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Short communication

Long-proboscid zhangsolvid flies in mid-Cretaceous Burmese amber (Diptera: Stratiomyomorpha)

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A B S T R A C T

Zhangsolvidae is an extinct family of brachycerous flies with long proboscis that is known only from the Cretaceous. This family is considered a pollinator of Cretaceous gymnosperms. Two new species, *Burmomyia rossi* gen. et sp. nov. and *Cratomyia zhuoi* sp. nov., are described in mid-Cretaceous Burmese amber from the Hukawng Valley in northern Myanmar. An updated key to all known genera and species of Zhangsolvidae is also given. Our study suggests that zhangsolvids had a relatively high diversity in the mid-Cretaceous and reveals zhangsolvid lacked distinct sexual dimorphism.

1. Introduction

The extinct family Zhangsolvidae was erected by Nagatomi & Yang (1998) based on the species *Zhangsolva cupressa* (Zhang et al., 1993) from the Lower Cretaceous Laiyang Formation of China. Zhangsolvidae were a very specialized family with long probosci, long antennae, and peculiar wing venations and are only found in the Cretaceous, especially at 99–125 Ma. The fossil record of this family is sparse, hitherto only seven species in four genera having been described as compression fossils (*Zhangsolva cupressa* from the Lower Cretaceous of China and *Cratomyia macrorrhyncha* and *Cratomyia cretacica* from the Lower Cretaceous of Brazil) and amber inclusions: *Buccinatormyia magnifica* and *Buccinatormyia soplaensis* from Early Cretaceous Spanish amber, and *Linguatormyia teletacta* and *Cratomyia mimetica* from mid-Cretaceous Burmese amber (Zhang, Zhang & Li, 1993; Mazzarolo & Amorim, 2000; Wilkommen & Grimaldi, 2007; Arillo et al., 2015; Peñalver et al., 2015; Grimaldi, 2016). Exceptional three-dimensional preservation has provided us with palaeoecological information about the lifestyle and micromorphology of this vanished group. The systematic position of Zhangsolvidae lies within the dipterous infraorder Stratiomyomorpha based on the phylogenetic analysis of 52 morphological characters (Arillo et al., 2015). The generic and specific diagnoses below are based on Arillo et al. (2015).

The best evidence of insect interaction with plants comes from insect mouthparts, as insect proboscis length commonly matches the floral tube length, Late Mesozoic long-proboscis scorpionflies having been already proposed as specialized pollinators and recently lacewings have revealed a high niche diversity of Mesozoic pollinating insects (Grimaldi and Engel, 2005; Labandeira, 2005; Ren, 2009; Liu et al., 2018a). Zhangsolvids were also undoubtedly specialized pollinators of plants as the recent study of the detailed structure of the long proboscis and co-occurrence of gymnosperm pollen clumps on one zhangsolvid fly has shown (Peñalver et al.,

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2015). Except for elongated mouthparts, additional specialized morphological adaptions such as wings with hovering flight, eyes with optimized frontal resolution, palpi with sensillar foveae on and elongated antennae for detecting scents of floral organs (Peñalver et al., 2015). In addition, mimicry behaviour is also suggested based on the vespid-like patterns on the abdomens of *B. soplaensis* Arillo et al. (2015) and *Cratomyia mimetica* Grimaldi (2016) (Arrilo et al., 2015; Peñalver et al., 2015; Grimaldi, 2016).

Burmese amber is one of the world's most important amber sources preserving one of the most important palaeobiotas in the world with 37 classes, 99 orders and 510 families of organisms having been described (Ross, 2018). Considerable insect palaeoethology has also been recorded in Burmese amber, such as debris-carrying camouflage in diverse lineages of insect larvae and liverwort mimesis in a lacewing larva (Wang et al., 2016; Liu et al., 2018b). Until now, only two species of zhangsolvids have been described from Burmese amber, *Linguatormyia teletacta* Grimaldi (2015) and *Cratomyia mimetica* Grimaldi (2016) (Arillo et al., 2015; Grimaldi, 2016); here we describe two new species, *Burmomyia rossi* gen. et sp. nov., and *Cratomyia zhuoi* sp. nov., from mid-Cretaceous Burmese amber with the first record of the entomologically important male genitalia of zhangsolvid flies.

2. Material and methods

The specimens described herein are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). They are from the Hukawng Valley of Kachin Province, northern Myanmar (locality in Kania et al., 2015: fig. 1). The geological age of Burmese amber is considered as earliest Cenomanian, about 99 Ma based on the radiometric date obtained from burmite-bearing sedimentary rock (Shi et al., 2012), but the actual age of the amber could be older than the enclosing volcanoclastic matrix, so we here adopt a mid-Cretaceous age for the inclusions.

The amber pieces have been polished with sand paper of different grain sizes and with polishing powder. Observations were made using a Zeiss Stemi 508 Microscope and photomicrographs were taken with a Zeiss Stereo Discovery V16 microscope system; in most instances, incident and transmitted light were used simultaneously. To overcome some reflected light caused by convex surfaces, we dropped glycerol on the amber, and then placed a cover glass on top for viewing. All images are digitally stacked photomicrographic composites of approximately 30 individual focal planes obtained using Helicon software for better illustration of the 3D structures. Measurements were taken using Zen software, and there is some approximation because of inclusion deformation and slight optical distortion. The figures were prepared with CorelDraw X7, Adobe Photoshop CS6 and SAI. Vein abbreviations follow Zhang et al. (1993). All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSIC: urn:lsid:zoobank.org:pub:37E291A0-498F-4279-9F8A-867886D650E1.

