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A new fossil psychodomorphan fly from Lower Barremian Lebanese amber elucidates the relationship of the Tanyderinae stat. nov. within the Psychodidae

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Abstract: A new species, †*Nannotanyderus granieri* sp. nov., belonging to the Tanyderidae (Diptera, Nematocera), from Lower Barremian amber of Bqaatouta (Lebanon), is characterized, described, figured, and its taxononomic position discussed. The possible confusion regarding the attribution of new fossils to either the Tanyderidae or the Psychodidae, in addition to the results of recent molecular phylogenies, have led us to re-evaluate the taxonomic position of the Tanyderidae and to consider it as a subfamily within the Psychodidae. The fossil described herein is a tiny tanyderine *sensu nov.* species, and the second one belonging to the genus *Nannotanyderus* from Lebanese amber. A tentative molecular phylogeny of recent Psychodidae and an exhaustive catalogue of fossil Tanyderinae *stat. nov.* are provided.

Keywords:

- Diptera;
- Tanyderidae;
- Psychodidae;
- Tanyderinae *stat. nov.*;
- Tanyderini;
- Nannotanyderini;
- Lower Cretaceous;
- Lebanon

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Résumé : ***Une nouvelle mouche psychodomorphe fossile de l'ambre Barrémien inférieur du Liban clarifie la relation des Tanyderinae stat. nov. au sein des Psychodidae.-*** Une nouvelle espèce, †*Nannotanyderus granieri* sp. nov., appartenant aux Tanyderidae (Diptera, Nematocera), provenant de

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l'ambre du Barrémien inférieur de Bqaatouta (Liban), est caractérisée, décrite et illustrée ; sa position taxonomique est discutée. En plus des résultats des phylogénies moléculaires récentes, la possible confusion concernant l'attribution de nouveaux fossiles soit aux Tanyderidae, soit aux Psychodidae, nous a amenés à réévaluer la position taxonomique des Tanyderidae et à les considérer comme une sous-famille au sein des Psychodidae. Le fossile décrit ici est une espèce tanydérine *sensu nov.* et le deuxième appartenant au genre *Nannotanyderus* de l'ambre libanais. Une phylogénie moléculaire provisoire des Psychodidae actuels et un catalogue exhaustif des Tanyderinae stat. nov. fossiles sont fournis.

Mots-clefs :

- Diptera ;
- Tanyderidae ;
- Psychodidae ;
- Tanyderinae *stat. nov.* ;
- Tanyderini ;
- Nannotanyderini ;
- Crétacé inférieur ;
- Liban

1. Introduction

The Tanyderidae Osten-Sacken, 1880, colloquially known as primitive crane flies, are a small relictual cryptic cosmopolitan family of mostly aquatic flies, with 39 known living species worldwide (Madriz *et al.*, 2018) across ten genera, *i.e.*, *Araucoderus* Alexander, 1929, *Eutanyderus* Alexander, 1928, *Mischoderus* Handlirsch, 1909, *Neoderus* Alexander, 1928, *Nothoderus* Alexander, 1928, *Peringueyomyina* Alexander, 1921, *Protanyderus* Handlirsch, 1909, *Protoplasa* Osten-Sacken, 1859, *Radinoderus* Handlirsch, 1909, and *Tanyderus* Philippi, 1865. The genus *Protanyderus* Handlirsch, 1909, is represented in both fossil and extant faunas (Alexander, 1932; Krzemiński & Judd, 1997; Exner & Craig, 1976). Immature stages of extant species are aquatic to semiaquatic, often associated with wet sandy soil and the outer layers of submerged rotting logs in streams (Krzemiński & Judd, 1997). Adults are small to large flies (5-35mm) and typically exhibit conspicuous mouthparts, with an elongated rostrum in some species. The family is characterized by elongate cervical sclerites in some species, creating the appearance of a long neck, which serves as the basis for the family name ['tany' from Greek (τανύω) meaning 'stretch', and 'dero' from Greek (δέρω) meaning skin]. Their legs are as long as, or longer than, the body. Males sometimes form large swarms in the evening, while spending daylight hours among riparian vegetation near stream borders. Little is known about the biology of these unusual flies.

The Tanyderidae have been understudied, which poses challenges for their placement within an evolutionary context (Madriz Villanueva, 2017). Considered among the rarest of Diptera (Crampton, 1926b; Krzemiński & Judd, 1997; Judd, 2004), tanyderids have long been described as 'primitive' (Crampton, 1930; Alexander, 1930; Williams, 1933; Colless & McAlpine, 1991; Rohdendorf, 1974; Exner & Craig, 1976). Phylogenetic hypotheses based on morphological characters of immature stages (Alexander, 1930), adult thoracic sclerites (Crampton, 1926a, 1926b, 1926c, 1930), and wing venation (Rohdendorf, 1974) have yielded inconsistent results regarding sister-group relationships, leading to a long-standing unresolved phylogenetic placement. Morphological phylogenetic analyses have suggested a close relationship between the Tanyderidae and Ptychopteridae (Hennig, 1973; Wood & Borkent, 1989; Oosterbroek & Courtney, 1995) and, more recently, the Blephariceridae (Lambkin *et al.*, 2013). In contrast, recent analyses based on molecular data strongly support a sister group relationship between the Blephariceridae and Tanyderidae + Psychodidae (Bertone *et al.*, 2008; Wiegmann *et al.*, 2011; Curler & Moulton, 2012).

