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Caddisflies with unusual hair-fans on the legs in Cretaceous Burmese amber (Insecta, Trichoptera)

WILFRIED WICHARD, MARIANNE ESPELAND & BO WANG

Abstract

We describe two caddisflies from mid-Cretaceous Burmese amber, with unusual hair fan modifications on the legs: *Cretaganonema dongi* nov. gen. et nov. sp. (Calamoceratidae) possesses greatly elongated hind legs with hair-tufts at the tarsal apex; *Cretahelicopsyche liuyani* nov. gen. et nov. sp. (Helicopsychidae) bears a hair-fan on the tibia of the middle legs. The functions of the leg modifications in the fossils are unknown, possibilities are briefly discussed. The species described here represent the third known calamoceratid and the first helicopsychid from the Cretaceous, thus increasing our scant knowledge on the Cretaceous Trichoptera biota and their adaptations.

K e y w o r d s: Calamoceratidae, Helicopsychidae, tarsal hair-tuft, tibial hair-fan, Cretaceous, Burmese amber.

1. Introduction

Legs of adult caddisflies are often densely setose; most species are covered with irregular hair coats, and often with numerous fine spines in rows along the femur, tibia and/or tarsus. Furthermore, all Trichoptera possess larger, movable spurs placed at the apex (apical spurs) and in the middle (preapical spurs) of the tibia. The variable "tibial spur formulae" consisting of the numbers of pre- and apical spurs of pre-, mid- and hindlegs are often important characteristics of genus and family classifications.

In this paper we present and describe two Cretaceous trichopteran species with remarkable hair-coat modifications of the legs, hitherto never seen in extant or fossil caddisflies. We briefly discuss the possible functions. We also propose the affiliations of the extinct species to extant families, although not all family characteristics are visible and substantiated on the fossil species embedded in amber.

2. Materials and methods

Burmese amber material was collected by local people in several districts of northern Myanmar, but most material comes from the amber mine located near Noije Bum Village, Tanaing Town (Kania et al. 2015: fig. 1; Jarzembowski et al. 2017: fig. S1). The age provided by U-Pb dating of zircons from the volcanoclastic matrix of the amber is early Cenomanian (98.8 \pm 0.6 Ma) (Shi et al. 2012).

The fossil specimens are embedded in small amber blocks which have been cut out from larger amber pieces. The studied specimens represent nearly complete adults, visible in ventral and dorsal view. The hindwings are partially covered by the forewings. Male genitalia are deeply embedded between the wings. Legs and antennae are totally or partially present. Photographs were taken using a Leica stereomicroscope M 420 Apozoom in combination with a Canon EOS 60D, EOS utility 3 software and the Zerene Stacker software. All images and figures were prepared with Adobe Photoshop CS4.

Terminology: Wing venation terminology generally follows Holzenthal et al. (2007): I – apical fork I; II – apical fork II; III – apical fork III; V – apical fork V; R – radius, Rs – radius sectori, M – media, Cul – cubitus anterior, Cu2 – cubitus posterior, A – analis, DC – discoidal cell, MC – median cell, TC – thyridial cell.

In male genitalia: inf ap – inferior appendages, cox – coxopodite, har – harpago, pr ap – preanal appendage (cercus), pha – phallic apparatus, X ap – mesodorsal processes of tergum X.

3. Systematic palaeontology

Order Trichoptera Kirby, 1815

Suborder Integripalpia Martynov, 1924

Family Calamoceratidae Ulmer, 1905

Calamoceratinae Ulmer, 1906

Genus Cretaganonema nov.

Etymology: The name Cretaganonema of the proposed genus refers to "creta" and "ganonema". "Creta" means the Cretaceous age and "Ganonema" indicates its resemblance to the extant calamoceratid genus Ganonema.