3. Systematic palaeontology

Order Diptera Linnaeus, 1758
Suborder Brachycera Zetterstedt, 1842
Infraorder Stratiomyomorpha Hennig, 1973
Family Zhangsolvidae Nagatomi & Yang, 1998

Key to the species of Zhangsolvidae

1. M_1 and M_2 diverging from a portion of M_{1+2} distad to cell d…2
– M_1 and M_2 diverging directly from cell d……………………….5
2. stem M_{1+2} long…………………………………………………….3
– stem M_{1+2} short…………………………………………………...4
3. cell d long…*Cratomyia macrorrhyncha* Mazzarolo & Amorim (2000)
– cell d short……………*Cratomyia cretacica* Wilkommen (2007)
4. Rs short; scape, pedicel and basal three flagellomeres uniform in size……………………….*Cratomyia mimetica* Grimaldi (2016)
– Rs long, basal three flagellomeres longer than scape and pedicel…………………………*Cratomyia zhuoi* sp. nov.
5. Antenna with more than 14 segments…*Zhangsolva cupressa* Nagatomi & Yang (1998)
– Antenna with less than 10 segments……………………………6
6. Antenna with five segments, without apical stylus…………………*Linguatormyia teletacta* Grimaldi, 2015
– Antennal segments with five to ten segments, apical stylus present or absent…………………………………………………..7
7. Antenna with eight segments, without apical stylus…………………………………….*Burmomyia rossi* sp. nov.
– Antenna with six segments and with apical stylus……………8
8. Antenna not flagellate and short, Sc ending at level of r-m crossvein, m_3 narrow, CuP well sclerotized……………*Buccinatormyia magnifica* Arillo et al. (2015)
– Antenna flagellate and elongate, Sc ending beyond level of r-m crossvein, cell m_3 broad, CuP weakly developed…*Buccinatormyia soplaensis* Arillo et al. (2015)

Genus ***Burmomyia*** Zhang and Wang, gen. nov.
(urn:lsid:zoobank.org:act:6436EA31-9FC9-46D6-BFB2-9D24C8EAF9DF)
Type species: *Burmomyia rossi* sp. nov.

Etymology. Derived from Burma and -myia, fly.
Diagnosis. body short and relatively stout; antenna with eight segments (six flagellomeres), without minute apical stylus; proboscis much stouter and relatively short compared to all known zhangsolvids; vein C ending just beyond M_1, veins M_1 and M_2 diverging directly from cell d; M_1 straight and long, cell m_3 narrow, M_3 fused to M_4 with a long petiole.

Burmomyia rossi Zhang and Wang, sp. nov.
Figs. 1 and 2
(urn:lsid:zoobank.org:act:1F311D87-0723-4C1F-8FB1-324DFCB2880C)

Etymology. Named after Prof. Andrew Ross, National Museum of Scotland, for his great contribution to cataloguing Burmese amber inclusions.
Material. Holotype specimen number NIGP169578 (female), stored at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.
Diagnosis. Proboscis bold but not very elongate (about 0.2 × body length); antenna not flagellate, about half length of wing; flagellomere II about 0.3 × flagellum length; costal vein ending just beyond M_1, all inner veins well sclerotized; cell m_3 narrow, closed before wing margin; R_{2+3} parallel to R_1, apex of cell r_{2+3} narrower than r_1; R_4 and R_5 bifurcated far behind cell d; cell cu closed before wing margin.
Description. (female; based on well preserved holotype). Body 3.3 mm long except for antennae; antennae 1.4 mm long; wing 3.2 mm long, 1.3 mm wide. Dark brown head and thorax, light brown abdomen (Fig. 1A, E–F).

Head broad, 0.86 mm wide. Eyes bare, bulging, widely separated, ventrally 0.4 mm wide between inner eye margins; eye facets undifferentiated; vertex deeply concave, without setae. Ocelli indiscernible. Clypeus large, bulging. Antennal bases widely separate, 2.5 × diameter of antennal socket

