multiple times in Brachycera (usually correlated with petiolate wings); and the basic wing venation of archisargoids is widespread (and probably plesiomorphic) in orthorrhaphous Brachycera, including the presence of cells dm, m (or m_3), and forked

R_{4+5} veins. In fact, seven characters indicate that Vermileonidae and *Zhenia* are not particularly related. In Vermileonidae: 1. The antennae are frontally (vs. dorsally) situated. 2. Eyes are not holoptic nor even nearly so in either sex. 3. There are two palpomeres (vs. one). 4. Cerci are 2-segmented (vs. 1). 5. Antennal flagellum has two or more flagellomeres (Stuckenberg, 1999) (vs. one). 6. Female terminalia are unmodified (vs. with piercing oviscapt). 7. Tibial spurs are present, as 1 : 2 : 2 (vs. entirely absent). An intriguing character is the clypeus in Vermileonidae, which forms part of the face, though discernible by a faint to obvious suture, particularly laterally. In *Zhenia* the clypeus is not apparent (but possibly not exposed beyond the oral margin), and no sutures occur on the face (fig. 3A). The clypeus was not mentioned in the description of *Zhenia* (Q.-Q. Zhang et al., 2016). Vermileonidae and some Archisargoidea apparently converged on a similar gracile body form. Vermileonidae probably is more phylogenetically basal, possibly the living sister group to Rhagionidae sensu stricto (Wiegmann et al., 2011).

Oberprielar and Yeates (2012) and Nagatomi and Yang (1998) discussed individual characters for estimating the relationships of Archisargidae and Archisargoidea (respectively) among orthorrhaphans. Oberprielar and Yeates (2012) assigned Archisargidae as either within or near the Stratiomyomorpha (this infraorder includes the Stratiomyidae, Xylomyidae, Pantophthalmidae, and the Cretaceous family Zhangsolvidae). Alternatively, Nagatomi and Yang (1998) concluded: “it seems that the Archisargoidea is identical with, or most closely related phylogenetically to, the Nemestrinoidea” (p. 163), albeit with the disclaimer (p. 190) that “the phylogenetic position is difficult [to determine] on the basis of wing only...” Nagatomi and Yang (1998) had a much more inclusive concept of Nemestrinoidea than is used today, which encompassed the Mesozoic families Sinonemestriidae, Rhagionemestriidae, and Archocyrtidae, and the (Mesozoic to Recent) Acroceridae, as well as the Archisargoidea and Nemestrinidae. No defining features of Nemestrinoidea sensu lato were provided.

The characters that Oberprielar and Yeates (2012) suggested might link Archisargidae with Stratiomyomorpha are the following:

1. Costalization of radial veins. This is a feature that occurs in only some Archisargoidea, and where it does occur veins Sc and R are not shortened as they are in Stratiomyidae.
2. Cell dm reduced in size. The size of cell dm in most Archisargoidea is actually rather large and elongate as in many other orthorrhaphans. The cell is shortened in some genera, like *Kovalevisargus*, *Novisargus*, and *Ovisargus*.
3. Costal vein ending near tip of wing (ie, at or near apex of vein R). Vein C definitely ends between the apices of veins R_5 and M_1 in *Zhenia*, but it is difficult to confirm if this is the case in lithified fossils of archisargoids (or if vein C is merely very thin beyond this point). A short vein C occurs in many orthorrhaphans; a circumambient C vein occurs in Asiloidea, Nemestrinoidea, Tabanomorpha, and Xylophagidae.
4. Loss of protibial spurs, which occurs in all Stratiomyomorpha. Tibial spurs are a significant character. Primitively, Brachycera have two spurs on the meso- and metatibiae, one on the protibia; these have been reduced to one or lost in several large lineages of Brachy-

