



Review

# Contributions to the Palaeobiodiversity of Psocodea ('Psocoptera') from Lebanese Amber: A Review

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**Abstract:** Psocodea has been globally reported in different Mesozoic and Cenozoic amber deposits, one of which is Early Cretaceous Lebanese amber. The latter is one of the oldest ambers, with rich biological inclusions, bringing about the discovery of multiple new taxa of arthropods, some representing the earliest known records of their lineages. A total of fourteen psocodean species (of which one is an unidentified immature species) have been described to date from this material, which we review and discuss in this paper. A key for the identification of psocodean species discovered in Lebanese amber is also provided.

**Keywords:** Insecta; Psocoptera; amber; Lebanon; Cretaceous; biodiversity; taxonomy

## 1. Introduction

### 1.1. Overview

Psocodea is an acercarian lineage commonly referred to as barklice, booklice and parasitic (or true) lice, englobing over 10, 800 discovered modern species. Barklice and booklice ('Psocoptera') are characterized from other acercarian orders by their rather primitive features, e.g., elongated antennae with numerous flagellomeres and mandibulate chewing mouthparts [1,2]. True lice ('Phthiraptera') are greatly derived forms, remarkably host-specific and adapted for parasitism with their small size, lack of wings, highly modified mouthparts for chewing or sucking, and highly adapted legs for grasping [3,4]. They display several losses or reductions in structures compared to barklice and booklice.

Barklice are typically encountered in warm and humid environments, e.g., in leaf litter, on or under tree bark and leaves, under rocks and in caves, mainly feeding on microflora, particularly green algae, fungi, and lichen, but also consuming organic detritus and, occasionally, pollen [1]. Booklice are apterous psocodean species, usually regarded as pests, infesting human homes, warehouses and facilities. They prey on (preferably moldy) stored grains, books, or other products, and when left unattended they can lead to minor or moderate damage and economic loss [5–11] or trigger health issues, particularly in allergic individuals [12–18]. Some species were reported on birds and mammals or in their nests [19–22], although they were not engaged in parasitism. On the other hand, the true lice are ectoparasites, some hematophagous while others feed on the oily secretions or keratin of their hosts, i.e., birds and mammals. They are associated with major human epidemic diseases and serious health issues in livestock, domesticated and laboratory animals [23–25].

### 1.2. Phylogeny and Classification

The systematics of Psocodea, notably the origin of parasitism in lice, are being thoroughly investigated through various morphological, molecular and phylogenomic approaches [26–40]. At present, Psocodea encompasses the three recognized suborders:



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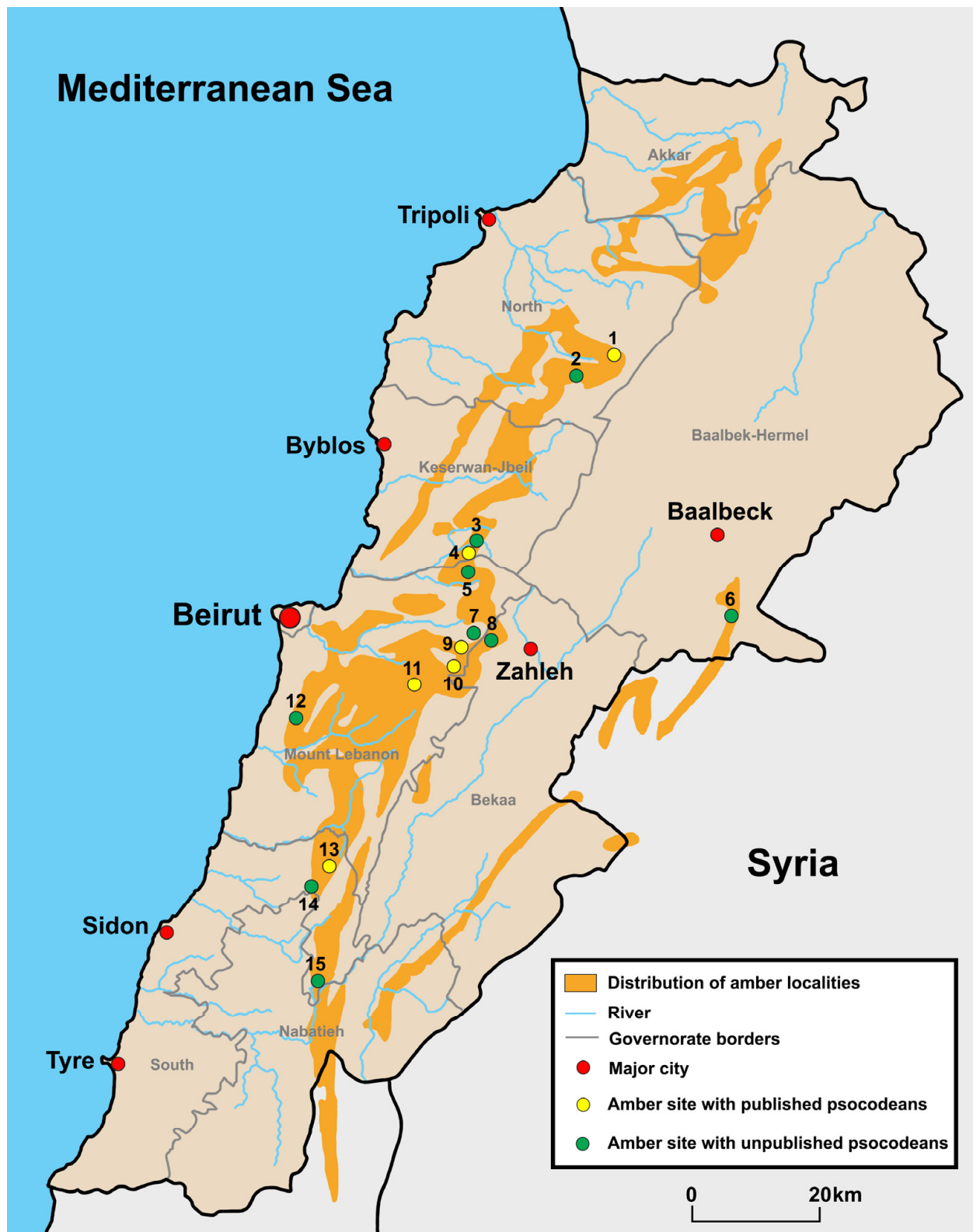
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Trogiomorpha, Troctomorpha, and Psocomorpha [36,41]. As the Phthiraptera are no longer considered at the taxonomic rank of order, they are now placed within Troctomorpha [27,36]. The latter, which was traditionally composed of only two infraorders, Amphientometae and Nanopsocetae (including the parasitic lice), is increased to five: Amphientometae, Liposcelidetae, Pachytroctetae, Phthiraptera, and Sphaeropsocetae [36]. Meanwhile, Trogiomorpha includes the three infraorders, Atropetae, Prionoglaridetae, and Psyllipsocetae, as well as the unassigned extinct family, Cormopsocidae [30,42]. Psocomorpha, on the other hand, is composed of six infraorders: Archipsocetae, Caeciliusetae, Epipsocetae, Homilopsocidea, Philotarsetae, and Psocetae [35]. Studies have confirmed the monophyly of Psocodea (Psocoptera + Phthiraptera) [27,36], yet some aspects of its phylogeny remain challenging as the exact relationships between some families and taxa are still unsettled, particularly when fossils are involved [30,35–39,42,43].

