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Unravelling the mishmash: A new phylogeny for the family Empheriidae (Psocodea, Trogiomorpha) with a new genus and species from Cretaceous Charentese amber

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Abstract

The order Psocodea, including barklice, booklice, and parasitic lice, is diverse and widely distributed since the Cretaceous. That is particularly the case for the speciose extinct family Empheriidae (Psocodea, Trogiomorpha, Atropetae), recently fused with the 'Archaeatropidae'. Understanding the evolution of barklice is dependent in part on studying this family, as its representatives have been found from the Early Cretaceous to the Eocene, surviving the K/Pg extinction event. The phylogenetic relationships of Empheriidae in relation to other families, such as Lepidopsocidae or Psoquillidae, have been extensively debated. However, distinguishing diagnostic characters for the Empheriidae has proven challenging. In this study, we describe the new empheriid *Santonipsocus mimeticus* **gen. et sp. nov.** from Cretaceous Charentese amber (France). It is the third empheriid species found in this locality. The new genus is compared with the other genera in the family, and *Proprionoglaris guyoti* and *Proprionoglaris axioperi erga* are revised based on the type material and new specimens. We explore the phylogeny of Empheriidae, both the relationships with other families and the inner relationships between the genera, through maximum parsimony analysis and Bayesian inference analysis. Our results suggest that Empheriidae may represent a paraphyletic evolutionary grade to the rest of Atropetae. The phylogenetic relationships between genera align with the biogeography of the family and support previous hypotheses. In addition, we discuss the possible biology of the members of the family, shedding light on the evolutionary history of Empheriidae.

Keywords

Insecta, Atropetae, biogeography, phylogenetic analysis, taxonomy, evolutionary history

1. Introduction

The Cretaceous is crucial in the evolutionary history of insects, as it marks a period of remarkable diversification in many insect orders, particularly Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (Grimaldi and Engel 2005). These diversification events are believed to be connected to the rise of angiosperms during the Angiosperm Terrestrial Revolution (ATR; Benton et al. 2022). While many insect orders thrived due to the changes brought about by the ATR, some likely faced challenges due to environmental shifts (Peris and Condamine 2024). From a broad perspective, the impact of this event on insect evolution remains poorly understood, largely due to limited knowledge about the past diversity of various ‘minor’ orders, such as Psocodea, before, during, and after the ATR (Schachat and Labandeira 2021). To gain a better understanding of how the ATR influenced insect diversity, it is crucial to thoroughly document Cretaceous palaeo-entomofaunas.

The order Psocodea includes barklice, booklice, and parasitic lice (Johnson et al. 2018). Recently, time-calibrated phylogenetic analyses consistently indicated that the order originated during the Early Carboniferous (e.g., Johnson et al. 2018; Yoshizawa et al. 2019). This age aligns with the discovery of their presumed oldest fossil species, which was described from the Late Carboniferous (Nel et al. 2013). This ancient origin indicates that psocodeans managed to survive numerous mass extinction events and periods of profound environmental changes. Notably, they survived the end-Permian mass extinction, the most severe experienced by the insects (Jouault et al. 2022). These extinction events are often associated with changes in palaeoflora, and both extant and fossil psocodean species are frequently known or interpreted to be herbivorous or detritivorous (New 1987). Given their diet, it is likely that psocodeans may have been affected by the ATR. However, considering the potential rise and impressive diversification of numerous psocodean families during this period, along with their extensive fossil record (with over 70 species documented; Álvarez-Parra et al. 2020, table 1), it is more plausible that they benefitted from the floral turnover during this time.

The fossil record of Psocodea exhibits spatial heterogeneity and a bias toward resiniferous forests (Álvarez-Parra et al. 2022). The fossil record of insects from the Cretaceous period is closely linked to abundant amber-bearing outcrops. During this time, in what is known as the “Cretaceous Resinous Interval” (Delclòs et al. 2023), resin production of conifers was stimulated due to a combination of abiotic and biotic factors. Consequently, forest-dwelling arthropods are more likely to be trapped in amber, which complicates our understanding of Psocodea diversity dynamics (e.g., Martínez-Delclòs et al. 2004). Recent studies have demonstrated a significant difference in species richness among psocid suborders during the Cretaceous compared to extant diversity (Álvarez-Parra et al. 2022). Moreover, barklice are overre-

presented in resin compared to the overall forest entomofauna (Solórzano Kraemer et al. 2018), possibly due to their typical habitats on tree bark (New 1987).

The family Empheriidae (Psocodea, Trogiomorpha, Atropetae) includes representatives from the Early Cretaceous to the Eocene (Baz and Ortuño 2001; Álvarez-Parra et al. 2022; Li et al. 2022), rendering it a key group for understanding the evolution of Psocodea. During the Cretaceous, Empheriidae were diverse and had a widespread distribution. They survived the K/Pg extinction, but after this event, their fossil record is limited to Europe, and their diversity probably greatly declined until the Eocene. Recently, the family ‘Archaeatropidae’ was synonymised under Empheriidae (Li et al. 2022). However, the precise diagnostic characteristics of this family are not well established yet.

The fossil record of barklice in France is represented by four species (belonging to Trogiomorpha and Troctomorpha) in ‘mid’-Cretaceous Charentese amber (Perrichot et al. 2003; Azar et al. 2009), four species (belonging to Trogiomorpha, Troctomorpha, and Psocomorpha) from Upper Cretaceous Vendean amber (Azar et al. 2014), and 12 species (also belonging to the three suborders) from the Eocene Oise amber (Nel et al. 2004, 2005; Álvarez-Parra and Nel 2023). Undetermined barklice have also been recorded in the French Cretaceous amber from various localities in the Charentes and Anjou regions (Perrichot et al. 2007).

In this study, we introduce a novel genus and species of empheriid barklice, providing valuable insights into psocodean diversity during the Cretaceous. Our investigation delves into its classification and relationships with other genera within the family. Additionally, we analyse the phylogeny of Empheriidae and discuss the biogeography, biology, and evolutionary history of this intriguing group.

2. Material and methods

2.1. Amber deposit and geology

The Charentes region in southwestern France has the highest concentration of amber deposits in France and most of them are of uppermost Albian–lowermost Cenomanian age (Perrichot et al. 2007, 2010). The amber pieces and specimens studied herein were found in the lignitic layers of the Font-de-Benon quarry, near the villages of Archingeay and Les Nouillers, which is dated as latest Albian–earliest Cenomanian (Néraudeau et al. 2002; Dejax and Masure 2005; Peyrot et al. 2019). The amber pieces were collected from the ‘lithological subunit A1’ in lignite sands and clay lenses that range from 0.1 to 1 m in thickness. This unit lays in discordance on the Jurassic substrate composed of a Tithonian calcareous-clay bedrock. The amber is collected in three subunits: (A1s11) consisting of sand with decimetric fragments of lignite and amber embedded in the sandy

matrix; (A1s12) comprising a large lignite lens, with amber and some pyritised oysters; and (A1s13) comprising lignite and amber embedded in the sandy matrix (Néraudeau et al. 2002).

The resin pieces and the associated fossil woods were deposited, after short biostratigraphic transport (parautochthony), in a coastal marine area, as indicated by sedimentary figures of tides and bioturbation, and the presence of oysters, teredinid bivalve holes in the woods, and marine foraminifera in the lignitic clay (Néraudeau et al. 2002; Perrichot 2005). However, the reduced abundance of burrows and oysters in amber levels suggests environments under continental influence (freshwater): the facies are compatible with those of an internal estuary (Dalrymple et al. 1992). Wood remains from Charentese amber outcrops have been associated with the morphogenera *Agathoxylon*, *Brachyoxylon*, *Podocarpoxylon*, and *Protopodocarpoxylon*, and the resin-producing tree has been related to Araucariaceae or Cheirolepidiaceae (Nohra et al. 2015).

2.2. Amber preparation, examination, and nomenclature

The amber pieces were polished using thin silicon carbide papers on a Buehler Metaserv 3000 polisher. The very small and thin amber pieces were removed from larger pieces using a scalpel and then mounted in Canada balsam between microscope slides and coverslips. The specimens were photographed with a Nikon D800 digital camera attached to a Nikon SMZ25 stereomicroscope. The photographs were processed using Capture NX-D software, version 1.5.3 and the software Helicon Focus 7.6.1 was used for stacking and compilation. The drawings of the wing venation were made through a Leica M205 C stereomicroscope with a camera lucida. The figures were prepared using Adobe Photoshop CS6. The anatomical nomenclature follows the works of Smithers (1972) and Mockford (1993). The holotype MNHN.F.A30180 (ARC-186.7) is housed in the MNHN – Muséum National d’Histoire Naturelle (Paris, France) and IGR.ARC-169 is housed in the IGR – Geological Department and Museum of the University of Rennes (France).

The type specimens of *Proprioglaris guyoti* Perrichot et al., 2003 (at MNHN) and new specimens (IGR.ARC-352.1, IGR.ARC-157, and IGR.ARC-355) belonging to this species (at IGR), from the uppermost Albian–lowermost Cenomanian amber of Archingeay-Les Nouillers, and the type specimens of *Proprioglaris axioperi erga* Azar et al., 2014 (at IGR), from the Turonian amber of Vendée (see details on the age in Néraudeau et al. 2017), have been revised.

