New psocids (Psocodea: Prionoglarididae, Psyllipsocidae) from Cretaceous Burmese amber deposits

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Abstract

Palaeosiamoglaris hkamtiensis sp. nov. of the family Prionoglarididae is described from Hkamti amber (ca. 110 Ma), together with *Psyllipsocus myanmarensis* sp. nov., the third fossil psyllipsocid species described from from Noije Bum Hill (ca. 98 Ma). Based on the current observations of *Palaeosiamoglaris hkamtiensis* sp. nov., we discuss the synapomorphic characters proposed to define the tribe Siamoglaridini. *Palaeosiamoglaris hkamtiensis* sp. nov. is, *inter alia*, characterized by the maxillary palpomere 3 ca. 0.66 time as long as maxillary palpomere 4, the second anal vein concavity turned toward posterior wing margin in forewing, Sc reaching R1 nearly at middle of radial cell. The new species *Psyllipsocus myanmarensis* sp. nov. is, *inter alia*, characterized by antennae with 11 segments, the radial cell closed and six-angled, and the quadrangular pterostigma.

Key words: Insecta, Psocodea, Prionoglaridetae, Psyllipsocetae, Hkamti,

1. Introduction

The Psocodea ('Psocoptera' + Phthiraptera) is an order relatively well known in the fossil record with 31 families and 101 genera known to date (www.fossilworks.org), and with more than 10,000 valid extant species (Johnson et al., 2020). The Psocodea should have arose during the late Devonian according to the recent result obtained from phylogenomic analysis (Misof et al., 2014) but the oldest fossil of the clade namely *Westphalopsocus pumilio* Azar et al., 2013 (in Nel et al., 2013) is from the Moscovian (Late Carboniferous), with the Permian *Zygopsocus permianus* Tillyard, 1935 as second described oldest record (Nel et al., 2012), and a third undescribed Middle Permian fossil from China (pers. obs.). Recently, de Moya et al., (2020) proposed a time-calibrated phylogeny of the crown Psocodea and estimate their arisen to the early Jurassic (de Moya et al., 2020: fig. 1) which is much younger than been previously proposed (e.g. Misof et al. 2014; Johnson et al., 2018; Yoshizawa et al., 2019) and may result from the partial integration of the fossil record as calibration points. This Jurassic dating, at most, can only concern the crown group of the extant Psocodea and not its stem group. However, de Moya et al. (2020) do not aim to refine the time divergence of the order but rather

investigate the appearance of the parasitism in the Psocodea. Therefore, we should take into account that the age obtained is not for Psocodea arising but rather for parasitism appearance. If it would have concerned the total group, it would be incongruent with all the recently proposed phylogenetic placements of the Psocodea, either as sister group of the clade (Permopsocida + (Thripida + Hemiptera)), or as sister group of the Holometabola, both these clades being already present in the late Carboniferous (Nel et al., 2013; Huang et al., 2016). This gap between the time divergence estimate of the clade or some of its constitutive families (viz. the Liposcelididae) and their oldest representatives reflects, as for many other insect orders, the discrepancy between the fossil record and the time divergence estimate which mainly results from the poor integration of the fossil record.

The growing interest in the study of insects in Burmese amber leads to considerably increase the number of known psocid fossil species (e.g. Ross, 2019, 2020; Yoshizawa and Lienhard, 2020), with representatives of the families †Archaeatropidae, Compsocidae, †Cormopsocidae, Liposcelididae, Manicapsocidae, Pachytroctidae, Prionoglarididae, Psyllipsocidae, Sphaeropsocidae, and Trogiidae.

Herein we described a new species of *Palaeosiamoglaris* Azar, Huang & Nel, 2017 from Hkamti amber namely *Palaeosiamoglaris hkamtiensis* sp. nov., and the third fossil psyllipsocid species from Burmese amber namely *Psyllipsocus myanmarensis* sp. nov.

2. Material and methods

The amber pieces containing the specimens come from two Myanmar deposits, viz. Noije Bum and and Hkamti site. Noije Bum is in the Hukawng Valley (26° 29′ N, 96° 35′ E), Kachin State, northern Myanmar (see detailed map in Grimaldi & Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing deposits (Shi et al. 2012). Some ammonites found in the amber-bearing bed and within amber corroborate a late Albian–early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019). Hkamti site is located in the Hkamti District in the Sagaing Region, Myanmar (see

detailed map in Xing & Qiu, 2020: fig 1). Zircon U-Pb analyses established an early Albian age (109.7 ± 0.4 Ma) for Hkamti amber, based on zircon analyses of clastic sediments at the surface (Xing & Qiu, 2020).

The two specimens are embedded in amber pieces of clear yellow amber. The amber pieces were polished to facilitate the observation of the specimens using a grinder polisher (Buehler EcoMet 30) with very thin silicon carbide sanding paper (grit size = 7000). The specimens were examined and photographed with a Leica MZ APO with an attached Canon EOS 5D Mark II camera, a Zeiss AXIO Zoom V16 stereo microscope and a Zeiss AXIO Imager Z2 compound microscope equipped with fluorescence laser. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 softwares. We follow the wing venation nomenclature of Yoshizawa and Lienhard (2020) for the 'Psocoptera'.

