

## Short communication

A new species of fossil *Corethrella* (Diptera, Corethrellidae) from mid-Cretaceous Burmese amberViktor Baranov <sup>a,\*</sup>, Gunnar M. Kvifte <sup>b</sup>, Patrick Müller <sup>c</sup>, Ximena E. Bernal <sup>b,d</sup><sup>a</sup> LMU Munich Biocenter, Department of Biology II, Großhaderner Str. 2, 82152, Planegg-Martinsried, Germany<sup>b</sup> Department of Biological Sciences, Purdue University, 915 West State Street, IN-47906, West Lafayette, United States<sup>c</sup> Amber Study Group, c/o Geological-Palaeontological Museum of the University of Hamburg, Bundesstraße 55, 20146, Hamburg, Germany<sup>d</sup> Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama

## ARTICLE INFO

## Article history:

Received 14 February 2019

Received in revised form

22 April 2019

Accepted in revised form 2 May 2019

Available online 9 May 2019

## Keywords:

Eavesdropping

Fossil

Frog-biting midges

Micropredator

Taxonomy

## ABSTRACT

Frog-biting midges (Diptera: Corethrellidae) are hematophagous flies in which females feed on anuran blood using the mating calls produced by calling male frogs. This family is of large ecological, evolutionary and ethological interest, but its geological history is poorly known. We describe a new species of frog-biting midge (Diptera, Corethrellidae), *Corethrella patula* sp. nov., from mid-Cretaceous Burmese amber (ca. 99 Ma). This new species is distinct from *Corethrella andersoni*, known from the same deposit, differing in having more slender mid femora and a triangular bifid tarsal segment 5 without scales. These two species, however, share an apparent synapomorphy in the wing: R<sub>2</sub> vein diverting from R<sub>2+3</sub> at 75° angle in relation to R<sub>3</sub>. The well-preserved male genitalia of the new species suggest *C. patula* and *C. andersoni* are a distinct, early lineage not easily placeable within either of the described subgenera of *Corethrella*.

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## 1. Introduction

The Cretaceous was a pivotal period in the history of the Earth given that it marks the origin of the biosphere as we know it (Butler et al., 2009). Many biotic interactions, such as plant-pollinator relationships (Angiosperm plants and insects) and brood care adaptations (e.g. cockroaches, ants), emerged during this period (Anderson, 2009; Grossnickle and Polly, 2013; Wang et al., 2015b). Another set of important biotic interactions that apparently emerged in the Cretaceous were host-parasite relationships between blood-feeding flies (Diptera) and vertebrates (Martinis-Neto, 2003; Borkent et al., 2013; Borkent and Grimaldi, 2004). The oldest records of true mosquitoes (Culicidae), biting midges (Ceratopogonidae), sand flies (Psychodidae: Phlebotominae) and horse flies (Tabanidae) are all of Cretaceous origin (Hennig, 1972; Martinis-Neto, 2003; Borkent et al., 2013; Borkent and Grimaldi, 2004).

Another group of bloodfeeding Diptera that made its first appearance in the Cretaceous is the frog-biting midges (Diptera, Corethrellidae) (Szadziewski, 1995). This group is a small

monobasic family of culicomorph Diptera represented by a single genus *Corethrella* Coquillett, 1902a (Borkent, 2008; Borkent and Gafe, 2012). Like many other Culicomorpha, Corethrellidae are haematophagous micropredators of vertebrate prey. Corethrellids, in particular, are specialized on feeding on frogs (McKeever, 1977; McKeever and Hartberg, 1980.; Bernal et al., 2006, 2007; Gafe et al., 2008). Together with a few Culicidae species from the genera *Uranotaenia* Lynch Arribálzaga, 1891, *Culex* Linnaeus, 1758 and *Mimomyia* Theobald, 1903, Corethrellidae are unique among bloodsucking Diptera in locating their prey mainly using sound rather than chemical cues (McKeever, 1977; McKeever and Hartberg, 1980; Toma et al., 2005; Borkent, 2008; Bartlett-Healy et al., 2008; Bernal and de Silva, 2015; Camp et al., 2018). Being eavesdropping micropredators of frogs and vectors of trypanosome blood parasites (Johnson et al., 1993; Bernal and Pinto, 2016), frog-biting midges are an important model system in acoustic ecology and co-evolution of prey, vectors and micropredators (Bernal et al., 2006; Gafe et al., 2008; de Silva et al., 2015; Leggett et al., 2018).