cera. Most Stratiomyidae and Muscomorpha have lost all tibial spurs (though some Bombyliidae retain them on the mesotibiae). Tibial spur formulas of Cretaceous stratiomyomorphs are the following: *Buccinotormyia* (Zhangsolvidae) 0-2-2; 0-2-1 in *Lysistrata*, and 0-2-0 in *Cretaceogaster* and 0-1-0 in *Parhadrestia* (basal Stratiomyidae). The presence of one or two hind tibial spurs has been reported in the following lithified archisargoids: *Mesosolva jurassica* (K.-Y. Zhang et al., 2010a), *Orientisargus illecebrosus* (J.-F. Zhang, 2012a), *Strenorhagio asymmetricus* (K.-Y. Zhang et al., 2010a), and *Uranorhagio* (K.-Y. Zhang et al., 2010a). Mostovski (1996b) reported 0-1-1 tibial spurs in *Sharasargus*(?) *spiniger*. Presence of these putative spurs needs to be confirmed. If indeed these species had true tibial spurs (i.e., articulating within the membrane between the tibia and basitarsomere), then the definitive absence of all tibial spurs in *Zhenia* is derived within Archisargoidea and not necessarily reflective of relationships. Since Tethepomyiidae also lack tibial spurs, the absence of tibial spurs in the amber archisargoids is interpreted here as a synapomorphy with Muscomorpha.

5. Short Rs, its origin opposite to (at same level as) or even distal to the origin of CuA₂. This is an interesting character that is shared between Stratiomyomorpha and Archisargoidea, although it does occur in various other families of orthorrhaphans: Acroceridae, Asiloidea, Nemestrinidae, and Vermileonidae, among others.

Other characters that appear to be significant are the following:

6. Antennal flagellum (postpedicel) with a single article, plus a minute terminal stylus. The true, apical stylus was observed in the AMNH specimen of *Zhenia* only under transmitted light using 400× magnification. A reduction to one flagellomere is found in Acroceridae and a few Schizophora, all clearly independently (Stuckenberg, 1999; McAlpine, 2002). Four flagellomeres is the groundplan condition in Cyclorrhapha and Nemestrinidae.

7. Maxillary palpus with a single segment. This character is found largely in Asiloidea + Eremoneura (the latter Empidoidea + Cyclorrhapha), though it also occurs secondarily in some pachygastrine Stratiomyidae. In Asiloidea a 1-segmented palpus occurs in at least some Apioceridae, Asilidae, Bombyliidae, Scenopinidae, Therevidae, and all Mydidae. It also occurs in some Acroceridae. Mouthparts were not fully observable in the *Zhenia* specimens used in its description (Q.-Q. Zhang et al., 2016).

8. Structure of empodium. An empodium (mediolobus) that is pulvilliform is the plesiomorphic state for Brachycera, which is the condition in *Zhenia*. A setiform empodium occurs in Asiloidea + Eremoneura. Interestingly, the preservation of pulvilli was observed in *Flagellisargus* spp. (J.-F. Zhang, 2012a), but the empodium was “invisible,” and pulvilli were “small” in *Sharasargus eximius* (K.-Y. Zhang et al., 2008). Most significantly, the empodium was reported as pulvilliform in *Uranorhagio* (K.-Y. Zhang et al., 2010a). In Tethepomyiidae the empodium is pulvilliform in *Tethepomyia thauma* in New Jersey amber (Grimaldi and Cumming, 1999) and *T. buruhandi* in Spanish amber (Grimaldi and

Arillo, 2008); it is not observable in the unique specimens of *Tethepomyia zigrasi* (Burmese amber) and *Tethepomima holomma* (Spanish amber), due to preservation (Grimaldi et al., 2011). The empodium structure in *Zhenia* would exclude it from the Asiloidea + Eremoneura, although basal Muscomorpha (Nemestrinidae, Acroceridae) retain a pulvilliform empodium.

9. Female cerci 1-segmented and modified into a long pair of ovipositor-like valves. The only orthorrhaphous brachyceran group with this form of cerci is the family Nemestrinidae, specifically the genera *Hirmoneura*, *Neorhynchocephalus*, and *Trichopsidea*. In Archisargoidea the cerci are very pointed and aculeate; in Nemestrinidae they are apically blunt. Furthermore, the cerci in *Zhenia* are 1-segmented (vs. primitively 2-segmented in Brachycera), which is a derived condition found in the Muscomorpha, including Nemestrinidae.

