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Short communication

A well-preserved minute litter bug in mid-Cretaceous Kachin amber from northern Myanmar (Heteroptera, Dipsocoromorpha)

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ABSTRACT

Although Dipsocoromorpha are one of the most ancient lineages of true bugs, their hitherto known fossil record was extremely scarce. Herein, *Kachinia cretacea* gen. et sp. nov., ascribed to Schizopteridae: Hypselosomatinae, is described based on a female adult in mid-Cretaceous Kachin amber from northern Myanmar. The new taxon shares some primitive traits with other Mesozoic schizopterids, but also derived a series of autapomorphic characteristics. The two Mesozoic schizopterid genera *Hexaphlebia* and *Lumatibialis*, which have not been assigned to subfamily level, are tentatively treated as early representatives of Hypselosomatinae based on their complex tegminal venation similar to that of the genus *Hypselosoma*. Additionally, a key to all known fossil species of Schizopteridae is provided on the basis of tegminal features. Our findings further confirm Schizopteridae as one of the basal clades of Dipsocoromorpha, being highly diversified and widespread by the late Mesozoic.

1. Introduction

The Dipsocoromorpha, collectively called minute litter bugs, is a lineage of very small insects (typically 1–2 mm long) commonly seen in humid tropical forests, but also found sporadically occurring in temperate rain forests or other cool temperate climates (Hill, 1980; Scudder, 2010; Weirauch and Fernandes, 2015). These tiny insects, as predators of small invertebrates, are usually ground and litter dwellers living in cryptic micro-habits (Schuh and Slater, 1995; Perrichot et al., 2007). The Dipsocoromorpha is confirmed as one of the most basal clades of Heteroptera (true bugs) on the basis of morphological and molecular evidence (Schuh, 1979; Wheeler et al., 1993; Wang et al., 2016; Li et al., 2017), thus it is important for the understanding the early evolutionary history of true bugs. Nevertheless, their high-level phylogenetic reconstruction based on recent dipsocoromorph groups has not received much attention to date (Weirauch and Štys, 2014). Moreover, their fossil record remains extremely scarce perhaps due to their small size and cryptic habits (Perrichot et al., 2007).

Up to now, 28 genera and 32 species attributed to 12 true bug families (Aradidae, Cimicidae, Cydnidae, Enicocephalidae, Gelastocoridae, Hydrometridae, Leptopodidae, Palaeoleptidae, Reduviidae, Schizopteridae, Tingidae and Velocipedidae) have been reported in Kachin amber (Heiss and Guilbert, 2018; Lis et al., 2018; Ross, 2018; Poinar, 2019; this study). The age of Kachin amber is now biostratigraphically considered to be mid-Cretaceous (e.g., Cruickshank and Ko, 2003; Grimaldi et al., 2005; Ross et al., 2010) and earliest Cenomanian (98.79 ± 0.62 Ma) based on a recent U–Pb zircon dating analysis (Shi et al., 2012).

We herein report a new fossil litter bug, *Kachinia cretacea* gen. et sp. nov., from the mid-Cretaceous Kachin amber of northern Myanmar (Table 1; Fig. 1). The new taxon belongs to Schizopteridae: Hypselosomatinae, which represents one of the ancient lineages of Dipsocoromorpha, providing us with useful information on the early evolution and palaeodiversity of these tiny insects (Weirauch and Štys, 2014).

2. Material and methods

The amber containing the new fossil is yellow and transparent originated from the Hukawng Valley, Kachin Province, northern Myanmar (locality in Kania et al., 2015: fig. 1).

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0195-6671/

Table 1
Fossil genera and species currently ascribed to the family Schizopteridae. Abbreviation: M., male; F., Female.

Horizon	Locality	Taxon	Gender	Reference
Miocene	Northern Dominican Republic[1]	*Hypselosoma dominicana* Poinar and Brown (2015)	M.	Poinar and Brown (2015)
		Schizoptera hispaniolae Poinar, 2015	M.	Poinar and Brown (2015)
		Schizoptera dominicana Poinar, 2015	F.	Poinar and Brown (2015)
Mid-Cretaceous	Kachin, Myanmar[2]	*Tanaia burmitica* Perrichot, Nel and Néraudeau (2007)	M.	Perrichot et al. (2007)
		Lumatibialis burmitis Poinar, 2015	M.	Poinar and Brown (2015)
		Hexaphlebia burmanica Poinar, 2015	M.	Poinar and Brown (2015)
		Kachinia cretacea gen. et sp. nov.	F.	This paper
	Charentes, France[3]	*Buzinia couillardi* Perrichot, Nel and Néraudeau (2007)	F. and M.	Perrichot et al. (2007)
Lower Cretaceous	central Lebanon[4]	*Libanohypselosoma popovi* Azar and Nel (2010)	F.? And M.	Azar and Nel (2010)

