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Review of the Cretaceous †Archaeatropidae and †Empheriidae and description of a new genus and species from Burmese amber (Psocoptera)

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Mesozoic;
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amber;
new genus;
new species;
taxonomy;
description.

Abstract. – The extinct bark lice families †Archaeatropidae and †Empheriidae are considered closely related, yet distinct based upon an ever-dwindling set of morphological features. To help highlight the known variability in venation for described species, we present brief discussions for each Cretaceous species for these two families, illustrations of their wing venation, and a key to species. While reviewing Cretaceous Psocopterans belonging to †Archaeatropidae and †Empheriidae, we found a consistent wing venation pattern not yet recognized, and therefore herein describe a new genus and species of extinct bark louse which is tentatively placed within †Archaeatropidae due to many of the forewing veins having a singular row of setae (although several veins also have double setae, a feature common to †Empheriidae) from Myanmar amber of the Late Cretaceous (Cenomanian stage). *Heliadesdakruon* **gen**. **nov**. shares features with both *Archaeatropos* Baz & Ortuño, 2000 and *Bcharreglaris* Azar & Nel, 2004 but can be differentiated from these two morphologically similar genera by the forewing vein separating the two closed cells as *Heliadesdakruon* **gen**. **nov**. has the vein strongly angled so that it is parallel with the posterior wing margin (not subparallel like in *Bcharreglaris* or perpendicular like in *Archaeatropos*). Within this new genus the new species *Heliadesdakruon morganae* **gen**. **et sp**. **nov**. is described as the solely known species at the present. Additionally, the species *Archaeatropos perantiqua* (Cockrell, 1919) is illustrated from a recently collected specimen which matches the original description which was based upon a poor condition specimen. This more complete specimen allows a better understanding of the taxonomic placement, and due to the darkened pterostigma, the long and narrow wings, lack of prominent forewing setae, and the long and thin distal closed forewing cell, this species is better placed within the recently described †Cormopsocidae Yoshizawa and Lienhard, 2020, and is therefore transferred to the single present genus within the family, creating the new combination *Cormopsocus perantiqua* (Cockrell, 1919) **comb**. **nov**.

Cumming R. T. & Le Tirant S., 2021. – Review of the Cretaceous †Archaeatropidae and †Empheriidae and description of a new genus and species from Burmese amber (Psocoptera). *Faunitaxys*, 9(16): 1 – 11.

ZooBank: http://zoobank.org/5D7C6CE7-E729-4193-B33E-797F8CF8C062

Introduction

The †Empheriidae was erected by Kolbe (1884) to originally accommodate several fossil and extant species. Subsequent reexaminations of contained genera have removed extant species and now this family is considered to only contain extinct taxa (Baz and Ortuño 2000). At present this family contains six Cretaceous species (maximum age ~113.0) and four Paleogene species (minimum age ~23.03 MYA) (Li et al. 2020; Cohen et al. 2013).

The †Archaeatropidae were first described as monotypic (a single genus and species) from amber collected from Alava Province, Spain, regarded as late Cretaceous in origin (Baz and Ortuño 2000). At present, the †Archaeatropidae now contains six genera with species known from Lebanese, French, Burmese, Jordanian, and Spanish ambers (Álvarez-Parra 2020; Kaddumi, 2007). To date, the †Archaeatropidae are only known from Cretaceous deposits, ranging from the Barremian (maximum age ~129.4) to the Cenomanian (minimum age ~93.9 MYA) and are regarded as extinct (Baz and Ortuño 2000; Cohen et al. 2013). The primary feature used for differentiating these two families is the setae of the forewing veins, with †Empheriidae classified by setae along both sides of the veins versus †Archaeatropidae with a single row of setae on the vein. Due to the propensity of Psocopterans to be polymorphic and that there are several species considered to be †Archaeatropidae (*Prospeleketor albianensis* Perrichot et al., 2003 and *Proprionoglaris axioperierga* Azar et al., 2014) that actually have two rows of setae, blurs the boundaries between these families.

As more Psocopterans species are described from the Cretaceous, the characteristics that define these families are not clarifying them but are instead blurring the distinctions between them. Recently the validity of the †Archaeatropidae has been questioned with the recent description of two new †Empheriidae species from Burmese amber which included a review of the features which link and those which supposedly differentiate these two families (Li et al. 2020).

Materials and Methods

Specimens. – The amber pieces containing the specimens were collected from the well-known Hukawng Valley in northern Myanmar, a prolific site of amber excavation (Grimaldi et al. 2002). The age of this amber deposit is estimated to be ~98.79 ± 0.62 million years old, within the Cenomanian stage of the Cretaceous (Shi et al. 2012). Specimens were morphologically reviewed using a 2x-225x trinocular boom stand stereo microscope (#ZM-4TW3-FOR-20MBI3) and photographs were taken with an attached high-speed 20MP camera (#MU2003-BI-CK) (AmScope, Irvine, USA). Illumination was from below

with a 3-3/4 Inch LED square light plate (#LED-SP) (AmScope, Irvine, USA). Measurements were taken using AmLite digital camera software for Mac OS X 10.8 64-bit which was calibrated with a microscope stage calibration slide (#MR095), 0.01mm div. (AmScope, Irvine, USA). Adobe Photoshop Elements 13 (Adobe Inc., San Jose, USA) was used as post-processing software.
The holotype specimen is deposited within the Montreal Insectarium, Montreal, Quebec, Canada (IMQC). Paratype depositions are listed within the material examined section.

Illustrations. – Illustrations were done by scientific illustrator Liz Sisk (Washington D.C., USA) using the original descriptions as well as their associated illustrations in order to present the many species of †Archaeatropidae and †Empheriidae illustrated herein side-by-side. Citations for the material used are discussed within each corresponding species discussion.

Taxonomy. – Higher level taxonomic authorships follow that presented in Lienhard and Yoshizawa (2019).

Abbreviations

– **IMQC**: Insectarium de Montréal, Montréal, Québec / Canada.
– **Coll RC**: Private collection of Royce T. Cumming / U.S.A.
– **Coll SLT**: Private collection of Stéphane Le Tirant / Canada.

Results

Systematic paleontology

Order **Psocodea** Hennig, 1966

Suborder **Trogiomorpha** Roesler, 1940

Infraorder **Atropetae** Pearman, 1936

Family †**Empheriidae** Kolbe 1884

Burmempheria densuschaetae Li, Wang & Yao, 2020

(Fig. 1A)

Approximate age. – Burmese (Cretaceous, Cenomanian, ~100.5–93.9 MYA).

Discussion. – This recently described genus and two species were the first †Empheriidae described from Burmese amber. This species can immediately be differentiated from the other †Empheriidae genera by the antennae which have more than 30 segments, as all other genera have 28 or fewer (Li et al. 2020). Interestingly, this genus has a mix of setae characteristics between the †Archaeatropidae and †Empheriidae in that the forewings have both double setae rows (SC, Cu, and A) and singular setae rows (the other wing veins; Li et al. 2020).
Fig. 1A is based upon the illustration and type photos presented within Li et al. (2020) which present full views of the venation and setae.

Burmempheria raruschaetae Li, Wang & Yao, 2020

(Fig. 1B)

Approximate age. – Burmese (Cretaceous, Cenomanian, ~100.5–93.9 MYA).

Discussion. – As above for discussion on this genus. To differentiate these two species, the number of setae on the wings, head, and legs is important for differentiation as *B. raruschaetae* is marked with less setae than *B. densuschaetae*.
Fig. 1B is based upon the illustration and type photos presented within Li et al. (2020) which present full views of the venation and setae.

Empheropsocus arilloi Baz & Ortuño, 2001

(Fig. 1C)

Approximate age. – Spanish (Albian, ~113.0–100.5 MYA).

Discussion. – This species is the type species for the genus and is considered closely related to its sister species below.
Fig. 1C is based upon the illustration within the original description which presents a nearly complete set of wings (Baz & Ortuño, 2001), the base of both the forewing and the hindwing are estimated within our illustration. Our hindwing illustration (Fig. 1C) is based upon the illustrations presented of two type specimens (MCNA-8814 and MCNA-9731) and is therefore a composite image.

Empheropsocus margineglabrus Baz & Ortuño, 2001

(Fig. 1D)

Approximate age. – Spanish (Albian, ~113.0–100.5 MYA).

