

Short communication

A new genus and species of Prosopistomatidae (Insecta: Ephemeroptera) from mid-Cretaceous Myanmar amber

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ABSTRACT

A new genus and species, *Proximicorneus rectivenius* gen. et sp. nov., in the family Prosopistomatidae of Ephemeroptera, is described from the mid-Cretaceous Myanmar (Burmese) amber. The new taxon is established primarily based on the following characters: Forewing Rs veins branched two times and AA vein situated almost at the tornus, legs well-developed with normal femur, tibia and 3-segmented tarsus, claws with one acute and hooked, the other blunt and straight, paracercus short and cerci multi-segmented. The new amber mayfly is the only and the earliest fossil record of Prosopistomatidae hitherto, dating back to the mid-Cretaceous and indicating the long-term presence of Prosopistomatidae in the Oriental region. This finding not only broadens the diversity of Prosopistomatidae, but also provides important morphological characters to enhance our understanding of the early evolutionary development of the Prosopistomatidae.

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1. Introduction

Ephemeroptera are a rather small insect order, comprising over 3124 described extant species in 42 families (Zhang, 2013) and over 218 extinct species in 40 families (including 20 extinct families) (Huang et al., 2007a). All of extant and most extinct mayflies belong to suborder Euplectoptera Kluge, 2000. Most of them are attributed to infraorder Anteriotorna Kluge, 1993, and others in infraorder Posteritorna Kluge, Studemann, Landolt & Gonser, 1995, based on their tornus of forewing situated behind CuP vein. Posteritorna are divided into two families, Prosopistomatidae and Baetiscidae (Kluge, 2004).

Prosopistomatidae, comprising 36 extant species in the genus *Prosopistoma* Latrielle, 1833 and distributed in Palaearctic, Oriental, Australian and Afrotropical, are rarely studied (Barber-James, 2009; Barber-James & de Moor, 2016). Most species are known by nymphs and only five species are recorded by winged imagoes, *P. pennigerum* Müller, 1785 (= *P. foliaceum* Foutcroy, 1785) recorded in male subimago and imago (Degrange, 1955; Fontaine, 1955) and female subimago (Vayssi re, 1881a, b), *P. africanum* Gillies, 1954 recorded in male and female all winged stages (Gillies, 1954,

1956), *P. pearsonorum* Campbell & Hubbard, 1998 recorded only in female subimago (Campbell & Hubbard, 1998), *P. mcaffertyi* Barber-James, 2010 recorded only in female subimago (Barber-James, 2010a) and *P. variegatum* Latreille, 1833 recorded in male and female all winged stages (Barber-James, 2010b). Female subimagoes appear to be sexually mature and do not turn into imagoes, while males are mature in imago stage (Barber-James, 2010a). What's more, mayflies of this family have sexual dimorphism in winged stage: male subimagoes and imagoes have two long intercalaries present by the sides of each long longitudinal vein forming fan-form radiating veins and several intercalaries present behind AA vein, while these intercalaries are absent in female subimagoes; long antenna with strongly enlarged pedicel in male subimagoes and imagoes while less expressed in female subimagoes (Gillies, 1954; Barber-James, 2010a, b).

Up to date, there are no firm fossil species described in Prosopistomatidae. Sinitshenkova assigned *Myanmarella rossi*, a mid-Cretaceous Myanmar amber, to Prosopistomatidae in 2000 (Sinitshenkova, 2000). Later in 2004, Kluge attributed this species to Baetidae (Kluge, 2004).

Mayflies might have higher diversity during the Mesozoic comparing to other fossil periods (Huang et al., 2007b, 2008). There are 40 families, 124 genera and 218 fossil species recorded worldwide till 2007, while 30 families, 75 genera and 127 fossil species recorded in the Mesozoic (Huang et al., 2007a). However, only three

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mayflies have been recorded in Myanmar (Burmese) amber hitherto, *Myanmarella rossi* (Sinitshenkova, 2000), *Nanophemera myanmarensis* in Australiphemeridae (McCafferty & Santiago-Blay, 2008) and *Vetuformosa buckleyi* in Baetidae (Poinar, 2011).