The Tanyderidae are relatively uncommon as fossils, yet they are well represented and diverse compared to recent extant tanyderids. The oldest known representative is *Nannotanyderus oliviae* Skibińska *et al.*, 2014, which was described from the Lower Jurassic of England (Sinemurian, ca. 199.5–192.9 Ma). To date, 34 fossil species, representing ten genera, have been described, including *Coramus* Skibińska, 2016, *Dacochile* Poinar & Brown, 2004, *Espanoderus* Skibińska *et al.*, 2019, *Macrochile* Loew, 1850, *Podemacrochile* Krzemiński & Kania *in* Krzemiński *et al.*, 2013, *Nannotanyderus* Ansorge, 1994, *Praemacrochile* Kalugina *in* Kalugina & Kovalev, 1985, *Protanyderus* Handlirsch, 1909, and *Similinannotanyderus* Dong *et al.*, 2015. A complete list of fossil Tanyderidae (or Tanyderinae *stat. nov.*) is provided in the appendix. The Psychodidae Newman, 1834, is a large family of small, hairy nematoceran dipterans, encompassing more than 2,600 described extant species (Azar & Maksoud, 2022a, 2022b). Presently, it is subdivided into seven subfamilies: Bruchomyiinae Alexander, 1920, Horaiellinae Enderlein, 1936, Phlebotominae Rondani, 1840, Psychodinae Newman, 1834, Sycoracinae Rondani, 1856, Trichomyiinae Tonnoir, 1922, and the extinct subfamily Datziinae (replacing Protopsychodinae Stebner *et al.*, 2015a) known thus far only from mid-Cretaceous Burmese amber (Stebner *et al.*, 2015a, 2015b).

Herein, we describe a new tiny tanyderine species (*sensu* the new classification proposed) that we assign to *Nannotanyderus* (based on wing shape and venation) from Lower Cretaceous amber of Bqaatouta. This marks the second species belonging to the genus *Nannotanyderus* recorded from Lebanese amber.

2. Material and methods

2.1. Material studied

The material described from Lebanese amber herein originates from the Bqaatouta outcrop (MAKSOUD *et al.*, 2022) in the Caza (District) of Kesserouan, Central Lebanon, from the MAALOUF collection. Syn-inclusions include a spider and a male chironomid dipteran. The amber piece containing the inclusion was cut, shaped, and polished before being placed between two cover slips in Canada balsam (following the method described by AZAR *et al.*, 2003).

Images in reflected light were captured using an AxioCam MRc 5 camera attached to a Zeiss Discovery V16 stereo microscope. Widefield fluorescence images were obtained using a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope with 488 nm Argon laser excitation line (CAI & HUANG, 2014; FU *et al.*, 2021). Photomicrographs were stacked using Helicon Focus 8.1.0. and processed with Adobe Photoshop CC 2019. The recent standard wing venation nomenclature of KVIFTE and WAGNER (2017) from the 'Manual of Afrotropical Diptera' was followed. All measurements are in micrometres (µm). The type specimen is housed in the collections of Natural History Museum of the Lebanese University, Faculty of Sciences II, located in Fanar, Lebanon.

2.2. Phylogenetic analysis

In order to assess the interrelationships among the subfamilies of the Psychodidae and its relationship with the closely related Tanyderidae, we conducted a phylogenetic analysis utilizing SANGER-sequencing data available in GenBank. This dataset included 3 outgroup taxa (each species for Limoniidae, Ptychopteridae, and Tanyderidae) and 43 ingroup taxa representing each subfamily with the Psychodidae (CURLER & MOULTON, 2012). Two nuclear genes, the large nuclear ribosomal subunit (*18S* rDNA) and bromodomain and PHD finger-containing protein (*Peregrin*), were selected and utilized in our analyses. GenBank sequence numbers mostly follow those provided in CURLER and MOULTON (2012), with the exception of the following gene sequences: 1) the *18S* rDNA gene of *Ptychoptera albimana* (KX453704) was incorporated with *Ptychoptera* sp., and 2) the problematic *Peregrin* gene of *Trichomyia* sp. nov. 2 (JF714438), which cannot be correctly aligned with the remaining species, was excluded from our analyses. All sequences were retrieved from GenBank using the Batch Entrez tool. The protein-coding gene (*Peregrin*) was aligned with respect to their codon structure using MACSE v2.06 (RANWEZ *et al.*, 2018). The ribosomal *18S* gene was aligned using the Q-INS-I algorithm in MAFFT (KATOH *et al*. 2002) available through the MAFFT online service (KATOH *et al*. 2019). The concatenated matrix included 46 taxa and 5,206 nucleotide sites.

The selection of evolutionary models for tree inference can significantly impact phylogenetic analyses. Previous studies (TIHELKA *et al.*, 2020, 2021) have demonstrated that different models make various assumptions about the nature of the data, and violations of these assumptions can lead to misleading topologies, even with high statistical support. Therefore, we employed the site-heterogeneous CAT-GTR model to analyze our data. This model accounts for compositional heterogeneity across sites and can mitigate common sources of phylogenetic error such as long-branch attraction (LARTILLOT *et al.*, 2007; TIHELKA *et al.*, 2021). The site-heterogeneous model CAT-GTR was implemented in PhyloBayes MPI1.7 (LARTILLOT *et al*., 2009), run at the Beijing Super Cloud Computing Center. Two independent MARKOV chain Monte Carlo (MCMC) chains were run until convergence. The bpcomp program was utilized to generate the largest (maxdiff) and mean (meandiff) values. The chains were considered to have converged when the maximum difference (maxdiff) was less than 0.3, with a recorded value of maxdiff = 0.13.