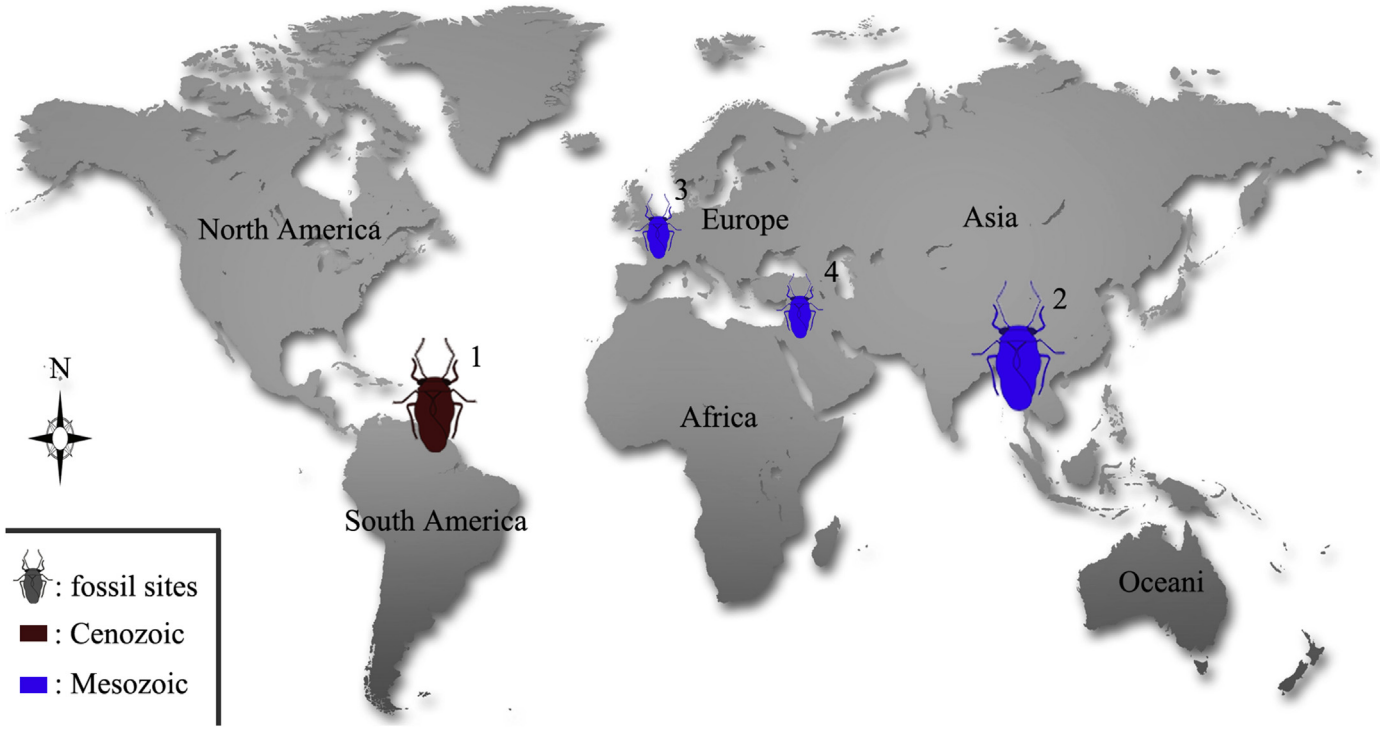

Fig. 1. Locations of fossil taxa of the family Schizopteridae. 1, Miocene of Dominican Republic; 2, mid-Cretaceous of Kachin, Myanmar; 3, mid-Cretaceous of Charentes, France; 4, Lower Cretaceous of central Lebanon. Size of pictogram of bug indicates the relative number of known species. See Table 1 for the detailed information on geographical and stratigraphical distribution of each species.

The amber specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP169518). This fossil specimen was examined and photomicrographed using the Zeiss Stereo Discovery V16 microscope system and Zen software, and VHX 5000 digital microscope platform, with incident and transmitted light. The measurements were made using the VHX 5000 digital microscope platform. The line drawings and reconstructions were prepared in two image-editing softwares (CorelDraw X7 and Adobe Photoshop CS6). The terminology used herein mainly follows that of Perrichot et al. (2007) and Azar and Nel (2010).

All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:48AF7516-81EB-47C4-8609-01826221AD94.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Dipsocoromorpha Miyamoto, 1961
Superfamily Dipsocoroidea Dohrn, 1859
Family Schizopteridae Reuter, 1891
Subfamily Hypselosomatinae Esaki and Miyamoto, 1959

Genus ***Kachinia*** Chen and Wang, gen. nov.
(urn:lsid:zoobank.org:act:552ED7A9-76D9-41E1-9E26-2E47B0C068D5)
Type species: *Kachinia cretacea* Chen and Wang, gen. et sp. nov.; by present designation and monotype.