Here, we describe a female subimago mayfly from the mid-Cretaceous Myanmar amber. This new species is the first and the earliest fossil record of Prosopistomatidae hitherto, providing more evidence of basal morphological characters of this family.

2. Materials and methods

The amber specimen studied in this paper was collected from Kachin (Hukawng Valley) of northern Myanmar, approximately 15 km southwest of the Village of Tanai (Cruickshank & Ko, 2003; Shi et al., 2012). The diversity of insects in Myanmar amber is very high. There are 29 orders, 184 families and 198 species of insect are known till 2010 (Ross et al., 2010). Recently, more and more insects are found in Myanmar amber, e.g. damselflies (Zheng et al., 2017), earwigs (Ren et al., 2017), stick insects (Engel et al., 2016; Chen et al., 2017) and moths (Zhang et al., 2017a). What's more, the amber insects also provide important characters to confirm the phylogenetic position (Prokop et al., 2017; Zhang et al., 2017b).

The amber-bearing deposit is dated as the earliest Cenomanian (98.79 ± 0.62 Ma) by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Cruickshank & Ko, 2003; Shi et al., 2012). Myanmar amber displays clear traces of redeposition and so it can be older than its enclosing rocks, e.g., could be of mid-Cretaceous age (Ross, 2015).

The mayfly was discovered in an orange–red flaky amber. The piece is 27 mm long and 14 mm at its maximum width. The mayfly is positioned almost at the upper edge, and far away from the lower surface. The maximum depth of the specimen area is 1 mm. Thus, dorsal view of mayfly is clear (Fig. 1A) but obscure at the ventral view (Fig. 2A). The specimen is deposited in the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). The specimen was examined under a Leica M205C dissecting microscope. Photographs were taken using a Nikon SMZ 25 microscope with a Nikon DS-Ri 2 digital camera system. Line drawings were prepared by using Adobe Illustrator CC and Adobe Photoshop CC graphics software.

In the text, higher rank group names use the Kluge classification (Kluge, 2004). Descriptive terminology, excluding wing venation, generally follows that presented by Kluge (2004). Wing venation follows the nomenclature of Tillyard (1932).

3. Systematic palaeontology

Order Ephemeroptera Latreille, 1810

Infraorder Posteritorna Kluge, Studemann, Landolt & Gonser, 1995

Superfamily Prosopistomatoidea Edmunds & Traver, 1954

Family Prosopistomatidae Lameere, 1917

Genus *Proxemicorneus* Lin, Shih & Ren gen. nov.

(Figs. 1–3)

Type species: *Proxemicorneus rectivenius* sp. nov.

Etymology. The new generic name is a combination of the Latin prefix “proxim-”, meaning “next to” and “corneus”, meaning “horn”. The name refers to AA vein situated at tornus in the forewing. The gender is masculine.

Diagnosis. Female subimago. Antenna well-developed, pedicel significantly elongated and expanded basally. Wing venation reduced. Subcostal area small, Sc situated closely to R₁ with two overlapped areas. The base of forewing thickened and Sc and R₁ veins forming a loop shape at the base. Rs veins branched two

times, R_{3b} contacting with R₂ together with R₄₊₅. All longitudinal veins behind Rs veins simple and detached. Crossveins, iMA and MA₂ completely absent. Single anal vein AA situated at almost tornus. Posterior margin fringed with long setae basally and short setae distally. Legs well-developed with normal femur, tibia and 3-segmented tarsus. One claw acute and hooked, another straight and blunt. Abdomen pisciform-shaped, abdomen segments broadened from segment I to segment III but tapered after. Cerci clearly multi-segmented with long irregular setae. Paracercus short, not segmented and without setae.

