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Cretacetrocta, a new genus of barklice from the Early Cretaceous Lebanese amber

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Abstract

Pachytroctidae is a diverse extant family of Troctomorpha, represented by few fossil taxa from the Cretaceous ambers of Myanmar and Lebanon, and a single species from the Eocene amber of France (Oise). Herein, we describe and illustrate a new monospecific genus *Cretacetrocta libanella* Hakim & Azar **gen. et sp. nov.** from the Lower Cretaceous Bqaatouta amber outcrop (Lebanon). The new taxon is tentatively assigned to Pachytroctidae, and the only hitherto record from Lebanese amber of the subfamily Tapinellinae. The new finding reveals potential unreliability of the character 'nodulus' as a key diagnostic characteristic of the family, at the very least among fossil representatives. On the other hand, sexual dimorphism, a common trait in modern species of the Pachytroctidae, remains unveiled among extinct taxa.

Keywords: Psocodea, Troctomorpha, Mesozoic, amber, taxonomy

Introduction

Lebanon is an important palaeontological hotspot, rich in a diversity of fossils—in relevance to the surface area—such as its famous Upper Cretaceous marine fish deposits (Patterson, 1967; Forey *et al*., 2003; Fuchs *et al*., 2009; Murray *et al*., 2022; El Hossny & Cavin, 2023), Lower Cretaceous continental dysodiles deposits (El Hajj *et al*., 2021a, b), and Lower Cretaceous amber outcrops yielding bioinclusions (Maksoud *et al*., 2022; Maksoud & Azar, 2020, 2023).

To date, 36 fossiliferous Cretaceous deposits have been reported across Lebanese territory revealing mainly arthropods—largely insects—preserved as rock adpressions or amber bioinclusions (Maksoud *et al*., 2022: fig. 1, table 1, 2024: fig. 1). Amber outcrops are quite abundant in Lebanon, with some 450 outcrops discovered, of which 19 outcrops belong to the Upper Jurassic (Kimmeridgian) and about 500 outcrops to the Lower Cretaceous (Barremian) (Azar *et al*., 2010; Nohra *et al*., 2013; Granier *et al*., 2016; Maksoud *et al*., 2017, 2022; Maksoud & Azar, 2020). The Lower Cretaceous fossiliferous amber outcrops, of which only 30 have been discovered thus far (Maksoud *et al*., 2022, 2024), are mainly found in three intervals in the upper part of the "Grès du Liban" (refer to Maksoud *et al*., 2017, 2022: fig. 18 for stratigraphic details). Reconstructions of the palaeoenvironment during the Cretaceous indicate a siliciclastic coastland estuarine depositional environment (based on co-occurrence of bioturbation, echinoids and bivalves in the transgressive marine layers and amber and lignite in the regressive layers) with a nearby dense resin-producing tropical forest (based on entomofaunal associations in amber and palynological data) (Azar *et al*., 2011; Maksoud *et al*., 2017, 2022).

Most phylogenetic studies involving Troctomorpha (Psocodea) have focused on modern fauna, and/or mainly explored the relationship between parasitic and non-parasitic lice, with few representatives from each family usually included (Murell & Baker, 2005; Grimaldi & Engel, 2006; Yoshizawa & Johnson, 2003, 2010; Yoshizawa & Lienhard, 2010; Moya *et al*., 2021). No analysis targeting troctomorphan 'psocopteran' families have been performed in recent years to explore the inter- and intra-relationships between the families and their assigned taxa—particularly after the description of multiple new extinct species—and provide solid synapomorphies to back up their classifications. The discovery of fossils increases the need for a taxonomic

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revision of Troctomorpha, along with a comprehensive morphological phylogenetic analysis taking both extant and fossil taxa into consideration.

The modern representatives of family Pachytroctidae (Troctomorpha) are widely distributed (Smithers, 1972; Nel *et al*., 2005), with *ca*. 90 recorded species (Azar *et al*., 2015: table 1). To date, described fossil pachytroctids are limited to the taxa *Libaneuphoris jantopi* Azar, Huang, Cai & Nel, 2015 from the Cretaceous (Barremian) Lebanese amber (Falougha locality in Baabda District, Governerate Mount Lebanon), *Atapinella garroustei* Azar, Huang, Cai & Nel, 2015 and *Burmipachytrocta singularis* Azar, Huang, Cai & Nel, 2015 from the mid-Cretaceous Burmese Kachin amber, and *Tapinella eocenica* Nel, Prokop, De Ploëg & Millet, 2005 from the Eocene French amber (Oise). *Cormopsocus perantiqua* (Cockerell, 1919) was initially assigned to genus *Psylloneura* Enderlein, 1903—currently placed in Pachytroctidae—, but was later moved to Archaeatropidae (genus *Archaeatropos* Baz & Ortuño, 2000) by Mockford *et al*. (2013) and finally to Cormopsocidae by Cumming & Le Tirant (2021) after their discovery of new matching material in a better state of preservation. On the other hand, the controversial species *Libanopsyllipsocus alexanderasnitsyni* Azar & Nel, 2011, discovered in Lebanese amber (Hammana-Mdeyrij locality in Baabda District, Governerate Mount Lebanon), was originally assigned to Psyllipsocidae by the original authors but was then transferred to Pachytroctidae by Mockford *et al*. (2013). However, Azar *et al*. (2015) and Hakim *et al*. (2018) reinstated this taxon to Psyllipsocidae after one of the original authors (DA) reexamined the type material. The discovery of additional specimens belonging to *Libanopsyllipsocus alexanderasnitsyni* will help resolve this polemic.