The genus *Corethrella* includes 110 species to date and has a semi-cosmopolitan distribution with the vast majority of extant species restricted to the tropics and subtropics (Borkent, 2008; Borkent and Gafe, 2012; Amaral and Pinho, 2015; Wang et al.,

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2015a; Baranov et al., 2016; Caldart et al., 2016; Kvifte and Bernal, 2018). The current distribution and phylogenetic relationships of lineages in this family indicate that they originated in the South-western Pacific. Since the earliest diverging extant species of *Corethrella* is found in New Zealand, which is also home to one of the two earliest lineages of frogs (Duellman and Trueb, 1994; Pyron and Wiens, 2011), it has been suggested that frog-biting midges and their anuran prey share a long evolutionary history together (Borkent and Szadziewski, 1992).

Frog-biting midges probably originated around the Jurassic/Cretaceous boundary about 145 Ma (Bertone et al., 2008). The oldest record from this family is *C. cretacea* Szadziewski, 1995, which was found preserved in 125–129 Ma Lebanese amber (Szadziewski, 1995; Maksoud et al., 2017). Indeed, all known fossil Corethrellidae are found in amber. The absence of specimens from this family in compression fossils has been attributed to the lifestyle of the known larvae which are largely arboreal and phytotelmatic, factors that do not make them amenable to preservation in lacustrine sediments (Lukashevich, 2000). Overall, however, this family is rare in the fossil record with fewer than 20 fossil specimens known in total, many poorly preserved (Borkent, 2014; Baranov et al., 2016). Among these, nine fossil species of *Corethrella* have been described, two from the Cretaceous, five from the Eocene and two more from the Miocene (Szadziewski, 1995; Borkent, 2008; Baranov et al., 2016). The rarity of Corethrellidae fossils makes it difficult to investigate the early evolutionary history of this family.

In this paper, we describe a new species of Corethrellidae from mid-Cretaceous Burmese amber from Myanmar, a deposit from which a different species of frog-biting midge had been previously described (*Corethrella andersoni* Poinar and Szadziewski, 2007). The new species provides new data on character evolution in the early evolutionary history of Corethrellidae, in particular concerning male genitalia. Finally, we compare the new species to other known fossil frog-biting midges and discuss the origin of frog-biting midges in relation to their feeding behavior.

## 2. Materials and methods

### 2.1. Geological context

Burmese amber from Myanmar is considered one of the most interesting amber deposits in the world given its animal inclusions, which represent the oldest biota known from tropical rainforests. Indeed, this deposit houses an astonishing diversity of species (916 described up to date, 849 of them Arthropoda – see Daza et al., 2016; Xing et al., 2016, 2018; Ross, 2019; Mey et al., 2018). While the age of Burmese amber has long been a matter of controversy, it is currently widely accepted to be from the Cretaceous period (see Ross, 2019). Palynological evidence suggests Burmese amber to be from Albian–Cenomanian deposits, and a *Mortoniceras* sp. ammonite suggests it is from the late Albian (Cruickshank and Ko, 2003). Similarly, radiometric zircon dating provides an age of ca.  $98.79 \pm 0.62$  Ma. Therefore, an earliest Cenomanian age is likely for Burmese amber (Shi et al., 2012).

The amber piece used in this study comes from Burmese deposits found in Hukawng Valley, Kachin State, Myanmar. (Cruickshank and Ko, 2003: fig. 1). The piece was bought by one of the authors (PM), and is now deposited in the American Museum of Natural History (permanent museum number AMNH Bu-VB01).