Abbreviations.— A for anal vein, CuA/P, cubitus anterior/posterior; M, median vein; R, radius; Rs radial sector posterior; Sc and Sc' basal and distal parts of subcostal vein respectively.

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3. Systematic paleontology

Suborder Trogiomorpha Roesler, 1940

Infraorder Prionoglaridetae Smithers, 1972

Family Prionoglaridídae Karny, 1930

Subfamily Prionoglaridinae Karny, 1930

Tribe Siamoglaridini Azar, Huang & Nel ,2017

Genus *Palaeosiamoglaris* Azar, Huang & Nel, 2017

Included species: *P. lienhardi* Azar, Huang & Nel., 2017 (type species), *P. burmica* Azar, Huang & Nel., 2017, *P. inexpectata* Azar, Huang & Nel., 2017, and *Palaeosiamoglaris hkamtiensis* sp. nov.

Palaeosiamoglaris hkamtiensis sp. nov.

(Figs 1-2)

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Etymology: Named after the originating deposit of the amber piece, Hkamti. The specific epithet is to be treated as a feminine adjective.

Holotype: IGR.BU-022, deposited in the Geological Department and Museum of the University of Rennes, France (IGR) (in a piece of amber measuring 12 × 7 × 2 mm).

Type locality: Hkamti site, Hkamti District, Sagaing Region, Myanmar.

Type horizon: Lower Albian (ca. 110 Ma), Lower Cretaceous.

Material.—Holotype only.

Diagnosis.—Maxillary palpomere 3 longer than half of palpomere 4 (ca. 0.66 time length of P4); Second anal vein concavity turned toward posterior wing margin in forewing; Sc reaching R1 nearly at middle of radial cell.

Description.—Winged (maybe male). Body 2.05 mm long. Head much longer than wide in frontal view, triangular-shaped; ocelli present but not conspicuous; compound eye ovoid, without color pattern, *ca.* 0.21 mm long; antenna with 18 antennomeres (hardly visible due to amber), at least 1.85 mm long; several flagellomeres with annulate sculpture weakly visible but present; scape (*ca.* 0.155 mm long) less than twice as long as pedicel (*ca.* 0.095 mm long); scape slightly wider than pedicel; frontal suture present; clypeus conspicuous; labrum thin covering mandibles in frontal view; distal margin of labrum with placoids, (maybe containing a very short conical sensillum); maxillary palps four-segmented, *ca.* 0.768 mm long; palpomeres respectively (from base to tip) 0.078, 0.26, 0.17, 0.26 mm long, with second one bearing a conical sensillum, and apical one slightly widened apically; labial palps two-segmented, not well-preserved. Thorax *ca*. 0.60 mm long. Legs with tibiae with

minute, strong spines; tarsi three-segmented, basal tarsomere the longest and apical one the shortest; tarsal claws asymmetrical, with preapical tooth, membranous extension of anterior preapical claws strongly developed. Forewing hyaline, glabrous, *ca.* 2.66 mm long, *ca.* 1.31 mm wide, with pterostigma not colored; wing apex broadly rounded; complete venation; Sc long, with its basal part strongly curved, distally fused with R1 in the middle of radial cell; Sc' straight, reaching wing margin at 1.87 mm from wing base and closing pterostigma; base of last R1 section separated from base of Sc' by a small section of R1; R1 reaching costal margin 2.15 mm from wing base; Rs bifurcating into R2+3 and R4+5 at 1.93 mm distal of wing base; R2+3 reaching wing margin at 2.46 mm; R4+5 slightly curved to straight, reaching wing margin at 2.66 mm; radial cell closed, heptagonal, longer than wide; M1+M2 bifurcating into M1 and M2 at 2.03 mm from wing base; M1 and M2 reaching wing margin respectively at 2.67 mm and 2.51 mm; M3 bifurcating from M at 1.84 mm and reaching wing margin at 2.24 mm; fork of CuA in CuA1 and CuA2 1.24 mm from wing base; CuA1 strongly curved and longer than CuA2, reaching wing margin at 1.87 mm; CuA2 straight to slightly curved, reaching wing margin at 1.53 mm; areola postica (AP) free; CuP straight, joining anal vein at posterior wing margin in a nodulus at 1.19 mm from wing base; A2 curved, joining wing margin at 0.57 mm with concavity directed toward wing base. Hind wing, hyaline, normally developed with complete venation, smaller than forewing, *ca.* 2.00 mm long and at least 0.64 mm wide; Sc short and ending free in membrane; R1 reaching costal margin at 1.31 mm from wing base; Rs fused with M for a short distance; Rs bifurcating into R2+3 and R4+5 at 1.67 mm apically; R2+3 and R4+5 reaching wing margin respectively at 1.74 and 2.01 mm; M bifurcating into M1 and M2 at 1.39 mm from wing base; M1 and M2 reaching wing margin respectively at 1.87 and 1.64 mm; CuA slightly curved medially, reaching wing margin at 1.33 mm apically; CuP reaching wing margin at 1.10 mm; A bifurcated into A1 and A2 respectively reaching wing margin at 0.90 and 0.67 mm. Abdomen *ca.* 1.30 mm long (including genitalia). Genitalia too much damaged to be described.

