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Myanmaro primus gen. *et* sp. nov., the first orthoclad (Diptera: Chironomidae) from Cretaceous Burmese amber

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Abstract

A fossil genus *Myanmaro* **gen. nov.**, with a species *M. primus* **sp. nov.** (Diptera, Chironomidae) is described from mid-Cretaceous Burmese amber (~100 Ma). The adult male of the new species shows the wing venation pattern lacking a cross-vein MCu, the fore leg ratio lower than 1, and the gonostylus folded inwards - features typical of the subfamily Orthocladiinae. A bifid gonostylus, with an articulate, likely movable inner branch, is the character indicating a close relationship between *Myanmaro* and *Diplocladius* Kieffer, 1908, the latter genus previously postulated as an early lineage in Orthocladiinae. Several characters, i.e. the structure of tergite IX and the anal point, are defined as generic autapom orphies for *Myanmaro*. A combination of the shape of hypopygial volsellae (or their absence) and the lack of tibial combs also separate this genus from related extant Orthocladiinae and from the only known Cretaceous extinct orthoclad genus *Lebanorthocladius* Veltz, Azar *et* Nel, 2007.

Key words: Diptera, Chironomidae, Orthocladiinae, systematics, Mesozoic, Burmite, Myanmar

Introduction

Based on the number of described taxa counted by Pape *et al.* (2011) and those published later, the family Chironomidae is the most species-rich group of aquatic insects and one of the largest dipteran families, with nearly 7,500 specific and 550 generic names. Within 12 chironomid subfamilies, the Orthocladiinae, commonly called "orthoclads", is the most diverse group. This subfamily includes nearly half the number of described extant chironomid species, clustered in 174 genera and 36 subgenera (Ashe & O'Connor 2012). In contrast to the well-studied extant fauna, Orthocladiinae are merely known from a couple of names coming from the Cretaceous. Unfortunately, the specific names by Boesel (1937) introduced on the basis of inclusions from Upper Cretaceous Canadian amber and originally attributed to the subfamily are suggested to be treated as Orthocladiinae with uncertain generic placement (Veltz *et al.* 2007, Zelentsov *et al.* 2012). The orthoclad evidenced as the oldest known and dated back to *ca.* 130 Ma, *Lebanorthocladius furcatus* Veltz, Azar *et* Nel, 2007, is thus the only representative of this subfamily recorded from the Cretaceous and described precisely enough to be regarded as definable on the background of potential further new taxa (Veltz *et al.* 2007). On the other hand, relatively high numbers of orthoclad specimens were reported from the Cretaceous, but determined only to the subfamily level (e.g. Kalugina 1974, 1976; Azar & Nel 2010).

Burmese amber, often referred to as "Burmite", is dated back to the beginning of the Upper Cretaceous (early Cenomanian) or perhaps even earlier, showing traces of redeposition, and thus being proposed to be called "mid-Cretaceous" (Shi *et al.* 2012, Smith & Ross 2018, Zhang *et al.* 2018). This amber, mined in the Hukawng Valley in Kachin State, Myanmar, until recently was regarded as rare. But new mines have produced scores of new amber specimens, and over the past several years the number of taxa described from Burmese amber has significantly