Discussion. – The only features given for differentiation of these two species was the difference in setae intensity along the forewing margin and that in *E. margineglabrus* the Sc' reaches to the Sc forming a polygonal cell, instead of reaching to the wing margin as in *E. arilloi*.
Fig. 1D is based upon the illustration within the original description which presents a dorsal habitus without setae (to allow better view of the veins) and upon an illustration with setae included (Baz & Ortuño, 2001).

Jerseyempheria grimaldii Azar, Nel & Petrulevicius, 2010

(Fig. 1E)

Approximate age. – New Jersey (Turonian, ~93.9–89.8 MYA).

Discussion. – This genus is unique among the †Empheriidae by having the membrane between the forewing veins setose, not the veins themselves. The lack of setae along the wing veins gives yet another difficult feature for differentiating the †Archaeatropidae from the †Empheriidae based on the setation of the forewings.
Fig. 1E is based upon the illustration presented within Azar et al. (2010) which presents a full view of the venation and setae clearly.

Preempheria antiqua Baz & Ortuño, 2001

(Fig. 1F)

Approximate age. – Spanish (Albian, ~113.0–100.5 MYA).

Discussion. – This monotypic genus was noted as being morphologically similar to *Empheria* Pictet-Baraban & Hagen, 1856 but notably differing in several aspects; having the forewing basal portion of the Sc setose, a crossvein from R1 to Rs, and a basiradial cell in the hindwing (Baz and Ortuño 2001). Mockford et al. (2013) regarded this genus and *Empheropsocus* as closely related or possibly synonyms.
Fig. 1F is based upon several type specimen illustrations from Baz and Ortuño (2001) and is a composite image (based upon specimens MCNA-8888 and MCNA-8872) due to the apparent slightly aberrant form of some of the veins in specimen MCNA-8888 (such as the Sc). Additionally, the base of the hindwing was not illustrated due to the condition of the specimens so our illustration includes an estimate of what the base might look like (appearing in dashed lines).

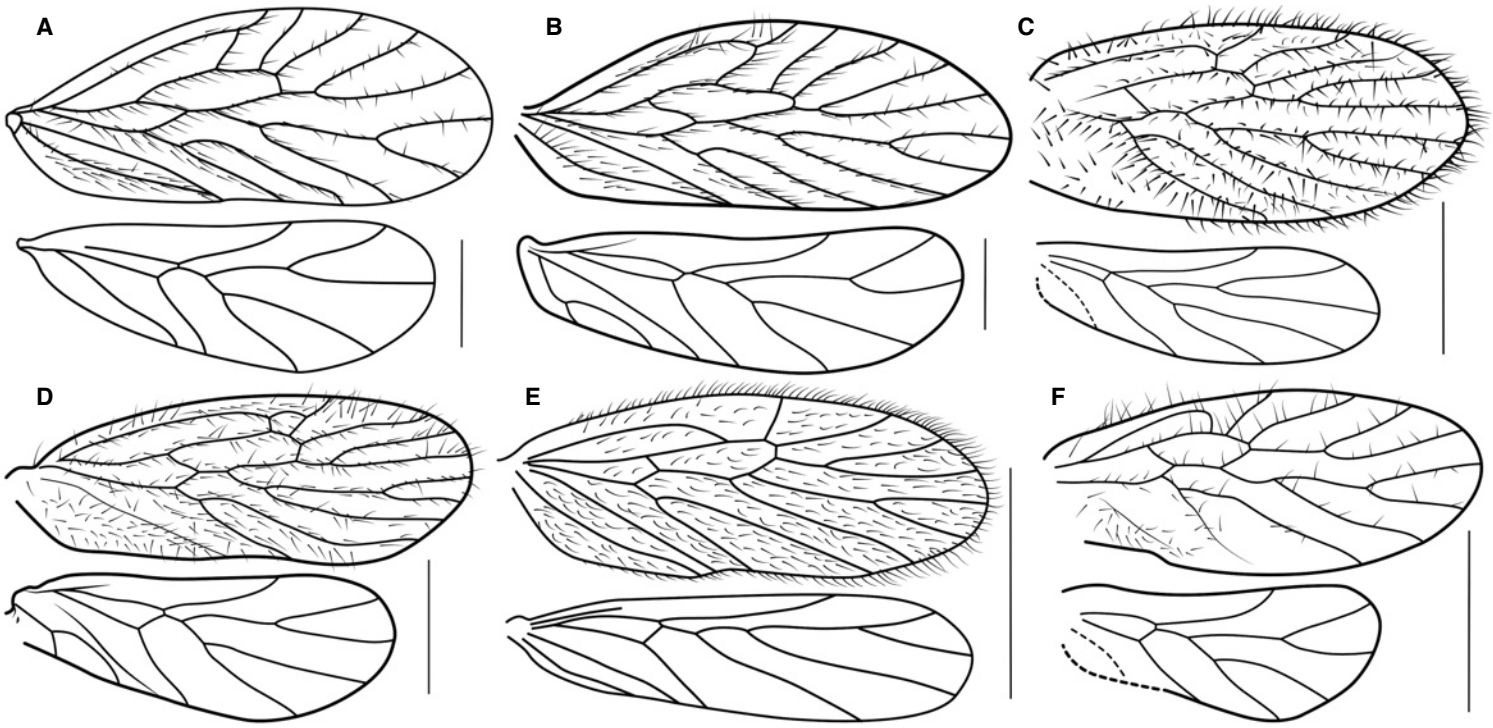

Fig. **1**. Cretaceous †Empheriidae wing venation. All scale bars 0.5 mm.
– **A**: *Burmempheria densuschaetae*. – **B**: *Burmempheria raruschaetae*. – **C**: *Empheropsocus arilloi*. – **D**: *Empheropsocus margineglabrus*.
– **E**: *Jerseyempheria grimaldii*. – **F**: *Preempheria antiqua.*

Order **Psocodea** Hennig, 1966

Suborder **Trogiomorpha** Roesler, 1940

Infraorder **Atropetae** Pearman, 1936

Family †**Archaeatropidae** Baz & Ortuño, 2000

Archaeatropos alavensis Baz & Ortuño 2000
(Fig. 6E)

Approximate age. – Spanish (Albian, ~113.0–100.5 MYA).

Discussion. – This is the type species of this genus and family. It has the interesting character of having the margin of the hindwing with dense setae along most of the margins, a feature that appears to not be present in any of the other Cretaceous †Archaeatropidae and †Empheriidae species (even those that are notably more heavily marked by setae).
Fig. 6E is based upon the illustration presented within Baz and Ortuño (2000) which presents a full view of the venation and setae clearly.

Archaeatropos randatae (Azar & Nel 2004)
(Fig. 6I)

Approximate age. – Lebanese (Barremian, ~129.4–125.0 MYA).

Discussion. – This species was originally described within *Libanoglaris* but was transferred to *Archaeatropos* by Mockford et al. (2013) due to the angle of the Sc' pointing towards the wing base, not the apex. Mockford et al. (2013) considered this feature a possible autapomorphy for the genus.
Fig. 6I is based upon the illustrations and figures presented within Azar and Nel (2004) which presents a full view of the venation and setae clearly.

Bcharreglaris amooni Kaddumi, 2007

Approximate age. – Jordanian (Albian, ~113.0–100.5 MYA).

Discussion. – This species and *Bcharreglaris haddadini* were not included within Álvarez-Parra (2020) checklist of Cretaceous Psocodea and are not currently listed within the Psocodea Species File Online (Johnson et al. 2021) and we wonder if these authors were simply unaware of the original description. Our own search for the original description of this species turned up fruitless and we hope that eventually this work and the specimens can be reviewed.

Bcharreglaris amunobi Azar & Nel, 2004
(Fig. 6D)

Approximate age. – Lebanese (Barremian, ~129.4–125.0 MYA).

Discussion. – This genus was originally monotypic based upon two specimens preserved in Lebanese amber. This species is unique in that in the forewing the Sc' reaches R1 at the same point as the R1 to Rs crossvein, which gives the closed radial cell six sides instead of the more common seven (due to the more typical Sc' not meeting at the same point).
Fig. 6D is based upon the illustrations and figures presented within Azar and Nel (2004) which presents a full view of the venation and setae clearly.

Bcharreglaris haddadini Kaddumi, 2007

Approximate age. – Jordanian (Albian, ~113.0–100.5 MYA).