Remark. The new species also differs from its relatives in its age (ca. 110 Ma vs. 98 Ma).

Infraorder Psyllipsocetae Smithers, 1972

Family Psyllipsocidae Kolbe, 1884

See detailed list of genera and species in Lienhard and Smithers (2002), Hakim et al. (2018) with the addition of Wang et al. (2019) and Álvarez-Parra et al. (2020).

Genus *Psyllipsocus* Selys-Longchamps, 1872

Psyllipsocus myanmarensis sp. nov.

Figures 3-6

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Etymology: Named after the originating country of the amber piece, Myanmar. The specific epithet is to be treated as a masculine adjective.

Holotype: IGR.BU-023 (female), deposited in Geological Department and Museum of the University of Rennes, France (IGR) (in a piece of amber measuring 11 × 5 × 2 mm); Paratype NIGP174915 (male) deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (NIGP).

Type locality: Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar.

Type horizon: upper Albian to lower Cenomanian (*ca.* 98 Ma), mid-Cretaceous.

Material.—Holotype only.

Diagnosis.—Antenna with 11 antennomeres; forewing with complete venation, sparse setation on veins; radial cell closed, six-angled; crossvein R1-Rs clearly separated from base of Sc', leading in an hexagonal radial cell; quadrangular pterostigma; Rs and CuA branched; elongated areola postica; nodulus present; hind wing venation developed with R, M, CuP, and A branched; R1 not sigmoidal; legs with three-segmented tarsi.

Description.—Female winged. Body *ca.* 1.25 mm long. Head as long as wide in frontal view (when eyes are included), triangular-shaped; vertex broad with ratio (distance between compound eyes/greatest width of postclypeus) = 1.47; ocelli arranged as an isosceles triangle with greatest

distance between lateral ocelli; compound eye ovoid, without color pattern, *ca.* 0.12 mm long; antennal socket with a dorsal ridge; antennae with 11 antennomeres, *ca.* 0.8 mm long; scape and pedicel of nearly same lengths, *ca.* 0.077 mm long, both of similar width; first flagellomere *ca.* 0.088 mm long; second flagellomere the longest, *ca*. 0.10 mm long, remaining ones decreasing in length toward apex with apical most flagellomere the smallest; frontal suture present; clypeus massive, bulging from head; labrum thin, covering mandibles in frontal view; maxillary palps four-segmented, *ca.* 0.30 mm long; palpomeres respectively (from base to tip) 0.039, 0.100, 0.050, 0.111 mm long, with second one lacking conical sensillum, and apical one slightly drop shape; labial palps two-segmented, terminal palpomere elongate with its length much more than twice its width. Thorax 0.440 mm long. Tibiae with minute strong spines; tarsi three-segmented, basal tarsomere the longest and middle one the shortest; preapical claws symmetrical, simple (viz. without preapical tooth). Forewing hyaline, with sparse setation on veins, *ca.* 1.30 mm long, *ca.* 0.45 mm wide, with pterostigma not particularly colored; wing apex rounded; complete venation; Sc short and not reaching R or wing margin but ending free in membrane; Sc' reaching wing margin at 0.69 mm from wing base and closing pterostigma; base of last R1 section separated from base of Sc' by a small section of R1; R1-Rs crossvein clearly separated from base of Sc'; R1 reaching costal margin 0.95 mm from wing base; Rs fused with M basally for a short distance; Rs bifurcating into R2+3 and R4+5 at 0.92 mm distal of wing base; R2+3 reaching wing margin at 1.09 mm; R4+5 slightly curved to straight, reaching wing margin at 1.17 mm; radial cell closed, hexagonal, with lateral sides the longest; M1+M2 bifurcating into M1 and M2 at 1.04 mm from wing base; M1 and M2 reaching wing margin respectively at 1.23 mm and 1.21 mm; M3 bifurcating from M at 0.90 mm and reaching wing margin at 1.14 mm; fork of CuA in CuA1 and CuA2 0.62 mm from wing base; CuA1 gently curved and longer than CuA2, reaching wing margin at 1.01 mm; CuA2 curved, reaching wing margin at 0.73 mm; areola postica (AP) free and elongate; CuP slightly curved medially, joining anal vein at posterior wing margin in a nodulus at 0.55 mm from wing base. Hind wing, hyaline, normally developed with complete venation, 1.19 mm long and at least 0.32 mm wide; Sc very short and ending

