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RESEARCH PAPER

Discovering a new fossil chironomid from Lower Cretaceous Lebanese Amber: *Electroneura pinhoi* sp. nov. Amaral, Silva & Baranov (Chironomidae: Tanypodinae)

Fabio Laurindo da Silva[1] · **André P. Amaral**[2] · **Dany Azar**[3,4] · **Viktor Baranov**[5]

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Abstract
Here we present new insights into Chironomidae (Insecta, Diptera) preserved in Lower Cretaceous Lebanese amber. We describe a new genus and species, *Electroneura pinhoi* gen. et sp. nov., seemingly related to Tanypodinae and offer an amended description of *Libanopelopia cretacica* Veltz, Azar and Nel, 2007. Moreover, our investigation highlights the challenges of assigning fossils to modern taxonomic groups, based on previous studies of Tanypodinae, underscoring the necessity of considering the geological context and utilizing, when possible, both morphological and molecular data from extant taxa to validate taxonomic assignments in paleontological studies.

Keywords Amber · Evolution · New taxa · Aquatic insects · Systematics · Non-biting midges

Introduction

Non-biting midges, members of the Diptera family Chironomidae, represent a highly diverse and abundant group of mainly aquatic insects. With over 7290 species described, out of which 7090 are aquatic (Lencioni et al. 2024), these insects inhabit a wide range of habitats, from the Antarctic Peninsula to the high Arctic. Remarkably, some species have even adapted to extreme conditions, demonstrating their resilience in environments with extremely cold temperatures, hot springs, or salt pans (Armitage et al. 1995).

Hence, this plasticity is reflected in their extensive distribution and abundance, making Chironomidae one of the most successful group of flies to have ever existed (Ashe and O'Connor 2009, 2012; Ferrington 2008). The fossil record shows that Chironomidae have been present at least since the Late Triassic, as evidenced by research conducted by Ansorge (1999), and Krzemiński and Jarzembowski (1999). This long evolutionary history has allowed Chironomidae to diversify into a wide variety of morphological adaptations and ecological niches. These include terrestrial, freshwater, and marine environments facilitated by their diverse morphological traits.

Compression fossils from the Jurassic, Cretaceous, Paleogene, and Neogene periods have contributed with numerous species of Chironomidae (Cockerell 1916; Lukashevich and Przhiboro 2011, 2012, 2015, 2018; Scudder 1890; Wappler et al. 2014), greatly enhancing our understanding of the evolution of the group. However, the most valuable insights into their evolutionary history come from chironomids preserved in amber (Azar and Nel 2010; Kalugina 1980; Seredszus and Wichard 2007; Veltz et al. 2007; Zakrzewska and Giłka 2015). The oldest known Chironomidae preserved in amber date back to the Barremian age, approximately 125.8–121.4 million years ago, and were found in Lebanese deposits

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✉ André P. Amaral
andre.amaral@campus.lmu.de

[1] Laboratory of Aquatic Insect Biodiversity and Ecology, Department of Zoology, Institute of Biosciences, University of São Paulo, São Paulo, Brazil

[2] Faculty of Biology, Biocenter, Ludwig-Maximilians-Universität München (LMU Munich), Großhaderner Str. 2, 82152 Munich, Germany

[3] State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Paleoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

[4] Faculty of Science II, Natural Sciences Department, Lebanese University, PO box 26110217, Fanar-El-Matn, Lebanon

[5] Estación Biológica de Doñana-CSIC, 41092 Seville, Spain

(Azar and Nel 2010; Azar et al. 2008; Maksoud et al. 2017; Veltz et al. 2007) and Wessex amber from the Isle of Wight (Baranov et al. 2019; Jarzembowski et al. 2008).

The Lebanese amber preserves a diverse array of well-preserved Chironomidae specimens, which offers valuable information on the evolutionary history and biodiversity of this group. The chironomid fauna found in the Lebanese amber is particularly diverse and well-documented, including several species representing the extinct group Aenneinae Ansorge 1999, as well as the recent Tanypodinae Skuse 1889, Orthocladiinae Kieffer 1911, and Prodiamesinae Sæther 1976. However, it is worth noting that there may be some reservations about the validity of Aenneinae as it was erected based on seemingly plesiomorphic wing characters.

Studies by Veltz et al. (2007) and Azar et al. (2008) argue that all Mesozoic fossils previously attributed to the Podonominae are either *incertae sedis* or representatives of Tanypodinae. While the authors suggest that the Podonominae is unrecorded before the Cenozoic era (66 million years ago to present), similarly to the large group Chironominae, recent findings by Giłka et al. (2022) indicate the presence of Chironominae in the Mesozoic era (from mid- to Upper Cretaceous deposits, ca. 99–83.6 Mya).

The richness of species of Chironomidae in Lebanese amber is currently only surpassed by the Eocene Baltic and Oise ambers (Azar and Nel 2010; Azar et al. 2010; Doitteau and Nel, 2007; Maksoud et al. 2017; Veltz et al. 2007; Wichard et al. 2009). Therefore, the aim of this study is to contribute to the understanding of the palaeofauna of Chironomidae and the diversification patterns of the family. To achieve this, we describe a new genus and species, *Electroneura pinhoi* gen. et sp. nov., a possible representative of the extant subfamily Tanypodinae. Additionally, we provide an amendment of the description of *Libanopelopia cretacica* Veltz, Azar and Nel, 2007.

Material and methods

Several keys and descriptions, including those authored by Brundin (1966), Doitteau and Nel (2007), Langton et al. (2007), Seredszus and Wichard (2007), Oliver and Dillon (1989), and Murray and Fittkau (1989) were used to determine the taxonomic affiliations of the specimens. The specific morphological terminology used in this study is largely based on Sæther (1980). Abbreviations are as follows: AR, antennal ratio: length of apical elongated flagellomere plus any element distal to it, divided by the combined length of the more basal flagellomeres, excluding the scape and pedicel; LR, leg ratio: length of tarsomere 1 divided by length of tibia. Wing veins: A_1: first branch of anal vein; bm-m: basal-medial crossvein; CuA: anterior branch of cubitus; M_{1+2}: fused first and second branches of medial vein; M_{3+4}: fused third and fourth branches of medial vein; m-cu: medial-cubital crossvein; R_2: second branch of radius; R_3: third branch of radius; R_{4+5}: fused fourth and fifth branches of radius; r-m: radial-medial crossvein; Sc: subcosta.

