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Short communication

Burmochlus gen. nov., the first Cretaceous member of the *Archaeochlus* cluster (Diptera: Chironomidae: Podonominae)

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ABSTRACT

A fossil genus, *Burmochlus* gen. nov., with a species *B. madmaxi* sp. nov. (Diptera, Chironomidae, Podonominae) is described from mid-Cretaceous amber of northern Myanmar (~100 Ma). The adult male of the new species/genus displays an interesting wing structure with a trace of the vein R_{2+3} (or R_3 alone), the character unique in the subfamily Podonominae. The wing squama with a process bearing a bunch of setae, the wing membrane covered with bi- or trifid spinulae-like microtrichia, the gonostylus with a collar-like ring and a pear-shaped distal part, the robust anal point and the extensive superior volsella are also characters defined as exclusive for *Burmochlus*. The antenna, thorax and several hypopygium structures found in male *Burmochlus* clearly resemble those known from *Archaeochlus* Brundin, here defined as the closest relative, as well as from *Afrochlus* Freeman and *Austrochlus* Cranston – both previously referenced to or derived from *Archaeochlus*, hence being postulated as close or sister taxa. In a view of several hypotheses on the time of divergence of the Podonominae and other related subfamilies, this is the oldest fossil record of a true Podonominae chironomid based on definition of male characters, and dated back to the "mid-Cretaceous". Along with *Furcobuchonomyia* Baranov, Góral *et* Ross (Buchonomyiinae) and *Myanmaro* Giłka, Makarchenko, Pankowski *et* Zakrzewska (Orthocladiinae), *Burmochlus* is the third genus described from Burmese amber, and the first known Podonominae chironomid described from this deposit.

1. Introduction

According to the most recently updated checklist by Ross (2019), 1,117 species of arthropods in 814 genera, 488 families and 67 orders were recorded in Burmese amber. Insects, as the most diverse group, are represented by 29 orders, 363 families, 646 genera and 823 species, including Diptera with 143 species, 110 genera and 49 families (Ross, 2019). The Chironomidae, one of the most species-rich dipteran families, however, is known only from three species described from this deposit until now. They are placed in the subfamily Buchonomyiinae and the genus *Furcobuchonomyia* Baranov, Góral *et* Ross, 2017 (Baranov et al., 2017; Giłka and Zakrzewska, 2017), and in the subfamily Orthocladiinae and the genus *Myanmaro* Giłka, Makarchenko, Pankowski *et* Zakrzewska, 2019 (Giłka et al., 2019). The new genus *Burmochlus* is thus the first representative of the chironomid subfamily Podonominae found in mid-Cretaceous Burmese amber.

In a view of several hypotheses on the time of divergence of the subfamily Podonominae (estimated from the Jurassic to the Cenozoic) (Kalugina and Kovalev, 1985; Veltz et al., 2007; Azar et al., 2008; Azar and Nel, 2010; Cranston et al., 2012), often difficult to separate from fossil chironomids of other related subfamilies, e.g. the Tanypodinae, and therefore referred to as "Podonominae or Tanypodinae" (e.g. Lukashevich and Przhiboro, 2018), an aim of our study is to evidence that true Podonominae existed in the Cretaceous.

2. Material and methods

2.1. Origin, processing and deposition of the type material

The specimen examined (Fig. 1A) is the inclusion preserved in Burmese amber, often referred to as "Burmite", mined in the

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Hukawng Valley in Kachin State, Myanmar (Kania et al., 2015: fig.1). It is dated back to the beginning of the Upper Cretaceous (Early Cenomanian, ca. 98.79 ± 0.62 Ma (Shi et al., 2012), or perhaps even earlier, showing traces of redeposition, and thus being proposed to be called "mid-Cretaceous" (Smith and Ross, 2018; Zhang et al., 2018).

The amber chunk was ground and polished manually so the inclusion could be viewed as clearly as possible and its diagnostic structures could be analysed. Measurements of the specimen are in micrometres, except for the total length (in millimetres). The body length was measured from the antennal pedicel to the end of the gonostylus, and the wing from the arculus to the tip. Lengths of leg segments were rounded off to the nearest 5 μm. The antennal and venarum ratios (AR, VR_{Cu}) were calculated to the first decimal place, and the leg ratios (LR_{1-3}) to the second digit after the decimal point. The morphological terminology and abbreviations follow Sæther (1980). The photographs were taken using the Leica M205A and the PZO Biolar SK14 microscopes under control of the LAS Montage multifocus and the Helicon Focus 6 image stacking software. The inclusion is part of the collection of the Laboratory of Systematic Zoology in the Department of Invertebrate Zoology and Parasitology (LSZ DIZP), University of Gdańsk, Poland. New nomenclatural acts and the paper were registered in Zoobank, in accordance with ICZN requirements (LSID: urn:lsid:zoobank.org:pub:FCE4D694-B2D6-4EE4-A762-1C355D74E396).

2.2. IR spectrum

The infrared spectra obtained from amber, with reference curve numbers registered and stored in collection archives is the procedure recommended for museum materials, especially for the name-bearing inclusions to support the validity of new taxa described. The spectrum (Fig. 1B) was obtained in the Laboratory of the International Amber Association (IAA), Gdańsk, Poland. For ATR (*Attenuated Total Reflection*) FT-IR spectrum registration a Nicolet iS10 FT-IR (diamond crystal) spectrometer was used. The resolution was 4 cm^{-1} and number of scans: 32. ATR spectrum was subjected to advanced ATR correction. The analyzed spectrum was baseline corrected and normalized, and all spectral operations were done using standard spectrophotometer software. The spectrum indicates that the analysed amber originates from the Cretaceous and shows characters typical of Burmite (Wagner-Wysiecka, pers. comm.).