2.3. Morphological data

The morphological data were taken and modified from Li et al. (2022) and extended with the genus *Brachyantennum* Liang and Liu, 2022 (in Zhang et al. 2022) and all

remaining genera of the family Empheriidae not included in the previous analysis by Li et al. (2022): *Bcharreglaris* Azar and Nel, 2004; *Eoempheria* Nel et al., 2005; *Empherium* Hakim et al., 2021; *Jerseyempheria* Azar et al., 2010; *Longiantennum* Liang et al., 2022; *Parallelopsocus* Hakim et al., 2024; *Preempheria* Baz and Ortuño, 2001; *Setoglaris* Azar and Nel, 2004; *Trichempheria* Enderlein, 1911; and the new genus described herein. It is important to note that Hakim et al. (2023) have proposed the synonymisation of the species *Latempheria kachinensis* Li et al., 2022 under *Burmempheria densuschaetae* Li et al., 2020, although we opt to consider the two genera as separated in our analyses. We used 39 characters (File S1), coded for the 28 ingroup taxa and the outgroup taxon: *Cormopsocus* Yoshizawa and Lienhard, 2020 (Table S1). All characters were treated as unordered and with equal weights. Inapplicable and unknown characters were coded with ‘–’ and ‘?’, respectively. The character matrix was established with Mesquite v.3.61 (Maddison and Maddison 2019). All consensus trees were visualised and drawn using Figtree v.1.4.4 (Rambaut 2009) and processed with Adobe Illustrator CC2019.

Some character descriptions presented by Li et al. (2022) were reviewed to make them more precise (File S1). In character 7, “mandible” has been changed to “maxillary palpus”. In character 29, “[M₁ and M₂ in hind wing fused only occurs in *Thylacella* and *Rhyopsocus*]” has been changed to “[M₁ and M₂ in hind wing not fused only occurs in *Jerseyempheria*, *Thylacella*, and *Rhyopsocus*]”. The character 39 “Anal vein in forewing” has been added to the list.

Some character states presented by Li et al. (2022) were reviewed and corrected (Table S1). (1) *Psyllipso-cus*, character 15 changed from state 0 to state 1, forewing veins have setae (Smithers 1972; Lienhard 2023). (2) *Empheria*, character 19 state 1 changed to “–”, this genus lacks basal section of Rs in forewing and, consequently, radial cell (Enderlein 1911; Smithers 1972); character 23 state 0 changed to 1, based also on its lack of radial cell in forewing (Smithers 1972). (3) *Libanoglaris*, character 13 state 0 changed to state 1, the shape of the areola postica is long (Perrichot et al. 2003; Álvarez-Parra et al. 2022). (4) *Thylacella* and *Thylax*, character 12 state 0 changed to state 1 and character 15 state 0 changed to state 1, as both genera show setae on forewing membrane and veins (Enderlein 1911; Smithers 1972). (5) *Psoquilla* and *Rhyopsocus*, character 10 state 0 changed to state 1 and character 15 state 0 changed to state 1, as both genera show setae on forewing margin and veins (Smithers 1972).

2.4. Maximum parsimony

Maximum parsimony (MP) analysis of the morphological dataset (Table S1) was conducted with PAUP v.4.0a166 (Swofford 2002). The outgroup taxon was treated as paraphyletic with respect to the ingroup. Tree searches were performed using a heuristic search method with the following options: maximum number of trees

saved equal to 10 000, only optimal trees retained, collapse of zero-length branches, and a tree bisection and reconnection (TBR) swapping algorithm. When searches produced more than one optimal cladogram (here 737), a strict consensus was performed. To measure the robustness of the parsimony cladograms, bootstrap analyses (Felsenstein 1985; Hillis and Bull 1993) were executed using the full heuristic search option for 100 replicates. We considered values of bootstrap support (BS) ≥ 70 as strong node supports (Hillis and Bull 1993).

2.5. Bayesian phylogenetic inference

We carried out Bayesian phylogenetic inference (BI) on the morphological dataset (Table S1) using MrBayes v.3.2.7a (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist et al. 2012). We performed our analysis with a Markov one-parameter (Mkv) model (Lewis 2001), with a gamma rate variation across characters. Other parameters were set on the by-default option. Because we try to estimate the position of the new genus and the relationships within the Empheriidae, we constrained the monophyly of the latter family. We considered polymorphism as a new character state (Kornet and Turner 1999).

The analysis comprised two runs and four Markov chains Monte Carlo (MCMC) and was launched for 20 million generations. The MCMC were sampled every 5000 generations, and a burn-in fraction of 0.25 was used. Convergence diagnostics were checked for each analysis, with the average standard deviation of split frequencies <0.01 , potential scale reduction factor (PRSF) close to 1.0 in MrBayes outputs, and an effective sample size >200 in tracer v.1.7.1 (Rambaut et al. 2018). Posterior probabilities (PP) are used to discuss the node support.

3. Systematic palaeontology

Order: Psocodea Hennig, 1966

Suborder: Trogiomorpha Roesler, 1940

Infraorder: Atropetae Pearman, 1936

Family: Empheriidae Kolbe, 1884

Genus *Santonipsocus* gen. nov.

<https://zoobank.org/0E610D78-0C6F-4058-A647-46BCEFE819B2>

Type species. *Santonipsocus mimeticus* sp. nov. by present designation and monotypy.

Etymology. A combination of ‘santoni-’ after the Santones, a Gallic tribe that inhabited the Saintonge within the Charentes region where the amber outcrop is located,

and ‘*Psocus*’, the common generic suffix in Psocodea. The name is masculine.

Diagnosis. Antenna with 17 flagellomeres without secondary annulations; no ocelli; compound eye not prominent and small; distal maxillary palpomere globose and rounded; elongate distal labial palpomere; forewing and hind wing of similar sizes, slightly surpassing distal part of abdomen; forewing with setae on margin; two rows of setae on veins; crossvein between Sc and margin emerging very close to meeting point of Sc with R_1 ; distal bent of basal section of Sc between the emerging of crossvein and meeting point with R_1 curved, not straight or perpendicular to R_1 ; vein 1A well developed, without nodulus; hind wing with bifurcation of Rs into R_{2+3} and R_{4+5} nearly at same level as R_1 reaching margin; tibiae with three to four spines; pretarsal claws lacking preapical tooth and pulvillus.

***Santonipsocus mimeticus* sp. nov.**

<https://zoobank.org/EB1D823F-33FF-4939-AFD6-1C8AF-D81C503>

Figures 1–4

Holotype. MNHN.F.A30180 (ARC-186.7), adult specimen, probably male (Figs 1–3), erroneously figured as a paratype of *Proprioglaris guyoti* in the PhD dissertation of Perrichot (2005, fig. 31b). Amber fragment cut from a larger amber piece (‘ARC-186’) and prepared in Canada balsam. Originally in syninclusion with the holotype of *Prospeleketor albianensis* Perrichot, Azar, Néraudeau and Nel, 2003 (specimen MNHN.F.A30111 [ARC-186.10]) and nine other arthropods (Diptera, Hemiptera, Coleoptera, and Pseudoscorpionida). In the article by Perrichot et al. (2003), it is indicated that the holotype of *P. albianensis* is together with the female paratype of *P. guyoti* as syninclusions. However, *P. guyoti* was described from the female holotype (MNHN.F.A30108 [ARC-58.2]) and two male paratypes (MNHN.F.A30109 [ARC-50.1] and MNHN.F.A30110 [ARC-201.2]), all in other amber pieces. All the above-mentioned material is housed in the palaeontological collection of the Muséum National d’Histoire Naturelle, Paris, France.

Other material. IGR.ARC-169, adult specimen, sex unknown (Fig. 4). From Archingeay-Les Nouillers amber deposit. Amber piece prepared in Canada balsam; the forewings are separated from the rest of the body. Undetermined arthropod leg as syninclusion. Housed in the Geological Department and Museum of the University of Rennes, France.

Locality and horizon. Font-de-Benon quarry, Archingeay-Les Nouillers, Charente-Maritime Department (Nouvelle-Aquitaine, France); level A1sl, uppermost Albian–lowermost Cenomanian, Cretaceous (Néraudeau et al. 2002).

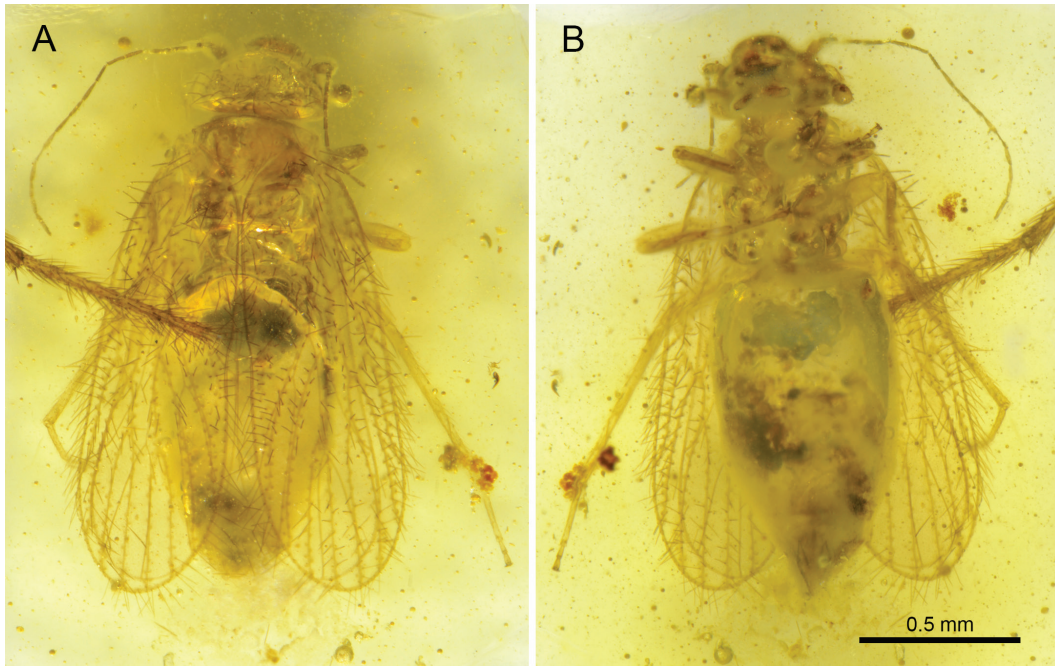


Figure 1. *Santonipsocus mimeticus* gen. et sp. nov. (Psocodea, Trogiomorpha, Empheriidae), holotype MNHN.F.A30180 (ARC-186.7), probably male; uppermost Albian–lowermost Cenomanian amber of Archingeay-Les Nouillers (France). **A** habitus from dorsal view; **B** habitus from ventral view. Both at same scale.

