



First description of the male of *Cretaconiopteryx grandis* Liu & Lu, 2017 (Neuroptera: Coniopterygidae) from the Cretaceous Burmese amber

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Abstract

The male of *Cretaconiopteryx grandis* Liu & Lu, 2017, which is the only representative species of the extinct dustywing subfamily Cretaconiopteryginae, is described for the first time from the Upper Cretaceous Burmese amber. The male genitalia, well preserved in the examined specimen, show a number of plesiomorphic characters, which support the sister group relationship between Coniopterygidae and the rest of extant lacewing families.

Key words: dustywing, Cretaconiopteryginae, genital characters, Myanmar

Introduction

Coniopterygidae (dustywings) is a distinctive family of Neuroptera characterized by the minute body-size, the waxy covering, and the reduction of wing venation. Currently, there are 571 described species around the world (Sziráki 2011; Engel 2016, 2018; Oswald 2018). The family is divided into four subfamilies, i.e. Aleuropteryginae, Coniopteryginae, Brucheiserinae, and Cretaconiopteryginae (an extinct subfamily from the Upper Cretaceous of Myanmar with only one species; Liu & Lu 2017). Coniopterygidae have been regarded as a morphologically specialized family belonging to the paraphyletic Hemerobiiformia (Aspöck *et al.* 2001; Haring & Aspöck 2004; Aspöck & Aspöck 2008; Zimmermann *et al.* 2009; Randolph *et al.* 2017), while many recent studies recovered dustywings as a sister group to remaining extant Neuroptera (Winterton *et al.* 2010, 2017; Wang *et al.* 2017).

Cretaconiopteryx grandis Liu & Lu, 2017 is an enigmatic fossil dustywing species from the Upper Cretaceous of Myanmar. This species is characterized by the rich number and configuration of crossveins, the origin of RP+MA near wing base in both fore- and hind wing, the forewing RA and RP terminally fused into a loop, and the proximally zig-zagged forewing CuP. Due to the peculiar combination of characters in *C. grandis*, a new subfamily, namely Cretaconiopteryginae, was erected based on this species. This subfamily was considered to be the basalmost lineage of all known dustywings because of the possession of some plesiomorphic characters, such as the denser cross-venation, the proximal origin of RP+MA in both fore- and hind wing, etc. (Liu & Lu 2017). However, Liu & Lu (2017) only described a female of *C. grandis*, while the male of this species has remained unknown. Here we firstly describe the male of *C. grandis* based on a well preserved specimen from the Burmese amber. A detail description of the male genitalia of this species is provided. Some characters incorrectly described in Liu & Lu (2017) are also revised based on re-examination of the holotype of this species. The present finding provides new evidence for understanding the phylogenetic position of Cretaconiopteryginae as well as Coniopterygidae.

Materials and methods

The amber specimens for this study come from the Hukwang Valley in Tanai Township, Myitkyina District of Kachin State, Myanmar (Kania *et al.* 2015: fig. 1). The age of this deposit has been investigated and dated to be

98.8±0.6 million years (the earliest Cenomanian) by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi *et al.* 2012). The male specimen of *C. grandis* is deposited in the Nanjing Institute of Geology and Palaeontology (NIPG), Chinese Academy of Sciences, Nanjing; and the holotype of this species (CAM BA-0008) is deposited in the Century Amber Museum (CAM), Shenzhen.

Photographs were taken by using a Zeiss SteREO Discovery V12 stereo microscope system and a Leica DM 2000 optical microscope with Nikon D90 digital camera. Wing drawings were prepared by Zeiss SteREO Discovery V12 stereo microscope system and genital drawings were made by Nikon SMZ745 stereoscope. The figures were prepared with Adobe Photoshop CC®.