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increased. According to the most recently updated checklist by Ross (2018), more than 1,000 species of fossil organisms classified in 777 genera, 525 families and 102 orders are known. Insects, as the most diverse group, are represented by 30 orders, 353 families, 556 genera and 693 species, including Diptera, with 47 families, 99 genera and 127 species (op. cit.). However, only two Chironomidae species have been described from Burmese amber to date. This could be due to the poor preservation of minute chironomid inclusions or the difficulty of examining their extremely small diagnostic structures. But it certainly is not an evidence of a low species richness of these dipterans in the mid-Cretaceous (cf. Grimaldi *et al.* 2002; authors' unpubl. data). The two chironomid species described from Burmese amber are placed in the extinct genus *Furcobuchonomyia* Baranov, Góral *et* Ross, 2017 (*F. saetheri* Baranov, Góral *et* Ross, 2017 and *F. pankowskii* Giłka *et* Zakrzewska, 2017) and in the subfamily Buchonomyiinae (Baranov *et al.* 2017, Giłka & Zakrzewska 2017). It was preliminarily estimated that this subfamily is abundant in amber from Myanmar, being more diverse in the Cretaceous (Zakrzewska & Giłka 2018, Baranov *et al.* 2019), contrary to the extant fauna merely known from three species worldwide (Brundin & Sæther 1978, Murray & Ashe 1985, Andersen & Sæther 1995). This clearly shows that the species richness or subfamily composition of Cretaceous and recent Chironomidae varies widely, with other differences noted previously, e.g. the extant second largest subfamily Chironominae absent or extremely rare in Cretaceous resins (cf. Kalugina 1974, 1976; Azar & Nel 2010). Our preliminary inventories confirm that Orthocladiinae appear among chironomid specimens found in Burmese amber. Nevertheless, no specific description of an orthoclad has so far been published from this deposit until now.

Material and methods

Origin, processing and deposition of the type material. The specimen examined is the inclusion preserved in Burmese amber (mid-Cretaceous, ~100 Ma), mined in the Hukawng Valley in Kachin State, Myanmar. The amber was ground and polished manually so that the inclusion could be viewed as clearly as possible and its diagnostic structures could be studied. Measurements of the specimen are in micrometres, except for the total length and the wing length given in Table 2 (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 and palpomeres were rounded off to the nearest 5 µm. The antennal, venarum and hypopygium ratios (AR, VR_C, VR_{Cu}, HR, HV) 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 PZO Biolar SK14 microscope and 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.

Geological context (IR spectrum). Today, infrared spectra obtained from amber, with reference curve numbers registered and stored in collection archives, is the procedure recommended for museum materials, particularly for the name-bearing specimens/inclusions to confirm their origin and to consolidate validity of new taxa described. For supporting the examined amber's identification, FT-IR spectrum (ATR, *Attenuated Total Reflection*) was presently obtained using the IS10 spectrometer (diamond crystal at resolution 4 cm^{-1}, with application of advanced ATR correction) in the Laboratory of the International Amber Association, Gdańsk, Poland (IAA). The spectrum (Fig. 1) indicates that the amber chunk analysed comes from the Cretaceous (Wagner-Wysiecka, pers. comm.). Relative to several samples compared, the analysed spectrum peaks at wavenumber values (cm^{-1}) ~1725, ~1455, ~1375, ~1025 and ~975 are the same or fall in the range typical of Burmite, while slight deviations at wavenumber bands ~1230 and ~1150 in the analysed sample are similar to those obtained for Lebanese amber (deviation range 1–4 and 1–5, respectively) and other Burmite samples compared (1–5 and 1–18). Thus, the presently examined spectrum shows characters typical of Burmite, and a detailed analysis of available data displays an interesting case of its spectral characteristics (Wagner-Wysiecka, pers. comm.).