Herein, we describe a new monospecific genus, *Cretacetrocta libanella* **gen. et sp. nov.**, from the Lower Cretaceous Lebanese amber, which we tentatively assign to the Pachytroctidae: Tapinellinae. With this classification, the taxon is the second representative of the family (if *Libanopsyllipsocus alexanderasnitsyni* is excluded) and the only representative of the subfamily collected from this amber material.

Material and methods

The studied material consists of one amber piece with a single psocodean individual, preserved as a bioinclusion in Lebanese amber, the latter collected by MM in the year 2021 from the discovered Bqaatouta amber outcrop (33º 58′0″ N, 35º47′13″ E, elevation at 1,177 m), located to the south-west near the Sannine Bottling Plant in Caza (= District) Kesserouan, Governorate of Jbeil-Kesserouan, Lebanon (Fig. 1; also refer to Maksoud *et al*., 2021: figs 1, 3 for additional imagery). The amber of this locality co-occurs along with lignite and plant debris in layers of dark shale and claystone (about 50 cm thick) in-between fluvial deposits of white and reddish sandstone (Maksoud *et al*., 2021, 2022: fig. 18). This outcrop is found in the lower interval of the upper part of the "Grès du Liban" and is dated to Early Cretaceous (early Barremian) (Granier *et al*., 2016; Maksoud *et al*., 2017, 2021).

The specimen was manually prepared, imbued with Canada balsam to fill cracks, and placed between two coverslips for long term preservation and clear observation under a microscope. The specimen was examined and photographed with a Zeiss AXIO Zoom V16 stereomicroscope (equipped with incident and transmitted lights) and a Zeiss AXIO Imager Z2 compound microscope, both equipped with Zeiss AxioCam HRc digital cameras. Photomicrographs with green fluorescence were obtained using a laser source connected to the compound microscope (eGFP mode; excitation/emission: 450–490/515–565 nm). The processing and treatment of illustrations were performed using Helicon Focus 8 and Adobe Photoshop CC 2019 software packages.

We mainly follow the wing venation and body structure nomenclature of Yoshizawa (2005), the systematic catalogue of Lienhard & Smithers (2002), and the keys to the families of Pachytroctidae by Lienhard (2005).

Systematic palaeontology

Order Psocodea Hennig, 1966
Suborder Troctomorpha Roesler, 1940
Infraorder Pachytroctetae Enderlein, 1905
Family Pachytroctidae Enderlein, 1905
Subfamily Tapinellinae Enderlein, 1908

Remarks. Moya *et al*. (2021), in an attempt to better unravel and organise the exact relationship between parasitic and non-parasitic lice, proposed a new classification of Psocodea in which they divided Nanopsocetae into three infraorders (Sphaeropsocetae, Pachytroctetae, and Liposcelidetae). Their main purpose was to avoid lowering the taxonomic rank of Phthiraptera, which fell within Nanopsocetae in their phylogenomics analysis, and retain its status as an infraorder along with the traditional subordinal names within it. However, they did not further elaborate on the status of the subordinal names within the three new infraorders of non-parasitic lice that they established. Given the lack of further information, and due to the major and delicate decision of elevating all subfamilies within Sphaeropsocetae, Pachytroctetae,