Terminology of wing venation generally follows Aspöck *et al.* (1980). Terminology of genitalia follows Aspöck and Aspöck (2008). Abbreviations used for wing veins are as following (Abbreviations in bracket refer to the venational terms used in Withycombe (1922), Tjeder (1931, 1957), Killington (1936), Meinander (1972), etc.): A, anal vein; C, costa; Cu, cubitus; CuA (Cu1), cubitus anterior; CuP (Cu2), cubitus posterior; M, media; MA (R4+5), media anterior; MP (M), media posterior; R, radius; RA (R1), radius anterior; RP (R2+3), radius posterior; Sc (Sc), subcosta. sc-r, crossvein between Sc and R stem; sc-ra, crossvein between Sc and RA; ra-rp, crossvein between RA and RP; rp-ma, crossvein between RP and MA; r-mp, crossvein between R stem and MP; ra-rp+ma, crossvein between RA and RP+MA; rp+ma-mp, crossvein between RP+MA and MP; ma-mp, crossvein between MA and MP; mp1-mp2, crossvein between MP1 and MP2; mp-cua, crossvein between MP and CuA; mp2-cua, crossvein between MP2 and CuA; cua-cup, crossvein between CuA and CuP; cup-a1, crossvein between CuP and A1; a1-a2, crossvein between A1 and A2.

Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Coniopterygidae Burmeister, 1839

Subfamily Cretaconiopteryginae Liu & Lu, 2017

Genus *Cretaconiopteryx* Liu & Lu, 2017

Cretaconiopteryx Liu & Lu, 2017: 382. Type species: *Cretaconiopteryx grandis* Liu & Lu, 2017: 382, original designation.

Cretaconiopteryx grandis Liu & Lu, 2017

(Figs. 1–3)

Cretaconiopteryx grandis Liu & Lu, 2017: 382.

Description of male. Body (Figs. 1A, B) length 4.3 mm; integument dark brown.

Head (Fig. 1C) nearly as long as wide, with prominent compound eyes; frons well-sclerotized between antennal insertions; gena elongated; vertex slightly domed. Antenna with scape stouter and longer than pedicel and flagellomeres, about twice as long as wide; pedicel nearly as long as wide; flagellum with 30 flagellomeres, each flagellomere subcylindrical, moderately setose, nearly as long as wide, but terminal flagellomere bullet-shaped, over three times longer than wide; mouthparts chewing mandibulate; terminal maxillary palpomere elongate elliptical, much longer and broader than preceding palpomeres; terminal labial palpomere elongate elliptical, much longer and broader than preceding palpomeres.

Prothorax slightly narrower than meso- and metathorax and slightly longer than wide. Legs slender, with numerous, short setae; pro- and mesotibiae nearly equal in length to pro- and mesofemora; metatibia longer than metafemur; profemur nearly equal in length to mesofemur but shorter than metafemur; protibia also nearly equal in

length to mesotibia but shorter than metatibia; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of remaining tarsomeres; tarsomere 4 (Fig. 1D) distally expanded and flattened, marginally with a row of setae; pretarsal claws short, simple; arolium absent.