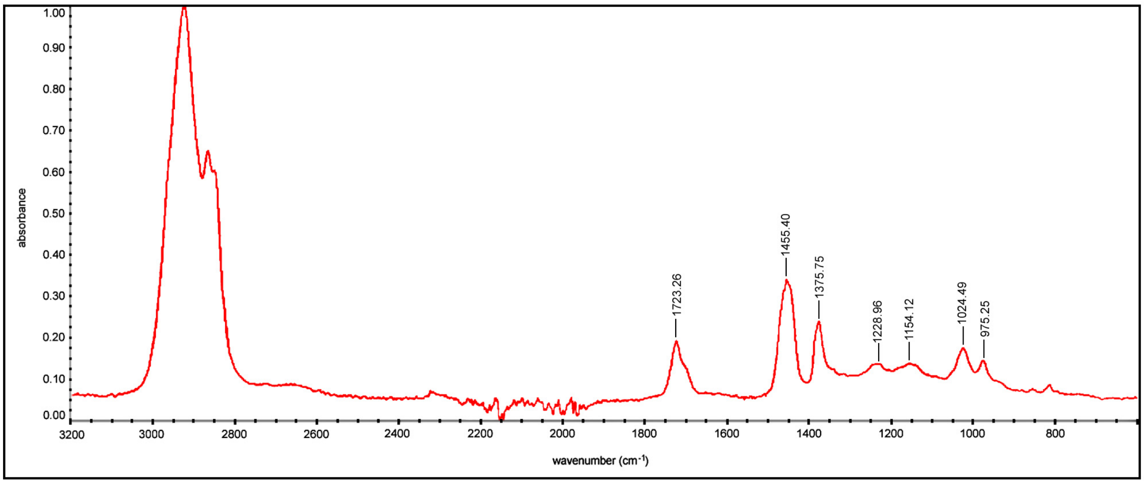

FIGURE 1. IR (ATR) spectrum (no. 13998 IAA) obtained from examined amber (mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar).

Results

Family: Chironomidae Newman, 1834
Subfamily: Orthocladiinae Kieffer, 1911

Myanmaro gen. nov.

Type species: *Myanmaro primus* sp. nov. (by present designation).

Derivatio nominis. From Myanmar, the amber's country of origin; noun suffixed with -o (masculine, 3rd declension in Classic Latin).

Diagnosis. Adult male. Small, total length ~2.2 mm, wing length: ~1185 µm. Eyes bare, with wedge-like dorsomedian extension. Antepronotum with setae in lateral position, Ac minute, Dc bi- or multiserial, Scts uniserial, Pa bristle-like, postnotum bare. Anal lobe of wing well-developed, squama with setae, membrane without setae, with fine punctation. Tibial combs absent; pseudospurs on mid leg tarsomeres only (absent on fore and hind leg tarsi); claws strongly curved apically. Tergite IX extensive, with membranous posterior shoulders and longitudinal double keel diverging into median pit; anal point broad at base, with membranous lateral parts and well-pigmented median section. Gonostylus bifurcate: main branch with beak-shaped apex bearing short subapical setae, megaseta absent; inner branch thumb-shaped, without setae, connected by distinct articulation with main branch. Inferior volsella with head-like dorsal part and extensive ventral lobe covered with dense protuberances and setae.

Myanmaro primus sp. nov.
Figures 2–4

Type material. Holotype, inventory no. F1a LSZ DIZP: adult male (complete specimen, thorax deformed, Fig. 2A, B) preserved in 11.5 x 8.5 x 3 mm piece of Burmese amber (mid-Cretaceous, ~100 Ma, IR spectrum no. 13998 IAA, Fig. 1) mined in Hukawng Valley, Kachin State, Myanmar. Syninclusion: Chironomidae adult (inventory no. F1b LSZ DIZP).

Derivatio nominis. This is the first described representative of the chironomid subfamily Orthocladiinae from Cretaceous Burmese amber.

Diagnosis. As for the genus.

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

Total length ~2.2 mm. Wing length: ~1185 µm. Total length/wing length ratio ~1.85.

Colouration. Body, including antenna, legs and haltere dark brown to black. Wing membrane yellowish, hyaline; C, M and radial veins distinctly darker, brown.