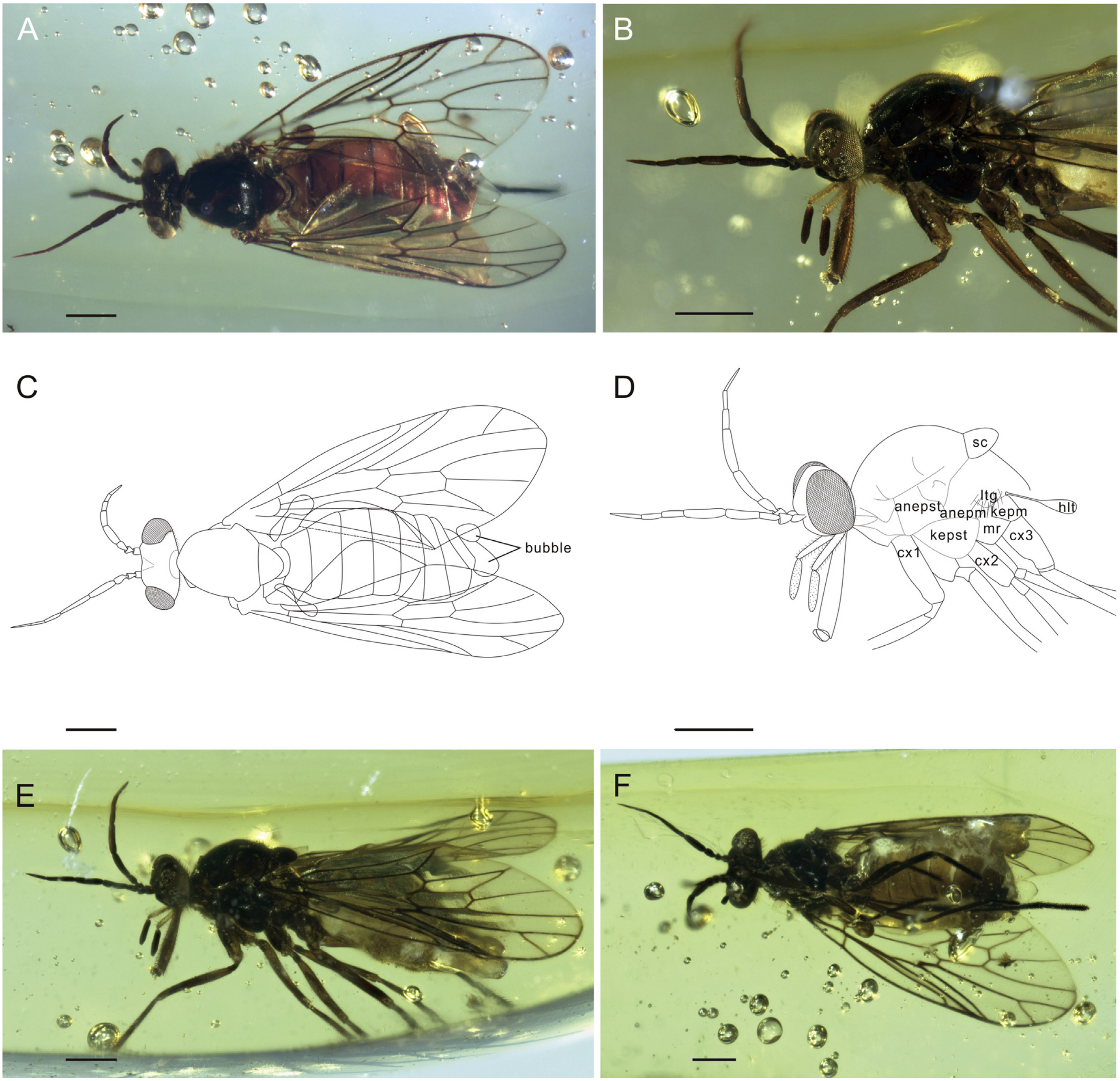

Fig. 1. *Burmomyia rossi* gen. et sp. nov., holotype 17070. A, photograph of dorsal features; B, photograph of head and thorax in lateral view; C, line drawings of body in dorsal view; D, line drawings of head and thorax in lateral view; E, photograph of lateral features; F, photograph of ventral features. aneps = anepisternum; cs = coxa; hlt = halter; kepst = katepisternum; kepm = katepimeron; ltg = laterotergite; mr = meropleurite. Scale bars represent 0.5 mm.

(Fig. 1A–D). Scape cylindrical, as long as wide; pedicel short, slightly shorter than scape; base of pedicel slender and apically widened, apically as wide as scape. Scape and pedicel covered by sparse and relatively strong setae. Flagellum long, comprising six flagellomeres: f I shortest, 0.13 mm long; f II widest, 0.27 mm long, 0.08 mm wide; f III longest, distinctly thinner than f II, 0.33 mm long; f IV 0.16 mm long; f V 0.13 mm long; f VI 0.21 mm long, tapered apically, without minute stylus (Fig. 2A and B). Proboscis directed forward in relation to head, 0.66 mm long, 0.12 mm wide. Proboscis covered by dense microtrichia, labellum as wide as haustellum. Maxillary palp flank base of proboscis; palp long, two segmented; basal palpomere long, about 0.5 × total palp length, covered by long, fine setae; apical part of palpomere apparently darker than basal part, club shaped, apex rounded, with several fine foveae present (Fig. 1B, D).

Thorax short and higher than head, 1.05 mm long, 0.72 mm wide, 0.8 mm high. Scutum short, convex in profile, trapezoidal in dorsal view (Fig. 1A and B). Scutellum large, triangular, suture between scutum and scutullum distinct. Scutum and scutullum densely pilose. Anterior part of thorax small, proepisternum large, subrectangular, hypochromic, covered with microtrichia; antepronotum oblong, small but bulging; proepimeron lateral to antepronotum, small. Transverse suture well developed in