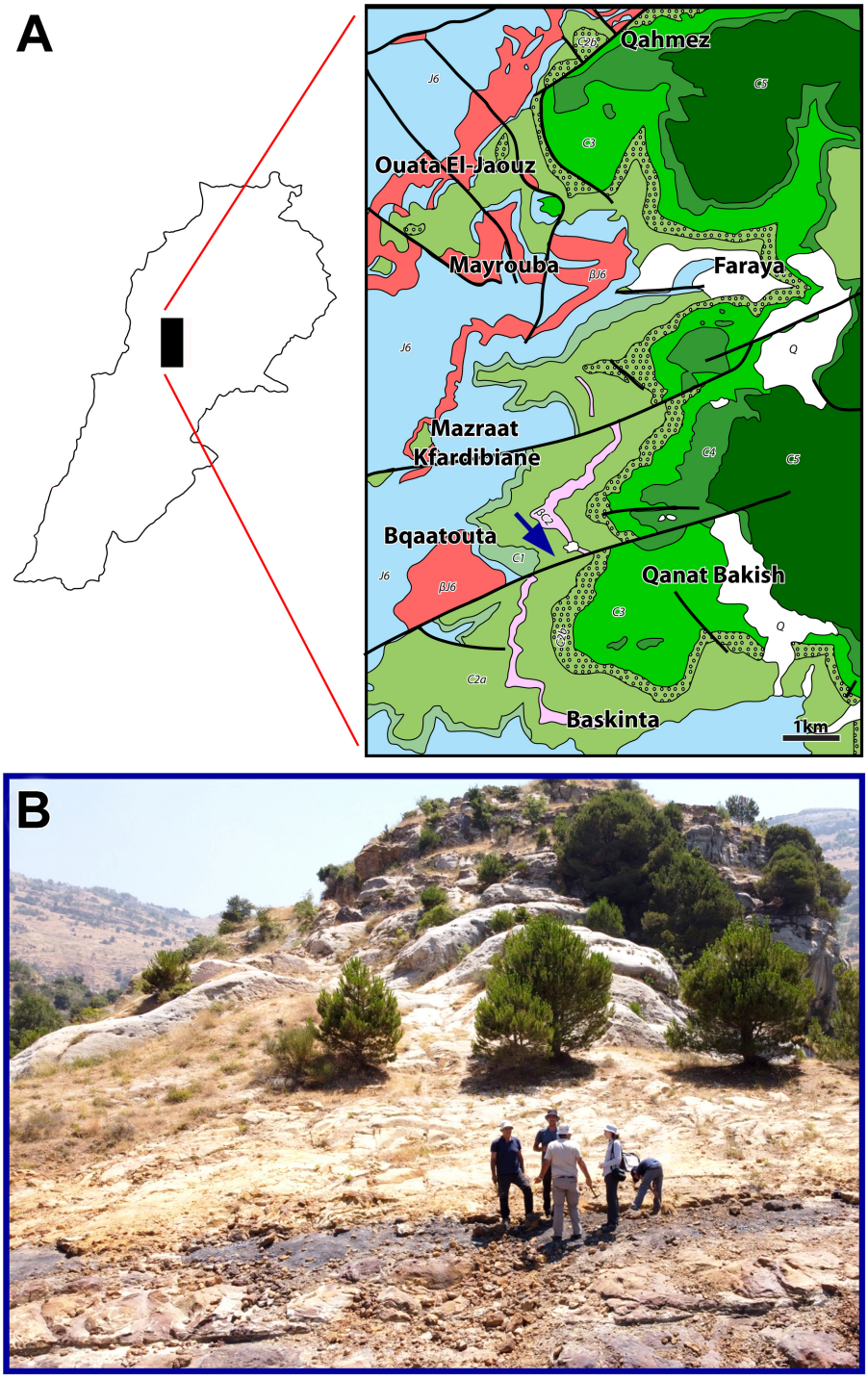

FIGURE 1. Bqaatouta amber outcrop, Lebanon. **A**, Geological map of the outcrop. **B**, Imagery of the site. (Maksoud *et al*., 2022)

and Liposcelidetae to family level without any careful consideration of each group or a detailed analysis aimed at them, we will continue in this work to adopt the traditional families Sphaeropsocidae, Pachytroctidae, and Liposcelididae and their included subfamilies (and lower ranks), while each is assigned to their respective infraorder Sphaeropsocetae, Pachytroctetae, and Liposcelidetae as established by Moya *et al*. (2021).

Genus *Cretacetrocta* Hakim & Azar, gen. nov.

Type species. *Cretacetrocta libanella* Hakim & Azar **sp. nov.**, by present designation and monotypy.

Etymology. The generic epithet is a combination of the term "Cretaceous", the age of the Lebanese amber studied herein, and the term "*trocta*" taken from "*Pachyctrocta*", deriving from the family name Pachytroctidae; gender feminine.

Diagnosis. Maxillary palpus without conical sensillum on second segment from base. Lacinia with outer cusp bidenticulate. Forewing with small pterostigma, not tinted; Rs separating before pterostigma; Rs and M connected by short crossvein; CuP and A meeting shortly before wing margin, wing-coupling structures present (nodulus present). Hindwing without vein Sc or basiradial cell. Claws asymmetrical, without pulvillus, one side with three small sharp spurs and one strong preapical tooth. Female subgenital plate with T-shaped sclerite.

***Cretacetrocta libanella* Hakim & Azar, sp. nov.**
(Figs 2–7)

Type material. Holotype, specimen number BKT-12A, female, Maalouf Collection, individual mostly complete, relatively well-preserved, except for abdomen (mostly broken off and very compressed), some areas overlapped with impurities and air bubbles (Fig. 2); syninclusions: two insects (one Hymenoptera and one Thysanoptera). The material is deposited at the Natural History Museum of the Lebanese University, Faculty of Science II, Fanar, Lebanon.

Etymology. The specific epithet is a combination of the term "Lebanon", where the amber was collected, and the extant genus "*Tapinella*" of the subfamily; gender feminine.

Diagnosis. As for the genus, *vide supra*.

Locality and horizon. Amber of Bqaatouta, Caza Kesserouan, Governorate of Jbeil—Kesserouan, Lebanon (Maksoud *et al*., 2022: fig. 6A, E); Lower Cretaceous, lower Barremian.

Description. Head: densely covered with thin setae. Epicranial suture indistinct, possibly absent or very weak. Compound eyes relatively small, slightly flattened dorso-ventrally, ellipsoid, 0.13 mm long and 0.09 mm wide, not very bulbous; numerous ommatidia present, without setae. Three large ocelli present, relatively spaced, disposed in a triangle (Fig. 3A). Antennae (both broken) bearing multiple thin setae, scape and pedicel about 2× width of flagellomeres, longest flagellum with 8–9 segments preserved, basal flagellomeres longer than apical segments, flagellomeres 2–4 the longest, weak traces of secondary annulations on basal flagellomeres. Postclypeus bulging. Maxillary palpus four-segmented (Fig. 3B), setose, second palpomere with no conical sensillum visible, fourth palpomere tapered apically (Fig. 3C); length (in mm): I: 0.02, II: 0.12, III: 0.08, IV: 0.12. Lacinia present, bicuspid; outer cusp bidenticulate (Fig. 3D).

Thorax: setose. Legs setose; tibiae with two apical spines; tarsus three-segmented, basal tarsomere the longest, middle and apical tarsomeres almost equal in length (Fig. 3E); claws asymmetrical, without pulvillus, one side with three short spurs in basal half and one sharp preapical tooth, second side without any spurs in basal half and one weak preapical tooth (Fig. 3F, G). Wings (Fig. 4A) macropterous. Forewing membranous, translucent, *ca*. 1.23 mm long and 0.49 mm wide, without setae on margin, membrane or veins; some veins thicker than others; Sc very short, free, not reaching wing margin or R; pterostigma present, small, 0.12 mm long and 0.05 mm wide, semi-triangular in shape, not opaque or tinted; Rs and M connected by short crossvein, 0.03 mm long; Rs and M two-branched, respectively forked at 0.93 mm and 0.98 mm; M and CuA separating at 0.47 mm; CuA two-branched, forked at 0.63 mm; CuA_1 very long, strongly curved, CuA_2 very short, straight; CuP and A meeting

FIGURE 2. *Cretacetrocta libanella* **gen. et sp. nov.**, holotype. **A**, **B**, Habitus. Scale bars: 0.5 mm.