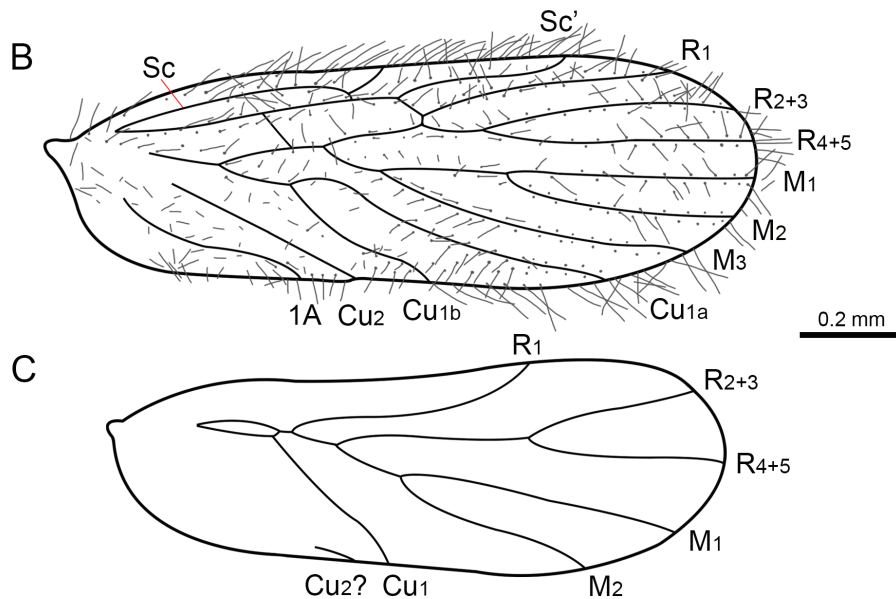
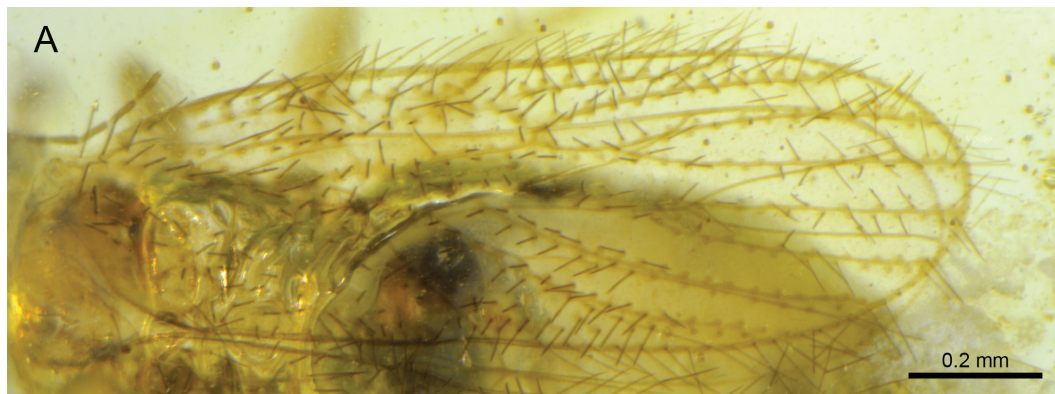


Figure 2. *Santonipsocus mimeticus* gen. et sp. nov. (Psocodea, Trogiomorpha, Empheriidae), holotype MNHN.F.A30180 (ARC-186.7), probably male; uppermost Albian–lowermost Cenomanian amber of Archingeay-Les Nouillers (France). **A** photograph of right fore- and hind wings, overlapped; **B** schematic drawing of forewing; **C** schematic drawing of hind wing. B and C at same scale.

Etymology. From the Greek μιμητικός, meaning ‘imitator’, based on the resemblance with other Cretaceous barklice species.

Diagnosis. As for the genus (vide supra).

Description. Probably male. Body length 1.75 mm from clypeus to genitalia (Fig. 1). — **Head:** almost twice wider than long, 0.26 mm long, 0.44 mm wide; vertex covered by setae; marked epicranial suture with indistinct anterior arms; no ocelli; compound eye not prominent and small; left antenna complete with 17 flagellomeres (Fig. 3A), right antenna with eight flagellomeres preserved; short setae on proximal flagellomeres; scape 0.04 mm long, pedicel 0.05 mm long; lengths of flagellomeres of left antenna: f1 0.04 mm, f2 0.04 mm, f3 0.05 mm, f4 0.07 mm, f5 0.07 mm, f6 0.06 mm, f7 0.06 mm, f8 0.07 mm, f9 0.06 mm, f10 0.07 mm, f11 0.07

mm, f12 0.04 mm, f13 0.06 mm, f14 0.06 mm, f15 0.05 mm, f16 0.04 mm, f17 0.04 mm; flagellomeres lacking secondary annulations (Fig. 3B); clypeus bulging; maxillary palps four-segmented, covered by short setae (Fig. 3C); lengths of maxillary palpomeres: I 0.02 mm, II 0.08 mm, III 0.02 mm, IV 0.07 mm; sensillum not present on second maxillary palpomere; distal maxillary palpomere globose and rounded; labial palps seemingly two-segmented, with the distal labial palpomere showing an elongate shape 0.06 mm long (Fig. 3C); a structure might correspond to lacinia. — **Thorax:** 0.46 mm long; pronotum bulging, covered by a few setae; macropterous (Fig. 2). — **Wings:** membrane hyaline with setae; forewing and hind wing with nearly the same size, surpassing the distal part of the abdomen only slightly (Fig. 1); forewing with margin covered by setae, veins with two rows of setae (Fig. 2A); hind wing glabrous (Fig. 2B). Forewing 3× longer than wide, 1.39 mm long