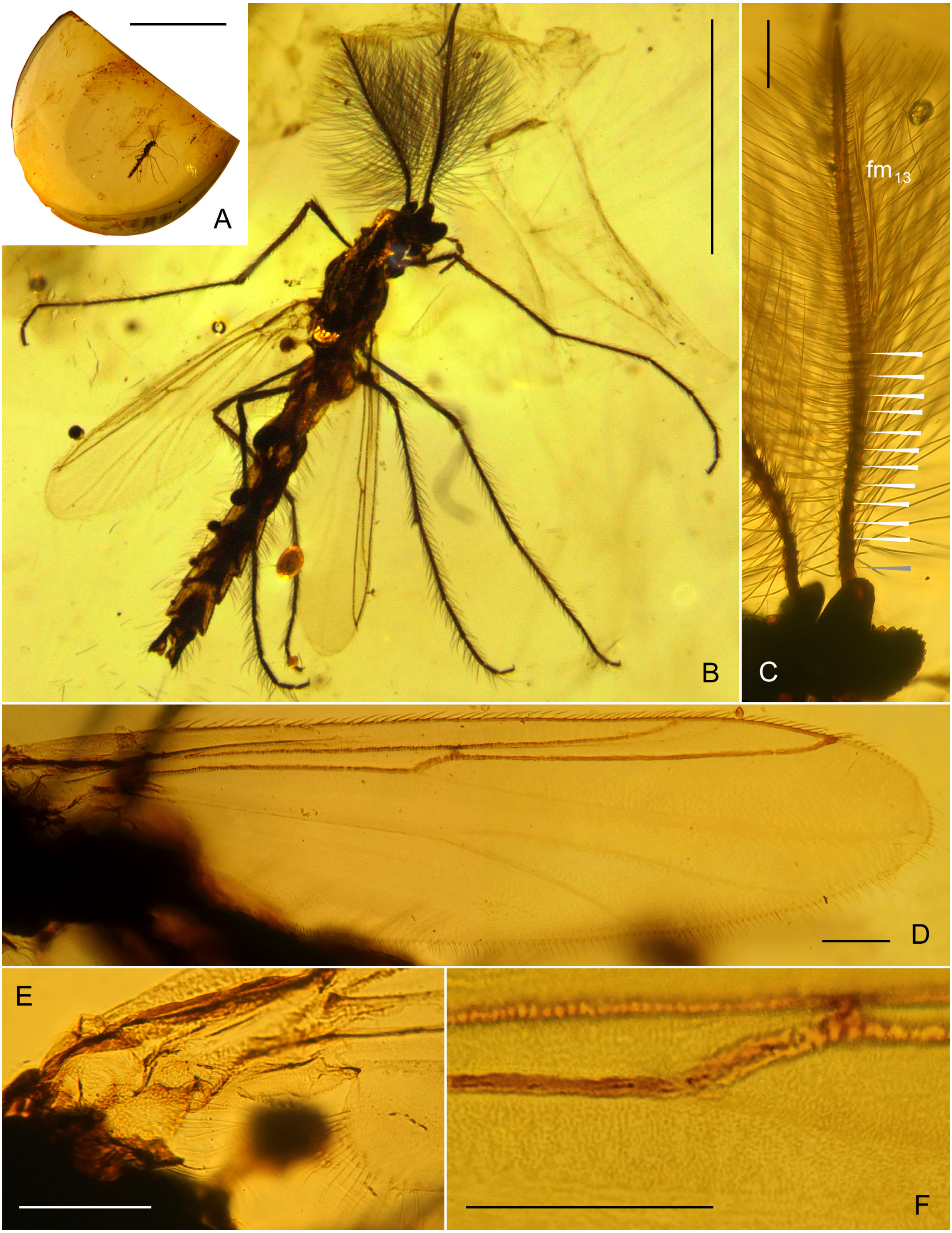

FIGURE 2. *Myanmaro primus* **sp. nov.**, holotype, adult male (F1a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar): **A** inclusion in amber, **B** habitus, **C** head and antenna (white arrows: borders between flagellomeres, grey arrow: incomplete fusion), **D** wing, **E** base of wing, **F** punctation of wing membrane below RM area. Scale bars: 5 mm (A), 1 mm (B), 100 µm (C–F).

Head (Fig. 2B, C). Eyes bare, with bluntly wedge-like dorsomedian extension. Antenna with 13 weakly discernible flagellomeres, proximal flagellomeres incompletely fused (Fig. 2C), ultimate flagellomere 468 µm long, AR ~1.3; pedicel pubescent, plume well-developed. Clypeals at least 12, numerous on clypeus margin. Length of palpomeres 3–5 (µm): ~75, 70, 130 (proximal palpomeres unobservable).

Thorax chaetotaxy. Aps 5–6 on each side laterally; Ac 4 pairs at least, minute; Dc 25 at least on each side, bi- or multiserial; Scts 4 at least; Pa 1 at least on each side, bristle-like. Postnotum bare. Other setae unobservable due to deformation of thorax.