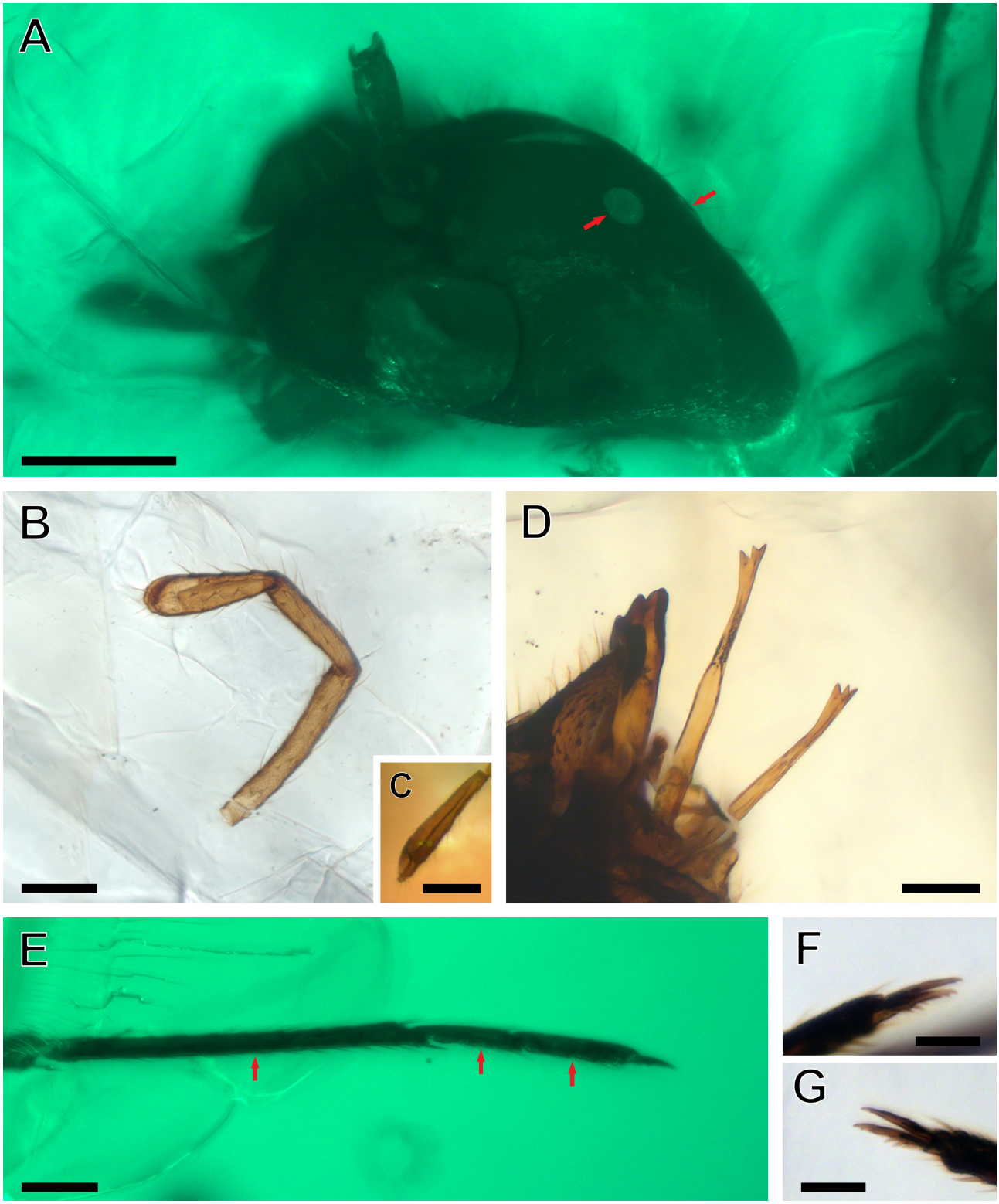

FIGURE 3. *Cretacetrocta libanella* **gen. et sp. nov.**, holotype. **A**, Head capsule; red arrows pointed at visible ocelli. **B**, **C**, Maxillary palpus; shape of fourth palpomere (in lower right). **D**, Lacinia. **E**, Tarsus. **F**, **G**, Claws respectively in middle leg and fore leg. Scale bars: 0.1 mm for **A**; 0.05 mm for **B**–**E**; 0.02 mm for **F**, **G**.

shortly before wing margin (Fig. 4B), wing-coupling structures present consisting of 7–8 separate spines (Fig. 4C); no second anal vein. Hindwing membranous, translucent, *ca*. 1.03 mm long and 0.34 mm wide, without setae on margin, membrane or veins; Sc absent; basiradial cell absent (Fig. 5); R_1 present, reaching margin; Rs forked into R_{2+3} and R_{4+5} at 0.75 mm; M, CuA and A simple.