10. Presence of a very short, weakly sclerotized crossvein sc-r in *Zhenia* is an obscure but significant feature, not originally mentioned though apparent in a published photomicrograph of a paratype wing (Q.-Q. Zhang et al., 2016: fig. 2b). This vein is not reported in any of the lithified Archisargoidea, or Tethepomyiidae, but if it was originally present it is doubtful that it would be preserved or be observable. The crossvein occurs in various genera of Asilidae, some Nemestrinidae (e.g., *Neorhynchocephalus*), various Bombyliidae, in *Evocoa* (Evocoidae), and it is widespread in Syrphidae. It seems to be associated with strong fliers.

11. Presence of (closed) cell m3: This is found in some Xylophagomorpha (Xylophagidae), Stratiomyomorpha (Xylomyidae, Pantophthalmidae, Zhangsolvidae), *Vermileo*, Nemestrinidae, some acrocerids, Asiloidea (Mydidae, Apiocera, many Asilidae, and some Therevidae). It is not found in Eremoneura. Presence of cell m is homoplasious, either plesiomorphic for Brachycera and lost many times or independently derived multiple times.

In summary, new evidence based on the new and previously described specimens of *Zhenia* indicates that the Archisargoidea is not closely related to Vermileonidae nor to Stratiomyomorpha. Based on the single-segmented palpi and cerci, loss of tibial spurs, and small sc-r crossvein, *Zhenia* and by extension the superfamily Archisargoidea is probably an extinct sister group to the Muscomorpha.

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APPENDIX 1

TAXONOMIC CATALOG

SUPERFAMILY ARCHISARGOIDEA

This superfamily is defined to include those species that are known to have a piercing, aculeate oviscapt, or presumed to have one based on venation similar to a species that does. Removed from Archisargoidea are the following: *Daohugosargus* J.-F. Zhang, 2012, *Orientisargus* J.-F. Zhang, 2012, and *Uranorhagio* K.-Y. Zhang et al., 2010. These are known to have a female oviscapt that is not aculeate.

FAMILY EREMOCHAETIDAE USSATCHOV

GENUS *EREMOCHAETUS* USSATCHOV, 1968

Eremochaetus asilicus Ussatchov, 1968: 618. Karabastau Formation, Kazakhstan.

GENUS *ALLEREMONOMUS* REN AND GUO, 1995

Alleremonomus xingi Ren and Guo, 1995: 301. Yixian Formation, China.

A. liaoningensis Ren and Guo, 1995: 306. Yixian Formation, China. Synonym by J.-F. Zhang, 2014.

GENUS *DISSUP* EVENHUIS, 1994 (replacement name for *Eremonomus* Kovalev, preocc. Wollaston, 1861)

Dissup irae (Kovalev) 1987: 106. As *Eremonomus irae* Kovalev. Turga Formation, Chita Region.

GENUS *EREMOCHAETOMIMA* MOSTOVSKI, 1996

Eremochaetomima incompleta Mostovski, 1996: 118. Karabastau Formation, Kazakhstan.

GENUS *EREMOCHAETOSOMA* KOVALEV, 1986

Eremochaetosoma mongolicum Kovalev, 1986: 149. Gurvan-Eren Formation, Mongolia.

GENUS *EREMOMUKHA* MOSTOVSKI, 1996

Eremomukha tsokotukha Mostovski, 1996: 118. Bon-Tsagan, Mongolia. Type species.

Eremomukha addita Mostovski, 1996: 120. Zaza Formation, Russia.

Eremomukha angusta J.-F. Zhang, 2014: 208. Yixian Formation, China. Originally considered by Zhang to be *E. tsokotukha*.

Eremomukha insidiosa Mostovski, 1996: 118. Gurvan-Eren Formation, Mongolia.

Eremomukha posita Mostovski, 1996: 120. Zaza Formation, Russia.

Eremomukha sorosi Mostovski, 1996: 120. Zaza Formation, Russia.

Eremomukha tenuissima J.-F. Zhang, 2014: 210. Yixian Formation, China.

GENUS *LEPTEREMOCHAETUS* REN

Lepteremochaetus lithoecius Ren, 1998: 78. Yixian Formation, China.

Lepteremochaetus elegans J.-F. Zhang, 2014: 207. Yixian Formation, China.