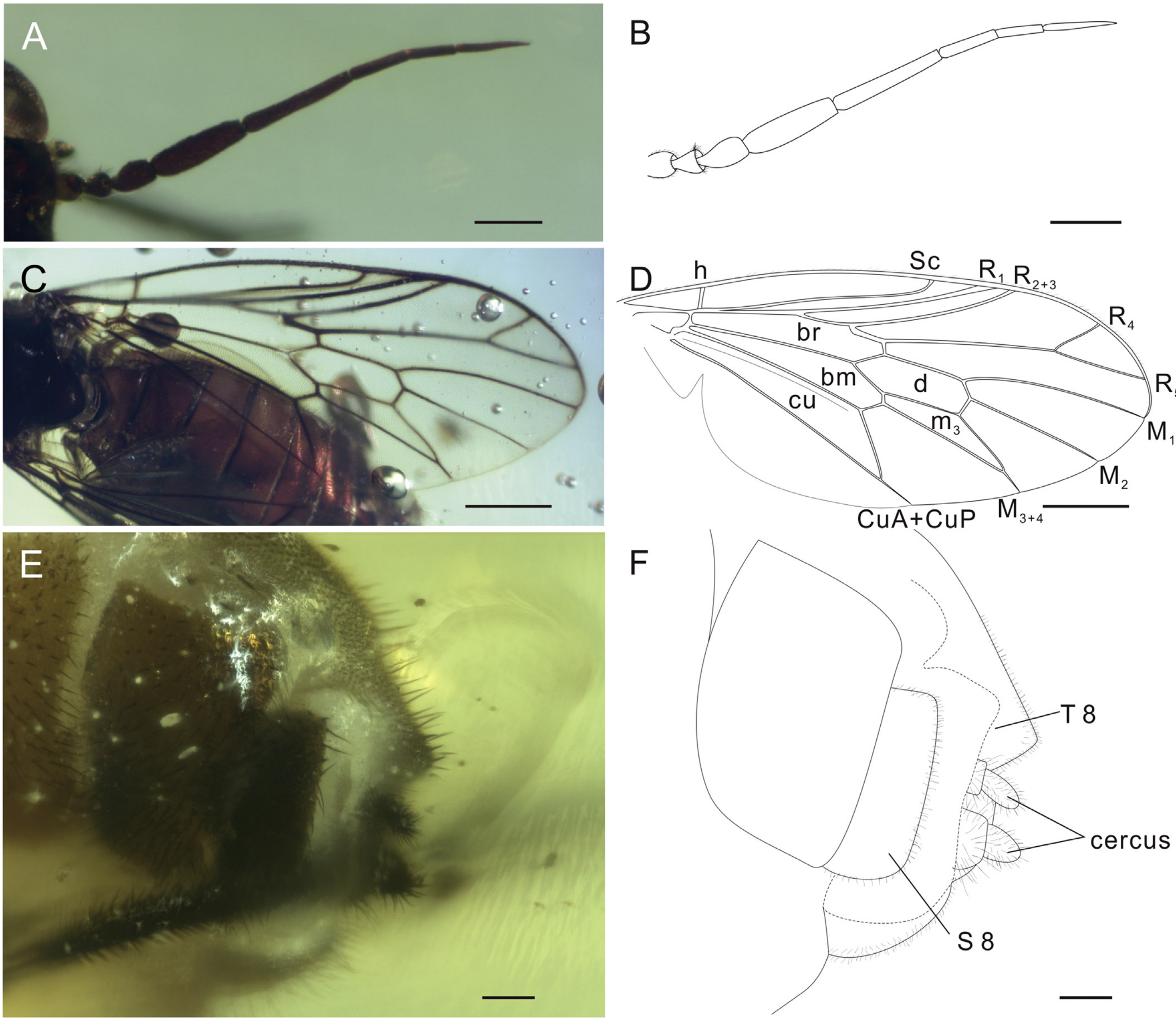

Fig. 2. *Burmomyia rossi* gen. et sp. nov., holotype 17070. A, photograph of antennae; B, line drawings of antennae; C, photograph of wing; D, line drawings of wing; E, photograph of genitalia in ventral view; F, ling drawings of genitalia in ventral view. Scale bars represent 0.2 mm in A and B, scale bars represent 0.5 mm in C and D, scale bars represent 0.1 mm in E and F.

meso- and metathorax, but faint dorsally. Anepisternum large, squarish. Anepimeron small, bulging. Katepisternum large, subtriangular, slightly bulging. Meropleurite much smaller than katepisternum. Laterotergite projecting, covered by thin, long setae (Fig. 1C and D).

Legs all covered by microtrichia. Procoxa slender, 0.4 mm long, apparently longer than meso- and metacoxa. Peg invisible on metacoxa. Trochanter small, slender. Femur and tibia slender, with decumbent setae, tibia without spurs. All tarsomeres missing (Fig. 1E). Wing membrane entirely hyaline, evenly covered with minute microtrichia. Wing length 3.13 mm, width 1.25 mm (Fig. 2C). Costal vein well sclerotized, tapered behind R_5, ending just behind M_1 vein. Crossvein h 0.12 mm long, well sclerotized. Vein Sc complete, apex abruptly upcurved, meeting wing margin just beyond the level of r-m. R_1 thickest, meeting costal vein opposite the distal part of cell d. Rs relatively long, 0.34 mm long (ca. 5 × length of r-m crossvein). R_{2+3} parallel to R_1. bR_{4+5} thick, as long as Rs. Bifurcation of R_{4+5} asymmetrical, R_4 0.28 mm long, R_5 0.53 mm long. Cross-vein r-m short, basal to cell d. Cells br and bm nearly equal in length, bm with four distal corners. Cell d narrow and long, 0.66 mm long, 0.07 mm wide. M_1 and M_2 diverging directly from cell d, long, nearly parallel, slightly divergent apically. Cell m_3 long and slender, 0.8 mm long, 0.15 mm wide. M_4 and M_3 join before meeting wing margin. CuA + CuP meeting wing margin just past midpoint of wing. Vein A faint, but recognizable, apically evanescent. Anal lobe and alula well developed (Fig. 2C and D). Haltere 0.4 mm long, apical knob rounded (Fig. 1D).

