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Acrotiarini trib. nov., in the Cixiidae (Insecta, Hemiptera, Fulgoromorpha) from mid-Cretaceous amber of northern Myanmar, with new insights in the classification of the family

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ABSTRACT

Three new genera and species of Cenomanian Cixiidae from Kachin amber (Myanmar) are described: *Acrotiara* Bourgoin & Luo gen. nov., type species *A. multigranulata* Luo & Bourgoin sp. nov., *Delphitiara* Bourgoin & Luo gen. nov., type species *D. tibiocoronata* Luo & Bourgoin sp. nov., and *Pentacarinus* Bourgoin & Luo gen. nov., type species *P. kachinensis* Luo & Bourgoin sp. nov. A key to identification of these new genera is provided. These cixiids with a pentacarinated mesonotum belong to a new tribe Acrotiarini Bourgoin & Luo trib. nov., type genus *Acrotiara* gen. nov., which is characterized by a specific set of characters, some being unique in the family Cixiidae such as the paired sublaterofrontal carinae and the arched RA on the tegmina. This new taxon prompts discussion of the current classification and phylogeny of the family, which remains widely unexplored, and of the evaluation of the placement of two older cixiid fossils currently known, *Karebodopoides aptianus* (Fennah, 1987) and *Cixius petrinus* Fennah, 1961. A new genus, *Barremixius* Bourgoin & Szwedo gen. nov., is proposed for the latter, resulting in the new combination *Barremixius petrinus* (Fennah, 1987). *Karebodopoides* Szwedo, 2001 and *Barremixius* gen. nov. are provisionally recognized as the oldest Cixiidae, respectively representative of the oecleinian lineage (including Bothriocerini trib. stat. nov.) and of the cixiinian lineage. Acrotiarini trib. nov. belongs to the pentastirinian lineage (including Borysthenini stat. nov.). All these fossils depict that the first main division that occurred in Cixiidae, occurred much earlier during the Cretaceous

1. Introduction

Planthoppers from mid-Cretaceous amber of Myanmar form a quite diverse and distinctive fauna. Most have been described as belonging to several new fossil families recently described: Dorytocidae Emeljanov & Shcherbakov, 2018 (Emeljanov & Shcherbakov, 2018; Song et al., 2021), Inoderbidae Shcherbakov & Emeljanov, 2021 (Shcherbakov and Emeljanov, 2021), Jubisentidae Zhang X., Ren & Yao, 2019 (Zhang X. et al., 2019), Katlasidae Luo, Jiang & Szwedo, 2020 (Luo et al., 2020b), Mimarachnidae Shcherbakov, 2007 (Shcherbakov, 2007b, Jiang et al., 2018, 2019; Zhang X. et al., 2018; Fu et al., 2019, Jiang et al., 2020; Fu & Huang, 2021), Perforissidae Shcherbakov, 2007 (Shcherbakov, 2007a, Zhang X. et al., 2017, Luo et al., 2020a) and Yetkhatidae Song, Szwedo & Bourgoin, 2019 (Song et al., 2019). Additionally, the recently described bizarre nymph (Luo et al., 2021) in the Fulgoridea, belongs probably to Neazoniidae Szwedo, 2007.

Interestingly, only few extant families are known from Myanmar amber. Recently a new tribe, Derbachilini Emeljanov & Shcherbakov, 2020 was proposed in the family Derbidae Spinola, 1839 for two Burmese amber genera (Emeljanov and Shcherbakov 2020) and several new taxa of the family Achilidae Stål, 1866, have been reported and are under investigation (Brysz and Szwedo 2019). A few other taxa are cited from Myanmar

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amber but were misidentified (Zhang W., 2017: Issidae Spinola, 1839, Tropiduchidae Stål, 1866, Kinnaridae Muir, 1922, Fulgoridae Latreille, 1807) or still remain to be described such as those within Dictyopharidae (Song et al., 2021). As expected for one of the older Fulgoroidea families, Cixiidae Spinola, 1839 are also present (Zhang W., 2017) but they yet remain to be described from mid-Cretaceous amber of Myanmar.

Cixiidae together with Delphacidae Leach, 1815 are considered to be the first ones to separate from the Fulgoroidea (Bartlett et al., 2018), in a very successful lineage that represents about one third of the current biodiversity of all planthoppers. Cixiidae themselves are worldwide distributed and the most successful planthopper family with over 2550 species and 247 genera (Bourgoin, 2021). The family is believed to be at least of Cretaceous origin (Szwedo *in* Urban and Cryan, 2012) or even older (Triassic: Bucher and Bourgoin, 2019). Surprisingly however, and despite their evolutionary success and their old age, only few fossils are known, and only about 30 different taxa have been described (Szwedo et al., 2004; Bourgoin, 2021). Cixiidae are at least attested in the fossil register since Barremian (129.4–125 Ma) (Fennah 1961, 1987; Maksoud et al., 2017; Maksoud and Azar, 2020) with the oldest Fulgoroidea fossils currently known: *Karebodopoides aptianus* (Fennah, 1987) and '*Cixius*' *petrinus* Fennah, 1961 (see taxonomic decisions below).

Monophyly of Cixiidae, respectively to Delphacidae, remains however in doubt (Muir, 1923; Asche, 1988; Bourgoin et al., 1997; Urban and Cryan 2007; Ceotto and Bourgoin, 2008; Ceotto et al., 2008; Urban et al., 2010; Bucher and Bourgoin, 2019) as no convincing morphological synapomorphies for the family have yet been proposed. Indeed, cixiids are diagnosed by a series of fulgoroid plesiomorphies, including an orthopteroid ovipositor, the presence of a median ocellus and wax pores on tergites VI–VIII of nymphs and IX of female adults (Emeljanov 2002). The family itself remains artificially divided into three subfamilies: Borystheninae Emeljanov, 1989, Bothriocerinae Muir, 1923 and Cixiinae Spinola, 1839. The latter is divided into sixteen tribes of various importance in terms of diversity as, for counting currently 245 genera, nine of them remain mono-, di- or three-generic only. Their relationships remain unclear and the topology of the family as proposed by Emeljanov (2002), was not recovered by Ceotto and Bourgoin (2008) and Ceotto et al. (2008).

Documentation of the earlier stages of character state development within the family Cixiidae with fossils therefore appears to be of great importance to better understand their evolution and also that of Fulgoroidea. Three new fossil genera from northern Burmese amber deposits are described here, representing a new cixiid lineage. Because a clear vision of the phylogenetic structure of Cixiidae is still lacking, we provisionally place these taxa into a new fossil tribe and discuss its relationships within the cixiid classification. Opportunity is taken to discuss the placement of two other cixiid fossils, *Karebodopoides aptianus* and '*Cixius*' *petrinus*. For the latter a new genus is proposed.

2. Material and methods

The material studied here consists of three pieces of burmite or Burmese (Myanmar) amber from the deposits of the Hukawng Valley of Kachin State of northern Myanmar (Cruickshank and Ko, 2003; Yu et al., 2019: fig.1). Palaeontological findings suggest that the amber is at most from late Albian, which is supported by evidence of amber redeposition and bivalve borings (Grimaldi and Ross, 2017; Smith and Ross, 2018). The Hukawng Valley amber deposit has been radiometrically dated using zircons to 98.8 ± 0.6 Ma 71, earliest Cenomanian (Shi et al., 2012), although this should be taken as a conservative minimum age of the deposit (Kania et al., 2015; Rasnitsyn et al., 2016; Mao et al., 2018a, b).

The Burma Terrane was part of a Trans-Tethyan island arc and stood at a near-equatorial southern latitude at about 100 Ma. The area of Kachin amber formation and deposition in the mid-Cretaceous times is considered to be an island or archipelago (Rasnitsyn and Öhm-Kühnle, 2018; Xing et al., 2018, 2020; Westerweel et al., 2019; Morley et al., 2020) suggesting island endemism for the Kachin amber biota. A warm, humid, nearshore marine setting with high species diversity has been proposed for the amber locality (Yu et al., 2019; Jiang et al., 2019; Bartel et al., 2021). The origin of the resin remains unclear, but Cupressaceae gymnosperms, very likely *Metasequoia* Hu & W.C. Cheng, 1948 or related taxa, were the trees exuding the resin at the time of burmite formation (Grimaldi and Ross, 2017) as well as trees of the families Araucariaceae and Taxodiaceae (Cruickshank and Ko, 2003; Poinar et al., 2007; Smith and Ross, 2018).

The amber specimens studied in the course of this work are deposited in the Insect Museum, Northwest A&F University (NWAFU), Yangling, China. The study follows the recommendations of the International Palaeoentomological Society (Szwedo et al., 2020).

The terminology for female terminalia and wing venation used herein respectively follows Bourgoin (1993) and Bourgoin et al. (2015) based on Nel et al. (2012) interpretation, with the following abbreviations for veins: CA, costal margin (costa anterior); Pc+CP, precosta + costa posterior; ScP+R, subcosta posterior + radius; RA, radius anterior; RP, radius posterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; Pcu, postcubitus; A_1, first anal vein; A_2, second anal vein. The metatibiotarsal formula LT-(Ti, Te)/Mt1/Mt2 provides the number of lateral spines on the metatibia (LT) - number of apical teeth of metatibia (T), eventually in two groups of internal (Ti) and external (Te) teeth separated with a diastema (Ti, Te)/on the apex of first metatarsomere (Mt1)/on the apex of second metatarsomere (Mt2).

3. Systematic paleontology

Order Hemiptera Linnaeus, 1758
Suborder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Latreille, 1807
Family Cixiidae Spinola, 1839

Acrotiarini Bourgoin & Luo, trib. nov.
urn:lsid:zoobank.org:act: A569D246-1595-4EE7-B40A-6D1E183FE18F.

Type genus. Acrotiara Bourgoin & Luo, gen. nov.
Composition. Acrotiara Bourgoin & Luo, gen. nov.; *Delphitiara* Bourgoin & Luo, gen. nov.; *Pentacarinus* Bourgoin & Luo, gen. nov.
Diagnosis. Medium sized specimens (5–10 mm) with wings largely surpassing body length, currently defined by the following characters shared by the three new taxa. Head capsule with paired sublaterofrontal carinae surrounding a more elevated area; median carina absent; at least laterodorsally part of frons visible in dorsal view, separated from vertex by one single transverse carina. Median ocellus present. Clypeus (not swollen) separated by a straight frontoclypeal suture from frons. Mesonotum pentacarinated. Forewing venation: common stalk ScP+R distad to basal cell; MP originating at the base of ScP+R or on the basal cell. CuA forking more or less at the same level as fork ScP and R; Pcu and A_1 joining distad of CuA fork. Terminals: RA(3), RP(2), MP(4), CuA(2). RA distinctly arched with C1 wider submedially than apically. Absence of true pterostigma (= sclerotized plate developed between ScP and the costal margin, including the corresponding area of the peripheral membrane). Veins with tubercles. Wrinkled peripheral 'vein' (Emeljanov, 2001: 67) ending distad to CuA_2. Hindwing

venation: with a regular cixiid pattern: RP(2), MP(2), CuA(3), CuP(1), Pcu(1), A_1(2), straight A_2 reaching the posterior margin. Metatibia lacking lateral metatibial spine, all apical teeth large, of same length except for slightly longer outermost teeth. No diastema. Male unknown. Female with an elongated pygofer, wax plates absent or very reduced. Gonoplacs shorter than gonapophysis VIII, themselves shorter than gonapophysis IX.
A differential diagnosis with the other cixiid tribes is provided in the discussion.