Etymology. After the region of Kachin Province in northern Myanmar where the amber piece containing the new bug was found.
Diagnosis. Head with crown extremely shorterned, two ocelli slightly sunk, touching compound eyes; two darkly stained muscle scars situated between ocelli, setae on third and fourth segments sparse but extremely long. Tegmina with only clavus sclerotized and other parts membranous; independent apical part of R and two terminal branches of M (M1 and M2) relatively short; basal *m-cu* connecting R + M instead of stem M; basal *cu-1v* connecting 1 V

just at its separation from 1 V+2 V, and middle *cu-1v* just distad of basal *m-cu*; median cells very long and sub-parallel to each other.

Key to species of fossil Schizopteridae based on tegmen:

1 Independent apical R and M1 almost transverse and perpendicular to R + M; just one median cell present……2
- Independent apical R and M1 oblique, not perpendicular to R + M; at least two median cells present……3
2 1 V reaching wing margin…*Schizoptera hispaniolae* Poinar, 2015
- 1 V not reaching wing margin…*Schizoptera dominicana* Poinar, 2015
3 R divided from R + M near wing base, long and fused with M1 apically; marginal cells just three in number…*Libanohypselosoma popovi* Azar and Nel, 2010
- R + M relatively long, bifurcating to R and M far away from wing base; R not fused with M1 apically; marginal cells at least four in number……4
4 M2 fused with Cu, forming a short stalk……5
- M2 and Cu not fused, connected to each other by a crossvein…7
5 Marginal cells five in number…*Hexaphlebia burmanica* Poinar, 2015
- Marginal cells four in number……6
6 Trapezoidal cell short…*Tanaia burmitica* Perrichot, Nel and Neraudeau, 2007
- Trapezoidal cell long and narrow…*Lumatibialis burmitis* Poinar, 2015
7 Trapezoidal cell absent…*Buzinia couillardi* Perrichot, Nel and Neraudeau, 2007
- Trapezoidal cell present……8
8 Basal crossvein *m-cu* near basal crossvein*cu-1v*; median cells not sub-parallel to each other…*Hypselosoma dominicana* Poinar and Brown, 2015
- Basal crossvein *m-cu* near middle crossvein *cu-1v*; median cells almost sub-parallel to each other…*Kachinia cretacea* Chen and Wang, gen. et sp. nov.

Kachinia cretacea Chen and Wang, gen. et sp. nov.
(urn:lsid:zoobank.org:act:F4E91C22-F0D4-4160-874D-2DF80DA7E2CE)
Figs. 2–6

Etymology. The specific epithet refers to the Cretaceous age of this bug.
Holotype. NIGP169518, a female adult insect with tegmina slightly outspread and hindwings folded.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; lowermost Cenomanian, Upper Cretaceous (Shi et al., 2012).
Diagnosis. As for genus as it is the only so far included species.
Description. Body (Fig. 2). Size small, somewhat stout. Surface densely covered with setae. Length about 1.28 mm, width about 0.58 mm (not including wings).
Head (Fig. 3). Width with compound eyes about 0.55 mm. Head densely setose and hairy, greatly declivous in lateral view. Crown extremely shortened. Two ocelli prominent and slightly sunk, touching compound eyes. Two distinct muscle scars situated between ocelli, darkly stained. Compound eyes large, touching margin of pronotum, ovaloid in dorsal and ventral view. Antenna four-segmented, with length about 0.05 mm, 0.07 mm, 0.22 mm and 0.32 mm; first and second segments extremely inflated, much shorter than third and fourth segments; fourth segment slight longer than third segment, setae on third and fourth segments sparse but extremely long. Labrum about 0.16 mm ong, with at least three macrosetae (not very clear). Labium short, about 0.18 mm ong.
Thorax (Fig. 4). Pronotum about 0.20 mm long, 0.53 mm wide, widest at its posterior margin, somewhat trapezoid-shaped; anterior margin slightly arched; posterior margin much longer than anterior margin, slightly concave at its middle; pronotal collar prominent, stained lighter than other parts of pronotum. Mesonotum with length about 0.19 mm, width about 0.32 mm; mesoscutellum sharp apically, covered densely with long setae. Prothoracic legs with coxae cylindroid; femora thick; tarsi just with two tarsomeres, with apical tarsomere much longer than basal tarsomere; two tarsal claws well developed; femora, tibiae, and tarsi with length about 0.18 mm, 0.19 mm, and 0.12 mm. Mesothoracic legs with femora slenderer than profemora; tibiae slightly longer than femora; tarsi just with two tarsomeres, with apical tarsomere much longer than basal tarsomere; two tarsal claws well-developed; femora, tibiae, and tarsi with length about 0.32 mm, 0.31 mm, and 0.10 mm. Metathoracic legs with femora somewhat slender; tibiae much longer than femora, with several strong, long and dark (probably sclerotized) lateral and apical spines; tarsi with three tarsomeres, with basal tarsomere very short and apical tarsomere longer than middle tarsomere; two well-developed tarsal claws; femora, tibiae, and tarsi with length about 0.32 mm, 0.50 mm, and 0.14 mm.
Wings (Fig. 5). Tegmina 1.16 mm long, densely covered with punctae and fine network and with only clavus sclerotized and other parts membranous. Clavus broad, about 0.46 mm long and 0.14 mm wide, with margin arched. Anterior margin with a row of strong setae and covered densely with short hair. Veins thick, with a row of strong setae. Longitudinal veins R, M, Cu, 1 V and 2 V present. Independent apical part of R and two terminal branches of M (M1 and M2) relatively short. 2 V fused with 1 V apically. Crossveins five in number. Basal crossvein between M and Cu (*m-cu*) long and connecting R + M, instead of stem M. Apical *m-cu* connecting M2. Crossveins between Cu and 1 V (*cu-1v*) three in number, long, with basal crossvein connecting 1 V just at its separation from 1 V+2 V, and middle one just distad of basal *m-cu*. Basal cell long and broad, about 0.40 mm long and 0.11 mm wide. Trapezoidal cell present and large. Median cells long, sub-parallel to each other, three in number. Marginal cells four in number. Hindwings membranous and finely netted, with venation weak, obscure.
Abdomen (Fig. 6). Abdomen flat, length about 0.66 mm, width about 0.58 mm spiracles not visible. Sterna densely covered with long setae. Pygofer short, with length much shorter than width; anal tube stout, with apex round; gonoplacs fused to near apices and round apically.