Abdomen pale-brown, all segments covered by fine microsetae. Abdomen broad, apparently broader than thorax, eight segments present, terminal covered by two bubbles in dorsal view (Fig. 1A). White emulsion present on tergum and sternum obscuring details in ventral view. Cerci small, two segmented, covered by fine setae (Fig. 2E and F).

Genus ***Cratomyia*** Mazzarolo and Amorim, 2000
Type species: *Cratomyia macrorrhyncha* Mazzarolo and Amorim (2000)

Cratomyia zhuoi Zhang and Wang, sp. nov.
(urn:lsid:zoobank.org:act:B000E114-31C5-45FA-B0CB-B3CB46B03374)
Figs. 3 and 4

Etymology. After Mr. Zhuo De who allowed us to study the unique type specimen.
Material. Holotype specimen number NIGP169579 (male), stored at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.
Diagnosis. Antenna with 7 annulations, apical with minute stylus; scape and pedicel shorter than flagellomeres; proboscis gracile, about 0.38 × body length; apex of R_{2+3} upcurved, join the costal

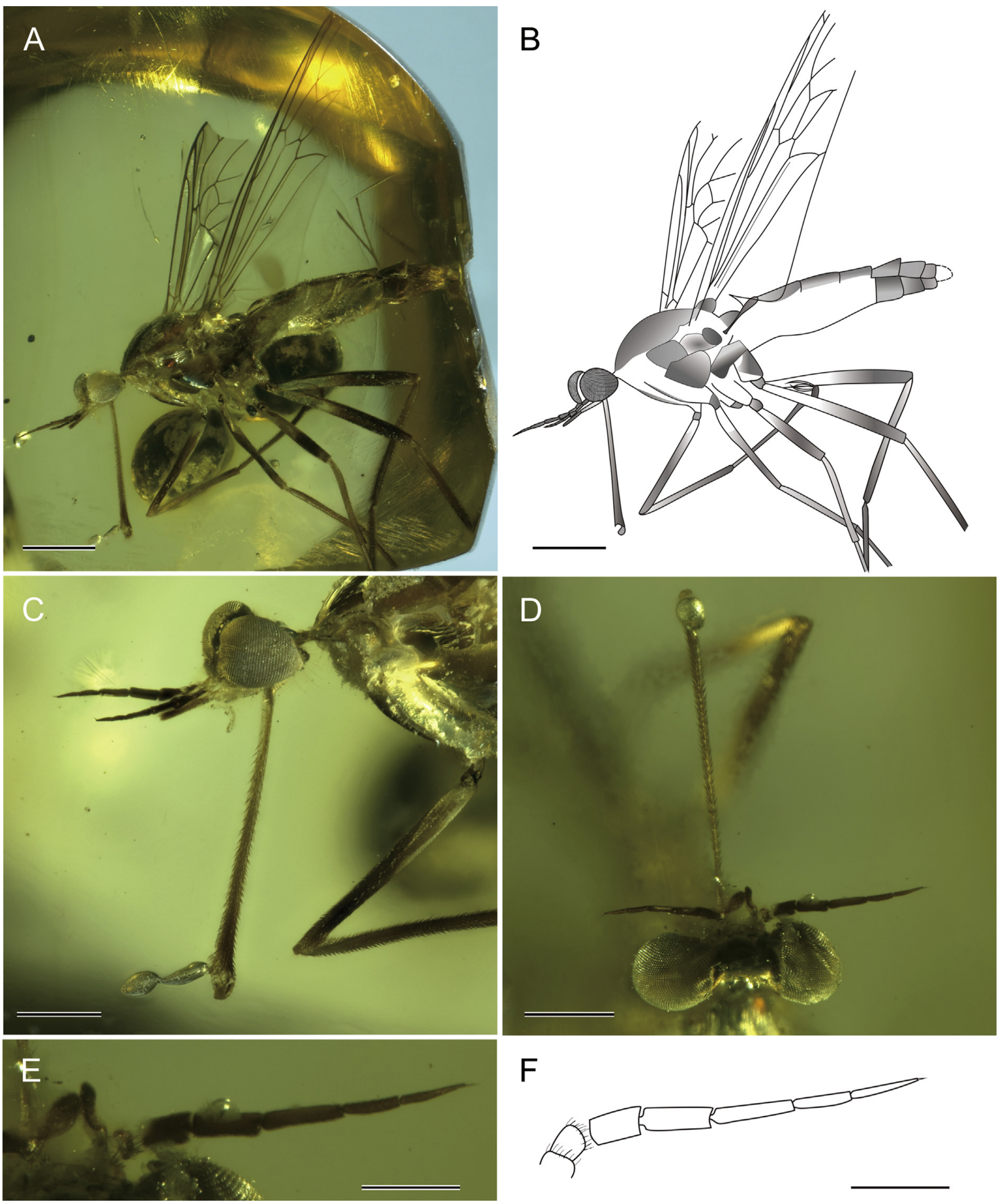

Fig. 3. *Cratomyia zhuoi* sp. nov., holotype 17100. A, photograph of lateral features; B, line drawings of lateral features; C, photograph of head in lateral view; D, photograph of head in dorsal view. Scale bars represent 1 mm in A and B, scale bars represent 0.5 mm in C and D, Scale bars represent 0.25 mm in E and F.