This study attends the requirement of the International Code of Zoological Nomenclature of registering new nomenclature acts on "Zoobank" to ensure the validity and recognition of the new species names.

Geological context

The specimens were recovered from Lower Cretaceous strata, from Ain Dara and Hammana-Mdeyrij outcrops, ascribed to the Barremian age, approximately 125.8–121.4 Ma (Maksoud et al. 2017). During this period, warm tropical climates and high sea levels resulted in widespread flooding and deposition of marine sediments. Lebanese amber deposits from the Lower Cretaceous strata provide paramount information about ancient forest ecosystems. The amber's entomofaunal associations suggest a thick resin-producing forest under warm tropical conditions (Azar et al. 2011). Lebanese amber deposits are mainly found in three intervals in the upper part of the "Grès du Liban". These intervals are rich in biological inclusions, mostly terrestrial arthropod remains, such as insects, spiders, and mites (Azar et al. 2010; Azar 1997a, 1997b), but also plants and vertebrate remains (Maksoud et al. 2022). The entomofaunal similarity of these three intervals suggests that they have very close, if not the same age (Azar, 2012; Azar et al. 2003; Veltz et al. 2013), and the amber pieces found in the middle and upper intervals were possibly relocated from the lower interval (Maksoud et al. 2022). Among the diverse collection of well-preserved inclusions in Lebanese amber, the Chironomidae specimens stand out, offering significant insights into the family's evolutionary history and biodiversity.

Repository and techniques

The material was borrowed from the Natural History Museum of the Lebanese University, Azar collection, Fanar, Lebanon.

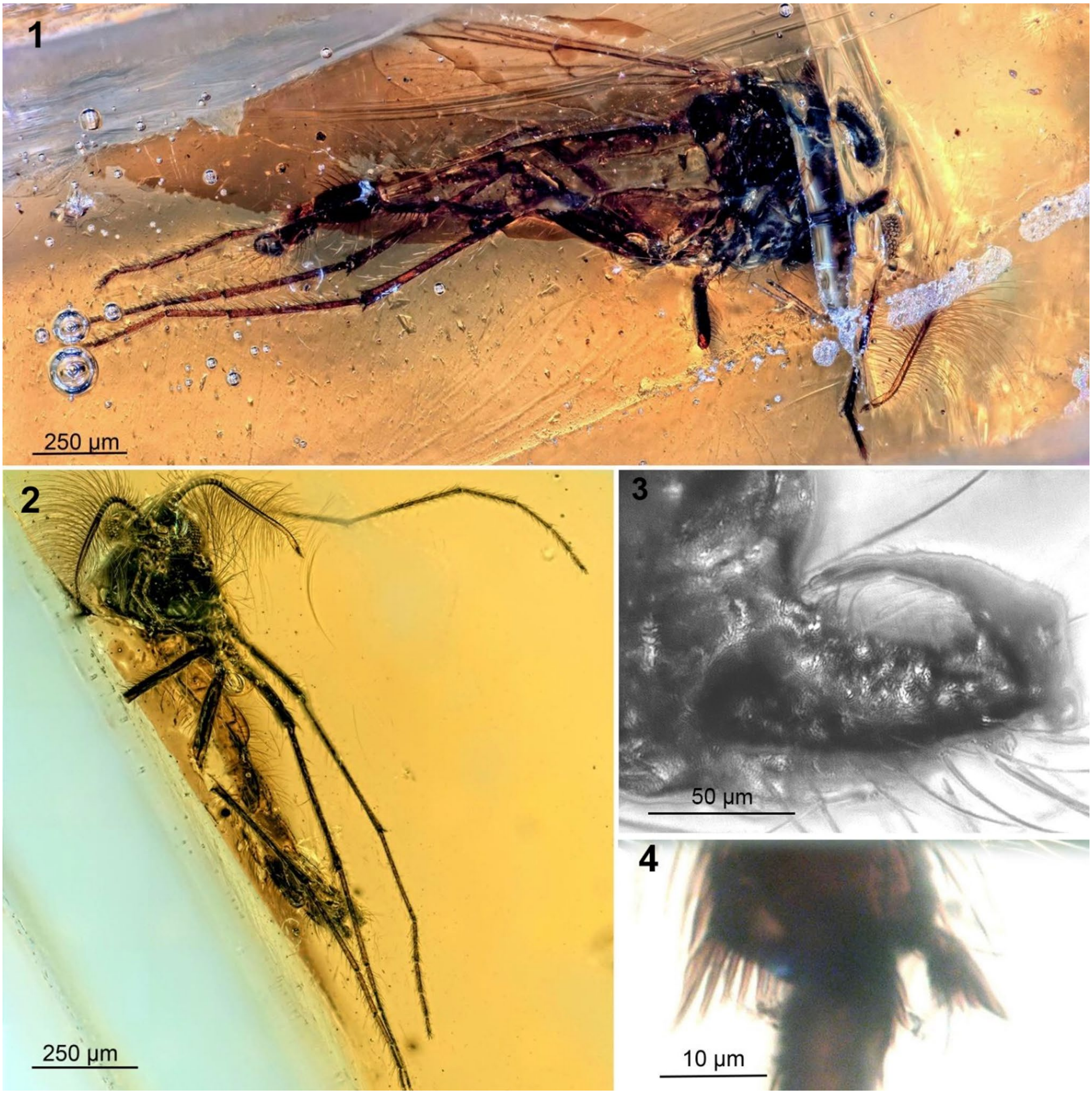
The amber pieces were fixed on a petri dish with modelling clay and prepared with a drop of glycerol and a coverslip on top, to even the surface and reduce reflections. A Keyence VHX-6000 Digital microscope was used to capture images of the mounted amber samples. To achieve the best possible contrast and resolution, the microscope was equipped with ring light-type illumination and cross-polarized co-axial illumination. The final images presented were produced using a combination of panorama functions, and deep-focus stacking, which were applied using the inbuilt software of the Keyence microscope. Additionally, to enhance the contrast and sharpness of some images, the HDR (high dynamic range) function was utilized.

Illustrations were made using the open-source software Inkscape. Images were treated for basic adjustments with Adobe Photoshop CS2, also used to create the figure plates.