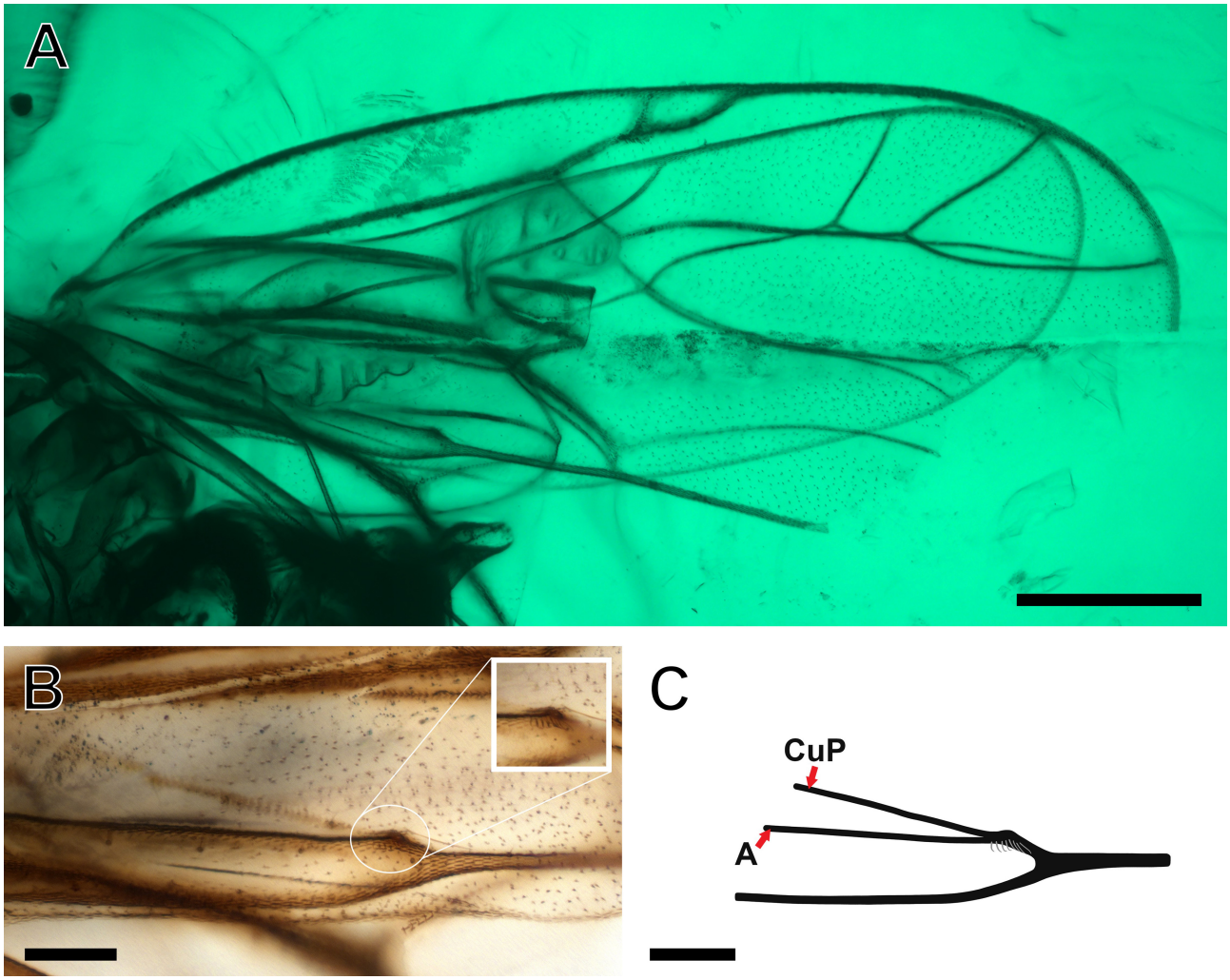

FIGURE 4. *Cretacetrocta libanella* **gen. et sp. nov.**, holotype. **A**, Wings, under green fluorescence. **B**, **C**, Details of forewing showing the meeting of veins CuP and A (and wing-coupling structures). Scale bars: 0.2 mm for **A**; 0.05 mm for **B**, **C**.

Abdomen: badly preserved (Fig. 6A). Female subgenital plate setose (Fig. 6B), with T-shaped sclerite (Fig. 6C); gonapophyses (ventral valvulae?) sclerotized, weakly visible through subgenital plate (Fig. 7).

Discussion

The classification of the new taxon is rather tricky as it does not fit well in any family. According to the keys to the families of 'Psocoptera' by Smithers (1990), the new taxon would fall into Psyllipsocidae when the character 'forewing with nodulus' is followed. However, if we exclude this character—which is normally absent in Pachytroctidae—and follow the character 'forewing without nodulus', the new taxon then falls into the Pachytroctidae. The wing venation pattern is quite different from that of psyllipsocids. *Cretacetrocta libanella* **gen. et sp. nov.** displays a more similar wing venation pattern to Pachytroctidae—vein M two-branched in forewing, basi-radial cell absent and vein A simple in hind wing (*vs*. vein M three-branched in forewing, basi-radial cell present and vein A forked in hind wing in Psyllipsocidae)—except for the presence of the wing-coupling structures (nodulus present) in the forewings (Smithers, 1972; Lienhard, 1998). The shapes of the pterostigma (small) and areola postica (very elongate with well curved CuA_1 and very short CuA_2) in *Cretacetrocta libanella* **gen. et sp. nov.** are slightly different as well—closer in shape to some fossil Electrentomoidea—, but these characters appear to be quite variable in Pachytroctidae (Azar *et al*., 2015), casting some doubt on their reliability in the case of this new taxon. On the other hand, the female subgenital plate with a T-shaped sclerite is distinctive of Troctomorpha (not found in Trogiomorpha) and common among the Pachytroctidae. Two curved and elongate sclerotized structures, which likely correspond to the