Key to Cretaceous Cixiidae of tribe Acrotiarini

1. Pedicel of antenna short, conical; on tegmen ScP+R and CuA forking at same level with cell C1 long and narrow: one transverse veinlet distad to RA fork between RA and R…… ……***Acrotiara*** Bourgoin & Luo, gen. nov.
-. Pedicel of antenna elongated-ovate; ScP+R fork distad of CuA fork……... **2**
2. Vertex almost twice as long as wide; apical metatibia teeth of equal length; on tegmen cell C1 shorter: two transverse veinlets between RA and R, first basad to RA fork; Pcu+A_1 meeting at the same level of CuA fork; Pcu+A1 stem long… ***Delphitiara*** Bourgoin & Luo, gen. nov.
-.Vertex as long as wide; outermost metatibia teeth longer than innermost ones; on tegmen cell C1 longer: one transverse veinlet between RA and RP, distad to RA fork; Pcu+A_1 meeting distad to CuA fork; Pcu+A_1 stem short…… …… ***Pentacarinus*** Bourgoin & Luo, gen. nov.

Acrotiara Bourgoin & Luo, gen. nov.

Type species. Acrotiara multigranulata Luo & Bourgoin, sp. nov.; by present designation and monotypy.
urn:lsid:zoobank.org:act: 04FD6CC4-D46C-4AD2-BB25-C1B7D1E0E9CA.

Etymology. Arbitrary composition from Ancient Greek *ἄκρος* (ákros, "highest, at the extremity") and the old Persian word تارە (*tara, tiara* in Latin, or *τιάρα* in Greek) referring to the elevated part of frons surrounded by the paired sublaterofrontal carinae. Gender feminine.
Diagnosis. Frons slightly elevated between two sublateral frontal carinae. Pedicel of antenna conical, with several *sensilla placodea.* Pterostigma absent, RA clearly arched with a relatively long and bent cell C1; veins with tubercles in groups of 3–5 at the basal and middle part of ScP+R, median portion of MP, median part of CuA_1 and CuA_2 and distal part of Pcu+A_1; all other veins and parts bearing only paired tubercles, one on each side of the vein with setae arranged in a V-formation along the vein. Basal fork of ScP+R and CuA in basal third of tegmen. Metatibia without lateral spines, with 6 apical teeth, without metatarsal diastema; Gonapophysis IX elongate, relatively wide, apical portion obtuse and curved dorsally.
Description. **Head.** Head including compound eye slightly narrower than pronotum. Vertex less than twice as long as wide, not surpassing level of anterior margin of compound eyes; anterior margin of vertex angulate, not reaching the sublaterofrontal carinae; vertex with a distinct median carina and two foliaceous lateral carinae. Frons, visible in dorsal view, forming a triple U-shaped margin (but not carinated); two median frontal carinae elevated, apical portion straight, converging to median ocellus but not reaching it; median ocellus distinct, large, slightly elevated. Lateral frontal carinae foliated, distinctly higher than the level of eyes. Frontoclypeal suture almost straight. Clypeus slightly convex, with a well-developed median carina, lateral carinae slightly ridged, converging but not fused. Rostrum long, surpassing metacoxae, probably reaching the seventh sternum (but this part appears to be damaged on the specimen). In lateral view, lateral ocelli distinct, situated below eyes. Scape of antenna very short, ring-shaped; pedicel oval, with several distinct *sensilla placodea*; in frontal view, pedicel not surpassing external margin of compound eyes; flagellum long, at least 2.5 times as long as pedicel, basal bulb of flagellum obtuse and large.
Thorax. Pronotum narrow, anterior margin straight, posterior one medially distinctly angulate, laterally widely convex; lateral carinae behind compound eyes delimitating an elevated lateral plate; median carina present. Tegulae large. Mesonotum with five distinct carinae, median carina present, submedian carinae evenly convex anteriorly, subparallel posteriorly, anteriorly approaching to median one well before anterior margin of mesonotum; lateral carinae not parallel to submedian carinae, sinuate anteriorly, basal and apical portion reaching margins.
Wings. Tegmen translucent, veins bearing many setae, arranged in a V-formation along the veins. Basal cell about 5 times as long as wide, stem ScP+R emerging from basal cell at same level as MP. ScP+R subparallel to costal margin, forked about $^1/_3$ of tegmen length; RA distinctly arched, trifid, with ScP-RA area wider apically than proximally, with 3 subcostal cells: stigma cell at least twice as large as two other cells. RP slightly curved medially (less curved than RA), with 2 terminals. One transverse vein (*ir*) between RA and RP, closing C1 apically. MP forked almost at nodal line, stem MP_{1+2} very short, stem MP_{3+4} long and curved; MP_1 and MP_2 subparallel; MP_1 reaching apex of tegmen; transverse veinlet imp_{1-2} in apical line distad to imp_{2-3}, which is shifted more basally; stem MP_{3+4} forked in apical $^1/_4$ of tegmen. Claval vein Pcu+A_1 meeting at same level as fork ScP+RA and RP, but slightly distad of CuA fork; stem Pcu+A_1 closes into posterior margin of tegmen, reaching it distinctly basad of CuP.
Costal cell wider than C1, radial cell and medial cell more or less same width, cell C5 slightly wider medially. C1 quite long, bent due to arched RA, almost starting at same level of C5, narrowing apically; C2 about 5 times as long as wide, slightly wider proximally; C3 and C4 arcuate, C5 closed by *icua.*
Legs. Metatibia narrow at base, widening towards apex, with small setae but without lateral spines, with six apical teeth, without metatarsal diastema; apical lateral metatibial teeth longer than the others. Basitarsomere widening apically, distinctly longer than combined length of second and apical tarsomeres. Second and third tarsomere wider apically, of same length. Metatibiotarsal formula: 0–6/8/8, first and second tarsomere with thin and acute setae (not platellae) behind teeth, absent in the two external spines.
Female terminalia. Ninth tergite conical, longer than wide. Anal tube longer than wide in dorsal view, narrow at base, and then widening apically; anal style almost as long as anal tube, finger-shaped apically. Ovipositor well-developed. Gonoplacs elongated, relatively wide, apical portion obtuse and curved dorsally.

Acrotiara multigranulata Luo & Bourgoin**,** sp. nov.
(Figs. 1–3)

Etymology. Referring to the numerous granules (tubercles) present on veins.
urn:lsid:zoobank.org:act: B49FBD53-968D-414D-A018-D5A7-134C0F43.
Type material. Holotype, HO221990. Female adult, in Myanmar amber, left tegmen outspread, with a thin inclined crack in its apical third. In dorsal view, head and thorax with slightly damaged right-side surface.
Horizon and locality. Lowermost Cenomanian, Upper Cretaceous, Kachin amber, Hukawng Valley, Kachin State, northern Myanmar.

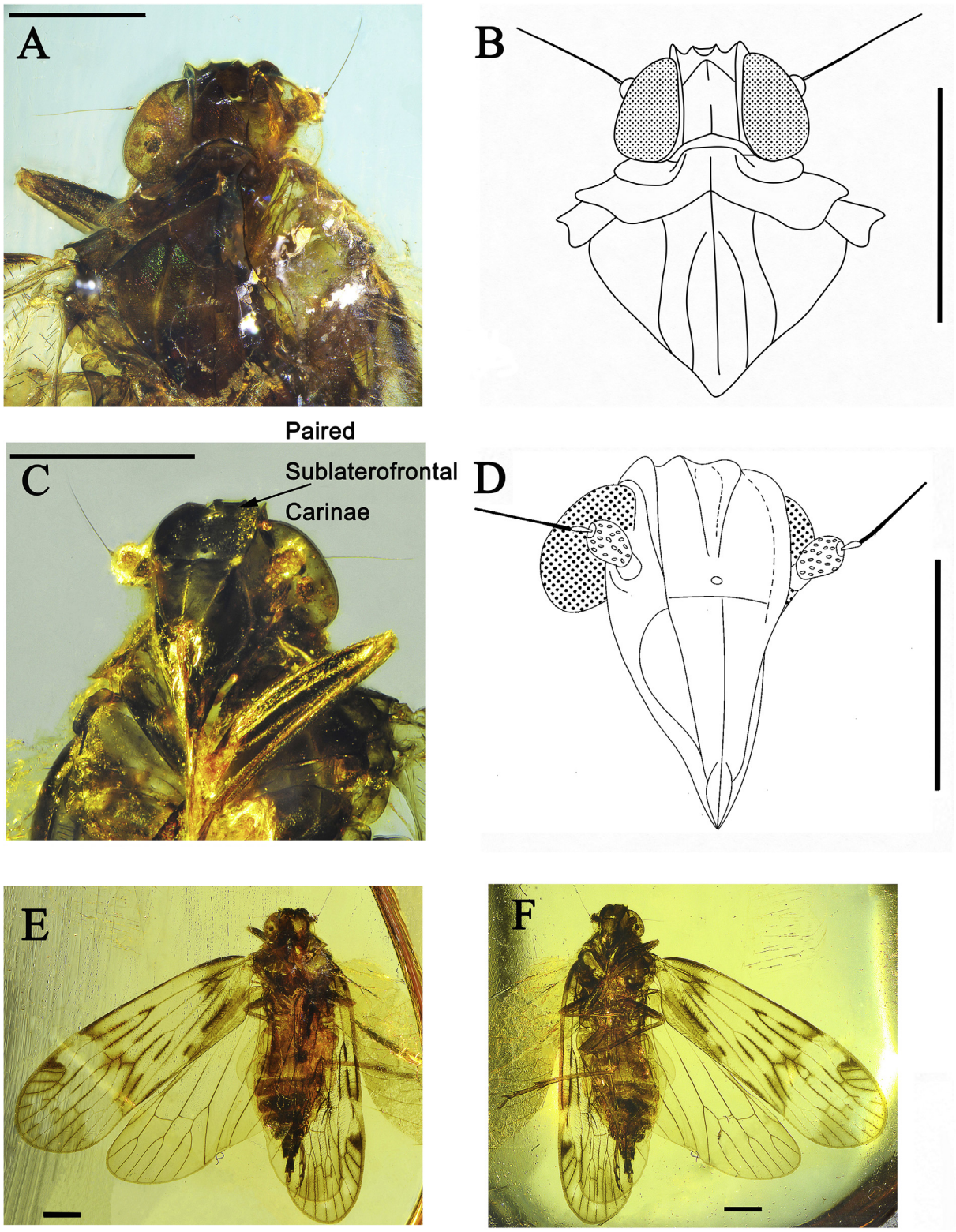

Fig. 1. *Acrotiara multigranulata* Luo & Bourgoin, sp. nov., holotype specimen HO221990. A, Head and thorax, in dorsal view. B, Line drawing of head and thorax, in dorsal view. C, Face, in ventrolateral view. D, Line drawing of face, in ventrolateral view. E. Female adult, in dorsal view. F. Female adult, in ventral view. Scale bar = 1 mm.