3. Results

Systematic palaeontology

Family: Chironomidae Newman, 1834.
Subfamily: Podonominae Thienemann *et* Edwards, 1937.

Burmochlus gen. nov.
LSID: urn:lsid:zoobank.org:act:A61350E1-5D10-41F6-AEBD-BCE73AEC2912
Type species. Burmochlus madmaxi sp. nov. (by present designation).

Derivation of name. From Burma, present Myanmar, the amber's country of origin; the genus belongs to the cluster of Podonominae chironomids possessing a well-developed, elongated proboscis.

Diagnostic description. Eyes bare, reniform, with wedge-like dorsomedian extension. Antennal flagellum with 14 flagellomeres, with ultimate flagellomere tapering to slender apex bearing strong seta; plume fully developed. Proboscis elongated, as long as head capsule (~200 μm). Postnotum with at least 10 setae in 2 longitudinal rows. Wing squama with process bearing a bunch of long setae; anal lobe well-developed, rounded; R_{2+3} (or R_3 alone) vestigial, visible as semitransparent streak, starting together with R_{4+5}, fading near end of R_1; membrane with simple, bi- or trifid spinulae-like microtrichia. Tibial spurs strong, covered with spinules; vestigial combs consisted of several short teeth, present only on hind leg; claws broadened near base, with inner spine-like setae. Gonocoxite robust, hemispherical; gonostylus with collar-like ring, pear-shaped distal part and minute megaseta; anal point stout, tapering towards incised apex, with longitudinal groove; superior volsella extensive, broadly fused with gonocoxite, with protuberances on median margin and stout posterolateral process; median volsella absent; inferior volsella broad at base, with setae on median margin and apex.

Burmochlus madmaxi sp. nov.
LSID: urn:lsid:zoobank.org:act:364D5817-2E20-4032-AA23-E960148084E7
Figs. 1A, 2–5

Type material. Holotype, inventory no. F2a LSZ DIZP: adult male (complete specimen, Figs 1A, 2A) preserved in 7 × 7 × 2.5 mm piece of Burmese amber (mid-Cretaceous, ~100 Ma; IR spectrum no. 16216 IAA, Fig. 1B) mined in Hukawng Valley, Kachin State, Myanmar. Syninclusions: Psychodidae, 1 adult female (F2b LSZ DIZP), Coleoptera, 1 adult (F2c LSZ DIZP).

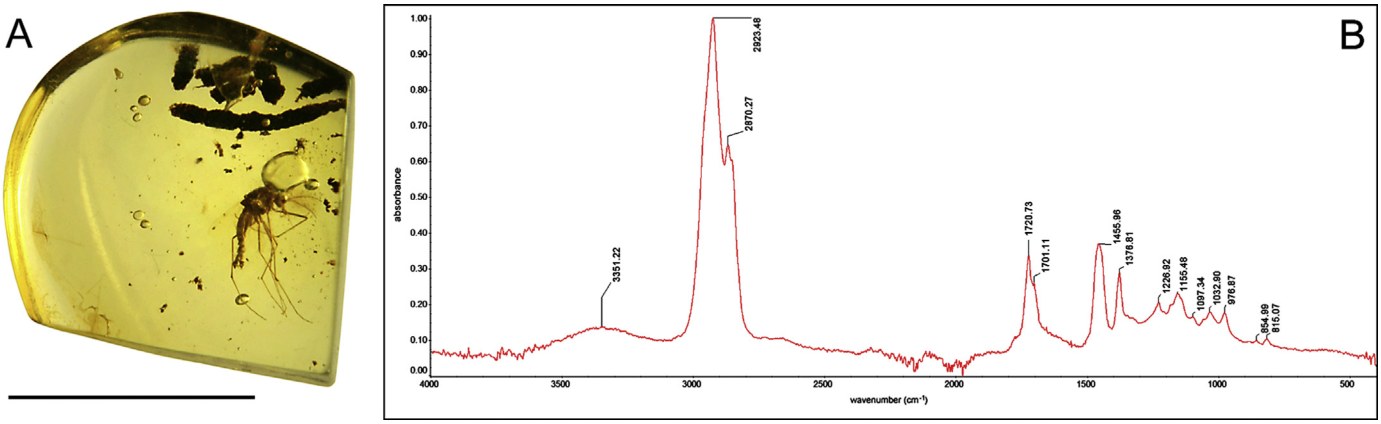

Fig. 1. *Burmochlus madmaxi* sp. nov., holotype, adult male (F2a LSZ DIZP). A: inclusion in amber. B: IR (ATR) spectrum no. 16216 IAA obtained from examined amber (mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar). Scale bar = 5 mm.