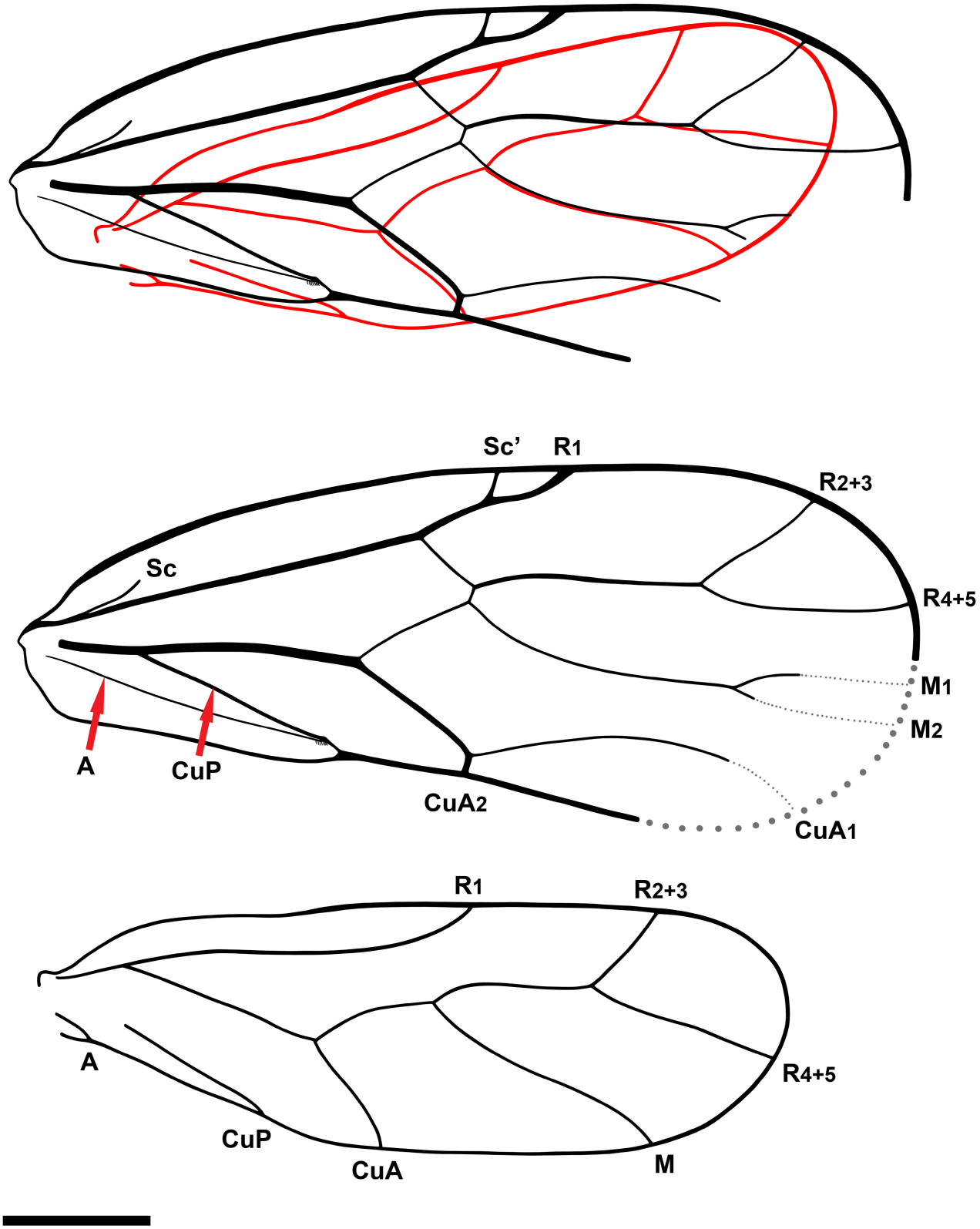

FIGURE 5. *Cretacetrocta libanella* **gen. et sp. nov.**, holotype. Hand drawings of forewing and hindwing. Scale bar: 0.2 mm.

female gonapophyses (ventral valvulae?), are weakly visible through the subgenital plate on either side of the T-shaped sclerite (Mockford *et al*., 2013).

The nodulus is commonly reported in families belonging to Amphientometae (Troctomorpha) (Smithers, 1972). Nonetheless, the new taxon does not fit in any of these families: Amphientomidae have the body and wings covered in scales, Musapsocidae have the tarsi two-segmented, while the rest (*i.e*., Compsocidae, Electrentomidae, Manicapsocidae, Protroctopsocidae,