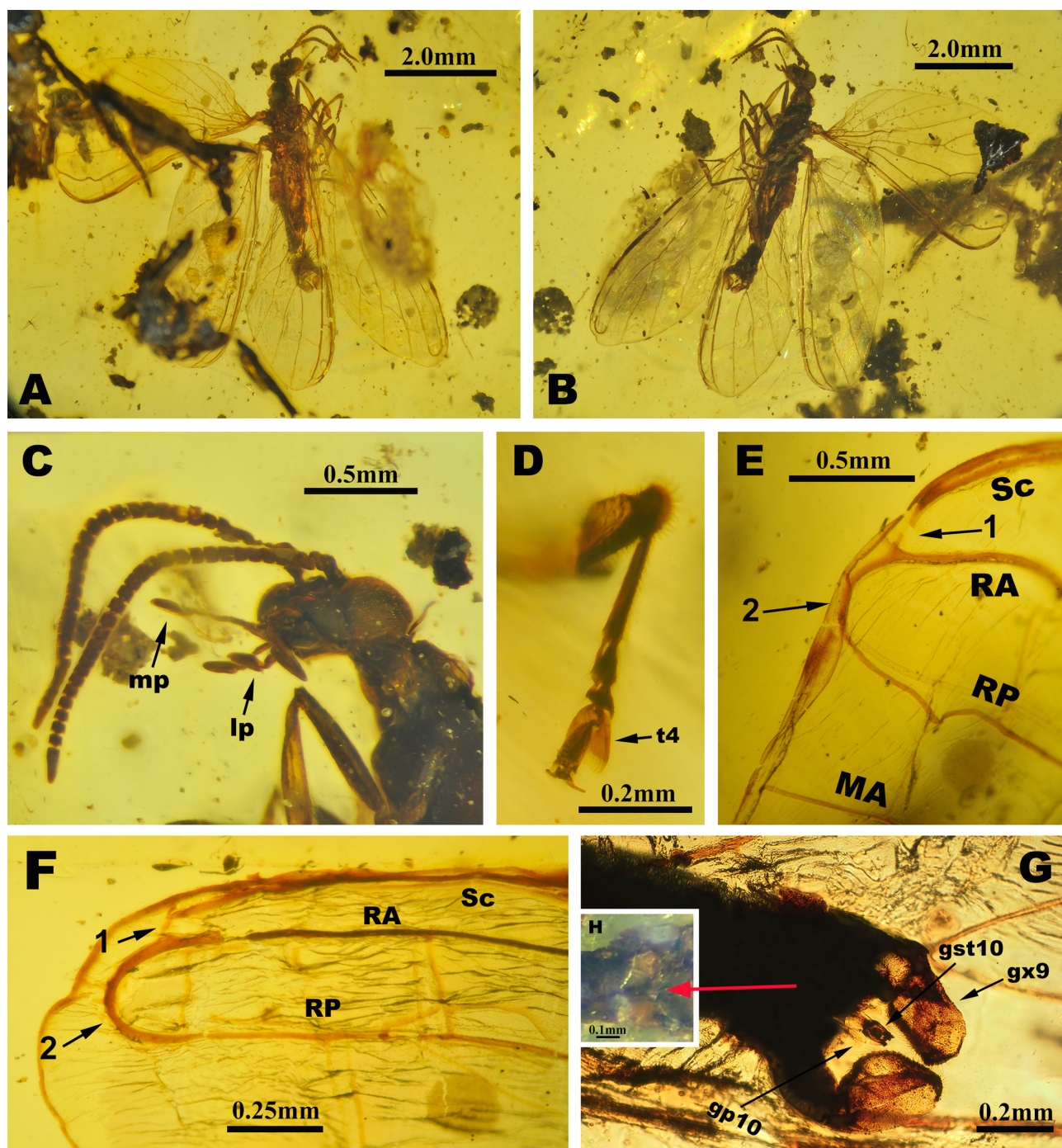


FIGURE 1. *Cretaconiapteryx grandis* Liu & Lu, male, NIGP 171206. A. Habitus photo, dorsal view; B. Habitus photo, ventral view; C. Photo of head, dorsal view; D. Photo of protarsus; E-F. Photos of apex of left (E) and right (F) forewings, arrow 1 indicates Sc terminally abruptly bending toward RA (or alternatively interpreted as connected by a crossvein with RA), arrow 2 indicates the loop formed by forewing RA and RP; G-H. Photo of genitalia, ventral view. gp: gonapophyses; gst: gonostylus; gx: gonocoxite; lp: labial palp; mp: maxillary palp; t: tarsomere.

Forewing (Figs. 1E, F, 2A, C) length 6.0 mm; membrane hyaline, slightly brownish throughout, with six distinct, ovoid, dark spots, respectively located at cell between RA and RP+MA, RP and MA, RP+MA and MP, MP1 and MP2, MP and CuA (or reaching MP slightly), CuP and A1; costal space proximally with two costal crossveins and several costal crossveins on distal half; Sc almost parallel to costal margin, terminally abruptly bending toward

RA (or alternatively interpreted as connected by a crossvein with RA); two sc-r, one sc-ra present at distal 1/4 of subcostal space; RA distally curved posteriad and connected with anteriorly curved RP forming a loop; one or two ra-rp present distad sc-ra; origin of RP+MA near wing base; RP simple, distally curved anteriorly; MA simple and curved posteriad slightly; one rp-ma present distad ra-rp; MP bifurcated at about distal 1/3; one or two r-mp, two rp+ma-mp and one ma-mp present; one mp1-mp2 present; RP/MA fork and MP1/MP2 fork generally similar in length, shape and size; stem of M nearly touching Cu; Cu fork near wing base; CuA straight and simple; CuP simple, proximally slightly protruding proximally in right forewing but not zig-zagged or protruding in left forewing (probably due to preservation condition); one mp-cua present on right forewing, absent on left forewing; one mp2-cua present on right forewing; two cua-cup present; A1 simple; three cup-a1 present; A2 with a long, distally bifurcated anterior branch and a short, strongly curved posterior branch; one a1-a2 present; distal-most crossveins among longitudinal veins from RA to A2 arrange into a gradate series; marginal setae present, and those on posterior margin much more widely spaced than those on costal margin.