Discussion. – See our discussion on *Bcharreglaris amooni* above discussing the mystery surrounding this species.

Heliadesdakruon Cumming & Le Tirant **gen**. **nov**.

ZooBank : http://zoobank.org/15C16020-E1E0-441B-9409-CA33FA508EC1

Type species: *Heliadesdakruon morganae* Cumming & Le Tirant **gen**. **et sp**. **nov**.

Type locality and horizon. – At present we are only aware of this genus being found in Myanmar amber from the Upper Cretaceous ~98.79 ± 0.62 million years old (Shi et al. 2012).

Diagnosis. – Antennae with 25 flagellomeres (27 antennomeres with two setae protruding from the distal end of each segment); fourth maxillary palp palpomere and second palpomere approximately the same length; wings hyaline with most cells lacking setae (only the cells around 1A in the forewing with notable setae present) and no obvious coloration of the wing membranes preserved; forewing with Sc running parallel with the anterior margin and then angling strongly backward and reaching the distal closed cell therefore Sc does not reach the wing margin (only Sc'); forewing proximal and distal cells elongated, approximately the same length, and each with a length at least three times longer than wide with the vein between the cells running parallel with the wing; forewing anal area covered with thin setae; all forewing veins with setae (either with setae on each side of the vein or singularly along the vein) only Cu2 is bare without setae; hindwing with a three or four-sided cell; hindwing lacking setae; tarsi three-segmented; first tarsal segment with ventral stout setae.

Differentiation. – Within the †Archaeatropidae *Heliadesdakruon* **gen**. **nov**. shares many morphological features with *Archaeatropos* Baz & Ortuño, 2000 (from Lebanese and Spanish amber) and *Bcharreglaris* Azar & Nel, 2004 (from Lebanese and Jordanian amber).
A feature which likens this new genus and *Archaeatropos* is the forewing vein Sc' not reaching R1 at the same point as the crossvein joining R1 to Rs, therefore giving the distal closed cell a seven-sided shape (versus *Bcharreglaris* which has these veins meeting at the same location, therefore giving the forewing distal closed cell a six-sided shape). *Heliadesdakruon* **gen**. **nov**. can easily be differentiated from *Archaeatropos* by the lack of setae along the hindwing margin, a feature which differentiates *Archaeatropos* from all other species within the family.
A feature which likens this new genus and *Bcharreglaris* is the forewing vein between the two closed cells is acutely angled (versus *Archaeatropos* which has this vein between the closed cells running perpendicular to the posterior wing margin). Additionally, *Heliadesdakruon* **gen**. **nov**. has similar forewing setation along the 1A vein in the cells around the vein (versus *Archaeatropos* which has the setae sparse, only along the 1A, not in the adjacent cells).
Heliadesdakruon **gen**. **nov**. can be differentiated from these two morphologically similar genera by the forewing vein separating the two closed cells as *Heliadesdakruon* **gen**. **nov**. has the vein strongly angled so that it is parallel with the posterior wing margin (not subparallel like in *Bcharreglaris* or perpendicular like in *Archaeatropos*) and can be differentiated from these two genera individually by the above discussed features.

Etymology. – Greek. Combination of Heliades (Ηλιάδες) meaning "children of the sun" and dakruon (δάκρυον) meaning "a teardrop". This name was chosen as reference to the ancient Greek mythology surrounding amber. Amber was said to be the tears of the Heliades sisters who wept greatly at the death of their brother Phaëthon who had attempted to drive Helios' sun chariot for a day, but he was unable to control the horses and Zeus struck it down in order to prevent disaster. This new genus name is neuter in gender following "dakruon".

Heliadesdakruon morganae Cumming & Le Tirant **gen**. **et sp**. **nov**.

(Fig. 2A-E, 3A-C, 4, 5A-F)

ZooBank : http://zoobank.org/94CA77F2-B724-4079-B946-474A6A910EE0

Holotype, ♀(?). – Amber specimen IMQC-BA-003 from northern Myanmar (Fig. 2). Partially complete yet well-preserved specimen which appears to be female (although the genitalia are partially damaged, so it is difficult to tell with confidence). Right wings well-preserved with only slight damage to the setae on the forewing, left wings with heavier damage. Right antennae fully preserved, left damaged with several segments missing. All legs well-preserved. Dorsal surface of head, thorax, and abdomen missing. Deposited in the Montreal Insectarium (IMQC). Amber piece containing the holotype also has a bristletail (Archaeognatha) inclusion, is roundly rectangular (21 by 11 mm), 1.34 grams, and with good visibility.

Paratypes [1 ♀; 16 undeterminable sex].

– IMQC-BA-007, amber specimen 0.9 grams, complete unsexed specimen, slight abdominal damage (Coll RC), Fig. 5A;

– IMQC-BA-006, amber specimen 0.55 grams, heavily damaged right wings, body and left wings decently preserved (Coll RC), Fig. 5B;

– IMQC-BA-008, amber specimen 3.43 grams, well preserved, only slight damage to the left antennae (Coll SLT), Fig. 5C;

– IMQC-BA-001, amber specimen 0.64 grams, damaged left wing tips and abdomen, remainder of the specimen is in good condition (Coll RC), Fig. 5D;

– IMQC-BA-002, amber specimen 1.8 grams, some leg damage and abdomen shriveled, all setae from forewings pulled off to one side of the specimen (Coll SLT), Fig. 5E;

– IMQC-BA-005, amber specimen 0.69 grams, one full, well-preserved specimen and one set of wings and a partial abdomen of a second close to the first (Coll SLT), Fig. 5F;

– IMQC-BA-034, amber specimen 1.14 grams, female specimen, well preserved with all setae and appendages intact (Coll RC), Fig. 3;

– IMQC-BA-015, amber specimen 0.13 grams, well-preserved but slight leg and abdomen damage (Coll RC);

– IMQC-BA-017, amber specimen 0.86 grams, well-preserved but slight damage to the setae on the forewings (Coll RC);

– IMQC-BA-021, amber specimen 0.45 grams, heavily damaged, missing legs, tip of abdomen, and antennae (Coll RC);

– IMQC-BA-024, amber specimen 0.38 grams, well-preserved but slight damage to right legs (Coll RC);

– IMQC-BA-025, amber specimen 0.44 grams, well-preserved only the tips of antennae missing (Coll RC);

– IMQC-BA-026, amber specimen 0.49 grams, well-preserved but slight damage to right legs (Coll RC);

– IMQC-BA-028, amber specimen 0.47 grams, well-preserved but with heavy damage to the abdomen and slight damage to the wings (Coll RC);

– IMQC-BA-030, amber specimen 0.91 grams, well-preserved no apparent missing limbs (Coll RC);

– IMQC-BA-035, amber specimen 0.93 grams, well-preserved but missing abdomen (Coll RC);

– IMQC-BA-036, amber specimen 1.18 grams, well-preserved but with abdomen damage (Coll RC).

Discussion. – At present this is the only species known from this genus. For differentiation from other known Cretaceous species see the above genus differentiation.

Type locality and horizon. – All type specimens are from Kachin State, Myanmar; Upper Cretaceous ~98.79 ± 0.62 million years old (Shi et al. 2012). At present we are only aware of this species being found in Myanmar amber from the Cretaceous.

Morphological description.

Morphology. – Description based upon the type specimens, see below discussion on intraspecific variation observed within paratypes. Measurements noted within are of the holotype specimen, all paratypes of a similar size with little variability.