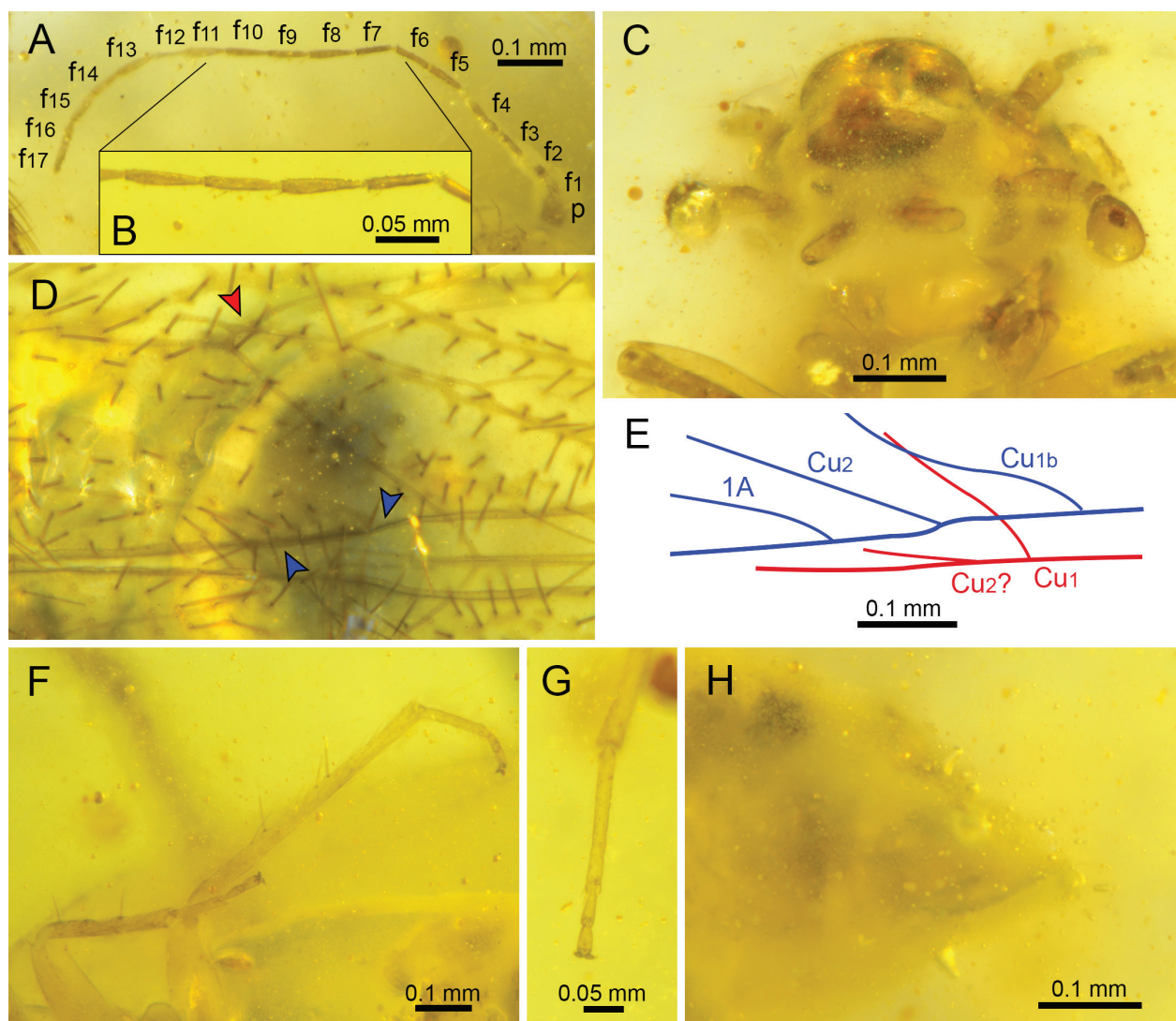


Figure 3. *Santonipsocus mimeticus* gen. et sp. nov. (Psocodea, Trogiomorpha, Empheriidae), holotype MNHN.F.A30180 (ARC-186.7), adult specimen, probably male; uppermost Albian–lowermost Cenomanian amber of Archingey-Les Nouillers (France). **A** photograph of left antenna; **B** detail of flagellomeres of left antenna; **C** head from ventral view; **D**, **E** photograph and schematic drawing, respectively, of nodulus area of right forewing, both at same scale, blue arrowheads: meeting point of veins Cu_2 and 1A with forewing margin, red arrowhead: emergence of R_1 in relation to basal cell in hind wing; **F** photograph of left midleg and hind leg; **G** photograph of tarsus of right hind leg; **H** genitalia in ventral view.

and 0.46 mm wide (Fig. 2A); basal section of Sc curved and joining R_1 at 0.60 mm from wing base, forming a narrow cell; a short, curved crossvein emerging from basal section of Sc, very close to the meeting point of Sc and R_1 , reaching margin at 0.67 mm from wing base; distal bent of basal section of Sc between emerging of crossvein and meeting point with R_1 curved, not straight or perpendicular to R_1 ; distal section of Sc separating from R_1 and joining wing margin at 1.02 mm from wing base showing a sigmoidal path; R_1 long reaching margin at 1.22 mm from wing base; basal section of Rs oblique, with crossvein between R_1 and Rs present, forming a six-angled radial cell; vein Rs+M 0.06 mm long; Rs bifurcating at 0.86 mm from wing base; R_{2+3} and R_{4+5} reaching margin at 1.34 mm and 1.37 mm from wing base, respectively; bifurcation of M_1 and M_2 at 0.90 mm from wing base, reaching margin at 1.38 mm and 1.34 mm from wing base, respectively; M_3 emerging from M at 0.65 mm from wing base and reaching margin at 1.26 mm from wing base; cells between R_{2+3} and R_{4+5} , and between M_1 and M_2 , elongate and relatively narrow; bifurcation of Cu_1 into Cu_{1a} and Cu_{1b} at 0.48 mm from wing base; elongate and narrow areola postica, with Cu_{1a} extending towards apex; Cu_{1a} and Cu_{1b} reaching margin at 1.11 mm and 0.79 mm from wing base, respectively; evanescent Cu_2 , without rows of setae, extending straight and reaching margin at 0.65 mm from wing base; vein

1A showing sigmoidal path and reaching margin at 0.56 mm from wing base; no nodulus (Fig. 3D, E); joining of Cu_2 with margin separated by 0.11 mm from joining of 1A with margin. Hind wing almost 3× longer than wide, 1.20 mm long and 0.42 mm wide (Fig. 2B); Sc not visible; basal cell closed, elongate and narrow, with three angles, 0.15 mm long and 0.03 mm wide; R_1 not emerging from apex of basal cell; R_1 fused to Rs+M for 0.03 mm; R_1 emerging from basal cell in specimen IGR.ARC-169; sigmoidal R_1 reaching margin at 0.83 mm from wing base; bifurcation of Rs into R_{2+3} and R_{4+5} at the same level as R_1 reaching margin; R_{2+3} and R_{4+5} reaching margin at 1.14 mm and 1.19 mm from wing base, respectively; cell between M_1 and M_2 elongate and narrow; M_1 and M_2 reaching margin at 1.12 mm and 0.97 mm from wing base, respectively; Cu_1 reaching margin at 0.62 mm from wing base; a vein reaching margin close to Cu_1 might correspond to Cu_2 ; anal vein not visible. — **Legs:** femora thick, without setae; tibiae thin, with three to four spines, and covered by setae; tarsi three-segmented, with first tarsomere covered by a few short setae (Fig. 3F, G); lengths of tarsomeres in foreleg: I 0.10 mm, II 0.04 mm, III 0.03 mm; lengths of tarsomeres in midleg: I 0.13 mm, II 0.03 mm, III 0.03 mm; lengths of tarsomeres in hind leg: I 0.18 mm, II 0.05 mm, III 0.04 mm; pretarsal claws lacking preapical tooth and pulvillus. — **Abdomen:** 1.03 mm long; genitalia poorly visible, although male charac-

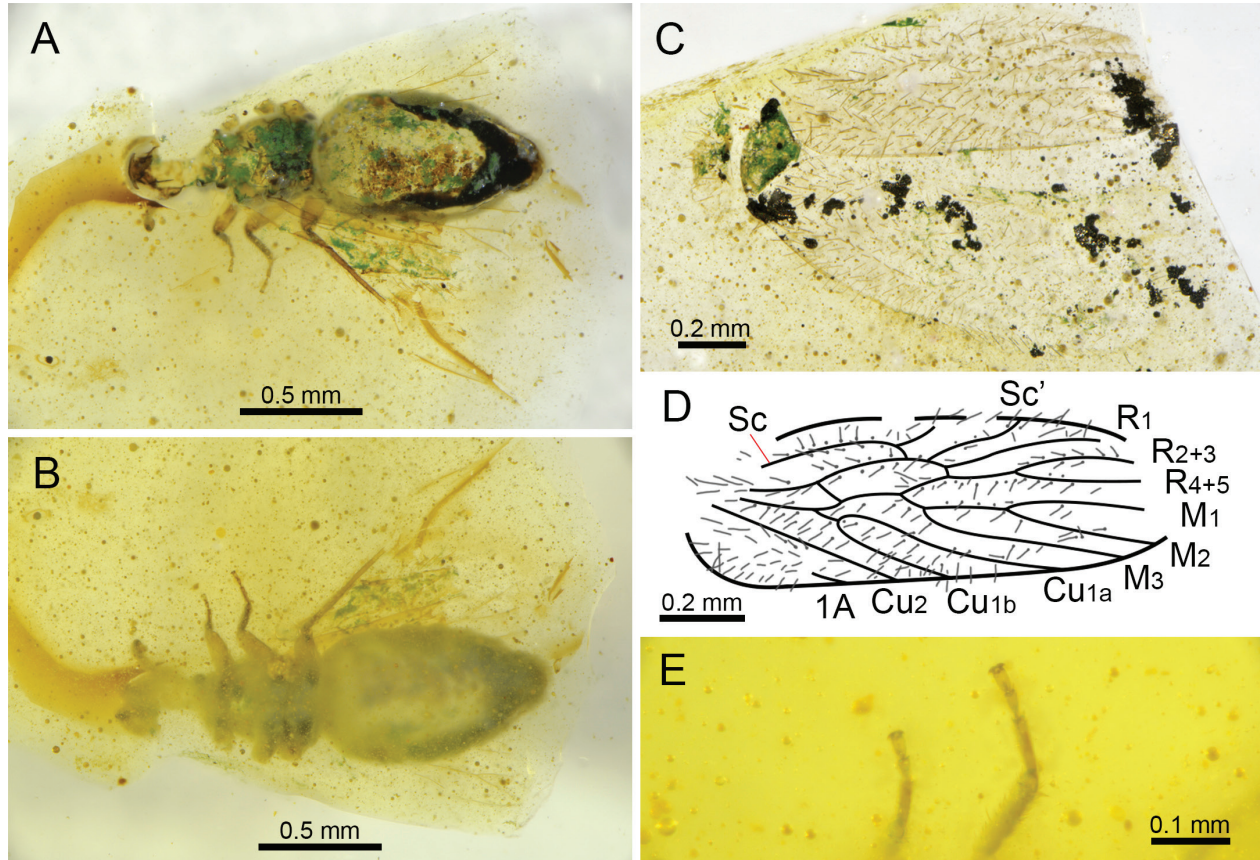


Figure 4. *Santonipsocus mimeticus* gen. et sp. nov. (Psocodea, Trogiomorpha, Empheriidae), specimen IGR.ARC-169, sex unknown; uppermost Albian–lowermost Cenomanian amber of Archingeay-Les Nouillers (France). **A** habitus from dorsal view; **B** habitus from ventral view; **C** photograph of wings; **D** schematic drawing of forewing; **E** photograph of the tarsi of right foreleg and midleg.

ters, such as hypandrium and paraprocts, are discernible (Fig. 3H).