3. Results

3.1. Systematic palaeontology

Order DIPTERA LINNAEUS, 1758
Infraorder PSYCHODOMORPHA HENNIG, 1968
Family PSYCHODIDAE NEWMAN, 1834
former family Tanyderidae OSTEN-SACKEN, 1880

Subfamily TANYDERINAE
OSTEN-SACKEN, 1880, stat. nov.
former family Tanyderidae OSTEN-SACKEN, 1880

Tribe NANNOTANYDERINI
SKIBIŃSKA, 2016, stat. nov.
former subfamily Nannotanyderinae
SKIBIŃSKA, 2016

Genus *NANNOTANYDERUS* ANSORGE, 1994

Type species. *Nannotanyderus krzeminskii* ANSORGE, 1994, Lower Jurassic (Toarcian), Grimmen, Germany.

***Nannotanyderus granieri* sp. nov.**
(Figs. 1-2)

Material. Holotype (specimen BKT-11A), female, part of the MAALOUF collection, Lebanese Lower Cretaceous amber found at the Bqaatouta outcrop, in the Caza (District) of Kesserouan, Central Lebanon. Syn-inclusions include a spider and a male chirbnomid dipteran. This material is housed in the collections of Natural History Museum of the Lebanese University, Faculty of Sciences II, located in Fanar, Lebanon.

Diagnosis. Female only. Head lacking an elongated neck; mouthparts well developed, longer than head, with well-developed sclerotized maxillae. R2 very short, slightly longer than half of R3, with R2+3 about 3 times longer than R2, hook-like at its basal part. Presence of cross-veins m-m and m-cu, as well as cell d.

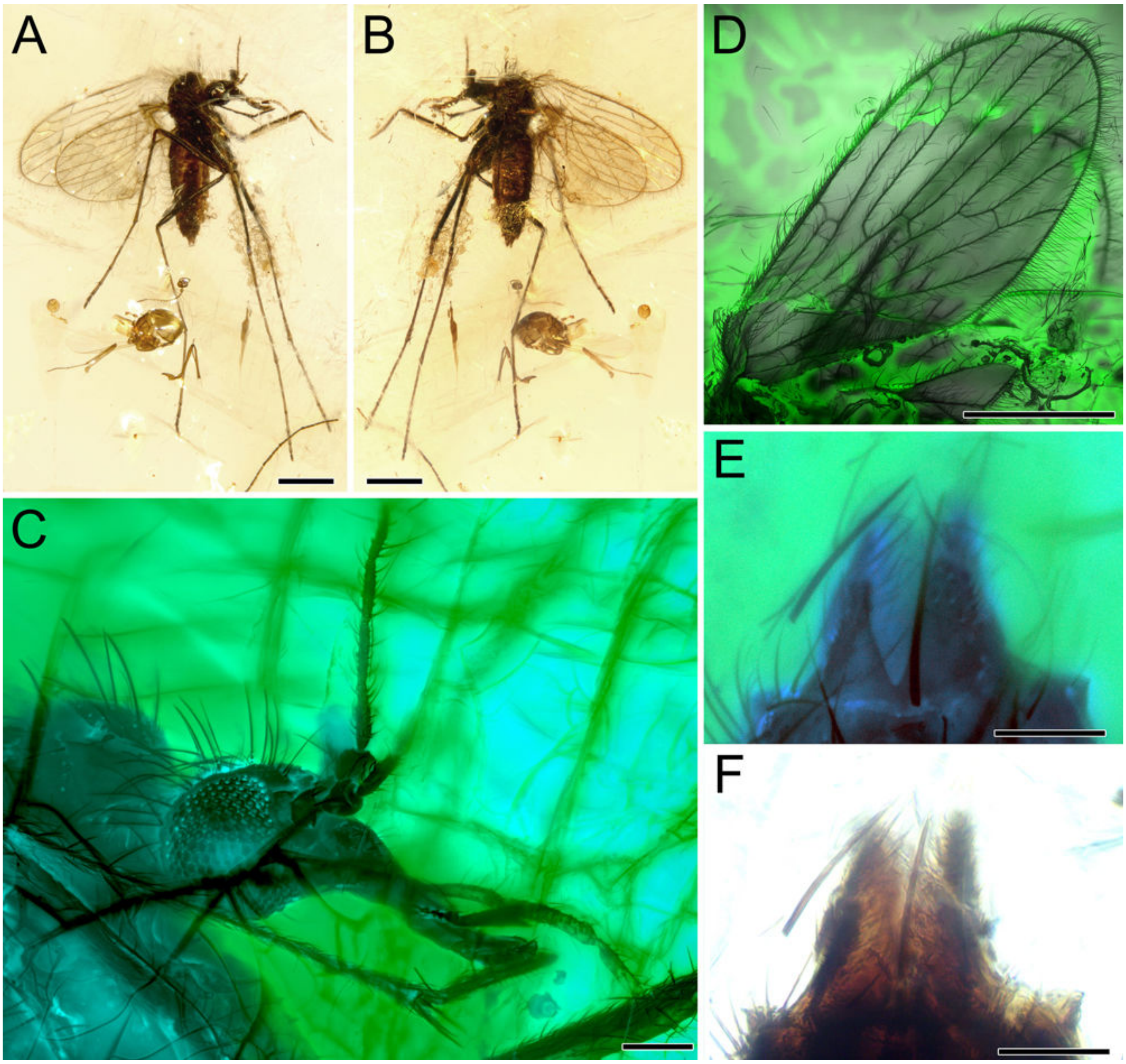


Figure 1: *Nannotanyderus granieri* sp. nov., holotype, female, specimen number BKT-11A. A) Habitus, right lateral side. Scale bar: 500 µm. B) Habitus, left lateral side. Scale bar: 500 µm. C) Head photomicrograph with confocal microscope. Scale bar: 100 µm. D) Wing photomicrograph with confocal microscope. Scale bar: 500 µm. E) Female terminalia, photomicrograph with confocal microscope. Scale bar: 50 µm. F) Female terminalia, photomicrograph with compound microscope. Scale bar: 50 µm.