free in membrane; R1 reaching costal margin at 0.76 mm from wing base; Rs fused with M for a distance; Rs bifurcating into R2+3 and R4+5 at 1.01 mm apically; R2+3 and R4+5 reaching wing margin respectively at 1.13 and 1.18 mm; M bifurcating into M1 and M2 at 0.76 mm from wing base; M1 and M2 reaching wing margin respectively at 1.08 and 0.86 mm; CuA curved, reaching wing margin at 0.61 mm apically; CuP very slightly curved, reaching wing margin at 0.45 mm; A bifurcated into A1 and A2 (wing membrane folded due to preservation). Abdomen ca. 0.65 mm long (including genitalia). Female genitalia with subgenital plate pointed apically, short, half-length of rounded and setose external valvula of gonapophyses, thin ventral valvula; dorsal valvula not discernable; paraprocts elongate, pointed apically.

Male genitalia setose, hypandrium simple with rounded posterior margin, parameres broad and well developed, trichobothrial field on paraprocts well developed.

Remarks: The reduced number of antennomeres is a unique feature among all known Psyllipsocidae. We can ensure this number based on three observations: (1) all the antennomeres shorten in length towards the apex, (2) the apical flagellomere does not present a hole at the apex allowing the insertion of an additional segment, and (3) the apex gradually becomes thinner, and is rounded. Additionally, this unique character is found on several specimens refuting the possibility that this condition represents abnormality.

4. Discussion

Several previous publications justified the family attributions of some fossils based only or mainly on the key of Smithers (1990) but several issues point off concerning this method: this key is an identification tool of extant taxa, based on characters without considering their apomorphic *vs.* plesiomorphic states. It would be more accurate to base our placements on the recent higher classification system of Trogiomorpha (Yoshizawa et al., 2006; Yoshizawa and Lienhard, 2020) defining several female synapomorphic characters supporting the Trogiomorpha: ventral and dorsal valves of gonapophyses strongly reduced or absent, external valves well-developed and setose;

subgenital plate short, covering at most basal part of external valves, which come close to ventral midline of abdomen, forming the ovipositor. However, these characters are not available in the holotype of *Palaeosiamoglaris hkamtiensis* sp. nov.

Recently, the tribe Siamoglaridini was erected based on fossil and extant species (Azar et al., 2017) and placed among the Trogiomorpha. If the synapomorphic characters used to define the suborder are not all recorded in the Siamoglaridini (e.g. the ventral valves of gonapophyses strongly reduced), its assignment to the subfamily Prionoglaridinae is obviously supported by the following apomorphies: long antennae composed of at most 13 flagellomeres and broadened and rounded forewing (apomorphies for the family Prionoglaridídae), adult lacinia reduced, asymmetric pretarsal claws, anterior claw with membranous extension, and phallosome consisting of cuticular sac with pair of posterolateral processes (apomorphies for the subfamily Prionoglaridinae) (Yoshizawa et al., 2006; Yoshizawa and Lienhard, 2020). Monophyly of Trogiomorpha including Prionoglaridídae is well supported morphologically and molecularly (Yoshizawa et al., 2006; Johnson et al., 2018; Yoshizawa and Lienhard, 2020; de Moya et al., 2020) so that there is no doubt about the placement of Siamoglaridini within the suborder Trogiomorpha.

Palaeosiamoglaris hkamtiensis sp. nov. is placed among the Siamoglaridini and among the genus *Palaeosiamoglaris* (see below) since it fits with the diagnosis of the tribe in having distal margin of labrum with placoids; legs lacking trichobothria; pretarsal claws asymmetric, lacking preapical tooth; forewing with pterostigma slightly opaque (difficult to observe due to amber preservation) and second anal vein A2 present. However, *Palaeosiamoglaris hkamtiensis* sp. nov. would differ from the other Siamoglaridini in having compound eyes with apparently uniform color pattern. This difference may, according to Lienhard (2004), be linked to the freshness of the specimen and therefore be lost if it took a long time to have it embedded in the resin. It should not be considered as a diagnostic character to exclude *Palaeosiamoglaris hkamtiensis* sp. nov. from the tribe. According to the datation of Hkamti amber deposit (*ca.* 110 Ma; Xing and Qiu, 2020), *Palaeosiamoglaris hkamtiensis* sp. nov. is the oldest Prionoglaridídae. Following the description of Azar et al. (2017),

Palaeosiamoglaris hkamtiensis sp. nov. fits with the diagnostic characters of *Palaeosiamoglaris* in having maxillary palp much longer than half of head length; maxillary palp 3 (P3) longer than half of maxillary palp 4 (P4); terminal labial palpomere elongate, with its length much more than twice its width.

