New Cretaceous empidoids and the Mesozoic dance fly revolution (Diptera: Empidoidea)

Davide Badano[a,b]*[,†], Bradley J. Sinclair[c], Qingqing Zhang[d,e,f]*, Francesca Palermo[g], Nicola Pieroni[g], Laura Maugeri[g], Michela Fratini[g] and Pierfilippo Cerretti[a,b]* [iD]

[a]*Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Piazzale A. Moro 5, 00185, Rome, Italy;* [b]*Museum of Zoology, Sapienza University of Rome, Piazzale Valerio Massimo 6, 00162, Rome, Italy;* [c]*Canadian National Collection of Insects & Canadian Food Inspection Agency, K.W. Neatby Bldg., C.E.F., 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada;* [d]*Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, South Waihuan Road, Chenggong District, Kunming, 650500, China;* [e]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing, 210008, China;* [f]*Institute of Geosciences, University of Bonn, 53115, Bonn, Germany;* [g]*CNR-Nanotec (Rome Unit) c/o Department of Physics, Sapienza University of Rome, Piazzale A. Moro, 5, 00185, Rome, Italy*

Abstract

Dance flies and relatives (Empidoidea) are a diverse and ecologically important group of Diptera in nearly all modern terrestrial ecosystems. Their fossil record, despite being scattered, attests to a long evolutionary history dating back to the early Mesozoic. Here, we describe seven new species of Empidoidea from Cretaceous Kachin amber inclusions, assigning them to the new genus *Electrochoreutes* **gen.n.** (type species: *Electrochoreutes trisetigerus* **sp.n.**) based on unique apomorphies among known Diptera. Like many extant dance flies, the males of *Electrochoreutes* are characterized by species-specific sexually dimorphic traits, which are likely to have played a role in courtship. The fine anatomy of the fossils was investigated through high-resolution X-ray phase-contrast microtomography to reconstruct their phylogenetic affinities within the empidoid clade, using cladistic reasoning. Morphology-based phylogenetic analyses including a selection of all extant family- and subfamily-ranked empidoid clades along with representatives of all extinct Mesozoic genera, were performed using a broad range of analytical methods (maximum parsimony, maximum-likelihood and Bayesian inference). These analyses converged in reconstructing *Electrochoreutes* as a stem-group representative of the Dolichopodidae, suggesting that complex mating rituals evolved in this lineage during the Cretaceous.

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Introduction

The Empidoidea (Eremoneura, Diptera) are a diverse, widespread and nearly ubiquitous group of true flies including approximately 12 000 described extant species (Sinclair and Cumming, 2006; Marshall, 2012). Most

empidoids are efficient flying or ground hunters of small soft-bodied arthropods or other invertebrates, with associated piercing mouthparts or raptorial legs. However, several genera and species feed chiefly or exclusively on nectar or pollen and might be important, yet overlooked, pollinators (Lefebvre et al., 2014). Although poorly known, immatures of many empidoids are typically damp-soil or dead-wood dwelling predators, whereas the larvae of several Empididae are aquatic (Robinson and Vockeroth, 1981; Steyskal and Knutson, 1981; Marshall, 2012; Grichanov and

Brooks, 2017; Sinclair and Cumming, 2017; Sinclair and Daugeron, 2017; Cumming et al., 2018).

Some adult empidoids are renowned for complex mating rituals involving nuptial swarms, ritual dances (Fig. 1) and exchanges of gifts from the male to the female, such as prey or silk balloons (Cumming, 1994; Marshall, 2012). Common names such as dance or balloon flies, which refer to Empididae, are based on these striking mating behaviours (Murray et al., 2022). Mating behaviours have probably played a key role in shaping the evolution of Empidoidea, as suggested by the preservation of silk-covered gifts and exaggerated secondary male sexual traits in Cretaceous species of the atelestid *Alavesia* Waters and Arillo, and of the dolichopodid *Schistostoma* Becker, respectively (Brooks et al., 2019; Tang et al., 2022).

The relationships and the circumscription of family-ranked taxa within Empidoidea are still debated as phylogenies inferred from morphological and molecular data yield conflicting results, as well as leaving several taxa of uncertain placement. The influential cladistic analysis of morphological traits by Sinclair and Cumming (2006) recognized five families: Atelestidae, Brachystomatidae, Dolichopodidae, Empididae and Hybotidae. Later studies classified certain genera of unclear affinities to family-rank, establishing the monotypic Homalocnemidae and Oreogetonidae and near monotypic Iteaphilidae (Pape et al., 2011; Sinclair and Shamshev, 2021). Molecular-based phylogenetic reconstructions have invariably reconstructed brachystomatids within empidids, but also have confirmed the monophyly of Dolichopodidae and Hybotidae. Recently, Wahlberg and Johanson (2018) erected the new family Ragadidae (also including *Iteaphila* Zetterstedt), recovering them as the sister group to monophyletic Empididae.

Molecular and fossil evidence suggest that empidoids diverged from the other Eremoneura in the Jurassic (Wiegmann et al., 2011; Wahlberg and Johanson, 2018). The oldest known fossils date back to the mid-Jurassic

Fig. 1. Secondary sexual traits of male Dolichopodidae and courtship behaviour. (a) *Dolichopus* sp. with enlarged and contrasted fore tarsi (Ontario); (b) *Tachytrechus* sp. with elongate and colourful antennae (Oregon); (c) *Neurigona quadrifasciata* (Rondani), male (above) showing to female (below) fore tarsi during mating (Netherlands); *N. quadrifasciata*, courtship and mating sequence (Netherlands), note contrasting fore tarsi and terminalia of male; (d) displaying male; (e) male touching female with forelegs; (f) mating, note how the male maintains hold on female. Photos by: (a)–(b) S.A. Marshall, (c)–(f) S. Lamberts.

of Kazakhstan, although the affinities of these specimens need to be reassessed by a thorough comparison with other Mesozoic dipterans using explicit cladistic arguments (Grimaldi and Cumming, 1999; Grimaldi and Engel, 2005). Definitive, crown-group empidoid fossils are relatively abundant and moderately diverse in virtually all Cretaceous deposits, with representatives of all extant, family-ranked clades (Carpenter, 1992; Grimaldi and Engel, 2005; Evenhuis, 2014). Interestingly, *Burmitempis* Cockerell and *Electrocyrtoma* Cockerell, two extinct, crown-group empidoids of uncertain affinities, are among the first inclusions described from the Burmese ambers, well before both the importance and Mesozoic age of these deposits were recognized (Cockerell, 1917a, b). Some morphologically conservative taxa apparently have an extensive stratigraphic occurrence, for example the extant atelestid *Alavesia*, the microphorine dolichopodid *Schistostoma* and the brachystomatid *Apalocnemis* Philippi are known from Cretaceous ambers, whereas the microphorine *Microphorites* Hennig is reported from the Cretaceous to the Eocene (Grimaldi and Cumming, 1999; Sinclair and Kirk-Spriggs, 2010; Perrichot and Engel, 2014; Brooks et al., 2019; Sinclair and Grimaldi, 2020; Shamshev and Perkovsky, 2022). Moreover, an impression fossil specimen from the Cretaceous of Botswana was assigned to the extant genus *Empis* based on wing characters (Waters, 1989). To date, Cenozoic deposits mostly yield "modern" empidoid forms, which have been assigned to extant genera (Carpenter, 1992), with a few exceptions (Cumming and Brooks, 2002; Solórzano-Kraemer et al., 2020; Shamshev and Perkovsky, 2022).

The relationships between some Cretaceous empidoids were studied using cladistic reasoning by Hennig (1971). Waters (1989) plotted the affinities of the then known fossil empidoids on the phylogenetic tree by Chvála (1983), whereas Grimaldi and Cumming (1999) reconstructed the affinities of several Mesozoic taxa. More recently, Cumming and Brooks (2002) investigated the phylogenetic relationships of fossil Microphorinae and Parathalassiinae through a cladistic analysis, and Zhang et al. (2021) tested the affinities of an atelestid preserved in Burmese amber. However, a comprehensive phylogenetic analysis incorporating Mesozoic empidoids has never been attempted, and the relationships of most fossil empidoids have been assessed through morphological comparisons with extant genera.

We here erect a new genus for seven new, morphologically derived, dance fly species based on Myanmar amber inclusions (Late Cretaceous from Kachin state, 98 ± 0.6 Ma; Shi et al., 2012). As for other Cretaceous insects (Pohl et al., 2021), these tiny flies have a chimeric combination of character states involving unusually large setae, unique wing venation and chaetotaxy, and striking sexually dimorphic features that make the reconstruction of their phylogeny challenging. We made use of traditional optical methods and X-ray phase-contrast microtomography to describe the fine morphology of these new taxa and to reconstruct their phylogenetic affinities using multiple analytical methods. We also assessed the phylogenetic placement of known Cretaceous empidoids preserved in amber, to provide explicit calibration points and to make inferences about the evolution of courtship rituals in this clade.

Materials and methods

Material, optical examination of amber inclusions and terminology

This study is based on specimens housed in the following institutions: State Key Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP); United States National Museum of Natural History, Washington D.C., USA (USNM). Specimens were examined, photographed, and measured with a Zeiss Axio Zoom v.16. Terminology follows Sinclair and Cumming (2006) and Cumming and Wood (2017).

X-ray phase-contrast microtomography

The X-ray phase-contrast tomography experiment was carried out at the TOMCAT beamline of the Swiss Light Source (Villigen, Switzerland). The incident monochromatic X-ray energy was 20 keV. A PCO edge 5.5 camera coupled with optics resulting in a pixel size of 1.625×1.625 μm^2 was set at a distance from the sample of 3 cm. The tomographic images were acquired with an exposure time of 90 ms covering a total angle range of 360°, which allows a near doubling of the image field of view. Data preprocessing, phase retrieval, and reconstruction were performed using the tomographic reconstruction software SYRMEP TOMOPROJECT (Brun et al., 2017). Flat-/dark-field correction was performed on raw data and each tomographic projection was normalized with the average value of the background outside the object. The tomographic reconstruction was used with Filtered Back Projection (FBP) method. The different electron densities of the tissues were rendered as grey levels in the phase tomograms images. To independently display the different tissues, image analysis and image segmentation were performed using the software ImageJ (https://imagej.net/Fiji), 3D slicer (https://www.slicer.org/) and Amira. For the 3D rendering, binarization was further applied over the reconstructed data.