N. granieri and *N. ansorgei* are the smallest members of the Tannyderidae, with female terminalia being simple, cerci terminating in a single lobe. The wing venation of *N. granieri* is very similar to that of *N. ansorgei* with the following differences: 1) R1 reaching costal margin is slightly beyond the fork of R2+3 into R2 and R3 in *N. granieri*, whereas it is opposite to it in *N. ansorgei*; 2) R2 slightly longer than half of R3 in *N. granieri*, whereas it is equal to half of R3 in *N. ansorgei*; 3) the bifurcation of R2+3 from Rs is slightly distal to the level where Sc meets the costal margin in *N. granieri*, whereas it is slightly basal to the level where Sc meets the costal margin in *N. ansorgei*; 4) the distance between the bifurcation of R2+3 from Rs to the base of R4 is smaller in *N. granieri*.

Etymology. The species is named after Prof. Bruno GRANIER, whose research has significantly advanced the dating of amber outcrops in Lebanon (*e.g.*, GRANIER *et al.*, 2015, 2016).

Description. The specimen is very small, measuring 1571 µm in length from the tip of the female genitalia to the thorax tip, with the head positioned beneath the thorax at 1890 µm (Fig. 1). The head is 411 µm wide and 211 µm high, featuring large eyes with a slight eye bridge, measuring 178 µm in diameter. The antennae are delicate and incomplete. The palpi are long, with the

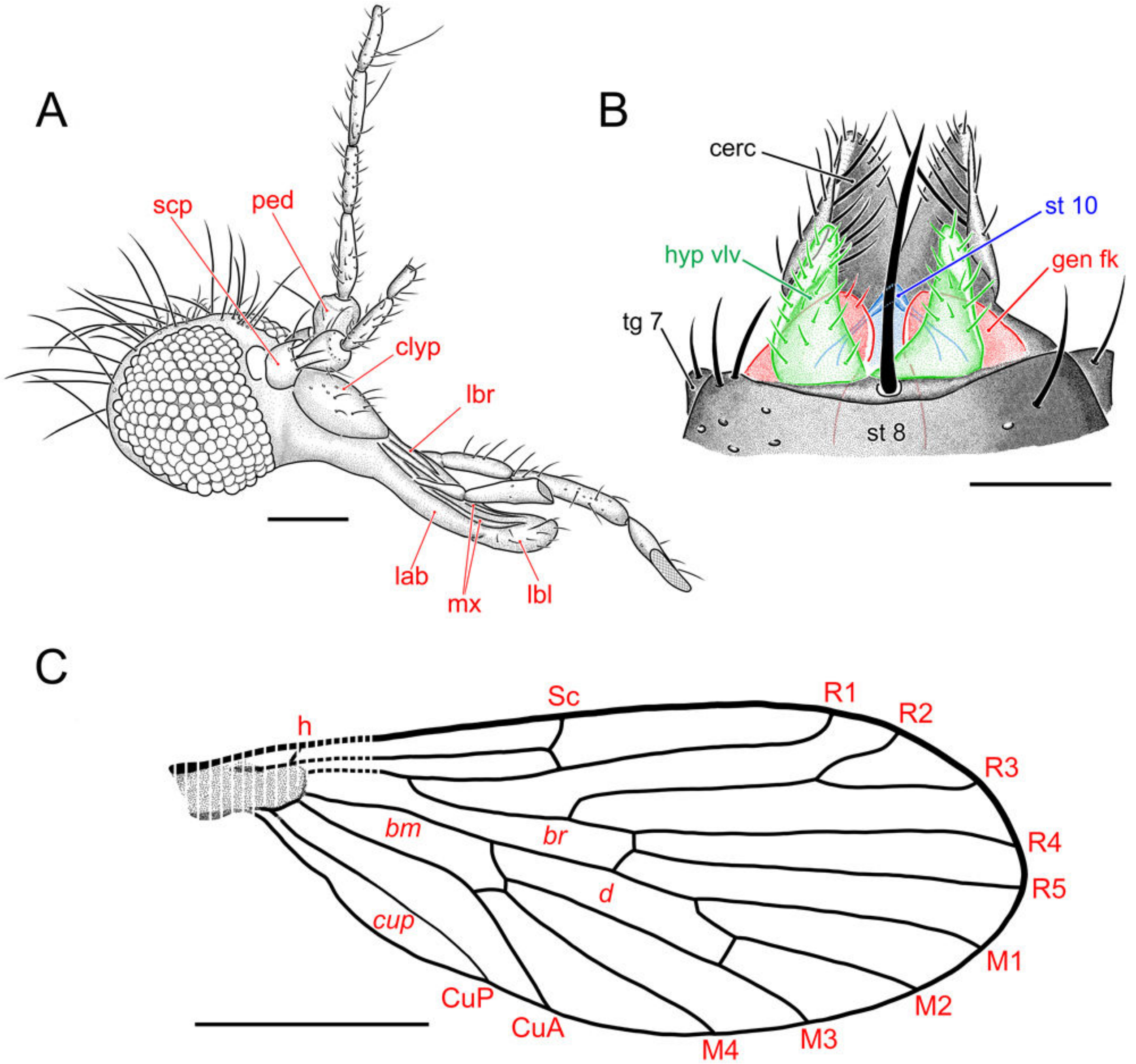
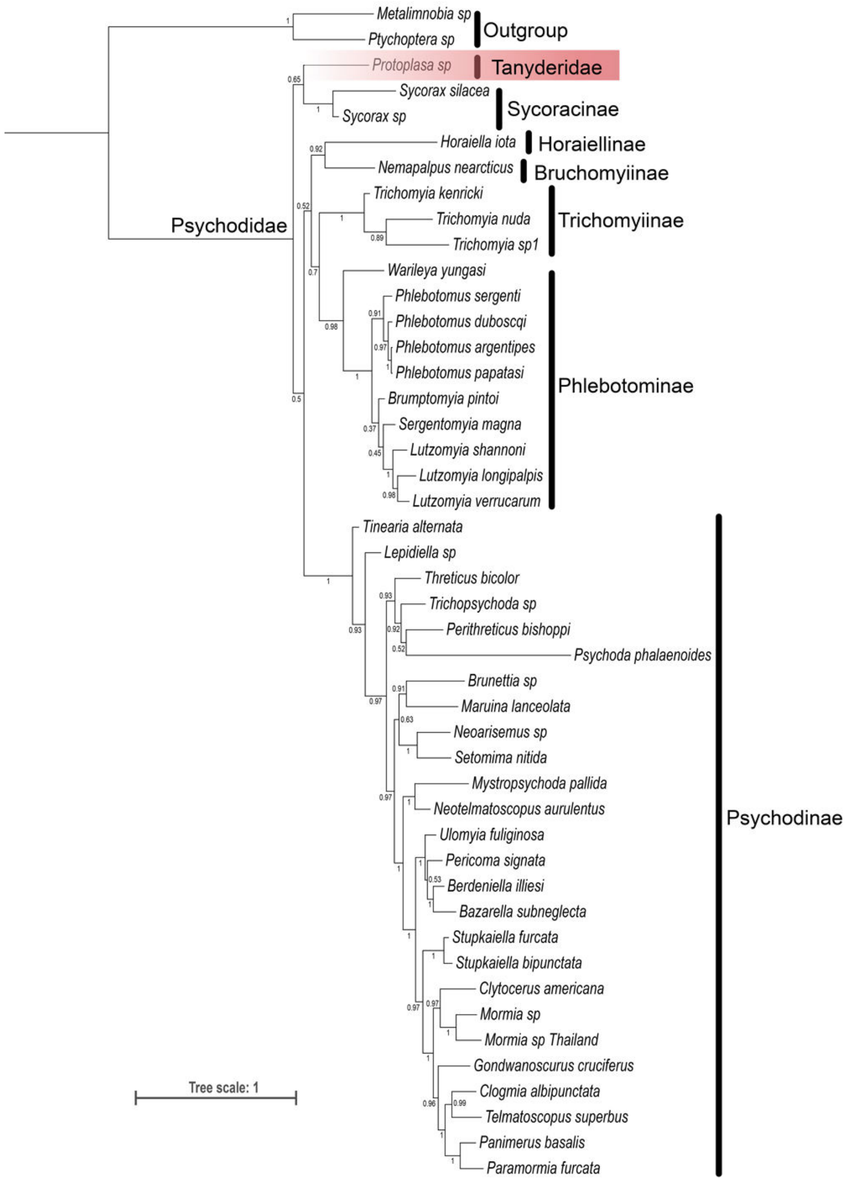