Results

Systematic paleontology

Diptera Linnaeus, 1758
Chironomidae Newman, 1834
Tanypodinae Skuse, 1889



Figs. 1–4 *Electroneura pinhoi* gen. et sp. nov. (**1**) Habitus, laterally. (**2**) Habitus, ventrally. (**3**) Hypopigum, left side, dorsally. (**4**) Hind leg spurs

Electroneura gen. nov. Amaral, Silva & Baranov
Figures 1–6
urn:lsid:zoobank.org:act:24D717F6-144E-43E1-A3A9-F3F2467139C9

Diagnosis. Electroneura gen. nov. can be distinguished from any modern or fossil genus of Tanypodinae by the following combination of characters: wing with R_{2+3} forked, forming with R_1 a closed cell on anterior margin of the wing; hind leg with 2 tibial spurs lyrate-like with outer tooth slightly longer than inner ones; scutal tubercle absent; postnotum bare; gonocoxite without volsellae; gonostylus curved, with strong hyaline megaseta.

Etymology. The name of this genus is a combination of the Greek word "electron", which means amber, and *Pentaneura,* an extant genus of the Tanypodinae, to which the new taxon bears resemblance.

Type species. Electroneura pinhoi sp. nov. (designation by monotypy).

Electroneura pinhoi sp. nov. Amaral, Silva & Baranov
Figures 1–6
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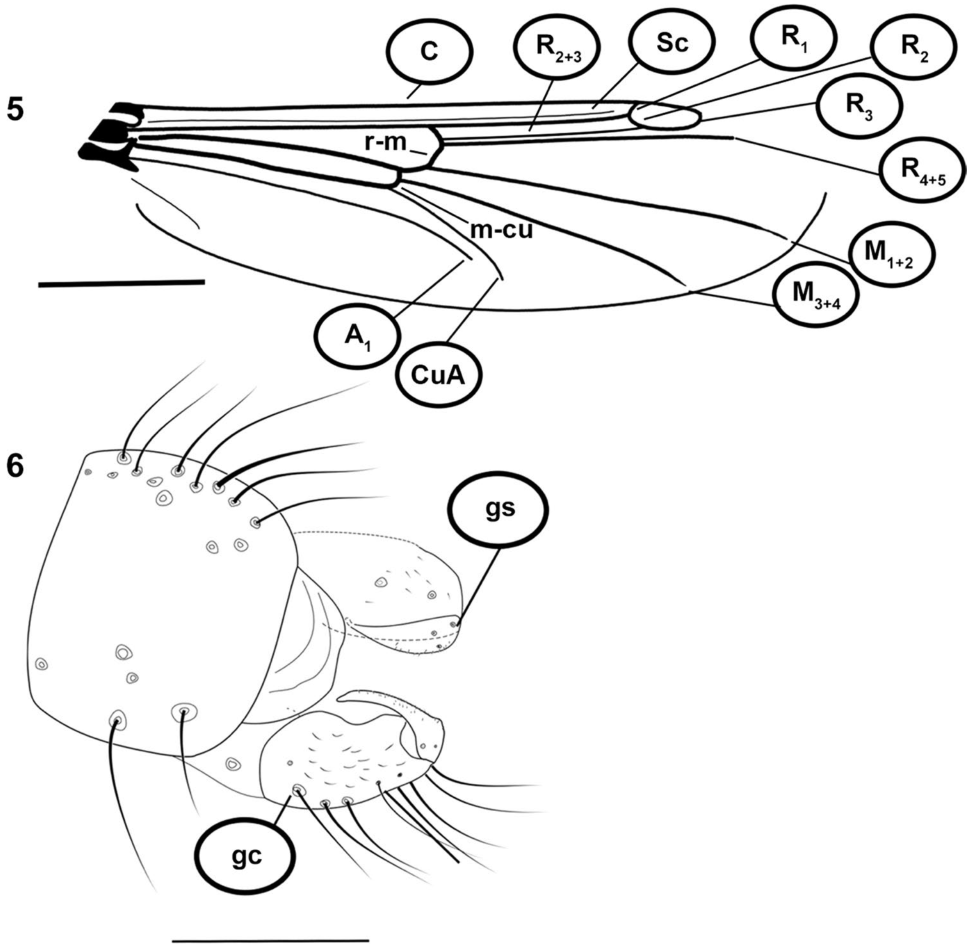
Diagnosis. As for genus, per monotypy.

Material examined. Holotype: adult male [AUBL AO 64]. deposited at Natural History Museum of the Lebanese University, Azar collection, Fanar, Lebanon.

Type locality and age. Ain Dara locality, central Lebanon. Lower Cretaceous, Early Barremian (about 125 Ma).

Etymology. Specific name honors the Brazilian entomologist Dr. Luiz Carlos de Pinho, in recognition of his prominent contribution to the study of Chironomidae and dedication to teaching at the University of Santa Catarina.

Condition of inclusion. Generally well-preserved. Tip of right wing, left wing missing. Right midleg missing distal from femur, left front leg present but unobservable, right



Figs. 5–6 *Electroneura pinhoi* gen. et sp. nov. (**5**) Wing. (**6**) Hypopygium, dorsally. Abbreviations: A_1: first branch of anal vein; CuA: anterior branch of cubitus; gc: gonocoxite; gs: gonostylus; M_{1+2}: fused first and second branches of medial vein; M_{3+4}: fused third and fourth branches of medial vein; m-cu: medial-cubital crossvein; R_1: first branch of radius; R_2: second branch of radius; R_3: third branch of radius; R_{2+3}: fused second and third branches of radius; R_{4+5}: fused fourth and fifth branches of radius; r-m: radial-medial crossvein; Sc: subcosta

front leg complete but detached at tibia. Piece without syninclusions.

Description. Adult male. Medium-sized insect, with generally midge-shaped body, with robust thorax, well-developed wings and legs, and long, thin abdomen. Body dark brown (Figs. 1, 2). Total length (frons to tip of abdomen) 1.53 mm.

Head. Eye kidney-shaped, bare, with long dorsomedial extension, three ommatidia wide. Ocelli absent. Antenna consisting of scape, pedicel and 14 flagellomeres. Ultimate flagellomere tapering at apex, penultimate flagellomere very long. Flagellomere 14 nearly 1/10 length of flagellomere 13. AR: 1.6. Plume well-developed. Mouthparts (cibarium and labium) scarcely seen. Palpus densely covered with long setae, with 5 palpomeres; length of palpomeres 2–5 (in µm): 60, 72, 148, 272.