Remarks. The specimen is identified as subimago for its posterior margin of forewings fringed with long setae and wing surface fulfilled with granular tubercles which is distinguishing feature for subimago (Edmunds & McCafferty, 1988). Because of the sexual dimorphism, here we only compare differences between recorded female and the new taxon. The new genus is distinguished from female *Prosopistoma* (Vayssière, 1881a, b; Gillies, 1954, 1956; Campbell & Hubbard, 1998; Barber-James, 2010a, 2010b) for having long antenna with significantly expanded pedicel and elongated pedicel and flagellum (vs. antenna in the same shape with shorter pedicel and flagellum); Rs veins branched two times, R_{3b} contacting with R₂ together with R₄₊₅ (vs. Rs veins branched only one time, R_{3b} contacting with R₂); AA vein of forewings situated almost at the tornus (vs. AA vein situated behind tornus); legs well-developed, with normal femur, tibia and 3-segmented tarsus; claws with one hooked and the other blunt (vs. legs reduced in great degree, tibia and tarsus fused to form an indefinite remnant but no more than 2-segmented tarsus, in *P. variegatum* and *P. mcaffertyi* without distinct segmented tarsus, with only one blunt claw or two claws both hooked); paracercus short (vs. paracercus well-developed and subequal to cerci) and cerci multi-segmented (vs. cerci have no distinct segmentation).

The loop shape formed by Sc and R₁ at the base and R_{3b} contact with R₂ forming a triad, AA vein situated almost at the tornus, legs well developed with 3-segmented tarsus, paracercus short, not segmented and without setae are all unique characters in the new taxon.

Proxemicorneus rectivenius Lin, Shih & Ren gen. et sp. nov.

(Figs. 1–3)

Etymology. The specific name is from a Latin word “rectivenius”, meaning “rectinerved”, referring to the simple and almost straight longitudinal veins of the wings.

Type material. Holotype: Female subimago. No. CNU-EPH-MA2017001. An almost complete specimen.

Diagnosis. As for the genus.

Description. Female subimago. Medium sized. Compound eyes widely separated but poorly preserved. Antenna well-developed, scape small, pedicel bottle-shaped and greatly elongated, broadened basally, slightly tapering to meet thread-like flagellum (Fig. 2B). Mouthparts vestigial, only clypeus prominent from below, rounded and disc-like (Fig. 2B).

Because of the poor preservation, pronotum, mesonotum and metanotum lost, only the shape of scutellum preserved. Prothorax small, mesothorax larger and metathorax the largest. Foreleg length 1.41 mm, middle leg length 1.53 mm, hind leg length 1.83 mm (Fig. 2C–F).

Forewing length 3.9 mm, width 2.0 mm at the widest point; hind wing length 1.5 mm. Forewings and hind wings partly folded as preserved. The wing venation of forewings and hind wings reduced. The wing surface fulfilled with granular tubercles. Sc and