### 2.2. Morphological preparation and description

The material was prepared as described by Baranov et al. (2016). The holotype of the new species was not mounted in any artificial

resins. The specimen was imaged using a Keyence VHX-6000 Digital microscope, with both ring light type and cross-polarized co-axial illumination. All photos presented in this paper are composite images assembled using cross-stitching and panorama functions to overcome limitations due to a restricted field of view under high magnifications ( $\times 200$ – $2000$ ). Each image detail was recorded by a stack of images of shifting focus to overcome limitations due to the depth of field (Haug et al., 2008; Haug and Haug, 2011; 2013). Fusion into sharp images and panorama stitching was performed with the microscope's built-in Keyence Image processing software. We also used the HDR function included in the Keyence microscope Keyence-VHX software. Thus, to achieve higher contrast and definition of the final images, every single frame is a composite from several images taken under different exposure times.

Morphological terminology is according to Borkent (2008, 2017). The new species was registered in ZooBank, as per ICBN requirements under unique lsid ID urn:lsid:zoobank.org:act: F6A16F8B-B5BF-48F8-AD37-1869FB0BF0DB.

## 3. Results

### 3.1. Systematic palaeontology

Order Diptera Linnaeus, 1758

Superfamily Culicoidea Meigen, 1818

Family Corethrellidae Edwards, 1932

Genus *Corethrella* Coquillett, 1902a

Type species: *Corethrella brakeleyi* (Coquillett, 1902b), by original designation.

***Corethrella patula*** Baranov & Kvifte, sp. nov. (Figs. 1 A–D, 2 A–D, 3 A–B, 4 A–D, 5)

**Diagnosis.** *Corethrella patula* can be easily differentiated from males of all other species of the genus *Corethrella* (Except *C. andersoni* Poinar and Szadziewski, 2007) based on the following combination of characters:  $R_2$  vein diverging from  $R_{2+3}$  at a  $75^\circ$  angle relative to  $R_3$ ,  $R_{2+3}$  distal of apex of  $R_1$ . In addition,  $M_{1+2}$  is much longer than in other species of frog-biting midges, with fork  $M_{1+2}$  reaching beyond  $R_{2+3}$  at 90% of the wing total length, in contrast to most other Corethrellidae, which have the branching point at about 70% of wing's total length. The new species, *C. patula*, can be distinguished from *C. andersoni* based on the thickness of the mid and hind femora and the structure of the fore and midleg  $Ta_5$ . In contrast to *C. andersoni*, the fore and mid femora in *C. patula* are not thicker than the hind femora, and the fore and mid leg  $Ta_5$  are triangular and bifid and lack scales.

**Material.**

**Holotype.** “Holotype, ♂, AMNH Bu-VB01. male, Burma amber”. Deposited the American Museum of Natural History, New York, USA.

**Locality and geological horizon.** Hukawng Valley, Kachin State, Myanmar; lowermost Cenomanian, mid-Cretaceous.

**Description.** Adult male. Well-preserved (Fig. 1A). Body coloration uniform, probably a preservation artifact. Frons blocked from sight by the antennae and forelegs. Habitus as shown in Fig. 1A, 1B. Body length: 1.7 mm, wing length: 1.1 mm, wing length/body length ratio = 0.64 (Fig. 1A, 1C).

**Head.** Clypeus and mouthparts not visible. Frons not visible, palpal segments 1 and 2 obscured from sight, lengths of palpal segments 3, 4, 5: 51:40:83  $\mu\text{m}$ . Total length of antennae 362  $\mu\text{m}$ . Pedicel 37  $\mu\text{m}$ , with 3 stout setae. Flagellum of antennae with 13 flagellomeres, apex of flagellomere 13 slightly bifid (Figs. 1B, 1D, 4B). Flagellomeres 1–10 with elongated setae in 3–5 concentric