GENUS *PAREREMOCHAETUS* USSATCHOV, 1968

Pareremochaetus minor Ussatchov, 1968: 619. Karabastau Formation, Kazakhstan.

GENUS *ZHENIA* Q.-Q. ZHANG, J.-F. ZHANG, FENG, ZHANG, AND WANG, 2016

Zhenia xiai Q.Q. Zhang et al., 2016: 2. Burmese amber, Myanmar.

FAMILY ARCHISARGIDAE ROHDENDORF, 1962

GENUS *ARCHISARGUS* ROHDENDORF, 1938

Archisargus pulcher Rohdendorf, 1938: 30. Karabastau Formation, Kazakhstan.

Archisargus maximus Mostovski, 1997: 75. Karabastau Formation, Kazakhstan.

Archisargus spuriventris K.-Y. Zhang, Yang, Ren, and Shih, 2007: 828. Daohugou Formation, China.

Archisargus strigatus K.-Y. Zhang, Yang, Ren, and Shih, 2007: 830. Daohugou Formation, China.

GENUS *ARCHIRHAGIO* ROHDENDORF, 1938

Archirhagio obscurus Rohdendorf, 1938: 37. Karabastau Formation, Kazakhstan. Type species.

Archirhagio mostovskii J.-F. Zhang, 2014: 4. Daohugou Formation, Mongolia.

Archirhagio striatus Zhang and Zhang, 2003: Daohugou, Jiulongshan Formation, China.

Archirhagio varius J.-F. Zhang, 2014: 5. Daohugou Formation, Mongolia.

Archirhagio zhangii K.-Y. Zhang, Yang, and Ren, 2009: 62. Daohugou Formation, Mongolia.

GENUS *CALOSARGUS* MOSTOVSKI, 1997

Calosargus tatianae Mostovski, 1997: 76. Karabastau Formation, Kazakhstan. Type species.

Calosargus antiquus K.-Y. Zhang, Yang, and Ren, 2007: 6. Daohugou Formation, Mongolia.

Calosargus bellus K.-Y. Zhang, Yang, and Ren, 2007: 3. Daohugou Formation, Mongolia.

Calosargus daohugouensis K.-Y. Zhang, Yang, and Ren, 2007: 9. Daohugou Formation, Mongolia.

Calosargus hani K.-Y. Zhang, Yang, and Ren, 2007: 15. Daohugou Formation, Mongolia.

Calosargus niger Mostovski, 1997: 76. Karabastau Formation, Kazakhstan.

Calosargus thanasymus Mostovski, 1997: 76. Karabastau Formation, Kazakhstan.

Calosargus tenuicellulatus K.-Y. Zhang, Yang, and Ren, 2007: 11. Daohugou Formation, Mongolia.

Calosargus validus K.-Y. Zhang, Yang, and Ren, 2007: 13. Daohugou Formation, Mongolia.

GENUS *DAOHUGOSARGUS* J.-F. ZHANG 2012

Daohugosargus eximius (K.-Y. Zhang et al.) 2008: 270 (orig. as *Sharasargus eximius*, n. comb., by J.-F. Zhang, 2012).

GENUS *FLAGELLISARGUS* J.-F. ZHANG, 2012

Flagellisargus sinicus J.-F. Zhang, 2012: 879. Daohugou Formation, China.

Flagellisargus robustus J.-F. Zhang, 2012: 881. Daohugou Formation, China.

Flagellisargus venustus J.-F. Zhang, 2012: 880. Daohugou Formation, China.

GENUS *HELEMPIS* REN, 1998

Helempis yixianensis Ren, 1998: 80. Yixian Formation, China. Placed by Ren in Protempididae.

Helempis eucalla Ren, 1998: 81. Yixian Formation, China. Placed by Ren in Protempididae.

GENUS *MESOSOLVA* HONG, 1983

Genus *Prosolva* Hong, 1983. Synonymy by Zhang, 2012.

Genus *Brevisolva* K.-Y. Zhang et al., 2010, Type species *B. daohugouensis* K.-Y. Zhang et al., 2010. Synonymy by J.-F. Zhang, 2012.