Type species: Cretaganonema dongi nov. sp., monotypic

Diagnosis and description: The new extinct genus *Cretaganonema* very likely belongs to the extant family Calamoceratidae as indicated by the following characteristics: Male with broad forewings, hindwings shorter and narrower than forewings. Head without ocelli. Antennae longer than forewings; scapus strong, more than twice as long as pedicellus. Maxillary palps 5-segmented. The wing venation complete (some hind wing veins and cross-veins covered, hence not visible). Tibial spur formula: 2/4/4. (Unfortunately the dorsum of the

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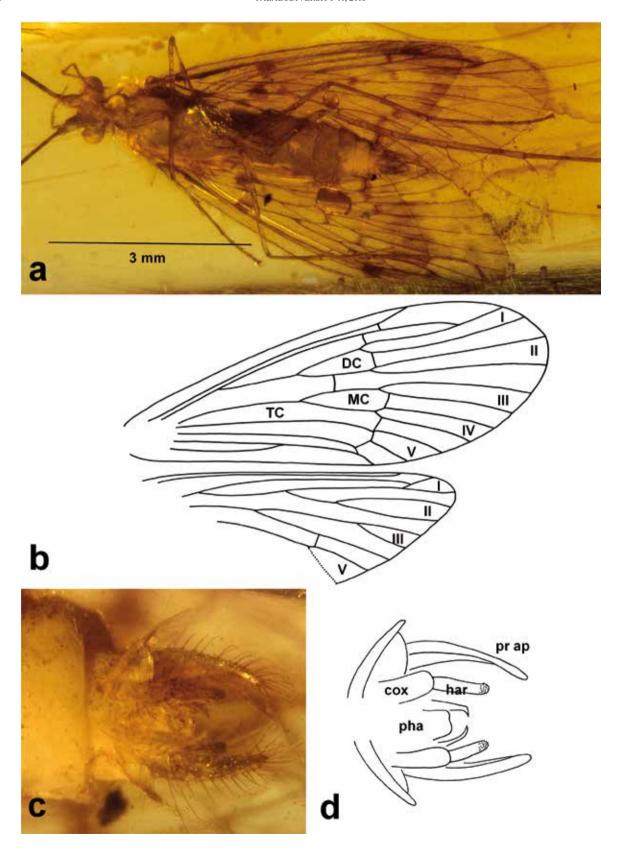


Fig. 1. Cretaganonema dongi nov. gen. et nov. sp. in Cretaceous Burmese amber, holotype, NIGP154571. **a:** Male adult in ventral view. **b:** Drawings of fore and hind wings. **c:** Male genitalia in ventral view. **d:** Drawing of male genitalia in ventral view.

head, the pronotum and the mesoscutum and mesoscutellum of the fossil specimen are rubbed away.)

Based on the visible characters of the maxillary palps, the tibial spur formula and the wing venation of the extinct species are closely related to the extant *Ganonema* (Prather 2002). In particular, the complete wing venation indicates a structural conformity with extant *Ganonema* species (OLAH & JOHANSON 2010; MALICKY 2010): In forewings R1 is recurrent into R2 before running in costal margin; forks, I, II, III, IV, V present; discoidal, median and thyridial cells closed; Cu2 fused with A1 at the apex before the wing margin. In the hindwing R1 is fused with R2 before the costal margin, forks I, II, III, V present; discoidal and median cells open.

Cretaganonema is, however, definitely distinguished from Ganonema in the male genitalia. In Ganonema the inferior appendages are 1-segmented (OLÁH & JOHANSON 2010; MALICKY 2010), Cretaganonema possesses 2-segmented inferior appendages with a basal coxopodite and an apical harpago (Fig. 1c, d). The family Calamoceratidae consists of genera with 1-segmented (e.g., Anisocentropus, Ganomnema) and genera with 2-segmented inferior appendages (e.g., Banyallaga, Phylloicus, as well as Cretaganonema nov. gen.). The extinct Cretaganonema nov. gen. is characterised by the combination of the complete wing venation as in Ganonema, with R1 fused with R2 and Cu2 fused with A1 before running to wing margin, and of the male genitalia with 2-segmented inferior appendages. As in most calamoceratid genera the spur formula is 2/4/4 and maxillary palps are 5-segmented.