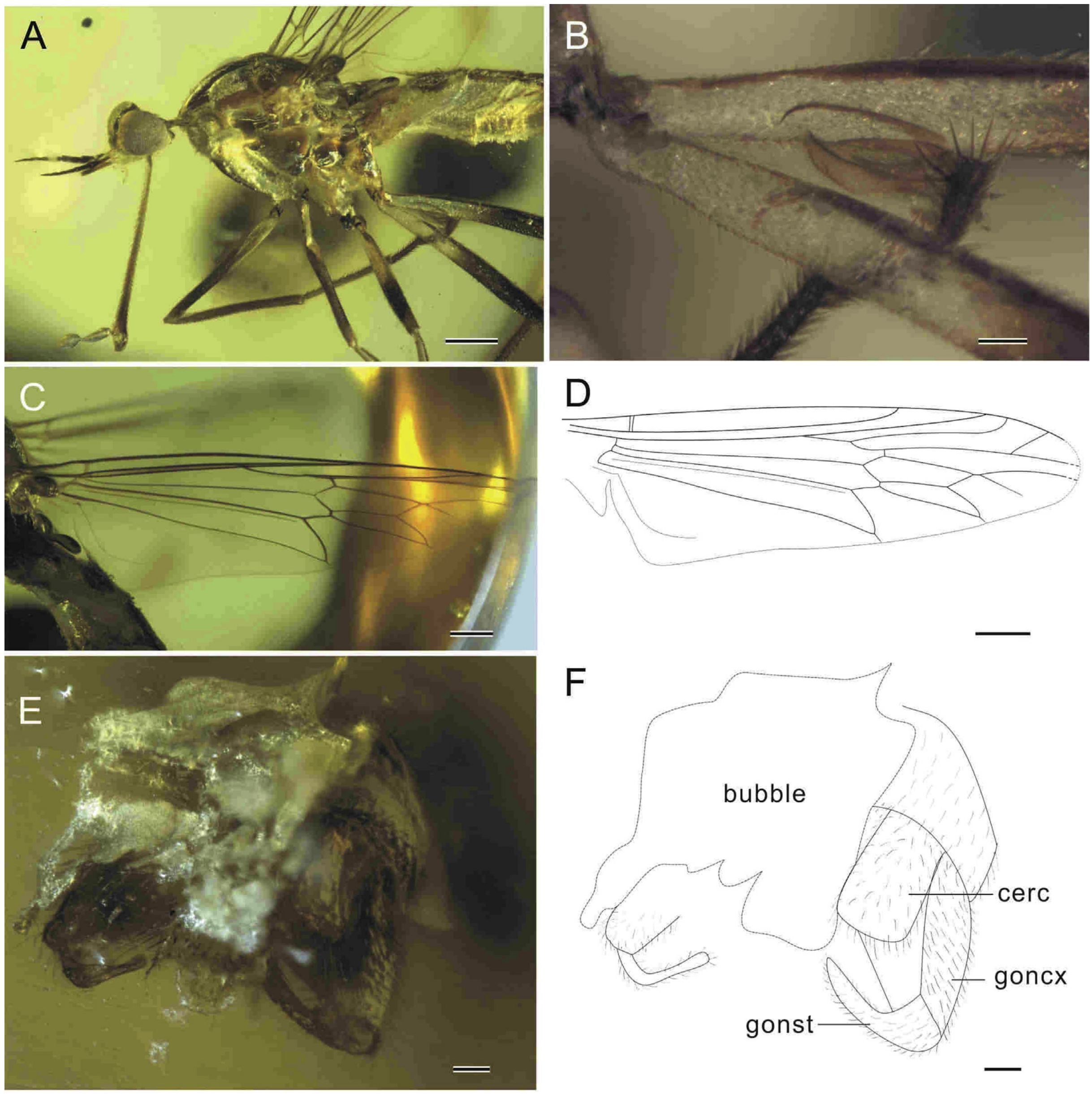

Fig. 4. *Cratomyia zhuoi* sp. nov., holotype 17100. A, photograph of head and thorax in lateral view; B, photograph of propretarsus; C, photograph of wing; D, line drawing reconstruction of wing; E, photograph of genitalia in dorsal view; F, line drawing of genitalia in dorsal view. gonst = gonostylus; goncx = gonocoxite; cerc = cercus. Scale bars represent 0.5 mm in A, C and D, scale bar represents 0.1 mm in B; scale bars represent 0.05 mm in E and F.

vein perpendicularly; M_1 slightly upcurved, ending just behind wing tip.

Description. (male, based on holotype). Body 5.5 mm long, except for antennae, antennae 1.2 mm long; wing 4.6 mm long, 1.2 mm wide. Body with colour pattern distinct, especially on abdomen and legs. Gracile flies, without macrosetae on body (Fig. 3A and B).

Head slightly wider than thorax, vertex deeply concave. Dichoptic, eyes widely apart, bulging, no differentiation between eye facets. Ocelli indiscernible. Antennal bases widely separated, 3× diameter of antennal sockets (Fig. 3D). Scape and pedicel not well preserved, short, cylindrical; apex of pedicel with a circle of setae. Flagellum comprising five flagellomeres, apical with a flimsy stylus: f I shortest, 0.14 mm long; f II 0.2 mm long; f III 0.21 mm long; f IV 0.13 mm long; f V 0.18 mm long (Fig. 3E and F). Proboscis thin and long, 1.9 mm long, 0.03 mm wide. Proboscis covered by dense microtrichia, labellum very small, about as wide as proboscis (Fig. 3C and D). Palp broad and long, two segmented, basal palpomere light, apical palpomere dark, the two palpomeres equal in length.