Mesosolva parva Hong, 1983: 133. Haifanggou Formation, Beipiao, China. Type species.

Mesosolva daohugouensis K.-Y. Zhang, Ren, and Shih, 2010: 79. Daohugou, Jiulongshan Formation, China. Name changed to *Mesosolva zhangae* by J.-F. Zhang (2012).

Mesolva huabeiensis (Hong), 1983: 134. Haifanggou Formation, Beipiao, China.

Prosolva huabeiensis Hong, 1983.

Mesosolva jurassica K.-Y. Zhang, Yang, and Shih, 2010: 77. Daohugou, Jiulongshan Formation, China.

Mesolva karataviensis (Mostovski), 1996: 120. Karabastau Formation, Kazakhstan. Originally as ?*Prosolva karataviensis* Mostovski.

Mesolva sinensis K.-Y. Zhang, Yang, and Ren, 2010: 76. Daohugou, Jiulongshan Formation, China.

GENUS *NOVISARGUS* J.-F. ZHANG, 2014

Novisargus rarus J.-F. Zhang, 2014: 9. Daohugou Formation, Mongolia.

GENUS *ORIGOASILUS* K.-Y. ZHANG ET AL., 2011

Origoasilus pingquanensis K.-Y. Zhang et al., 2011: 995. Yixian Formation, China.

GENUS *OVISARGUS* MOSTOVSKI, 1996

Genus *Helempis* Ren, 1998. Synonymy by J.-F. Zhang, 2012.

Ovisargus gracilis Mostovski, 1996: 121. Karabastau Formation, Kazakhstan.

Ovisargus singulus J.-F. Zhang, 2014: 11. Daohugou Formation, Mongolia.

GENUS *PARVISARGUS* MOSTOVSKI, 1996

Parvisargus malus Mostovski, 1996: 123. Karabastau Formation, Kazakhstan.

Parvisargus peior Mostovski, 1996: 123. Karabastau Formation, Kazakhstan.

GENUS *PAUROMYIA* REN, 1998

Pauromyia orebesia Ren, 1998: 72. Yixian Formation. Ren noted that the species was like *Archirhagio*. Called *oresbius* by J.-F. Zhang, 2014.

GENUS *SHARASARGUS* MOSTOVSKI, 1996

Sharasargus ruptus Mostovski, 1996: 124. Shara-Teg, Mongolia. Type species.

Sharasargus eximius K.-Y. Zhang, Yang, and Ren, 2008: 270. Daohugou, Jiulongshan Formation, China.

Sharasargus fortis K.-Y. Zhang, Yang, and Ren, 2008: 271. Daohugou, Jiulongshan Formation, China.

Sharasargus maculus J.-F. Zhang, 2014: 12. Daohugou Formation, Mongolia.

Sharasargus? spiniger Mostovski, 1996: 124. Karabastau Formation, Kazakhstan.

GENUS *TABANISARGUS* J.-F. ZHANG, 2014

Tabanisargus daohugouensis J.-F. Zhang, 2014: 15. Daohugou Formation, Mongolia.

GENUS *SINALLOMYIA* J.-F. ZHANG, 2012 (new name for *Allomyia* Ren, preoccupied by *Allomyia* Banks)

Sinallomyia ruderalis (Ren) 1998: 68.

FAMILY KOVALEVISARGIDAE MOSTOVSKI

GENUS *KOVALEVISARGUS* MOSTOVSKI, 1997

Kovalevisargus clarigenus Mostovski, 1997: 77. Karabastau Formation, Kazakhstan. Type species.

Kovalevisargus brachypterus J.-F. Zhang 2011: 166. Haifanggou Formation, Beipiao, China.

Kovalevisargus haifunggouensis J.-F. Zhang, 2014: 18. Haifanggou Formation, Beipiao, China.

Kovalevisargus macropterus J.-F. Zhang, 2011: 164. Haifanggou Formation, Beipiao, China.

GENUS *KEROSARGUS* MOSTOVSKI, 1997

Kerosargus argus Mostovski, 1997: 77. Karabastau Formation, Kazakhstan. Type species.

Kerosargus sororius J.-F. Zhang, 2011: 167. Haifanggou Formation, Beipiao, China.