### 1.3. Studies on Fossil Taxa

The earliest records from this order are the stem psocodeans *Westphalopsocus pumilio* Azar, Nel, Engel and Bourgoïn, 2013 [44], from the Late Carboniferous (Pennsylvanian, Moscovian, Westphalian) of France (Avion, Pas-de-Calais), and *Zygopsocus permianus* Tilliard, 1935, from the Late Permian of Australia (Newcastle Coal) [45,46]. Jouault et al. (2021) also mentioned an undescribed record from the Middle Permian of China [47]. The discovered biodiversity of Psocodea in the Mesozoic and Cenozoic is significantly higher, with fossils collected from various localities and horizons. Taxa from the Mesozoic are reported from the Late Jurassic of Kazakhstan [48] and the Cretaceous ambers of Canada, France, Lebanon (Table 1), Myanmar, Russia, Spain, and the USA [37,49–52]. Taxa from the Cenozoic are reported from the Eocene limestone of England (Isle of Wight) [53], the Eocene ambers of the Baltic region, China (Fushun), France (Oise), Germany (Bitterfeld amber) and Ukraine (Rovno amber) [54–60], and the Miocene ambers of Mexico, Costa Rica and the Dominican Republic [29,61–65]. In the last two decades, the earliest definitive undisputed record of parasitic lice was *Megamenopon rasnitsyni* Wappler, Smith and Dalgleish, 2004, from the Eocene of Germany (Eckfeld maar) [66,67], although, the recent discovery of *Archimenopon myanmarensis* Zhang, Rasnitsyn, Zhang, Song, Shih, Ren, Wang, Li and Gao, 2024, assigned to the new stem family Archimenoponidae, from Burmese amber set back their oldest record to the mid-Cretaceous [68]. The youngest fossils attributed to Psocodea were discovered in the Quaternary, preserved in Colombian and Zanzibar (or Tanzanian?) copal [69–71].

To date, thirteen named fossil species from imago and one unidentified species from an immature, collected from six Lower Cretaceous amber outcrops across Lebanese territory (Figure 1), have been described and assigned to different families in Trogiomorpha and Troctomorpha. Several fossil psocodeans were also found in other amber outcrops in Lebanon (Figure 1), but they are yet to be studied and published. While some fossiliferous outcrops have not yielded any psocodean inclusions, it is most likely a result of under-sampling. Representatives of this order might be collected from those localities after new excavations in the future. The described immature specimen was also the subject of study for camouflage behavior, which has been observed among immatures in modern forms [72].



**Figure 1.** Distribution of fossil Psocodea in Lebanese amber outcrops. Yellow dots represent the amber outcrops from which fossil Psocodea have been described and green dots represent the amber outcrops from which fossil Psocodea have not yet been studied: 1, Bcharreh; 2, Hadath El-Joubbeh; 3, Ouata El-Jaouz; 4, Bqaatouta (El-Shqif); 5, Baskinta (Qanat Bakish); 6, Esh-Sheaybeh; 7, Kfar Selouan; 8, Bouarij (Tarchich); 9, Falougha; 10, Hammana–Mdeyrij; 11, Ain Dara; 12, Sarhmoul; 13, Jouar-Ess-Souss (Jezzine); 14, Maknouniyeh; 15, Rihaneh.

**Table 1.** Checklist of described psocodeans from Lebanese amber.

Species	Family	Type Locality	Remarks
<i>Archaeatropos randatae</i> (Azar & Nel, 2004)	Empheriidae (Trogiomorpha)	Jouar-Ess-Souss (Jezzine) outcrop	
<i>Asphaeropsocites neli</i> Azar, Engel & Grimaldi, 2010	Sphaeropsocidae (Troctomorpha)	Hammana–Mdeyrij outcrop	
<i>Bcharreglaris amunobi</i> Azar & Nel, 2004	Empheriidae (Trogiomorpha)	Bcharreh outcrop	
<i>Cretacetrotrocta libanella</i> Hakim & Azar, 2024	Pachytroctidae (Troctomorpha)	Bqaatouta outcrop	The assignment to Pachytroctidae is tentative; authors noted some similarities to electrentomoids as well.
<i>Libaneuphoris jantopi</i> Azar, Huang, Cai & Nel, 2015	Pachytroctidae (Troctomorpha)	Falougha outcrop	
<i>Libanoglaris chehabi</i> Azar & Nel, 2004	Empheriidae (Trogiomorpha)	Hammana–Mdeyrij outcrop	
<i>Libanoglaris mouawadi</i> Azar, Perrichot, Néraudeau & Nel, 2003	Empheriidae (Trogiomorpha)	Hammana–Mdeyrij outcrop	
<i>Libanomphientomum nudus</i> Choufani, Azar & Nel, 2011	Family <i>Incertae sedis</i> (Amphientometae, Troctomorpha)	Hammana–Mdeyrij outcrop	
<i>Libanopsyllipsocus alexanderasnitzyi</i> Azar & Nel, 2011	Psyllipsocidae (Trogiomorpha)	Hammana–Mdeyrij outcrop	Belongs to Pachytroctidae (Troctomorpha) according to Mockford et al. (2013) [73]
<i>Palaeosiamoglaris hammanaensis</i> Hakim, Huang & Azar, 2022	Prionoglarididae (Trogiomorpha)	Hammana–Mdeyrij outcrop	
<i>Paramesopsocus lu</i> Azar, Hajar, Indary & Nel, 2008	Electrentomidae (Troctomorpha)	Hammana–Mdeyrij outcrop	
<i>Setoglaris reemae</i> Azar & Nel, 2004	Empheriidae (Trogiomorpha)	Hammana–Mdeyrij outcrop	
<i>Sphaeropsocites libanensis</i> Grimaldi & Engel, 2006	Sphaeropsocidae (Troctomorpha)	Jouar-Ess-Souss (Jezzine) outcrop	
Sp. 1 (Nymph)	Family <i>Incertae sedis</i>	Ain Dara outcrop	