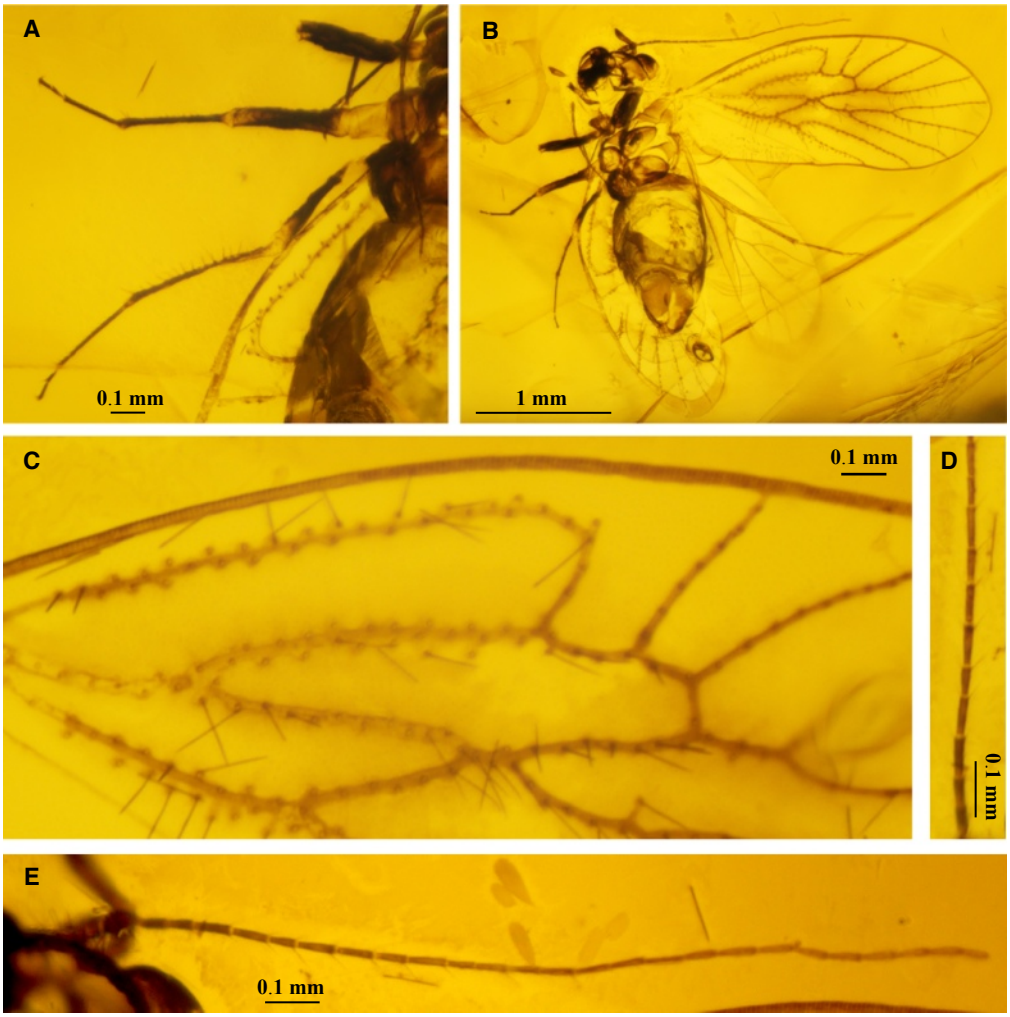

Fig. **2**. Holotype *Heliadesdakruon morganae* **gen**. **et sp**. **nov**., IMQC-BA-003.
– **A**: Detail of the meso- and meta- legs, dorsolateral view. – **B**: Habitus, dorsal view (note that the dorsal surface is gone so the ventral details are visible so the specimen appears to be viewed from the ventral surface). – **C**: Details of the forewing, note the margin segmented texture, the veins with setae on each side, and the veins with a singular set of setae along them, dorsal view. – **D**: Details of the right antenna basal segments, dorsal. – **E**: Right antenna in full, dorsal.

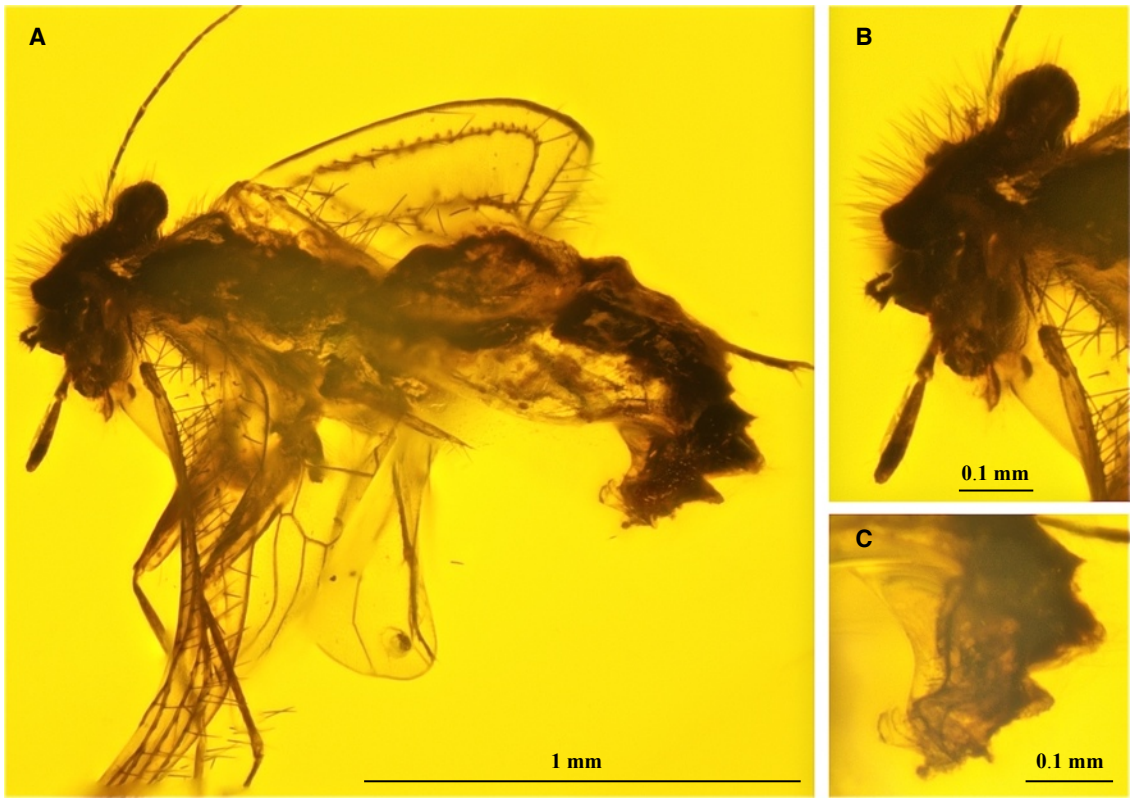

Fig. **3**. Paratype *Heliadesdakruon morganae* **gen**. **et sp**. **nov**. female, IMQC-BA-034.
– **A**: Habitus, lateral. – **B**: Details of the head, lateral. – **C**: Details of genitalia, lateral.

Head. – Roundly triangular head, maximum width 0.63 mm. Head with two prominently protruding spherical compound eyes, maximum diameter 0.15 mm; with three ocelli centrally located between them and slightly protruding from the head capsule (Fig. 3B). Head capsule densely covered with numerous setae, each approximately 0.1 mm long (Fig. 3B). Anterior with prominent, gibbous postclypeus; labial palps short with few setae at the tips (Fig. 3B); maxillary palps four-segmented, first 0.03 mm, second 0.13 mm, third 0.06 mm, fourth 0.11 mm, fourth palpomere with round apex and only slightly clavate. Antennae with 25 flagellomeres (27 antennomeres), 1.73 mm long (Fig. 2E), segments bare except for two fine setae protruding from the apex of each segment (Fig. 2D); scape and pedicel mostly bare, with only a few short and thin setae near their distal ends.

Thorax. – Thorax heavily damaged in the holotype, in the paratypes which are well-preserved the pronotum is distinctly triangular and smooth, lacking distinct features. Pronotum appears approximately level with the head, mesonotum raised slightly, and metanotum lowered.