Wing (Fig. 2D–F). Fully-developed, ellipse-shaped (Fig. 2D), with anal lobe distinct (Fig. 2E). Veins ending as follows (in order from base to tip): An and Sc (distal sections fading), Cu_1, R_1, R_{2+3}, M_{3+4}, R_{4+5}, M_{1+2}; FCu under RM; An reaching FCu at most. VR_C ~2.2. VR_{Cu} ~1.1. Setae present only on wing margin incl. costa, other veins bare. Brachiolum with several setal tubercles (1 long seta preserved). Squama with 10 setae (Fig. 2E). Wing membrane without setae, but with fine punctation forming an ornament, as shown on Fig. 2F.

Legs (Figs 2B, 3A–H). Tibial combs absent. Spurs and pseudospurs smooth, straight or slightly curved. Fore leg tibia with short spur (12–15 µm) (Fig. 3A, B); mid leg tibia with two spurs (15 and 25 µm long) (Fig. 3C); hind leg tibia with two unequally long spurs (25 and 40 µm long) and shorter (~20 µm) pseudospur between (Fig. 3D). Pseudospurs on mid leg tarsomeres 1–4 arranged as follows: ta_1 with 2 pseudospurs (Fig. 3E), ta_2: 1 (Fig. 3F), ta_3: 1 (Fig. 3G), ta_4: 3 pseudospurs (Fig. 3H); pseudospurs on tarsomeres of fore and hind legs absent. Pulvilli absent. Claws simple, strongly curved apically. For length of leg segments and leg ratios see Table 1.