4. Discussion

The new taxon *Kachinia* gen. nov. in mid-Cretaceous Kachin amber can be ascribed to Schizopteridae: Hypselosomatinae (big-eyed minute litter bugs) on the basis of the following morphological characteristics: exceedingly large eyes overlapping anterolateral margin of pronotum, and tegmen with relatively complex venation, defining a series of median and marginal cells (Esaki and Miyamoto, 1959; Emsley, 1969; Štys, 1995; Perrichot et al., 2007; Azar and Nel, 2010; Hoey-Chamberlain and Weirauch, 2016; Weirauch et al., 2018).

As the second largest subfamily of Schizopteridae, Hypselosomatinae currently comprises 13 extant genera (*Hypselosoma* Reuter, 1891; *Ommatides* Uhler, 1894; *Glyptocombus* Heidemann, 1906; *Pateena* Hill, 1980; *Rectilamina* Hill, 1984; *Cryptomannus* Hill, 1984; *Duonata* Hill, 1984; *Lativena* Hill, 1984; *Macromannus* Hill, 1984, *Ordirete* Hill, 1984; *Williamsocoris* Carpintero and Dellapé, 2006; *Hypselosomops* Hoey-Chamberlain and Weirauch, 2016; *Hypsohapsis* Hoey-Chamberlain and Weirauch, 2016). The new genus remarkably differs from all