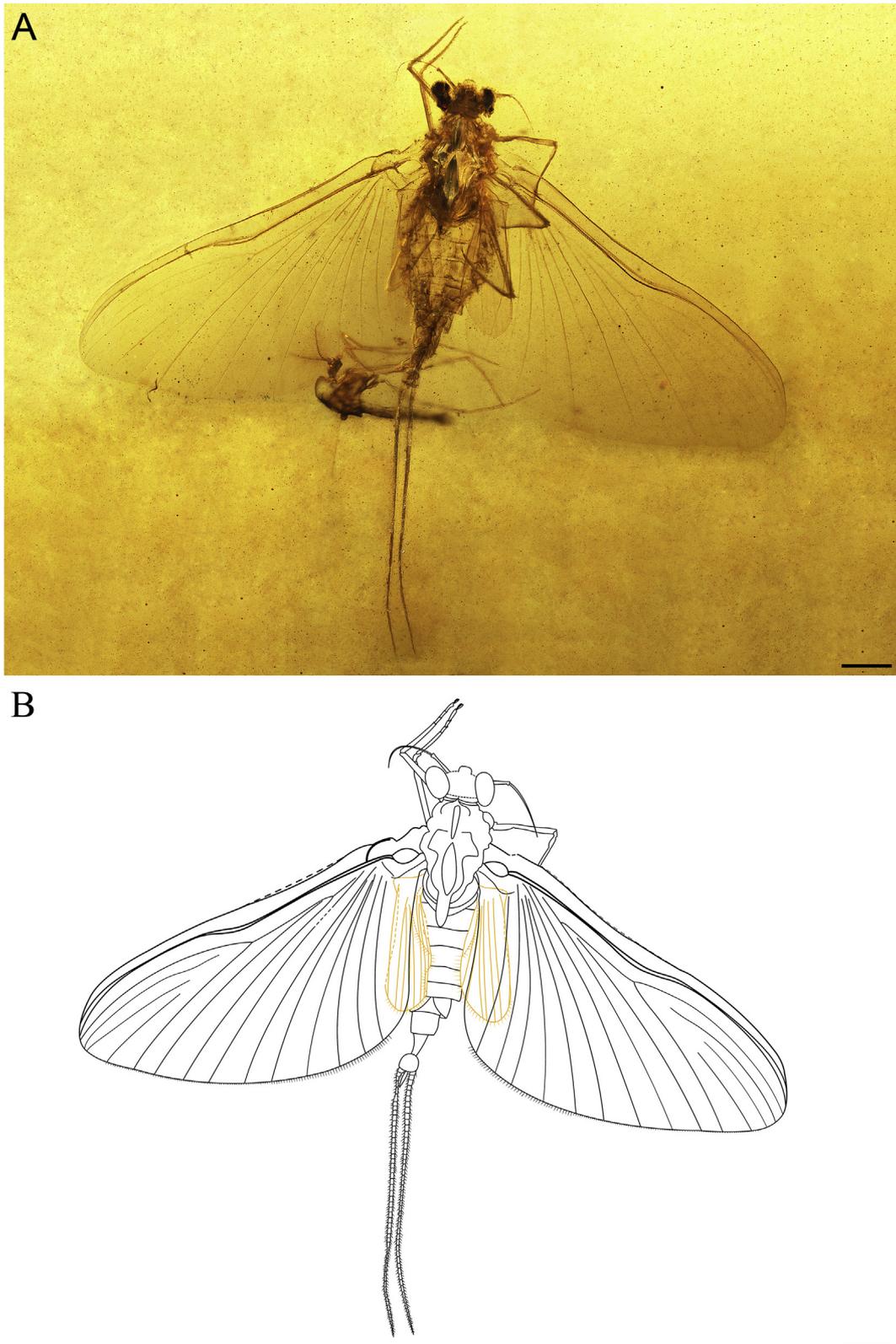


Fig. 1. *Proximicorneus rectivenius* gen. et sp. nov. Holotype CNU-EPH-MA2017001. A, Photograph of habitus in dorsal view. B, Line drawing of dorsal view (Scale bars = 0.5 mm).

R_1 arising from the wing base, thickened and overlapping in basal and distal parts. R_s veins branched two times, R_2 contacting with R_{3b} together with R_{4+5} . R_3 detached with R_{3b} . All longitudinal veins behind R_s veins simple and detached. The intercalary vein iMP also arising from the wing base, just as long as the longitudinal veins.

CuP vein situated before the tornus apex. The posterior margin of forewings fringed with two kinds of setae in length, the distal part short but basal part long (Fig. 3A, B). The posterior margin of hind wing fringed with longer setae than those in forewings. Intercalary veins absent in hind wings (Fig. 3C).