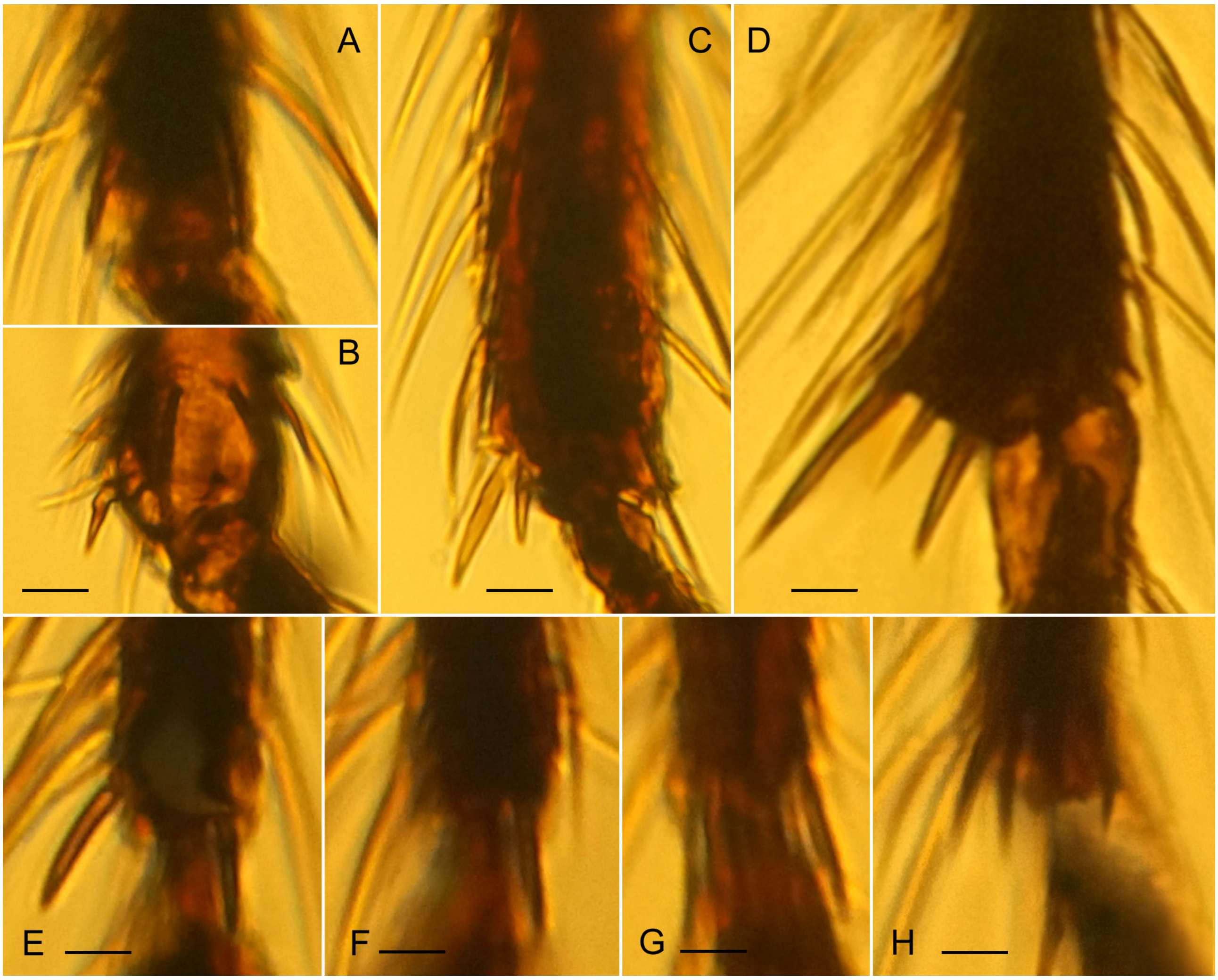

FIGURE 3. *Myanmaro primus* **sp. nov.**, holotype, adult male (F1a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar): **A–D** tibial spurs of fore (**A**, **B**), mid (**C**) and hind leg (**D**); **E–H** pseudospurs of mid leg tarsomere 1 (**E**), 2 (**F**), 3 (**G**) and 4 (**H**). Scale bar: 10 µm.

FIGURE 4. *Myanmaro primus* **sp. nov.**, holotype, adult male (F1a LSZ DIZP, mid-Cretaceous Burmese amber, ~100 Ma; Hukawng Valley, Kachin State, Myanmar). Hypopygium in dorsal (**A**) and ventral view (**B**), **C** gonocoxite (grey) and gonostylus (blue) with articulate lobe (green), **D** distal part of anal tergite and anal point, **E** inferior volsella. Scale bars: 50 µm (A, B), 25 µm (C–E).

TABLE 1. Lengths of leg segments (µm) and leg ratios of male *Myanmaro primus* **sp. nov.**

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	425	560	425	255	195	120	90	0.76
p_2	570	570	310	180	140	75	65	0.54
p_3	415	610	370	190	140	80	80	0.61

Hypopygium (Fig. 4A–E). Tergite IX extensive, with membranous posterior shoulders surrounding subtriangular anal point, and longitudinal double keel diverging into median pit with two minute protuberances and ribs running towards anal point apex; anal point broad at base, with membranous lateral parts and well-pigmented median section, as show in Fig. 4A, B, D. Gonocoxite ~205 µm long, slender but slightly swollen in proximal section, with two setae placed near apex ventrally. Gonostylus bifurcate: main branch ~75 µm long, curved at mid length, with slightly broadened distal section, apex beak-shaped bearing 2 short subapical setae, megaseta absent; inner branch ~25 µm long, thumb-shaped, without setae, connected by distinct articulation with main branch (Fig. 4A–C). Inferior volsella ~70 µm long and 35 µm wide, with head-like dorsal part and extensive ventral lobe covered with dense protuberances and setae (Fig. 4A, B, E). HR ~2.7, HV ~2.9.

Discussion

Several characters of the examined adult male, i.e. the lack of the wing MCu crossvein, the LR_1 ratio lower than 1, and the gonostylus folded inwards, clearly indicate that *Myanmaro* belongs to the subfamily Orthocladiinae. This most speciose subfamily still has, however, weakly-understood internal structure with a two-tribe system of Orthocladiini and Metriocnemini (Cranston *et al.* 1989, 2012). Thus, until the proposed division and the phylogenetic relationships between Orthocladiinae genera are tentative (op. cit.), a tribal membership of *Myanmaro* must remain open.