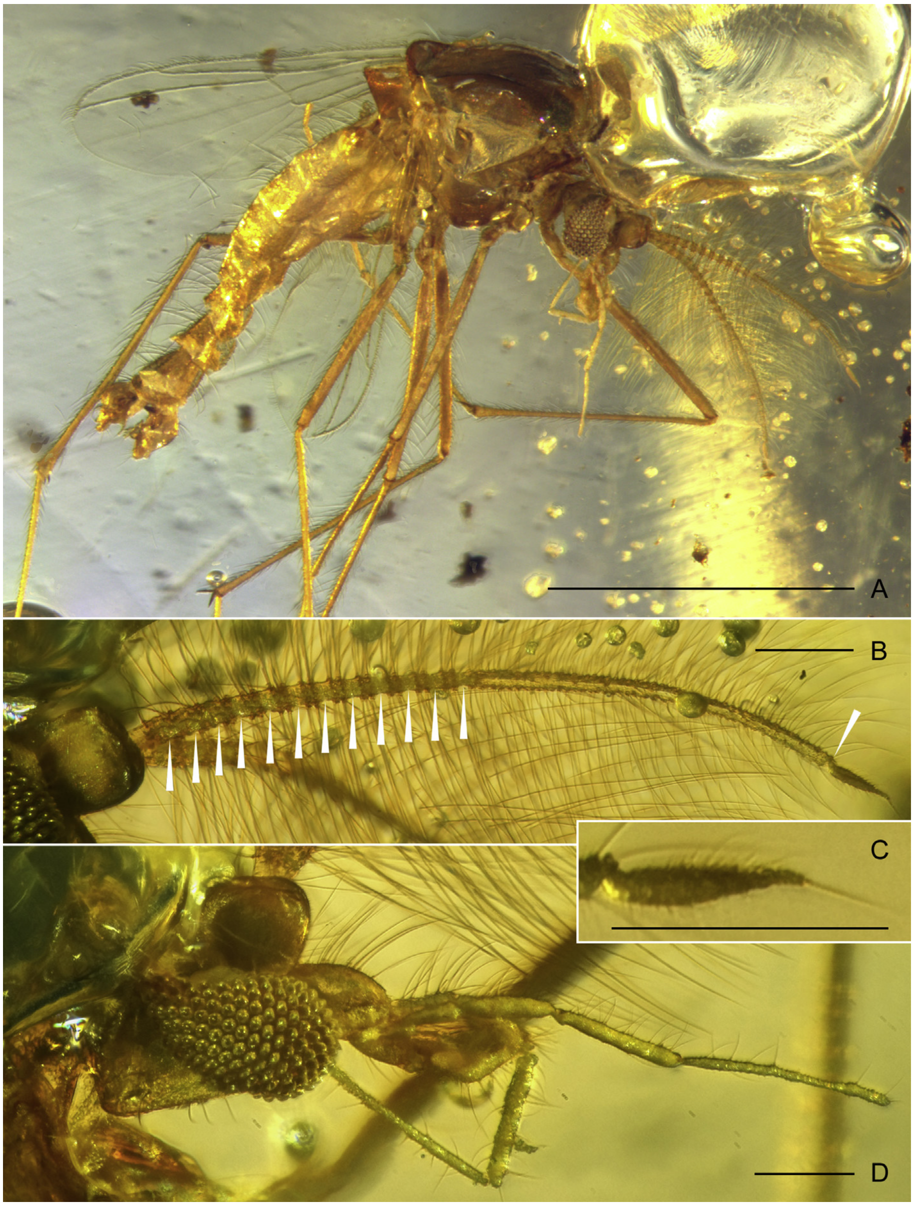

Fig. 2. *Burmochlus madmaxi* sp. nov., holotype, adult male (F2a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar). A: habitus in dorsolateral view. B: antenna (arrows: borders between flagellomeres). C: ultimate flagellomere (fm_{14}). D: head with elongated proboscis. Scale bars = 1 mm (A), 100 µm (B–D).

Derivation of name. We dedicate the specific name to Madeline and Maximilian Pankowski (Rockville, USA), the donators of amber inclusions housed in the collection of the LSZ DIZP.

Diagnosis. As for the genus.

Description. Adult male (n = 1, holotype).

Total length ~2.3 mm, wing length 1200 µm; total length/wing length ratio ~1.9.

Colouration. Yellowish brown to dark brown, wing membrane transparent (Fig. 2A).

Head (Fig. 2B–D). Eyes bare, reniform, with short wedge-like dorsomedian extension. Antenna (Fig. 2B) with pedicel 95 µm long, pubescent; flagellum with 14 well discernible flagellomeres (fm_{1-14}): fm_{1-12} 357 µm long, fm_{13} 394 µm long, fm_{14} 72 µm long and 12 µm wide, slightly swollen in proximal half, tapering to slender apex bearing strong, 32 µm long seta (Fig. 2C); AR ~1.30; plume fully developed, with setae arranged in distinctly separated whorls on fm_{1-12}. Clypeus elongated, convex, with at least 14 strong clypeals. Proboscis elongated, as long as head capsule (~200 µm) (Fig. 2D). Length of palpomeres 2–5 (µm): 56, 94, 141, 215.

Thorax (Fig. 3A). Setae mostly missing, only some setal tubercles observable: several on acrostichal area (mostly hidden in air bubble), at least 13 on humeral-prealar area (Dc and/or Pa, poorly differentiated); at least 8 on margin of scutellum; at least 10 in 2 longitudinal rows on postnotum.