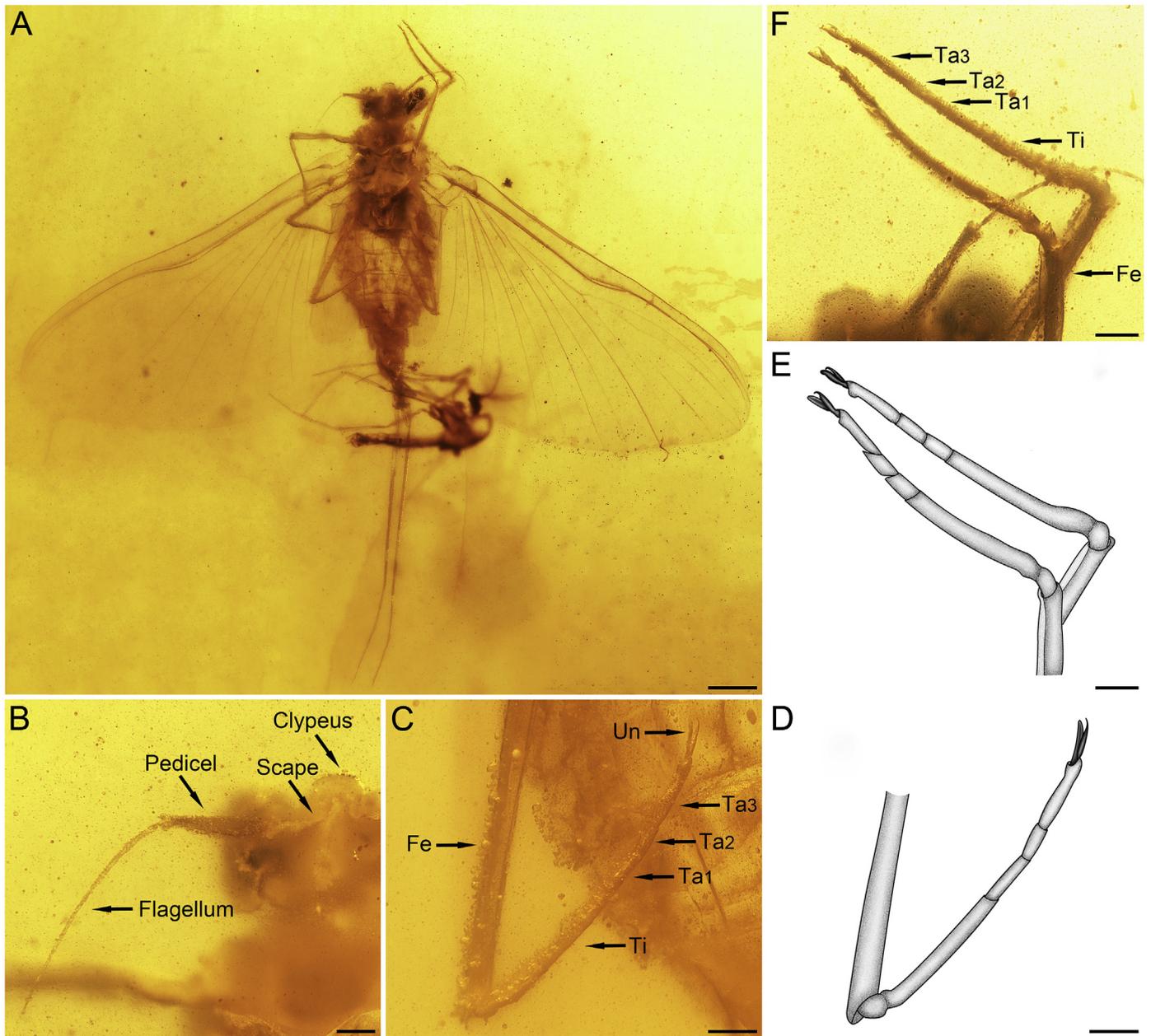


Fig. 2. *Proximicorneus rectivenius* gen. et sp. nov. Holotype CNU-EPH-MA2017001. A, Photograph of habitus in ventral view. B, Antenna and labrum. C, Hind leg. D, Line drawing of hind leg. E, Line drawing of fore leg and middle leg. F, Fore leg and middle leg. Ta1-Ta3: Tarsus I–III; Ti: Tibia; Fe: Femur; Un: Claw (Scale bar for A = 0.5 mm, scale bars for B to F = 0.1 mm).