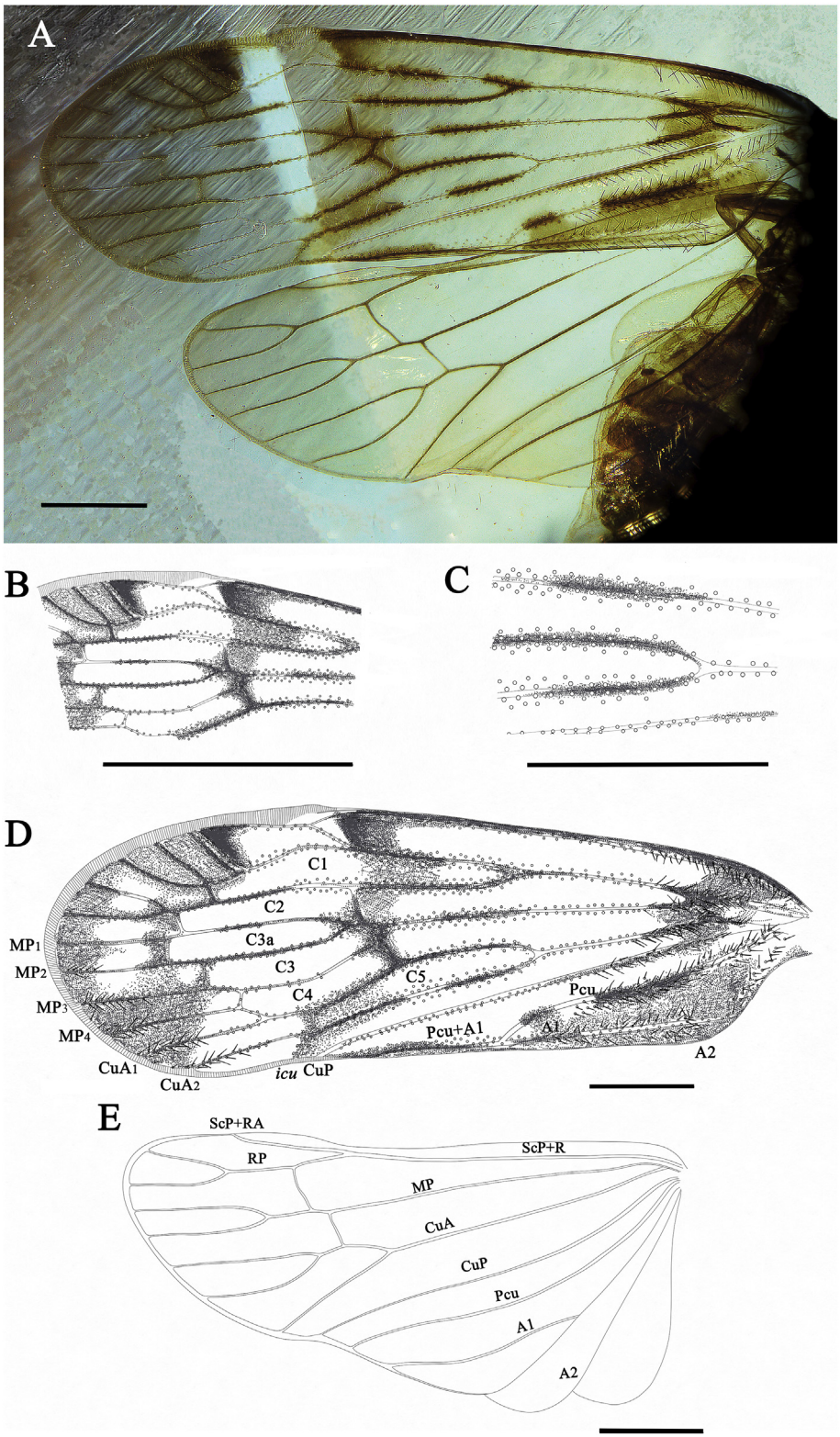

Fig. 2. *Acrotiara multigranulata* Luo & Bourgoin, sp. nov. (HO221990). A, Left forewing and hind wing. B, Pterostigma part of forewing. C, basal fork of CuA vein of forewing. D. Left forewing. E, Left hind wing. Scale bar = 1 mm.

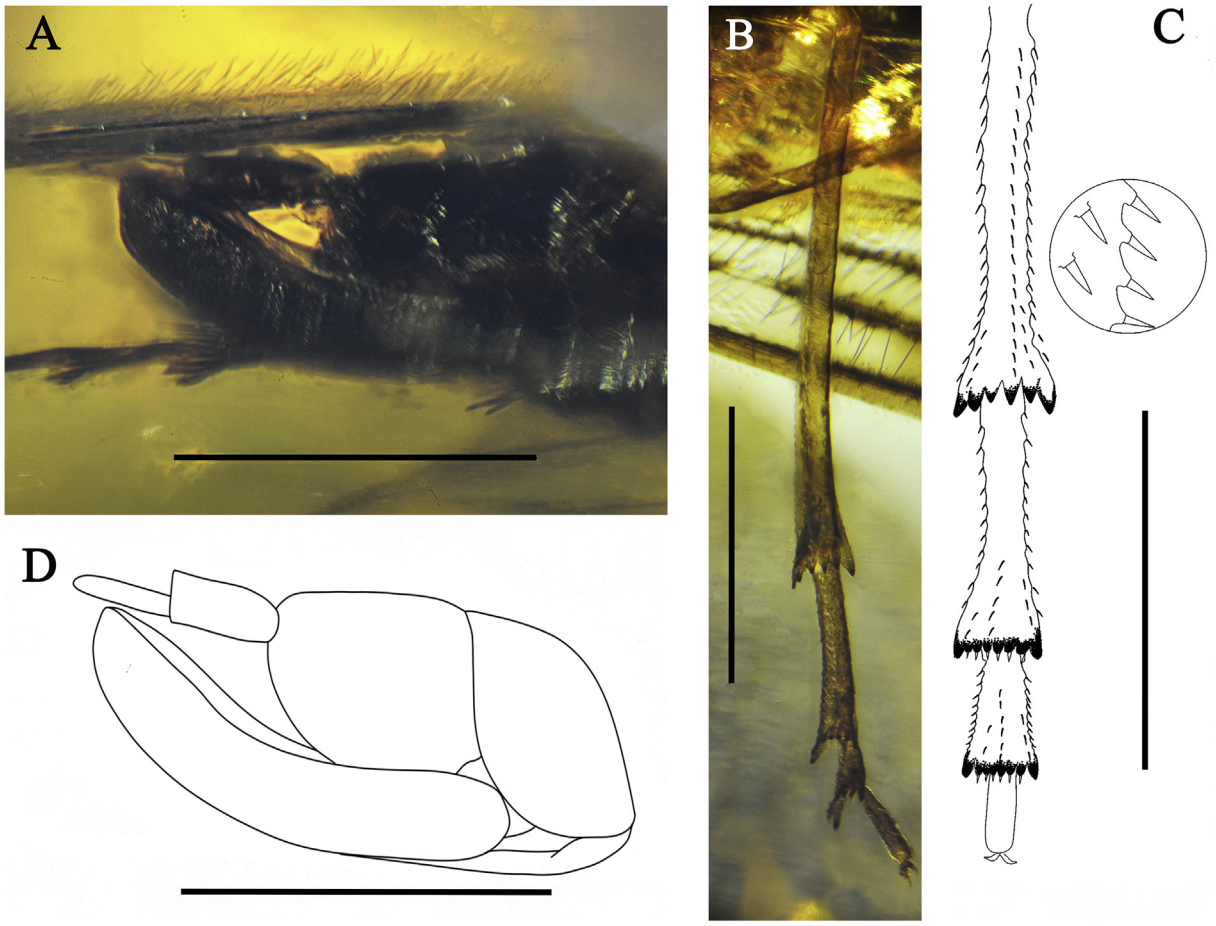

Fig. 3. *Acrotiara multigranulata* Luo & Bourgoin, sp. nov. (HO221990). A, D, Female terminalia. B, C, Hind tibia. Scale bar = 1 mm.

Diagnosis. General color fuscous, tegmina hyaline, with three darker bands (basally, medially including nodal line, and apically. A clear dark patch in distal corner of first subcostal cell. Hindwing hyaline. Veins covered with numerous tubercles, particularly medially arranged in groups of three to five. Wings surpassing end of body.

Description. Length of body 8.55 mm. Head including compound eyes 1.39 mm wide, length of vertex in midline 0.57 mm, width of vertex at anterior margin 0.40 mm, at posterior margin 0.50 mm. Length of face in mid line 1.40 mm; frons 0.37 mm long in mid line, 0.52 mm at widest point at level of lateral ocelli; clypeus 0.96 mm long in mid line; rostrum 3.23 mm, apical segment shorter, 0.96 mm. Pronotum length/width: 1.85/0.32 mm; mesonotum length/width: 1.99/1.66 mm. Tegmen length/width: 7.82/2.66 mm. Hind femur 1.27 mm, metatibia 2.07 mm, hind tarsus 1.29 mm long, basitarsomere 0.73 mm long, mid and apical tarsomere 0.56 mm. Ninth tergite 0.56 mm long, 0.53 mm wide at basal portion, 0.32 mm wide at apical portion, anal tube 0.41 mm long, 0.14 mm wide at narrowest portion, anal style length/width: 0.25/0.11 mm. Gonoplacs 1.22 mm long.

Basal cell and basal portion of ScP, R, M and CuA stems with brown fumations. A brown oblique band extending from base of tegmen to junction of claval veins. A second transverse median band from apical anterior angle of costal cell, median part of tegmen to level of *icu* vein covered with irregular brown suffusion following the first transverse veins *rp-mp*$_1$ and *mp-cua*$_1$. Stigma cell between ScP and RA apically dark-brown. A third band of obsolete suffusions in apical $^1/_5$ of tegmen. Veins yellowish, except at the level of darker bands where some segmental dark-brown marks are present. Tegmen about 2.9 times as long as wide, narrow at base and then expanded apically. Costal margin slightly curved at base, and then almost straight, slightly concave at ScP terminal, apex of tegmen rounded, longest at first terminal of MP, apex of clavus arcuate, posterior margin straight.

Delphitiara Bourgoin & Luo, gen. nov.

Type species. Delphitiara tibiocoronata Luo & Bourgoin, sp. nov.; by present designation and monotypy.
urn:lsid:zoobank.org:act: 64909796-9136-43C0-86D1-0CF29B83FE7D.

Etymology. Arbitrary composition referring to the paired sublaterofrontal carinae also present in Delphacidae and the old Persian word تاره (*tara, tiara* in Latin, or *τιάρα* in Greek) referring to the elevated part of frons surrounded by the paired sublaterofrontal carinae. Gender feminine.