Wing (Fig. 3B–F). Broadest at 2/3 length, width: 350 µm, length/width ratio 3.43. Squama with process bearing a bunch of several long setae (Fig. 3B). Anal lobe well-developed, rounded. Costa slightly extending beyond end of R_{4+5} to wing apex; subcosta developed, but fading apically; R_{2+3} (or possibly R_3 alone) vestigial, visible as semitransparent streak, starting together with R_{4+5}, fading near end of R_1 (Fig. 3C, D); R_{4+5} curved posteriorly to terminate close to wing apex; FCu placed slightly proximally of RM;

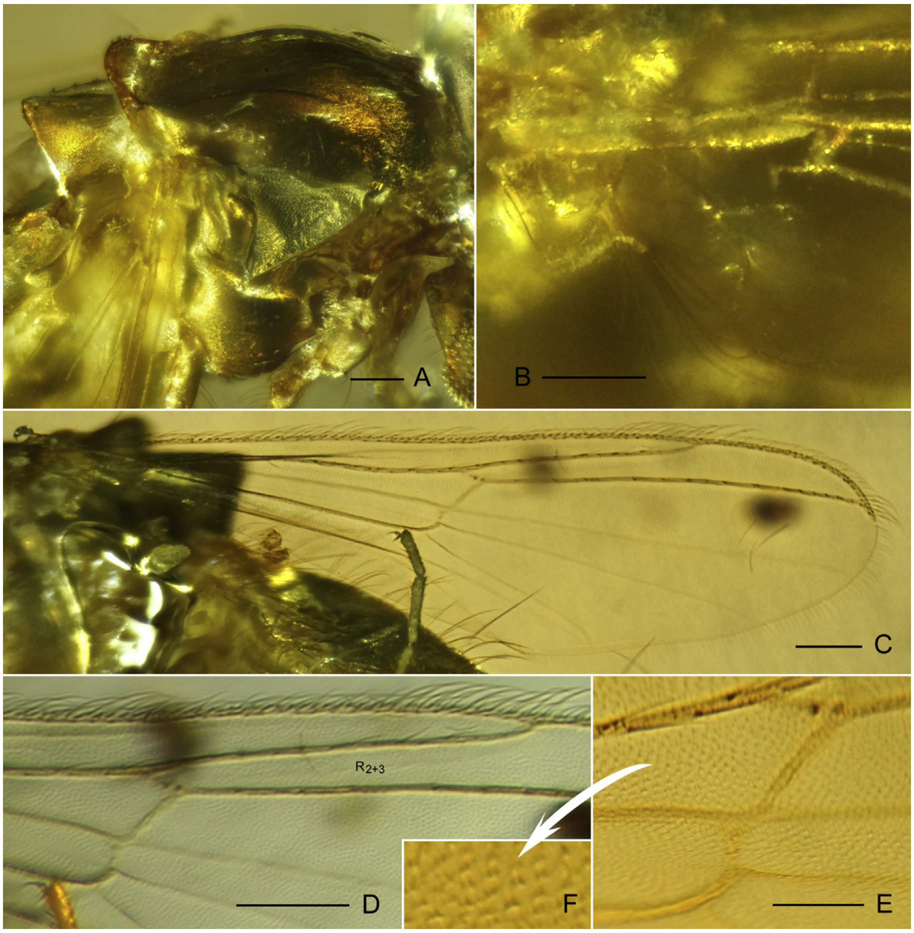

Fig. 3. *Burmochlus madmaxi* sp. nov., holotype, adult male (F2a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar). A: thorax in dorsolateral view. B: base of wing, with squama bearing a bunch of setae. C: wing, venation pattern. D: median area of wing, with vestigial vein R_{2+3}. E, F: RM and MCu area of wing, with membrane covered with spinulae-like microtrichia (magnified twice on F). Scale bars = 100 μm (A, C, D), 50 μm (B, E).

cross veins RM and MCu arranged as shown on Fig. 3C–E. VR_{Cu} close to 1.0. Setae present on wing margin including costa and whole length of R (with 25 setae), R_1 (15 setae) and R_{4+5} (20 setae), other veins bare. Wing membrane without macrotrichia, covered with simple, bi- or trifid spinulae-like microtrichia (Fig. 3E, F).

Legs (Fig. 4A–N). Fore leg tibia with ~50 μm long spur; spurs of mid and hind leg unequal: ~60 μm and ~50 μm long (mid leg), ~40 μm and ~30 μm long (hind leg); spurs strong, covered with spinules, as shown on Fig. 4A–F. Vestigial combs consisted of a couple of short spine-like teeth (up to 30 μm long) present only on hind leg tibiae (Fig. 4E, F). Pseudospurs only on ta_1 and ta_2 of mid leg and on ta_1 of hind leg (Fig. 4G, H). Sensilla chaetica not observed. Pulvilli absent. Claws simple, distinctly broadened near base, strongly curved apically, with inner spine-like setae (Fig. 4I–N). For length of leg segments and leg ratios see Table 1.

Hypopygium (Fig. 5A–E). Gonocoxite robust, hemispherical. Gonostylus ca. 120 μm long, strongly setose basally, with collar-like ring at 2/3 length, and pear-shaped distal part tapering towards narrow tip bearing minute megaseta (Fig. 5A, C). Tergite IX broad and relatively short, semicircular, with posterolateral margins bearing strong setae, median area with shorter setae. Apodemes (aedeagal lobe and phallapodeme) strongly sclerotized, observable in part, as shown on Fig. 5A. Anal point stout, parallel-sided at base, slightly tapering from mid-length towards incised apex, with longitudinal groove (Fig. 5A). Superior volsella broadly fused with gonocoxite, extensive, with distinct protuberances on median margin and stout posterolateral process, all with strong curved setae (Fig. 5A, D). Median volsella absent. Inferior volsella broad at base, reaching end of gonocoxite, with several strong setae on median margin and apex; posterolateral part translucent (Fig. 5A, B, E).