## 2. Lebanese Amber

### 2.1. Locality and Age

Extensive geological surveys have revealed over 450 amber outcrops in Lebanon [74], dating from the Late Jurassic [75,76] or Early Cretaceous [77–79]. The Jurassic amber was collected from nineteen localities [74] (fig. 1) in the lens of lignite mixed with laterites and pyrite, recovered from volcano–basaltic complex soil [75,76]. No inclusions were found yet in this amber. The Cretaceous amber was discovered from over 430 localities in layers of silts and dark clay mixed with lignite and vegetal remains, recovered from three intervals in the upper part of the ‘Grès du Liban’ [79]. Studies on the entomofaunal associations and palynological analysis indicate deposition took place in a warm environment corresponding to a humid and dense tropical forest [78,80]. Inclusions have been reported from a total of thirty fossiliferous Cretaceous outcrops scattered across the country [81] (fig. 1).

### 2.2. Scientific Significance of Lebanese Amber

Bioinclusions are quite frequent in Lebanese amber, with arthropods—particularly insects—found in every 25 to 30 pieces in the fossiliferous localities, often well preserved for scientific study [79]. A total of 19 orders and no less than 270 species of insects have been

recorded to date, entrapped either individually or as aggregations [79,82–87]. In addition, Lebanese amber was formed along with the rise and radiation of angiosperms, which correlates to the origin of multiple modern families of insects [4]. Consequently, these inclusions proved to be valuable in the study of palaeobiodiversity, palaeodistribution, and, sometimes, palaeoecological behavior and associations [88] occurring during the Early Cretaceous, and ultimately, in retracing the evolution of these extant insect lineages.

### 2.3. Lebanese Amber Collections

The Lebanese amber inclusions were hitherto collected by different people and are therefore part of four scientific collections: Acra collection, Azar collection, Estephan collection, and Maalouf collection. All the described materials are housed in public repositories (refer to the following section for details). More psocodean inclusions are still under study from the various Lebanese amber outcrops.

## 3. Systematic Paleontology

Order **Psocodea** Hennig, 1966 [89]

Suborder **Trogiomorpha** Roesler, 1940 [90]

Infraorder **Psyllipsocetae** Smithers, 1972 [30,91]

Family **Psyllipsocidae** Kolbe, 1884 [92]

Genus *Libanopsyllipsocus* Azar and Nel, 2011 [93]

Type species. *Libanopsyllipsocus alexanderasnitzyi* Azar and Nel, 2011 [93]; by original designation.

*Libanopsyllipsocus alexanderasnitzyi* Azar & Nel, 2011 [93] (figs 1–12)

(Figure 2A)

**Material.** Specimen 30 (holotype); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrij, Baabda District (= Caza), Mount Lebanon Governorate (= Mohafazat), Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** *Libanopsyllipsocus alexanderasnitzyi* is mainly differentiated from fossil psyllipsocids by their wing traits (forewing with pterostigma absent, and M two-branched; hind wing with R1 absent, and M simple). It is noteworthy that *Concavapsocus parallelus* Wang, Li, Ren and Yao, 2019 also lacks a pterostigma in the forewing and has vein M simple in the hind wing, but the latter species differs from *L. alexanderasnitzyi* in multiple other venation traits (e.g., R2+3 forked, M simple, CuA simple, and veins CuP and A fused forming a long Y-shape in the forewings; R simple and basi-radial cell absent in hind wings) [94]. In terms of the wing venation, *L. alexanderasnitzyi* is closer to Pachytroctidae. The forewing venation of *L. alexanderasnitzyi* appears closest to that of pachytroctid *Libaneuphoris jantopi* Azar, Huang, Cai and Nel, 2015 [95]. Nonetheless, it is distinguished from it in the absence of the anal lobe, longer basi-radial cell, and shorter common stem of Rs-M in the hind wing. It can also be differentiated from the other four fossil pachytroctids by the absence of the pterostigma in the forewing (present in the rest) and the presence of the basi-radial cell in the hind wing (absent in the rest), as well as some other wing and body features that vary depending on the taxa.

Azar and Nel (2011) described this taxon as a highly unusual psyllipsocid with wing characteristics very similar to Pachytroctidae [93]. They assigned it to Psyllipsocidae mainly due to the presence of ‘two distinct sclerotized filaments on the hypopharynx’, ‘nodule in the forewings’, and ‘Pearman’s coxal organ in hind legs’, all features characteristically absent from Pachytroctidae. They also identified an ‘anal spine on each paraproct’ and stated the specimen to be male with the ‘phallosome having two curved arms not fused anteriorly’. However, the classification of this species remains under debate. Mockford et al. (2013) rejected this attribution, stating that these traits, as presented in the illustrations, are absent and/or incorrectly identified [73]. They advocated for the specimen being female and moved the species to the Pachytroctidae. The original authors (D.A. and A.N.) rejected this decision and reinstated the taxon back to Psyllipsocidae in Azar et al. (2015) and

later in Hakim et al. (2018) [95,96]. To date, *Libanopsyllipsocus* remains monospecific and assigned to Psyllipsocidae; the discovery of new well-preserved individuals belonging to *L. alexanderasnitsyni* or other closely related species is crucial to solving this polemic of opposing opinions and finally clarifying the true nature of the structures involved for a better understanding of the appropriate classification.