Diagnosis. The new genus is similar to the genus *Acrotiara* Bourgoin & Luo, gen. nov., but differs by a longer vertex surpassing anterior margin of compound eyes (shorter and not surpassing this level in *Acrotiara* gen. nov.); pedicel of antennae oval (longer than in *Acrotiara*); veins with pairs of tubercles, bearing long setae, arranged in V-formation along the veins (groups of 3–5 tubercles at basal and middle portions in *Acrotiara*). Basal fork of SC+R and CuA in basal $^1/_4$ of the tegmen. All metatibial apical teeth of equal length (outermost apical teeth longer than innermost ones in *Acrotiara*); metatibiotarsal formula: 0–8/10/10 (0–6/8/8 in *Acrotiara*). Gonoplacs narrow, apical portion arcuate (versus wide and apical portion obtuse in *Acrotiara*).

Head. Head including compound eye narrower than pronotum. Vertex almost twice as long as wide, anterior margin angulate reaching dorsal sublaterofrontal carinae; a distinct median carina not reaching anterior margin and two foliaceous lateral carinae. Frons visible in dorsal view on each side of vertex, forming a triple U-shaped margin (but not carinate); two median frontal carinae elevated, slightly converging to median ocellus but not reaching it, slightly diverging medially; median ocellus distinct, large, slightly elevated. Lateral frontal carinae foliated, distinctly higher than level of eyes. Frontoclypeal suture almost straight. Clypeus slightly convex, with a well-developed median carina, lateral carinae slightly ridged, converging but not fused. Rostrum long surpassing tip of hind coxae, probably by 3 or 4 segments, apical segment almost as long as subapical segment. In lateral view, lateral ocelli distinct, under the eyes. Scape of antenna very short ring-shaped, pedicel oval, with several *sensilla placodea*; in frontal view, pedicel not surpassing external margin of compound eyes; flagellum long, at least twice as long as pedicel, basal bulb of flagellum obtuse and large.

Thorax. Pronotum narrow, anterior margin almost straight, posterior one medially distinctly angulate; lateral carinae behind compound eyes present but this area flattened and damaged; median carina present. Tegulae large. Mesonotum with five distinct carinae, median carina present and complete; submedian carinae of mesonotum S-shaped, apex almost reaching posterior margin of pronotum, distal part clearly diverging; lateral carinae slightly and evenly convex, basal and apical portion reaching to the margins.

Wings. Tegmen translucent, veins bearing many setae, arranged in V-formation along the veins. Costal margin slightly and evenly convex, apex of tegmen rounded, longest between RA and MP_1, posterior margin straight. Basal cell about 2.5 times as long as wide, stem ScP+R emerging from basal cell at same level as stem MP, ScP+R forked about ¼ of tegmen length, and subparallel to costal margin; RA trifid, subcostal stigma cell as long as the two others combined; RA distinctly arched bearing many setae, with tubercles arranged in pairs; RP more or less parallel to costal margin, forked at level of apical line; two terminals. One or two (left wing) *ir* transverse veinlets. MP forked slightly basad of apex of clavus, in nodal line; stem MP_{1+2} quite short, MP_{3+4} longer and curved; $imp_{1\text{-}2}$, distad to $imp_{2\text{-}3}$; Pcu+A_1 meeting distad of fork ScP+RA+RP, but at same level the forking of CuA; stem Pcu+A_1 running close to the posterior margin merging with it far basad of CuP.

Costal cell slightly narrower than C1 in its medial part, radial cell and medial cell more or less same width, C5 slightly wider. Cell C1 quite long and starting slightly basad of C5, narrower on apical portion, and close by transverse veinlet *im*; C2 almost rectangular about 5 times as long as width, slightly wider proximally; C3 and C4 parallel, arcuate; C5 long, medially wider.

Legs. Metatibia narrow at base, then widening apically, without lateral spines, with 8 apical teeth of equal length; basitarsomere widening apically, distinctly longer than combined length of second and third tarsomeres. Second and third tarsomere wider apically, of same length. Metatibiotarsal formula: 0–8/10/10, first and second tarsomere with setae (no platellae), absent in the two lateral teeth.

Female terminalia. Ninth tergite longer than wide. Anal tube longer than wide in dorsal view, narrow at base, widening towards apex; anal style shorter than anal tube, finger-shaped. Ovipositor well-developed. Gonoplacs elongate, relatively narrow, apical portion arcuate and curved dorsally.

Delphitiara tibiocoronata Luo & Bourgoin, sp. nov.
(Figs 4–6)

Etymology. Referring to the metatibial crown formed by the apical spines.

urn:lsid:zoobank.org:act: BABBFC50-5E61-4A4D-A9F1-E0650AB81932.

Type material. Holotype, HO221991. Female adult, in Myanmar amber. The specimen is well preserved in a piece of yellow amber with some impurities.

Horizon and locality. Lowermost Upper Cretaceous, Cenomanian; Kachin amber, Hukawng Valley, Kachin State, Myanmar.

Diagnosis. Female adult. General color fuscous, tegmina hyaline with basal cell and basal portion of ScP+R, M and CuA stems with brown fumations; with a Y-shaped band covering nodal line area. A wide dark patch covering half of distal part of first subcostal cell. Hindwing hyaline. Veins covered with tubercles arranged in pairs. Wings largely surpassing end of the body.

Description. Length of body 5.87 mm. Head with compound eyes 0.88 mm wide, length of vertex in mid line 0.30 mm, width of vertex at anterior margin 0.21 mm, at posterior margin 0.29 mm. Length of face in mid line 1.54 mm; frons 0.57 mm long in mid line, 0.45 mm at widest point at level of lateral ocelli, clypeus 0.91 mm long in mid line; rostrum 1.85 mm, apical segment shorter, 0.69 mm. Pronotum length/width 0.65/0.11 mm; mesonotum length/width 0.86/0.64 mm. Tegmen length/width 4.96/1.87 mm. Hind femur 1.26 mm, metatibia 1.76 mm, hind tarsus 1.13 mm, basitarsomere 0.63 mm, second and third tarsomere 0.5 mm. Gonoplacs 1.9 mm.

Tegmen about 2.7 times as long as wide. Basal cell and basal portion of CP, veins of basal cell, dark brown. CP, ScP+RA and CuA_2 with veins alternatively pale yellowish and dark brown; RP, MP_{1+2} at the nodal level and imp_1-cua_1 dark brown. A Y-shaped band of darker suffusion at nodal line area with second distal half of stigma cell darker. Rostrum distinctly surpassing hind coxae. Metatibia widened towards apex, without lateral spines, metatibiotarsal formula: 0–8/10/10, second and third tarsomere both with 8 setae.

Pentacarinus Bourgoin & Luo, gen. nov.

Type species. Pentacarinus kachinensis Luo & Bourgoin, sp. nov.; by present designation and monotypy.

urn:lsid:zoobank.org:act: DAB6C65D-0CDE-4CEC-9D3A-D3966F49F420.

Etymology. Arbitrary composition referring to the penta-carinated mesonotum. Gender masculine.

Diagnosis. The new genus is similar to *Acrotiara*, gen. nov., but differs by vertex wider than long (versus narrower in *Acrotiara*), not reaching the level of anterior margin of compound eyes; pedicel of antenna elongated, surpassing lateral margin of compound eye (reaching or not reaching in *Acrotiara*); tubercles on tegmina less numerous and arranged in pairs, ScP+R fork more proximal in basad $^1/_5$ of the tegmen, well basad of CuA fork (first $^1/_3$ in *Acrotiara* and aligned with CuA fork); a short Pcu+A_1 stem (long in *Acrotiara*).

Description. **Head.** Vertex including compound eye narrower than pronotum. Vertex as long as wide, anterior margin roundly angulate, reaching dorsal part of sublaterofrontal carinae; with a distinct median carina, not reaching anterior margin and two foliaceous lateral carinae. Frons visible in dorsal view, divided in three compartments by sublaterofrontal carinae, forming a triple U-shaped margin (but not carinate). Median ocellus visible. Lateral frontal carinae foliated, distinctly higher than level of eyes. Clypeus convex, with a well-developed median carina, lateral carinae slightly ridged, converging but not fused. Rostrum, just reaching hind coxae. Scape of antenna very short, ring-shaped, pedicel elongated-ovate, with several *sensilla placodea*; in front view, pedicel surpassing external margin of compound eyes; flagellum long, at least 1.5 times as long as pedicel, basal bulb of flagellum elongated and large.

Wings. Tegmen translucent, veins bearing many setae, arranged alternatively in V-formation along the veins. Costal margin

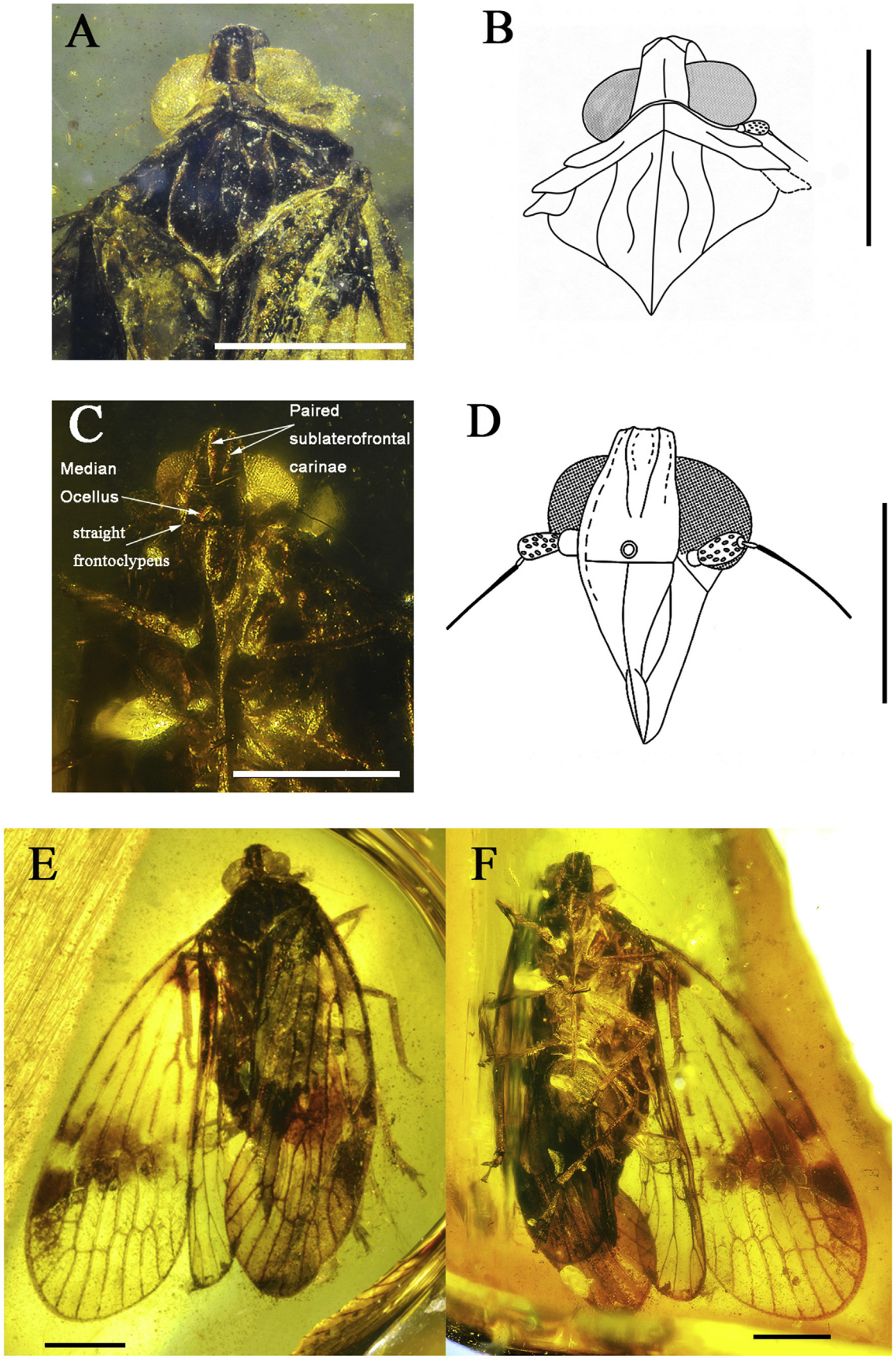

Fig. 4. *Delphitiara tibiocoronata* Luo & Bourgoin, sp. nov., holotype specimen HO221991. A, B, Head and thorax, in dorsal view. C, D, Face, in ventral view. E. Female adult, in dorsal view. F. Female adult, in ventral view. Scale bar = 1 mm.