Data matrix

We implemented an updated version of the morphological character dataset originally produced by Sinclair and Cumming (2006) using Mesquite v.3.61 software (Maddison and Maddison, 2021) by including an additional 21 taxa (Appendix S5), 19 of which are extinct and two extant but also known from Cretaceous amber deposits (Table 1). The information concerning the morphology of fossil taxa was drawn mainly from the literature (Appendix S3), while in the case of the genus *Electrochoreutes* it was based on the examined specimens. Moreover, we added four new morphological

Table 1
List of genera of Empidoidea reported from Mesozoic amber included in the phylogenetic analysis

Genus	Type species	Type locality and age	Time range (Ma)	Species	Occurrence	Former classification	Present classification
Atelestites Grimaldi and Cumming, 1999	*A. senectus* Grimaldi and Cumming, 1999	Bchare Mountain; Barremian	130.0–125.4	1	Cretaceous: Lebanon	Atelestidae Atelestinae	Atelestidae Atelestinae
Phaetempis Grimaldi and Cumming, 1999	*P. lebanensis* Grimaldi and Cumming, 1999	Bchare Mountain; Barremian	130.0–125.4	1	Cretaceous: Lebanon	Atelestidae Nemedininae	Atelestidae Nemedininae
Trichinites Hennig, 1976	*T. cretaceus* Hennig, 1976	Jezzine; Barremian	130.0–125.4	1	Cretaceous: Lebanon	Hybotidae	Atelestidae Atelestinae
Avenaphora Grimaldi and Cumming, 1999	*A. hispida* Grimaldi and Cumming, 1999	Bchare Mountain; Barremian	130.0–125.4	1	Cretaceous: Lebanon, France	Dolichopodidae Microphorinae	Dolichopodidae
Microphorites Hennig, 1971	*M. extinctus* Hennig, 1971	Jezzine; Barremian	130.0–48.6	9	Cretaceous: Lebanon, Spain, France, Myanmar; Eocene: Czech Republic, France	Dolichopodidae Microphorinae	Dolichopodidae
Alavesia Waters and Arillo, 1999	*A. subiasi* Waters and Arillo, 1999	Peñacerrada outcrop I; Albian	105.3–0	16	Cretaceous: Spain, Myanmar. Present: Brazil, Namibia	Atelestidae Atelestinae	Atelestidae Atelestinae
Cretoplatypalpus Kovalev, 1978	*C. archaeus* Kovalev, 1978	Nizhnyaya River; Cenomanian	99.7–70.6	2	Cretaceous: Russia, Canada	Hybotidae Tachydromiinae	Hybotidae Tachydromiinae
Schistostoma Becker, 1902	*S. eremita* Becker, 1902	Egypt: present	98.6–0	24	Cretaceous: Myanmar; present: Afrotropical, Palaearctic, Nearctic	Dolichopodidae Microphorinae	Dolichopodidae Microphorinae
Pouillonhybos Ngô-Muller, Engel and Nel, 2021	*P. venator* Ngô-Muller, Engel and Nel, 2021	Hukwang Valley; Cenomanian	98.6	1	Cretaceous: Myanmar	Hybotidae Ocydromiinae	Hybotidae
Electrochoreutes **gen.n.**	*E. trisetigerus* **sp.n.**	Hukwang Valley; Cenomanian	98.6	7	Cretaceous: Myanmar	–	Stem-group Dolichopodidae
Pristinmicrophor Tang et al., 2019	*P. hukawngensis* Tang et al., 2019	Hukwang Valley; Cenomanian	98.6	1	Cretaceous: Myanmar	Dolichopodidae Microphorinae	Dolichopodidae
Neoturonius Grimaldi and Cumming, 1999	*N. asymmetrus* Grimaldi and Cumming, 1999	Sunrise Landing; Turonian	94.3–89.3	3	Cretaceous: USA	Atelestidae Nemedininae	Atelestidae Nemedininae
Emplita Grimaldi and Cumming, 1999	*E. casei* Grimaldi and Cumming, 1999	White Oaks Pit; Turonian	94.3–89.3	1	Cretaceous: USA	Empididae	Crown-group Empidoidea
Turonempis Grimaldi and Cumming, 1999	*T. styx* Grimaldi and Cumming, 1999	White Oaks Pit; Turonian	94.3–89.3	1	Cretaceous: USA	Empididae	Crown-group Empidoidea
Archichrysotus Negrobov, 1978	*A. hennigi* Negrobov, 1978	Yantardakh Hill; Santonian	94.3–70.6	3	Cretaceous: Russia, Canada	Dolichopodidae Parathalassiinae	Dolichopodidae
Cretomicrophorus Negrobov, 1978	*C. rohdendorfi* Negrobov, 1978	Yantardakh Hill; Santonian	94.3–70.6	3	Cretaceous: Russia, France, USA	Dolichopodidae Parathalassiinae	Dolichopodidae
Cretodromia Grimaldi and Cumming, 1999	*C. glaesa* Grimaldi and Cumming, 1999	Cedar Lake; Late Cretaceous	84.9–70.6	1	Cretaceous: Canada	Atelestidae Nemedininae	Atelestidae Nemedininae

Table 1
(Continued)

Genus	Type species	Type locality and age	Time range (Ma)	Species	Occurrence	Former classification	Present classification
Nemedromia Grimaldi and Cumming, 1999	*N. campania* Grimaldi and Cumming, 1999	Grassy Lake; Late Cretaceous	84.9–70.6	3	Cretaceous: Canada, USA	Atelestidae Nemedininae	Atelestidae Nemedininae
Prolatomyia Grimaldi and Cumming, 1999	*P. elongata* Grimaldi and Cumming, 1999	Cedar Lake; Late Cretaceous	84.9–70.6	1	Cretaceous: Canada	Atelestidae Nemedininae	Atelestidae Nemedininae
Mesoplatypalpus Grimaldi and Cumming, 1999	*M. carpenteri* Grimaldi and Cumming, 1999	Cedar Lake; Late Cretaceous	84.9–70.6	1	Cretaceous: Canada	Hybotidae Tachydromiinae	Hybotidae Tachydromiinae
Apalocnemis Philippi, 1865	*A. obscura* Philippi, 1865	Chile; present	84.9–0		Cretaceous: Canada; Eocene: Russia; Present: Neotropical	Brachystomatidae	Brachystomatidae

characters, namely, character 124 (vein Rs), character 125 (cell r-m), character 126 (veins R and M) and character 127 (vein r-m; Appendix S5). In addition, several original characters were redefined, and scorings updated. The final version of the dataset included 82 taxa and 127 characters, 80 of which were binary and 47 multistate (Appendix S5).

Phylogenetic analyses

Maximum parsimony (MP) analyses of the dataset were conducted using the software TNT v1.5 (Goloboff and Catalano, 2016) under both equal (EW) and implied (IW) weights. Heuristic tree searches were run under the "traditional search option" with the following settings: general RAM of 1000 Mbytes, memory holding 1 000 000 trees, 1000 replicates with tree bisection-reconnection (TBR) branch swapping and saving 1000 trees per replicate. Under IW, we analysed the dataset enforcing a broad range of concavity *k*-values of the weighting function, from $k = 3$ to $k = 20$, selecting the best fitting one with the TNT script "setk.run" (Santos et al., 2015). Multistate characters were treated as unordered and zero-length branches were collapsed. Bremer support values under EW were calculated in TNT from 10 000 trees up to ten steps longer than the shortest trees obtained from the "traditional search", using the "trees from RAM" setting. Character state changes were mapped with WinClada v.1.00.08 (Nixon, 2002). Consistency (CI) and retention (RI) indexes for matrix were calculated with TNT.

Bayesian inference (BI) analyses were performed in MrBayes v.3.2.7 on the Extreme Science and Engineering Discovery Environment at Cyberinfrastructure for Phylogenetic Research (Miller et al., 2010). The analyses were run under the Mk1 model (Lewis, 2001) with scoring set for variable morphological characters. Four Markov chain Monte Carlo (MCMC) chains, of which one was cold and three heated, were run for 10^6 generations, setting a burn-in fraction of 50% and sampling the chains every 1000 generations. The convergence of independent runs was assessed through the average standard deviation of split frequencies (<0.01) and potential scale reduction factors (approaching 1).

Maximum-likelihood (ML) analyses were performed in IQ-TREE (v.2.1.1; Minh et al., 2020) on the IQ-TREE web server (Trifinopoulos et al., 2016). The selected model enforced was computed through the Model Finder option implemented in IQ-TREE (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017).

Results

Systematic palaeontology

Diptera Linnaeus, 1758
Eremoneura Lameere, 1906
Empidoidea Latreille, 1804
Dolichopodidae Latreille, 1809 (stem group)

Electrochoreutes **gen.n.**
Zoobank ID: *urn:lsid:zoobank.org:act:BE5F7A1D-9065-4F38-B26A-5896B2FD190*
(Figs 2–4 and S1–S12)

Type species. *Electrochoreutes trisetigerus* **sp.n.**, Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Etymology. The genus name is masculine, and it is a composite word from Greek, with prefix "electro", i.e. amber, and suffix "choreutes", i.e. dancer, hence "amber dancer" referring to complex mating rituals of empidoids.

Description. Male dichoptic. Inner margin of eye with shallow notch opposite base of antenna. Antennal pedicel without conus; postpedicel with strong dorsal seta at base, longer than stylus; arista-like stylus at tip of postpedicel, with one basal article (occasionally two), apex of stylus without sensillum (Fig. 3d,e). Labellum enlarged, with pseudotracheae (in form of small rings), obscuring labrum. Epipharyngeal blades present. Proepisternal seta present. Male fore tarsus often highly modified with processes and/or enlarged setae, tarsomere 5 flattened, apically truncate, with large claws and pulvilli (Fig. S1a). Sc complete. Costa reaching R_5, pterostigma absent. Rs origin opposite humeral crossvein (Fig. S1b). R_{4+5} unbranched. Crossvein r-m beyond middle of cell dm, three veins emitted from cell
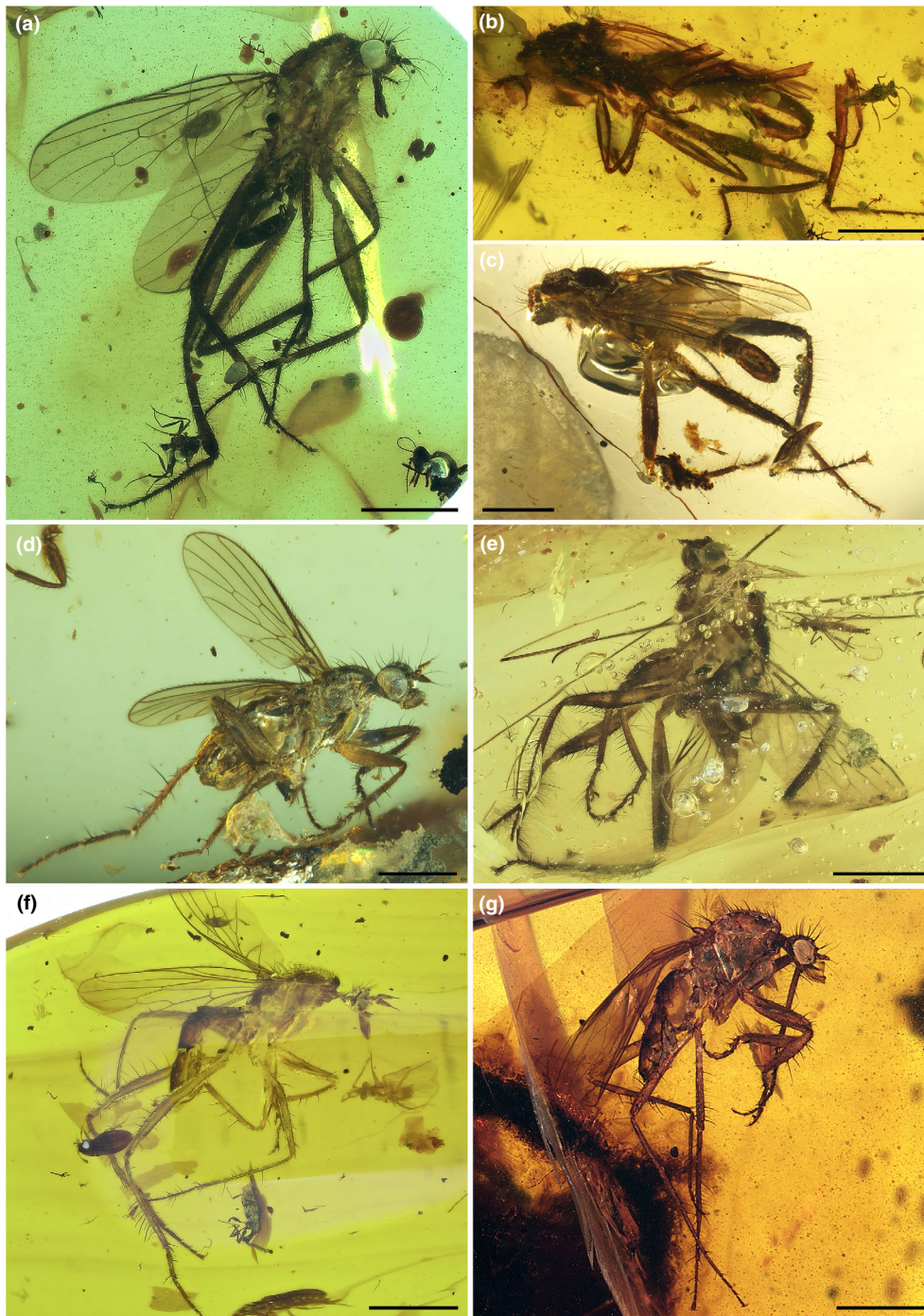
Fig. 2. Habitus of *Electrochoreutes* species, holotypes. (a) *Electrochoreutes trisetigerus* **sp.n.**; (b) *Electrochoreutes hamatus* **sp.n.**; (c) *Electrochoreutes planitibia* **sp.n.**; (d) *Electrochoreutes electroechinus* **sp.n.**; (e) *Electrochoreutes furcillatus* **sp.n.**; (f) *Electrochoreutes falculigerus* **sp.n.**; (g) *Electrochoreutes pankowskii* **sp.n.** Scale bars = 1 mm.