Thorax. Antepronotal setae present. With 15 acrostichals. At least 17 dorsocentral setae present, arranged in two rows on posterior portion. With 10 prealars. Supraalar setae present, scutellum with at least 14 strong setae arranged in two rows. Postnotum bare.

Wing. Well-developed (Figs. 1, 5). Wing length (arculus to tip) 1.22 mm. Wing length/total body length ratio: 0.80. Apex of C unobservable; R_{2+3} forked, forming with R_1 a closed cell on anterior margin; medial-cubital crossvein aligned with fork of Cubital vein. Wing coarsely punctuated with microtrichia. Halter well-developed.

Legs (Figs. 1, 2). *Foreleg*: femur 474 µm long, tibia 500 µm long, tibia with 1 prominent lyrate spur; tibial comb absent; Ta_1 400 µm long, Ta_2 176 µm long, Ta_3 116 µm long, Ta_4 83 µm long, Ta_5 60 µm long. LR: 0.8. *Midleg*: femur 460 µm long, tibia 450 µm long, with 2 lyrate spurs, 23–26 µm long; tibial comb absent; Ta_1 320 µm long, Ta_2 146 µm long, Ta_3 100 µm long, Ta_4 66 µm long, Ta_5 60 µm long. LR: 0.73. *Hind leg*: femur 416 µm long, tibia 333 µm long, tibia with 2 lyrate spurs 26–23 µm long, tibial comb present (Fig. 4), with outer tooth slightly longer than inner ones; Ta_1 366 µm long, Ta_2 157 µm long, Ta_3 113 µm long, Ta_4 73 µm long, Ta_5 60 µm long. LR: 1.1.

Hypopygium (Figs. 3, 6). Tergite IX with rounded posterior margin, without anal point. Gonocoxite about 100 µm long. Inner margin of gonocoxite without membranous volsellae. Gonostylus 63 µm long, with blunt hyaline megaseta (Fig. 3). Gonostylus gently curved, basally expanded, tapering towards apex, and reaching about 0.6 of the length of the gonocoxite.

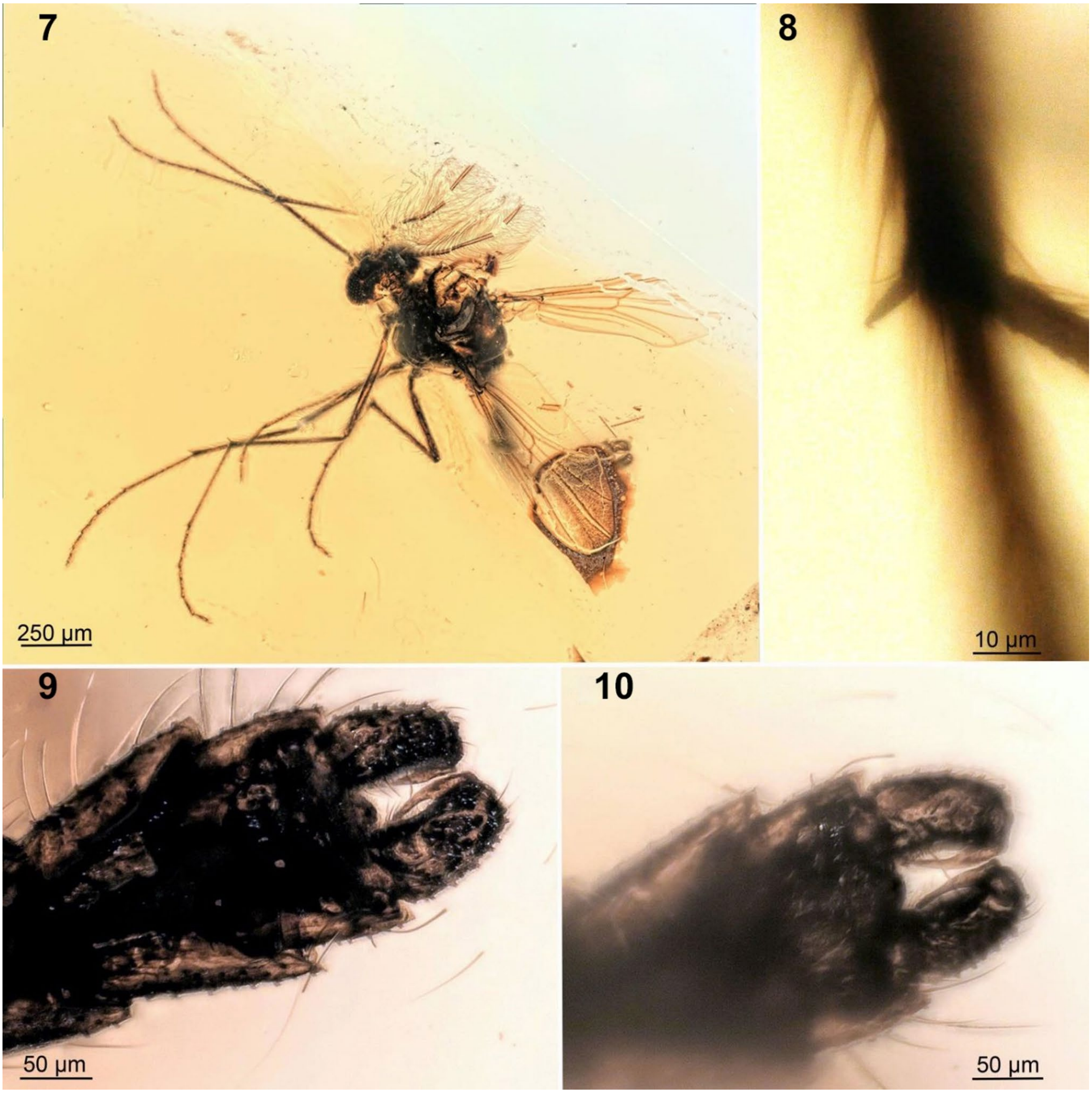
Remarks. Electroneura gen. nov. is considered a representative of the Tanypodinae based on diagnostic features such as the presence of medial-cubital crossvein and R_{2+3}, as well as tibial spurs with multiple spines (Murray and Fittkau 1989; Silva and Ekrem 2016). However, determining the precise placement of *Electroneura* within a Tanypodinae tribe is challenging due to wing damage, which hampers observation of the costa vein ending. This feature is essential for distinguishing between the Macropelopiini and Pentaneurini tribes. Typically, in Macropelopiini, the wing's costa extends beyond R_{4+5}, usually at least as long as crossvein r-m, whereas in Pentaneurini, the costa ends at R_{4+5} or extends for a shorter distance than r-m. Notably, *Electroneura* exhibits lyrate tibial spurs, with the outer tibial spur approximately equal in length to the inner one, a characteristic only recorded so far in Pentaneurini. Therefore, despite this drawback, we assign the new genus to the Pentaneurini.