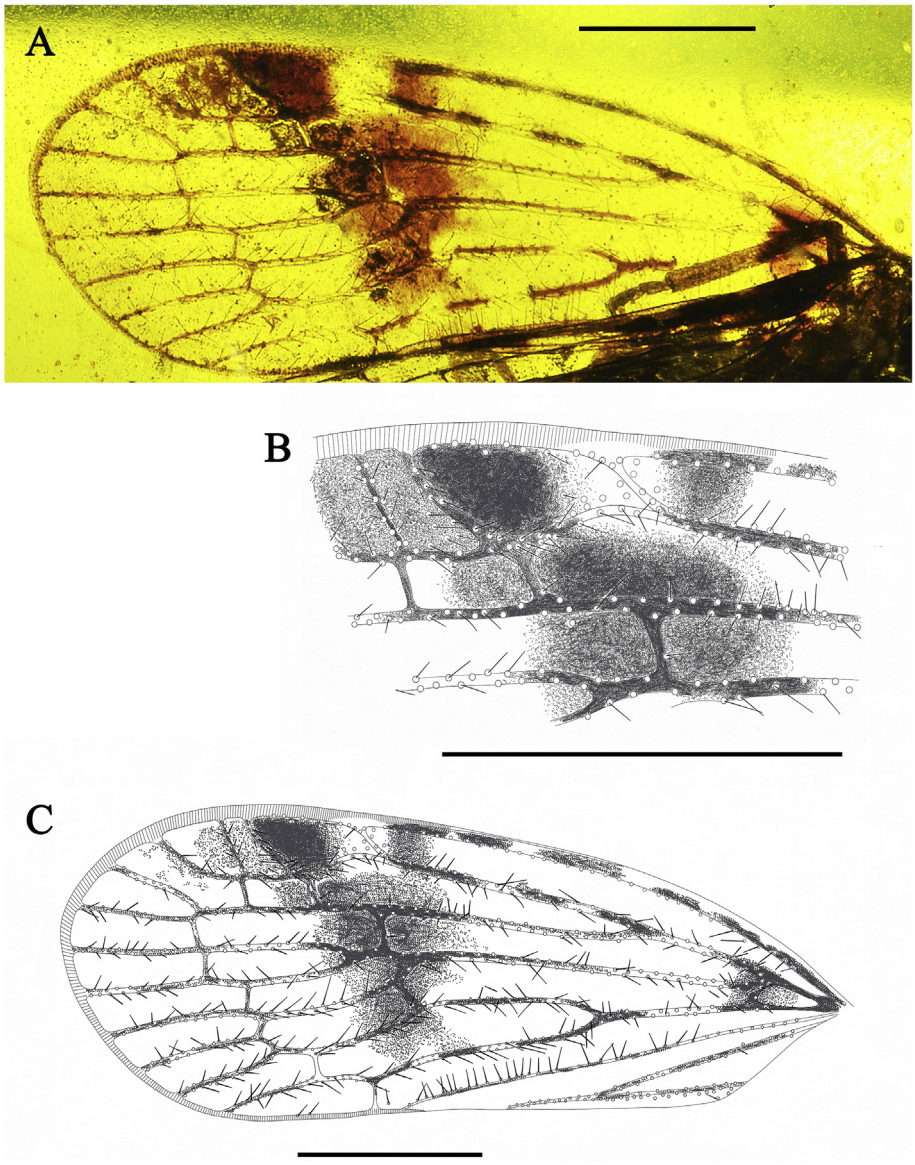

Fig. 5. *Delphitiara tibiocoronata* Luo & Bourgoin, sp. nov. (HO221991). A, Left forewing. B, Line drawing of pterostigma portion of forewing. C, Line drawing of left forewing. Scale bar = 1 mm.

slightly and evenly curved, wide, CA without setae, CP with setae, apical anterior angle of costal cell rounded; apex of tegmen rounded, tornus arcuate, posterior margin straight. Basal cell wide and large, about 3.4 times as long as wide; ScP+R forked about $^{1}/_{5}$ of tegmen length, subparallel to costal margin; RA trifid, subcostal stigma cell slightly longer as the two others combined; RA distinctly arched bearing setae with tubercles arranged in pairs; RP more or less parallel to costal margin, forked at level of apical line: RP(2). One *ir* transverse veinlet. MP leaving basal cell at same point as ScP+R, forked at level of apex of clavus, in the nodal line; MP_{1+2} long, stem MP_{3+4} relatively short (C3 shorter than C3′) and curved; $imp_{1\text{-}2}$ distad to $imp_{2\text{-}3}$; CuA_1 sinuated; $Pcu{+}A_1$ meeting distad of forking of ScP+RA+RP and forking of CuA; stem $Pcu{+}A_1$ short, running close to posterior margin, merging with it far basad of CuP. Basal cell longer than wide, almost quadrate.

Costal cell slightly wider than C1, radial cell and medial cell more or less with same width; C5 long, wider at nodal line level, narrowing on its apical portion; C2 about 4.7 times as long as wide, slightly wider at base; C3 more or less as long as C4; C5 long, wider at nodal line level.

Legs. Metatibia widening apically, without lateral teeth but with minute setae, with 5–6 apical teeth, outermost one slightly longer than the others; basitarsomere slightly widening apically, distinctly longer than combined length of second and third tarsomeres; second and third tarsomere same length. Metatibiotarsal formula: 0-(5–6)/6/(7–8), no setae under lateral teeth of basitarsomere, second tarsomere with setae under all teeth.

Female terminalia. Ninth tergite rounded, conical. Anal tube more or less as long as wide in dorsal view, almost four times longer in lateral view. Anal style long, slender and tubular. Ovipositor with gonapophysis VIII elongate, apical portion acute, slightly curved dorsally. Gonapophysis IX with sinuated inner margin, angulated at $^{1}/_{4}$ of apex and wider in its basal $^{1}/_{3}$ portion. Gonoplacs shorter, wide and robust, ventral external margin punctuated/pointed.

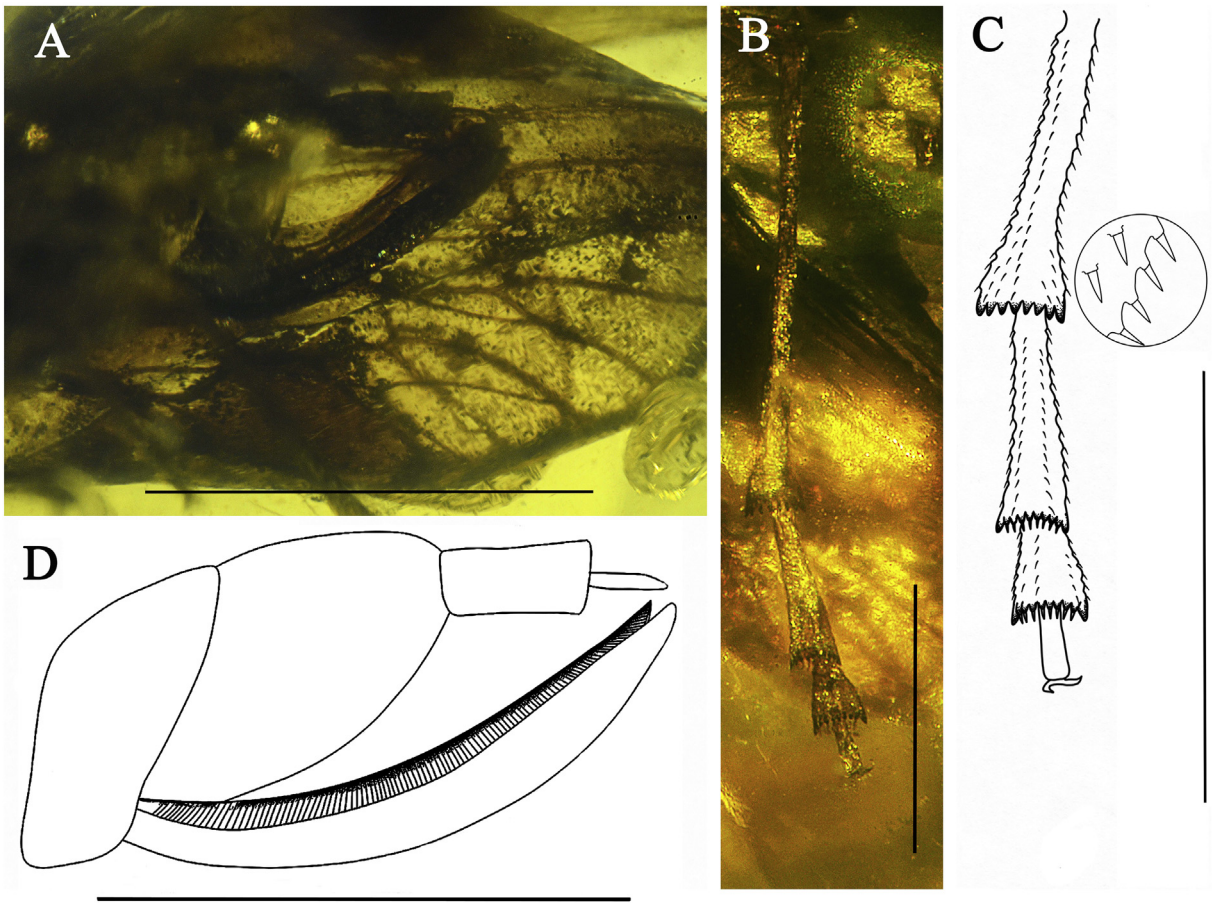

Fig. 6. *Delphitiara tibiocoronata* Luo & Bourgoin, sp. nov. (HO221990). A, D, Female terminalia. B, C, Hind tibia. Scale bar = 1 mm.