4. Discussion

On the basis of the comparative characteristics of *Burmochlus* with other chironomid genera we attribute the new genus to the cluster consisted of *Archaeochlus* Brundin, *Afrochlus* Freeman and *Austrochlus* Cranston. According to a recent concept, *Archaeochlus* + *Afrochlus* are the sister clad to *Austrochlus*, all in the subfamily Podonominae (Cranston et al., 2012).

4.1. Structures/characters of systematic importance

The distinctly elongated proboscis found in the adult male of *Burmochlus* may suggest feeding on liquid nourishment. Recently, several concepts of possible trends in evolution of feeding behaviour, including the haematophagy in chironomids were postulated (e.g. Azar et al., 2008; Szadziewski et al., 2018). This is not, however,

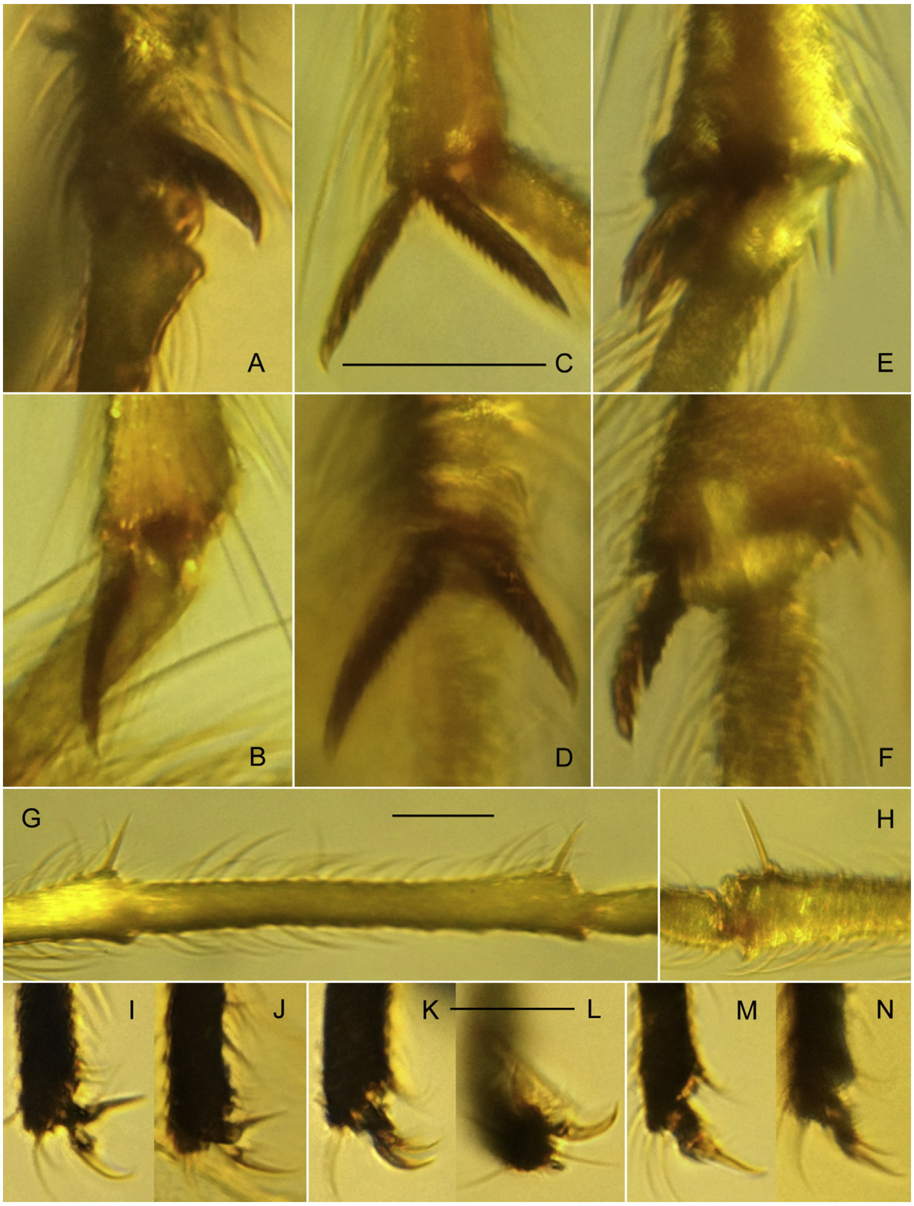

Fig. 4. *Burmochlus madmaxi* sp. nov., holotype, adult male (F2a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar). A–F: tibial apices of fore (A, B), mid (C, D) and hind leg (E, F), with spurs and spine-like comb's teeth. G, H: pseudospurs on mid (G) and hind leg (H). I–N: ultimate tarsomere and claws of fore (I, J), mid (K, L) and hind leg (M, N). Scale bars = 50 μm (same for A–F, G–H, I–N).

an aim of our study – based on adult males, which, contrary to females, usually demonstrate a non-feeding behaviour and/or have the biting mouthparts reduced. Except for the elongated proboscis, no toothed mandibles or serrated mouthpart structures have been observed in the examined *Burmochlus* male. Nevertheless, the proboscis of *Burmochlus* (Fig. 2D) resembles that found in males of other genera of the *Archaeochlus* cluster, in which serrated mouthparts are also reduced (Brundin, 1966, 1989; Cranston et al., 1987) or are not developed in adults of both sexes (Cranston and Edward, 1998).