Palaeosiamoglaris hkamtiensis sp. nov. differs from *P. lienhardi* in having P3 longer than P4 half length (P3 *ca.* 0.66 times P4 *vs.* 0.49 in *P. lienhardi*); Sc reaching R1 at middle of radial cell (*vs.* more distally). It also differs from *P. burmica* in having P3 proportionally longer (P3 *ca.* 0.66 times P4 *vs.* 0.59 in *P. burmica*) Sc reaching R1 at middle of radial cell (*vs.* more basally). *Palaeosiamoglaris hkamtiensis* sp. nov. differs from *P. inexpectata* in having P3 longer than P4 half length (*vs.* P3 more than twice as long as P4); Sc reaching R in R1 at middle of radial cell (*vs.* reaching R basally of the radial cell), CuA1 gently curved and not converging toward CuA2.

Psyllipsocus myanmarensis sp. nov. has all the synapomorphic characters supporting the Trogiomorpha (viz. ventral valvula of gonapophyses very thin, dorsal valvula strongly reduced or absent, external valvula well-developed and setose; subgenital plate short, half-length of external valves, which come close to ventral midline of abdomen, forming the ovipositor). *Psyllipsocus myanmarensis* sp. nov. is assigned to the Psyllipsocetae and to the family Psyllipsocidae but the autapomorphy proposed to define the infraorder: spermathecal sac lacking glandular accessory bodies, with complicated sclerifications at origin of duct and often with accessory vesicle (Yoshizawa et al. 2006), cannot be observed in our specimen due to the preservation in amber. However, *Psyllipsocus myanmarensis* sp. nov. has the additional characters proposed to define the infraorder, viz. the second maxillary palpomere without conical spur sensillum; basal segment of forewing Sc short, ending free in membrane; nodulus present; hind wing vein A bifurcate; wing pilosity developed (partially preserved on our specimen); female external valve of gonapophyses broad.

To date, there are three psyllipsocid genera described from Burmese amber, namely *Annulipsyllipsocus* Hakim et al., 2017 (two species: Hakim et al., 2017), *Concavapsocus* Wang et al., 2019 (one species: Wang et al., 2019) and *Psyllipsocus yoshizawai* Álvarez-Parra et al., 2020.

Psyllipsocus myanmarensis sp. nov. differs from *Annulipsyllipsocus* in lacking secondary annulations of antennomeres, in having a longer pterostigma and a hexagonal radial cell, R1-Rs crossvein clearly separated from base of Sc', and an elongated areola postica. It differs from *Concavapsocus* in the forewing venation complete, with radial cell closed (vs. reduced and opened), M forked with three section (*vs.* simple), CuA1 forked (*vs.* simple), nodulus present; hind wing with R forked (*vs.* simple), M forked with two section (*vs.* simple), CuA and CuP both present (*vs.* CuP absent), A bifurcated (*vs.* absent). In fact, the wing venation of *Concavapsocus* is completely different from those of all Psyllipsocidae and probably does not belong to this family (Dany Azar pers. comm.).

The extant and fossil genus *Psyllipsocus* Selys-Longchamps, 1872 shows a high disparity in the wing venation, with or without radial cell, Sc', etc. (Mockford, 2011; Lienhard and Ferreira, 2013, 2014; Lienhard and García-Aldrete, 2016). *Psyllipsocus* is characterized by a broad vertex, with ratio (distance between compound eyes/greatest width of postclypeus) = 1.41 or more (Mockford, 1993: 52); which is the case for *Psyllipsocus myanmarensis* sp. nov.

Psyllipsocus myanmarensis sp. nov. has a forewing venation rather similar to that of the third Burmese amber Psyllipsocidae (*P. yoshizawai*) but it differs in the forewing veins R2+3, R4+5 and M3 longer, the hind wing vein R1 simply curved vs. sigmoidal, veins M1 and M2 distinctly longer, M2 having a different orientation (Álvarez-Parra et al., 2020: fig. 2), and in the number of antennomeres (11 *vs.* at least 16).

Psyllipsocus myanmarensis sp. nov. cannot be placed in the other Cretaceous Psyllipsocidae genus *Khatangia* Vishniakova, 1975 since having a hexagonal radial cell (*vs.* pentagonal) and a long and wide triangular pterostigma (vs. short and quadrangular) (Vishniakova, 1975: figs 7-14). Additionally, the genus *Khatangia* lacks the nodulus in forewing (i.e. CuP and A reaching wing margin separately; see Vishynakova, 1975) while representatives of the genus *Psyllipsocus* have a nodulus.

Psyllipsocus myanmarensis sp. nov. also differs from the extant genus *Pseudopsyllipsocus* Li, 2002 in having female fully winged (vs. apterous) and claws simple (*vs.* with a preapical tooth) (Li, 2002:

58 & 1766). *Psyllipsocus myanmarensis* sp. nov. cannot be placed in the extant genera *Dorypteryx* Aaron, 1883, *Psocathropos* Ribaga, 1899, and *Pseudorypteryx* García-Aldrete, 1984 since having normal wing with complete venation (*vs.* narrow elongate wings with a reduced venation) (García-Aldrete, 1984; Li and Liu, 2009; Lienhard and Ferreira, 2015).