Infraorder **Prionoglaridetae** Smithers, 1972 [30,91]

Family **Prionoglarididae** Karny, 1930 [97]

Subfamily **Prionoglaridinae** Karny, 1930 [97]

Tribe **Siamoglaridini** Azar, Huang and Nel, 2017 [98]

Genus *Palaeosiamoglaris* Azar, Huang and Nel, 2017 [98]

Type species. *Palaeosiamoglaris lienhardi* Azar, Huang and Nel, 2017 [98]; by original designation.

*Palaeosiamoglaris hammanaensis* Hakim, Huang and Azar, 2022 [99] (figs 1–6) (Figure 2B)

**Material.** Specimen 1308 (holotype), specimen 164C, specimen 904A, specimen 1095B, specimen 1428A, specimen 728A (paratypes); Azar collection, deposited at the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrij, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** This species is mainly differentiated from other taxa of the genus by the features of the wings and, with some, the absence of a conical sensillum in the maxillary palpomeres. The wing venation patterns of *Palaeosiamoglaris hammanaensis* are very similar to those of *Palaeosiamoglaris lienhardi* Azar, Huang and Nel, 2017; both species clearly have CuP and A reaching the margin separately while the nodulus is present [98] (fig. 3B) [99] (fig. 3C). The illustration of the nodulus of *Palaeosiamoglaris burmica* Azar, Huang and Nel, 2017 [98] (fig. 8B) does not clearly show whether CuP and A meet or reach the margin separately due to the overlapping of the hind wing margin; thus, we can only speculate that it is possibly the same as in *P. burmica* and *P. hammanaensis*. Species *Palaeosiamoglaris inexpectata* Azar, Huang and Nel, 2017 and *Palaeosiamoglaris hkamtiensis* Jouault, Yoshizawa, Hakim, Huang and Nel, 2021 are both described as having a nodulus—CuP and A joining at the margin in *P. hkamtiensis* stated in the text—but no detailed pictures for the nodulus area are presented [47,98].

**Additional remarks.** This genus also includes four fossil species from Burmese amber: the three species *P. burmica*, *P. inexpectata*, and *P. lienhardi* from Kachin amber, and the one species *P. hkamtiensis* from Hkamti amber.

Infraorder **Atropetae** Pearman, 1936 [100]

Family †Empheriidae Kolbe, 1884 [92]

(= †**Archaeatropidae** Baz and Ortuño, 2000) [101]

**Remarks.** *Bcharreglaris*, *Libanoglaris* and *Setoglaris* were initially not classified in a family and were suggested for attribution to either Prionoglarididae or Archaeatropidae by the original authors [43,102]. Mockford et al. (2013) later placed the genera and their respective species in Archaeatropidae based on the presence of macropterous setose wings—without scales – with the forewings having vein Sc curved apically joining R1, and the nodulus present [73]. For *Setoglaris*, they also listed the presence of well-developed female valvulae.

Genus *Archaeatropos* Baz and Ortuño, 2000 [101]

Type species. *Archaeatropos alavensis* Baz and Ortuño, 2000 [101]; by original designation.

*Archaeatropos randatae* (Azar and Nel, 2004) [102] (figs 4–14)

(Figure 2C)

**Material.** Specimen JS 203/2 BM 904 (holotype); Acra collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon. Specimen JG 21/12 BM 753, specimen JG 21/7 BM 698, specimen JG 21/4 BM 738, specimen JG 21/8 BM 678, specimen JG 21/3 BM 669 A, specimen JG 21/3 BM 669 B, specimen JS 108 BM 35, specimen JG 21/10 BM 709 (paratypes); Acra collection, deposited in the American Museum of Natural History, New York, NY, USA.

**Locality and age.** Jouar-Ess-Souss (Jezzine), Jezzine District, South Lebanon Governorate, Southern Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** This species is mainly distinguished from those of *Bcharreglaris*, *Libanoglaris* and *Setoglaris* by varying combinations of features of the wings (e.g., shape of the pterostigma, and presence/absence of setae in pterostigmal and anal areas) and antennae (number of flagellomeres, and presence/absence of secondary annulations). Azar and Nel (2004) originally assigned *Archaeatropos randatae* to *Libanoglaris* due to the absence of secondary annulations on flagellomeres and the presence of a distinct preapical tooth on the claws [102]. Mockford et al. (2013) transferred *A. randatae* to *Archaeatropos* due to the vein Sc' being strongly curved backwards, reaching to the wing margin, a trait observed in *Archaeatropos alavensis* Baz and Ortuño, 2000, while the taxa of *Libanoglaris* have Sc' more perpendicular to the wing margin [43,73,101–103]. Species *A. randatae* also differs from *A. alavensis* in the absence of a fringe on both wings (the presence of setae on the wing margins is not stated in the description of *A. randatae* nor illustrated in [102] (figs 12 and 13)), and the length and orientation of R1 in the forewing [101–103].

**Additional remarks.** *A. alavensis* is the only other species included in this genus, described from inclusions in Spanish amber of different outcrops [103].

Genus *Bcharreglaris* Azar and Nel, 2004 [102]

Type species. *Bcharreglaris amunobi* Azar and Nel, 2004 [102]; by original designation.

*Bcharreglaris amunobi* Azar and Nel, 2004 [102] (figs 1–3)

(Figure 2D)

**Material.** Specimen 21a (holotype), specimen 21b (paratype); Estephan collection, deposited in the American Museum of Natural History, New York, NY, USA.

**Locality and age.** Bcharreh, Bcharreh District, North Lebanon Governorate, Northern Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** This species is mainly characterized from other Cretaceous empheriids by its triangular (three-angled) pterostigma.