According to the taxonomic key by Murray and Fittkau (1989), *Electroneura* falls into Pentaneurini. Due to the missing tip of the wing, the key leads to either couplet 31, to *Pentaneura* Philippi, 1865, or 39 to *Trissopelopia* Fittkau, 1962. This determination is based on shared traits such as bare eyes, absence of scutal tubercule, unmarked wings, median-cubital crossvein opposite to fork of Cubital veins, and a bare postnotum. However, *Electroneura* can be differentiated from both genera by its remaining wing venation, which features a forked R_{2+3} vein forming a closed cell with R_1 and C at the anterior margin of the wing. Furthermore, *Electroneura* can be distinguished from *Pentaneura* by its basally expanded gonostylus (Silva and Ferrington 2018), and from *Trissopelopia* by the presence of a tibial comb on the hind leg.

Moreover, the diagnostic characters shared by *Electroneura* and the Pentaneurini are not considered as autapomorphies of the group (Silva and Ekrem 2016), indicating that they are likely ancestral traits. This implies that *Electroneura* could represent either a primitive lineage within the Pentaneurini tribe or an extinct sister group closely related to the Tanypodinae, from which this tribe evolved.

Libanopelopia cretacica Veltz, Azar and Nel, 2007
Figures 7–13

Diagnosis. From Veltz et al. (2007): Eye bare. Costa (Figs. 7, 11) produced beyond R_{4+5} by a distance less than the length of cross-vein *rm*, ending slightly before M_{1+2}; R_{2+3} well separated from R_1 and R_{4+5}, apically divided into R_2 and R_3, with R_2 rather long and well distinct. Hind tibial comb disposed in one row (Fig. 8); two tibial spurs on both mid and hind leg with lateral comb-like teeth, outer tibial spur half as long as inner spur, those of hind legs not flattened. Inferior volsella small or absent (Figs. 9–10, 12–13); gonostylus distinctly shorter than gonocoxite.

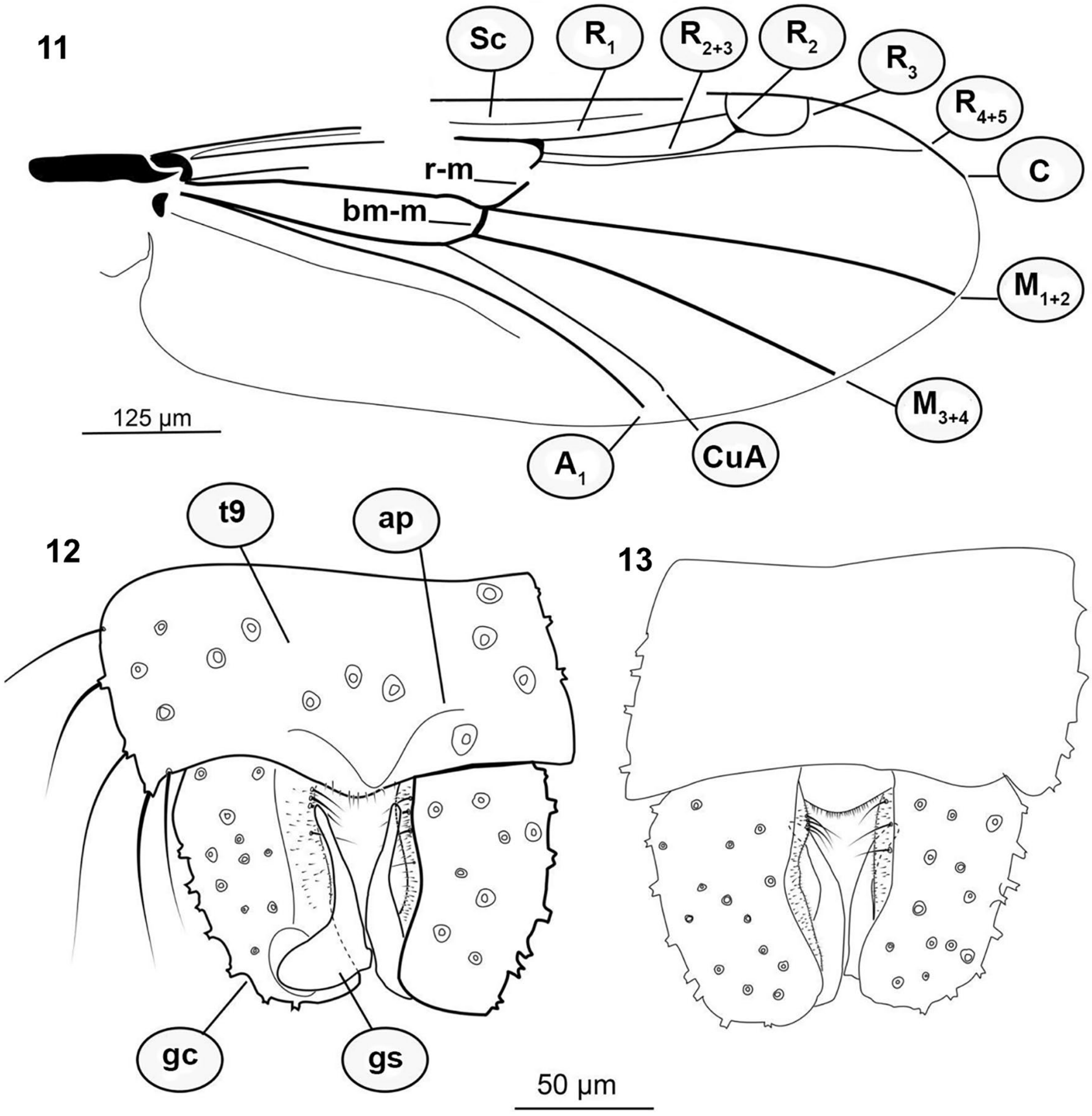


Figs. 7–10 *Libanopelopia cretacica* Veltz, Azar and Nel, 2007. (**7**) Habitus, dorsally. (**8**) Hind leg tibial spur. (**9**) Hypopygium, ventrally. (**10**) Hypopygium, dorsally

Material examined. Adult male [AUBL 1698 E], deposited at Natural History Museum of the Lebanese University, Azar collection, Fanar, Lebanon.