5. Conclusion

The new fossils demonstrate that the Prionoglarididae are rather an old group existing at least from the Albian (Lower Cretaceous) with a diversity surely underestimated in fossil ages. Similarly *Psyllipsocus myanmarensis* sp. nov. by displaying a unique wing venation for Cretaceous Psyllipsocidae and a striking reduction of the number of antennomeres highlights the underestimated diversity of the family during the Cretaceous. This unprecedented number of antennomeres (unknown in extant Psyllipsocidae) surely indicates a peculiar biology and behavior. It is possibly an adaptation to a special ecological niche. Therefore, *Psyllipsocus myanmarensis* sp. nov. highlights also the underestimated ecological diversity of this family during the Cretaceous. Recently, numerous phylogenetic analyses have been proposed for the Psocodea but none fully integrates the information from the fossil record resulting in underestimated time divergence for the constitutive families. It would be interesting to propose a total-evidence dating or tip-dating approach to refine these estimates of the time of divergence, and thereby reduce the gap between fossil data and molecular clocks.

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Figure caption

Fig. 1. *Palaeosiamoglaris hkamtiensis* sp. nov., holotype IGR.BU-022 (female). Habitus in ventro-lateral view. Scale bar: 0.5 mm.

Fig. 2. *Palaeosiamoglaris hkamtiensis* sp. nov., holotype IGR.BU-022 (female). A: Detailed view of mouthparts (arrow pointing labrum and location of placoids). B: Wing venation. C: Antenna. D: Detailed view of hind tarsus. E: Labelled line drawing of wings venation. F: Line drawing of distal part of tarsus with pretarsal claws. Scale bars 0.5 mm (A,B,C,D,E), 0.03 mm (F)

Fig. 3. *Psyllipsocus myanmarensis* sp. nov., holotype IGR.BU-023. Habitus in right-lateral view. Scale bar 0.5 mm.

Fig. 4. *Psyllipsocus myanmarensis* sp. nov., holotype IGR.BU-023. A: Detailed view of mouthparts. B: Detailed view of left antenna. C: Detailed view of wing venation. D: Labelled line drawing of wing venation. Scale bars 0.25 mm.

Fig. 4. *Psyllipsocus myanmarensis* sp. nov., paratype NIGP174915 (male). Habitus in frontal view. Scale bar 0.2 mm.

Fig. 4. *Psyllipsocus myanmarensis* sp. nov., paratype NIGP174915 (male). A: Detailed view of head in frontal view. B: Head in full face view. C: Detailed view of fore tarsus. D: Apical part of abdomen. E: Forewing. F: Labelled line drawing of forewing venation. G: Hind wing. H: Labelled line drawing of forewing venation. Scale bars 0.1 mm (A, D); 0.2 mm (B, F, H); 0.02 mm (C); 0.5 mm (E, G).

Figure 1

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Figure 2

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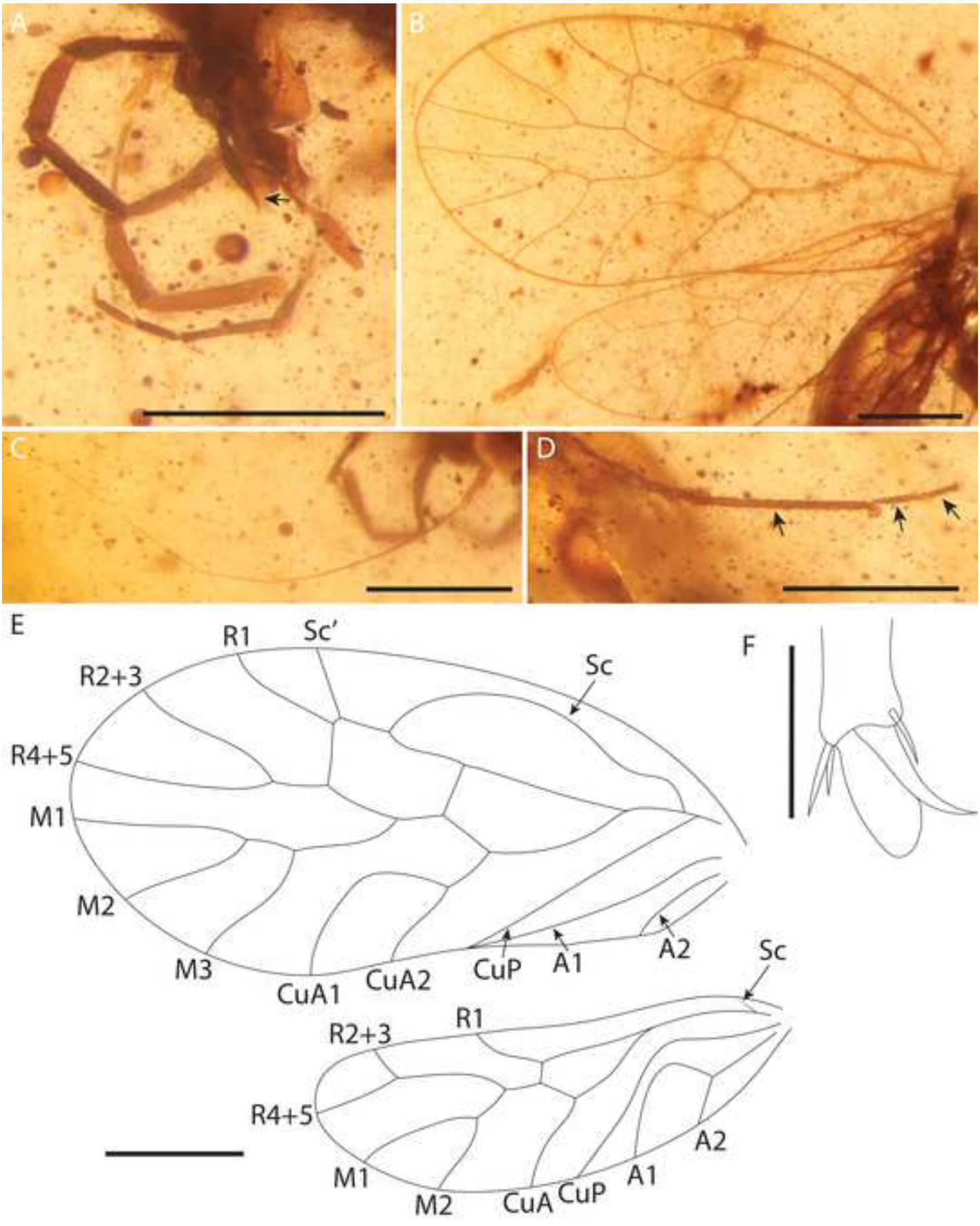