**Additional remarks.** Two additional species *Bcharreglaris amooni* Kaddumi, 2007 and *Bcharreglaris haddadini* Kaddumi, 2007 have been described from the co-eval Jordanian amber [104]. However, these species are considered by several psocodean experts to be *nomen nudum* since the work is not peer-reviewed and the type material is not accessible to the public or experts for examination.

Genus *Libanoglaris* Azar, Perrichot, Néraudeau and Nel, 2003 [43]

Type species. *Libanoglaris mouawadi* Azar, Perrichot, Néraudeau and Nel, 2003 [43]; by original designation.

**Remarks.** In addition to the taxa described from Lebanese amber, this genus also includes *Libanoglaris hespericus* Álvarez-Parra, Peñalver, Nel and Delclòs, 2022 discovered from Spanish amber [103].

*Libanoglaris chehabi* Azar and Nel, 2004 [102] (figs 15–22)

(Figure 2E)

**Material.** Specimen 117B (holotype), specimen 1194A (paratype); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrij, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** This species is mainly distinguished from others assigned to *Libanoglaris* by the characteristics of the forewings, e.g., the presence of three setae arranged in a triangle in the pterostigmal cell (vs. no setae), Sc' weakly directed backwards toward wing base and R1 almost perpendicular to margin (vs. Sc' perpendicular to wing margin and R1 directed forwards), and the fork of CuA1 and CuA2 occurring before the fork of Rs and M (vs. fork of CuA1 and CuA2 almost at the same level as the fork of Rs and M in *L. hespericus*) [43,102,103]. Refer to Álvarez-Parra et al. (2022) for comparative drawings of the forewings of the three *Libanoglaris* species [103] (fig. 8).

*Libanoglaris mouawadi* Azar, Perrichot, Néraudeau and Nel, 2003 [43] (figs 10–19)  
(Figure 2F)

**Material.** Specimen 420 (holotype), specimen 58, specimen 713A, specimen 714, specimen 423, specimen 378 (paratypes); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrij, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** Refer to the discussion above for the differences from *L. chehabi*. Species *L. mouawadi* also differs from *L. hespericus* by having the fork of CuA1 and CuA2 occurring before the fork of Rs and M (vs. almost at the same level).

Genus *Setoglaris* Azar and Nel, 2004 [102]

Type species. *Setoglaris reemae* Azar and Nel, 2004 [102]; by original designation.

*Setoglaris reemae* Azar and Nel, 2004 [102] (figs 23–27)

(Figure 3A)

**Material.** Specimen 1197 (holotype); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrij, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** This species is distinguished from other empheriids in Lebanese amber in terms of the characteristics of the antennae and forewing venation. In particular, the main known differences from *Libanoglaris* are the presence of secondary annulations on the flagellomeres, the forewing vein Rs basally perpendicular (not oblique), and the presence of a single seta in the pterostigmal area [43,102,103], which might not be enough to support a separate genus. *Setoglaris* is monospecific, based on a singular individual. Therefore, the discovery of new material is crucial for assessing the true value of the diagnostic characters and retaining the validity of the generic and specific taxa.

Suborder **Troctomorpha** Roesler, 1940 [90]

Infraorder **Amphientometae** Pearman, 1936 [100]

Family **Electrentomidae** Enderlein, 1911 [70]

(= †**Paramesopsocidae** Azar, Hajar, Indary and Nel, 2008) [48]

**Remarks.** Lienhard and Smithers (2002) synonymized Manicapsocidae with Electrentomidae as well, but Azar et al. (2017) suggested to continue following the traditional classification, referring to Manicapsocidae and Electrentomidae as distinct families, until this synonymy is backed up by phylogenetic analyses [41,105].

Genus *Paramesopsocus* Azar, Hajar, Indary and Nel, 2008 [48]

Type species. *Paramesopsocus lu* Azar, Hajar, Indary and Nel, 2008 [48]; by original designation.

*Paramesopsocus lu* Azar, Hajar, Indary and Nel, 2008 [48] (figs 1–19)

(Figure 3B)

**Material.** Specimen 746C (holotype), specimen 422, specimen 427A, specimen 886 (paratypes); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