dm. Cell cua longer than cell bm, lower angle acute, ending distant from wing margin. CuA arched. CuA + CuP reaching wing margin. Anal lobe well-developed, alula present (Fig. S1b). Abdominal plaques present. Male pregenital segments tubular (Figs 2a and 3a,b). Male sternite 7 bare. Male terminalia symmetrical, elongate, tubular-shaped, unrotated, and folded ventrally beneath abdomen (Figs 2a and 3a,b). Male terminalia with robust, prominent, sometimes apically forked, cerci, and without strong setae. Female with apical abdominal segments retracted within segment 6 (Fig. 3c). Acanthophorites absent.
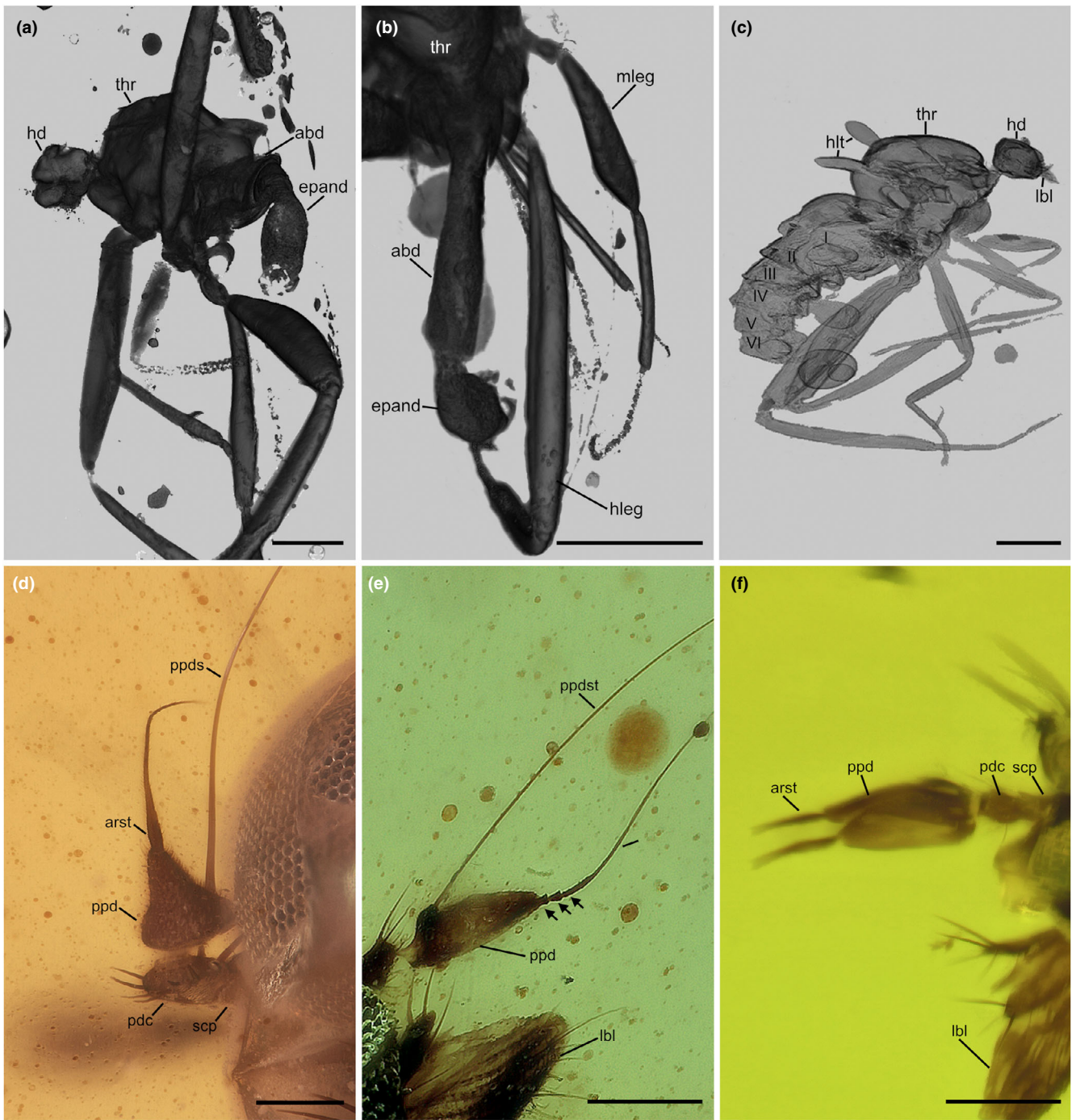
Fig. 3. Morphology of *Electrochoreutes* **gen.n.** 3D XPCT rendering. (a) *Electrochoreutes furcillatus* **sp.n.**, holotype, caudal view with abdomen and terminalia in evidence; (b) *E. furcillatus* **sp.n.**, holotype, abdomen in dorsal view; (c) *Electrochoreutes* sp., female (BA16150). Morphology of antenna. (d) *Electrochoreutes* sp., female (BA16150) antenna; (e) *Electrochoreutes pankowskii* **sp.n.**, 3-segmented aristal stylus; (f) *Electrochoreutes falculigerus* **sp.n.**, antenna without postpedicel seta. Scale bars for (a)–(c) = 1 mm, scale bars for (d)–(f) = 0.25 mm. abd, abdomen; arst, arista-like stylus; epand, epandrium; hd, head; hleg, hindleg; hlt, halter; lbl, labellum; mleg, midleg; pdc, pedicel; ppd, postpedicel; ppst, postpedicel seta; thr, thorax.

Remarks. *Electrochoreutes* **gen.n.** is characterized by a unique combination of features, a mixture of plesiomorphic and derived traits, clearly setting it apart from any other extinct or living Diptera. The representatives of this genus differ, sometimes conspicuously, in male secondary sexual traits; however, the different species are constant in overall morphology.
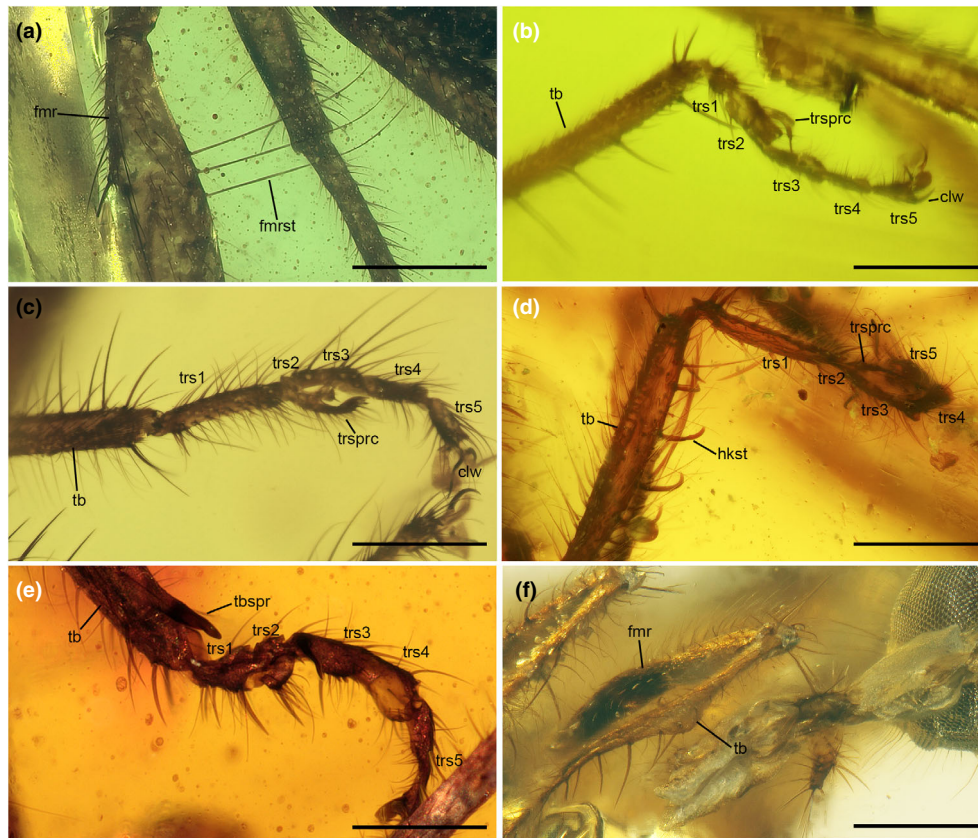
Fig. 4. Secondary leg sexual characters of *Electrochoreutes* species. (a) *Electrochoreutes trisetigerus* **sp.n.**, detail of fore femur; (b) *Electrochoreutes falculigerus* **sp.n.**, holotype, fore tarsus; (c) *Electrochoreutes furcillatus* **sp.n.**, holotype, fore tarsus; (d) *Electrochoreutes hamatus* **sp.n.**, holotype, fore tibia and tarsus; (e) *Electrochoreutes pankowskii* **sp.n.**, holotype, fore tarsus; (f) *Electrochoreutes planitibia* **sp.n.**, holotype, fore leg. Scale bars = 0.25 mm. clw, claw; fmr, femur; fmrst, femur seta; hkst, hooked seta; tb, tibia; tbspr, tibial spur; trs, tarsomere; trsprc, tarsal process.