Remarks. Although the specimen IGR.ARC-169 is poorly preserved (Fig. 4A, B), it is preliminary considered conspecific with holotype MNHN.F.A30180 (ARC-186.7) based on coincident diagnostic characters of the new genus: body length from clypeus to genitalia (1.75 mm holotype vs. 1.72 mm); distal maxillary palpomere globose and rounded; forewing with setae on margin, two rows of setae on veins, and very similar venation (Fig. 4C, D), particularly presence of a cross-vein between Sc and margin emerging very close to meeting point of Sc with R_1 , distal bent of basal section of Sc curved between emerging of crossvein and meeting point with R_1 , not straight or perpendicular to R_1 , without nodulus; and pretarsal claws lacking preapical tooth and pulvillus (Fig. 4E). The forewing venation of IGR.ARC-169 is nebulous and difficult to see, but it can be discerned using a combination of transmitted and reflected light under a stereomicroscope. We consider the distal maxillary palpomere globose and rounded and the lack of nodulus as key characters of the new genus. Two differences in wing venation can be related to intraspecific variability or ter-

atism typical in barklice (Smithers 1972): forewing with basal section of Rs placed more proximal in IGR.ARC-169 than in holotype and hind wing with four-angled basal cell in IGR.ARC-169 in comparison with three-angled basal cell in the holotype. Based on the coincident characters and the poor preservation of IGR.ARC-169, we believe that the most parsimonious option is to place this specimen, at least preliminarily, in the same species as the holotype, yet refraining from including it within the type material.

Notes on *Proprioglaris guyoti* and *Proprioglaris axioperierga*. The presence of a nodulus in forewing is confirmed for both species (Fig. 5). The species *P. guyoti* was described as possessing only one row of setae along veins in forewing (Perrichot et al. 2003). However, a detailed re-examination has allowed us to distinguish two rows of setae along veins in all the type specimens. Therefore, the diagnosis must be emended replacing “setae arranged in one row on veins” with “setae arranged in two rows on veins” in forewing. The species *P. axioperierga* was originally described with two rows of setae along veins in forewing (Azar et al. 2014).

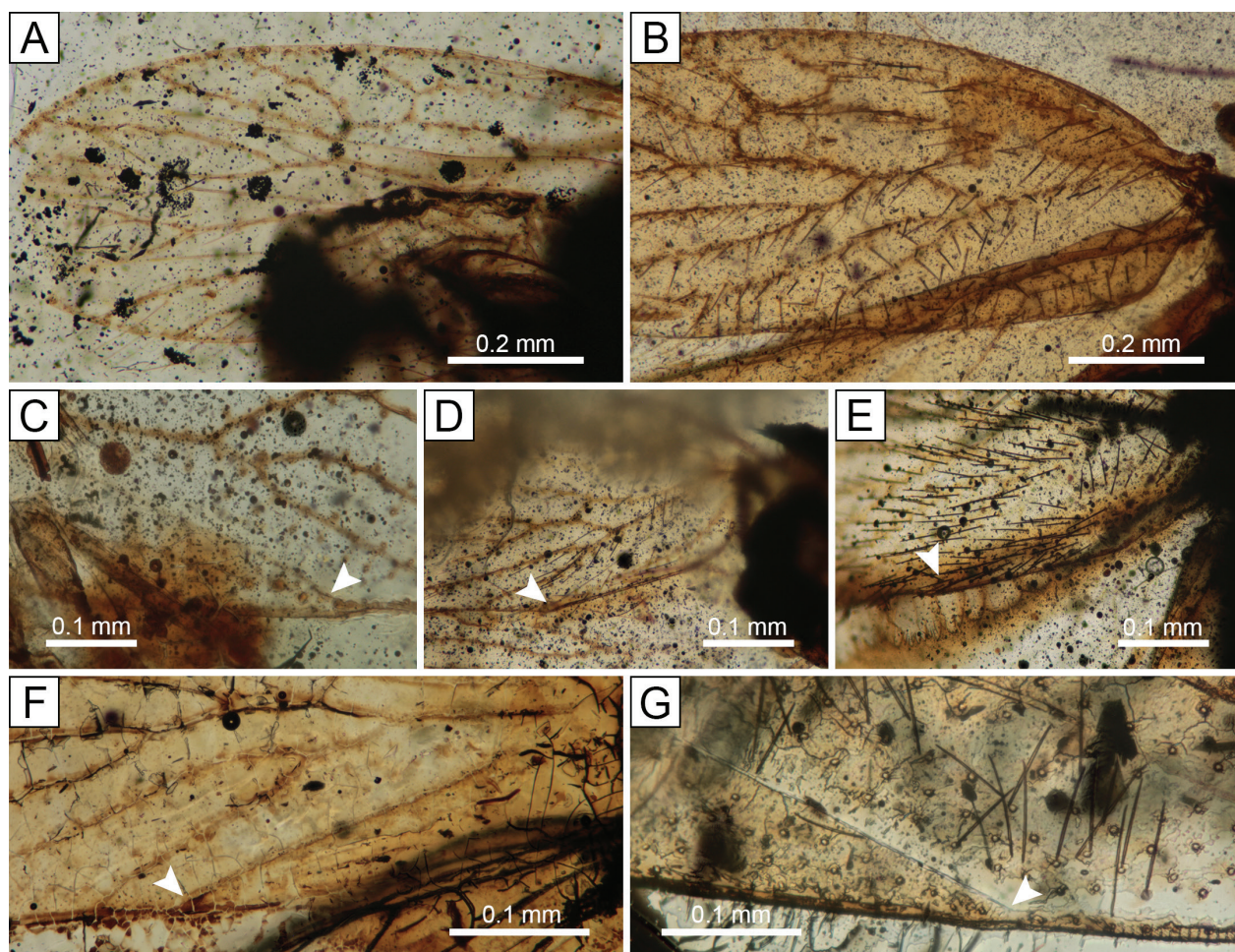


Figure 5. Forewings of *Proprioglaris guyoti* and *Proprioglaris axioperierga* (Psocodea, Trogiomorpha, Empheriidae). **A** holotype of *P. guyoti*, female, MNHN.F.A30108 (ARC 58.2 R); **B** paratype of *P. guyoti*, male, MNHN.F.A30109 (ARC 201.2); **C–E** new specimens of *P. guyoti*, sex unknown, IGR.ARC-352.1, IGR.ARC-157, and IGR.ARC-355, respectively; **F** holotype of *P. axioperierga*, female, IGR.GAR-69; **G** paratype of *P. axioperierga*, sex unknown, IGR.GAR-39. White arrowheads: nodulus.

4. Phylogenetic results

4.1. Maximum parsimony

The positions of *Brachyantennum* (incertae sedis within Trogiomorpha) and *Siamoglaris* are relatively well supported (Fig. 6A). *Brachyantennum* is not nested or associated with any family but occupies a position of sister lineage to the moderately supported clade (BS = 60) encompassing the (Psyllipsocidae + Lepidopsocidae + Trogiidae + Lepidopsocidae + Empheriidae). The genus *Siamoglaris* is found as the sister lineage to the clade (*Brachyantennum* (Psyllipsocidae + Lepidopsocidae + Trogiidae + Lepidopsocidae + Empheriidae)) (BS = 88). The monophyly of the family Trogiidae is well supported (BS = 81). The Psoquillidae are found paraphyletic with respect to the Trogiidae. The families Trogiidae and Psoquillidae are grouped in a moderately supported clade (BS = 62). The monophyly of the Lepidopsocidae is well supported (BS = 84). The monophyly of the family Empheriidae and the relationships between its constitutive genera are poorly supported (BS <50). However, the relationships between *Empheropsocus* and *Preempheria* received moderate bootstrap support (BS = 64).

4.2. Bayesian phylogenetic inference

The positions of *Brachyantennum* (incertae sedis within Trogiomorpha) and *Siamoglaris* are well supported (Fig. 6B). *Brachyantennum* is not nested or associated

with any family but occupies a position (PP = 0.99) of sister lineage to the well-supported clade encompassing the (Psyllipsocidae + Lepidopsocidae + Trogiidae + Lepidopsocidae + Empheriidae). The clade (Psyllipsocidae + Lepidopsocidae + Trogiidae + Lepidopsocidae) is well supported as the sister lineage to the Empheriidae (PP = 0.96). The genus *Siamoglaris* is found as the sister lineage to the clade (*Brachyantennum* (Psyllipsocidae + Lepidopsocidae + Trogiidae + Lepidopsocidae + Empheriidae)) (PP = 1). The monophyly of the Lepidopsocidae and Trogiidae is well supported (PP respectively = 1 and = 0.97). On the other hand, the Psoquillidae are found paraphyletic with respect to the Trogiidae (PP = 0.76). The genus *Psyllipsocus* (Psyllipsocidae) occupies a sister position to the clade (Lepidopsocidae + Psyllipsocidae + Trogiidae) but this position is poorly supported (PP = 0.6). Within the Empheriidae, the relationships between genera are poorly supported (PP between 0.06 and 0.77). The genus *Longiantennum* occupies the position of the earliest diverged genus within the family (PP = 1), followed by *Archaeatropos* (PP = 0.77). Two monophyletic clades of Empheriidae are found (PP = 0.2). The first clade presents the following topology ((*Libanoglaris* + *Setoglaris*) (*Bcharreglaris* (*Burmempheria* (*Heliadesdakruon* + *Latempheria*)))) with posterior probabilities ranging between 0.12 and 0.61. Within the second clade (PP = 0.56), *Santonipsocus mimeticus* **gen. et sp. nov.** occupies a position of early diverging taxon (PP = 0.56), then the clade (*Propionoglaris* + *Prospeleketor*) is poorly supported (PP = 0.4) and found as sister lineage to the more inclusive empherid clade encompassing ((*Jerseyempheria* (*Empheria* (*Eoempheria* + *Trichempheria*))) + (*Empherium* (*Paralellopsocus* (*Empheropsocus* + *Pre-*