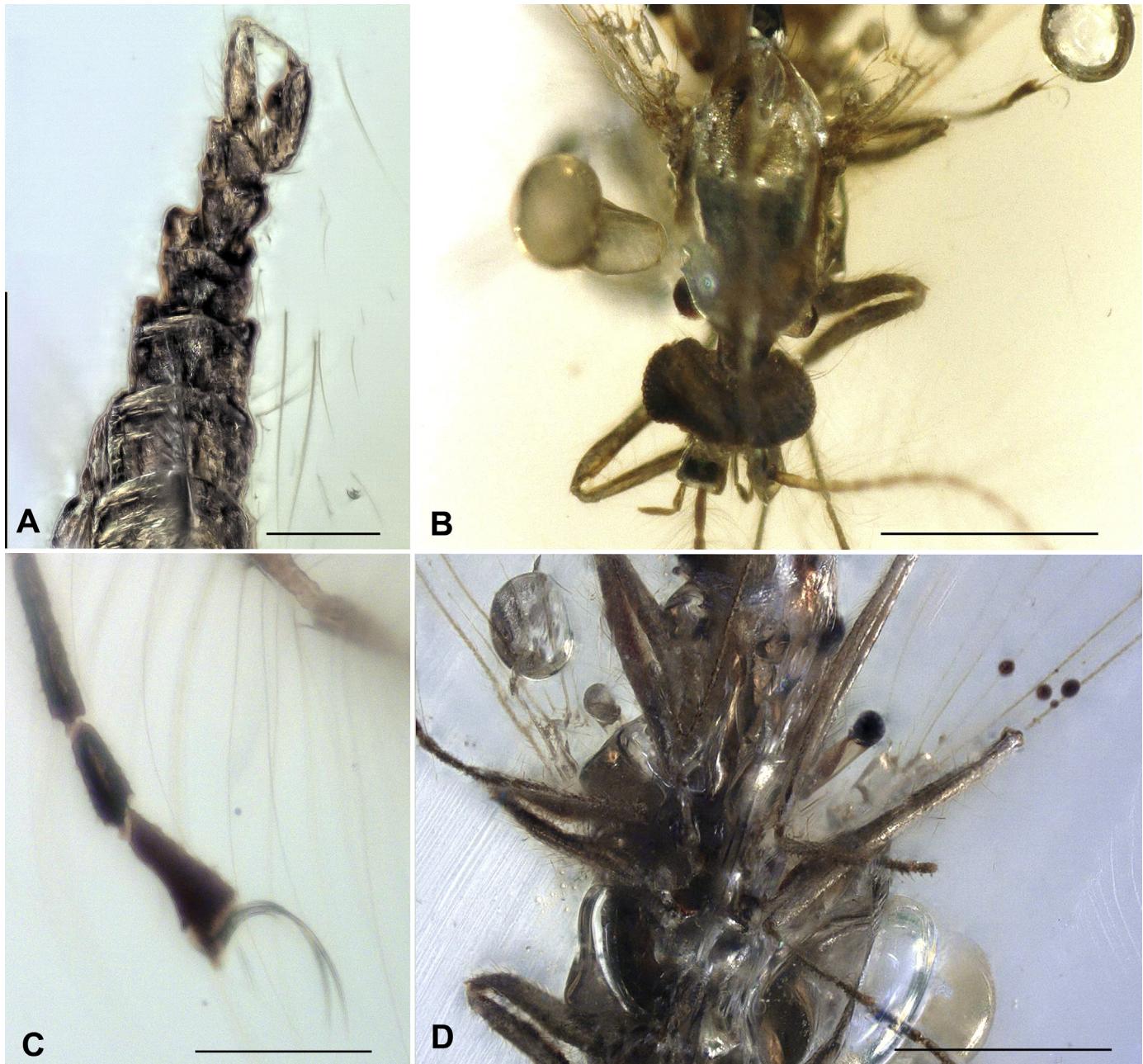
**Fig. 1.** *Corethrella patula* sp. nov., male, holotype, AMNH Bu-VB01. A. Habitus. B. Head. C. Wing. D. Basal flagellomeres with rings of strong setae. Scale bars = 100 µm.

circles (Fig. 1D). Lengths of flagellomeres 1–13 as follows: 36:23:23:24:23:32:24:24:24:27:21:17:22 µm. Head with 9 strong occipital setae, not divided into inner and outer verticals.