Cretaganonema dongi nov. sp. Figs. 1, 2

E t y m o l o g y : The specific epithet honours the collector, $\mbox{\sc Huabao}$ Dong.

Holotype: Male NIGP154571, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Burmese amber, Upper Cretaceous, Cenomanian; from a mine near Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, Myanmar, 26150N, 96330E.

Diagnosis: Cretaganonema donginov. sp. is an extinct new species from Cretaceous Burmese amber and characterised by the greatly elongated tarsal segments of the hind legs, with a hair tuft at the tarsal apex (Fig. 2a, b).

R e m a r k s: This is the third known calamoceratid species from the Cretaceous and distinguished from the two described Cretaceous calamoceratid species by the forewing venation: Calamodontus grandaevus Botosaneanu & Wichard, 1983 was described from Taimyr amber dated into the Santonian, and Palaeocentropus placidus Sukatsheva & Jarzembowski, 2001 from the Purbeck Limestone Group and Wealden Supergroup of southern England (Berriasian). Additionally, there is a record of an indeterminate calamoceratid pupa from the Lower Cretaceous Koonwarra fossil bed in Australia (Jell & Duncan 1986). The oldest evidence (wing fragments) of the family Calamoceratidae comes from the Jurassic/Cretaceous insect fossil site Chernovskie Kopi in Transbaikalia (Sukatsheva & Vassilenko 2011).

Description: Head: Ocelli absent. Antennae longer than forewings. Scapus strong, more than twice as long as the pedicellus, first flagellomere twice as long as subsequent cylindrical flagellomeres, each coated with fine setae. Maxillary palps 5-segmented with 1st segment shorter than 2nd segment (in most calamoceratids 1st and 2nd segments are of approximately

equal length), 2nd and 3rd equal in length, 4th segment shorter than 2nd or 3rd segment and terminal segment longest of all. The dorsum of the head, the pronotum and the mesoscutum and mesoscutellum of the fossil specimen are rubbed away.

Wing venation (Fig. 1b): Forewings broad, about 6 mm in lengths, hindwings similarly broad, however, shorter. In forewing Sc strong, R1 recurrent into R2 before costal margin; forks I-V present; crossveins sc-r, r, s, r-m, m, m-cu visible, discoidal, median and thyridial cells closed; A1 meets Cu2 before wing margin. Forewing with small pigmented spots on some crossveins and forking points of longitudinal veins; hindwing immaculate. In hindwing Sc strong, R1 connected to R2 before apical cell margin. Forks I, II, III and V present; fork I small, about one-third as long as fork II. Crossveins r-m, m-cu present; discoidal and median cells open.

Legs: Fore legs nearly half as long as mid legs; hind legs unusually long (Fig. 2a, b), more than twice as long as mid legs, particularly the 5-segmented hind tarsus with a length of 7 mm, at the apex the tarsus bears a 2.5 mm long hair-tuft covering the leg from the lower half of the 3rd tarsal segment to the tarsal claw. Only one hind leg present, the other one lost. Tibial spur formula: 2/4/4.

Male genitalia, visible in ventral view (Fig. 1c, d): Inferior appendages 2-segmented, coxopodite stocky; harpago cylindrical, apically rounded, covered with short, dark spines on the apical surface. The preanal appendages are laterodorsally present, in shape of elongate scales bent inward, bearing lengthwise long setae. As far as visible, the phallic apparatus is small, subsquare, apical margin undulated. Posterior to the phallic apparatus two elongate processes probably of tergite X, pointed at the apex, curved mesad.

Family Helicopsychidae Ulmer, 1906

Genus Cretahelicopsyche nov.

Etymology: The name *Cretahelicopsyche* of the proposed genus refers to "*creta*" and "*helicopsyche*". "*Creta*" means the Cretaceous age and "*helicopsyche*" indicates its placement in the family Helicopsychidae.

Type species: Cretahelicopsyche liuyani nov. sp., monotypic.