Wings. – Forewing and hindwings hyaline. Forewing length 2.32 mm and maximum width 0.96 mm (Fig. 2B), all cells transparent. Costa thickened, about two times as thick as any of the internal veins, and with a ribbed texture throughout its length, occasionally up to four setae can be found on the basal half of the wing's costa, but not always present (Fig. 2C). Subcosta running parallel with the costa until the midline of the wing, at which point it abruptly bends acutely and connects with the distal closed forewing cell, not reaching the wing margin (Fig. 4). Subcosta with setae on each side of the vein for most of the length but following the acute bend the vein has a singular line of setae along it (Fig. 2C). A continuation of the subcosta (Sc') runs from the distal closed cell to the wing margin, reaching the costa at a perpendicular or slightly sub-perpendicular angle (0.32 mm); marked with a singular line of setae along the vein (Fig. 2C). Pterostigma of similar color and form as the rest of the wing, bounded by Sc' and R1 with the broad costal end approximately two times the width of the internal side (Fig. 4). Closed forewing cells of similar lengths and widths, both more than three times longer than wide, with the vein separating them running parallel with the wing giving these cells an acute meeting point (Fig. 4). The proximal cell is four-sided, and the distal cell is seven-sided with the veins making up these cells marked by double setae or singular setae (Fig. 2C). First radial (R1) emerges from the closed distal cell near the distal most end approximately 0.1 mm from where Sc' emerges and runs slightly diverging away from Sc', resulting in a slightly longer R1 than Sc' (0.48 mm and 0.32 mm respectively); R1 is marked with a singular line of setae. R2+3+4+5 emerges from the distal end of the distal closed cell and runs for 0.13 mm before splitting into the R2+3 and R4+5. R2+3 runs straight to the wing margin without strongly curving (0.57 mm), R4+5 slightly curved on the proximal quarter of the length, then straightens and runs to the wing margin (0.72 mm). All radial veins are marked with a single line of setae. The media and first cubitus (M + Cu1) is marked with setae on each side of the vein and runs from the wing base for 0.65 mm then splits into M and Cu1a+b; the media runs upward for 0.27 mm and connects with the distal closed cell near the middle of the cell, and the media is marked with a single line of setae. The media branches from the closed distal cell about three fifths of the way through and runs for 0.26 mm before splitting into the M1+2 and M3 (with M3 running slightly undulating, not perfectly straight to the wing margin; length 0.76 mm). M1+2 runs for 0.30 mm then splits into the M1 and M2 which run steadily diverging to the wing apex (0.70 mm and 0.65 mm long respectively). All medial veins are marked with a single line of setae. Cu1a+b is marked with double setae and splits into Cu1a and Cu1b 0.18 mm from where it split from the media. Cu1a is longer than Cu1b (0.88 mm and 0.55 mm respectively); Cu1a bends immediately and then runs straight to the margin and is marked with a single line of setae, Cu1b runs straight from the branching point to the wing margin and is doubly marked with setae. The second cubitus (Cu2) is 1.07 mm long, is the only vein which is not marked with setae, and it runs straight from the wing base to the margin. The first anal is incredibly faint and in most specimens could not be seen, it appears to run slightly arcing from the wing base to end near where Cu2 does on the wing margin. It is made more difficult to see due to the anal wing area being heavily marked by thin setae. Hindwing paddle-shaped; transparent; 1.79 mm long and a maximum width of 0.60 mm; margins thin, lacking setae, and texture; all veins are bare, not marked with setae. The first radial (R1) arcs upward, reaching the wing margin 1.23 mm from the wing base. The closed central cell is three or four-sided (sometimes the distal end has a short, blunted end (Fig. 4) or can end with a point (Fig. 2B)), the cell is narrow at the base and steadily broadens until about four fifths of the way through its length. R2+3+4+5 and M run fused from the closed cell for 0.09 mm then bifurcate. The radial splits about halfway through its length into the R2+3 and R4+5 which run to the wing margin slightly diverging from each other, with lengths 0.52 mm and 0.58 mm, respectively. The media (M) runs for 0.14 mm before splitting into M1 and M2; M1 is curved very slightly originally but then runs straight to the margin with a length of 0.63 mm; M2 is slightly sigmoidal until joining the wing margin with a length of 0.45 mm. M + Cu1 runs fused for 0.27 mm before splitting, at which point Cu1 runs gently arcing to the wing margin with a length of 0.49 mm. Cu2 arcing smoothly, reaching the wing margin with a length of 0.62 mm. Anal veins not visible in any specimens, it appears as though any anal veins are very thin and transparent.

Legs. – Femora thick and approximately as long as the tibiae; tibiae half as thick as the femora and about as long, except the metatibiae which is slightly longer than the metafemora. All tibiae with two distinct lateral spurs on the distal ends (Fig. 2A), the spurs on the pro- and mesotibiae are distinctly longer than the setae along the tibiae lengths, but the setae along the metatibiae are approximately as long as the lateral distal spurs (Fig. 2A). The tibiae setae are double rowed and uniformly spaced (Fig. 2A). Tarsi three-segmented; basitarsi distinctly longer than the other tarsi (as much as four times as long) and marked with ventral short setae. Terminal tarsomere with two pretarsal claws and appearing to lack a preapical tooth (Fig. 2A).

Abdomen. – Abdomen approximately 1.15 mm long with segments distinctly visible. Female genitalia on paratype specimen IMQC-BA-034 well-preserved with subgenital plate smooth, external valvulae J-shaped and marked with slight setae (Fig. 3C).

Intraspecific variation. – In addition to the holotype, 17 paratypes were examined from the same deposit. For Pscopids it is often noted that between the left and right side of a specimen and oftentimes intraspecifically the wing venation can differ drastically (Cockrell 1919). Interestingly, we did not find this trend within our rather significant paratype sampling with venation present rather stable.

The only subtle differences we observed within the series were slight differences in setae on the tibiae (with some specimens with evenly spaced and sized setae and some with fewer, but this could be due to damage to the rather small setae) and several specimens with a slight difference in the hindwing venation with the radial veins not splitting from the closed central cell immediately but originating from a small crossvein (for example see the hindwings in Fig. 2B, 5A). All other examined specimens were quite stable in their morphology for these veins, so we have illustrated the most common morphology encountered (Fig. 4).

Etymology. – Patronym, named to thank Morgan Brock-Smith, partner to the first author, for her years of love and support of the first author's passion for entomology.

Libanoglaris chehabi Azar & Nel, 2004

(Fig. 6H)

Approximate age. – Lebanese (Barremian/Aptian, ~129.4–113.0 MYA).

Discussion. – This species can easily be identified from its congeneric *L. mouawadi* by the presence of three setae in the pterostigmal cell (a feature which is not wholly unique as other species such as *Archaeatropos randatae* also have a similar ornamentation in the pterostigmal cell; Fig. 6I).

Fig. 6H is based upon the illustrations and figures presented within Azar and Nel (2004) which presents a full view of the venation and setae clearly.

Libanoglaris mouawadi **Azar** Perrichot, Néraudeau & Nel, 2003

(Fig. 6G)

Approximate age. – Lebanese (Barremian/Aptian, ~129.4–113.0 MYA).

Discussion. – This genus and species was originally tentatively

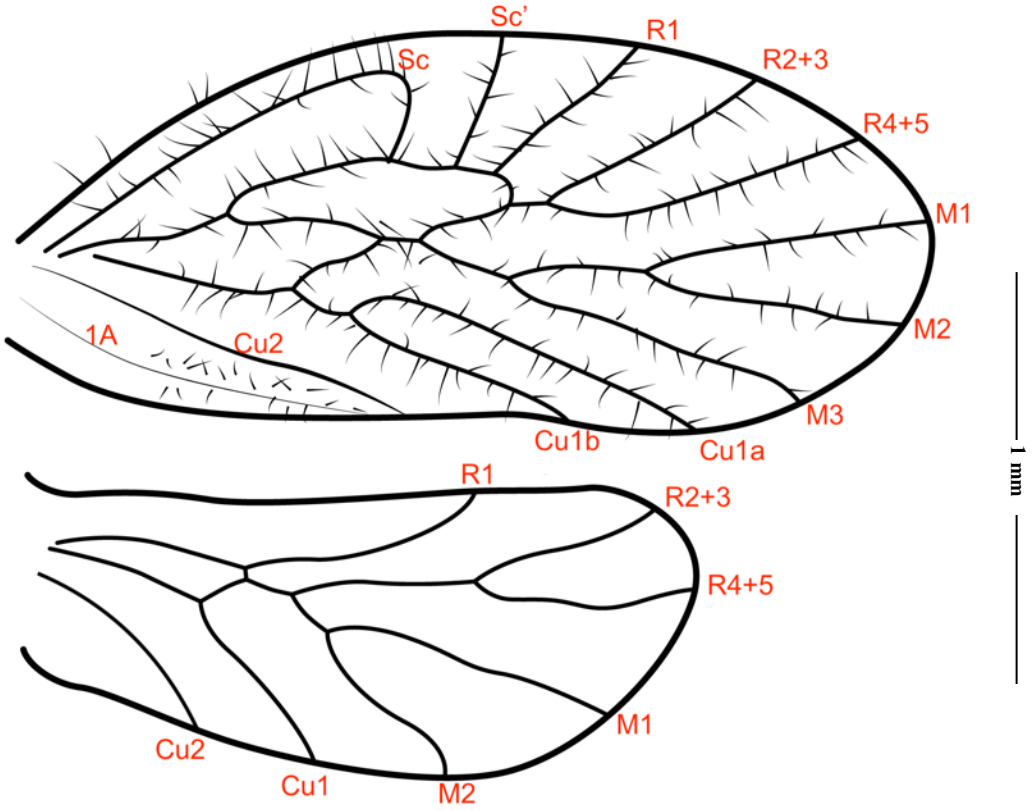

Fig. **4**. Wing venation for *Heliadesdakruon morganae* **gen**. **et sp**. **nov**. based upon type material.