Pentacarinus kachinensis Luo & Bourgoin, sp. nov.
(Figs. 7–9)

urn:lsid:zoobank.org:act: A1A80FEA-0EAD-49E5-9E5F-41DB7E642BD9.

Etymology. Referring to Myanmar state, Kachin, where the fossil was found.

Type material. Holotype, HO221992. Female adult, in Myanmar amber. Specimen well preserved, with the left tegmen stretched and apical portion folded; face and end of abdomen are covered by several air bubbles.

Horizon and locality. Lowermost Upper Cretaceous, Cenomanian; Kachin amber, Hukawng Valley, Kachin State, Myanmar.

Diagnosis. Female adult: General color ochraceous. Tegmina hyaline with one dark brown patch in distal part of subcostal stigma cell. Tegmina longest at apex of MP_1. Costal margin wide with an internal row of setae. Veins densely covered with tubercles arranged in pairs. MP_{1+2} almost absent. $CuP+A_1$ long, covering almost $^1/_3$ of clavus. Hind wing hyaline. Wings largely surpassing end of the body.

Description. Length of body 7.10 mm. Head with compound eyes 1.40 mm wide, length of vertex in mid line 0.35 mm, width of vertex at anterior margin 0.46 mm, at posterior margin 0.57 mm. Length of face in mid line 1.79 mm; frons 0.65 mm long in mid line, 0.63 mm at widest point at level of lateral ocelli, clypeus 1.11 mm long in mid line; rostrum 1.64 mm, apical segment shorter, 0.77 mm. Pronotum length/width 1.53/0.14 mm; mesonotum length/width 1.48/1.55 mm. Tegmen 5.93 mm long. Metafemur 1.24 mm, metatibia 1.58 mm, metatarsus 1.41 mm with basitarsomere 0.72 mm, second and third tarsomere 0.69 mm. IXth tergite 0.24 mm long, 0.75 mm wide at basal portion, 0.30 mm wide at apical portion, anal tube 0.24 mm long, 0.23 mm wide at narrowest portion, anal style length/width 0.30/0.11 mm. Gonapophysis VIII 1.40 mm, gonapophysis IX 0.79 mm long; gonoplacs 0.68 mm.

General color ochraceous. Tegmen about 2.5 times longer than wide, hyaline; Veins brownish, bearing setiferous tubercles, more or less alternatively distributed on each side of vein; dark brown patch in distal part of subcostal stigma cell.

Family Cixiidae Spinola, 1839
Tribe Cixiini Spinola, 1839

Barremixius Bourgoin & Szwedo, gen. nov.
(Figs 10B)

Type species. Cixius petrinus Fennah, 1961, by present designation and monotypy.
urn:lsid:zoobank.org:act: 2D85B037-B7A7-4A22-9082-DE410B704E7C.

Etymology. Arbitrary composition referring to the stratum in which the fossil was found (Barremian) and the generic name *Cixius*. Gender: masculine.

Diagnosis. Tegmen with costal margin slightly and evenly convex, longest between MP_1 and MP_2, posterior margin straight. Branches: ScP(1), RA(3), RP (2), MP(6), CuA(2), *icu* long, joining margin distad of apex of clavus. Pcu+ A_1 relatively short, not running close to posterior margin. ScP+R and MP leaving basal cell at same point, both forking at first ¼ of the tegmen; Pcu and A_1 meeting distad. Pterostigma absent. MP_{1+2} and MP_{3+4} forking at same level, one

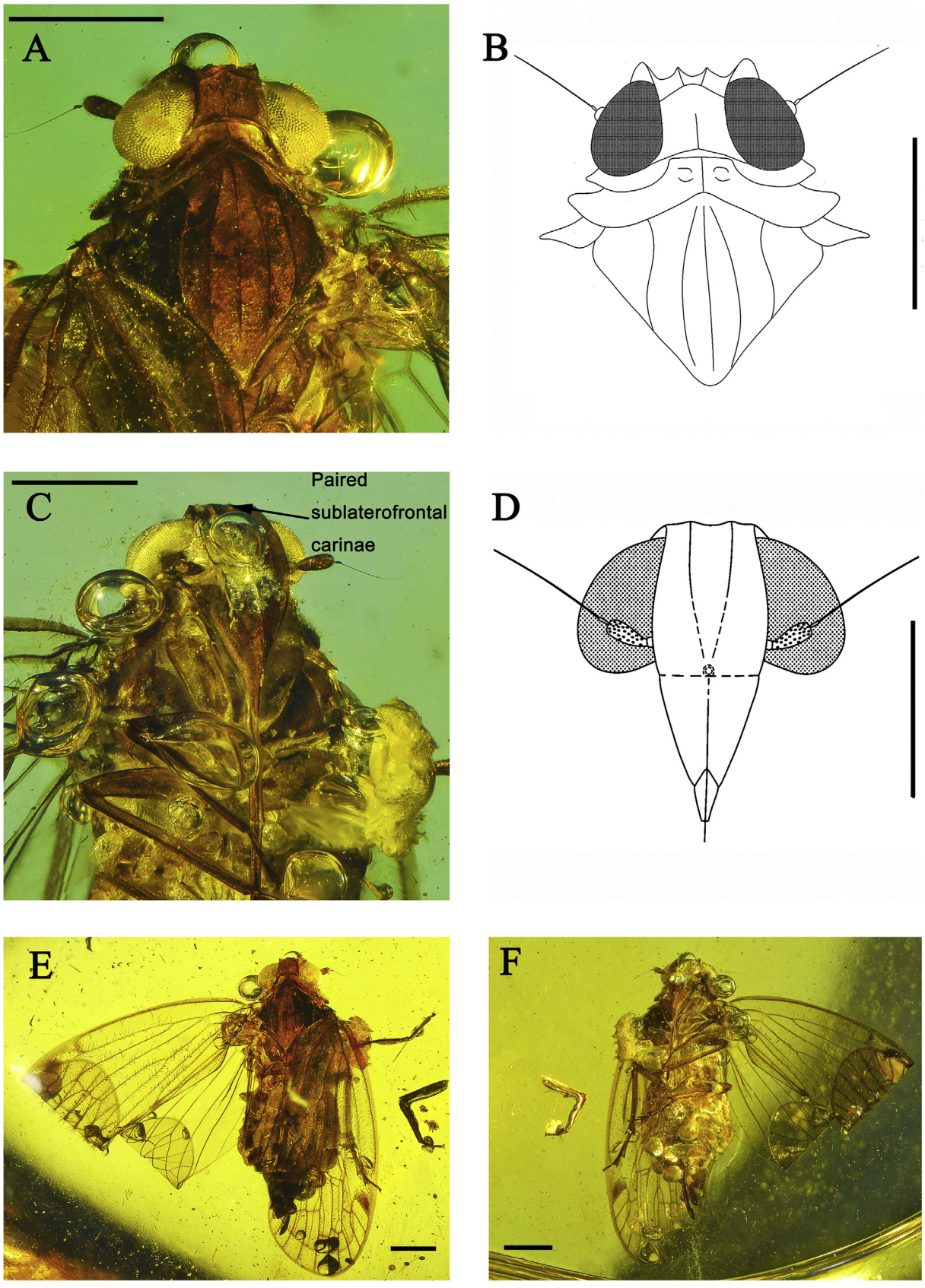

Fig. 7. *Pentacarinus kachinensis* Luo & Bourgoin, sp. nov., holotype specimen HO221992. A, B, Head and thorax, in dorsal view. C, D, Face, in ventral view. E. Female adult, in dorsal view. F. Female adult, in ventral view. Scale bar = 1 mm.

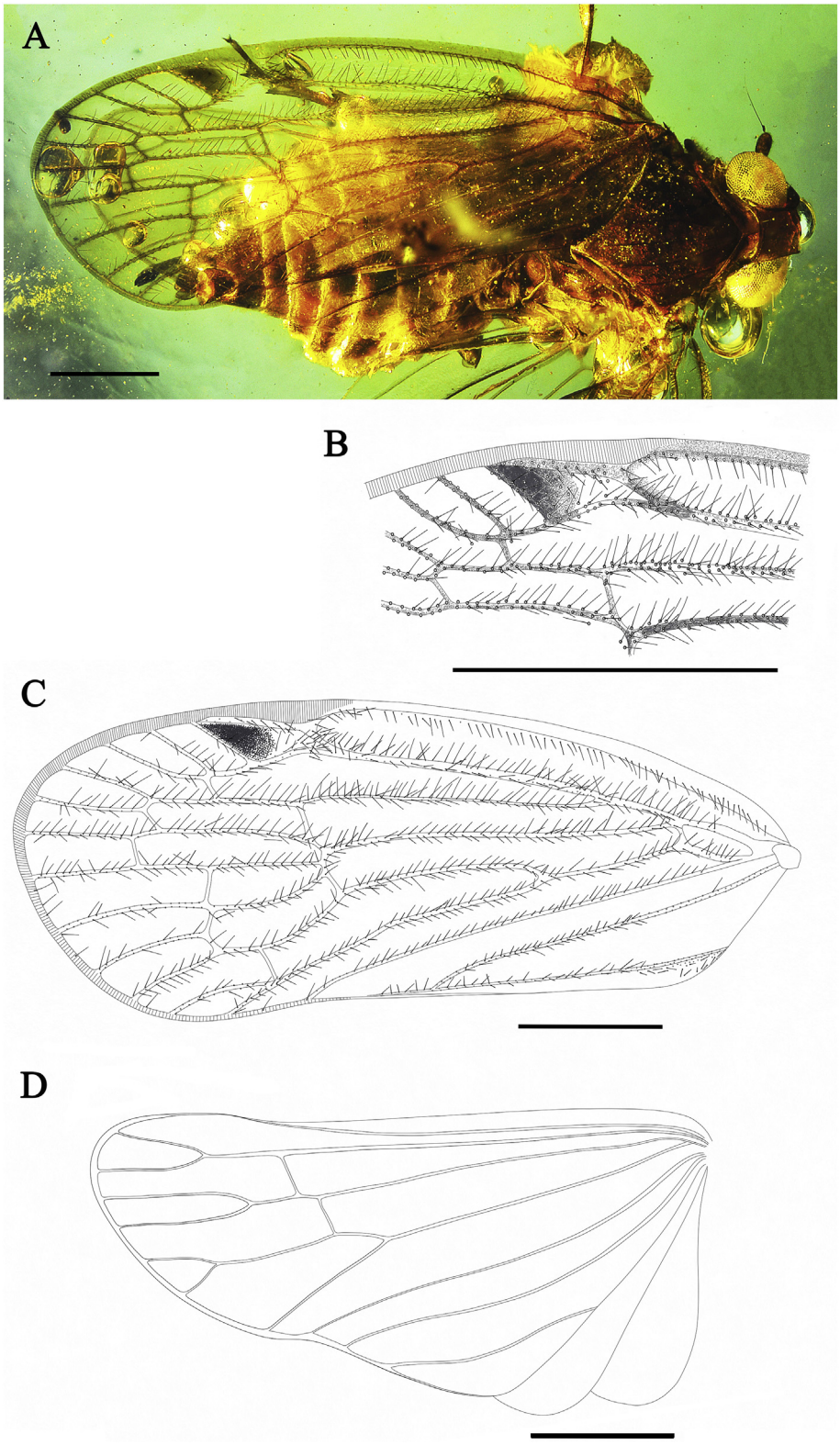

Fig. 8. *Pentacarinus kachinensis* Luo & Bourgoin, sp. nov. (HO221992). A, Left forewing. B, Pterostigma part of forewing. C, Left forewing. D, Left hind wing. Scale bar = 1 mm.

imp between MP_2 and MP_3; MP_4 with two terminals. C1 with RA not arched, of same width medially and apically; C3 proximad to C3a. Wing with *rp-mp* distad to MP fork, but we could not observe this character reported by Fennah (1961).