The wing vein R_{2+3} is one of crucial characters in delimitation of chironomid subfamilies (Sæther et al., 2000). The vein, with few exceptions (when R_3 and/or R_2 are absent), is well-developed or branched into R_2 and R_3 in Tanypodinae, but considered to be completely lacking in Podonominae (Brundin, 1989). In *Burmochlus*, the R_{2+3} (or possibly R_3 alone) is present, but vestigial, visible as semitransparent simple streak starting together with R_{4+5} and fading near the end of R_1 (Fig. 3C, D). Besides, the venation pattern of the radial area found in *Burmochlus* is typical of the majority of Podonominae, particularly of the *Archaeochlus* cluster, in which the R_{4+5} is widely separated from R_1, curved posteriorly to terminate close to wing apex and ending distally to end of M_{3+4} or even to M_{1+2}. The vestigial vein in *Burmochlus* may thus be defined as a plesiomorphic character derived from a Tanypodinae or other subfamily ancestor having the R_{2+3} or R_3 developed.

The hypopygial anal point is the portion of terminal tergite, i.e. part of tergite IX, or the anal point consists of tergite X (Sæther, 1980). In *Burmochlus*, the anal point is distinct (Fig. 5A) and we see no reason to call this structure as an extension of tergite IX, neither to consider the anal point to be absent, as it was in other related genera of the *Archaeochlus* cluster. However, we believe that the extending median portion of tergite IX, described previously in

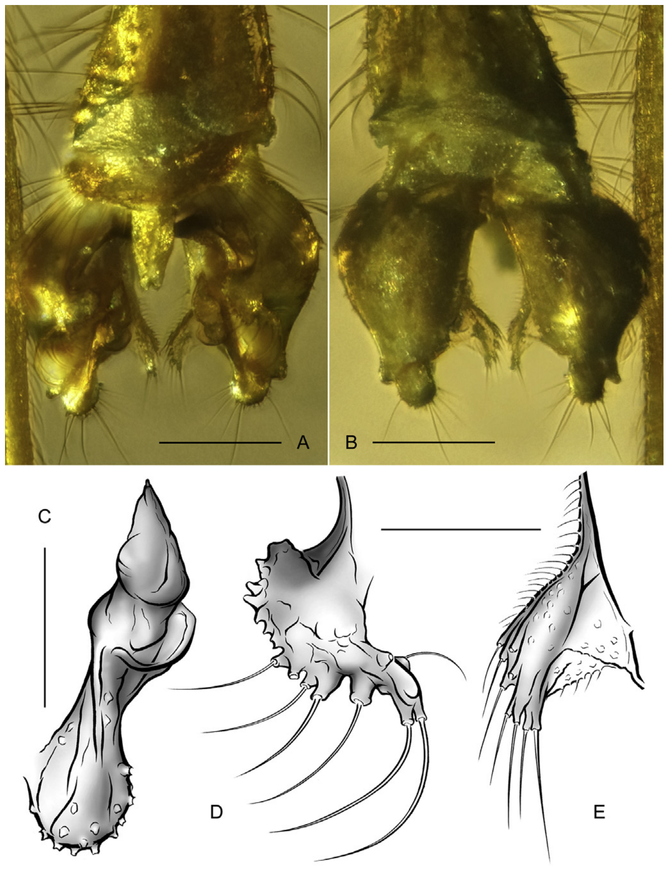

Fig. 5. *Burmochlus madmaxi* sp. nov., holotype, adult male (F2a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar). A, B: hypopygium in dorsal (A) and ventral view (B). C: gonostylus. D: superior volsella. E: inferior volsella. Scale bars = 100 μm (A, B), 50 μm (C–E).

Table 1
Leg segment lengths (μm) and leg ratios of male *Burmochlus madmaxi* **sp. nov.** p_1–p_3 = pair of legs 1–3, fe = femur, ti = tibia, ta_1–ta_5 = tarsomeres 1–5, LR = leg ratio.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	700	810	560	230	165	110	90	0.69
p_2	705	815	460	180	135	110	75	0.56
p_3	610	860	560	270	200	135	90	0.65

the *Archaeochlus* genera group and the anal point found in *Burmochlus*, both similarly developed (with the characteristic longitudinal groove), are homologous.

Other characters, including these defined as exclusive for *Burmochlus*, i.e. the wing squama with the process bearing the bunch of setae, the membrane covered with bi- or trifid spinulae-like microtrichia (Fig. 3B–F), the gonostylus with the collar-like ring and pear-shaped distal part (Fig. 5A, C) and the extensive superior volsella (Fig. 5A, D) (see diagnostic description of the genus) are compared below with those known from related genera.