Locality and age. Hammana-Mdeyrij outcrop, Baabda District, Mount Lebanon Governorate, Central Lebanon. Lower Cretaceous, Late Barremian (about 125 Ma).

Amended description. Based on additional material from the from Lower Cretaceous Lebanese amber, generic description



Figs. 11–13 *Libanopelopia cretacica* Veltz, Azar and Nel, 2007. (**11**) Wing. (**12**) Hypopygium, dorsally. (**13**) Hypopygium, ventrally. Abbreviations: A_1: first branch of anal vein; ap: anal point; bm-m: basal-medial crossvein; CuA: anterior branch of cubitus; gc: gonocoxite; gs: gonostylus; M_{1+2}: fused first and second branches of medial vein; M_{3+4}: fused third and fourth branches of medial vein; R_1: first branch of radius; R_2: second branch of radius; R_3: third branch of radius; R_{2+3}: fused second and third branches of radius; R_{4+5}: fused fourth and fifth branches of radius; r-m: radial-medial crossvein; Sc: subcosta; t9: tergite 9

to the adult male of the monotypic *Libanopelopia cretacica* Veltz, Azar and Nel, 2007 should be amended as follows: gonocoxite without volsellae, only dense group of long setae basally on medial region (Figs. 9–10, 12–13). With 4 densely clustered setae on right, 3 more widely spaced on left.

Remarks. Although the structure of the gonocoxite of *Libanopelopia cretacica* has been elucidated and confirmed to lack inferior volsellae, this feature alone does not provide conclusive evidence for determining whether *Libanopelopia* represents the tribe Macropelopiini or Pentaneurini, since that is possibly a plesiomorphic trait within Tanypodinae. As noted by Veltz et al. (2007), the classification of *Libanopelopia* remains unclear. The absence of inferior volsellae is found in both tribes, suggesting that the genus could be related to a common ancestor of these tribes. This hypothesis is supported by the dated phylogeny presented in studies by Krosch et al. (2017, 2022). These phylogenetic reconstructions estimated that the divergence between Pentaneurini and remaining tribes within Tanypodinae occurred approximately 119 million years ago (135–105 Mya), during the

Lower Cretaceous when *Libanopelopia* species existed. In particular, both *Libanopelopia* Veltz, Azar and Nel, 2007 and *Cretapelopia* Veltz, Azar and Nel, 2007 have setation and hypopygium structure typical of the crown-group Pentaneurini (Veltz et al. 2007), combined with wing venation and tibial spur structure common to the Macropelopiini, as documented by Silva and Ekrem (2016) and Veltz et al. (2007). Therefore, it is possible that the genus represents an early lineage that preceded the divergence of these two tribes. Further research and analysis may help clarify the relationships between *Libanopelopia* and other members of the Tanypodinae.

Discussion

The study of Chironomidae has been paramount in advancing our understanding of phylogenetics and historical biogeography. Brundin's groundbreaking work in the 1960s and 1970s (Brundin 1966, 1976) demonstrated the importance of integrating geological evidence and fossil records with phylogenetic hypotheses to infer the evolutionary relationships of Chironomidae (Cranston et al. 2010, 2012; Giłka et al. 2022; Krosch et al. 2017). Recent progress in molecular techniques has significantly improved our ability to reconstruct phylogenies with higher accuracy and resolution than ever before (Smith and O'Meara 2012). In addition, Bayesian analyses have allowed for the development of complex models of molecular evolution, enabling hypotheses of evolutionary relationships to be tested and further refined (Bouckaert et al. 2014). Moreover, the use of calibration points derived from fossils has enabled researchers to estimate the pace of diversification and the timing of key evolutionary events (Giłka et al. 2022). These calibration points provide critical anchors for molecular clocks, allowing us to more accurately infer when lineages diverged (Cranston et al. 2010, 2012; Krosch et al. 2017, 2022; Silva et al. 2024) and have revolutionized our understanding of the evolutionary history of Chironomidae.

Krosch et al. (2022) calculated that the initial divergence of Tanypodinae occurred approximately 119 (135–105) million years ago, during the Early Cretaceous. Considering the lack of recognized morphological synapomorphies for adult males (Silva and Ekrem 2016), it is plausible that fossils with that age bearing diagnostic characters (not necessarily apomorphic) of Tanypodinae could instead represent an outgroup. Hence, in paleontological studies, it is central to consider the geological context of the fossils and use both morphological and molecular evidence, when possible, to reconstruct phylogenies in order to support taxonomic assignments.

Conclusions

The discovery of a new chironomid species reinforces the idea that extant major lineages, generally treated as subfamilies and tribes of chironomids radiated during the Cretaceous. This finding contributes to our growing understanding of Chironomidae diversity and distribution in the past, providing insights into their evolution. Furthermore, the analysis of the hypopygium structure in *Libanopelopia cretacica* raises concerns about the inclusion of chironomid fossils in modern taxonomic classifications.

A comprehensive phylogeny of these major lineages, using cutting-edge methods, with a thorough discussion of character transformation and synapomorphies is still notably absent for the Chironomidae. Such a study would provide an important basis for understanding the evolution of the group and help associating fossil species to their respective lineages, based on well-defined apomorphic characters.

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Author contributions Fabio Laurindo da Silva: conceptualization (equal); investigation (equal); project administration (supporting); writing original draft (lead); taxonomy (supporting); writing—review and editing (equal). André Pereira do Amaral: conceptualization (equal); data curation (equal); investigation (equal); project administration (lead); writing original draft (supporting); taxonomy (lead); writing—review and editing (equal). Dany Azar: material collection in the field (lead); writing—review and editing (supporting). Viktor Baranov: data curation (equal); investigation (equal); taxonomy (supporting); writing—review and editing (supporting). Image preparation (lead).

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Data availability All the data used is already included in the article.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest and no competing interests.