Electrochoreutes shares with Dolichopodidae several synapomorphies, including Rs originating opposite to humeral crossvein (56 : 1, homoplasious; Fig. S1b), and male with sternite 7 bare (71 : 1, non-homoplasious) and tubular pregenital segments (73 : 1, non-homoplasious). Moreover, the females of *Electrochoreutes* are characterized by the invagination of the apical abdominal segments within segment 6, a condition also observed in the dolichopodids, *Schistostoma* Becker and *Amphithalassius* Ulrich (69 : 2, homoplasious). However, *Electrochoreutes* notably differs from all dolichopodids in several characters, such as unrotated male genitalia, symmetrical hypopygium (Fig. 3a, b) and large wing basal cells (Fig. S1b). The forward placement of crossvein r-m in the new genus also is unique among all Empidoidea and is more typical of "lower" Brachycera.

Electrochoreutes is readily distinguished by the presence of a large dorsal seta on the postpedicel that is longer than the head and more robust than the arista-like stylus (Fig. 3d,e), and the male with tubular and folded apical abdominal segments (Fig. 3a,b). However, this seta is absent in *E. falculigerus* **sp.n.** (Fig. 2f), although this species hardly differs from congeners in overall morphology. Moreover, *E. pankowskii* **sp.n.** noticeably differs from congeners and most empidoids by the arista-like stylus composed of three articles (Fig. 3e). Among empidoids, a three-articled stylus occurs only in a few Atelestidae (e.g. *Meghyperus* Loew, *Acarteroptera* Collin) and in the Cretaceous *Turonempis* Grimaldi and Cumming (the apparently three-segmented stylus of *Trichinites* Hennig is a preservation artefact; see Solórzano-Kraemer et al., 2023). In half of the *Electrochoreutes* species, vein M_{1+2} is proximally upcurved (e.g. *E. electroechinus* **sp.n.**, *E. furcillatus* **sp.n.**, *E. planitibia* **sp.n.**, *E. trisetigerus* **sp.n.**), whereas in the other half M_{1+2} is straight (e.g. *E. falculigerus* **sp.n.**, *E. pankowskii* **sp.n.**). In the males of *Electrochoreutes*, the last abdominal segments are folded beneath the abdomen and usually provided with prominent apical claspers, which can be apically forked (e.g. *E. trisetigerus*; Fig. S2f) or bearing spine-like setae (e.g. *E. falculigerus*; Fig. S4g).

The males of *Electrochoreutes* are characterized by remarkable male sexual secondary traits which are

clearly species-specific. Most species, including *E. falculigerus*, *E. furcillatus* and *E. pankowskii*, are characterized by strongly modified tarsi, provided with prominently curved, sometimes bilobed, processes and modified robust setae (Fig. 4). Instead, *E. planitibia* and *E. trisetigerus* are characterized by unmodified tarsi, although they are provided with male secondary sexual traits on legs, i.e. tibia with lateral expansion in the former and femur with hair-like setae in the latter. Moreover, *E. pankowskii* is easily set apart from congeners by the swollen femora. Finally, *E. electroechinus* is devoid of leg or chaetotaxy modifications of any kind.

The females of *Electrochoreutes* differ from crown-group Dolichopodidae in lacking acanthophorite spines on the terminalia (Fig. 3c).

Note. Further *Electrochoreutes* specimens not assignable to species are described in Appendix S1 and figured in Appendix S2 (Figs S10–S12).

Electrochoreutes trisetigerus sp.n.

Zoobank ID: urn:lsid:zoobank.org:act:676fd80-1DFC-4FF5-9D48-1E9E77EA43D9

Etymology. The specific epithet is a Latin compound adjective meaning "bearing three setae" after the hair-like setae on base of the male fore femur.

Type material. Holotype, male, NIGP 201456. A well-preserved male specimen, with the thorax crossed by a crack line.

Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Fore femur with three long posteroventral setae which are longer than femur width. Facial bristle anterior to ocellar triangle absent. Palpus with long, erect stout setae. Fore tibia slender. R_1 with dorsal setae. Wing vein M_{1+2} bowed into cell dm proximal to crossvein r-m.

Description. Male. Head without interfrontal setae. Ocellar triangle halfway between vertex and antennal sockets, with pair of stout ocellar setae on short tubercles posterior to anterior ocellus; pair of setulae behind posterior ocellus. Strong vertical seta, longer than occipital setae. Occiput with vertical row of setae, stouter dorsally. Face shorter than frons, without setae. Antenna with scape and pedicel subequal in length, with dorsal setae; postpedicel pointed ovate, basal width half as long as length; postpedicel seta longer than length of head; arista-like stylus more than twice length of postpedicel, with one basal article. Proboscis with cylindrical palpus, clothed in long, stout, erect setae; labellum longer than eye height, with several pseudotracheae visible.

Thorax somewhat hunched in shape; chaetotaxy strong and thickened: one postpronotal seta; one posthumeral seta; one presutural supra-alar seta; acrostichal setae uniserial, extending onto prescutellar depression, with pair of prescutellar setae; dorsocentral setae numerous, alternating long and short; two notopleural setae; one postsutural supra-alar seta; one thin postalar seta; a pair of scutellar setae; one proepisternal seta; laterotergite bare.

Fore coxa with fine, silky anterior setae; mid coxa with strong lateral seta. Foreleg not shortened. Fore femur shorter than mid and hind femora, with strong dorsal setae; base with three long ventral setae, longer than width of femur. Fore tibia narrower than femur, with strong anterodorsal and posterodorsal setae; apex without subapical anterodorsal spur-like process, ventrally with stout posteroventral apical seta. Fore tarsomeres not modified: tarsomeres 1 twice length of tarsomere 2, with stout ventral seta; tarsomere 2 with stout ventral seta; tarsomere 3 less than half length of tarsomere 1, cylindrical, base with stout seta; tarsomere 4 cylindrical. Midleg with numerous strong, erect setae. Mid tibia and tarsus with row of fine, elongate anteroventral setae. Base of mid tarsomere 1 with pair of stout ventral setae; tarsomeres 1–3 with pair of strong, preapical ventral setae. Hindleg similar to midleg; hind tibia clavate, with fine, elongate ventral setae, longer than width of tibia.

Wing with one basal costal seta; stem vein without several dorsal setae; vein R_1 with dorsal setae; vein M_{1+2} bowed into cell dm proximal to crossvein r-m; crossvein dm-m sinuous.

Abdomen with long posteromarginal setae; pregenital segments tubular, folded tightly beneath. Tergite 7 bare. Apex of terminalia with pair of claw-like projections, lower process forked.

Electrochoreutes electroechinus sp.n.

Zoobank ID: urn:lsid:zoobank.org:act:C58DAAF4-06F8-4AEF-BE71-A8108B13DF3C

Etymology. The species name is a composite word from Greek, with prefix "electron", i.e. amber, and suffix "echinus", i.e. urchin, hence "amber urchin" referring to the characteristic spine-like setae covering the head and the thorax.

Type material. Holotype, male, NIGP 201457. Paratype, female, NIGP 201458. The amber piece contains two well-preserved specimens: the male holotype, and a female.

Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Strong erect interfrontal setae anterior to ocellar triangle. Palpus without strong, erect setae. Fore tibia narrower than femur. M_{1+2} not bowed into cell dm proximal to crossvein r-m. Male fore tarsomeres 3–4 slightly modified.

Description. Male. Compound eye with narrow median furrow. Head with pair of stout interfrontal setae on short tubercles; ocellar triangle halfway between vertex and antennal sockets, with pair of stout

ocellar setae on short tubercles posterior to anterior ocellus; pair of setulae behind posterior ocellus. Strong vertical seta, longer than collar setae. Occiput with vertical row of setae, stouter dorsally. Face shorter than frons, without setae. Antenna with scape and pedicel subequal in length, with dorsal setae; postpedicel elongate ovate, basal width half as long as length; postpedicel seta longer than length of head; arista-like stylus subequal to length of postpedicel, with one basal article. Proboscis with palpus with rounded tip; labellum shorter than compound eye width.

Thorax not strongly hunched in shape; setae strong and thickened. One postpronotal seta; one posthumeral seta; one presutural supra-alar seta; acrostichal setae uniserial, extending onto prescutellar depression, with pair of prescutellar setae; dorsocentral setae short; two notopleural setae, long and thin; one postsutural supra-alar seta; one postalar seta; one pair of scutellar setae; laterotergite bare.

Fore coxa with fine, silky anterior setae. Foreleg slightly shorter than other legs, not raptorial. Fore femur shorter than mid and hind femora, with strong, dorsal posterodorsal and posteroventral setae. Fore tibia narrower than femur, with two strong posterodorsal setae; apex with pair of spine-like ventroapical setae. Fore tarsomeres 3–4 slightly modified: tarsomere 1 1.5 times longer than tarsomere 2; tarsomere 2 quadrate with spine-like ventral seta and short ventral process; tarsomere 3 longer than tarsomeres 1 and 2 combined, with strong setae, base with stout anterior seta; tarsomere 4 laterally flattened with peg-like setae. Midleg with numerous strong, erect setae. Hindleg similar to midleg; hind tarsomere 1 with one erect, outstanding dorsal seta on distal third.

Wing with one basal costal seta; M_{1+2} not bowed into cell dm proximal to cell dm; stem vein with several dorsal setae; R_1 with dorsal setae; alula not developed; crossvein dm-m gently curved.

Abdomen with long posteromarginal setae; six pregenital segments before terminalia folded tightly beneath.

Female. Similar to male except without modified fore tarsomeres and tubular abdomen.

Electrochoreutes falculigerus **sp.n.**
Zoobank ID: urn:lsid:zoobank.org:act:9EDF603F-F313-4F62-A1FA-85F3B1DF50BD
Etymology. The species name is a composite adjective from Latin, meaning "sickle bearer" referring to the sickle-shaped process on tarsomere 2 of male foreleg.
Type material. Holotype, male, NIGP 201459. Well-preserved, complete specimen.
Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Postpedicel flattened 2.5 times longer than wide, without dorsal seta, stylus with one basal segment. Tarsomere 2 of male foreleg robust, subcylindrical with unforked, arched process with an apical spine-like seta. Tarsomere 3 of male foreleg notched at base. M_{1+2} nearly straight (except for a gentle curvature proximally beyond cell dm), not bowed into cell dm proximal to crossvein r-m.

Description. Male. Compound eye with deep anterior notch. Head with pair of stout interfrontal setae on short tubercles; ocellar triangle halfway between vertex and antennal sockets, with pair of stout ocellar setae on short tubercles posterior to anterior ocellus; pair of setulae behind posterior ocellus. Strong vertical seta, longer than occipital setae. Occiput with vertical row of setae, stouter dorsally. Face shorter than frons, bare. Antenna with scape and pedicel subequal in length, with dorsal setae; postpedicel conical, 2.5 times longer than maximum width at base, without dorsal seta; stylus half-length of postpedicel, with one basal article. Proboscis with palpus cylindrical, clothed in long, thin setae, and with three strong apical setae; labellum longer than eye length.