Diagnosis: The new extinct genus Cretahelicopsyche very likely belongs to the extant family Helicopsychidae as indicated by the following characteristics: ocelli absent, antennae about as long as forewings, maxillary palps 3-segmented, VIth abdominal sternal process present, short and stump as in Rakiura. Cephalic warts, setal warts of pronotum as well as mesoscutal and mesoscutellar warts of the fossil specimen are damaged and not clearly visible. Forewing venation generally conform to Helicopsychidae and expecially to Rakiura McFarlane, 1973, which represents the sister group of all other Helicopsychidae (JOHANSON 1998; JOHANSON et al. 2017). The modification of R2 fused with R1 in which basal R2 forming a "crossvein", is present in Rakiura just as in the Cretaceous Cretahelicopsyche. Furthermore, the extinct genus is characterised by the tibial spur formula: 1/2/4, distinguished from most extant species of the family Helicopsychidae (Johanson et al. 2017). Although 2/2/4 is the most commonly found spur formula in Helicopsychidae, 1/2/4 as found in this species, is not uncommon among Oriental and Palaearctic genera (Johanson 1998).

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Fig. 2. Cretaganonema dongi nov. gen. et nov. sp. in Cretaceous Burmese amber, holotype, NIGP154571. **a:** Male adult with left long hind leg and (arrow) apical hair-tuft; right hind leg lost. **b:** Tarsal apical hair tuft of hind leg.

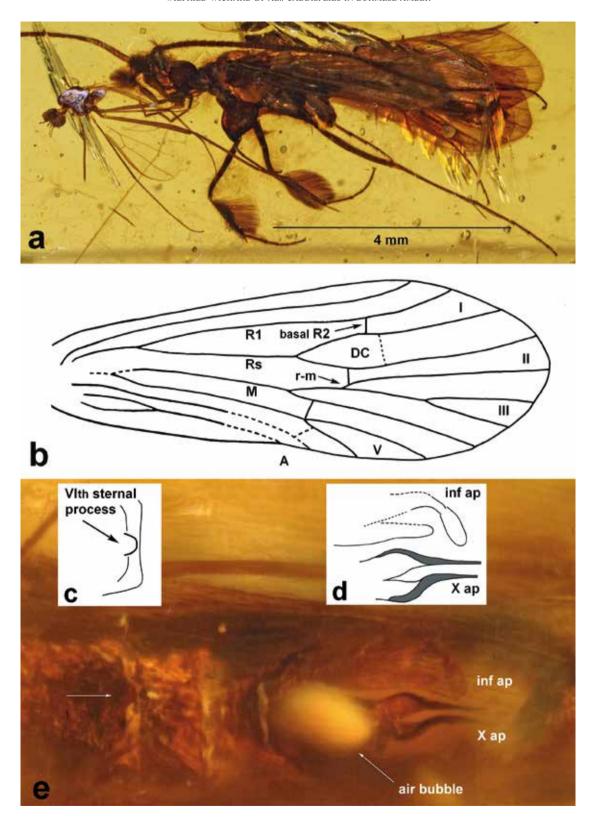


Fig. 3. Cretahelicopsyche liuyani nov. gen. et nov. sp. in Cretaceous Burmese amber, holotype, RPX18001. **a:** Male adult in lateral view (in front a cut midge), arrow: bilateral hair fans of the fore legs tibia. **b:** Drawing of fore wing. **c:** Drawing of male VIth sternal process. **d:** Drawing partial of male genitalia in ventral view. **e:** Male abdomen in ventral view with VIth sternal process and outer genitalia, so far as visible.



Fig. 4. Cretahelicopsyche liuyani nov. gen. et nov. sp. in Cretaceous Burmese amber, holotype, RPX18001. **a:** Head in lateral view with compound eye, labial and maxillary palps inclusive (arrow) the modified 3rd segment apically covered by a strong hair-tuft. **b:** Bilateral hair fans of the fore leg tibiae, one folded together and one partially unfolded.