References

Ansorge, J. (1999). *Aenne liasina* gen.et sp.n.—the most primitive non biting midge [Diptera: Chironomidae: Aenneinae subfam.n.]—from the Lower Jurassic of Germany. *Polskie Pismo Entomologiczne, 68*, 431–443.

Armitage, P. D., Cranston, P. S., Clive, L., & Pinder, V. (Eds.). (1995). *The Chironomidae*. Springer. https://doi.org/10.1007/978-94-011-0715-0

Ashe, P., & O'Connor, J. P. (2009). *A world catalogue of Chironomidae (Diptera), Part 1: Buchonomyiinae, Chilenomyiinae, Podonominae, Aphroteniinae, Tanypodinae, Usambaromyiinae, Diamesinae, Prodiamesinae and Telmatogetoninae*. Irish Biogeographical Society and National Museum of Ireland.

Ashe, P., & O'Connor, J. P. (2012). *A world catalogue of Chironomidae (Diptera), Part 2: Orthocladiinae (Sections A and B)*. Irish Biogeographical Society and National Museum of Ireland.

Azar, D. (1997a). *Lebanese amber*. Strasbourg: Meganeura.

Azar, D. (1997b). A new method for extracting plant and insect fossils from Lebanese amber. *Palaeontology, 40*(4), 1027–1029.

Azar, D. (2012). Lebanese amber: A "Guinness Book of Records." *Annales Universitatis Paedagogicae Cracoviensis, Folia, 111*, 44–60.

Azar, D., & Nel, A. (2010). Two new non-biting midges from the Early Cretaceous Lebanese amber (Diptera: Chironomidae). *Annales De La Société Entomologique De France (NS), 46*, 198–203. https://doi.org/10.1080/00379271.2010.10697658

Azar, D., Nel, A., & Gèze, R. (2003). Use of Lebanese amber inclusions in paleoenvironmental reconstruction, dating and paleobiogeography. *Acta Zoologica Cracoviensia, 46*, 393–398.

Azar, D., Veltz, I., & Nel, A. (2008). Mandibulate chironomids: Primitive or derived? (Diptera: Chironomidae). *Systematic Entomology, 33*, 688–699. https://doi.org/10.1111/j.1365-3113.2008.00438.x

Azar, D., Gèze, R., & Acra, F. (2010). Lebanese Amber. In D. Penney (Ed.), *Biodiversity of Fossils in Amber from the major world deposits* (pp. 271–298). Siri Scientific Press.

Azar, D., Dejax, J., & Masure, E. (2011). Palynological analysis of amber-bearing clay from the lower cretaceous of central Lebanon. *Acta Geologica Sinica - English Edition, 85*, 942–949. https://doi.org/10.1111/j.1755-6724.2011.00497.x

Baranov, V., Giłka, W., Zakrzewska, M., & Jarzembowski, E. (2019). New non-biting midges (Diptera: Chironomidae) from Lower Cretaceous Wealden amber of the Isle of Wight (UK). *Cretaceous Research, 95*, 138–145. https://doi.org/10.1016/j.cretres.2018.11.012

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M. A., Rambaut, A., & Drummond, A. J. (2014). BEAST 2: a software platform for bayesian evolutionary analysis. Edited by Andreas Prlic. *PLoS Computational Biology, 10*, e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Brundin, L. (1966). *Transantarctic relationships and their significance, as evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae*. Almqvist & Wiksell.

Brundin, L. (1976). A Neocomian Chironomid and Podonominae-Aphroteniinae (Diptera) in the Light of Phylogenetics and Biogeography. *Zoologica Scripta, 5*, 139–160. https://doi.org/10.1111/j.1463-6409.1976.tb00691.x

Cockerell, T. D. A. (1916). Some American fossil insects. *Proceedings of the United States National Museum, 51*, 89–106. https://doi.org/10.5479/si.00963801.51-2146.89

Cranston, P. S., Hardy, N. B., & Morse, G. E. (2012). A dated molecular phylogeny for the Chironomidae (Diptera). *Systematic Entomology, 37*, 172–188. https://doi.org/10.1111/j.1365-3113.2011.00603.x

Cranston, P. S., Hardy, N. B., Morse, G. E., Puslednik, L., & McCluen, S. R. (2010). When molecules and morphology concur: The 'Gondwanan' midges (Diptera: Chironomidae). *Systematic Entomology, 35*, 636–648. https://doi.org/10.1111/j.1365-3113.2010.00531.x

Doitteau, G., & Nel, A. (2007). Chironomid midges from early Eocene amber of France (Diptera: Chironomidae). *Zootaxa, 1404*, 1–66.

Ferrington, L. C. (2008). Global diversity of non-biting midges (Chironomidae; Insecta-Diptera) in freshwater. *Hydrobiologia, 595*, 447. https://doi.org/10.1007/s10750-007-9130-1

Giłka, W., Zakrzewska, M., Lukashevich, E. D., Vorontsov, D. D., Soszyńska-Maj, A., Skibińska, K., & Cranston, P. S. (2022). Wanted, tracked down and identified: Mesozoic non-biting midges of the subfamily Chironominae (Chironomidae, Diptera). *Zoological Journal of the Linnean Society, 194*, 874–892. https://doi.org/10.1093/zoolinnean/zlab020

Jarzembowski, E. D., Azar, D., & Nel, A. (2008). A new chironomid (Insecta: Diptera) from Wealden amber (Lower Cretaceous) of the Isle of Wight (UK). *Geologica Acta*. https://doi.org/10.1344/105.000000257

Kalugina, N. S. (1980). Cretaceous Aphroteniinae from north Siberia (Diptera, Chironomidae). *Electrotenia brundini* gen. nov., sp. nov. *Acta Universitatis Carolinae, 12*, 89–93.

Krosch, M. N., Cranston, P. S., Bryant, L. M., Strutt, F., & McCluen, S. R. (2017). Towards a dated molecular phylogeny of the Tanypodinae (Chironomidae, Diptera). *Invertebrate Systematics, 31*, 302–316. https://doi.org/10.1071/IS16046

Krosch, M. N., Silva, F. L., Ekrem, T., Baker, A. M., Bryant, L. M., Stur, E., & Cranston, P. S. (2022). A new molecular phylogeny for the Tanypodinae (Diptera: Chironomidae) places the Australian diversity in a global context. *Molecular Phylogenetics and Evolution, 166*, 1–11. https://doi.org/10.1016/j.ympev.2021.107324

Krzemiński, W., & Jarzembowski, E. (1999). *Aenne triassica* sp.n., the oldest representative of the family Chironomidae [Insecta: Diptera]. *Polskie Pismo Entomologiczne, 68*, 445–449.