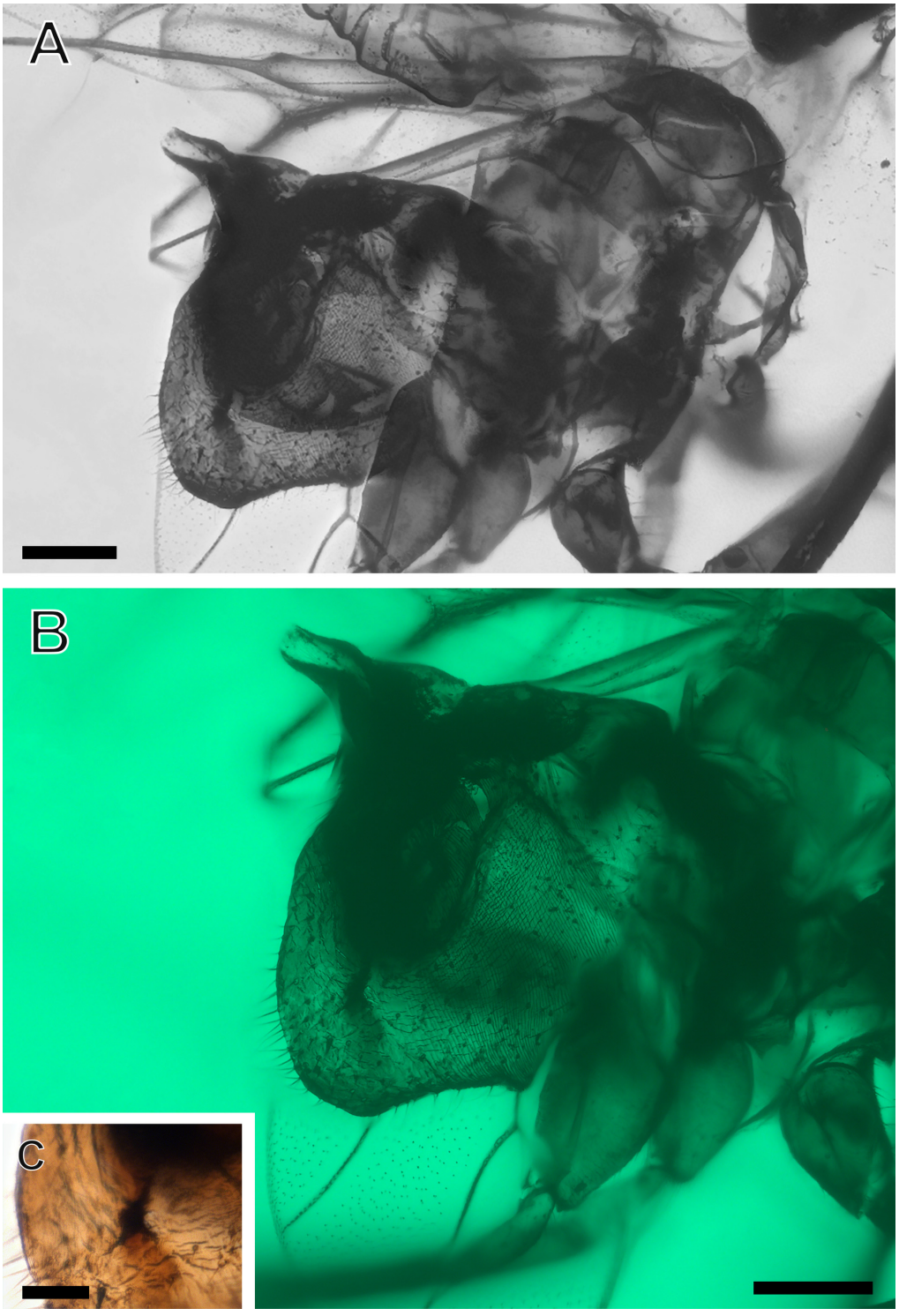

FIGURE 6. *Cretacetrocta libanella* **gen. et sp. nov.**, holotype. **A**, Thorax and abdomen. **B**, Genitalia, under green fluorescence. **C**, T-shaped sclerite. Scale bars: 0.1 mm for **A**, **B**; 0.04 mm for **C**.

and Troctopsocidae) typically have Sc meeting R, vein M three-branched, and two anal veins in the forewing. Among the Amphientometae, *Cretacetrocta libanella* **gen. et sp. nov.** appears to resemble the genus *Palaeomanicapsocus* Azar *et al*., 2017 the closest; *Palaeomanicapsocus*, reported from Burmese amber, is distinguished from other manicapsocids (and most Amphientometae) with forewing vein M two-branched, but it possesses the characters 'Sc meeting R' and 'two anal veins' in the forewing as it is typical in the family Manicapsocidae. The genus *Arcantipsocus* Azar, Nel & Néraudeau, 2009 from the Charente-Maritime amber also has M two-branched but is also significantly different in other wing venation characteristics, *i.e*., forewing membrane setose with veins

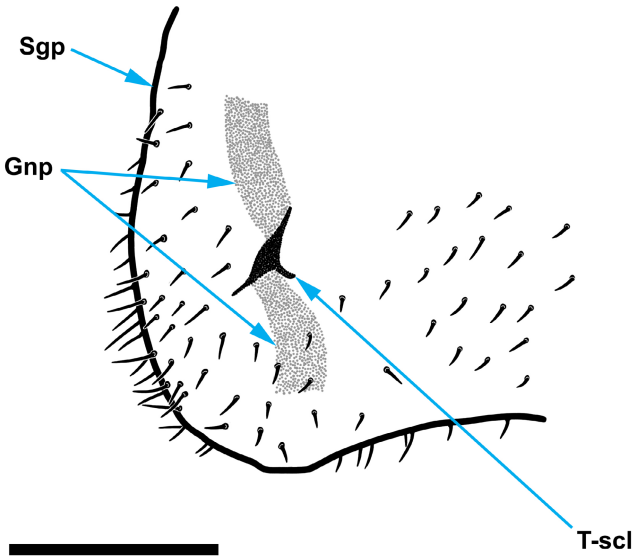

FIGURE 7. *Cretacetrocta libanella* **gen. et sp. nov.**, holotype. Hand drawing of genitalia (Sgp: subgenital plate; Gnp: gonapophyses; T-scl: T-shaped sclerite). Scale bar: 0.1 mm.

basally evanescent, pterostigma thickened, and hind wing with M bifurcated. At present, several attributions of the new taxon to different families can be made depending on the characters prioritised for classification. With the exception of the nodulus, *Cretacetrocta libanella* **gen. et sp. nov.** would fit the Pachytroctidae rather well. Thus, we believe that assigning the taxon to this family is appropriate at the moment, until further phylogenetic analysis can reveal more insight into this group.

One possibility is placing *Cretacetrocta libanella* **gen. et sp. nov.** in a separate new family, but we currently lack reliable proof to support the establishment of a taxon at a higher rank than genus, based on a monospecific genus described from one specimen. Another valid option is to leave *Cretacetrocta libanella* **gen. et sp. nov.** as *incertae sedis*, but we do not believe that there are enough major disparities to Pachytroctidae (other than the nodulus, as stated previously)—or possibly an electrentomoid family—to justify refraining from making a familial placement.

Recent studies on fossil Psocodea have suggested that the nodulus could be a variable character within some Trogiomorphan families (*e.g.*, the Empheriidae, after it was synonymised with Archaeatropidae) and thus could be an unsuitable character for diagnostic use in some cases at family level, requiring more investigation and re-evaluation (Wang *et al*., 2019; Álvarez-Parra *et al*., 2024). However, such a variation was not recorded in troctomorphan families. This discovery of a potential pachytroctid with wing-coupling structures could be a first occurrence of such a case.