4.2. *Burmochlus* and related genera of the *Archaeochlus* cluster

Morphological characters crucial in the delimitation of *Burmochlus* and other genera of the *Archaeochlus* cluster are presented in Table 2. The comparison provided indicates that *Burmochlus* and *Archaeochlus* (and *Austrochlus*, the genus derived from *Archaeochlus*) can be defined as the closest genera, in which some similar or the same features can be found. They are as follows: eyes bare; antenna with 14 flagellomeres and well-developed plume, ultimate flagellomere with strong apical seta; proboscis elongated; 5 palpomeres; costa extending beyond end of R_{4+5} to wing apex, subcosta developed but apically fading, anal lobe well-developed, squama with setae, VR close to 1.0; pulvilli absent, claws simple, with inner spine-like setae, spines or teeth. On the other hand, several characters found in *Burmochlus* are unique and/or differ distinctly from those in the genera compared, main of which are as follows (opposite characters of *Archaeochlus* and *Austrochlus* are given in brackets): eyes reniform, with short wedge-like dorsomedian extension (dorsomedian extension parallel-sided); proboscis distinctly elongated, ca. 200 μm long (proboscis shorter); 3rd palpomere without sensilla capitata (sensilla capitata present); wing membrane with bi- or trifid spinulae-like microtrichia but without macrotrichia (macrotrichia present); the vein R_{2+3} or R_3 present (absent, see the above subchapter); alula without setae (setae present); hind leg tibial comb vestigial, consisted of a few short teeth (4–8 spines); LR_1 0.69 (LR_1 close to 0.5–0.6); stout anal point present (see the above subchapter); gonostylus with strong setae basally, collar-like ring and pear-shaped distal part bearing minute megaseta, ‘x’ and ‘y’ setae absent [gonostylus without strong setae basally, simple, relatively narrow (or with large extension in distal half in *Archaeochlus bicirratus* Brundin), with distinct megaseta and the ‘x’ and ‘y’ setae].

All the extant representatives of the *Archaeochlus* cluster share an unusual ecology and mating behaviour (Freeman, 1964; Brundin, 1966; Cranston et al., 1987, 2002; Cranston and Edward, 1998). The adult male of the fourth genus, *Afrochlus*, morphologically particularly differs within the cluster, demonstrating characters typical of chironomids with a limited ability to fly or non-flying adults (Cranston and Edward, 1998). The characters best separating *Afrochlus* from other genera compared are the small reniform eyes, the abbreviated antenna with the reduced plume and indistinctly separated palpomeres, as well as the set of hypopygial features, as given in Table 2.

4.3. *Burmochlus* as the oldest known true Podonominae

The oldest known fossil Chironomidae, often displaying a mosaic of characters of the subfamily importance (derived from or defined mostly on the basis of extant taxa), may cause a hesitation in their diagnostics. According to some authors, the oldest Podonominae and Tanypodinae are morphologically particularly hard to distinguish from each other (Kalugina and Kovalev, 1985) due to weak separation in the past, the trend being supposed to last up to the Early Cretaceous (Lukashevich and Przhiboro, 2018). The genera ascribed to one or both of these subfamilies, using the “transitional diagnostic characters” or character combination, supported that hypothesis (Lukashevich and Przhiboro, 2018).

Since when the genus *Libanochlites* Brundin has been described (Brundin, 1976), several concepts on the time of divergence of the Podonominae and a possible oldest member of this subfamily were presented. However, *Libanochlites* and several genera describedlater were at first included in Aphroteniinae/Podonominae (*Libanochlites*), or in Podonominae/Buchonomyiinae (*Dungeyella* Jarzembowski, Azar *et* Nel in Jarzembowski et al., 2008), but finally placed in Buchonomyiinae (Baranov et al., 2019); a subfamily status of several taxa remains open, i.e. these

Table 2

Comparison of diagnostic characters of male *Burmochlus* gen. nov. and related genera of the *Archaeochlus* cluster: *Archaeochlus* Brundin, *Austrochlus* Cranston and *Afrochlus* Freeman. [1]Brundin (1966), [2]Cranston et al. (1987), [3]Cranston and Edward (1998), [4]Cranston et al. (2002).