Thorax slightly hunched-shaped; chaetotaxy strong and thickened: one postpronotal setae; one posthumeral setae; one presutural supra-alar seta; *c.* 18 acrostichal setae uniserial, short, extending onto prescutellar depression, with pair of prescutellar setae; 12 dorsocentral setae short and stout; two notopleural setae; one postsutural supra-alar seta; one postalar seta; one pair of scutellar setae; two proepisternal seta; laterotergite bare.

Foreleg shorter than other legs, slightly swollen. Fore femur shorter than mid and hind femora, swollen. Fore tibia narrower and slightly shorter than femur, with strong anterodorsal and posterodorsal setae; apex with stout setae, ventrally with stout posteroventral apical seta. Fore tarsomeres 1–4 partly modified: tarsomeres short, with robust setae; tarsomere 2 stout, subcylindrical, with curved ventral process bearing apical spine; tarsomere 3 slightly longer than tarsomere 2, clothed with thin setae; tarsomere 4 shorter than tarsomere 3, clothed with thin setae; tarsomere 5 shorter than tarsomere 4, with thin setae. Midleg with numerous strong, erect setae. Mid tibia and tarsus long and thin, with row of fine, elongate anteroventral setae. Mid tarsomere 1 with both thin and stout ventral setae. Hindleg similar to midleg, except femur more robust.

Wing with one basal costal seta; M_{1+2} not bowed into cell dm proximal to crossvein r-m; stem vein with several dorsal setae; R_1 without dorsal setae; crossvein dm-m gently curved.

Abdomen with six pregenital segments before terminalia folded tightly beneath. Apex of terminalia with

pair of claw-like projections, bearing apical spine-like processes.

Electrochoreutes furcillatus **sp.n.**

Zoobank ID: urn:lsid:zoobank.org:act:7AAE8030-7743-4B7B-821C-57B38361EB88

Etymology. The specific epithet is a Latin adjective meaning "biforked", referring to the tarsal process on foreleg.

Type material. Holotype, male, NIGP 201460. Relatively well-preserved male specimen, partly obscured by bubbles and impurities, dorsal side only partially visible.

Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Tarsomere 2 of male foreleg with forked process. Palpus with erect stout setae. Fore tibia narrower than femur. M_{1+2} strongly bowed into cell dm to proximal to r-m crossvein.

Description. Male. Head without interfrontal setae; ocellar triangle halfway between vertex and antennal sockets, ocellar setae lost. Antenna with scape and pedicel subequal in length, with dorsal setae; postpedicel pointed ovate, longer than basal width; postpedicel seta shorter than length of head; arista-like stylus twice length of postpedicel, with one basal article. Proboscis with cylindrical palpus, clothed in long, strong, erect setae and stout erect apical seta; labellum longer than eye length, with several pseudotracheae visible.

Thorax slightly hunched-shaped; setae poorly preserved and barely recognizable; most setae thin. Fore coxa with fine, silky anterior setae; mid coxa with strong lateral seta. Foreleg with femur as broad as mid and hind femora. Fore femur shorter than mid and hind femora, with strong dorsal, posterodorsal and posteroventral setae. Fore tibia narrower than femur, with row of strong, erect dorsal setae; apex with stout, posteroventral apical seta. Fore tarsomeres 1–3 modified: tarsomere 1 longer than other tarsomeres, with tuft of ventrobasal setae; tarsomere 2 very short, with long, forked sickle-shaped process; tarsomere 3 concave opposite process, with pair of elongate dorsal setae. Midleg with numerous strong, erect setae; tarsomere 4 subcylindrical; tarsomere 5 shorter than tarsomere 4, of same width. Mid tibia and tarsus clothed in fine, elongate setae. Base of mid tarsomere 1 with pair of long and strengthened ventral setae; tarsomeres 1–3 with pair of strong, preapical ventral setae. Hindleg similar to midleg, without fine, elongate anteroventral setae.

Wing vein M_{1+2} bowed into cell dm proximal to crossvein r-m; stem vein with several dorsal setae; R_1 without dorsal setae; crossvein dm-m sinuous.

Abdomen with long posteromarginal setae; segments before terminalia folded tightly beneath. Apex of terminalia with pair of claw-like projections.

Electrochoreutes hamatus **sp.n.**

Zoobank ID: urn:lsid:zoobank.org:act:18040FC6-6004-4628-A763-36EB028AFB7E

Etymology. The specific epithet is a Latin adjective meaning "hooked".

Type material. Holotype, male, NIGP 201461. Poorly preserved specimen, lacking most of the head, with poorly recognizable wing venation and chaetotaxy and with disarticulated and broken mid- and hindlegs.

Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Male fore femur and tibia slightly swollen, with a row of stout, hook-shaped dorsal setae on tibia. Male hind tibia with preapical row of thickened ventral setae.

Description. Male. Most of head damaged and lost. Occiput with stout setae.

Thorax slightly hunched in shape; chaetotaxy strong and thickened.

Foreleg shorter than other legs, slightly swollen. Fore femur shorter than mid and hind femora, with row of thin, erect dorsal setae, longer than width of femur; anteroventrally with row of thickened setae. Fore tibia slightly swollen and shorter than femur, with strong anterodorsal and posterodorsal setae and distal row of at least four very robust and hooked dorsal setae; apex with ventral spine-like posteroventral apical seta. Fore tarsomere 1 longer than other tarsomeres, base with stout setae, covered with thin setae; tarsomeres 2–4 shorter, subcylindrical covered in thin setae; tarsomere 5 shorter than tarsomere 4 and wider. Midleg thinner than other legs, with numerous long, thin setae. Mid tibia with thin, elongate anteroventral setae and at least two long and robust setae. Base of mid tarsomere 1 with pair of stout ventral setae. Hindleg longer and more robust than midleg, with swollen femur. Hind tibia not swollen, with several strong dorsal setae and numerous thin ventral setae, longer than width of tibia; apex with ventral row of at least six evenly spaced and similar sized short, robust setae. Hind tarsomere 1 with spine-like preapical ventral setae.

Abdomen with six pregenital segments before terminalia folded beneath.

Remarks. Despite the poor state of preservation, *E. hamatus* can be assigned to *Electrochoreutes* based on the shape of pregenital segments and wing vein Rs originating at humeral crossvein.

Electrochoreutes pankowskii **sp.n.**

Zoobank ID:urn:lsid:zoobank.org:act:FAE4F0CF-B5D9-4F09-BCEA-C56DF01A7C6A

Etymology. The specific epithet is named in honour of Max Pankowski, who kindly donated the specimen used in this study.

Type material. Holotype, male, USNM PAL 726876 (USNM). Paratype, male, NIGP 201462. Both well-preserved specimens.

Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Postpedicel 1.5–2 times as long as wide. Arista-like stylus with two basal articles. Strong erect interfrontal setae anterior to ocellar triangle. Male fore tibia as broad as femur with anterodorsal preapical process. Wing vein M_{1+2} not bowed into cell dm proximal to crossvein r-m.

Description. Male. Head with pair of stout interfrontal setae on short tubercles; ocellar triangle halfway between vertex and antennal sockets, with pair of stout ocellar setae on short tubercles posterior to anterior ocellus; pair of setulae behind posterior ocellus. Strong vertical seta, longer than occipital setae. Occiput with vertical row of setae, stouter dorsally. Face shorter than frons, without setae. Antenna with scape and pedicel subequal in length, with dorsal setae; postpedicel pointed ovate, 1.5 times longer than basal width; postpedicel seta longer than length of head; arista-like stylus twice length of postpedicel, with two basal articles. Proboscis with palpus tapered, clothed in long, slender setae; labellum longer than eye length, with possibly six visible pseudotracheae.

Thorax somewhat hunched in shape; chaetotaxy strong and thickened: two postpronotal setae; two posthumeral setae; two presutural supra-alar setae; acrostichal setae uniserial, extending onto prescutellar depression, with pair of prescutellar setae; 13 dorsocentral setae, alternating long and short; two notopleural setae with two lower fine setae; one postsutural supra-alar seta; one postalar seta; pair of scutellar setae, with several apical setulae; one proepisternal seta; laterotergite bare.

Fore coxa with fine, silky anterior setae; mid coxa with strong lateral seta. Foreleg appears shortened, somewhat swollen. Fore femur shorter than mid and hind femora, with strong dorsal, posterodorsal and posteroventral setae. Fore tibia stocky as wide as and shorter than femur, with strong anterodorsal and posterodorsal setae, longer than width of tibia; apex with subapical, anterodorsal spur-like process, ventrally with spine-like posteroventral apical seta. Fore tarsomeres 1–4 highly modified: tarsomeres 1 and 2 shortened, with spine-like ventral seta; tarsomere 3 longer than tarsomeres 1 and 2 combined, apical half flattened and expanded, mid-length with row of peg-like setae, base with anterior, sinuous, spine-like seta; tarsomere 4 laterally flattened with truncate-tipped preapical ventral process, subequal to width of tarsomere. Midleg with numerous strong, erect setae. Mid tibia and tarsus with row of fine, elongate anteroventral setae. Base of mid tarsomere 1 with pair of spine-like

ventral setae; tarsomeres 1–3 with pair of strong, preapical ventral setae. Hindleg similar to midleg, without fine, elongate anteroventral setae.

Wing with 1 basal costal seta; vein M_{1+2} not bowed into cell dm proximal to crossvein r-m; stem vein with several dorsal setae; R_1 without dorsal setae; crossvein dm-m gently curved.

Abdomen with long posteromarginal setae; six pregenital segments before terminalia folded tightly beneath. Apex of terminalia with pair of claw-like projections.

Electrochoreutes planitibia **sp.n.**
Zoobank ID: urn:lsid:zoobank.org:act:A9EDBE04-4535-4ACE-8819-09AAFE540342

Etymology. The specific epithet is a Latin compound name meaning "flattened tibia", after the shape of the fore tibia.

Type material. Holotype, male, NIGP 201463. A poorly preserved male, partly deformed and covered in impurities.

Type locality and horizon. Northern Myanmar, Kachin Province, Hukawng Valley, *c.* 100 km west of the town of Myitkyina; Late Cretaceous (98 ± 0.6 Ma).

Diagnosis. Fore tibia with expanded, flat anterior ridge near mid-length. Hind tibia with fine, elongate silky setae. Wing vein M_{1+2} bowed into cell dm proximal to crossvein r-m.

Description. Male. Head with pair of stout interfrontal setae on short tubercles. Occiput with vertical row of setae, stouter dorsally. Proboscis with palpus cylindrical, clothed in long, erect setae.

Thorax slightly hunched-shaped; chaetotaxy only partly appreciable; one posthumeral seta; one presutural supra-alar seta; acrostichal setae uniserial, with pair of prescutellar setae; dorsocentral setae dense, short and thin, two notopleural setae; one postsutural supra-alar seta; laterotergite bare.