*Thorax.* Dc weak, 28–30 setae in 3–4 rows. Scutellum with 4 strong setae (some setae appear to be lost). Scutum with 5 strong, closely placed, setae, next to the posterior end of dorsocentral setae row. Postnotum with 10 strong marginal setae (Fig. 2B). Details of shape and setation of pleural sclerites unclear.

*Wing.* R<sub>1</sub> short, not reaching level of R<sub>2+3</sub> fork (Fig. 1C, 4A). R<sub>2</sub> and R<sub>3</sub> short, R<sub>3</sub> diverging at a 75° angle from stalk of R<sub>2+3</sub>. Hind margin carries simple setae, no traces of scales anywhere at the wing (veins might be denuded).

*Legs.* Leg segments lengths in µm as in Table 1. Midfemur not wider than hind femur, both ca 28 µm wide. Legs with leaf-shaped scales on fore femur and Ta<sub>1</sub> of all legs. Ta<sub>2–5</sub> bare. Tibial comb not visible on any of the tibias. Midtibia without spur. Setae on posterior face of hind tibia undifferentiated. All femora with narrow scales. Foreleg with length ratio Ta<sub>3</sub>/Ta<sub>4</sub> < 2.0. Tarsomere<sub>5</sub> of fore and-mid leg triangular in shape, expanding from base to apex, apically divided (Fig. 2C), empodium not discernable, possibly absent or broken away. Tarsal claws of the foreleg of equal length (18 µm), with weak inner tooth, without basal prong. Tarsomeres of the foreleg also bearing non-plumose protrusion which could be a terminal seta. Midleg tarsomere<sub>3</sub>/tarsomere<sub>4</sub> ratio = 1.3.



**Fig. 2.** *Corethrella patula* sp. nov., holotype, AMNH Bu-VB01. A. Abdomen, ventral view. B Thorax, dorsal view. C. Midleg tarsomere<sub>5</sub> and claws. D. Thorax, ventral view. Scale bars = 100 µm.

Empodium not observable. Ta<sub>5</sub> of forelegs with no ventrobasal swelling. Claws of midlegs of equal length (25 µm), with weak inner tooth and without empodium or prongs. Terminal tarsomeres of hind legs not preserved.

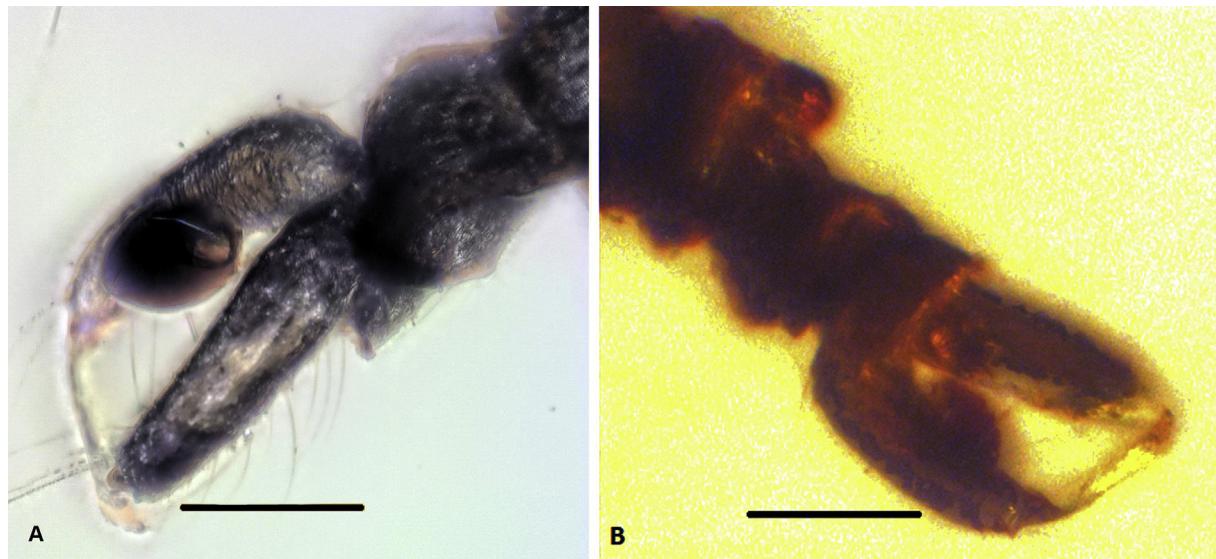
**Hypopygium** (Figs. 3A, 3B, 4C, 4D). Gonocoxite parallel-sided, 117 µm long. Dorsal row consists of 3 strong, simple setae. Dorsomedial seta 35 µm long, straight, about 1.5 times thicker than setae of the dorsal row. Gonostylus 72 µm long, elongate, with a strong apical peg (megaseta), subbasal seta absent. Aedeagus tapering to a point. Aedeagus and parameres overlaying well-developed triangular expansion of tergite IX, which appears “warty” due to numerous insertion points of setae.