FAMILY TETHEPOMYIIDAE GRIMALDI AND ARILLO

GENUS *TETHEPOMYIA* GRIMALDI AND CUMMING, 1999.

Tethepomyia thauma Grimaldi and Cumming, 1999: 6. Raritan Formation, New Jersey. Type species.

Tethepomyia buruhandi Grimaldi and Arillo, 2008: 259. Escucha Formation, Spain.

Tethepomyia zigrasi Grimaldi and Arillo, in Grimaldi et al., 2011: 323. Kachin, Myanmar.

GENUS *TETHEPOMIMA* GRIMALDI AND ARILLO, 2008.

Tethepomima holomma Grimaldi and Arillo, 2008: 261. Escucha Formation, Spain.

APPENDIX 2

DATA MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23	24	25	26	27	28	29	30	31	32
<i>Alleremonomus xingi</i>	1	0	1	1	?	?	?	?	0.34	0	0	0.19	0	N/A	1	1	1	1	0	0.37	N/A	1	0	0	1	1	0	?	?	0	2
<i>Allomyia ruderalis</i>	0	1	0	?	?	?	?	?	0.37	0	0	0.1	0	0	0	0	0	0	0	0.2	0.12	0	0	0	1	0	0	?	0	0	?
<i>Archirhagio mostovskii</i>	1	0	1	1	1	1	0	?	0.3	0	0	0.15	0	0	0	0	0	0	0	0.37	0.43	0	0	0	0	1	0	0.33	1	1	?
<i>Archirhagio varius</i>	1	0	1	1	1	0	0	?	0.25	0	0	0.13	0	0	0	0	0	0	0	0.3	0.3	0	0	0	0	0	0	0.27	1	?	?
<i>Archirhagio zhangii</i>	1	0	1	1	1	0	0	?	0.24	0	0	0.17	0	0	0	0	0	0	0	0.22	0.51	0	0	0	0	0	0	0.34	1	1	?
<i>Archisargus pulcher</i>	1	?	?	?	?	?	?	?	0.26	0	0	0.2	0	1	0	0	0	0	0	0.34	0.55	0	0	0	1	0	0	?	?	0	?
<i>Archisargus spuriventris</i>	1	0	1	1	1	1	0	?	0.25	0	0	0.16	0	1	0	0	0	0	0	0.23	0.34	0	0	0	?	1	0	0.32	1	1	?
<i>Archisargus strigatus</i>	1	0	1	1	?	?	?	?	0.33	0	0	0.13	0	1	0	0	0	0	0	0.33	0.47	1	0	0	1	1	0	?	?	0	?
<i>Archocyrtus gibbosus</i>	0	?	?	?	?	?	?	?	0.4	0	1	0.16	0	0	0	1	0	0	0	0.35	N/A	0	1	0	0	0	0	0.15	0	0	?
<i>Calosargus bellus</i>	1	0	1	1	?	?	?	?	0.33	0	0	0.21	0	N/A	1	0	0	0	0	0.48	0.37	0	1	0	0	0	0	?	?	1	?