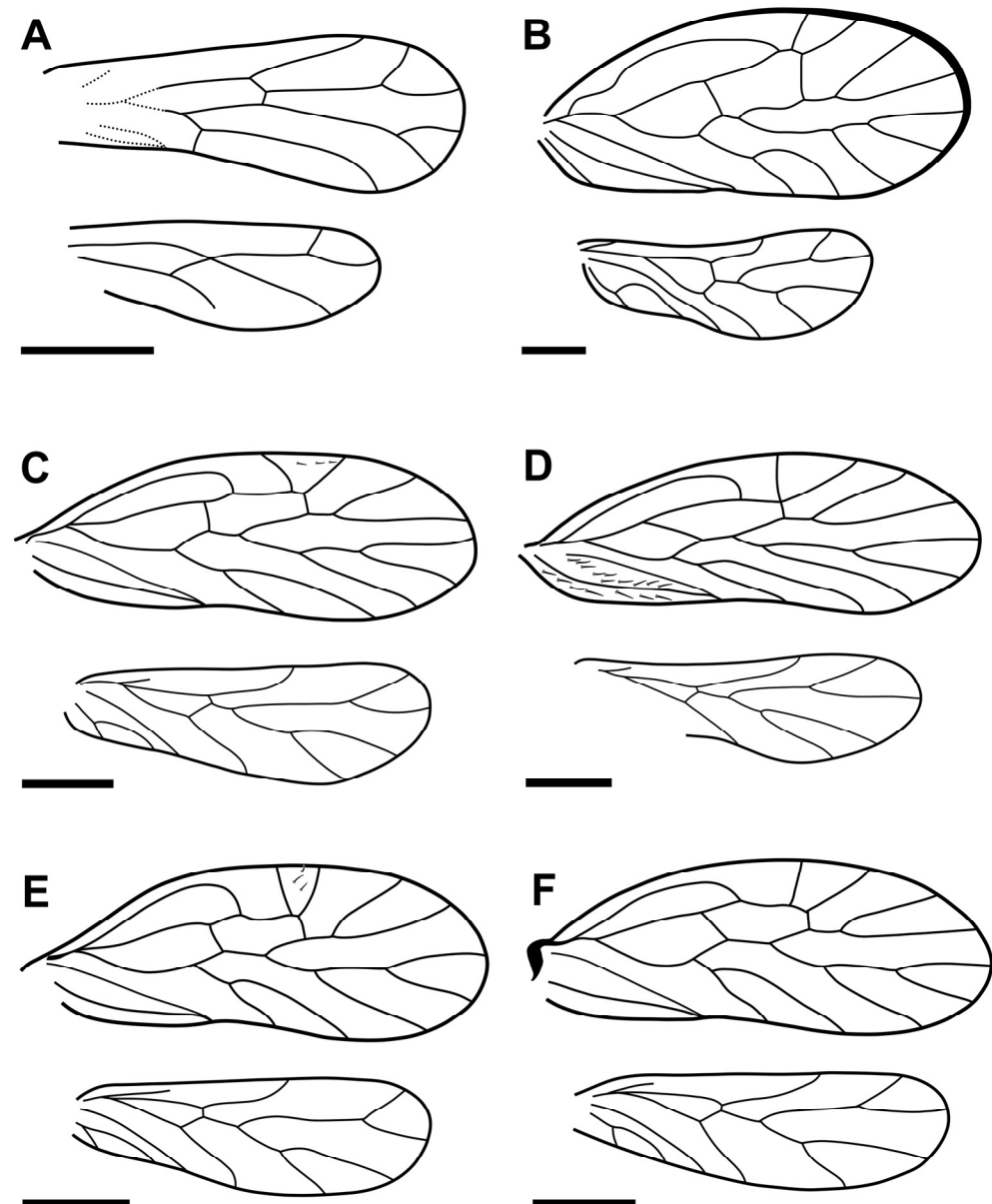
**Locality and age.** Hammana–Mdeyrij, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** Azar et al. (2008) described this species as possessing characteristics of both Troctomorpha (e.g., antennae with 13 flagellomeres) and Psocomorpha (e.g., presence of thickened and sclerotized pterostigma) [48]. Ultimately, they assigned it to Psocomorpha—while noting some similarities to Mesopsocidae—mainly due to the presence of a thickened and sclerotized pterostigma with nodus, and a hooked nodulus in the forewing. They discussed the fact that the characteristics shared with Troctomorpha are either plesiomorphic or found in both suborders, but they noted that excluding the characters of the pterostigma would place the genus near the electrentomoids. Mockford et al. (2013) later transferred *Paramesopsocus*—which was assigned by the original authors to a new



family, Paramesopsocidae—to Electrentomidae, thus synonymizing the two families based on the presence of several characteristics of Troctomorpha in *Paramesopsocus*, notably the forewing venation pattern (presence of a well-developed Sc and A2) [73], stating that the character ‘thickened and sclerotized pterostigma with nodus’ cannot be used as an autapomorphy of Psocomorpha as it was also detected in some extant and fossil Troctomorpha [73] (p. 14–15, remarks section of *Arcantipsocus*).

**Additional remarks.** This genus also includes one other species, *Paramesopsocus adibi* Azar, Hajar, Indary and Nel, 2008, preserved as adpressions from the Late Jurassic of Karatau, South Kazakhstan [48].



**Figure 2.** Wing drawings of Lebanese amber psocodean species: (A) *Libanopsyllipsocus alexanderanitsyni*. (B) *Palaeosiamoglaris hammanaensis*. (C) *Archaeatropos randatae*. (D) *Bcharreglaris amunobi*. (E) *Libanoglaris chehabi*. (F) *Libanoglaris mouawadi*. (Scale bars = 0.3 mm).

Infraorder **Pachytroctetae** Enderlein, 1905 [36,106]

Family **Pachytroctidae** Enderlein, 1905 [106]

Subfamily **Tapinellinae** Enderlein, 1908 [107]

**Remarks.** The subfamily also includes the three fossil species *Atapinella garroustei* Azar, Huang, Cai and Nel, 2015 and *Burmipachytracta singularis* Azar, Huang, Cai and Nel, 2015 from the Cretaceous Burmese amber, and *Tapinella eocenica* Nel, Prokop, De Ploëg and Millet, 2005 from the Eocene amber of Oise (France) [55,95].

Genus *Cretacetrocta* Hakim and Azar, 2024 [108]

Type species. *Cretacetrocta libanella* Hakim and Azar, 2024 [108]; by original designation.

*Cretacetrocta libanella* Hakim and Azar, 2024 [108] (figs 2–7)

(Figure 3C)

**Material.** Specimen BKT-12A (holotype); Maalouf collection, deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Bqaatouta, Kesserouan District, Jbeil—Kesserouan Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** Hakim and Azar (2024) tentatively placed the taxon in Pachytractidae while noting that it does not fit well in any family of Troctomorpha [108]. They discussed that the presence of a nodulus (CuP and A joining at margin) is not typical in the family, but it is rather common in Amphientometae. However, unlike Amphientometae, e.g., electrentomoid families, the taxon has forewings' Sc not joining R, vein M-two branched, and A<sub>2</sub> seemingly absent. The genus is currently monospecific.

Subfamily **Libanophorinae** Azar, Huang, Cai and Nel, 2015 [95]

Genus *Libaneuphoris* Azar, Huang, Cai and Nel, 2015 [95]

Type species. *Libaneuphoris jantopi* Azar, Huang, Cai and Nel, 2015 [95]; by original designation.

*Libaneuphoris jantopi* Azar, Huang, Cai and Nel, 2015 [95] (figs 4–17)

(Figure 3D)

**Material.** Specimen FAL-11A (holotype); Azar collection, deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Falougha, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** Azar et al. (2015) mainly distinguished this species from other pachytractids by characters relevant to the shape and venation of the hind wings [95]. They also noted the presence of the female T-shaped sclerite, a feature shared with the subfamily Tapinellinae. To date, the subfamily and genus remain monospecific. The discovery of more material belonging to this group from Lebanese amber or other deposits is necessary for further cementing the validity of the subfamily.