Hind wing (Figs. 2B, D) length 4.2 mm, similar to forewing, while immaculate; costal space proximally with two costal crossveins and at least five costal crossveins on distal half; Sc largely parallel to costal margin, terminally abruptly bending toward RA (or alternatively interpreted as connected by a crossvein with RA); one sc-ra present; RA distally slightly curved posteriad; two ra-rp+ma and one ra-rp present; origin of RP+MA near wing base; RP simple, distally feebly curved anteriorly; MA simple, slightly curved posteriad; one rp-ma present distad ra-rp; MP bifurcated at about distal 1/3; at least one rp+ma-mp and one ma-mp present; one mp1-mp2 present; RA/MA fork and MP1/MP2 fork generally similar in shape and size, while length of former fork is slightly longer than that of latter one; Cu forked near wing base; two mp-cua and one mp2-cua present; CuA and CuP both simple and slightly curved anteriorly; four cua-cup present; A1 simple, slightly curved anteriorly; two cup-a1 present; two a1-a2 present; A2 distally bifurcated, with a short crossvein between stem of A2 and posterior margin; distal-most crossveins among longitudinal veins from RA to CuA arranged into a gradate series; marginal setae present, and those on posterior margin much more widely spaced than those on costal margin.

Abdomen (Figs. 1G, 3A, B) with plicature invisible. Genital segments largely preserved except tergum 9. Putative ectoproct unpaired, broad and rounded, slightly domed in dorsal view. Sternum 9 with short and rectangular, medially longitudinally elevated (probably not natural condition). Hypandrium glabrous, present as a posteriorly expanded, subtriangular sclerite, which is bifid posteriorly and posterolaterally bears a pair of lobes, each lobe rounded distally. Gonocoxites 9 present as a pair of large, external sclerites, which are probably connected with tergum 9 proximally; distal half of gonocoxite 9 distinctly expanded into a subquadrate lobe, medially curved, with a secondary elevated lobe with sparse setae on inner surface, distal margin densely setose. Putative gonapophyses 10 [= parameres in Meinander (1972)] at least with posterior part paired, slender, laterally curved, and slightly inflated into an obtuse tip. Putative gonostyli 10 (= penis) present as a long, narrow sclerite, slightly narrowed posteriad; apex modified into an ovoid structure, with a pair of tiny subquadrate processes at tip and a hole in dorsal view, laterally with slightly sclerotized expansion and internally with paired slender rods.

Material examined. Holotype, CAM BA-0008, female, it is polished in the form of a nearly elliptical transparent cabochon, with length×width about 10.2×8.0 mm, height about 5.3 mm, Lowermost Cenomanian, Tanai Village, Hukawng Valley, northern Myanmar. NIGP 171206, amber piece with a complete male adult and a psocid, a beetle, a cockroach, a caddisfly, four aphids, a spider, and a scorpion. It is polished in the form of ovoid cabochon, transparent, with length×width about 37.52×22.01 mm, height about 6.30 mm, Lowermost Cenomanian, Tanai Village, Hukawng Valley, northern Myanmar.

Discussion

The male dustywing herein described is placed in *Cretaconiopteryx* based on the following characters: 1) the relatively large body size; 2) the tarsomere 4 distally expanded and flattened, marginally with a row of setae; 3) the number and configuration of crossveins; 4) the origin of RP+MA near wing base both in fore- and hind wing; 5) the forewing RA and RP terminally fused into a loop; 6) the same branching condition of forewing A2; 7) Sc terminally abruptly bends toward RA (or alternatively interprets as connected by a crossvein with RA) both in fore- and hind wing [only mentioned in hind wing in Liu & Lu (2017)]. Moreover, we identified this male as *C. grandis* based on the similar position of six distinct ovoid dark spots in the forewing; However, there are also some subtle differences

between male and female of this species except their genitalia. For example, in the male of *C. grandis*, the body size is slightly smaller than female (forewing length 6.0 mm in male but 6.7 mm in female); the antenna is 32-segmented while 39-segmented in female [incorrectly described as 27-segmented in Liu & Lu (2017)]; the terminal flagellomere is over three times as long as wide but twice as long as wide in female; a small dark spot at distal cell between forewing RP+MA and MP is absent, but present in female; CuP is not zig-zagged on forewing as in the female but only protruding proximally in right forewing, which may be a deformation caused by the amber preservation.