Gonostylus/Gonocoxite length ratio = 0.61.

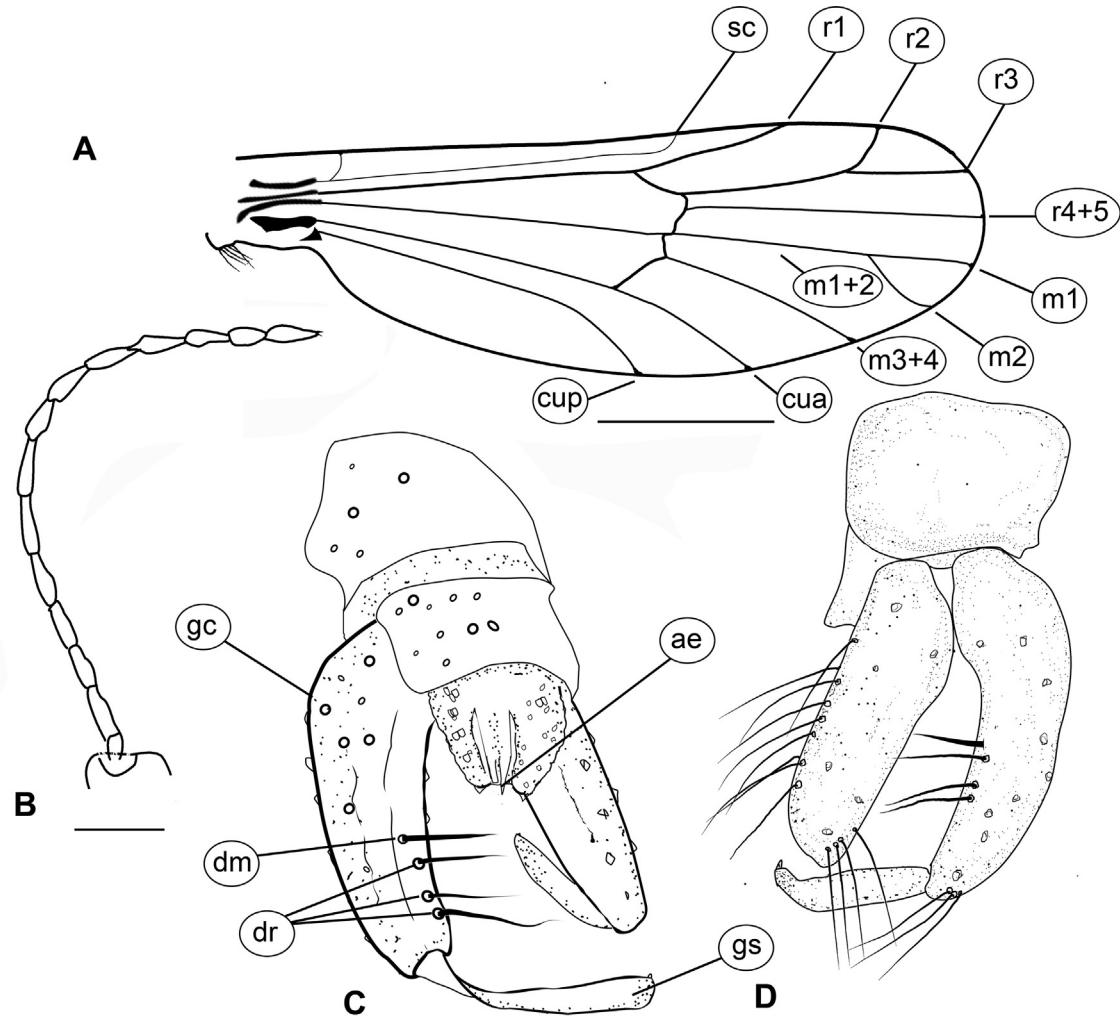
**Etymology.** from Latin «*patula*», open, referring to the wide R<sub>2+3</sub> fork.