Cretahelicopsyche liuyani nov. sp. Figs. 3, 4

E t y m o l o g y : The specific epithet honours the collector, Yan Liu.

Holotype: Male RPX18001, housed in the Ruipoxuan Amber Museum in Jinan. Burmese amber, Upper Cretaceous, Cenomanian; from a mine near Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, Myanmar, 26150N, 96330E.

Diagnosis: Cretahelicopsyche liuyani nov. sp. is characterised by the modification of the terminal segment of the 3-segmented maxillary palps bearing apically a rounded knot with a hair-tuft, and furthermore by possessing tibial hair fans on the forelegs (Fig. 4a, b).

R e m a r k s: *Cretahelicopsyche liuyani* nov. sp. from Cretaceous Burmese amber is the oldest fossil Helicopsychidae described so far and probably closely related to *Rakiura vernale* McFarlane, 1973 which presents "the most basal taxon within the Helicopsychidae" (Johanson 1998). Further extinct species have hitherto been described from Eocene Baltic amber (Ulmer 1912; Johanson & Wichard 1997; Wichard 2013).

Description: Head: Antennae slightly longer than forewings. Scapus broad and about 0.4 mm long, much longer than the pedicellus and the following flagellomeres. Flagellum consisting of about 34 flagellomeres, completely covered with a fine hair-coat, densely setose. Male maxillary palps 3-segmented, 1st segment about 0.3 mm long, a little smaller than the 2nd segment with a length of about 0.4 mm; 3nd segment twisted, sinusoidal, at its apex with a strong rounded knot, which is covered by a strong hair-tuft (Fig. 4a).

Wing venation (Fig. 3b): Forewings about 5 mm long, hindwings slightly shorter. In forewings R2 fused with R1 in which basal R2 forming a "crossvein" (compare *Rakiura*, JOHANSON 1998), therefore apical forks I, II, III and V present; discoidal and thyridial cells closed; discoidal cell short, about half as long as the stem; thyridial cell long. Crossveins r-m and m-cu visible. Cu2 and A1 free to wing margin (with vague details). Hindwings covered by forewings; venation not visible.

Legs: well-developed, with tibial spur formula 1/2/4 and uniformly covered by trichoid serrate setae. Fore legs are modified (Fig 4 b), bearing hair-fans lengthwise and bilaterally on the tibia. The bilateral hair-fans are densely packed with parallel running long setae, which seemingly could be folded together.

Abdomen (Fig. 3c, d): Surface structures of IInd sternite not visible in amber. Male VIth sternal process located medially, its shape is short and stump.

Male genitalia (Fig. 3d, e): In ventral view, the genitalia are deeply embedded between the right and left wings and partially covered by artefacts. As far as visible, Xth tergum centrally arranged, basal broad, in amber covered ventrally by a light air bubble, apex divided into two lateral lobes, each subtriangular long drawn-out, following spicular and apically pointed. Inferior appendages laterally arranged, curved mediad at the apex, probably with a basomedian branch, digitiform; both appendages gleaming laterally.

4. Discussion

Many extant caddisflies briefly skate on the water surface when they emerge from their pupal exuviae or when

females lay eggs at the water surface, and some species temporarily skip across the surface (Morse & Chuluunbat 2007), but none of these possess any specific adaptations for this life style. The few caddisflies species that spend most of their adult life on the water surface have modified legs and often also reduced wings rendering them flightless (reviewed in Morse & Chuluunbut 2007). Both species described here have modified legs, with hair tufts, which could possibly indicate a skating lifestyle, but the wings are fully developed and they were likely able to fly. The leg modifications on extant skating caddisflies are. however, found on the middle legs (Morse & Chuluunbat 2007), which is not the case in the species described here (fore legs and hind legs, respectively). There are a number of other possible interpretations of the modified legs such as involvement in courtship behaviour, pheromone production or communication in swarms, but these must all remain hypothetical. Similar modifications to what is described here are not present in any known extant species.

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