Composition. Barremixius petrinus (Fennah, 1961) comb. nov.
Remark. Holotype. BMNH In. 59335, collected by C. Flood-Page in June 1959; apical portion of a wing overlying a substantially complete tegmen, as exposed from below.

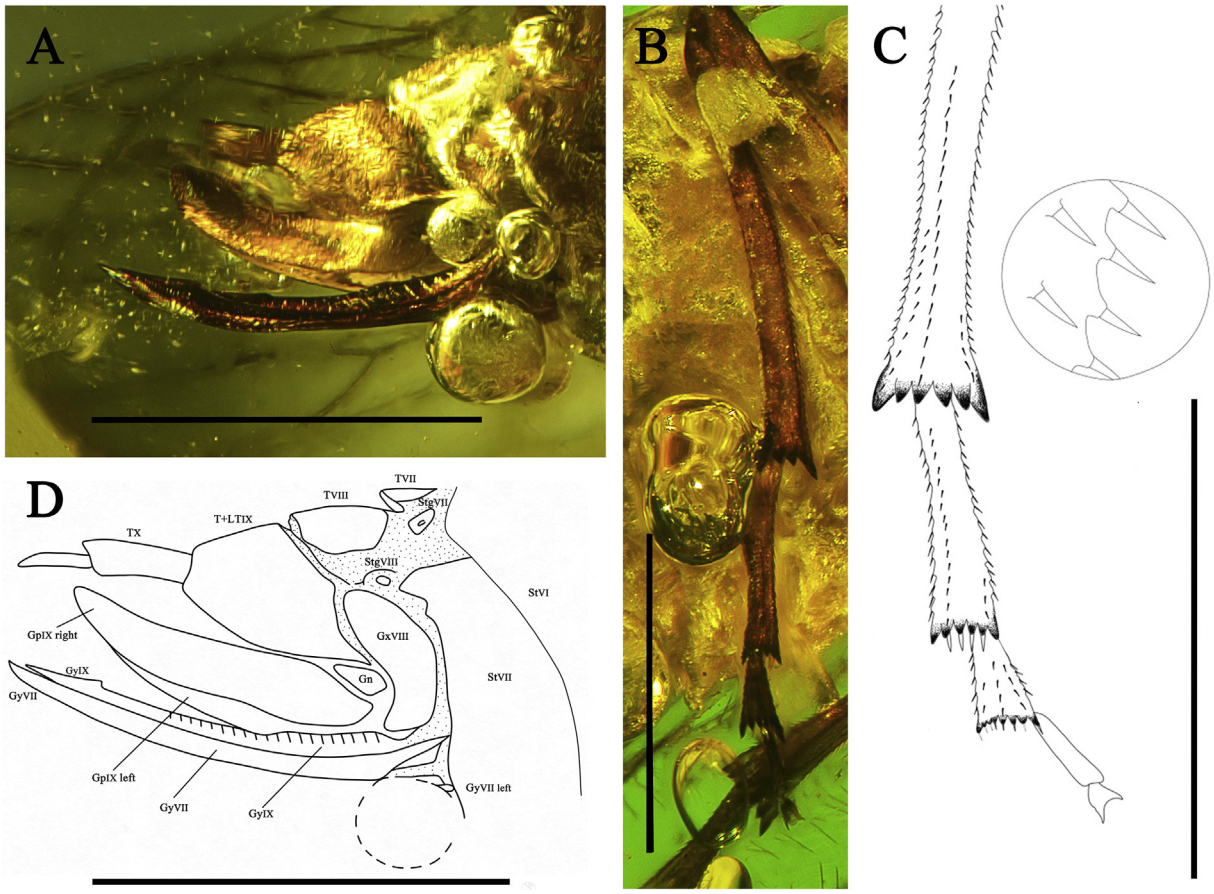

Fig. 9. *Pentacarinus kachinensis* Luo & Bourgoin, sp. nov. (HO221992). A, D, Female terminalia, B, D, Hind tibia. Scale bar = 1 mm. Gn: Gonangulum; GpIX right, GpIX left: Right gonoplac, left gonoplac; GxVIII: Gonocoxa VIII; Gy VIII, GyIX: gonapophysis VIII, gonapophysis IX; St VI, St VII: Sternite VI, sternite VII; Stg VII, Stg VIII: stigmate VII, stigmate VIII; T+LTIX: tergite and laterotergite IX (pygofer); TVII, VIII: Tergite VII, tergite VIII; TX: Anal tube (segment X).

Horizon and locality. Barremian; Lamb's Brickworks, locality 170/348485, Upper Member of Weald Clay Formation, South Godstone, Tandridge, Surrey, England, United Kingdom.

4. Discussion

4.1. Where to place these three newly described fossils and Acrotiarini?

With their venation pattern, veins covered with tubercules and their habitus, the three fossils from Kachin amber described above should be placed within the Cixiidae which are currently divided into 3 subfamilies and 16 tribes (Emeljanov, 2002; Holzinger et al., 2002; Bourgoin, 2021). Following the diagnoses of these different groups, habitus of the fossils and the character state 'membrane of the tegmen (wrinkled peripheral 'vein') not extending beyond the line of the commissural margin of clavus' excludes the fossils from both Bothriocerinae and Borystheninae and should place them into the Cixiinae *sec.* Emeljanov, 1989.

However, the Cixiidae phylogeny is not well understood (Löcker et al., 2006a: 60). The prelimary phylogram of Emeljanov (2002: 111) remains incomplete, not including the subfamily Borystheninae and the tribes Bennarellini Emeljanov, 1989 Gelastocephalini Emeljanov, 2000, and Mnemosynini Emeljanov, 1992. It is also not in agreement with the few phylogenetic analyses of the family, although these did not provide any conclusive and congruent results: 1) the morphological approach (Ceotto and Bourgoin, 2008) did not show any clear grouping of the previously recognized tribes, particularly for Pintaliini Stål, 1862 and Cixiini, which were scattered all over the tree; Bothriocerinae and Borystheninae were grouped together in a terminal portion of the tree depicting their very probable non-subfamilial rank, and 2) the molecular approach (Ceotto et al., 2008) differing greatly from the morphological one, with paraphyletic Cixiidae in which Bothriocerinae are placed as sister group to the rest of Cixiidae that also include Delphacidae and Borystheninae. However, these last two phylogenetical studies suffer sampling bias not allowing thorough testing of Emeljanov's hypothesis.

Following Fennah, 1987's approach, we also examined Muir, 1925's dichotomous key to the genera. The three fossil species would key out as cixiid with female pygofer longer than wide (couplet 12) but with tegmina held flat and apical margins not coming together when at rest (couplet 37), which makes them incompatible with Muir's key. Finally, from a phenetic approach, and in absence of a clear system of classification to follow apart from that of Emeljanov (2002), the closest placement of these fossils to the current tribes would be Oecleini Muir, 1922 with which they share the absence of lateral metatibial spines (Bahder

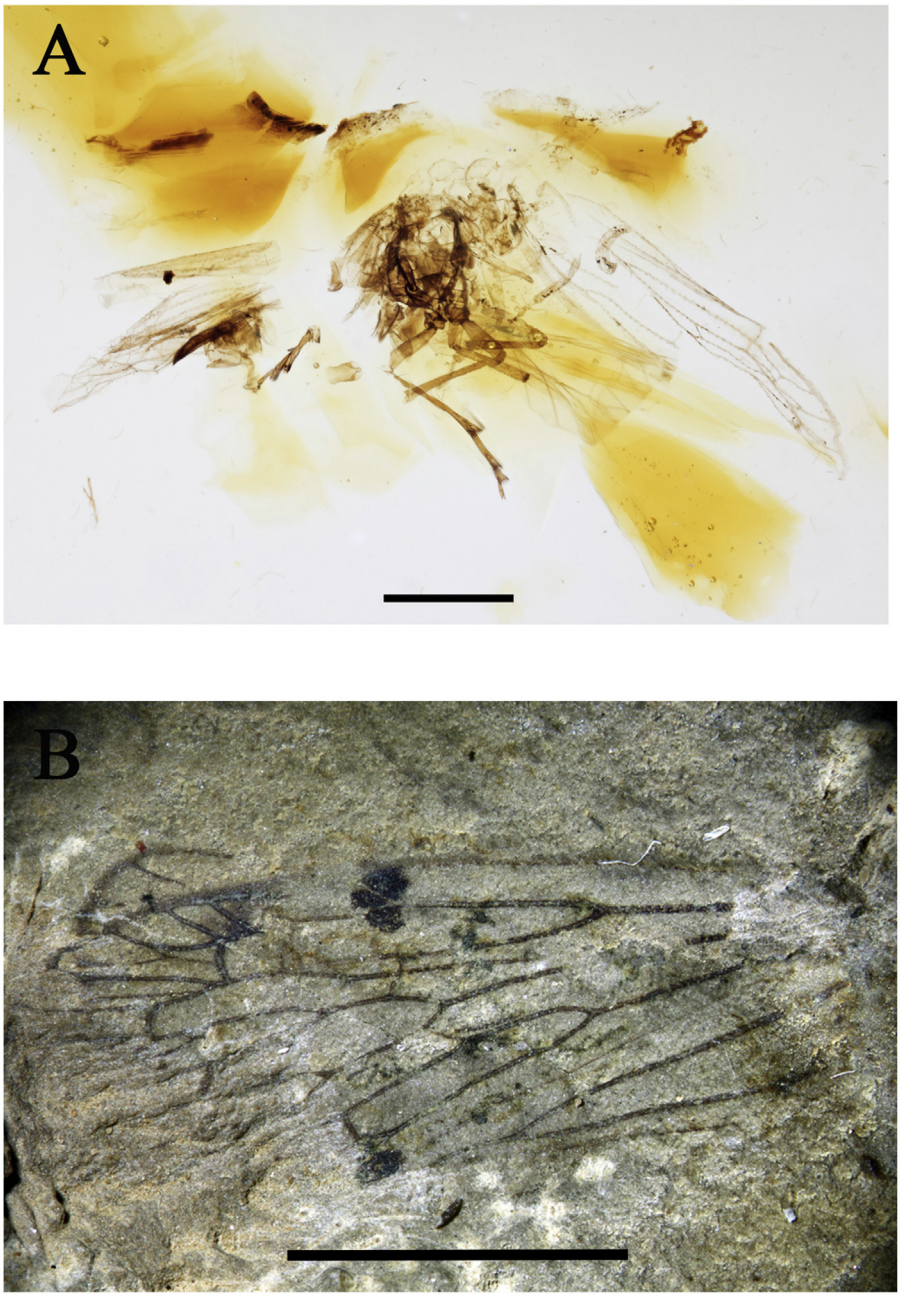

Fig. 10. A, *Karbopodoides aptianus* (Fennah, 1987) [NHMUK PI II.535(1)]. Photograph of lateral view. Photo Claire Mellish (NHM). B. *Barremixius petrinus* (Fennah, 1961) comb. nov., holotype specimen BMNH In. 59335. Left tegmen and part of hind wing. Photo Vladimir Blagoderov (NHM). Scale bar = 1 mm.