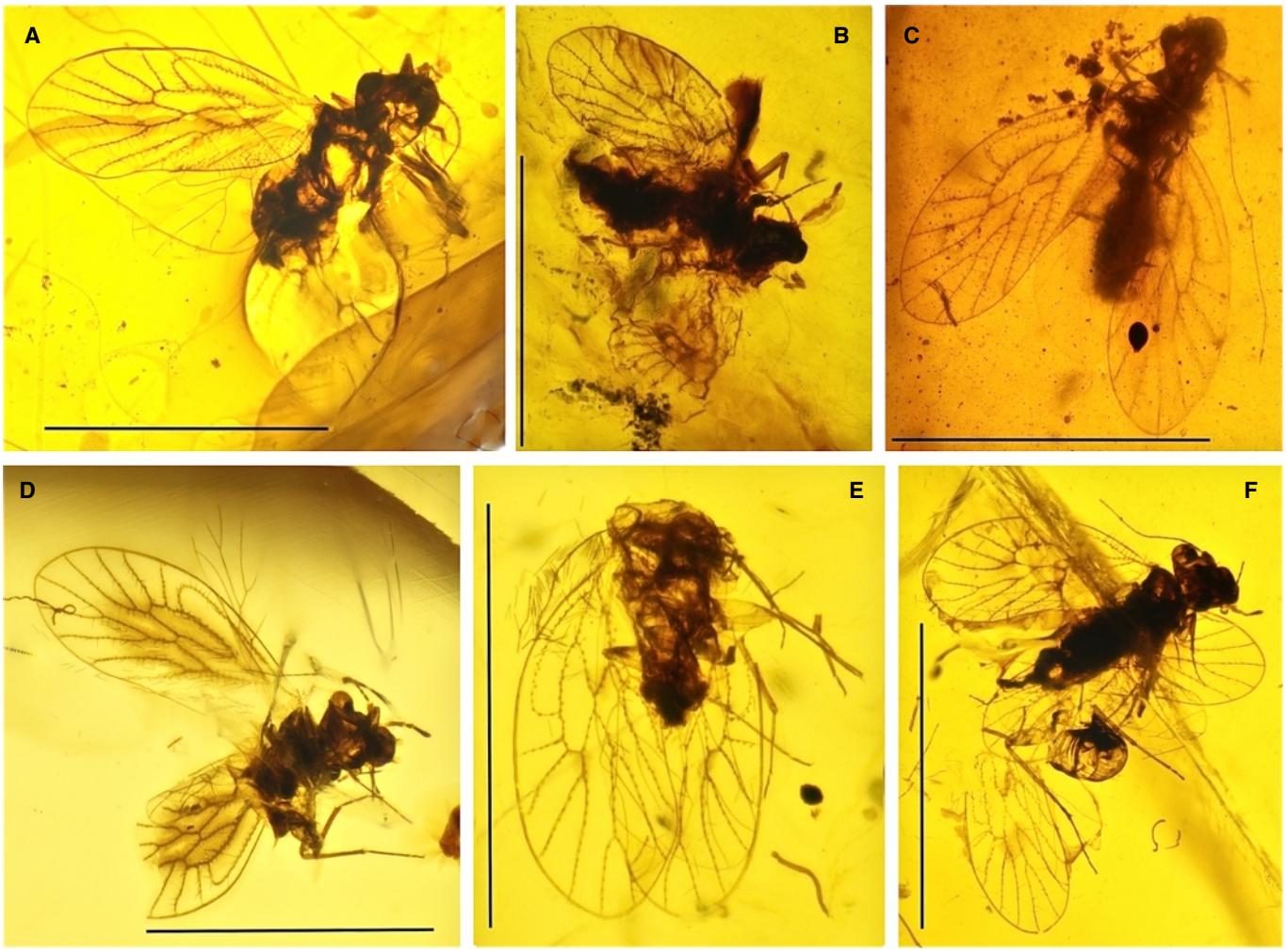

Fig. **5**. Select *Heliadesdakruon morganae* **gen**. **et sp**. **nov**. paratypes. All scale bars 2.0 mm.
– **A**: IMQC-BA-007, dorsal. – **B**: IMQC-BA-006, dorsal. – **C**: IMQC-BA-008, dorsal. – **D**: IMQC-BA-001, ventral.
– **E**: IMQC-BA-002, ventra. – **F**: IMQC-BA-005, ventral.

placed within Prionoglarididae or †Archaeatropidae according to Perrichot et al. (2003) but was latter move to †Archaeatropidae by Mockford et al. (2013) due to multiple features (see page 6 in Mockford et al. (2013) for the long list of features). Additionally, discussed was the presence of the nodulus in the forewing which has been considered a diagnostic feature for differentiation of †Archaeatropidae from †Empheriidae (Baz and Ortuño 2000) but within more recent reviews of Trogiomorpha this feature has been questioned as some clades are variable in their presence or absence of this feature (Wang et al. 2019).
Fig. 6G is based upon the illustrations and figures presented within Perrichot et al. (2003) which presents a full view of the venation and setae clearly.

Proprionoglaris axioperierga Azar, Nel & Perrichot, 2015
(Fig. 6A)

Approximate age. – French (Albian/Cenomanian, ~113.0–93.9).

Discussion. – Azar et al. (2015) followed the placement of this genus within †Archaeatropidae as was proposed by Mockford et al. (2013), but Azar et al. (2015) emphasized that further review is necessary in order to confidently place this genus. Interestingly, its sister species (*P. guyoti*) has the typical setae of †Archaeatropidae, but this species on many of the forewing veins has two rows of setae (indicating possible †Empheriidae). It is likely these mixing of features within a single genus which leads to the uncertainty on the uniqueness of these families.
Fig. 6A is based upon the illustrations and figures presented within Azar et al. (2015) which presents a full view of the venation and setae relatively clearly, with only certain portions of the wings obscured due to debris on the specimens.

Proprionoglaris guyoti Perrichot, Azar, Néraudeau & Nel, 2003
(Fig. 6B)

Approximate age. – French (Albian/Cenomanian, ~113.0–93.9).

Discussion. – See above discussion for the placement of this genus. This species can be differentiated from its sister species by the notable difference in size (3.0 mm long forewing in this species versus the smaller *P. axioperierga* which is almost half the size; 1.64 mm forewing length; Azar et al. 2015).
Fig. 6B is based upon the illustrations and figures presented within Perrichot et al. (2003) which presents a full view of the venation and setae clearly.

Prospelektor albianensis Perrichot, Azar, Néraudeau & Nel, 2003
(Fig. 6C)

Approximate age. – French (Albian/Cenomanian, ~113.0–93.9).

Discussion. – Interestingly this species has forewings with two rows of setae (indicating possible †Empheriidae placement instead of within †Archaeatropidae known for their singular setae row) and within its original description a family placement was not attempted (Perrichot et al. (2003) speculated that it was likely within Prionoglarididae or †Archaeatropidae). Mockford et al. (2013) placed this species within †Archaeatropidae due to the significant setae on the forewing and the presence of a nodulus.
Fig. 6C is based upon the illustrations and figures presented within Perrichot et al. (2003) which presents a full view of the venation and setae clearly.