<i>Calosargus hani</i>	1	0	1	1	?	?	?	?	0.29	0	0	0.18	0	N/A	1	0	0	0	0	0.23	0.29	0	1	0	0	0	0	?	?	1	?
<i>Callosargus tatianae</i>	1	1	?	1	1	1	0	0.29	0	0	0.26	0	0	N/A	1	0	0	0	0	0.41	0.28	0	0	0	0	0	0	0.32	0	1	?
<i>Calosargus thanasymus</i>	1	0	1	1	?	?	?	?	0.28	0	0	0.2	0	N/A	1	0	0	0	0	0.37	0.42	0	1	0	0	0	0	?	?	1	?
<i>Calosargus validus</i>	1	0	1	1	?	?	?	?	0.31	0	0	0.15	0	N/A	1	0	0	0	0	0.42	0.48	0	1	0	1	0	0	0.2	1	1	2
<i>Zhenia xiai</i>	1	1	0	1	1	1	0	0.28	0	0	0.11	0	0	N/A	1	0	1	1	0	0.42	0.69	0	0	0	0	0	0	0.28	1	?	?
<i>Daohugosargus eximius</i>	1	?	?	?	?	?	?	?	0.27	0	0	0.33	0	1	0	0	0	0	0	0.3	N/A	1	0	0	1	0	0	?	?	1	2
<i>Dissip clausus</i>	1	0	1	?	?	?	?	?	0.42	0	0	0.29	1	N/A	1	1	1	1	0	0.36	0.33	0	0	0	1	0	0	0.32	1	1	?
<i>Eremomukha angusta</i>	1	0	1	1	?	?	?	?	0.27	0	0	0.09	0	0	0	1	1	1	0	0.36	N/A	0	1	0	1	0	0	0.26	1	1	?
<i>Eremomukha sorosi</i>	1	1	0	1	1	1	0	0.27	0	0	0.06	0	0	0	0	1	1	1	0	0.32	N/A	0	1	0	1	0	0	0.33	1	1	?
<i>Eremomukha tenuissima</i>	1	0	1	1	?	?	?	?	0.28	0	1	0.09	0	0	0	1	1	1	0	0.35	N/A	0	1	0	1	0	0	0.25	1	1	2
<i>Eremomukha tsokotukha</i>	1	0	1	1	1	1	0	?	0.24	0	0	0.06	0	1	0	0	1	1	0	0.35	0.33	0	1	0	?	?	?	?	1	?	
<i>Flagellisargus robusta</i>	1	0	1	1	0	0	?	0.34	0	0	0.11	0	0	0	0	0	0	1	0	0.31	0.19	0	1	0	0	0	0.32	0	0	?	
<i>Flagellisargus sinicus</i>	1	0	1	1	0	0	?	0.28	0	0	0.18	0	0	0	0	0	0	1	0	0.27	0.19	0	0	0	0	0	0.23	0	0	?	
<i>Kerosargus argus</i>	0	?	?	?	?	?	?	?	0.37	0	1	0.08	0	1	0	0	0	N/A	1	0.13	0.41	0	0	0	0	0	0.21	1	1	?	
<i>Kovalevisargus haifan-</i> <i>gouensis</i>	1	1	0	1	1	1	0	?	0.35	0	1	0.13	0	1	0	0	0	N/A	1	0.36	N/A	0	0	0	0	0	0	0.17	1	0	?