Infraorder **Sphaeropsocetae** Kolbe, 1883 [36,109]

Family **Sphaeropsocidae** Kolbe, 1883 [109]

Genus *Asphaeropsocites* Azar, Engel and Grimaldi, 2010 [110]

Type species. *Asphaeropsocites neli* Azar, Engel and Grimaldi, 2010 [110]; by original designation.

*Asphaeropsocites neli* Azar, Engel and Grimaldi, 2010 [110] (figs 1 and 2)

(Figure 3E)

**Material.** Specimen 1513-A (holotype); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrj, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** To date, the genus remains monospecific. The species shares multiple characteristics of the head and wings with *Sphaeropsocites lebanensis* Grimaldi and Engel, 2006, but is clearly distinguished from the latter by others traits (e.g., presence of a distinct frontal suture, areolate surface of the head and wings, absence of a claval furrow, and all the veins reaching the wing margin except R) [110,111]. Consequently, Azar et al. (2010) suggested a more derived placement of *Asphaeropsocites neli* compared to *S. lebanensis*, not as sister taxa, although *A. neli* still retains multiple plesiomorphic traits to warrant a basal position, albeit related, to the other Sphaeropsocidae [110].

Genus *Sphaeropsocites* Grimaldi and Engel, 2006 [111]

Type species. *Sphaeropsocites lebanensis* Grimaldi and Engel, 2006 [111]; by original designation.

*Sphaeropsocites lebanensis* Grimaldi and Engel, 2006 [111] (figs 2E and 6) (Figure 3F)

**Material.** Specimen AMNH JS284 (holotype); Acra collection, deposited in the American Museum of Natural History, New York, NY, USA.

**Locality and age.** Jouar Ess-Souss (Jezzine), Jezzine District, South Lebanon Governorate, Southern Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** To date, the genus remains monospecific. Grimaldi and Engel (2006) proposed *Sphaeropsocites lebanensis* to be a sister group to all the Sphaeropsocidae as it retains plesiomorphic features in the wings in comparison to the other taxa [111]. Also refer to the previous discussion on *Asphaeropsocites neli*.

Family *Incertae sedis*

Genus *Libanomphientomum* Choufani, Azar and Nel, 2011 [112]

Type species. *Libanomphientomum nudus* Choufani, Azar and Nel, 2011 [112]; by original designation.

*Libanomphientomum nudus* Choufani, Azar and Nel, 2011 [112] (figs 1–8) (Figure 3G)

**Material.** Specimen 1646 (holotype); Azar collection, currently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Hammana–Mdeyrij, Baabda District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Diagnostic remarks.** *Libanomphientomum nudus* is distinguished by the combination of different features of the head, body and wings, particularly the lack of scales, 14 antennomeres, forewing venation pattern (e.g., Sc joining R distally, presence of a well-developed pterostigma, and two separated anal veins), and ventral row of ctenidiobothria on the basal tarsomere [112]. Choufani et al. (2011) assigned the species to Amphientometae but refrained from placing the taxon in any family, suggesting multiple possible options “when considering different sets of characters” [112]. Mockford et al. (2013) agreed with the choice of infraorder by further placing *L. nudus* in the superfamily Electrentomoidea [73]. To date, the genus remains monospecific.

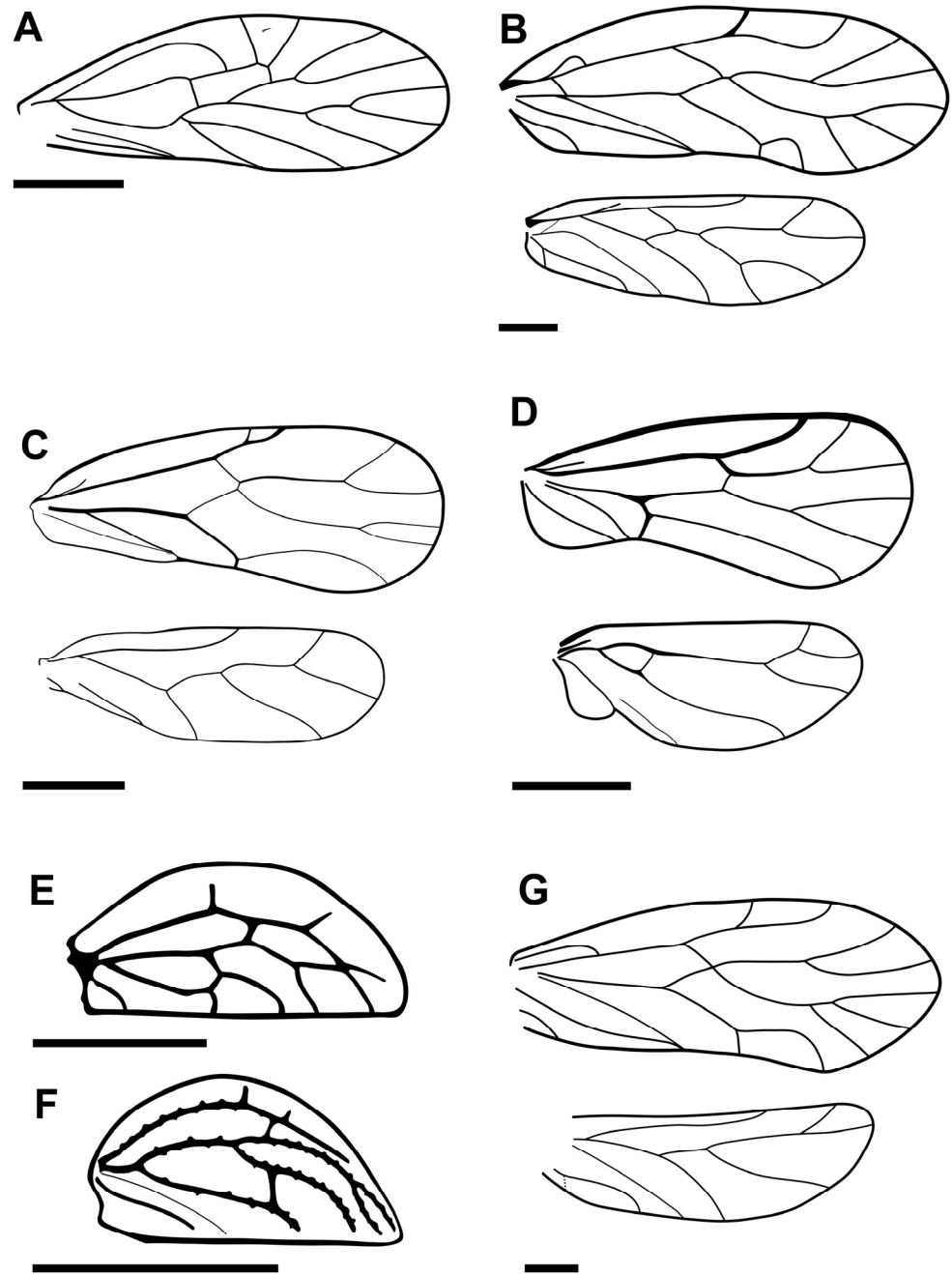
Sp. 1 (immature) [72] (figs 1–3)