Figure 2: *Nannotanyderus granieri* sp. nov., holotype, female, specimen number BKT-11A, head, line drawings. A) Head; abbreviations: clyp = clypeus; lab = labium; lbl = labellum; lbr = labrum; mx = maxilla; ped = pedicel; scp = scape. Scale bar: 100 µm. B) Wing, abbreviations: bc = basal costal cell; bm = basal medial cell; br = basal radial cell; CuA = anterior branch of cubitus vein; cup = posterior cubital cell; CuP = posterior branch of cubitus vein; d = discal cell; h = humeral crossvein; M1, M2, M3, M4 = distal branches of medial vein; R1, R2, R3, R4, R5 = distal branches of radius; Sc = ubcostal vein. Scale bar: 500 µm. C) Female terminalia; abbreviations: cerc = cercus; gen fk = genital fork; hyp vlv = hypogynial valve; st 8 = sternite 8; st 10 = sternite 10; tg 7 = tergite 7. Scale bar: 50 µm.

right palpus having two incomplete palpomeres preserved and the left palpus with four incomplete palpomeres preserved. The thorax is 548 µm long. The wing is hyaline, lacking a stigma (Fig. 2), measuring 1788 µm in length and 712 µm in width. The humeral cross vein (h) reaches the wing margin at 224 µm from the wing base. The subcosta (Sc) is short, measuring 800 µm in length, with the cross-vein sc-r present. R1 ends in the wing margin at about 1368 µm from the wing base, slightly beyond the fork of R2+3 into R2 and R3. R2 and R3 reach the costal margin at 1504 µm and 1680 µm from the wing base, respectively. R4 is more than 5 times longer than R4+5, and both R4 and R5 are straight reaching the wing apex at 1752 µm and 1760 µm, respectively. M1 is longer than the discal cell (d) with the d cell closed. M1-M4 reach the wing margin at 1680 µm, 1544 µm, 1312 µm, and 1104 µm apically, respectively. The cup cell is narrow. CuA and CuP reach the wing posterior margin at 768 µm and 632 µm, respectively. The legs are longer than the body and feature two apical tibial spurs. The abdomen is 1071 µm long, with simple female terminalia (typical of most Psychodidae), and the cerci terminate in a single lobe measuring 62 µm in length.



◀ **Figure 3:** Phylogenetic relationships of Tanyderidae (highlighted with red background) and subfamilies of Psychodidae based on data mainly from CURLER and MOULTON (2012) analyzed under a site-heterogeneous CAT-GTR model in PhyloBayes. Posterior probabilities are reported aside each node.