#### 4. Discussion

Synamorphies common to *C. patula* and other *Corethrella* suggest that this new species belongs to Corethrellidae rather than Chaoboridae. In particular, we consider that the presence of the following synapomorphies supports the placement of *C. patula* in this family: elongated setae of male basal flagellomeres 1–10 arranged into several circles (Fig. 1D), dorsomedial setae present on the gonocoxite (Fig. 4 C, D) (Borkent, 2008; Borkent, 2012). The latter character is of particular interest as it is a synapomorphy for *Corethrella* s. str. and *C. (Fossilcorethrella)* – lacking from



**Fig. 3.** *Corethrella patula* sp. nov., holotype, AMNH Bu-VB01. A. Hypopygium, ventral view. B. Hypopygium, dorsal view. Scale bars = 100 µm.



**Fig. 4.** *Corethrella patula* sp. nov., holotype, AMNH Bu-VB01. Drawings of details. A. Left wing. B. Right antenna. C. Hypopygium, dorsal view. D. Hypopygium, ventral view. Scale bars = 4A – 200 µm, 4B – 20 µm, 4C-D – 100 µm. Abbreviations: r1-r4+5: radial veins 1 through 4 + 5; m1-m3+4: medial veins 1 through 3 + 4; cua—anterior branch of the cubital vein; cup—posterior branch of the cubital vein; sc—subcostal vein; gc—gonocoxite; gs—gonostylus; ae—adeagus; dm—dorso-medial setae; dr—dorsal row of setae.



**Fig. 5.** Speculative reconstruction of *Corethrella patula* sp. nov. as a micropredator of a hypothetical Alytoidea frog. Male in the foreground, females sitting at the frog. Reconstruction and art by Gabriel Ugueto.

**Table 1**

Leg segments lengths, in  $\mu\text{m}$  (“Pe<sub>1</sub>”–“Pe<sub>3</sub>” Fore, Mid and Hindlegs. “Fe”–femur; “Ti”–tibia, “Ta<sub>1–5</sub>” – tarsomeres 1–5.).

	Fe	Ti	Ta <sub>1</sub>	Ta <sub>2</sub>	Ta <sub>3</sub>	Ta <sub>4</sub>	Ta <sub>5</sub>	Claws
Pe <sub>1</sub>	126	136	110	47	31	16	32	18
Pe <sub>2</sub>	86	117	100	32	22	17	28	25
Pe <sub>3</sub>	161	162	101	42	45	59	–	–

*Corethrella* (*Notocorethrella*). Other characters of possible relevance for resolving the earliest Corethrellidae divergences are the mid-tibia without a spur (apomorphy 5 *sensu* Borkent, 2008, missing from *C. (Fossilcorethrella)*) and the male's fifth tarsomeres of fore and mid legs short and squat (apomorphy 8 *sensu* Borkent, 2008, missing from *C. (Fossilcorethrella)*). Among the synapomorphies defining Corethrellidae, however, *C. patula* lacks the subbasal seta of the gonostyli and the mid femora are not thickened relative to other femora. Given all the other synapomorphies with Corethrellidae, however, *C. patula* clearly belongs in this family.