**Material.** Specimen AD-33; Azar collection, deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

**Locality and age.** Ain Dara, Aley District, Mount Lebanon Governorate, Central Lebanon; early Barremian, Early Cretaceous [79].

**Remarks.** This specimen is the first and only immature psocodean described from Lebanese amber thus far. While the authors could not classify it, they were able to investigate the camouflage behavior, common among immatures in modern taxa, as the individual was carrying some debris, leaving the dorsal side of the abdomen exposed for examination of the involved structures.

Identification of psocodean immatures in fossils is extremely difficult since the morphological characters are not always well preserved for observation, if preserved at all. The accessibility of diagnostic characters necessary for accurate identification at the generic and specific levels is limited. Moreover, many taxa in modern fauna are known only from their imago forms and not much information—such as keys, descriptions and diagnoses—on their earlier stages is published for comparison with the fossil records.



**Figure 3.** Wing drawings of Lebanese amber psocodean species: (A) *Setoglaris reemae*. (B) *Paramesopsocus lu*. (C) *Cretacetrocta libanella*. (D) *Libaneuphoris jantopi*. (E) *Asphaeropsocites neli*. (F) *Sphaeropsocites lebanensis*. (G) *Libanomphientomum nudus*. (Scale bars = 0.3 mm).

Key to psocodean species from Lebanese amber:

- 1- Compound eyes reduced; forewings elytriform, hemispherical, with inner margins touching for entire length and not divergent apically, wing surface with dense areolation or punctation; hind wings absent ..... 2
- 2- Compound eyes normal; forewings elongated, wing surface membranous without any areolation or punctation; hind wings present ..... 3
- 2- Developed frontal suture present, surface of head and wings areolate, claval furrow absent, all veins reaching margin except R ..... *Asphaeropsocites neli*
- Frontal suture absent, surface of head not areolate, surface of wings punctate, claval furrow present, all veins not reaching margin ..... *Sphaeropsocites lebanensis*

- 3- Forewing Sc not joining R, vein M two-branched .....4  
 Forewing Sc joining R, vein M three-branched .....6
- 4- Forewing with pterostigma; hind wing with vein R1 present, basiradial cell absent  
 ..... *Cretacetrocta libanella*  
 Forewing without pterostigma; hind wing with vein R1 absent, basiradial cell present  
 .....5
- 5- Forewings tinted; hind wings with anal lobe protruding and well developed, Rs and M  
 fused for a length ..... *Libaneuphoris jantopi*  
 Forewings not tinted; hind wings with anal lobe normal, not protruding, Rs and M  
 fused briefly ..... *Libanopsyllipsocus alexanderasnitnyi*
- 6- Forewing Sc short, crossvein r1-rs absent .....7  
 Forewing Sc very elongate, crossvein r1-rs present .....8
- 7- Fifteen antennomeres; forewing with pterostigma thickened and sclerotized; hind  
 wing with M branched ..... *Paramesopsocus lu*  
 Fourteen antennomeres; forewing with pterostigma not thickened or sclerotized; hind  
 wing with M simple ..... *Libanomphientomum nudus*
- 8- Forewings with setae on veins and (sometimes) membrane, base of Sc straight, one anal  
 vein present .....9  
 Forewings without setae on veins or membrane, base of Sc sigmoidal, two anal veins  
 present ..... *Palaeosiamoglaris hammanaensis*
- 9- Forewing pterostigma four-angled, axillar and anal area without long setae .....10  
 Forewing pterostigma three-angled, axillar and anal area with long setae .....  
 ..... *Bcharreglaris amunobi*
- 10- Forewing Sc' strongly arched backwards, three aligned setae present in pterostigmal  
 cell ..... *Archaeatropos randatae*  
 Forewing Sc' weakly curved and directed forwards or backwards (almost perpendicu-  
 lar to margin), different setation in pterostigmal cell (see below) .....11
- 11- Without secondary annulations on flagellomeres; forewings with base of Rs strongly or  
 weakly oblique .....12  
 With secondary annulations on flagellomeres; forewings with base of Rs perpendicular,  
 one seta present in pterostigmal cell ..... *Setoglaris reemae*
- 12- Forewing Sc' slightly directed backwards, three setae present, disposed in triangle in  
 pterostigmal cell ..... *Libanoglaris chehabi*  
 Forewing Sc' slightly directed forwards, no setae present in pterostigmal cell .....  
 ..... *Libanoglaris mouawadi*

#### 4. Conclusions

Psocodeans are quite diverse in Lebanese amber. To date, the described psocodean fauna includes two suborders, 6 (or 5?) recognized families (+two undetermined), 12 genera and 14 species (of which one is an unidentified immature). Moreover, some genera are co-occurring in other Cretaceous outcrops, i.e., Jordanian amber, Burmese amber (Kachin and Hkamti) and Spanish amber.

With 30 fossiliferous outcrops hitherto identified in Lebanon, new taxa belonging to this insect order are expected in the future. These discoveries would prove valuable in accessing the entomofaunal biodiversity of the region during the Early Cretaceous, retracing the evolutionary history of the Psocodean lineages, as well as further cementing the validity of the established taxa, their diagnoses and phylogenetic relationships.

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