3.2. Molecular phylogeny analysis

Our phylogenetic analysis of the Tanyderidae and Psychodidae utilized a site-heterogeneous CAT-GTR model (Fig. 3) in PhyloBayes. This model yielded a moderately resolved topology with strong statistical support at shallow nodes. Consistent with CURLER and MOULTON (2012), the monophyly of the Psychodidae was not upheld in relation to the Tanyderidae, with the Tanyderidae being identified as a sister group to the subfamily Sycoracinae. However, contrary to CURLER and MOULTON (2012), the Horaiellinae were determined to be a sister group to the subfamily Bruchomyiinae (Bayesian posterior probability [BPP] = 0.92), rather than to the remaining subfamilies of the Psychodidae + Tanyderidae. Within the monophyletic Psychodinae, the genus *Tinearia* was found to be a sister group to the remaining sampled genera, with *Lepidiella* represented a second diverging lineage within the subfamily (BPP = 0.93).

4. Discussion

Specimens of the Tanyderidae are rare in entomological collections, and this group has been consistently understudied. Placing these dipterans in their evolutionary context presents a formidable challenge, with various evolutionary placements proposed by different authors. These placements have primarily relied on larval features, but especially on adult wing characters, which we consider to be plesiomorphic. Unfortunately, the Tanyderidae remains the only family of extant Diptera for which species-level identification is routinely achievable solely through wing characters (ALEXANDER, 1927). With the exception of one genus (*Peringueyomyina* ALEXANDER, 1921), all extant tanyderids (in the usual sense) exhibit patterned wings. Existing keys have traditionally been constructed based on the notion that these flies exhibit one of the most 'primitive' conditions of wing venation (MACGILLIVRAY, 1923; ROHDEN-

DORF, 1974; KRZEMIŃSKI, 1992). However, there has been no concerted effort to incorporate other structures, such as terminalia, for species-level discrimination. On one hand, phylogenetic hypotheses based on morphological characters of immature stages (ALEXANDER, 1930), adult thoracic sclerites (CRAMPTON, 1926a, 1926b, 1926c, 1930), and wing venation (ROHDENDORF, 1974) have yielded unreliable results regarding sister-group relationships, leading to an uncertain phylogenetic placement. For instance, a close relationship between the Tanyderidae and Ptychopteridae (HENNIG, 1973; Wood & BORKENT, 1989; OOSTERBROEK & COURTNEY, 1995), based on mesonotal suture and the foldability of the last tarsomere in males, and more recently with the Blephariceridae (LAMBKIN *et al.*, 2013), has been suggested.

On the other hand, recent analyses based on molecular data strongly support a sister group relationship between the Blephariceridae and Tanyderidae + Psychodidae (BERTONE *et al.*, 2008; WIEGMANN *et al.*, 2011; CURLER & MOULTON, 2012). In all molecular analyses, the families Tanyderidae and Psychodidae are strongly supported as a monophyletic group. Moreover, a possible character uniting these three families is the presence of mandibles in the adult Bertone *et al.*, 2008. Indeed, in the lower Diptera, mandibulate adults only occur in the Culicomorpha, Blephariceridae, Psychodidae, and Tanyderidae (DOWNES & COLLESS, 1967). As Mecoptera (the outgroup of Diptera) have mandibles, this character is likely a symplesiomorphy. Support for a relationship between the Tanyderidae and Psychodidae is not surprising. For example, fossil Tanyderidae and Psychodidae are remarkably similar (ANSORGE, 1994; GRIMALDI & ENGEL, 2005; KRZEMIŃSKI *et al.*, 2013), to the extent that confusion of fossil taxa has occurred (WOODLEY, 2005). This confusion is understandable, as some tanyderid (in the usual sense) fossils exhibit more 'plesiomorphic' characters akin to the Psychodidae rather than to the Tanyderidae, where features such as size, wing venation, head shape, absence of neck stretching, and inversion of male genitalia observed in some fossils are characteristic of the Psychodidae. Some other fossil psychodids described from Lebanese amber with m-m crossvein could also be considered by some workers as tanyderids (in the usual sense). Some of the earliest described tanyderids were incorrectly placed in the Ptychopteridae (LOEW, 1850; ALEXANDER, 1913). In 1879, OSTEN-SACKEN proposed that Tanyderina included three genera: *Macrochile* LOEW, 1850, *Protoplasa* OSTEN-SACKEN, 1859, and *Tanyderus* PHILIPPI, 1865. ALEXANDER (1920) recognized Tanyderina as a family and divided it into two subfamilies, Tanyderinae and Bruchomyiinae. Later, he acknowledged that the Bruchomyiinae belong to the family Psychodidae (ALEXANDER, 1965). Recently, SKIBIŃSKA (2016) correctly subdivided the Tanyderidae into two subfamilies, the Tanyderinae and Nannotanyderinae. This last subfamily comprises tanyderids with unique male genitalia featuring elongate gonopods without patterned wings. *Nannotanyderus granieri* sp. nov. could be assigned to the Tanyderidae in this sense, based on wing venation, arrangement of setae on flagellomeres, absence of ascoids, presence of cross-vein m-m, presence of m-cu cross-vein, presence of discal cell (d), and spurs on the tibiae. It is noteworthy to state that *N. granieri* sp. nov. can be easily confused with members of the family Psychodidae, with whom it shares some features, such as, small size, absence of well-developed anal lobe, inverted genitalia, immaculate wings, and a general aspect of venation. Within the Tanyderidae in the usual sense, *Nannotanyderus granieri* sp. nov. can be attributed to the Nannotanyderinae in the usual sense, due to the striking similarity in wing venation with members of the genus *Nannotanyderus* in general, and particularly with *N. ansorgei* KRZEMIŃSKI *et al.*, 2013. *N. granieri* sp. nov. shares with all members of *Nannotanyderus* its small size, absence of well-developed anal lobe, and Sc reaching the wing margin at about the half of the wing length (Fig. 4). *N. granieri* sp. nov. differs from all known *Nannotanyderus* species (except *N. ansorgei* and *N. incertus*) by its considerably smaller wings. *N. granieri* sp. nov. differs from *N. incertus* by the much more proximal position of CuA in the latter. The wing venations of *N. granieri* are very similar to those of *N. ansorgei*, with the following differences: 1) R1 reaching the costal margin slightly beyond the fork of R2+3 into R2 and R3 in *N. granieri*, versus opposite to it in *N. ansorgei*; 2) R2 slightly longer than half of R3 in *N. granieri*, versus equal to half of R3 in *N. ansorgei*; 3) R2+3 bifurcation from Rs slightly distal to level where Sc meets costal margin in *N. granieri*, versus slightly basal to the level where Sc meets the costal margin in *N. ansorgei*; 4) the distance between the bifurcation of R2+3 from Rs to the base of R4 is smaller in *N. granieri*. *N. granieri* and *N. ansorgei* are to date the smallest known for tanyderid flies.