We tentatively assign *Cretacetrocta libanella* **gen. et sp. nov.** to Pachytroctidae based on the presence of the following combination of diagnostic characters (Smithers, 1972, 1990; Mockford, 1993; Lienhard, 1998): 1) Body and wings without flattened scales, body not flattened dorsoventrally, hind legs extending beyond apex of abdomen; 2) Ocelli present, spaced; 3) Compound eyes relatively well-developed; 4) Lacinia present, with few apical teeth; 5) Maxillary palpus without sensillum on second segment; 6) Wings macropterous, elongate, apically rounded, with complex and distinct venation; 7) Forewing membranous, pterostigma not thickened, vein M two-branched, areola postica elongate, one anal vein present; 8) Tarsi three-segmented; 9) Subgenital plate with T-shaped sclerite.

We assign *Cretacetrocta libanella* **gen. et sp. nov.** to Tapinellinae based on the keys to the subfamilies of Pachytroctidae by Lienhard (2005): 1) Winged female morphs; 2) Compound eyes with numerous ommatidia; 3) Female subgenital plate with T-shaped sclerite. Furthermore, the shape of the lacinia is alike to some modern species of *Tapinella* (Smithers, 1972: fig. 4.277), although the claws are dissimilar, contrary to *Tapinella* where they have a normal and similar shape (Mockford, 1993: 58–59; Lienhard, 1998: 176–177). Cretaceous fossil species *Burmipachytrocta singularis*, likewise assigned to Tapinellinae, was also described with asymmetrical claws (Azar *et al*., 2015). *Cretacetrocta libanella* **gen. et sp. nov.** is differentiated from the Pachytroctinae by having the subgenital plate with a T-shaped sclerite (Lienhard, 2005) and from the Libaneuphorinae in several diagnostic characteristics of the wings (Azar *et al*., 2015); no winged forms belonging to Thoracotroctinae are known (Lienhard, 2005).

Cretacetrocta libanella **gen. et sp. nov.** differs mainly from all Pachytroctidae by having the forewing veins CuP and A meeting together at the wing margin, with the presence of the wing-coupling structures. This feature is uncharacteristic in other Pachytroctidae. The nodulus has been reported in the polemic species *Libanopsyllipsocus alexanderasnitsyni* (Azar & Nel, 2011), also from Lebanese amber (Hammana-Mdeyrij amber outcrop), but Mockford *et al*. (2013) refuted the presence of the nodulus (*in* Azar & Nel, 2011: fig. 5), along with some other interpretations of the authors, and consequently stated that *Libanopsyllipsocus alexanderasnitsyni* should belong in Pachytroctidae instead of Psyllipsocidae where it was assigned originally. Regardless, the new taxon is clearly distinguished from the latter species, most notably by the features of the claws (symmetrical in *Libanopsyllipsocus*) and the wings (absence of a pterostigma and shape of areola postica in forewings and absence of R_1 and presence of basi-radial cell in hind wings in *Libanopsyllipsocus*).

The new species is further differentiated from the fossil pachytroctids by other characteristics, mainly the length of the flagellomeres and maxillary palpomeres, and multiple variations in wing venation patterns. For example, *Libaneuphoris jantopi* has the forewings tinted with the pterostigma absent, and the hind wings with a clearly protruding anal lobe, vein R_1 absent and the basi-radial cell present (*vs*. no tint, pterostigma present but small, no protruding anal lobe, R_1 present and basi-radial cell absent in *Cretacetrocta libanella* **gen. et sp. nov.**). On the other hand, *Atapinella garroustei* and *Burmipachytrocta singularis* both have the forewings with a longer pterostigma and a longer vein CuA_2, and the hind wing with Sc present (*vs*. smaller pterostigma, shorter CuA_2 and vein Sc absent in *Cretacetrocta libanella* **gen. et sp. nov.**). Additionally, *Burmipachytrocta singularis* has veins Rs and M fused for a length in the forewings instead of being connected by a crossvein like in other fossil taxa, *Cretacetrocta libanella* **gen. et sp. nov.** included.

Sexual dimorphism in wing size is very common among modern representatives of Pachytroctidae, in which females typically can be fully winged while males are always apterous. This matter is not reflected in discovered fossil material yet as only females (winged morphs) have been reported, from which the Mesozoic and Cenozoic species have been described and established. Whether it is a result of bias in preservation—*e.g.*, because males lived in different habitats than females (not on the bark of resin-producing trees where they could easily get captured by the viscous resin)—or simply a result of males getting overlooked or unidentified as pachytroctids by psocodean experts because of their apterous nature remains uncertain. They would have to be recognized based on other diagnostic morphological features aside from wing characteristics, which could sometimes prove challenging to observe clearly in amber, if these traits are preserved. The discovery of an amber piece with co-occurring male and female adult pachyctroctid syninclusions would be valuable in retracing the origin of wing sexual dimorphism in the family, thereby further unveiling the evolutionary history of Pachytroctidae and, in larger scope, Psocodea.

Conclusion

Our knowledge of the Troctomorpha and their diversity during the Cretaceous increases with this newly described taxon. The discovery of more pachytroctid material from different localities will be crucial for our understanding of the biology and biogeographic distribution of fossil representatives, thus providing more necessary clues in unveiling the family (and suborder) evolutionary history. The latter, coupled with the recovery of male individuals in fossil records, is vital for tracing back the origin of the sexual dimorphism within this group.

On the other hand, new material belonging to *Cretacetrocta libanella* **gen. et sp. nov.** would help collect more data on this species and genus, for a better understanding of their taxonomic placement and, in a broader context, for a proper re-evaluation of the lineages within ‘psocopteran’ Troctomorpha, their assigned taxa and diagnostic characters.

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