A set of features crucial in the delimitation of *Myanmaro* and several presumably close Orthocladiinae genera is presented in Table 2. The head, thorax, wing, legs, and male hypopygium characters compared suggest that the new genus is close to the fossil *Lebanorthocladius* Veltz, Azar *et* Nel, 2007 and several extant, primitive genera that all have a bifurcate gonostylus: *Eurycnemus* van der Wulp, 1874, *Euryhapsis* Oliver, 1981, *Brillia* Kieffer, 1913, *Xylotopus* Oliver, 1982, *Plhudsonia* Sæther, 1982 and, more likely, *Diplocladius* Kieffer, 1908. The latter genus was postulated as an early branch in Orthocladiinae, though, as requiring to be sampled for its DNA, it was not treated in the Bayesian tree presented by Cranston *et al.* (2012). Nevertheless, the sets of morphological crucial characters presently analysed indicate that *Diplocladius* and *Myanmaro* show the largest number of common features within the genera compared (Table 2).

The bi- or trifid gonostylus consisting of non-movable, stiffly connected branches/lobes is known from phylogenetically distant Chironomidae groups (cf. Baranov *et al.* 2017, Giłka & Zakrzewska 2017), as well as from other related nematocerans (e.g. Dominiak *et al.* 2014, Szadziewski *et al.* 2015). This character should be thus regarded as an adaptation developed as an effective tool for junction of male–female copulatory structures during mating rather than a phylogenetic trend or character state of family, subfamily or tribe importance. However, it can certainly be analysed within taxa of lower rank independently, e.g. in/between Orthocladiinae genera or species. Interestingly, the bilobed gonostylus, with the articulate, likely movable inner branch (Fig. 4A–C), is a rare character known from *Diplocladius* and *Myanmaro*.

The genital apparatus of *Myanmaro* has also a unique structure of its tergite IX, with the double keel diverging into median pit, and the anal point broad at base, bearing membranous lateral parts and well-pigmented median section (Fig. 4A, D). The inferior volsella has a head-like dorsal part and extensive ventral lobe covered with protuberances and setae (Fig. 4A, B, E), while the superior volsella is completely undeveloped. The gonostylus bears short setae on a beak-shaped apex lacking a megaseta (Fig. 4A–C). The structure of tergite IX and the anal point can be defined as generic autapomorphies for *Myanmaro*. The shape of hypopygial volsellae, or their absence, form a unique character combination unknown from other genera.

TABLE 2. Comparison of diagnostic characters of male *Myanmaro* **gen. nov.** and related Orthocladiinae genera. [1]Veltz et al. (2007), [2]Cranston et al. (1989), [3]Oliver (1981), [4]Oliver (1985), [5]Sæther (1982, 1992).