Based on the comparison between male and female of *C. grandis*, all characters distinguished from the other three dustywing subfamilies (proposed in Liu & Lu 2017) are obvious and stable. In particular, the peculiar configuration of forewing RA and RP that are terminally fused into a loop is a normal feature of *C. grandis* but not caused by the preserved condition of the amber. Nevertheless, there is a variation of the number of forewing ra-rp crossvein in the male of *C. grandis*—right forewing of the examined male has only one ra-rp as the same as female but two in left forewing (Fig. 1F, 2C). Such crossvein variation is common in Neuroptera.

The male genitalia of *C. grandis* is significant for understanding the phylogenetic position of Cretaconiopteryginae as well as Coniopterygidae. The general configuration of the male genitalia of *C. grandis* is similar to some species of *Helicoconis* Enderlein, 1905 (Aleuropteryginae), such as *H. (Ohmopteryx) pseudolutea* Ohm, 1965 and *H. (Fontenellea) hispanica* Ohm, 1965 in having similar relatively small hypandrium, a pair of slender and elongate gonapophyses 10, and elongate gonostyli 10. Liu & Lu (2017) mentioned that *Cretaconiopteryx* shares more character states with Aleuropteryginae. Thus, morphological similarity of the male genitalia between *Cretaconiopteryx* and Aleuropteryginae further suggests possible close relationship between Cretaconiopteryginae and Aleuropteryginae.

The major difference from male genitalia between *C. grandis* and all the other dustywing species except *Spiloconis eominuta* Grimaldi *et al.*, 2013 (Aleuropteryginae) refers to the large external gonocoxites 9. In some genera of Aleuropteryginae (e.g. *Aleuropteryx* Low, 1885; see Aspöck & Aspöck 2008: fig. 25), the male gonocoxites, gonapophyses and gonostyli 9 form an internal structure associated with gonocoxites 11 (gonarcus), while in some other genera of Aleuropteryginae (e.g. *H. lutea* Wallengren, 1871; see Meinander 1972: figs. 64D, G) as well as all known extant genera of Coniopteryginae and Brucheiserinae, the male gonocoxites 9 are present as a pair of external sclerites, connected with ectoproct (Aspöck & Aspöck 2008: p. 106, figs. 26-30; Sziráki 2007). However, in the aforementioned dustywing groups with external male gonocoxites 9, these sclerites are small and appendage-like. The gonocoxites 9 of extant species of *Spiloconis* Enderlein, 1907 are fused with gonocoxites 11 (gonarcus) and usually contracted inside the genital chamber, e.g. *S. notata* Navás, 1926, or disappear, e.g. in *S. sexguttata* Enderlein, 1907 (see Meinander 1972: fig. 79A, B, C; fig. 81B, C). Interestingly, the fossil species *S. eominuta* from the Eocene Cambay amber possesses paired large external gonocoxites 9 similar to that in *C. grandis*, which is not surprising because this character state is plesiomorphic and could be present in some fossil or primitive species. Besides, *S. eominuta* may represent a different genus due to the great differences of the genital characters in comparison to the extant species of *Spiloconis*. Additionally, the male gonocoxites 9 of *C. grandis* and *S. eominuta* are similar to Raphidioptera and basal groups of Neuroptera, i.e. Nevrothidae, Sisyridae and Osmylidae [Aspöck & Aspöck 2008: p. 103-104, figs. 3-6 (Raphidioptera); figs. 7-15 (Megaloptera); figs. 16-20 (Nevrothidae); figs. 21, 22 (Sisyridae); figs. 23, 24 (Osmylidae)], being a pair of large external sclerites. Aspöck & Aspöck (2008) considered this character state to be plesiomorphic. In recent phylogenetic studies of Neuroptera (Wang *et al.* 2017; Winterton *et al.* 2017) the lacewing families with distinct external male gonocoxites 9 (i.e. Nevrothidae, Sisyridae and Osmylidae) are recovered to be the sister group of the other extant families except Coniopterygidae which is recovered to be the sister group of all the other extant lacewing families. However, the genital characters of Coniopterygidae in most species are generally highly specialized, and no characters from the genitalia have yet been found to support the basal-most position of this family (i.e. the sister group between Coniopterygidae and all the other extant lacewing families). Therefore, the external male gonocoxites 9 in *C. grandis* might provide further evidence to support the recent recovery of the phylogenetic position of Coniopterygidae. Nevertheless, it should be mentioned that similar external male gonocoxites 9 are also present in some recently described Burmese amber Kalligrammatidae (Liu *et al.* 2018), which belongs to Psychopsoidea (one of the crown groups of Neuroptera). Whether the external male gonocoxites 9 are widely developed in ancient lacewings could be an interesting question for future investigation.