Thorax short and deep, 1.6 mm long, 0.86 mm wide, 1.3 mm high. Scutum short, convex in profile. Scutellum projected, well above abdomen, 0.3 mm in length (Fig. 3A and B). Thorax without pilosity except on laterotergite. Anepisternum, anepimeron, laterotergite, katepisternum and meropleurite all black coloured. Laterotergite fusiform, with long setae (Fig. 4A). Haltere long, apical knob club shaped. Wing membrane entirely hyaline, evenly covered with minute microtrichia. Wing relatively narrow, length 4.6 mm, width 1.2 mm. Costal vein well sclerotized beyond R_4, fading away near M_1 (due to incomplete preservation). Cross-vein h thick but faint, Rs relatively long compared to *C. mimetica*, 0.81 mm long; M_2 apparently incomplete. Stem of M_{1+2} quite short. Vein A faint, parallel to anal lobe, faded away in the mid of the anal lobe; anal lobe and alula well developed. Upper calypter large, erect to wing base (Fig. 4C and D).

Leg slender, coxa patterned like *Cratomyia mimetica*, pro- and mesocoxa light, metacoxa dark dorsally; mesocoxa slightly closer to metacoxa than to procoxa, not contacting either one; knob present on metacoxa. Trochanter dark; colouration on femur relatively distinct, lower part of pro- and metafemur dark, mesofemur lighter. Tibial colouration lighter, not as dark as femur, gradually darker from top to bottom; formula of tibial spurs 0-2-2, spurs quite slender. Only foretarsus preserved, pretarsus with claws well developed; pulvillus well developed, about same size as claws. Empodium pulvilliform, about same size as pulvillus and claws (Fig. 4B).

Abdomen slightly wider than thorax in dorsal view; 8 segments visible; T II longest, T VIII shortest. Terminalia with one-segmented setose cerci, cerci broad and flat; gonocoxite setose, broad and distinctly longer than cercus; gonostylus thin and long, about equal in length with gonocoxite (Fig. 4E and F).

4. Discussion

Reduction in the number of flagellomeres comprising the antennal flagellum is a trend throughout the Diptera (Yeates, 1994). *Burmomyia rossi* gen. et sp. nov. with antennae possessing 8 segments (versus described species mainly with 6 or 5 annulations except *Zhangsolva cupressa* which have 12 segments) evidently represents the primitive state of this group. *B. rossi* is the smallest species in body size based on all records of Zhangsolvidae with a body length of only 3.3 mm (normally more than 10 mm). Also, the mouthparts of *B. rossi* are much stouter and shorter compared to other zhangsolvids (0.66 mm long vs 10 mm or longer).

Cratomyia zhuoi is very similar to *Cratomyia mimetica* in both body shape and colour pattern on the thorax and legs, but differs from *C. mimetica* in antenna having 7 annulations, scape and pedicel being much shorter than the flagellomeres (vs scape, pedicel and basal three flagellomeres being uniform in size and shape); wing being narrower with W/L ratio 0.26 (vs 0.36); Rs relatively long (vs very short); area between Sc and R_1 without any darkening (vs entire area darkened, including basal area); apex of M_1 straight (vs sinuous, apex upcurved); vein A concave, nearly parallel to anal lobe (vs straight); annula well developed (barely observable in *C. mimetica*); tibial spurs slender (vs relatively robust); and pulvilli about same size as claws (vs shorter than claws).

C. mimetica is a female mentioned by Grimaldi, but without any description of the genitalia: “terminalia obscured by bubbles, largely retracted into sternite/tergite 8” (Grimaldi, 2016). *C. zhuoi* is undoubtedly male with genitalia well preserved and it's also the first definite male zhangsolvid known. If *C. mimetica* is a female, then the male and female lack distinct sexual dimorphism as they have very similar colour patterns on the body, *C. zhuoi* also possessing dichoptic eyes and facets without any differentiation. Sexual dimorphism is, however, quite common in extant flies, in orthorrhaphous flies commonly involving eye types (male holoptic, female dichoptic), differentiation of facets (male usually with enlarged facets on upper area, female without any differentiation), and body/wing colouration. *Linguatormyia teletacta* without the abdomen preserved was supposed to be a female based on dichoptic eyes (Arillo et al., 2015) by analogy with extant brachycerous flies. However, with our discovery of a dichoptic male zhangsolvid, the analogy is questionable.

The fossil record of Zhangsolvidae is summarized by Peñalver et al. (2015): (Their fig. 4B), involving three localities in Laurasia (in northeast China, Spain and Myanmar) and one locality in Gondwana (Brazil): a widespread distribution suggesting successful plant colonisation. The mouthpart lengths of Zhangsolvidae are varied, ranging from 0.66 mm to 7 mm, even in Burmese amber ranging from 0.66 mm to 4.37 mm, and are gracile to stout. Insect proboscis length commonly matches that of floral tubes suggesting diverse plant hosts (Liu et al., 2018a); as nectar feeding is linked to pollination, diverse proboscis length implies pollination niche partitioning.