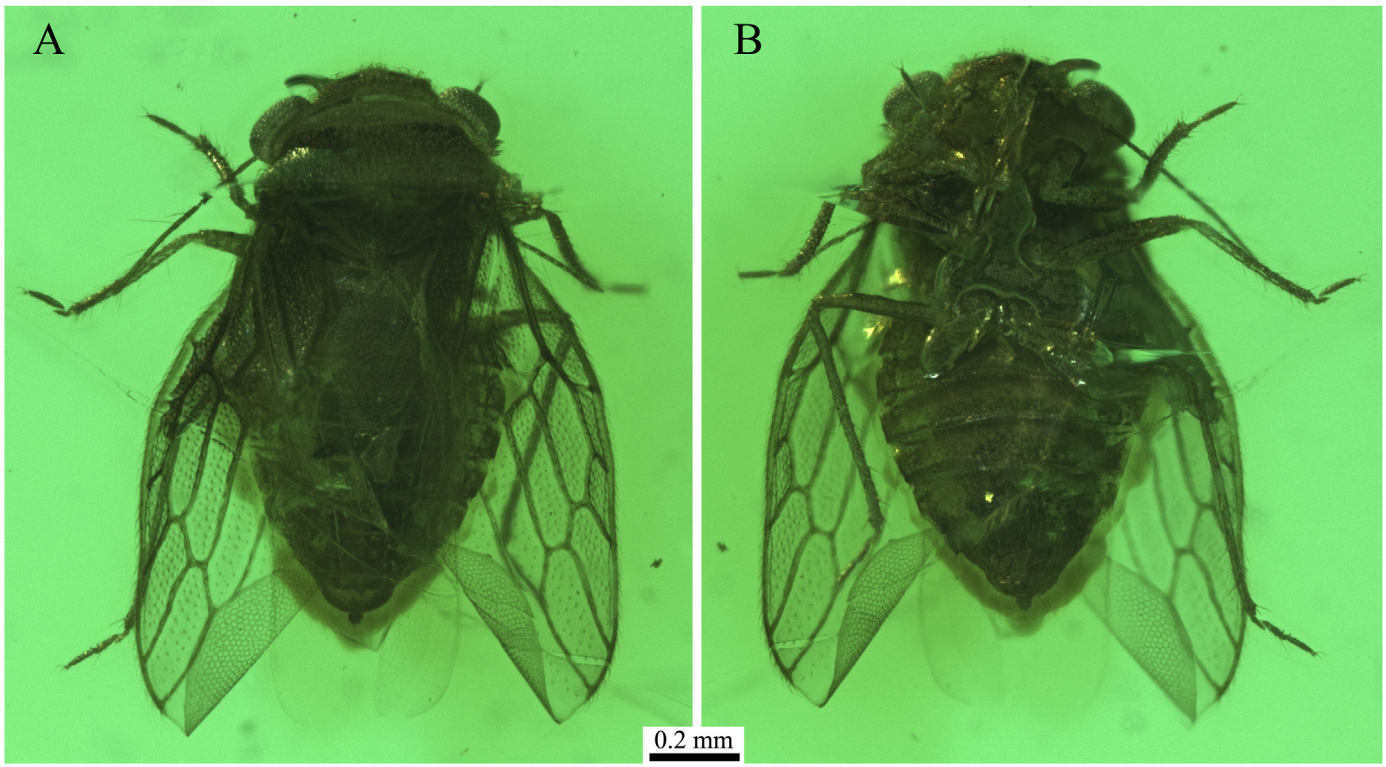

Fig. 2. Photographs of holotype of *Kachinia cretacea* gen. et sp. nov. (A), dorsal view; (B), ventral view. All to scale bar.

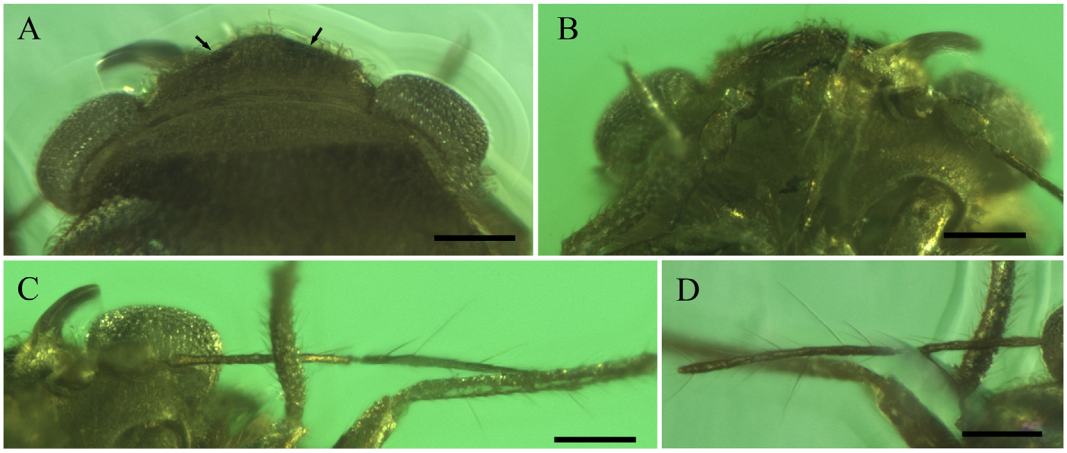

Fig. 3. Head of holotype of *Kachinia cretacea* gen. et sp. nov. (A), dorsal view, muscle scars indicated by arrows; (B), ventral view; (C), enlarged left antenna in ventral view; (D), enlarged left antenna in dorsal view. Scale bars = 0.1 mm.

extant genera with the crown extremely shorterned, two ocelli touching compound eyes, and tegmina with only clavus sclerotized and other parts membranous. *Kachinia* gen. nov. resembles the recent genera *Hypselosoma*, *Hypselosomops* and *Williamsocoris* in possessing similar tegmina (macropterous type) with six thick longitudinal veins (R, M1, M2, Cu, 1 V and 2 V), five crossveins (two crossveins between M and Cu and three crossveins between Cu and 1 V), and extensive cells (three median cells and four marginal cells). However, the new genus distinctly differs from the three extinct genera in body structures, such as compound eyes ovaloid in dorsal and ventral view, ocelli slightly sunk and touching compound eyes, and pronotum with posterior margin slightly concave at middle.