The only taxon of modern or fossil Culicoidea with a somewhat similar state of the R<sub>2+3</sub> is *Corethrella* (*Corethrella*) *brevivena* Borkent, 2008, which possesses many derived characters as part of the well-supported *C. rotunda* species group (Borkent, 2008, Baranov et al., 2016). The short R<sub>2</sub> and R<sub>3</sub> in *C. brevivena* are parallel as in other, long-forked *C. rotunda* group species, and we deem the shortening of R<sub>2</sub> to be a homoplastic character between *C. brevivena* and the fossil species. The shortened and divergent R<sub>2</sub> and R<sub>3</sub>, however, is probably a synapomorphy of the distinct species group of the Burmese amber species *C. patula* and *C. andersoni* within

*Corethrella*. The relationship of this putative species group with the named subgenera of Corethrellidae, however, remains unclear.

In general, the gonostyli of *C. patula* is very different from all known fossil *Corethrella*, with the exception of *C. cretacea*. Both *C. patula* and *C. cretacea* males have elongated gonostyli with bluntly rounded distal ends and an apical peg (“megaseta”) at the tip (Szadziewski, 1995; Borkent, 2008). In contrast, the rest of fossil *Corethrella*, such as *C. miocenica* Szadziewski, Krzeminski and Kutscher, 1994 or *C. baltica* Borkent, 2008, have less elongated gonostyli, often with a club-shaped expansion distally (Borkent, 2008; Baranov et al., 2016). Unfortunately, critical features from the wings and genitalia are missing, impeding a more complete comparison of both genitalia and wings among fossil species. For instance, the male hypopygium of *C. andersoni* and the wing venation of *C. cretacea* are unknown (Szadziewski, 1995; Szadziewski and Sontag, 2018). Additional specimens are required to elucidate the relationships between the earliest divergences of *Corethrella*, i.e. *C. (Fossilcorethrella) cretacea*, *C. patula* + *C. andersoni*, *C. (Notocorethrella) novaezealandiae* and *C. s. str.*

The appearance of *Corethrella* in the geological record is preceded by the appearance of their main prey, frogs. The Anuran lineage of amphibians are known from the Permian onwards (Anderson et al., 2008), while the sister group of Corethrellidae, Culicidae + Chaoboridae, is known from as early as the Early Jurassic. Burmese amber is the oldest geological deposit where both frog-biting midges and frogs have been recorded (Poinar and Szadziewski, 2007; Xing et al., 2018). Indeed, the presence of Alytoidea Fitzinger, 1843 frogs in the Burmese Cretaceous rainforest suggest there was ample opportunity for *C. patula* and *C. andersoni*.

to feed on amphibian prey, should they be blood-feeding. We currently, however, only have circumstantial evidence for the interactions between frogs and frog-biting midges at that time. Unless a frog-midge syninclusion is found, no indisputable link can be proven. Nevertheless, both phylogenetic and geological evidence suggest that prey-micropredator interactions between frogs and corethrellids in Burmese amber forest were not only possible but probable (Fig. 5).

## 5. Conclusion

The discovery of *Corethrella patula* sp. nov. in Burmese amber provides valuable insights into the geological history of frog-biting midges. Morphological similarity between *C. andersoni* and *C. patula* suggests the presence of a monophyletic group of Corethrellidae species in the Burmese amber forest, but their phylogenetic affinities to other Corethrellidae are not clear from the character evidence.

The discovery of this new Corethrellidae, together with the recent discovery of Alytoidea frogs from Burmese amber, provides an unprecedented look into likely prey-predator relationships between these two groups in the mid-Cretaceous.

## Acknowledgements

We are grateful to Joachim Haug (LMU Munich) for his kind assistance in the high resolution imaging of the holotype. We would also like to express our gratitude to Art Borkent and Peter Cranston for suggestions on an early version of the manuscript. All authors express our gratitude to Gabriel Ugueto, whose incomparable artwork is gracing this paper. We are thankful to Ross Piper (Royal Geographical Society) for the acquisition of the holotype for the AMNH, and to David Grimaldi for assisting with holotype deposition. Funding for this study was partially provided by NSF IOS#1433990 to XEB. Authors are grateful to the Editor – Eduardo Koutsoukos and two anonymous reviewers for their efforts in improving this manuscript.

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