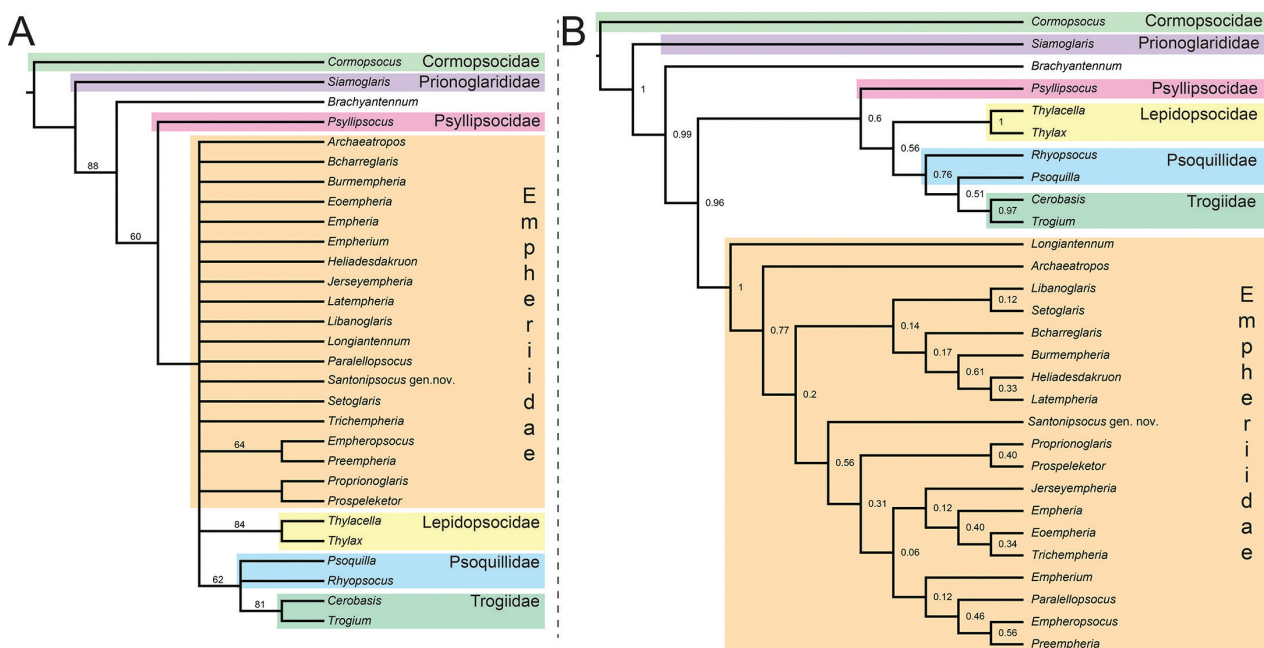


Figure 6. Phylogeny of Trogiomorpha (Psocodea), focused on Empheriidae, considering 39 characters coded for 28 ingroup taxa and one outgroup taxon (File S1; Table S1). **A** strict consensus tree based on 737 trees constructed under with parsimony analysis; (L 126 steps; consistency index 0.4286; retention index 0.5909); values at nodes represent bootstrap percentages > 50% (majority-rule consensus); **B** relationships reconstructed under Bayesian inference, constraining monophyly of Empheriidae; values at nodes represent posterior probabilities.

empheria))) (PP = 0.31). The supports for the relationships within these clades are low with posterior probabilities ranging between 0.12 and 0.56.

5. Discussion

5.1. Systematic placement of the new taxon

Santonipsocus mimeticus **gen. et sp. nov.** shows characteristics typical of the family Empheriidae (Trogiomorpha, Atropetae) (Baz and Ortuño 2001; Li et al. 2022). It is considered that members of Trogiomorpha have more than 18 flagellomeres on antennae (Smithers et al. 1972; Mockford 1993; Yoshizawa et al. 2006). However, having fewer flagellomeres, as the holotype MNHN.F.A30180 (ARC-186.7), is not sufficient to exclude a specimen from this group as a reduction of the number of flagellomeres (specialisation) is documented for some species of this suborder (e.g., Jouault et al. 2021). Mockford (1993) indicated that trogiomorphans have two-segmented labial palps with a rounded distal segment, but Yoshizawa et al. (2006) qualified this statement by indicating that the distal segment can be rounded or somewhat elongated. Interestingly, *Santonipsocus mimeticus* **gen. et sp. nov.** has an elongate distal labial palpomere (Fig. 3C), which would not be typical of the Trogiomorpha (sensu Mockford 1993).

The infraorder Atropetae is considered monophyletic based on autapomorphies related to the genitalia (Yoshizawa et al. 2006). Noteworthy characteristics of Atropetae, as noted by Smithers (1972) and Mockford (1993), include the presence of a sensillum on the second maxillary palpomere and the absence of nodulus in the forewing. However, observing the presence of the sensillum in fossil taxa can be challenging, and it is sometimes omitted in descriptions (Álvarez-Parra et al. 2022). Additionally, the presence vs. absence of a nodulus in the forewing has been found to be variable in Atropetae, particularly in fossil taxa (Li et al. 2022). It is present in some members of Empheriidae, especially in genera previously grouped under the polyphyletic group ‘Archaeatropidae.’ According to Li et al. (2022), the monophyly of Atropetae is supported by the presence of a sensillum in the second maxillary palpomere, forewing with M_{1+2} longer than the second section, long areola postica, and long and thin female external valves. *Santonipsocus mimeticus* **gen. et sp. nov.** exhibits long forewing with M_{1+2} longer than the second section and long areola postica, but it lacks sensillum in the second maxillary palpomere.

Considering the four families within Atropetae, *Santonipsocus mimeticus* **gen. et sp. nov.** can be excluded from Lepidopsocidae, Psoquillidae, and Trogiidae, but it can be included in the family Empheriidae. In the cladistics analysis conducted by Li et al. (2022), the clade (Lepidopsocidae + Psoquillidae + Trogiidae) was supported by the absence of radial cell in forewing and a

broad pulvillus. Our specimens have a radial cell and minute pulvilli precluding their placement in this clade. Similarly, the analysis supported the monophyly of the clade (Psoquillidae + Trogiidae), characterised by R_s and R_1 not being connected by a short crossvein in the forewing (Li et al. 2022). Our specimens display a well-preserved crossvein, refuting affinities with these families. Furthermore, the study suggested that the monophyly of the family Lepidopsocidae is supported by the following characters: ocelli arranged far apart, forewing pointed, body covered by scales (Li et al. 2022). In contrast, our specimens lack ocelli and scales on the body, and have rounded forewings, providing clear evidence that they do not share affinities with the Lepidopsocidae.

The placement above is further corroborated by the presence of numerous characters used to define Empheriidae or support its monophyly in cladistics analysis. These characters include: wings rounded at apex, forewing with membrane and veins setose, vein Sc well developed with a basal section long and curved joining R_1 and a distal section directed forward and reaching margin, crossvein between R_1 and R_s , Cu_1 bifurcating close to wing base resulting in a long areola postica, hind wing glabrous, and pretarsal claws without preapical tooth (Baz and Ortuño 2001; Li et al. 2022).

The forewing venation of *Santonipsocus mimeticus* **gen. et sp. nov.** is characterised by the presence of a crossvein between the basal section of Sc and wing margin, and the absence of nodulus (Cu_2 and 1A reaching margin separately). The only empheriid genera having a crossvein between the basal section of Sc and wing margin are *Burmempheria* (three species), *Empheropsocus* (two species), *Latempheria* (one species), and *Propriionoglaris* (two species), all of them also lacking preapical tooth on pretarsal claws (Baz and Ortuño 2001; Perrichot et al. 2003; Azar et al. 2014; Li et al. 2020, 2022). The genera *Burmempheria*, *Latempheria*, and *Propriionoglaris* have forewing with Cu_2 fused to 1A or joined in a nodulus (Perrichot et al. 2003; Azar et al. 2014; Li et al. 2020, 2022), while the genus *Empheropsocus* lacks vein 1A (Baz and Ortuño 2001). Therefore, *Santonipsocus mimeticus* **gen. et sp. nov.** is unique within Empheriidae, supporting its description as a new genus and species. However, the new genus has a wing venation very similar to that of the species *Empheropsocus arilloi* (from the upper Albian of Spain) and *Propriionoglaris axioperi erga* (from the Turonian amber of France). The three species show forewings with two rows of setae on veins, similar crossvein between basal section of Sc and wing margin, bifurcation of R_s (into R_{2+3} and R_{4+5}) and M (into M_1 and M_2) relatively basal and both nearly at the same level resulting in long cells, hind wing with basal cell narrow and bifurcation of R_s (into R_{2+3} and R_{4+5}) nearly at the same level as R_1 reaching margin (Baz and Ortuño 2001; Azar et al. 2014). Interestingly, the species *Empheropsocus margineglabrus* differs from the new species mainly because of its glabrous forewing margin and crossvein between the basal and distal section of Sc, as the crossvein does not reach the margin (Baz and Ortuño 2001). The species *Propriionoglaris guyoti* (from the same outcrop

as the new species) has hind wings with bifurcation of R_s distal to R_1 reaching margin (Perrichot et al. 2003).