Character/genus	*Burmochlus*	*Archaeochlus*[1,2]	*Austrochlus*[1,2,4]	*Afrochlus*[1,3]
Total length (mm)	2.3	3–6	4.2–6.2	3.6–4.8
Wing length (mm)	1.2	1.9–3.3	2.2–3.3	1.7–2.0
Eyes	bare, reniform, with short wedge-like dorsomedian extension	bare, with parallel-sided dorsomedian extension	bare, with parallel-sided dorsomedian extension	bare, reniform, with slight dorsomedian extension
Antenna	14 flagellomeres; plume well-developed; ultimate flagellomere with strong apical seta; AR ~1.3	14 flagellomeres; plume well-developed; ultimate flagellomere with strong apical seta; AR 0.25–1.15	14 flagellomeres; plume well-developed; ultimate flagellomere with strong apical seta; AR 0.99–1.27	14 flagellomeres; plume reduced to single whorl; ultimate flagellomere longer than, but indistinctly separated from penultimate, without strong apical seta; AR 0.07–0.09
Proboscis	elongated, as long as head capsule, ~200 μm long	extended	extended	extended
Palp	5 palpomeres, 3rd palpomere without sensilla capitata	5 palpomeres, 3rd palpomere with subapical deep pit containing up 10 sensilla capitata	5 palpomeres, 3rd palpomere with subapical deep pit containing up 10 sensilla capitata	5 palpomeres, but distal palpomeres short and partly fused; palpomere 1 bilobed, 3rd palpomere with apically deep pit containing numerous sensilla capitata
wing	Membrane without macrotrichia, covered with simple, bi- or trifid spinulae-like microtrichia; R_{2+3} (or possibly R_3 alone) present, but vestigial, visible as semitransparent streak, starting together with R_{4+5}, fading near end of R_1; costa slightly extending beyond end of R_{4+5} to wing apex; subcosta developed but apically fading; VR close to 1.0. Alula without setae; squama with process bearing bunch of several long setae; anal lobe well-developed, rounded.	Membrane with good visible micro- and macrotrichia; R_{2+3} completely absent; costa extending beyond end of R_{4+5} to wing apex; subcosta strongly developed, but apically attenuated; VR close to 1.0. Alula and squama with setae; anal lobe strongly developed.	Membrane with good visible micro- and macrotrichia at least towards the apex of cell r_{4+5},; usually in apex of m_{1+2}; R_{2+3} absent; costa extending beyond end of R_{4+5} to wing apex; subcosta strongly developed, but apically attenuated; VR close to 1.0. Alula and squama with setae; anal lobe strongly developed.	Membrane without macrotrichia, with good visible microtrichia; R_{2+3} absent; costa extending weakly beyond end of R_{4+5} to wing apex. Alula with 1 seta; squama with few setae; anal lobe gently rounded.
Legs	Pulvilli absent. Claws simple, with inner spine-like setae. Hind vestigial tibial comb with a couple of short teeth. LR_1 0.69.	Pulvilli absent. Claws with inner spines or teeth. Hind tibial comb with 4–8 spines. LR_1 close to 0.5.	Pulvilli absent. Claws with inner spines or teeth. Hind tibial comb with 4–8 spines. LR_1 0.51–0.62.	Pulvilli present. Claws with inner spine. Hind tibial comb with 4–8 spines. LR_1 close to 0.5.
Hypopygium	Segment IX broad and relatively short, semicircular, with posterolateral margins bearing strong setae, median area with shorter setae; anal point stout, parallel-sided at base, slightly tapering from mid-length towards incised apex, with longitudinal groove. Superior volsella broadly fused with gonocoxite, extensive, with distinct protuberances on median margin and stout posterolateral process, all with strong curved setae. Median volsella absent. Inferior volsella broad at base, reaching end of gonocoxite, with several strong setae on median margin and apex; posterolateral part translucent. Gonostylus strongly setose basally, with collar-like ring at 2/3 length, and pear-shaped distal part tapering towards narrow tip bearing minute megaseta, without ‘x’ and ‘y’ setae.	Segment IX broad and relatively narrow (short), with tendency for the median area to be bare or have shorter and weaker setae than elsewhere; without anal point (but with distinctly extending median portion of tergite IX in *A. bicirratus* Brundin and *A. drakensbergensis* Brundin, and with slightly extending median portion of tergite IX in *A. biko* Cranston, Edward *et* Colless). Gonocoxite with 2–3 volsellae, median volsella present only in one species; superior volsella more ventro-lateral on gonocoxite than inferior volsella. Gonostylus simple, long, relatively narrow (or with large extension in distal half in *A. bicirratus* Brundin), bearing apical megaseta and the ‘x’ and ‘y’ setae.	Segment IX typically annulate but excised ventrally, containing large, broad inverted U- or V-shaped sternapodeme; without anal point (but with slightly extending median portion of tergite IX in *A. brundini* Cranston, Edward *et* Colless and *A. parabrundini* Cranston, Edward *et* Cook); phallapodeme narrow, elongate, with poorly sclerotized apodeme lobe, extending into gonocoxite. Gonocoxite with two volsellae. Gonostylus simple, long, relatively narrow, bearing apical megaseta and the ‘x’ and ‘y’ setae	Segment IX comprising a very narrow sclerotized lateral strap, slightly broader ventrally, broad and deep dorsally although poorly sclerotized medially with patches of setae, without anal point (but with extending median portion of tergite IX in *A. harrisoni* Freeman). Apodemes (strongly sclerotized, particularly the phallapodeme and aedeagal lobe. Gonocoxite with 2 volsellae: distal (? superior volsella) extends from strongly setose, anteriorly directed, lobe in medio-dorsal position on gonostylus via sclerotized ridge to posteriorly directed mesal lobe; more apical lobe (? inferior volsella) ovoid, densely setose, with group of stout setae lying at base of lobe. Gonostylus simple, long, sinuous, bearing an apical megaseta, densely setose without discernible ‘p’, ‘x’ or ‘y’ setae.

defined as Tanypodinae/Podonominae (*Podonomius* Kalugina in Kalugina *et* Kovalev, 1985; *Langtonius* Lukashevich *et* Przhiboro, 2018) or is considered debatable being based on questionable name assignation of immatures or adults alone within the same genera independently and/or based on more or less complete specimens (Veltz et al., 2007). As a result, all the fossil genera, at first ascribed to Podonominae, one by one were postulated to be excluded from this subfamily. Also *Libanochlites*, defined previously as the unique remaining Mesozoic Podonominae, was finally transferred to Tanypodinae (Azar et al., 2008). In a view of this concept, the subfamily Podonominae was concluded as not recorded before the Cenozoic (Azar et al., 2008). Our Cretaceous record of *Burmochlus* — the genus evidenced as the member of the *Archaeochlus* cluster, now refutes, however, this hypothesis and shows that the subfamily Podonominae should be dated back to the turn of the Lower and Upper Cretaceous at least. The record is consistent with results obtained by Cranston et al. (2010: fig. 2, 3; 2012: fig. 2, 3), where the divergence time of the *Archaeochlus* cluster, estimated on the basis of molecules derived from extant chironomids, was dated back to the "mid-Cretaceous".

5. Conclusions

An aim of our study was to evidence that true Podonominae existed in the Cretaceous. Indeed, a wing venation pattern found in *Burmochlus*, crucial in understanding the subfamily diagnostics, may support close relations between Podonominae and Tanypodinae. However, a set of characters of the head and genital apparatus, common for *Burmochlus* and several close genera of the *Archaeochlus* cluster, all included in the Podonominae, clearly shows that this subfamily should be dated back to the turn of the Lower and Upper Cretaceous at least. The new genus can presumably be considered the most plesiomorphic within the group, possibly even predating the ancient *Archaeochlus*.

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