Figure 3

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Figure 4

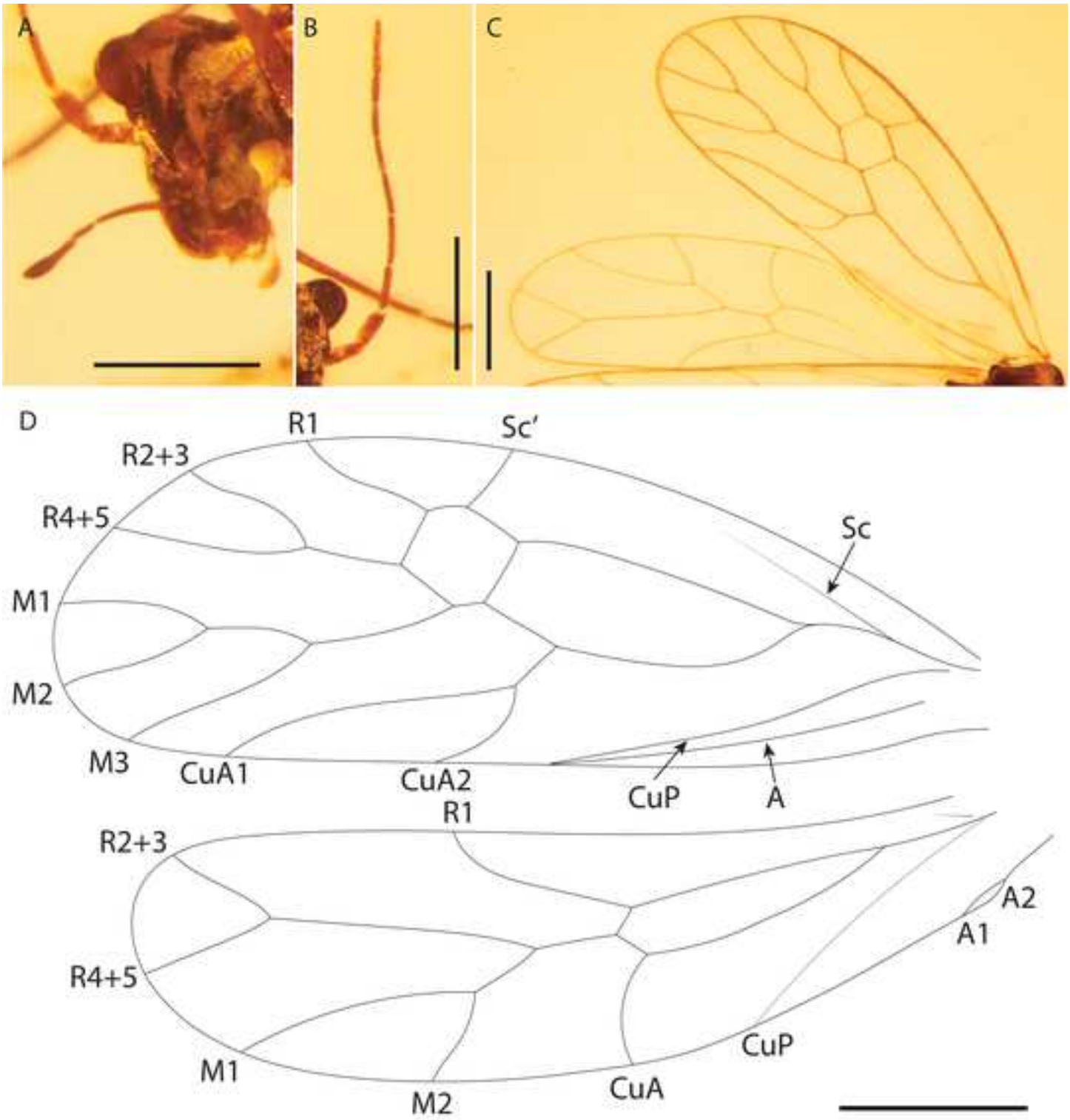

Figure 5

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Figure 6

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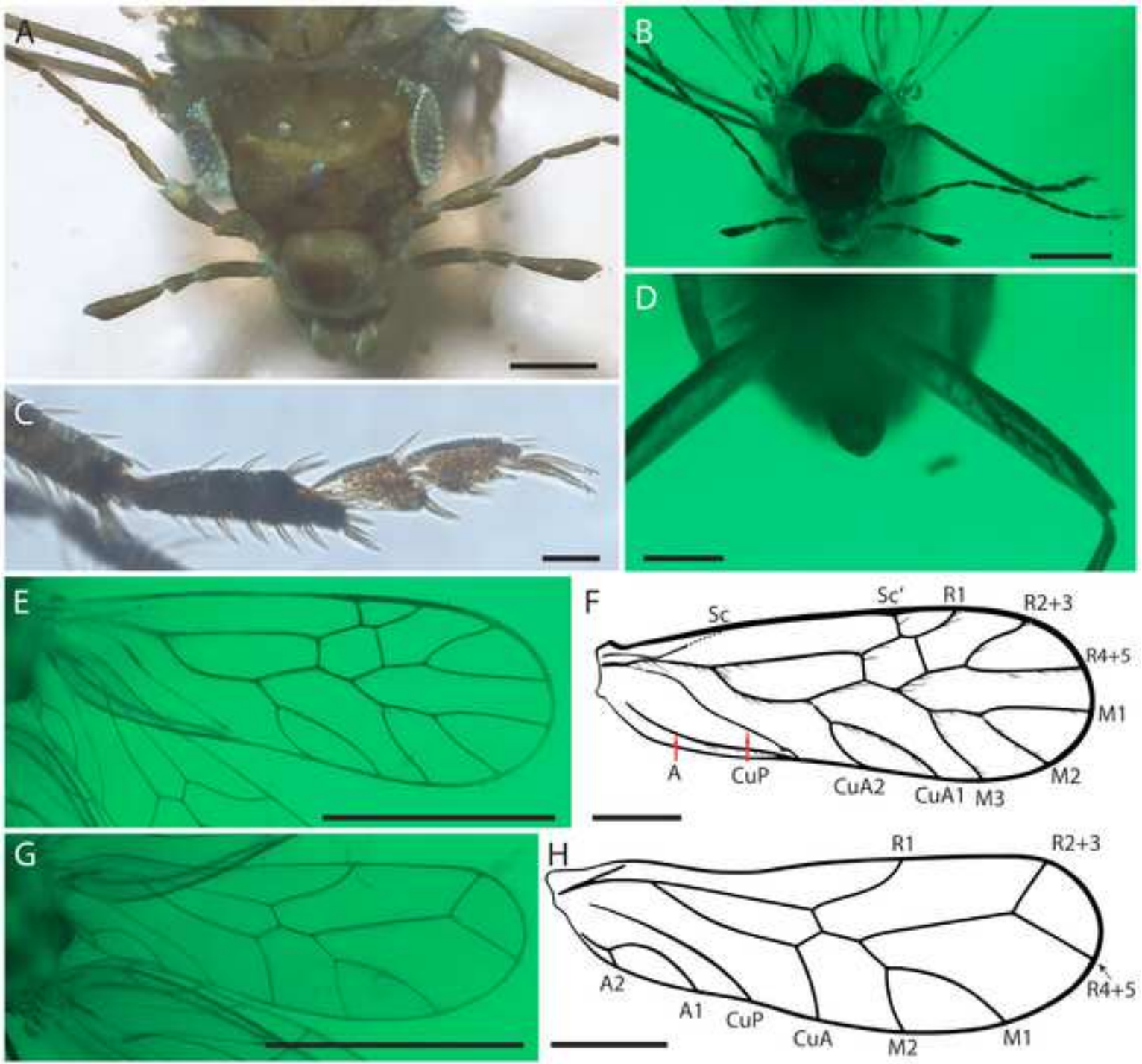

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CJ: Conceptualization, Data curation, Investigation, Methodology, Visualization, Writing - original draft & review. KY: Data curation, Investigation, Methodology, Writing - original draft & review. MH: Data curation, Investigation, Methodology, Visualization, Writing review. DH: Data curation, Investigation, Methodology, Visualization. AN: Supervision, Data curation, Methodology, Investigation, Writing - original draft & review.