Up to now, five extinct genera ascribed to Schizopteridae have been reproted from the Mesozoic, including *Tanaia* Perrichot, Nel and Neraudeau (2007), *Buzinia* Perrichot, Nel and Neraudeau (2007), Libanohypselosoma Azar and Nel (2010), *Hexaphlebia* Poinar, 2015, and *Lumatibialis* Poinar, 2015. Of these taxa, *Tanaia*, *Buzinia*, and Libanohypselosoma were originally attributed to the subfamily Hypselosomatinae, but *Hexaphlebia* and *Lumatibialis* have not been assigned at subfamily level. Based on their complex tegminal venation similar to the genus *Hypselosoma*, we tentatively treat these two genera as representatives of Hypselosomatinae. *Kachinia* gen. nov. can be distinguished from all known Mesozoic genera in the following tegminal features: three median cells long, almost longitudinal, and similar in shape; the basal crossvein between M and Cu and the middle crossvein between Cu and 1 V almost at same level; and basal cell very long and broad. Additionally, the new genus is distinctly different from Libanohypselosoma in having a tegmen with R free apically, not fused with M1,

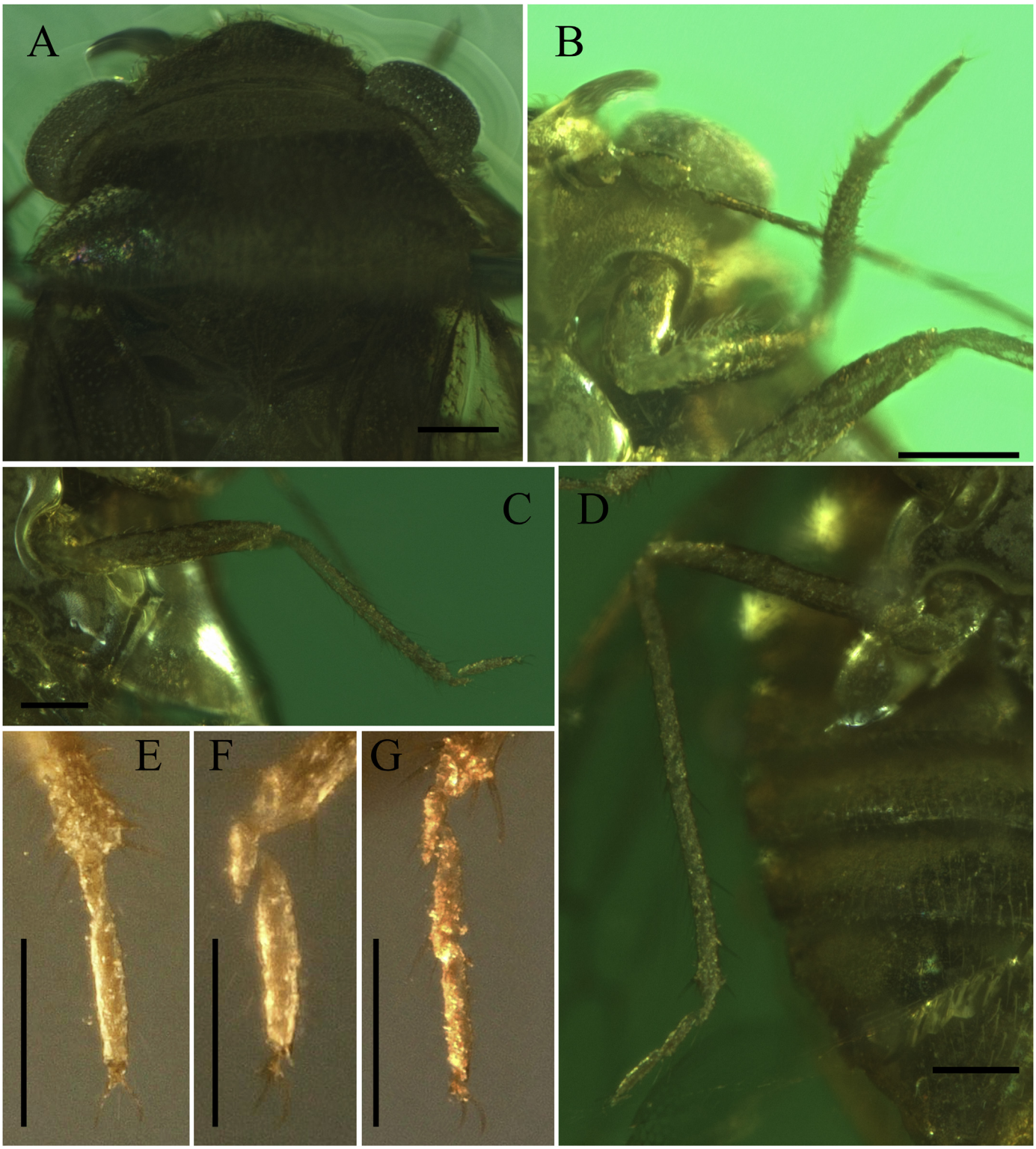

Fig. 4. Thorax of holotype of *Kachinia cretacea* gen. et sp. nov. (A), thorax in dorsal view; (B), left prothoracic leg; (C), left mesothoracic leg; (D), right metathoracic leg; (E), enlarged left protarsus; (F), enlarged left mesotarsus; (G), enlarged left metatarsus. Scale bars = 0.1 mm.

from *Buzinia* with trapezoidal cell present, from *Tanaia* and *Lumatibialis* with M2 and Cu not fused, but connected to each other by a crossvein, and from *Hexaphlebia* with 2 V fused with 1 V apically, not ending at tegminal margin.

The holotype of *Kachinia cretacea* gen. et sp. nov., is the third definite Mesozoic female schizopterid individual (Table 1), bearing the 2/2/3 tarsal formula, just like the female specimens of *Buzinia couillardi*, which however possesses the 3/3/3 tarsal formula, with mesotarsi trimerous but incrassate in the male (= '4-segmented' *sensu* Esaki and Miyamoto, 1959; 'pseudotetramerous' *sensu* Emsley, 1969) (Perrichot et al., 2007). Tarsal formulae are variable among different species or even sexually dimorphic within