The discovery of very small Tanyderidae, which share several structural characters with Psychodidae such as the absence of neck, wing venation, and inversion of male genitalia, alongside primitive Psychodidae from the Jurassic and Cretaceous periods, has enhanced our understanding of the close phylogenetic relationship between the Tanyderidae and Psychodidae, as previously stated by KRZEMIŃSKI (1992), KRZEMIŃSKI and EVENHUIS (2000), and KRZEMIŃSKI and KRZEMIŃSKA (2003). It is worth recalling that the Bruchomyiinae, now considered as a psychodid subfamily, was initially classified within the Tanyderidae by ALEXANDER (1920). Furthermore, in all molecular phylogenies conducted since 2008 (BERTONE *et al.*, 2008; WIEGMANN *et al.*, 2011; CURLER & MOULTON, 2012), Tanyderids consistently appear as a sister-group to the Psychodidae, forming a monophyletic clade. Considering all these findings, and

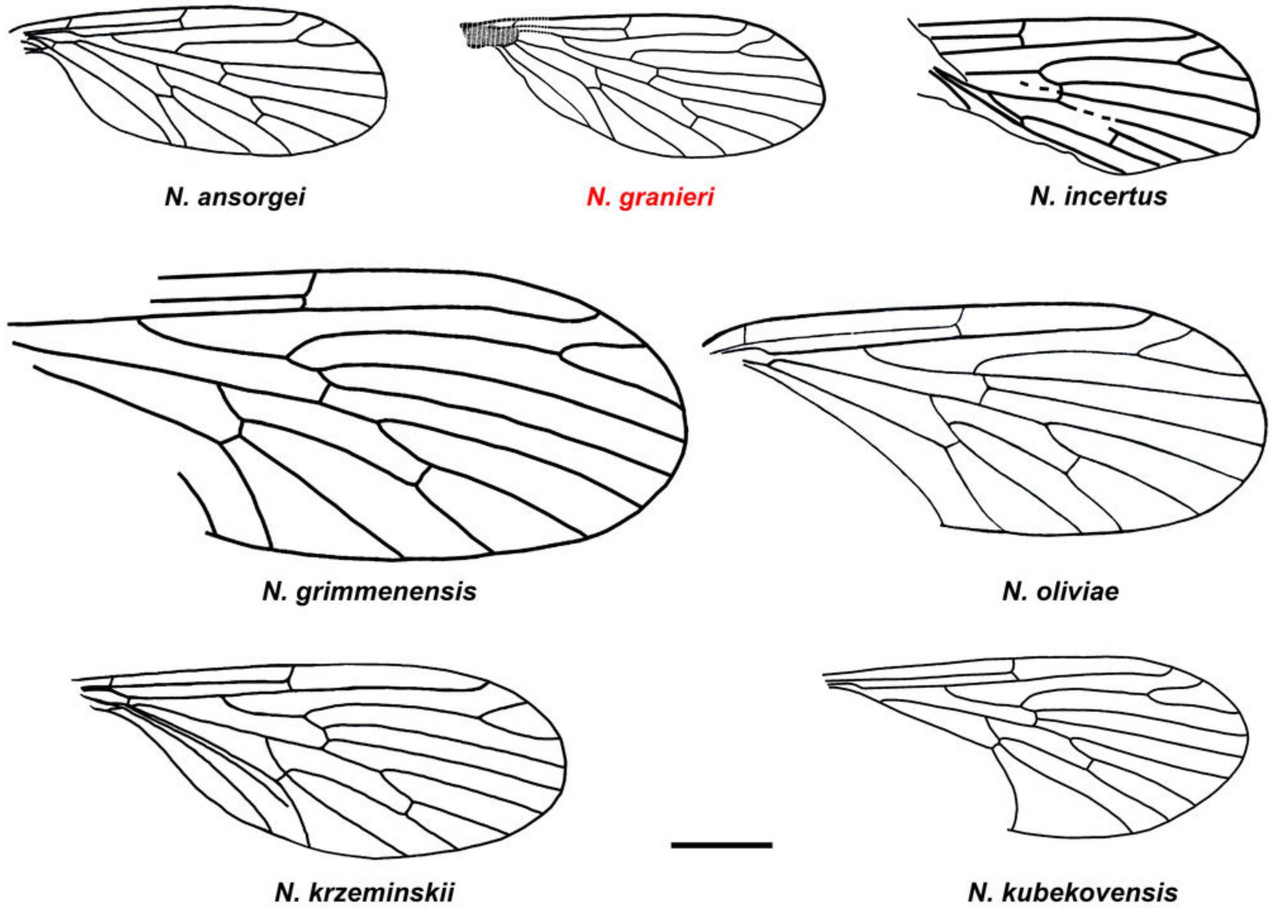


Figure 4: Line drawings of wings of all known species of *Nannotanyderus* (Scale bar = 500 µm).

given the possibility of confusion in the classification of present-day tanyderids and psychodids with the discovery of fossil material, we find it legitimate to downgrade the Tanyderidae to the rank of a subfamily within the Psychodidae. In this case, the two existing subfamilies of the Tanyderidae would be considered as the tribes Tanyderini OSTEN-SACKEN, 1880, and Nannotanyderini SKIBIŃSKA, 2016, instead of the subfamilies Tanyderinae OSTEN-SACKEN, 1880, and Nannotanyderinae SKIBIŃSKA, 2016, respectively.