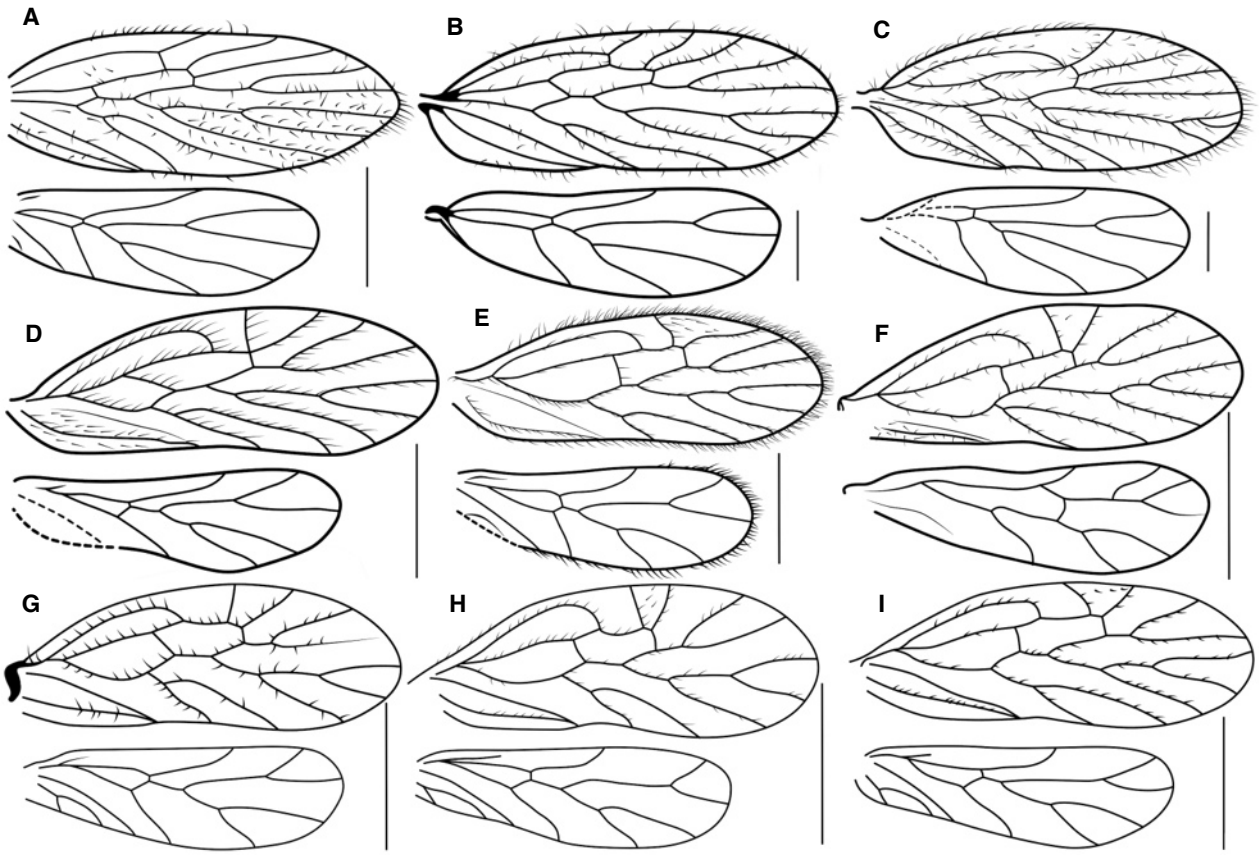

Fig. **6**. Cretaceous †Archaeatropidae wing venation. All scale bars 0.5 mm.
– **A**: *Proprionoglaris axioperierga*. – **B**: *Proprionoglaris guyoti*. – **C**: *Prospeleketor albianensis*. – **D**: *Bcharreglaris amunobi*.
– **E**: *Archaeatropos alavensis*. – **F**: *Setoglaris reemae*. – **G**: *Libanoglaris mouawadi*. – **H**: *Libanoglaris chehabi*.
– **I**: *Archaeatropos randatae*.

Key to species of Cretaceous †Archaeatropidae and †Empheriidae

Presented as a single key due to the lack of consistent characters for reliable differentiation of these two families and several species contain features that do not readily designate them to one or the other. *Bcharreglaris amooni* and *Bcharreglaris haddadini* could not be included due to inability to examine the original description and literature.

1. Forewing with Sc and Sc' terminating at the wing margin therefore there is a Sc crossvein to the distal closed cell present **2**

— Forewing with Sc' only reaching the wing margin (Sc present, but running back and connecting to the distal closed cell instead of the wing margin; therefore only Sc' reaches the wing margin) **6**

2(**1**). Forewing, crossvein between the Sc and the distal closed cell equal in length or longer than the Sc running to the wing margin from that branching point **3**

— Forewing, crossvein between the Sc and the distal closed cell shorter than the Sc running to the wing margin from that branching point **4**

3(**2**). Vertex with long setae; tibiae covered with long dense setae ..... ***Burmempheria densuschaetae***

— Vertex sparsely marked by long setae; tibiae lack long setae ..... ***Burmempheria raruschaetae***

4(**2**). Small species; forewing length ca. 1.5 mm; hindwing fork of R2+3 and R4+5 deep, occurring near the middle or deeper (proximally) within the radial length **5**

— Large species; forewing length 3.0 mm; hindwing fork of R2+3 and R4+5 shallow occurring near the distal two fifths of the radial length ..... ***Proprionoglaris guyoti***

5(**4**). Forewing distal closed cell long and narrow, approximately five times longer than wide ..... ***Proprionoglaris axioperierga***

— Forewing distal closed cell broader, distinctly less than four times longer than wide ..... ***Empheropsocus arilloi***

6(**1**). Forewing cells with setae present throughout, nearly no setae along the wing veins ..... ***Jerseyempheria grimaldii***

— Forewing with most cells empty, lacking setae, at most with the cell formed by R1 and Sc' with a few setae and the anal area of the forewing with setae but most setae are present only on the veins or on each side of the veins **7**

7(**6**). Forewing with small crossvein present between the arcing Sc and the Sc' creating a small closed cell just above the large distal cell ..... ***Empheropsocus margineglabrus***

— Forewing without small crossvein present between the arcing Sc and the Sc', instead only Sc' running to the wing margin and no additional small closed cell **8**

8(**7**). Forewing Sc' running acutely towards the wing margin, not perpendicular, sub-perpendicular, or distinctly towards the wing base **9**

— Forewing Sc' running perpendicular to the wing margin, sub-perpendicular, or distinctly towards the wing base **10**

9(8). Forewing branching of R2+3 from R4+5 happens at the base of those veins ..... ***Prospelektor albianensis***

— Forewing branching of R2+3 from R4+5 happens approximately one third of the way through the length not immediately ..... ***Preempheria antiqua***

10(**8**). Forewing, the distal closed cells proximal end is strongly tapered to a fine point due to the vein between the cells being highly angled and nearly parallel with the wing base, not blunted with the vein between the cells nearly perpendicular to the wing base; the distal and proximal cells can be about the same length, or the distal cell can be longer than the proximal cell **11**

— Forewing, the margin between the two closed cells is blunted with the vein between the cells nearly perpendicular to the wing base; the basal cell is notably longer than the distal closed cell **12**

11(**10**). Forewing Sc' reaching R1 at same point as crossvein joining R1 to Rs ..... ***Bcharreglaris amunobi***

— Forewing Sc' reaching R1 proximally to the crossvein joining R1 to Rs ..... ***Heliadesdakruon morganae*** **gen. et sp. nov.**

12(**10**). Forewing, the R2+3 / R4+5 split occurs proximal to the level of the M3 from M1 and M2 split ..... ***Setoglaris reemae***

— Forewing, the R2+3 / R4+5 split occurs at the level between the M3 from M1 and M2 split **13**

13(**12**). Forewing, Sc' distinctly arcing towards the wing base (not straight) **14**

— Forewing, Sc' straight, running perpendicular to or slightly sub-perpendicular to the wing margin, not arcing in either direction **15**

14(**13**). Forewing, R1 runs straight, approximately at a 45-degree angle to the wing margin, therefore, the cell between R1 and R2+3 is wider at the wing margin than on the proximal portion ..... ***Archaeatropos randatae***

— Forewing, R1 is distinctly bent, strongly angled towards the apex of the wing and reaching distinctly towards R2+3, therefore, the cell between R1 and R2+3 narrows as it reaches the wing apex with the basal section wider ..... ***Archaeatropos alavensis***

15(**13**). Forewing, presence of three setae within the pterostigmal cell; forewing Sc' slightly directed towards wing base; forewing R1 and Sc' about the same length to wing margin ..... ***Libanoglaris chehabi***

— Forewing, pterostigmal area bare, lacking setae; forewing Sc' slightly directed towards wing apex; forewing R1 notably longer than Sc' ..... ***Libanoglaris mouawadi***

Setoglaris reemae Azar & Nel, 2004

(Fig. 6F)

Approximate age. – Lebanese (Barremian, ~129.4–125.0 MYA).