Langton, P.H., & Clive, L., Pinder, V. (2007). *Keys to the adult male Chironomidae of Britain and Ireland*. 2 vols. Freshwater Biological Association Scientific Publication no. 64. Ambleside: Freshwater Biological Association.

Lencioni, V., Adler, P. H., & Courtney, G. W. (2024). Chapter 15—order Diptera. In A. Maasri & J. H. Thorp (Eds.), *Identification and ecology of freshwater arthropods in the Mediterranean basin* (pp. 503–639). Elsevier. https://doi.org/10.1016/B978-0-12-821844-0.00001-6

Lukashevich, E. D., & Przhiboro, A. A. (2011). New Chironomidae (Diptera) with elongate proboscises from the Late Jurassic of Mongolia. *ZooKeys*. https://doi.org/10.3897/zookeys.130.1555

Lukashevich, E. D., & Przhiboro, A. A. (2012). Pupae of Mesozoic *Jurochlus* Kalugina, 1985 (Diptera: Chironomidae), with description of four new species. *Zootaxa, 3478*, 434–452. https://doi.org/10.1164/zootaxa.3478.1.39

Lukashevich, E. D., & Przhiboro, A. A. (2015). A new tribe of Diamesinae (Diptera: Chironomidae) from the Lower Cretaceous of Mongolia. *Cretaceous Research, 52*, 562–569. https://doi.org/10.1016/j.cretres.2014.03.016

Lukashevich, E. D., & Przhiboro, A. A. (2018). A new genus of Chironomidae (Insecta: Diptera) from the Lower Cretaceous of

Mongolia. *Paleontological Journal, 52*, 1401–1407. https://doi.org/10.1134/S0031030118120110

Maksoud, S., Azar, D., Granier, B., & Gèze, R. (2017). New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld, 26*, 331–338. https://doi.org/10.1016/j.palwor.2016.03.003

Maksoud, S., Granier, B. R. C., & Azar, D. (2022). Palaeoentomological (fossil insects) outcrops in Lebanon. *Carnets De Géologie (notebooks on Geology), 22*, 699–743.

Murray, D.A., & Fittkau, E.J. (1989). 5. The adult males of Tanypodinae (Diptera: Chironomidae) of the Holarctic region — Keys and diagnoses. In *The adult males of Chironomidae (Diptera) of the Holarctic region—Keys and diagnose*, ed. Torgny Wiederholm, Suppl. 34:37–123. Entomologica Scandinavica.

Oliver, D.R., & Dillon, M.E. (1989). 2. The adult males of Chironomidae (Diptera) of the Holarctic region-Key to subfamilies. In *The adult males of Chironomidae (Diptera) of the Holarctic region—Keys and diagnose*, ed. Torgny Wiederholm, Suppl. 34:11–15. Entomologica Scandinavica.

Sæther, O.A. (1980). Glossary of chironomid morphology terminology (Diptera: Chironomidae). *Entomologica scandinavica, Supplement*: 1–51.

Scudder, S. H. (1890). *The Tertiary insects of North America*. Government Printing Office.

Seredszus, F., & Wichard, W. (2007). Fossil chironomids (Insecta, Diptera) in Baltic amber. *Palaeontographica Abteilung A, 279*, 49–91. https://doi.org/10.1127/pala/279/2007/49

Silva, F. L., & Ekrem, T. (2016). Phylogenetic relationships of non-biting midges in the subfamily Tanypodinae (Diptera: Chironomidae) inferred from morphology: Phylogenetic relationships in the subfamily Tanypodinae. *Systematic Entomology, 41*, 73–92. https://doi.org/10.1111/syen.12141

Silva, F. L., & Ferrington, L. C. (2018). Systematics of the new world genus *Pentaneura* Phillip (Diptera: Chironomidae: Tanypodinae): Historical review, new species and phylogeny. *Zoologischer Anzeiger, 274*, 60–89. https://doi.org/10.1016/j.jcz.2017.11.010

Silva, F. L., De Medeiros, B. A. S., & Farrell, B. D. (2024). Once upon a fly: The biogeographical odyssey of *Labrundinia* (Chironomidae, Tanypodinae), an aquatic non-biting midge towards diversification. *Molecular Phylogenetics and Evolution, 194*, 1–16. https://doi.org/10.1016/j.ympev.2024.108025

Smith, S. A., & O'Meara, B. C. (2012). treePL: Divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics, 28*, 2689–2690. https://doi.org/10.1093/bioinformatics/bts492

Veltz, I., Azar, D., & Nel, A. (2007). New chironomid flies in Early Cretaceous Lebanese amber (Diptera : Chironomidae). *African Invertebrates* 48. Council of the Natal Museum: 169–191. https://doi.org/10.10520/EJC84582.

Veltz, I., Paicheler, J.-C., Maksoud, S., Gèze, R., & Azar, D. (2013). Context and genesis of the Lebanese amberiferous palaeoenvironments at the Jurassic-Cretaceous transition. *Terrestrial Arthropod Reviews* 6. Leiden, The Netherlands: Brill: 11–26. https://doi.org/10.1163/18749836-06021055.

Wappler, T., Grímsson, F., Wang, Bo., Nel, A., Ólafsson, E., Kotov, A. A., Davis, S. R., & Engel, M. S. (2014). Before the 'Big Chill': A preliminary overview of arthropods from the middle Miocene of Iceland (Insecta, Crustacea). *Palaeogeography, Palaeoclimatology, Palaeoecology, 401*, 1–12. https://doi.org/10.1016/j.palaeo.2014.03.006

Wichard, W., Gröhn, C., & Seredszus, F. (2009). Chironomidae—Non-Biting Midges—Zuckmücken. In *Wasserinsekten im Baltischen Bernstein. Aquatic Insects in Baltic Amber*, 224–271. Kessel, Germany: Verlag.

Zakrzewska, M., & Giłka, W. (2015). The Tanytarsini (Diptera: Chironomidae) in the collection of the Museum of Amber Inclusions, University of Gdańsk. *Zootaxa, 3946*, 347–360. https://doi.org/10.11646/zootaxa.3946.3.3