Abdomen length 2.3 mm (excluding long cerci), short, pisciform-shaped. First segment covered by metathorax (Fig. 1). Segment III the widest, the segment I slightly wider than the segment VI. Segments VII–IX with postero-lateral margins produced to form tergal spurs. Segments VIII and IX produced posteriorly. Cerci length 2.8 mm, paracercus 0.2 mm in length, almost one fourteenth of cerci.

4. Discussion

In this paper, we described a new genus and species of the Prosopistomatidae from Myanmar amber. Because of CuP vein situated before tornus, the specimen is attributed to the infraorder

Posteritorna which only include two families: Baetiscidae and Prosopistomatidae. The new genus can be placed easily within Prosopistomatidae for its autapomorphies: elongated and basally expanded pedicel; unique wing venation, crossveins and intercalary veins absent in both forewing and hind wing, iMA and MA₂ of forewing completely absent in female (Fig. 3A–B). Owing to the well-preserved characters, the new taxon provides a better understanding of morphological characters of the family. It shares some characters with female *Prosopistoma*: venation reduced in both forewing and hind wing, AA vein unbranched and nearly parallel to MP₂; all longitudinal veins simple and arising from the wing base (Fig. 3A–B) and legs partially atrophied and reduced in great degree (Fig. 2C–F). However, the new genus is differentiated

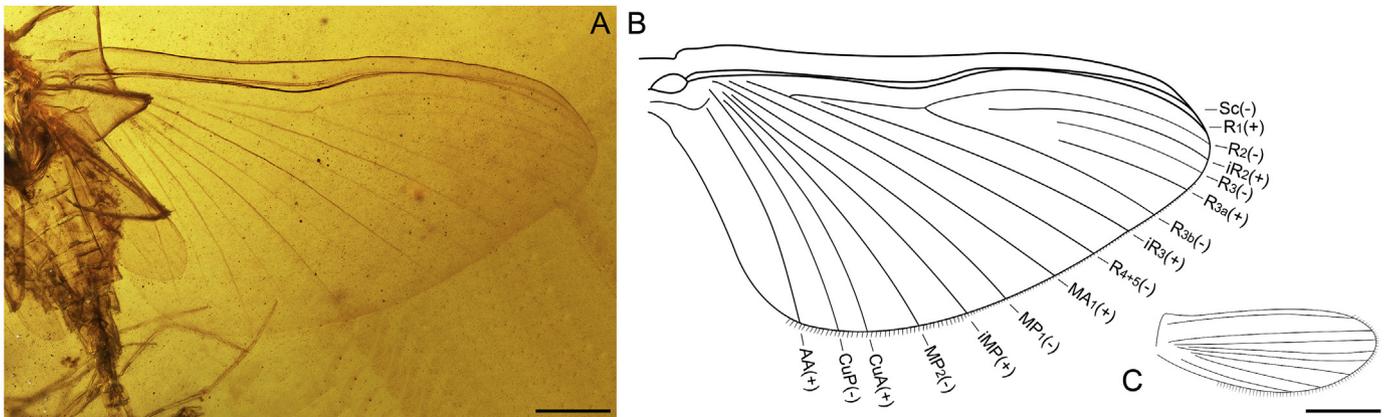


Fig. 3. *Proximicorneus rectivenius* gen. et sp. nov. Holotype CNU-EPH-MA2017001. A, Photograph of forewing and hind wing. B, Forewing reconstruction. C, Hind wing reconstruction (Scale bars = 0.5 mm).

from *Prosopistoma* based on: significantly expanded pedicel and elongated pedicel and flagellum (Fig. 2B); Rs system branched two times, R_{3b} contacting with R_2 together with R_{4+5} , AA vein situated almost at the tornus (Fig. 3A–B); legs well-developed, with normal femur, tibia and 3-segmented tarsus (Fig. 2C–F) and paracercus short and cerci multi-segmented (Fig. 1).