Considering this information, it is possible that *Santonipsocus mimeticus* **gen. et sp. nov.** is related to both the genera *Empheropsocus* and *Proprionoglaris*. Additionally, within the family Empheriidae, *Empheropsocus*, and *Preempheria* are considered to form a subgroup characterised by the absence of vein 1A in the forewing (Mockford et al. 2013; Álvarez-Parra et al. 2022). However, *Santonipsocus mimeticus* **gen. et sp. nov.** has wings that only slightly extend beyond the distal part of the abdomen, which sets it apart from the genera *Empheropsocus* and *Proprionoglaris* (Baz and Ortuño 2001; Perrichot et al. 2003; Azar et al. 2014). We agree with previous authors (e.g., Li et al. 2020, 2022) that the presence or absence of a nodulus in the forewing is not a useful character for distinguishing families (as demonstrated for ‘Archaeatropidae’ and Empheriidae). However, we believe that this character is valuable for distinguishing genera. Therefore, we find it justified to describe a new genus rather than assigning the studied specimen to the genus *Proprionoglaris*. Moreover, the separation of these genera is supported by other characters, not only the presence/absence of a nodulus, which are detailed in the diagnosis of the new genus.

5.2. Phylogeny of Empheriidae

The suborder Trogiomorpha is considered monophyletic, characterised by many plesiomorphic characters and a few autapomorphies (Yoshizawa et al. 2006, 2019; Johnson et al. 2018; Yoshizawa and Lienhard 2020; de Moya et al. 2021). This suborder includes the families Cormopsocidae, Prionoglaridae, Psyllipsocidae, Empheriidae, Lepidopsocidae, Psoquillidae, and Trogiidae (Yoshizawa and Lienhard 2020; Li et al. 2022). The families Psyllipsocidae, Empheriidae, Lepidopsocidae, and Trogiidae have been considered monophyletic (Yoshizawa et al. 2006; de Moya et al. 2021; Li et al. 2022). However, the family Prionoglaridae is found paraphyletic in molecular-based phylogenies (Yoshizawa et al. 2006; de Moya et al. 2021). Further investigation is needed to explore the monophyly of the families Cormopsocidae and Psoquillidae (Yoshizawa et al. 2006; Yoshizawa and Lienhard 2020). The monophyly of the infraorder Atropetae, grouping Empheriidae, Lepidopsocidae, Psoquillidae, and Trogiidae, is well supported and placed as sister group to Psyllipsocidae (Smithers 1972; Yoshizawa et al. 2006; de Moya et al. 2021; Li et al. 2022). The relationships of the extant families within Atropetae remain uncertain, with some analyses supporting the clade (Psoquillidae (Lepidopsocidae + Trogiidae) (Yoshizawa et al. 2019; de Moya et al. 2021), while other analyses indicating an alternative topology (Lepidopsocidae (Psoquillidae + Trogiidae)) (Smithers 1972; Yoshizawa et al. 2006; Li et al. 2022). In the analysis conducted by Li et al. (2022) and our results (Fig. 6), it has been revealed that the family Psoquillidae is paraphyletic. Additionally, the enigmatic genus *Brachyantennum*, previously considered

incertae sedis within Trogiomorpha (Zhang et al. 2022), does not belong to any established family (Fig. 6). We concur with Zhang et al. (2022) that the most appropriate course of action is to refrain from describing a new family for this species until similar specimens are discovered in the future.

Most of the Cretaceous barklice species have been included in the ‘Archaeatropidae’ or Empheriidae (Cumming and Le Tirant 2021; Álvarez-Parra et al. 2022). However, the boundaries between these ‘clades’ have been considered somewhat ambiguous, primarily relying on the presence of one/two rows of setae on forewing veins and the presence/absence of nodulus in the forewing (Baz and Ortuño 2000, 2001). Recently, the validity of ‘Archaeatropidae’ as a distinct lineage has been questioned (Li et al. 2020, 2022; Álvarez-Parra et al. 2022; Liang et al. 2022), and a phylogenetic analysis has led to the synonymisation of ‘Archaeatropidae’ under the family Empheriidae, which was considered monophyletic (Li et al. 2022). However, the monophyly of Empheriidae was only supported by two characters (Li et al. 2022): (1) forewing membrane with setae, and (2) forewing veins with setae. Moreover, Li et al. (2022) did not revise the diagnosis of Empheriidae, which raises concerns about it potentially becoming a ‘waste-basket’ clade. Our own phylogenetic analyses also support the synonymisation of ‘Archaeatropidae’ under the family Empheriidae (Fig. 6).

The characterisation of the family Empheriidae poses challenges because the first species included in this family were described in old works. The species *Empheria reticulata* Hagen, 1856, found in Baltic amber, was the first to be described (Pictet-Baraban and Hagen 1856). Kolbe (1883) proposed the group ‘Empheriini’, and the name Empheriidae was introduced by Kolbe (1884). However, no formal diagnosis was provided in his work, only a general statement: “Prothorax free, distinct and somewhat elongated. Ocelli absent or present. Antennae with mostly numerous segments. Maxillary ark unequally 2 to multi-pointed” (Kolbe 1884). Subsequently, the term Empheriidae was also mentioned by Enderlein (1906) without a proper diagnosis. Roesler (1944) and Smithers (1972) regarded this taxon as a subfamily within Trogiidae. The first comprehensive diagnosis for the family Empheriidae was provided by Baz and Ortuño (2001), offering key characteristics to distinguish it from other families. Due to this historical development, it is not entirely clear if the original diagnosis of Empheriidae corresponds to the original description of *Empheria reticulata* (Pictet-Baraban and Hagen 1856), the vague characters stated by Kolbe (1884), or the diagnosis by Baz and Ortuño (2001).

Li et al. (2022) identified two characters as putative autapomorphies for Empheriidae, but it is worth noting that these characters are also found in Lepidopsocidae and Psoquillidae. Both *Thylacella* and *Thylax* display forewing membrane and veins with setae (Enderlein 1911; Smithers 1972), and similarly, *Psoquilla* and *Rhyopsocus* possess forewing veins with setae (Smithers 1972). Surprisingly, in the matrix used by Li et al. (2022), these characters were not considered for *Thylacella*, *Thylax*, *Pso-*

quilla, and *Rhyopsocus*. As a result, forewing membrane and veins with setae were labelled as autapomorphies for Empheriidae, while they should be more accurately regarded as symplesiomorphies of these related groups.

Based on the information presented and the results obtained from our MP phylogenetic analysis, where the monophyly of Empheriidae is poorly supported (Fig. 6A), it is highly probable that the Empheriidae taxon represents an evolutionary grade, rendering it a paraphyletic group. This might explain the morphological disparity of the empheriids, such as the wing venation, which hinders the identification of diagnostic characters and autapomorphies. Our MP analysis supports the monophyly of Atropetae and positions the empheriids as a grade within the rest of the Atropetae (Fig. 6A). Interestingly, Smithers (1972: 276) placed *Empheria* and *Trichempheria* (the only known empheriid genera at that time) in the Psoquillidae-Trogiidae lineage and suggested a “transformation series in which increasing wing glabrosity is achieved” for them. He also proposed that “they clearly must have arisen near the origin of the lines giving rise to the other genera of the Atropetae” and that “early psoquillids must have been *Empheria*-like” (Smithers 1972: 277). Similarly, Enderlein (1911) proposed a close relationship between empheriids and psoquillids. The Thylacellinae are a distinct group within Lepidopsocidae, characterised by a densely setose body and wings, unlike the scales found in the rest of lepidopsocids (Smithers 1972; Mockford 1993; Álvarez-Parra and Nel, 2023). Hence, we believe that the idea of an ‘empheriid grade’ in relation to the rest of Atropetae presents a plausible evolutionary hypothesis, connecting them to the thylacellines and psoquillids that diversified during the Cenozoic or possibly during the Late Cretaceous. However, to support the hypothesis that this group is paraphyletic, a broader consensus, the description of new specimens related to Empheriidae, and additional phylogenetic analyses are needed. Moreover, molecular phylogenies involving a greater number of extant representatives within Atropetae will be essential for resolving the relationships between Lepidopsocidae, Psoquillidae, and Trogiidae. For the time being, we choose to continue considering Empheriidae as a clade, but we propose a new hypothesis that may provide clearer insights into the relationships of this group in the future.

The inner relationships within Empheriidae remain poorly understood. The initial phylogenetic analysis by Li et al. (2022) considered only nine genera, placing the genus *Latempheria* as sister to the rest of the empheriids. Within the Empheriidae, they identified two clades: one comprising *Libanoglaris* and *Archaeatropos*, and the other including *Propriionoglaris*, *Prospeleketor*, *Heliadesdakruon*, *Empheria*, *Empheropsocus*, and *Burmempheria* (Li et al. 2022). In our expanded phylogenetic analyses, which include 19 empheriid genera, the inner relationships of Empheriidae receive weak support in the MP analysis (Fig. 6A). Hence, we discuss the results from the BI analysis with the constrained monophyly for Empheriidae (Fig. 6B).