5. Conclusion

The discovery of new fossils has caused confusion in the classification of modern tanyderids and psychodids. Moreover, all recent molecular phylogenies consistently show a sister-group relationship between the Tanyderidae and Psychodidae within a monophyletic clade. These findings prompt us to consider the Tanyderidae and Psychodidae as a single family, with the Tanyderidae being regarded as a subfamily (Tanyderinae) within the Psychodidae.

The ongoing discovery of new fossils and recent material continues to provide valuable insights into the true evolutionary history of tanyderids and psychodids.

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Appendix

List of all 34 described fossil Tanyderinae stat. nov.

Genus	Species	Author(s)	Age	Origin
Coramus	*gedanensis*	Skibińska, 2016	Upper Eocene	Baltic amber
Dacochile	*browni*	Skibińska & Krzemiński, 2018	mid-Cretaceous	Burmese amber
D.	*microsoma*	Poinar & Brown, 2004	mid-Cretaceous	Burmese amber
D.	*poinari*	Skibińska & Krzemiński, 2018	mid-Cretaceous	Burmese amber
Espanoderus	*barbarae*	Skibińska *et al.*, 2019	Lower Cretaceous	Álava, Spanish amber
E.	*orientalis*	Men & Hu in Men *et al.*, 2020	mid-Cretaceous	Burmese amber
Macrochile	*hornei*	Krzemiński *et al.*, 2013	Upper Eocene	Baltic amber
M.	*spectrum*	Loew, 1850	Upper Eocene	Baltic amber
Nannotanyderus	*ansorgei*	Krzemiński *et al.*, 2013	Lower Cretaceous	Bkassine, Lebanese amber
N.	***granieri***	**This work**	**Lower Cretaceous**	**Bqaatouta, Lebanese amber**
N.	*grimmensis*	Ansorge & Krzemiński, 2002	Lower Jurassic	Western Pomerania, Germany
N.	*incertus*	Lukashevich, 2011	Upper Jurassic	Share Teg, Mongolia; Durlstone Bay, England
N.	*krzeminskii*	Ansorge, 1994	Lower Jurassic	Germmen, Germany; Dobbertin, Germany
N.	*kubekorensis*	Skibińska & Krzemiński, 2013	Middle Jurassic	Kubekovo, Russia
N.	*oliviae*	Skibińska *et al.*, 2014	Lower Jurassic	Dorset, England
Podemacrochile	*baltica*	(Podenas, 1997)	Upper Eocene	Baltic amber
Praemacrochile	*ansorgei*	Lukashevich & Krzemiński, 2009	Middle or Upper Jurassic	Karatau, Kazakhstan; Shar-Teg, Mongolia
Praem.	*chinensis*	Krzemiński & Ren, 2001	Middle Jurassic	Daohugou, China
Praem.	*decipiens*	(Bode, 1953)	Lower Jurassic	Dobbertin, Germany
Praem.	*dobbertinensis*	Ansorge & Krzemiński, 2002	Lower Jurassic	Dobbertin, Germany
Praem.	*dryasis*	Dong *et al.*, 2015	Middle Jurassic	Daohugou, China
Praem.	*kaluginae*	Lukashevich & Krzemiński, 2009	Middle or Upper Jurassic	Karatau, Kazakhstan
Praem.	*stackelbergi*	Kalugina, 1985	Lower or Middle Jurassic	Siberia, Russia
Protanyderus	*astictum*	Dong *et al.*, 2015	Middle Jurassic	Daohugou, China
Prot.	*invalidus*	Lukashevich & Krzemiński, 2009	Middle Jurassic	Siberia and Kubekovo,
Prot.	*mesozoicus*	Kalugina, 1988	Upper Jurassic or Upper Cretaceous	Khutel Khara, Mongolia
Prot.	*nebulosus*	Lukashevich & Krzemiński, 2009	Upper Jurassic	Shar-Teg, Mongolia
Prot.	*savtchenkoi*	Lukashevich & Krzemiński, 2009	Middle or Upper Jurassic	Karatau, Kazakhstan
Prot.	*senilis*	Kalugina, 1992	Upper Jurassic	Shar-Teg, Mongolia
Prot.	*vetus*	Kalugina, 1992	Upper Jurassic	Shar-Teg, Mongolia
Prot.	*vulcanium*	Zhang, 2004	Middle Jurassic	Daohugou, China
Similinannotanyderus	*lii*	Dong *et al.*, 2015	mid-Cretaceous	Burmese amber
S.	*longitergata*	Men & Hu in Men *et al.*, 2020	mid-Cretaceous	Burmese amber
S.	*zbigniewi*	Skibińska & Krzemiński, 2018	mid-Cretaceous	Burmese amber

Nomenclatural note:
Life Sciences Identifier (LSID)
https://zoobank.org/References/86D9B493-1246-4427-915E-2AF0EC0286BC

- *Nannotanyderus granieri* AZAR, MAKSOUD, HUANG, MAALOUF & CAI, 2024

https://zoobank.org/NomenclaturalActs/8D2EDB55-372C-4EFD-B3FE-F51BB2BE1822