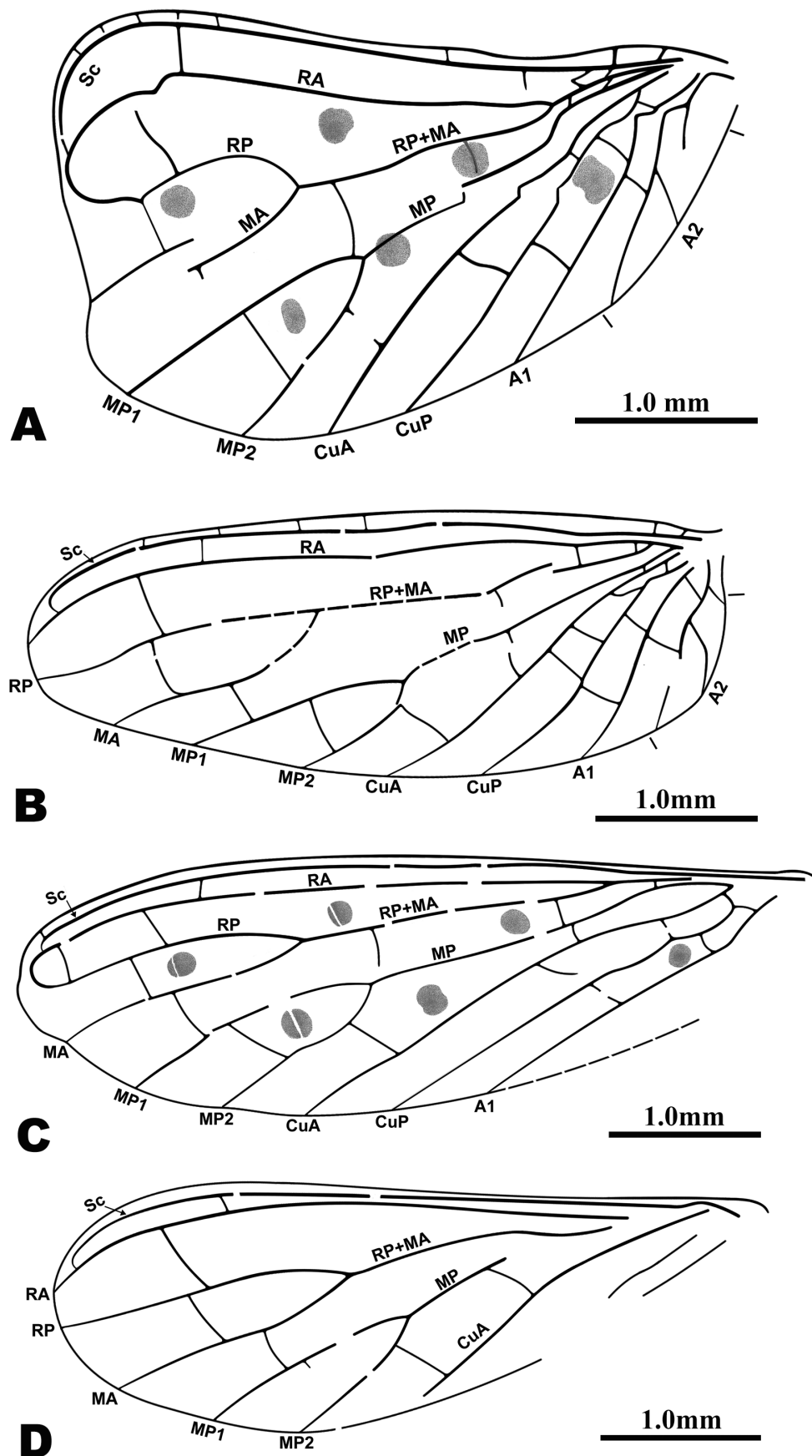


FIGURE 2. Drawings of fore- and hind wings of *Cretaconiopteryx grandis* Liu & Lu, male, NIGP 171206. A. Left forewing; B. Left hind wing; C. Right forewing; D. Right hind wing.