The specialized parasitoid eremochaetid flies also occur only in the Mesozoic, with the latest records in Burmese amber, similar to Zhangsolvidae (Zhang et al., 2016). The extinction of specialized flies such as Zhangsolvidae and Eremochaetidae evidently before the K/T boundary event, may be linked to floral turnover and competition from newly devolved groups that dominant in the extant ecosystems (Zhang et al., 216; Zhang & Wang, 2017).

5. Conclusion

The discovery of *Burmomyia rossi* gen. et sp. nov. and *Cratomyia zhuoi* sp. nov. greatly augments the fossil record of Zhangsolvidae, supporting the diversity of this family in the mid-Cretaceous. The new discovery also enriched zhangsolvids proboscis length in Burmese amber, confirmed the niche diversity between these flies. *Cratomyia zhuoi* is the first male record of Zhangsolvidae, settling the issue of sexual dimorphism in zhangsolvids.

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References

Arillo, A., Peñalver, E., Pérez-de la Fuente, R., Delclòs, X., Criscione, J., Barden, P.M., Riccio, M.L., Grimaldi, D.A., 2015. Long-proboscid brachyceran flies in Cretaceous amber (Diptera: Stratiomyomorpha: Zhangsolvidae). Systematic Entomology 40, 242–267.
Grimaldi, D.A., 2016. Diverse orthorrhaphan flies (Insecta: Diptera: Brachycera) in amber from the Cretaceous of Myanmar: Brachycera in Cretaceous amber, part VII. Bulletin of the American Museum of Natural History 408, 1–131.
Grimaldi, D.A., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, New York, p. 755.
Hennig, W., 1973. 31. Diptera (Zweiflügler). In: Helmcke, J.G., Starck, D., Wermuth, H. (Eds.), Handbuch der Zoologie, IV. Arthropoda–2. Insekta. De Gruyter, Berlin, p. 337.
Kania, I., Wang, B., Szwedo, J., 2015. Dicranoptycha Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. Cretaceous Research 52, 522–530.
Labandeira, C.C., 2005. Fossil history and evolutionary ecology of Diptera and their associations with plants. In: The Evolutionary Biology of Flies, vol. 9, pp. 217–273.
Linnaeus, C., 1758. Systema naturae per regna tria naturae, secumdum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentius Salvius, Holmiae, p. 824.
Liu, Q., Lu, X.M., Zhang, Q.Q., Chen, J., Zheng, X.T., Zhang, W.W., Liu, X.Y., Wang, B., 2018a. High niche diversity in Mesozoic pollinating lacewings. Nature Communications 9, 3793.
Liu, X.Y., Shi, G.L., Xia, F.Y., Lu, X.M., Wang, B., Engel, M.S., 2018b. Liverwort mimesis in a Cretaceous lacewing larva. Current Biology 28, 1475–1481.
Mazzarolo, L.A., Amorim, D.S., 2000. *Cratomyia macrorrhyncha*, a Lower Cretaceous brachyceran fossil from the Santana Formation, Brazil, representing a new species, genus and family of the Stratiomyomorpha (Diptera). Insect Systematics and Evolution 1, 91–102.

Nagatomi, A., Yang, D., 1998. A review of extinct Mesozoic genera and families of Brachycera (Insecta, Diptera, Orthorrhapha). Entomologists' Monthly Magazine 134, 95–192.
Peñalver, E., Arillo, A., Pérez-de la Fuente, R., Riccio, M.L., Delclòs, X., Barrón, E., Grimaldi, D.A., 2015. Long-proboscid flies as pollinators of Cretaceous gymnosperms. Current Biology 25, 1917–1923.
Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A., Shih, C.K., Bashkuev, A., Logan, M.A.V., Hotton, C.L., Dilcher, D., 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. Science 326, 840–847.
Ross, A., 2018. Burmese (Myanmar) amber taxa, on-line checklist v.2018.2, p. 104. https://www.nms.ac.uk/media/1158001/burmese-amber-taxa-v2018_2.pdf.
Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.
Wang, B., Xia, F.Y., Engel, M.S., Perrichot, V., Shi, G.L., Zhang, H.C., Chen, J., Jarzembowski, E.A., Wappler, T., Rust, J., 2016. Debris-carrying camouflage among diverse lineages of Cretaceous insects. Science Advances 2, e1501918.
Willkommen, J., Grimaldi, D.A., 2007. Diptera: true flies, gnats and crane flies. In: The Crato Fossil Beds of Brazil – Window into an Ancient World, vol. 11.20. Cambridge University Press, pp. 369–387.
Yeates, D.K., 1994. The cladistics and classification of the Bombyliidae (Diptera: Asiloidea). Bulletin of the American Museum of Natural History 191.
Zetterstedt, J.W., 1842. Diptera Scandinaviae disposita et descripta. Officina Lundbergiana Lundae 1, 1–894.
Zhang, Q.Q., Wang, B., 2017. Evolution of lower brachyceran flies (Diptera) and their adaptive radiation with angiosperms. Frontiers in Plant Science 8, 1–6.
Zhang, J.F., Zhang, S., Li, L.Y., 1993. Mesozoic gadflies (Insecta: Diptera). Acta Palaeontologica Sinica 32, 662–672.
Zhang, Q.Q., Zhang, J.F., Feng, Y.T., Zhang, H.C., Wang, B., 2016. An endoparasitoid Cretaceous fly and the evolution of parasitoidism. The Science of Nature 103, 1–7.