et al., 2019), the straight frontoclypeal carina and the elongated female terminalia (pygofer and genitalia) without wax plates. These three characters are however very probably plesiomorphic and therefore cannot depict any sister-relationship with Oecleini. Moreover the fossils differ from Oecleini by the *icu* vein joining the wing margin distad of the apex of the clavus - but Löcker (2006a: 155) showed this character to be prone to intraspecific variation - and the absence of a diastema in the apical metatibia teeth (Emeljanov, 2002: fig. 12-5). This last character, as well as the presence of a median ocellus, a long anal style and the absence of lateral metatibial spines also exclude the fossils from Gelastocephalini (Löcker 2006a: 156). The unarmed metatibia and elongated female pygofer exclude the Stenophlepsiini Metcalf, 1938 (Tsaur 1989). Further, the three fossils lack the basal concavity of the anterior margin of the forewings as present in Eucarpiini Emeljanov, 2002 (Emeljanov, 2002; Löcker et al., 2010: 26), as well as the convexity between the apex of clavus and *icu* characteristic of Pintaliini (Emeljanov, 2002; Löcker et al., 2010: 26). Finally, all of the fossils exhibit a pentacarinated mesonotum usually characteristic of Pentastirini Emeljanov, 1971 (Emeljanov 2002: 109). However, contrarily to Pentastirini, they do not have a pterostigma (Emeljanov, 2015: fig. 9.1), such as is the case in Bennini Metcalf, 1938 (Hoch, 2013: fig. 20) or Borystheninae (Emeljanov, 2002: fig. 6) from which they can be obviously excluded by their general habitus. In addition, they clearly exhibit a long ovipositor, corrugated gonapophyses IX (in a different configuration from Cixiini)

with an elongated laterotergal-tergal IX pygofer (Emeljanov, 1971: 350; Löcker et al., 2006b:103) that also excludes them from Pentastirini.

Clearly, the combination of all character states observed remains unique within the Cixiidae and may even justify description of a new family for these three fossils. In absence of a reliable phylogenetical structure for the family Cixiidae, that would allow a better assessment of the relationships between the taxa involved, we currently prefer suggesting only a new tribe, that we provisionally place as sister to Pentastirini based on the only apomorphic character they share with them: the pentacarinated mesonotum.

Currently, and from analysis of yet unpublished molecular data, that still needs to be completed (in prep), and in line with Emeljanov (2002) we currently recognize three main lineages in Cixiidae: the oecleinian lineage (including Duiliini Emeljanov, 2002, Cajetini Emeljanov 2002, Stenophlepsini, Oecleini, Bothriocerinae, but probably not Gelastocephalini) sister to a pentastirinian (with Pentastirini, Mnemosynini, and probably Borystheninae) and a cixiinian lineage (including all other cixiid tribes). Both of these lineages might be considered at least with a subfamilial rank in the future or even with a familial one. Both Bothriocerinae, belonging to the oecleinian lineage, and Borystheninae, to the pentastirinian one, should be downgraded to tribal rank only as Bothriocerini trib. stat. nov. and Borysthenini stat. nov. The place of Delphacidae remains problematic, either as sister to Cixiidae, or within Cixiidae, rendering them paraphyletic.

From a morphological point of view, Acrotiarini Bourgoin & Luo, trib. nov. differs from the oecleinian lineage by the absence of the metatibial diastema and it shares with the (pentastirinian + cixiinian) one, an open cubital cell by the displacement of the intercubital *icu* vein (*cua-cup* transverse vein) distal to the apex of clavus marked by the apex of CuP and joining the wing margin. The pentacarinated mesonotum allow to place it in the Pentastirinian lineage but as a separate lineage by the unique presence of the paired sublaterofrontal carinae, the arched RA, and perhaps the absence of laterometatibial spines (while this last one may also be observed in some Cixiini).

4.2. Placement of the two oldest cixiid fossils

One of the oldest cixiid fossils known is *Karebodopoides aptianus* (Fennah, 1987) from Lebanese amber, which was dated from Aptian (125-113 Ma) when first described. However, the deposit was re-analyzed recently and dated from Barremian: 129.4–125 Ma (Maksoud et al., 2017; Maksoud and Azar, 2020).

When Fennah (1987) described this fossil under the new genus *Mundopoides*, he photographed it and stated (Fennah, 1987: 1237) that the specimen was unfortunately separated in various parts: “head and pronotum detached, the tegmina and wings open, the abdomen apparently complete, but distorted and collapsed, and the anal segment and one of the third valvulae of the ovipositor slightly detached”. However, the amber piece itself was also not in good conditions, full of fractures, and a few years later, the specimen yet unregistered, was falling apart in pieces. In an attempt to save it, Andrew Ross (pers. comm.) asked David Gray (Palaeontology Conservation Unit) in 1994 to mount it on a Canada Balsam slide. At that time it became first registered in the NHM catalogue (old database). In 2007, with the implementation of a new collections' management system, its registration details changed to ‘NHMUK PI II.535(1) Cretaceous, Early Cretaceous, Aptian, Lebanese amber’. Thanks to Claire Mellish (NHM Earth Sciences department) a new set of photos was produced in July 2018 and a full view of the specimen is published here (Fig. 10A). However, the specimen appears even more damaged and several characters, previously listed by Fennah (1987), are now uncheckable.

Fennah suggested close relationships of *Karebodopoides* with *Mundopa* Distant, 1906 (Oecleini), however without formally placing the fossil into the tribe Oecleini. It remains difficult to place *K. aptianus* within the Cixiidae classification/phylogeny. Its three-carinated mesonotum, the absence of paired sublaterofrontal carinae and the tegmina venation (RA unibranched, not arched) excludes the fossil from Acrotiarini trib. nov., and it is currently kept within the oecleinian lineage until new fossil specimens are discovered and described.

More interestingly, we are also aware of an undescribed specimen from Lebanese amber (Szwedo, in preparation) which might belong to Acrotiarini trib. nov. (arched RA, but RA remains unforked; head capsule and thorax are not observable). This undescribed fossil suggests that the tribe was already present more than 125 Ma ago and at least distributed in the Laurasia Southern margin.

In 1961, Fennah described another Cixiidae fossil, ‘*Cixius*’ *petrinus* Fennah, 1961, from the United Kingdom (Weald Clay Formation), also dated from Barremian. Although it was described from a wing and tegmen imprint only, Fennah assigned it as belonging ‘with confidence’ to the Cixiina subtribe and ‘tentatively’ referred to it as genus *Cixius*. A photo of this specimen is included in this paper (see Fig. 10B) as Fennah only published drawings. The venation of the tegmen with a non-arched RA, a six-branched MP, with its secondary forks at almost the same level, and the *r-m* transverse veinlet distad to the basal fork of MP exclude *C. petrinus* from belonging to Acrotiarini as well as from the genus *Cixius* Latreille 1804, asking to place this taxon in a new genus, *Barremixius*, in the cixiinian lineage and provisionally kept in Cixiini.

5. Conclusions

Over the last 100 years, and particularly in the past two decades, Kachin amber has received worldwide scientific interest with nearly 600 families of invertebrates, vertebrates, protists, plants, and fungi reported from it (Ross, 2019, 2020a, b; Yu et al., 2019). Burmese amber preserves one of the most diverse Cretaceous fossil insect assemblages in terms of the number of described species (Gimmel et al., 2019; Ross, 2019, 2020a, b; Bartel et al., 2021).

Kachin amber gives us new insights into the very important period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organization times (Szwedo & Nel, 2015) and provides ideal materials for studying the Cretaceous Terrestrial Revolution, which is marked by the radiation of angiosperms, parasitic and social insects and early mammals (Lloyd et al., 2008; Meredith et al., 2011; Rust and Wappler, 2016; Jiang et al., 2018; Bao et al., 2019; Pohl et al., 2020; Genise et al., 2020; Sendi et al., 2020).

We hope that the combination of a better taxonomic knowledge of past faunas, coupled with molecular approaches relating to current faunas, will make it possible to propose a sound phylogenetic hypothesis of the evolution of Cixiidae. Despite being the most successfully diversified family of planthoppers and presumably one of the oldest of the extant ones, the classification and phylogeny of the currently known taxa remain unsatisfactory: whether all recognized tribes are valid taxa, and how they group together, remains to be investigated further. Currently, Cixiidae are assumed to belong to the basal extant Fulgoroidea families as sister to Delphacidae, although their monophyly/paraphyly with respect to Delphacidae remains to be further analyzed. With our current knowledge, the authors foresee Cixiidae as grouping in three major lineages: the oecleinian sister to the pentastirinian and the cixiinian ones, that might take respectively a formal subfamily or even family rank in the future. Oecleinian lineage includes Bothriocerini trib. stat. nov. and Borysthenini stat. nov. would probably belong to

the pentastirinian one. Accordingly, Acrotiarini trib. nov. should take a basal position to the family, sister to Pentastirini (and perhaps Mnemosynini). *Karebodopoides* Szwedo 2001 and *Barremixius* gen. nov. are provisionally recognized as the oldest representatives of the oecleinian and cixiinian lineages respectively.

CRediT authorship contribution statement

Yang Luo: Conceptualization, interpretation, writing, Writing – original draft, Providing material and palaeoenvironmenal interpretation, Taxonomy and phylogeny. **Thierry Bourgoin:** Conceptualization, interpretation, writing, Writing – original draft, Taxonomy and phylogeny. **Jacek Szwedo:** Conceptualization, interpretation, writing, Writing – original draft, Providing material and palaeoenvironmenal interpretation; Ji-Nian Feng, Conceptualization, interpretation, writing, Writing – original draft preparation.

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The authors thanks Claire Mellish (NHM Earth Sciences department) for providing information and new photos for *Karebodopoides aptianus* (Fennah, 1987). We are specially indebted to B. Löcker, H. Hoch and anonymous reviewers for their valuable comments and precisions provided in early draft and review of the paper. The principal phase of this research was supported by the Pilot Project of Standardized Curation, Data Integration and Resource Sharing of Zoological Collections (2015FY210300) by the Ministry of Science and Technology of China and China Scholarship Council (201906300092).

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