Our results differ significantly from those of Li et al. (2022). We find *Longiantennum* and *Archaeatropos* oc-

cupying ‘basal’ positions within the group, and two main clades are distinguished (Fig. 6B). Interestingly, a sub-clade within the first main clade includes three empheriid genera from the lower Cenomanian Burmese amber (*Burmempheria*, *Heliadesdakruon*, and *Latempheria*). In the first main empheriid clade, we also find the genera *Libanoglaris*, *Setoglaris*, and *Bcharreglaris*, all represented in the Barremian Lebanese amber. At the ‘basal’ part of the second main empheriid clade, we have three genera from the upper Albian–Turonian French amber (*Propriionoglaris*, *Prospeleketor*, and *Santonipsocus* gen. nov.) forming a grade to the rest of the genera in this clade. *Propriionoglaris* and *Prospeleketor* are nested in a monophyletic group. The genus *Jerseyempheria* is placed as sister to a monophyletic group comprising the three known empheriid genera from the Eocene (*Empheria*, *Eoempheria*, and *Trichempheria*), characterised by the lack of the basal section of Rs in the forewing and a closed cell in the hind wing (Mockford et al. 2013). The genera *Empheropsocus* and *Preempheria*, from Albian Spanish amber, form a monophyletic group, as previously proposed based on the lack of anal vein in the forewing (Mockford et al. 2013; Álvarez-Parra et al. 2022), and form a clade together with *Empherium* and *Paralellopsocus*. These results seem plausible as they align with the biogeography of the family and support previous hypotheses regarding close relationships. Nevertheless, we consider these results as an initial step towards a better understanding of the evolution of the Empheriidae, and further discoveries and analyses are required to thoroughly test these hypotheses.

5.3. Biogeography and biology of Empheriidae

The evolutionary history of Psocodea remains poorly understood in general, primarily due to the limited representation of fossils, which are namely preserved in amber from the Cretaceous, Eocene, and Miocene periods. Other time periods are relatively depauperate, maybe because of the small sizes of these insects and taphonomic processes that affect their preservation (Álvarez-Parra et al. 2022). Fossilised barklice found in compression/imprint outcrops are rare and often poorly preserved.

The pre-Cretaceous record of barklice is a subject of debate, with some specimens mistakenly classified as other groups, such as Lophioneurida (e.g., Ansoerge 1966). When excluding the pre-Cretaceous barklice, there are only three known extinct psocodean families: Cormopsocidae, Electrentomidae, and Empheriidae. The family Cormopsocidae was recently described (Yoshizawa and Lienhard 2020) and is found to be highly diverse in lower Cenomanian Burmese amber, with three genera and seven species documented (e.g., Liang and Liu 2022). The status of the family Electrentomidae remains problematic. Some authors suggest that it includes the extant manicapsocid barklice (Mockford et al. 2013), while others choose to continue following the traditional separation of Electrentomidae and Manicapsocidae until a phylogenetic

ic study is established to support the merging (Hakim et al. 2020). In the latter scenario, Electrentomidae would consist of the genera *Paramesopsocus* (Late Jurassic and Barremian), *Electromum* (Eocene), and *Parelectromum* (Eocene). Given this context, the family Empheriidae becomes pivotal in understanding the evolution and palaeobiology of Psocodea, as it is an extinct group represented by 19 genera and 27 species found in the Early Cretaceous, Late Cretaceous, and Eocene periods. This survival of the family up to the K/Pg extinction further emphasises its significance in shedding light on the ancient history of Psocodea.

Cretaceous empheriids have a worldwide distribution, with species found in North America (New Jersey), northern Gondwana (Lebanon), Eurasia (Spain, France, and Siberia), and the Burma Terrane (Myanmar). However, Eocene empheriids are primarily restricted to Europe, as they have only been discovered in Oise, Baltic, and Rovno ambers (Álvarez-Parra et al. 2022, table 1), which correspond with the Eocene ambers richest in bioinclusions, other ambers from this age having fewer bioinclusions. The palaeoenvironments where the Cretaceous resin accumulated are believed to be transitional sedimentary environments under subtropical and temperate palaeoclimatic conditions (Delclòs et al. 2023). These inferred environmental conditions are similar to those where modern barklice are found today (New 1987), suggesting that the palaeobiology of Cretaceous empheriids may have resembled that of their living counterparts. Interestingly, the barklice fauna from Charentese amber differs from that of the Spanish amber in Iberia Island, and there is no occurrence of shared genera despite the proximity of these palaeogeographic regions during the ‘mid’-Cretaceous (Álvarez-Parra et al. 2023). The faunistic differences between French and Spanish ambers have been also observed for other insect groups (Peris et al. 2016). The palaeoclimate during the late Albian–early Cenomanian of the Charentese region was inferred as warm and humid (Néraudeau et al. 2002; Peyrot et al. 2019), while those from Iberia Island ranged from humid to arid influences (Barrón et al. 2015, 2023; Álvarez-Parra et al. 2021), and these differences are reflected in the respective botanical communities as inferred from palynoflora studies (Barrón et al. 2015). Therefore, the differences in the barklice fauna between these regions could be related to environmental factors (Álvarez-Parra et al. 2023).

The co-occurrence of Empheriidae genera in different amber outcrops is limited. There are only four known instances: (1) *Archaeatropos* in the Barremian Lebanese amber and in several Albian Spanish ambers (Álvarez-Parra et al. 2022), (2) *Libanoglaris* in the Barremian Lebanese amber and in the Albian Spanish amber (Álvarez-Parra et al. 2022), (3) *Proprioglaris* in upper Albian–lower Cenomanian Charentese amber and Turonian Vendean amber (Perrichot et al. 2003; Azar et al. 2014), and (4) *Trichempheria villosa* in Eocene Baltic and Rovno ambers (Engel and Perkovsky 2006). Consequently, biogeographic studies of empheriid barklice are challenging due to these scarce co-occurrences, and more data are needed to understand the factors influencing their distri-

bution and to determine whether they originated from Laurasian or Gondwanan regions.

It is evident that empheriids lived in forests composed of resin-producing trees of several affinities, including Araucariaceae and Cheirolepidiaceae, during the Cretaceous, and conifers and angiosperms during the Eocene. This suggests that they were likely generalists and not specific to a particular type of forest ecosystem. Moreover, polymorphism, which is common in some living barklice species (Smithers 1972), has not been detected in empheriids thus far. Recently, Hakim et al. (2023) described specimens of *Burmempheria densuschaetae* preserved in copula and specimens of *Longiantennum fashengi* Liang et al., 2022 in an alleged mating position. No sexual dimorphism has been noted for empheriids apart from a slightly smaller size of females in some species (Hakim et al. 2023).

Inferring the biology and behaviour of Empheriidae, an extinct family, poses challenges due to the lack of a comparative framework. Closest relatives such as Psocullidae and thylacelline Lepidopsocidae are typically found in leaf litter, on or under the bark of living or dead trees, and even in bird nests within tropical to subtropical environments (Smithers 1972). It is a plausible hypothesis that barklice, including empheriids, dwelled in bird nests during the Cretaceous, similarly to some living psocodean species (New 1987), but there is currently no definitive evidence supporting this hypothesis (Peñalver et al. 2023). Considering the extensive diversity and distribution of empheriids during the Cretaceous and their subsequent decline and extinction in the Cenozoic, it is possible that they occupied a particular niche within the forest ecosystems. The Cenozoic diversification of Psocomorpha implied niche competition and led them to occupy marginal habitats, much like the rest of Trogiomorpha (Álvarez-Parra et al. 2022), until their eventual extinction, which likely occurred during the Eocene–Oligocene transition due to a combination of abiotic and biotic factors (Prothero and Berggren 1992; Ivany et al. 2000).

6. Conclusions

The family Empheriidae, consisting of 19 genera and 27 species from the Early Cretaceous to the Eocene, is primarily represented in amber inclusions. It exhibited significant diversity and widespread distribution during the Cretaceous, and while some members survived the K/Pg extinction event, their numbers declined in the early Cenozoic, likely leading to their eventual extinction around the Eocene–Oligocene boundary. Currently, the phylogenetic relationships and biology of empheriid representatives remain poorly understood. They may correspond to an evolutionary grade (paraphyletic group) occupying specific niches in various forest ecosystems. However, more research is needed to thoroughly investigate the phylogeny and ecology of Empheriidae, and for now, we adopt a conservative approach and maintain it as

a family. Comprehensive phylogenetic analyses that integrate morphological data from fossil specimens and molecular data from living Trogiomorpha may shed light on the relationships between Empheriidae and other groups, as well as the internal relationships among empheriid genera. Studies of the wing venation disparity and the in-flight wing-coupling structure (nodulus) will provide important information for comparison with fossil representatives allowing us to understand their lifestyle. The observed diversity of empheriids in each amber outcrop may indicate species avoiding niche competition. Furthermore, identifying syninclusions in amber pieces containing empheriids and discovering and describing these barklice in compression outcrops will aid in unravelling the enigmatic evolutionary history of Empheriidae.

7. Competing interests

The authors have declared that no competing interests exist.

8. Author contributions

Sergio Álvarez-Parra: Conceptualization, Investigation, Methodology, Data curation, Visualization, Writing-original draft, Writing-review and editing. — **André Nel:** Investigation, Methodology, Supervision, Validation, Writing-review and editing. — **Vincent Perrichot:** Investigation, Methodology, Visualization, Validation, Writing-review and editing. — **Corentin Jouault:** Investigation, Methodology, Formal analysis, Software, Visualization, Writing-original draft, Writing-review and editing.

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Supplementary Material 1

File S1

Authors: Álvarez-Parra S, Nel A, Perrichot V, Jouault C (2024)

Data type: .pdf

Explanation notes: Description of the characters linked to the phylogenetic analyses. Modified from Li et al. (2022).

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Link: <https://doi.org/10.3897/asp.82.e114849.suppl1>

Supplementary Material 2

Table S1

Authors: Álvarez-Parra S, Nel A, Perrichot V, Jouault C (2024)

Data type: .xlsx

Explanation notes: Matrix of characters and states linked to the phylogenetic analyses. Modified from Li et al. (2022).

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