character/genus	***Myanmaro***	***Lebanorthocladius***[1]	***Diplocladius***[2]	***Eurycnemus***[2]	***Euryhapsis***[2,3]	***Brillia***[2]	***Xylotopus***[2,4]	***Plhudsonia***[5]
wing length (mm)	1.19	0.84	up to 2.9	up to 4.5	up to 2.8	up to 3.3	up to 5.0	up to 2.3
eye (hairs / pubescence; dorsomedian extension)	bare; wedge-like	bare; small	hairy; slight or absent	bare; long, almost parallel-sided	bare, or partly pubescent; long, almost parallel-sided	bare; long, almost parallel-sided	bare or partly pubescent; almost parallel-sided	bare; bluntly wedge-like
thorax chaetotaxy	Aps lateral, Ac minute; Dc bi- or multiserial; Pa 1 at least, bristle-like; Scts 4 at least	Aps ?, Ac and Dc not visible, probably absent	Aps lateral, Ac short, often difficult to see; Dc uniserial; Pa 1–2; Su 0. Scts uniserial	Aps median & lateral, Ac absent; Dc and Pa multiserial; Su 2–3; Scts multiserial	Aps median & lateral, Ac absent; Dc and Pa bi- to multiserial; Su 1; Scts multiserial	Aps median & lateral, Ac absent; Dc and Pa uni- to multiserial; Su 1; Scts multiserial	Aps median & lateral, Ac absent; Dc uni- to multiserial; Pa multiserial; Su 1; Scts multiserial	Aps lateral, Ac short or vestigial; Dc 7–8; Pa 2–3; Scts uniserial
wing	anal lobe distinct, membrane without setae, squama with setae	anal lobe not produced, membrane and squama without setae	anal lobe right-angled, membrane without setae; squama without or with few setae	anal lobe rounded obtuse; membrane with long setae; squama with setae	anal lobe rounded; membrane with setae; squama with setae	anal lobe oblique; membrane with setae; squama with setae	anal lobe rounded; membrane with setae; squama with setae	anal lobe slightly produced; membrane without setae; squama with setae
p_3 tibial comb	absent	present	present	absent	present	present	present	present
gonostylus	bifurcate; inner branch connected by distinct articulation with main branch	bifurcate, folded inward, short	bifurcate; inner branch appearing to articulate with main branch bearing simple setae	bifurcate, inner branch with stout apical lamellate setae and long subapical setae	bifurcate, inner branch with lamellate setae	bifurcate, main branch without lamellate setae	bifurcate	bifurcate
megaseta	absent	absent	absent	absent	absent	absent	1 or 2	absent
anal point	broad at base, subtriangular, with membranous lateral parts and well-pigmented median section	large, triangular	short, triangular	absent	absent	absent	absent	low rounded hump instead of anal point, sometimes short AP ending with spine
superior volsella	absent	(?) large, digitiform	absent	well-developed, elongate, narrow	well-developed, elongate, narrow	well-developed, elongate, narrow	elongate, narrow	long
inferior volsella	with head-like dorsal part and extensive ventral lobe	apparently absent	long, lobe-like	adpressed to inner margin of gonocoxite	adpressed to inner margin of gonocoxite	adpressed to gonocoxite	strongly diverging medially from gonocoxite	long, lobe-like

Except for the hypopygium structure, the male of *Myanmaro* can be separated from the compared Orthocladiinae genera by a set of other features, namely, the bare eyes, with distinct wedge-like dorsomedian extensions, the antepronotum bearing only lateral setae, the thorax chaetotaxy (lateral antepronotals, minute acrostichals, bi- or multiserial dorsocentrals, scutellars in a single row), the wing with the anal lobe well-developed and with the membrane without setae, the lack of tibial combs (Fig. 3A–D), and the arrangement of pseudospurs on mid leg tarsomeres (Fig. 3E–H).

Males of only three mentioned genera, *Lebanorthocladius*, *Diplocladius* and *Plhudsonia*, similarly to *Myanmaro*, have the hypopygial anal point developed, but those of the first genus have a tibial comb of hind leg developed, the anal lobe of wing not produced, the superior volsella is present, but the inferior volsella is absent. The two latter genera have a similarly structured gonostylus (bifurcate) and inferior volsellae, the antepronotum bearing only lateral setae, and the wing membrane bare. However, the *Diplocladius* males have hairy eyes, the tibial combs developed and the anal point short and triangular (Cranston *et al.* 1989). The male of *Plhudsonia*, like *Myanmaro*, has bare eyes, with wedge-like dorsomedian extension and vestigial acrostichals, but contrary to *Myanamro*, the tibial combs are present, the superior volsella is developed, and a low rounded hump sometimes ending with a spine is observed instead of the anal point (Sæther 1982, 1992). In all other compared Orthocladiinae genera, i.e. *Eurycnemus*, *Euryhapsis*, *Brillia* and *Xylotopus*, the eyes are bare, with long, almost parallel-sided dorsomedian extensions, but the anal point is not developed, the superior volsella often is present, the acrostichals are absent, and the wing membrane is covered with setae (Cranston *et al.* 1989) (Table 2).

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