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23	24	25	26	27	28	29	30	31	32
<i>Leptermochaetus elegans</i>	1	1	0	1	?	?	?	?	?	0.28	0	0	0.21	1	N/A	1	1	1	0	0.34	0.34	0	1	0	1	0	0	0.13	0	0	?
<i>Helempis eucalla</i>	1	1	0	1	1	1	0	?	0.4	0	0	0.11	0	0	0	0	0	0	0	0.42	0.37	1	0	0	0	1	0	0.27	0	?	?
<i>Mesosolva jurassica</i>	1	?	?	?	?	?	?	?	0.29	0	0	0.18	0	0	0	0	0	0	0	0.28	0.3	1	0	0	0	0	0	0.27	0	?	?
<i>Mesosolva parva</i>	1	?	?	?	1	?	1	0	?	0.37	0	0	0.21	0	0	0	0	0	0	0.28	0.46	0	1	0	0	0	0	0.25	?	1	2
<i>Novisargus rara</i>	1	1	0	1	1	1	0	?	0.31	0	0	0.22	0	0	0	0	0	N/A	1	0.42	0.05	1	0	0	0	0	0	0.27	1	1	0
<i>Orientisargus illecebrosus</i>	1	1	0	?	0	0	?	?	0.26	0	1	0.07	0	0	0	0	0	N/A	1	0.13	0.77	1	1	0	0	0	0	?	0	0	?
<i>Origoastlus pinguanensis</i>	1	?	?	?	?	?	?	?	0.31	0	0	0.27	0	0	0	0	0	0	0	0.28	0.48	0	1	0	1	0	0	0.33	1	0	2
<i>Ovisargus gracilis</i>	?	?	?	?	?	?	?	?	0.32	0	0	0.17	0	0	0	0	0	1	0	0.48	0.48	0	1	0	1	0	0	0.31	1	1	2
<i>Ovisargus singulus</i>	1	1	0	1	?	?	?	?	0.33	0	0	0.2	0	0	0	0	0	1	0	0.46	0.59	0	1	0	0	0	0	?	?	0	?
<i>Pauromyia oresbia</i>	0	?	?	?	?	?	?	?	0.23	0	0	0.23	0	0	0	0	0	0	0	0.28	0.26	1	0	0	0	0	0	0.22	0	0	?
<i>Prosolva huabeiensis</i>	1	?	?	?	?	?	?	?	0.37	0	0	0.21	0	0	0	0	0	0	0	0.21	0.68	0	1	0	0	0	0	0.26	1	0	?
<i>Sharasargus eximius</i>	1	0	1	?	?	?	?	?	0.26	0	0	0.32	0	1	0	0	0	0	0	0.29	0.28	0	1	0	0	0	0	0.24	?	1	?
<i>Sharasargus fortis</i>	1	?	?	?	?	?	?	?	0.32	0	0	0.18	0	1	0	0	0	0	0	0.3	0.52	0	1	0	0	0	0	?	?	0	?
<i>Sharasargus maculus</i>	0	0	1	1	1	0	?	?	0.27	0	0	0.21	0	1	0	0	0	0	0	0.26	0.56	0	1	0	0	0	0	0.2	?	0	?
<i>Sharasargus? spiniger</i>	0	0	1	?	1	1	0	0.21	0	0	0.24	0	1	0	0	0	0	0	0	0.24	0.38	0	0	0	0	0	0	0.35	0	0	?
<i>Tabanisargus daohugouensis</i>	0	0	1	1	?	?	?	?	0.35	0	0	0.16	0	0	0	0	0	0	0	0.41	N/A	N/A	1	1	N/A	0	1	0.34	0	0	?
<i>Tethepomima holomma</i>	1	1	0	1	0	0	1	1	0.42	1	0	0.15	N/A	0	0	0	N/A	N/A	1	N/A	N/A	N/A	1	1	N/A	0	1	N/A	0	0	?
<i>Tethepomymia buruhandi</i>	1	1	0	1	0	0	1	1	0.4	1	0	N/A	N/A	N/A	N/A	0	N/A	N/A	1	N/A	N/A	N/A	1	1	N/A	0	?	N/A	0	0	?
<i>Tethepomymia thauma</i>	1	1	0	1	0	0	1	1	0.33	1	0	N/A	N/A	N/A	N/A	0	N/A	N/A	1	N/A	N/A	N/A	1	1	N/A	0	1	N/A	0	0	3
<i>Tethepomymia zigrasi</i>	1	1	0	1	0	0	1	1	0.43	1	0	N/A	N/A	N/A	N/A	0	N/A	N/A	1	N/A	0.43	0	0	0	0	0	?	?	1	1	?
<i>Uranorhagio daohugouensis</i>	1	0	1	?	?	?	?	?	0.3	0	0	0.27	0	0	0	0	0	0	0	0.3	0.38	1	1	0	1	0	0	0.32	0	0	0
<i>Rachicercus obscuripennis</i>	0	1	0	0	0	0	0	0.38	0	0	0.21	0	0	0	0	0	0	0	0	0.27	0.41	0	1	0	1	0	0	0.38	0	0	0
<i>Beris fuscipes</i>	0	0	1	0	0	0	0	0.37	0	1	0.14	0	1	0	0	0	0	0	0	0.41	0.26	0	1	0	0	0	0	0.26	0	0	0
<i>Symphoromyia hirta</i>	0	0	0	0	0	0	0	0.4	0	0	0.15	0	0	0	0	0	0	0	0	0.26	N/A	1	1	0	1	0	0	0.36	0	0	0
<i>Neorhynchocephalus volaticus</i>	0	0	1	0	0	0	0	0.28	0	0	0.04	0	0	0	0	0	0	0	0	0.29	0.29	1	1	0	0	0	0	0.22	1	1	1
<i>Vermileo tibialis</i>	1	1	0	0	0	0	0	0.28	0	0	0.1	0	0	0	0	0	0	0	0	0.18											

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