Discussion. – This species was also originally not placed within a family (Azar and Nel 2004) but was later transferred to †Archaeatropidae due to the Sc shape and the setae of the forewing (Mockford et al. 2013).
Fig. 6F is based upon the illustrations and figures presented within Azar and Nel (2004) which presents a full view of the venation and setae clearly.

Order **Psocodea** Hennig, 1966

Suborder **Trogiomorpha** Roesler, 1940

Family †**Cormopsocidae** Yoshizawa & Lienhard, 2020

Cormopsocus perantiqua (Cockerell, 1919) **comb**. **nov**.

(Fig. 7)

Approximate age. – Burmese (Cretaceous, Cenomanian, ~100.5–93.9 MYA).

Discussion. – This species was originally tentatively placed within *Psylloneura* by Cockrell (1919) and was transferred to *Archaeatropos* by Mockford et al. (2013) (a placement which they were both uncertain about due to the missing details of the type specimen). Mockford et al. (2013) believed that the reason the illustration was so vague likely was due to that portion of the wing being damaged or restricted from Cockrell's view and that its likely this specimen is a †Archaeatropidae due to the shapes of the closed cells in the forewings.
Recently we were presented with a specimen (Fig. 7A) which morphologically matches well with the original description of Cockrell (1919). Now with additional features available for review, the higher taxonomy of this species comes into more clarity. Firstly, the forewing appears to lack setae, a feature which removes this species from †Archaeatropidae and †Empheriidae. Instead, the features of this species place it more clearly within the recently described †Cormopsocidae Yoshizawa and Lienhard, 2020 due to the darkened pterostigma, the long and narrow wings, lack of prominent forewing setae, the long and thin distal closed forewing cell, and the Sc well developed and strongly arched (Fig. 7B). Therefore, we transfer this species to the single presently known genus within the family, creating the new combination *Cormopsocus perantiqua* (Cockrell, 1919) **comb**. **nov**.

Conclusion

With our knowledge on the diversity of ancient bark lice continuing to grow, the clarity of their taxonomic higher classifications should begin to solidify. At the present some of the family level classifications appear to instead have their boundaries beginning to blur due to the diversity now known. When single unique genera/species are located, sometimes features may stand out as incredibly unique, and therefore warranting a unique higher-level classification as well. However, as the knowledge of diversity grows, it seems for the case of these extinct bark lice, these distinctions are becoming less significant.
We expect that future, thorough cladistic analyses will be able to bring clarity to these extinct lineages and clarify their higher-level taxonomy as additional specimens/species are discovered/described.

Acknowledgments

We thank scientific illustrator Liz Sisk (USA) for illustrating all of the venation presented within this work. We thank Terry Su (China) for providing images of a *Cormopsocus perantiqua* specimen used within. We thank our peer reviewers for prompt and helpful feedback for this work. We thank Lionel Delaunay for his collaboration in the layout of this article and for the creation of this scientific journal. Thank you to Morgan Brock-Smith for her years of love and support to the first author, your kindness and enthusiasm make every day special.

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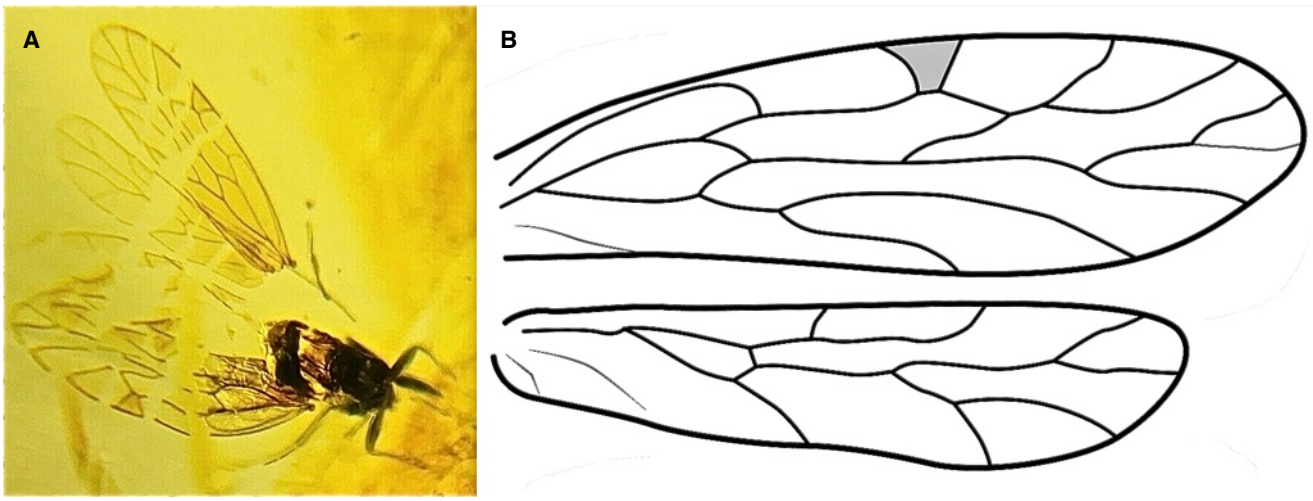

Fig. **7**. Recently collected specimen presumed to be the poorly known *Cormopsocus perantiqua* (Cockerell, 1919) **comb**. **nov**. based upon the vague original description. – **A**: photograph of the specimen by Terry Su (China). – **B**: illustration of the wing venation, drawn by Liz Sisk (USA).

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Résumé

Cumming R. T. & Le Tirant S., 2021. – Révision des †Archaeatropidae et des †Empheriidae du Crétacé avec la description d'un nouveau genre et d'une nouvelle espèce de Psoque en provenance d'un morceau d'ambre Birman (Psocoptera). *Faunitaxys*, 9(16) : 1 – 11.

Les familles fossiles †Archaeatropidae et †Empheriidae sont considérées comme étroitement apparentées. La principale caractéristique morphologique qui les distingue est la conformation des soies des nervures des ailes antérieures. Chez les †Empheriidae, ces soies sont positionnées le long de chaque côté des nervures, alors que les †Archaeatropidae ne présentent qu'une seule rangée de soies, positionnée sur la nervure elle-même. Nous discutons du polymorphisme chez les psocoptères, et présentons des illustrations et des clefs d'identification.
L'examen les psocoptères du Crétacé appartenant à ces deux familles, nous conduit à proposer un modèle cohérent de nervation des ailes. Nous décrivons un nouveau genre et une nouvelle espèce de l'ambre du Myanmar du Crétacé supérieur (stade Cénomanien) que nous plaçons provisoirement dans la familles †Archaeatropidae, en raison des nombreuses nervures des ailes antérieures ayant une rangée simple de soies.
Le genre *Heliadesdakruon* **gen**. **nov**. partage des caractéristiques avec les genres *Archaeatropos* Baz & Ortuño, 2000 et *Bcharreglaris* Azar & Nel, 2004. Au sein de ce nouveau genre, la nouvelle espèce *Heliadesdakruon morganae* **gen**. **et sp**. **nov**. est décrite comme la seule espèce connue à l'heure actuelle. De plus, l'espèce *Archaeatropos perantiqua* (Cockrell, 1919) est illustrée à partir d'un spécimen récemment collecté qui correspond à la description originale basée sur un spécimen en mauvais état. Ce spécimen plus complet permet une meilleure compréhension du placement taxonomique, et en raison du pterostigma noirci, des ailes longues et étroites, du manque de soies avant proéminentes, et de la cellule distale longue et mince de l'aile antérieure fermée, cette espèce est positionnée dans le genre unique de la famille †Cormopsocidae Yoshizawa et Lienhard, 2020 récemment décrite, créant la nouvelle combinaison *Cormopsocus perantiqua* (Cockrell, 1919) **comb**. **nov**.

Mots-clés. – Psocoptera, Empheriidae, Arcaetropidae, Crétacé, Birmanie, Mésozoïque, fossile, ambre, genre nouveau, espèce nouvelle, taxonomie, description.

Derniers articles publiés

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