Fore coxa with fine, silky anterior setae; mid coxa with strong lateral seta. Foreleg appears shortened. Fore femur shorter than mid and hind femora, with strong dorsal, posterodorsal and posteroventral setae. Fore tibia slender, with expanded, flat anterior ridge near mid-length; strong anterodorsal and posterodorsal setae. Fore tarsomeres not modified, subcylindrical, covered in long setae. Midleg with numerous strong, erect setae. Mid tibia and tarsus with fine, elongate setae. Base of mid tarsomere 1 with pair of spine-like ventral setae; tarsomeres 1–3 with pair of strong, preapical ventral setae. Hindleg similar to midleg, with fine, elongate setae.

Wing with vein M_{1+2} bowed into cell dm proximal to crossvein r-m; stem vein with several dorsal setae; R_1 without dorsal setae; crossvein dm-m gently sinuous.

Abdomen with long posteromarginal setae; six pregenital segments before terminalia folded beneath abdomen.

Key to the males of the species of *Electrochoreutes*

1. Fore tibia with stout hook-shaped setae (Fig. 4d)..............................*E. hamatus*

• Fore tibia without stout hook-shaped setae (Fig. 2a, c–f)... 2

2. Postpedicel with long dorsal hair-like seta (Fig. 3d)...................................... 3

• Postpedicel without long dorsal hair-like seta (Fig. 3f)............................ *E. falculigerus*

3. Arista-like stylus with two basal articles (Fig. 3e); fore tibia swollen with anteroventral spur-like process (Fig. 4e)........................ *E. pankowskii*

• Arista-like stylus with one basal article (Fig. 3d); fore tibia not swollen, without anteroventral spur-like process 4

4. M_{1+2} not dipped into cell dm proximal to crossvein r-m (Figs 2d and S3)............................... *E. electroechinus*

• M_{1+2} dipped into cell dm proximal to crossvein r-m (Figs 2a and S2e) 5

5. Fore tarsomere 2 with forked, sickle-shaped process (Fig. 4c)............................. *E. furcillatus*

• Fore tarsomere 2 without process.. 6

6. Fore femur with three long ventrobasal setae; fore tibia without expanded ridge (Fig. 4a)............................. *E. trisetigerus*

• Fore femur without three long ventrobasal setae; fore tibia with expanded, flat anterior ridge (Fig. 4f)................................. *E. planitibia*

Phylogenetic analyses

The MP analysis under equal weights produced 7904 most-parsimonious trees (tree length = 662 steps; consistency index for matrix, CI = 0.302; retention index for matrix, RI = 0.71). The strict consensus cladogram is shown in Appendix S4. Under implied weights, the search yielded different topologies depending on the selected *k*-value of the default weighting function. The tree obtained under the best fitting *k*-value (*k* = 14.785) as recovered by the "setk.run" algorithm was chosen to discuss the relationships among empidoids. Under these conditions, the analysis yielded 24 most-parsimonious trees with a total fit of 104.518 and tree length of 665 steps, whose strict consensus tree is shown in Fig. 5. Equal and implied weight MP analyses mostly differ in the relationships within family-ranked clades (Fig. 5, Appendix S4).

All phylogenetic analyses consistently recovered Empidoidea as monophyletic, albeit with low support. Overall, the phylogenetic backbone of empidoids remained poorly resolved (Figs 5 and 6; Appendix S4).

Atelestidae were retrieved as monophyletic in all analyses (MP Bremer support value: 1; BI posterior probability: 0.97; ML bootstrap resampling percentile: 95). Depending upon the analytical method employed the atelestid clade is recovered as nested within the empidoids and sister to Hybotidae (MP, under both EW and IW), or as part of a basal trichotomy with *Homalocnemis* Philippi and the rest of the empidoids (BI and ML). Within Atelestidae, Nemedininae were recovered as monophyletic in all analyses, whereas Atelestinae were only recovered as monophyletic under IW. *Trichinites* and *Atelestites* Grimaldi and Cumming were consistently recovered as crown-group atelestid in all analyses. *Alavesia* was recovered as the sister taxon to all the other Atelestinae (also including *Trichinites*) under IW. The Nemedininae were recovered as monophyletic in virtually all analyses also gaining high support (MP Bremer support value: 3; BI posterior probability: 1; ML bootstrap resampling percentile: 98). The latter clade included the extant *Nemedina* Chandler and several Cretaceous extinct taxa, namely, *Cretodromia* Grimaldi and Cumming, *Nemedromia* Grimaldi and Cumming, *Neoturonius* Grimaldi and Cumming, *Phaetempis* Grimaldi and Cumming and *Prolatomyia* Grimaldi and Cumming. Under MP, *Nemedina* appears nested within the Mesozoic taxa.

The Empididae are never recovered as monophyletic, nor are the empidid subfamilies represented in our dataset. The Mesozoic *Emplita* Grimaldi and Cumming and *Turonempis* were recovered as nested within Empidinae + Tachydromiinae under both ML and BI. However, MP analyses gave conflicting results regarding their affinities.

The family Brachystomatidae, including *Apalocnemis*, turned out to be monophyletic in all analyses (MP Bremer support value: 1; BI posterior probability: 0.98; ML bootstrap resampling percentile: 94), but their affinity with respect to other empidoids remained unresolved (Figs 5 and 6; Appendix S4).

The Hybotidae were poorly (MP Bremer support value: 1) to strongly (BI posterior probability: 0.99, ML bootstrap resampling percentile: 96) supported as monophyletic in all analyses, although their internal relationships remained unclear, as the different phylogenetic methods yielded contrasting topologies (Figs 5 and 6; Appendix S4). *Cretoplatypalpus* Kovalev, *Pouillonhybos* Ngô-Muller, Engel and Nel and

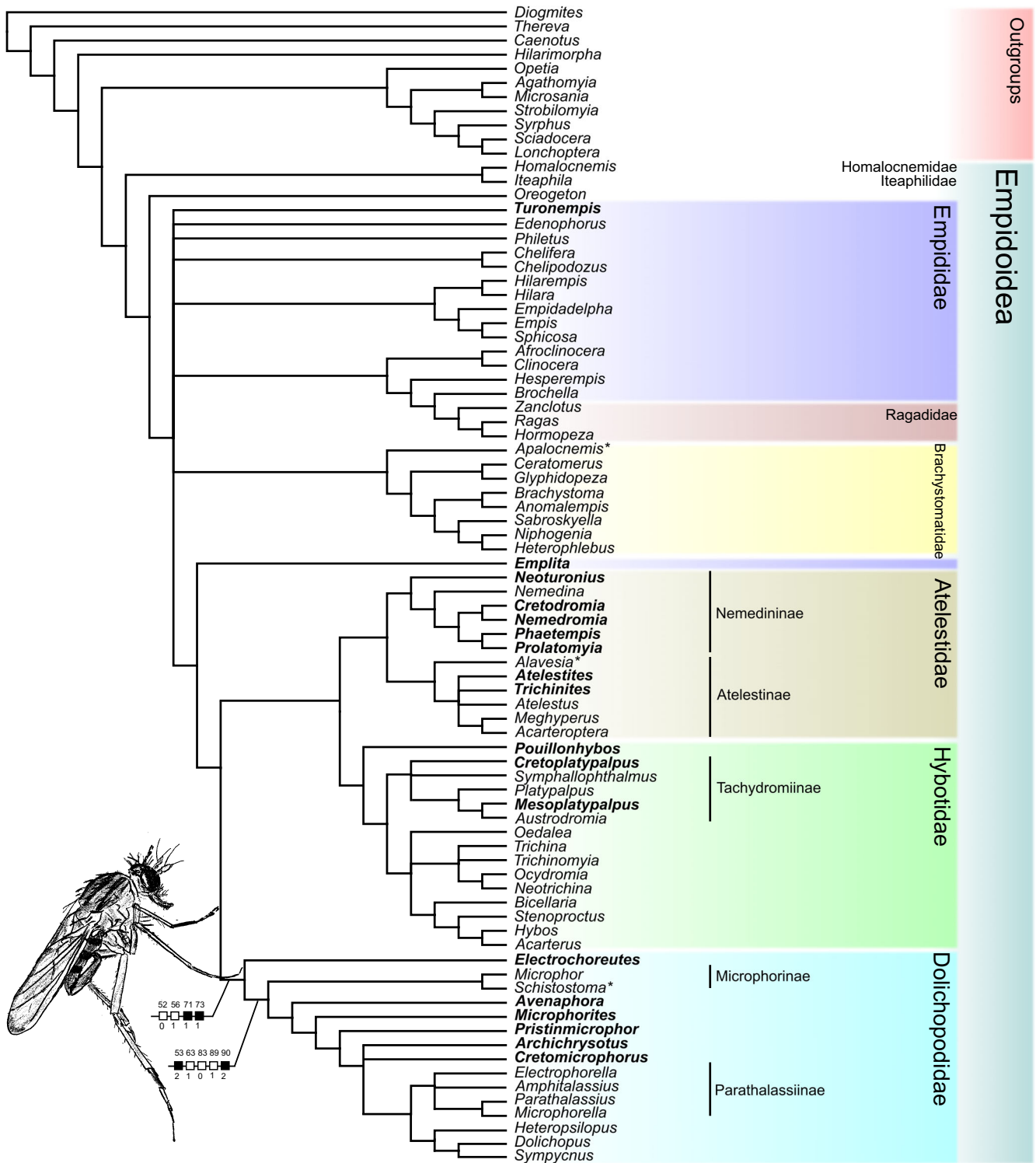*Badano D. et al. | Cladistics 0 (2023) 1–21*