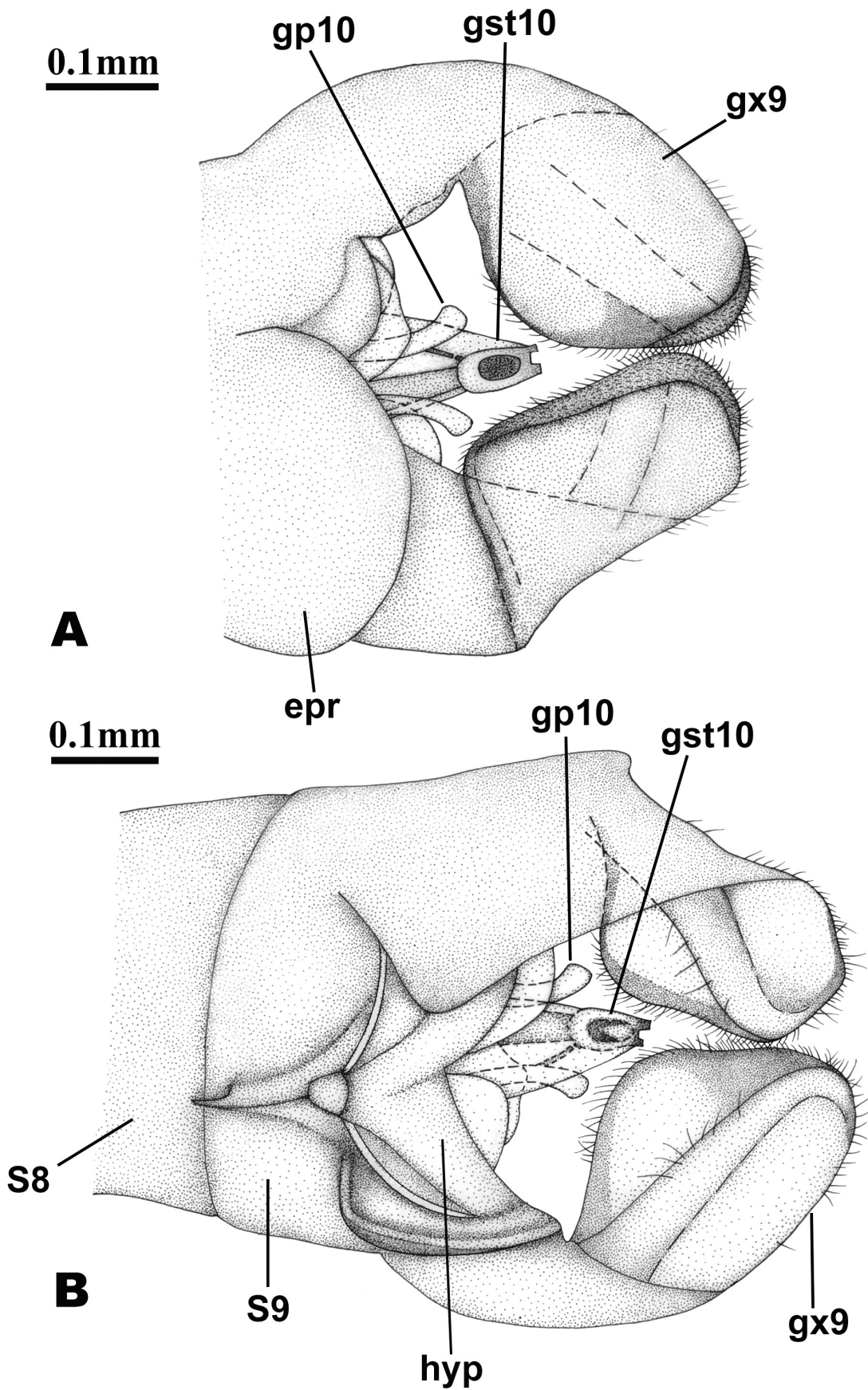


FIGURE 3. *Cretaconiapteryx grandis* Liu & Lu, male, NIGP 171206. A. Drawing of genitalia, dorsal view; B. Drawing of genitalia, ventral view. T: tergum; S: sternum; epr: ectoproct; gp: gonapophyses; gst: gonostyli; gx: gonocoxites; hyp: hypandrium.

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