The legs of extant taxa in Prosopistomatidae are partly atrophied as tibia and tarsus fused to form an indefinite remnant. The tarsus of male is consisted of two tarsi while the 1st segment fused with tibia, and female legs are degraded in greater degree. Only forelegs of male subimago and imago are functional to help mating, while middle and hind legs are non-functional. Legs of female subimago are all non-functional. Male subimago has a pair of hooked claws but the claws of male imago are bulbous in the terminal, preceded by a small thumb-like apophysis (Gillies, 1954, 1956; Barber-James, 2010a, 2010b). However, the legs of *Proximicorneus rectivenius* gen. et sp. nov. are well-developed with normal femur, tibia and 3-segmented tarsus, claws with one blunt and the other hooked. It is suggested that the legs of female mayflies might have been functional in the Mesozoic, but degraded since then.

5. Conclusion

The new mayfly, *Proximicorneus rectivenius* gen. et sp. nov., from the mid-Cretaceous Myanmar amber is documented. To date, this is the only and the earliest prosopistomatid fossil record, dating the family back to the mid-Cretaceous and indicating the long-term presence of Prosopistomatidae in the Oriental Region. Furthermore, the new genus and species provides new evidence to enhance our understanding of the early evolutionary development of important morphological characters, e.g. female legs, in Prosopistomatidae. Most characters between *Prosopistoma* and *Proximicorneus* gen. nov. are in common, so it is postulated that the new mayfly may have the basal ground pattern of Prosopistomatidae.

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References

- Barber-James, H.M., 2009. A preliminary phylogeny of Prosopistomatidae (Ephemeroptera) based on morphological characters of the larvae, and an assessment of their distribution. *Aquatic Insects* 31 (1), 149–166.
- Barber-James, H.M., 2010a. Two new species of Prosopistomatidae (Ephemeroptera) from South Africa and Swaziland. *African Entomology* 18 (1), 147–165.
- Barber-James, H.M., 2010b. Neotype erection, redescription of the larva and first description of the winged stages of *Prosopistoma variegatum* Latreille, 1833 (Insecta: Ephemeroptera) from Madagascar. *Aquatic Insects* 32 (3), 215–243.
- Barber-James, H.M., de Moor, F.C., 2016. Mating behaviour and life history of the Prosopistomatidae (Ephemeroptera) derived from studies of morphology. In: Proceedings of the Joint XIII International Conference on Ephemeroptera, XVII International Symposium on Plecoptera, At Biology of Inland Waters, vol. 3, pp. 13–31.
- Campbell, I.C., Hubbard, M.D., 1998. A new species of *Prosopistoma* (Ephemeroptera: Prosopistomatidae) from Australia. *Aquatic Insects* 20 (3), 141–148.
- Chen, S., Zhang, W.W., Shih, C.K., Ren, D., 2017. Two new species of Archipseudophamatidae (Insecta: Phasmatodea) from Upper Cretaceous Myanmar amber. *Cretaceous Research* 73, 65–70.
- Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Science* 21 (5), 441–455.
- Degrange, C., 1955. Sur la morphologie de *Prosopistoma foliaceum* Fourc. *Comptes rendus des séances de l'Académie des Sciences* 240, 1668–1669.
- Edmunds, G.F., McCafferty, W.P., 1988. The mayfly subimago. *Annual Review of Entomology* 33 (33), 509–529.
- Engel, M.S., Wang, B., Alqarni, A.S., 2016. A thorny, 'anareolate' stick-insect (Phasmatidae s.l.) in Upper Cretaceous amber from Myanmar, with remarks on diversification times among Phasmatodea. *Cretaceous Research* 63, 45–53.
- Fontaine, J., 1955. Les formes ailées de *Prosopistoma foliaceum* Fourcroy (Epheméroptère). *Bulletin Mensuel de la Société Linnéenne de Lyon* 24, 60–65.
- Gillies, M.T., 1954. The adult stages of *Prosopistoma* Latreille (Ephemeroptera), with descriptions of two new species from Africa. *Transactions of the Royal Entomological Society of London* 105, 355–372.
- Gillies, M.T., 1956. A supplementary note on *Prosopistoma* Latreille (Ephemeroptera). *Proceedings of the Royal Entomological Society of London* 31, 165–166.
- Huang, J.D., Ren, D., Sun, J.H., 2007a. Progress in the study of Ephemeroptera (Mayfly) fossils. *Acta Zootaxonomica Sinica* 32 (2), 391–404 (In Chinese with English abstract).
- Huang, J.D., Ren, D., Sinitshenkova, N.D., Shih, C.K., 2007b. New genus and species of Hexagenitidae (Insecta: Ephemeroptera) from Yixian Formation, China. *Zootaxa* 1629, 39–50.
- Huang, J.D., Ren, D., Sinitshenkova, N.D., Shih, C.K., 2008. New fossil mayflies (Insecta: Ephemeroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *Insect Science* 15, 193–198.
- Kluge, N., 2004. *The Phylogenetic System of Ephemeroptera*. Springer Netherlands 61–68.
- McCafferty, W.P., Santiago-Blay, J.A., 2008. A new Cretaceous mayfly from Burmese amber (Ephemeroptera: Australiphemeridae). *Entomological News* 119 (5), 492–496.
- Poinar, G., 2011. *Vetuformosa buckleyi* n. gen., n. sp. (Ephemeroptera: Baetidae; Vetuformosinae n. subfam.), a new subfamily of mayflies in Early Cretaceous Burmese amber. *Historical Biology* 23 (4), 369–374.
- Prokop, J., Pecharová, M., Garrouste, R., Beattie, R., Chintauanmarquier, I.C., Nel, A., 2017. Redefining the extinct orders Miomoptera and Hypoperlida as stem acercarian insects. *BMC Evolutionary Biology* 17 (205), 1–20.
- Ren, M.Y., Zhang, W.T., Shih, C.K., Ren, D., 2017. A new earwig (Dermaptera: Pygidicranidae) from the Upper Cretaceous Myanmar amber. *Cretaceous Research* 74, 137–141.