Fig. 5. Phylogeny of Empidoidea under MP, including fossils. Strict consensus cladogram of 24 trees obtained under implied weights. Inferred character state changes for Dolichopodidae mapped at base of dolichopodid branch; white squares indicate non unique apomorphies; black squares indicate unique apomorphies. Genera in bold are Cretaceous fossils; taxa with asterisks represent extant genera also known from Cretaceous amber.
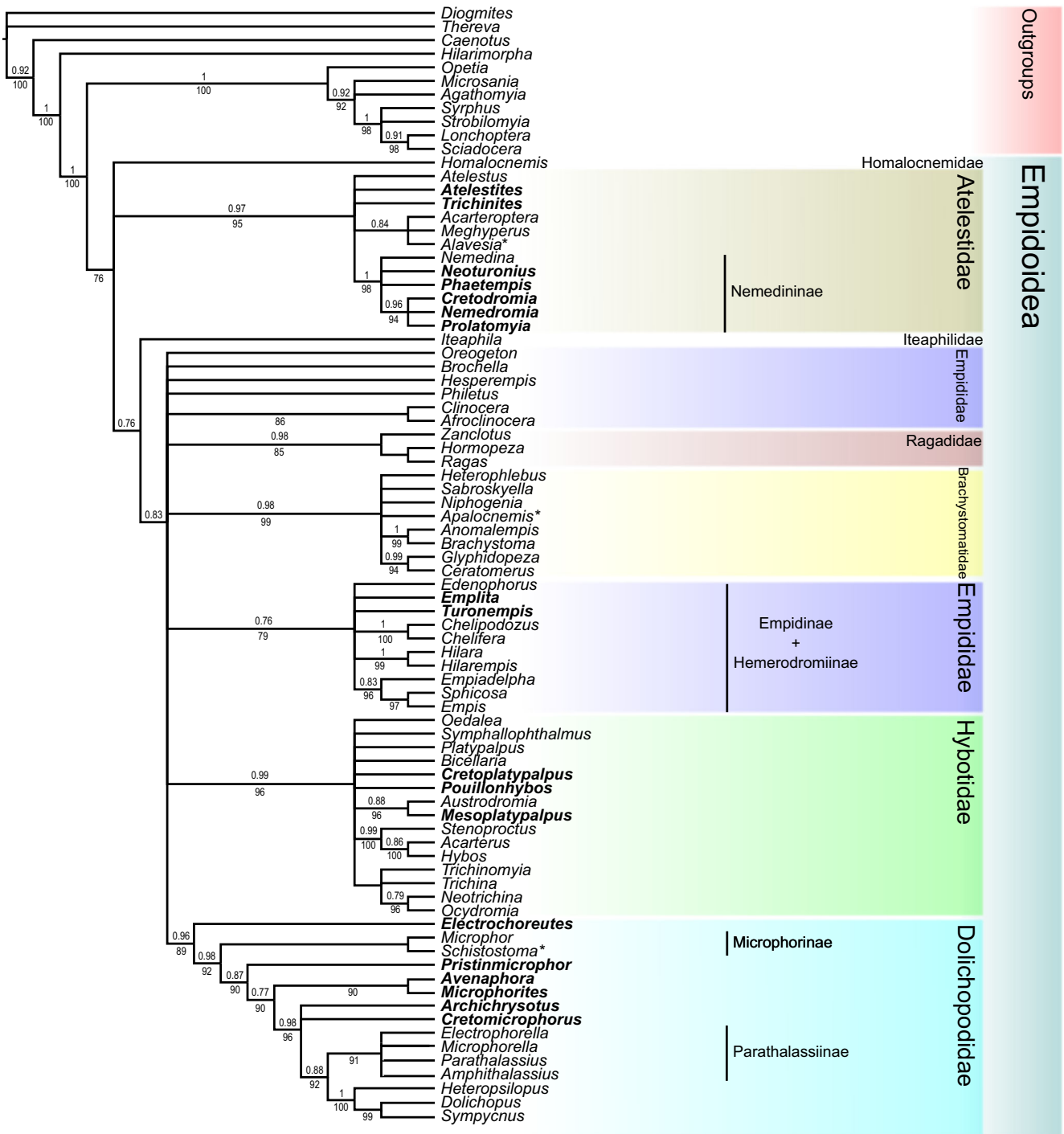
Fig. 6. Phylogenetic tree of Empidoidea, including fossils, obtained under ML and BI. Numbers above branches are Bayesian posterior probabilities; numbers below branches are ML bootstrap supports. Branches below 75 thresholds were collapsed. Genera in bold are Cretaceous fossils; taxa with asterisks represent extant genera also known from Cretaceous amber.

Mesoplatypalpus Grimaldi and Cumming were recovered as part of the hybotid radiation. MP analysis recovered *Pouillonhybos* as the sister taxon to all hybotids, whereas *Cretoplatypalpus* and *Mesoplatypalpus* were recovered nested within the Tachydromiinae. *Mesoplatypalpus* was consistently reconstructed as sister to the extant *Austrodromia* Collin in all analyses.

Electrochoreutes clustered sister to the crown-group Dolichopodidae in all analyses (Figs 5 and 6; Appendix S4). Under IW, *Electrochoreutes* shared with crown-group Dolichopodidae two unique (71 : 1, male with sternite 7 bare; 73 : 1 male with segment 7 tubular) and three homoplasious synapomorphies (52 : 0; 56 : 1; 69 : 2; Fig. 5). The monophyly of crown-group Dolichopodidae was strongly supported in the BI (posterior probability: 0.98) and ML (bootstrap resampling percentile: 92); under MP the monophyly of crown-group Dolichopodidae received a Bremer support value of 1 (Figs 5 and 6; Appendix S4). Under IW, crown-group Dolichopodidae were characterized by two unique (53 : 2, costal spine single; 90 : 2, male genitalia rotated at 90°–180°) and three homoplasious (63 : 1; 83 : 0; 89 : 1) synapomorphies (Fig. 5). Several Cretaceous taxa—*Pristinmicrophor*, *Avenaphora*, *Microphorites*, *Archichrysotus* and *Cretomicrophorus*—formed a progressive grade, between the extant *Microphor* and *Schistostoma*—which were recovered as sister in all analyses—and the rest of Dolichopodidae.

Discussion

Fossil placement

Our phylogenetic analyses retrieved empidoids and most of the family-ranked taxa as monophyletic, with extinct forms clustering invariably as stem- or crown-groups of these taxa (Figs 5 and 6; Appendix S4). Notable exceptions are the fossil empidids *Emplita* and *Turonempis*, whose relationships remained unclear in a context where the empidids themselves are not monophyletic. Nevertheless, ML and BI reconstructions weakly supported both *Emplita* and *Turonempis* as nested within Empidinae + Hemerodromiinae—the "core" empidids—in agreement with Grimaldi and Cumming (1999; Fig. 6). Atelestidae, one of the best-represented groups of empidoids in Mesozoic ambers, were confirmed to be monophyletic with Mesozoic *Trichinites* nested within them. This latter taxon was originally assigned to Hybotidae by Hennig (1970), but was later moved by Hennig (1971) as sister to a clade composed by hybotids and atelestids. Grimaldi and Cumming (1999) instead proposed that *Trichinites* might be a stem-group hybotid. We recovered a well-supported Hybotidae, encompassing three Cretaceous fossils: *Cretoplatypalpus*, *Mesoplatypalpus* and *Pouillonhybos*. Our reconstruction confirmed that *Cretoplatypalpus* and *Mesoplatypalpus* are nested within Tachydromiinae in agreement with Grimaldi and Cumming (1999), who highlighted the plesiomorphic condition of the chaetotaxy of these genera in contrast with extant tachydromiines. The phylogenetic position of *Pouillonhybos* varied with phylogenetic inference method; however, in

contrast to Ngô-Muller et al. (2021) we did not recover it as closely related to Ocydromiinae. In addition to atelestids, dolichopodids are well-represented in Cretaceous amber deposits. Most of these fossil taxa, such as *Pristinmicrophor*, *Avenaphora*, *Microphorites*, *Archichrysotus* and *Cretomicrophorus*, have been assigned to the subfamily Microphorinae based on morphological evidence (Grimaldi and Cumming, 1999). However, the inclusion of this diverse assemblage of Mesozoic taxa within Microphorinae has been debated (Cumming and Brooks, 2002; Shamshev and Perkovsky, 2022). Cumming and Brooks (2002), using cladistic arguments, reconstructed the Microphorinae as paraphyletic, with *Microphorites* forming a clade with *Microphor* and *Schistostoma*, while *Cretomicrophorus* and *Archichrysotus* were recovered as Parathalassiinae, which also included the Eocene *Electrophorella* (Figs 5 and 6; Appendix S4). We also never recovered the "traditional" Microphorinae as monophyletic in our reconstructions, as the fossil taxa never clustered with the extant microphorines *Microphor* and *Schistostoma*. However, our analyses did not reconstruct *Cretomicrophorus* and *Archichrysotus* as parathalassiines, finding them in a polytomy with a clade that included *Dolichopus* Latreille, *Heteropsilopus* Bigot, *Sympycnus* Loew and the representatives of the Parathalassiinae (Figs 5 and 6; Appendix S4). We therefore propose that *Pristinmicrophor*, *Avenaphora*, *Microphorites*, *Archichrysotus* and *Cretomicrophorus* represent a diverse assemblage of Dolichopodidae *incertae sedis* (see also Grimaldi and Cumming, 1999). In our analyses, the crown-group Dolichopodidae consistently received moderate to high support (Figs 5 and 6; Appendix S4).

Electrochoreutes: a puzzling Mesozoic fly

Dolichopodidae are the most diverse group of empidoids and are widespread in modern ecosystems. Dolichopodid monophyly, including Microphorinae and Parathalassiinae—two groups whose affinities have been long debated—appears strongly supported by both morphological and molecular evidence (Sinclair and Cumming, 2006; Moulton and Wiegmann, 2007; Wahlberg and Johanson, 2018). Mesozoic amber show that dolichopodids were already quite diverse in the Cretaceous, being represented by Microphorinae (e.g. *Schistostoma*) and a diverse assemblage of microphorine-like taxa (e.g. *Pristinmicrophor*, *Avenaphora*, *Microphorites*, *Archichrysotus*, *Cretomicrophorus*; Grimaldi and Cumming, 1999; Tang et al., 2019; Shamshev and Perkovsky, 2022). Our phylogenetic reconstructions consistently recover *Electrochoreutes* as an early representative of the dolichopodids (Figs 5 and 6; Appendix S4). This Mesozoic genus displays a mosaic combination of empidoid traits, being characterized by a rather plesiomorphic habitus with respect to other

Mesozoic and modern dolichopodids, and resembling a generalized empidid-like or brachystomid-like fly in body shape; yet, it also possesses a highly derived and unique antenna, wing venation and male terminalia (Figs 2 and 3).

Empidoidea, and Dolichopodidae in particular, vary greatly in the shape of postpedicel and in the placement of the arista-like stylus, which can be terminal or dorsal in position (Sinclair and Cumming, 2006). *Electrochoreutes* is the only representative of this clade with a large mechanoreceptor originating on the dorsal side of the postpedicel that is thicker than the stylus and much longer than the head. This very large seta is the most remarkable autapomorphic feature of *Electrochoreutes* (Fig. 3d,e).

Electrochoreutes shares with crown-group Dolichopodidae a major synapomorphic character, namely the first radial wing vein originating toward the base of the wing, opposite the humeral vein (Fig. S1d). The importance of this venation character in the identification of dolichopodids has long been recognized (Sinclair and Cumming, 2006). All fossil and living Dolichopodidae are characterized by small basal and cubital cells, and by crossvein r-m situated at the proximal quarter of the wing. By contrast, *Electrochoreutes* species have large basal and cubital cells—which is likely to be a plesiomorphic condition of empidoids— and crossvein r-m situated more distally (i.e. beyond half of wing length), thus recalling the condition shared by "basal" brachycerans, such as Asiloidea and Nemestrinoidea.

Empidoidea exhibit a wide diversity in the structure of male terminalia and copulatory behaviour across lineages. Hybotidae, Dolichopodidae, the brachystomatid *Trichopeza* Rondani (and related genera) and the Cretaceous atelestid *Neoturonius* exhibit varying degrees of asymmetry of the male terminalia, which are likely to have evolved multiple times independently in these groups (Sinclair and Cumming, 2006; Huber et al., 2007). The asymmetry in Hybotidae and Dolichopodidae is associated with rotation of the last abdominal segments around the longitudinal body axis (45°–90° in Hybotidae, 90°–180° in Dolichopodidae). In male Dolichopodidae the pregenital segments are partially stretched and twisted to the right, the hypopygium is asymmetrical with reduced gonocoxal apodemes, the subepandrial sclerites are fused to the hypandrium, and the terminalia are flexed beneath the abdomen (Ulrich, 1974; McAlpine, 1981; Sinclair and Cumming, 2006; Huber et al., 2007). Male *Electrochoreutes* share flexed terminalia, but apparently evolved a different configuration characterized by long and tubular pregenital segments, which are much narrower than preceding segments, and a symmetrical hypopygium (Figs 3a,b, S4g, S6f and S7d). The structure of male terminalia and pregenital segments of *Electrochoreutes* appears unique across Empidoidea and is highly apomorphic.

Electrochoreutes differs from crown-group dolichopodids in the absence of acanthophorites— spiny hemitergites on syntergite 9 + 10 of female, functionally associated with oviposition—which are shared by many lineages of Eremoneura. Acanthophorites also characterize several non-eremoneuran Brachycera, such as the Asiloidea, and may represent a groundplan apomorphy of the Brachycera that has experienced multiple independent losses (including Atelestinae, Hybotidae and Empididae among empidoids) or shape changes (e.g. seta-like as in Microphorinae) during the radiation of various lineages (Sinclair and Cumming, 2006). The lack of acanthophorites in *Electrochoreutes* may represent just another case of independent loss, perhaps associated with specialized oviposition behaviour or larval habits.

Lim et al. (2010) hinted at a rapid diversification of the dolichopodid over a short time, which is supported by their diversity in Mesozoic amber deposits. The unusual morphological features of *Electrochoreutes*, which blend plesiomorphic and apomorphic traits, and its phylogenetic affinities suggest that it might be one of the earliest lineages to branch off from the dolichopodid evolutionary tree.

A wealth of Mesozoic compression fossils has been assigned to Empidoidea, some of which date back to the Middle Jurassic, while others have been assigned to present-day genera (e.g. Waters, 1989). Reconstructing phylogenetic affinities of these fossils often is problematic, as the only reliable features are wing veins, which are rather conservative across the clade and therefore largely uninformative. Unsurprisingly, several fossils originally described as representing Empidoidea were later reassigned to other Diptera groups (Zhang, 2012). In this difficult context, well-preserved amber specimens such as those of *Electrochoreutes*, shed light on the diversification of lineages and the evolution of morphological and ethological traits. *Electrochoreutes* is a stem-group lineage of the Dolichopodidae, and therefore represents a potentially useful calibration point for marking the diversification events of this clade.

Secondary sexual characters and species recognition

Sexual dimorphism and exaggerated secondary sexual traits can evolve as the result of sexual selection, by means of direct competition between individuals of the same sex or owing to mate choice by the opposite sex (Jones and Ratterman, 2009; Henshaw et al., 2022). Sexually selected characters also can play a role in interspecific identification and as a potential driver in speciation, facilitating the avoidance of interbreeding between related species (Boake, 2002). Diptera show an exceptional diversity of secondary sexual

traits and mating behaviours, such as swarming, court-ships or fights, making them a pivotal group for the study of the evolution of these traits (Burk, 1981; Sivinski, 1997; Wilkinson and Dodson, 1997; Wilkinson and Johns, 2005; Marshall, 2012).

Males of extant Dolichopodidae perform a variety of mating behaviours and often are endowed with distinctive secondary sexual traits involving antennae, legs, wings and terminalia; the latter are often spectacularly modified (Fig. 1). Most of these sexually dimorphic characters are involved in elaborate courtship and ritual dances (Steyskal, 1938, 1946; Lunau, 1996; Zimmer et al., 2003; Fig. 1d–f). Unlike most dolichopodids, the Microphorinae do not have complex courtship behaviour and mate in swarms, a condition that appears plesiomorphic among the Eremoneura (Marshall, 2012). However, the males of two *Schistostoma* species recently described in Burmese amber, *S. burmanicum* Brooks, Cumming and Grimaldi and *S. foliaceum* Brooks, Cumming and Grimaldi, are characterized by enlarged, lamellate fore tibia, suggesting that signalling behaviour also may have been present in the early Microphorinae (Brooks et al., 2019).

Mating rituals differ considerably among the dolichopodids. Males of some genera, such as *Sybistroma* Meigen, perform ritualized nuptial flights while being observed by females resting on the substratum (Lunau, 1996). Males of flight-dancing species often are characterized by modified and exaggerated antennae, which may be swollen or elongated (Fig. 1b; Lunau, 1996; Grichanov and Brooks, 2017). In other genera, such as *Poecilobothrus* Mik, courtship behaviour involves a dance on the substratum, during which the male rhythmically displays and waves his wings, which often are coloured, or modified in shape (Lunau, 1996; Zimmer et al., 2003; Lunau et al., 2006). In other cases, such as *Neurigona* Rondani, male mating dances also include ritual movements of the legs, sometimes in synchrony with the wings. These mating rituals are associated with the evolution of sometimes highly exaggerated secondary sexual modifications of the legs, which appear to have independently evolved on each pair of legs as swellings, tarsal projections, modified setae or enlarged pretarsal claws. For instance, the fore tarsus is provided with swollen tarsomeres or projections in *Campsicnemus* Haliday and *Telmaturgus* Mik, with a tuft of long setae in *Hercostomus* Loew or provided with enlarged pretarsal claws in *Peloropeodes* Wheeler (Lunau, 1996; Grichanov and Brooks, 2017). Similar modifications involve the midleg in *Dolichopus*, *Sciapus* Zeller and *Teuchophorus* Loew, and the hindleg in *Chaetogonopteron* de Meijere. In several cases (e.g. *Dolichopus, Neurigona* and *Sciapus*), the modified tarsi also are conspicuously pigmented to enhance visual contrast of the signalling structures (Lunau, 1996; Grichanov and Brooks, 2017; Fig. 1a, c–f).

However, in other dolichopodids, male secondary sexual traits might be involved in more active, antagonistic behaviours. Indeed, the males of some species defend their territories by chasing away any intruding conspecific male, while others guard their female partner after copulation by holding her with forelegs to prevent her mating with others (e.g. *Hydrophorus* Fallén; Dyte, 1988).

Electrochoreutes is unique among Diptera in having a long seta arising from postpedicel (Fig. 3d,e). This seta is present in both sexes of all species but *E. falculigerus* (Fig. 3f). During the Cretaceous, various lineages of flies independently evolved unusual antennal features; for example, exaggerated antennal traits characterized several extinct species of *Alavesia* from Burmese amber (Grichanov and Brooks, 2017; Sinclair and Grimaldi, 2020). Elongated or swollen antennae in extant dolichopodids are a secondary sexual trait occurring in males and are usually involved in nuptial dances performed in flight (Lunau, 1996; Fig. 1b). The postpedicel seta in *Electrochoreutes* is not sexually dimorphic and is likely to have been used as a specialized mechanoreceptor.

Leg modifications often are species-specific and highly variable in shape within the same genus, suggesting that they play important roles in species recognition and act as important pre-mating barriers. Some dolichopodid genera are characterized by a wide range of variation in leg features. For example, the genus *Campsicnemus* includes both species with unmodified forelegs (e.g. *C. pusillus* Meigen) and others with conspicuous modifications involving processes, protuberances and modified setae (e.g. *C. magius* Loew; Lunau, 1996; Sivinski, 1997).

Electrochoreutes show that highly derived species-specific secondary sexual traits of the legs in the Dolichopodidae evolved during the Mesozoic. Males of all of the described species of *Electrochoreutes*, with the only exception of *E. electroechinus*, are characterized by modified forelegs. The great interspecific variability in structure, shape, position (i.e. article involved), and size of secondary sexual characters in male forelegs suggests that these features may have played important roles in intraspecific recognition and/or courtship rituals, and potentially acting as premating barriers. *Electrochoreutes pankowskii* differs from congeners in having swollen fore tibia (Fig. 2g). Given the presence of well-developed epipharyngeal blades, *Electrochoreutes* species are likely to have been predators, so a raptorial function of foreleg cannot be ruled out in this species. However, its swollen fore tibia could have been involved in courtship rituals as well. Unfortunately, we could not recognize any female specimens as conspecific with *E. pankowskii* to understand whether raptorial-looking forelegs were sexually dimorphic. Tarsal modifications are present in

E. falculigerus (Fig. 4b), *E. furcillatus* (Fig. 4c) and *E. pankowskii* (Fig. 4e). *Electrochoreutes furcillatus* is characterized by a highly modified second tarsomere, bearing a deeply forked process, representing the most elaborate sexual feature in this genus. *Electrochoreutes planitibia* and *E. trisetigerus* are provided with leg features that appear poorly suited for grasping purposes, whereas *E. electroechinus* apparently lacks any modification. The fore tibia of *E. planitibia* are provided with an anterior swollen ridge at about mid-length (Fig. 4f), which might have had a signalling function, and *E. trisetigerus* has three hair-like setae arising from the ventral side of the femur (Fig. 4a), which might have played a role in display or tactile communication during courtship or mating. Finally, the poorly preserved *E. hamatus* stands apart from congeners in having hook-shaped setae on the fore tibia (Fig. 4d), which might again play a similar role in communication or be used for grasping during mating.

The shapes and the great interspecific variability of sexually dimorphic traits in *Electrochoreutes* mirror those of many extant dolichopodids and other empidoid lineages. Therefore, we suggest that male leg features in *Electrochoreutes* are most likely to have been involved in signalling during courtship. It is possible that males of this group might have performed complex, ritualized nuptial dances involving rhythmic movements, as in many extant relatives (Lunau, 1996; Sivinski, 1997). The diversity of leg and other secondary sexual traits in *Electrochoreutes* imply that mating rituals may have played a prominent role in their speciation and diversification.

Conclusions

Amber deposits provide valuable pieces making up the complex and still largely incomplete mosaic of the history of life. The specimens examined in this work have shown us a glimpse of a diverse radiation of an extinct lineage of Dolichopodidae characterized by unique secondary sexual traits, probably involved in mating rituals. We recognized seven, previously undescribed, species from Kachin amber and proposed to erect the new genus *Electrochoreutes* for them. However, a reconstruction of the evolution of courtship rituals and sexually dimorphic characters in empidoid lineages is still premature for two reasons: (i) poor phylogenetic resolution of the empidoid clade, and (ii) sparse and biased behavioural data at the species-level. The sexually dimorphic characters of *Electrochoreutes* involve the same body parts and interspecific variation as observed in present-day dolichopodids, suggesting that these extinct species were subjected to similar selective pressures that shaped their body and behaviours in the same ways. Our results show that complex secondary sexual characters had already appeared

in the stem-group dolichopodids during the Cretaceous and might have facilitated diversification across the entire dolichopodid clade.

Conflict of interest

None declared.

Data availability statement

The data that supports the findings of this study are available in the supporting information of this article.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Description of specimens of *Electrochoreutes* **gen.n.** not assigned to species.

Appendix S2. Morphology of specimens of *Electrochoreutes* **gen.n.**

Appendix S3. Main references for the morphological information for fossil genera of Empidoidea included in the phylogenetic analysis.

Appendix S4. Phylogeny of Empidoidea, including fossils. Strict consensus cladogram of 7904 trees obtained under equal weights.

Appendix S5. Morphological data matrix in nexus format.