- Ross, A., 2015. Insects in Burmese amber. In: Schmitt, T., Blank, S.M., Kohler, A., Kramp, K., Weyer, J. (Eds.), *Entomologentagung 02.–05.03.2015 Frankfurt/M. Programm und Abstracts, Frankfurt/Main (2015)*, p. 72.
- Ross, A., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, UK, pp. 208–235.
- Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L., Li, X.H., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Sinitshenkova, N.D., 2000. The first fossil prosopistomatid mayfly from Burmese amber (Ephemeroptera; Prosopistomatidae). *Bulletin of the Natural History Museum, London (Geology)* 56 (1), 25–28.
- Vayssière, A., 1881a. Etude sur l'état parfait du *Prospistoma punctifrons*. *Annales des Sciences Naturelles Series 6* (11), 1–15 (in French).
- Vayssière, A., 1881b. On the perfect state of *Prospistoma punctifrons*. *Annals of Natural History* 5, 73–85 (Translated by W.S. Dallas).
- Zhang, W.T., Wang, J.J., Shih, C.K., Ren, D., 2017a. Cretaceous moths (Lepidoptera: Micropterigidae) with scales from Myanmar amber. *Cretaceous Research* 78, 166–173. <https://doi.org/10.1016/j.cretres.2017.06.016>.
- Zhang, W.T., Li, H., Shih, C.K., Zhang, A.B., Ren, D., 2017b. Phylogenetic analyses with four new Cretaceous bristletails reveal inter-relationships of Archaeognatha and Gondwana origin of Meinertellidae. *Cladistics* 1–23. <https://doi.org/10.1111/cla.12212>.
- Zhang, Z.Q., 2013. Phylum Athropoda. In: Zhang, Z.Q. (Ed.), *Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013)*. *Zootaxa*, 3703, pp. 017–026.
- Zheng, D.R., Nel, A., Jarzembowski, E.A., Chang, S.C., Zhang, H.C., Xia, F.Y., Liu, H.Y., Wang, B., 2017. Extreme adaptations for probable visual courtship behaviour in a Cretaceous dancing damselfly. *Scientific Reports* 7, 1–8. <https://doi.org/10.1038/srep44932>.