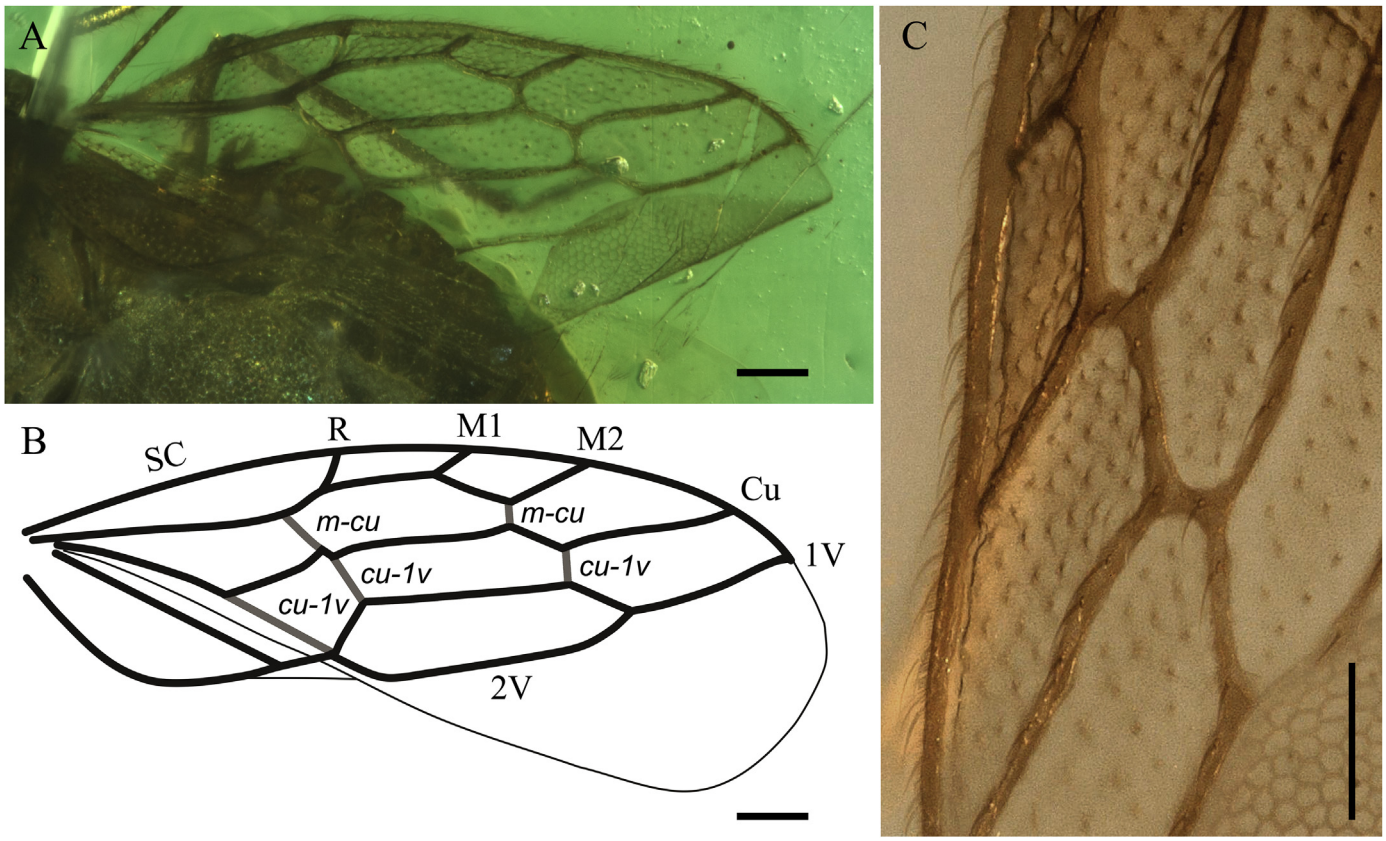

Fig. 5. Tegmen of holotype of *Kachinia cretacea* gen. et sp. nov. (A), photograph of right tegmen; (B), line drawing of tegmen; (C), enlarged part of left tegmen, showing a row of setae on tegminal margin and veins, and punctae and fine network on membrane. Crossveins are shown in grey line. Scale bars = 0.1 mm.

Dipsocoromorpha (Zheng, 1999). For modern Hypselosomatinae, the tarsal formula is one of the useful characters for distinguishing genera: for example, the 2/2/3 tarsal formula is shared by females of *Glyptocombus* and *Hypselosomps*; in contrast, the formula is 3/3/3 in males of *Glyptocombus* but 2/3/3 in males of *Hypselosomps* (Hoey-Chamberlain and Weirauch, 2016). Poinar and Brown (2015) reported *Lumatibialis* with a 3/4/5 tarsal formula; the 4-segmented mesotarsi and 5-segmented metatarsi are extremely unusual for

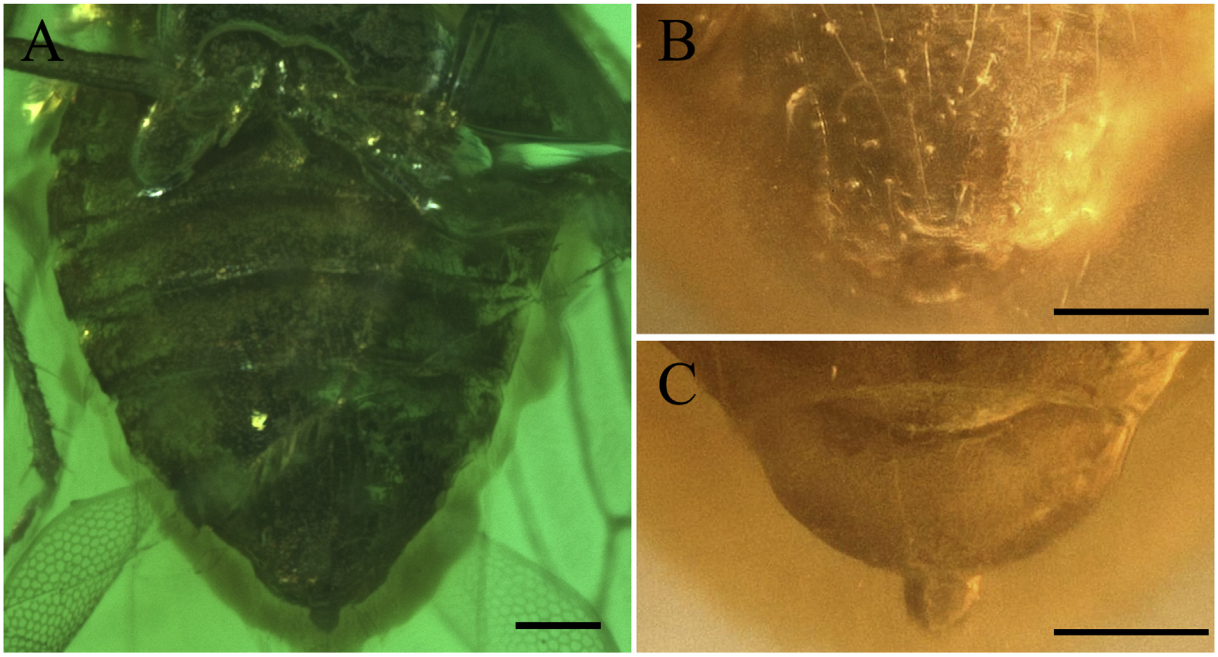

Fig. 6. Abdomen of holotype of *Kachinia cretacea* gen. et sp. nov. (A), abdomen in ventral view; (B), enlarged pygofer in ventral view; (C), enlarged pygofer in dorsal view. Scale bars = 0.1 mm.

hemipteran insects, and might be the result of pseudo-tetramery (Emsley, 1969; Perrichot et al., 2007; Azar and Nel, 2010) and pseudo-pentamery and/or distortion by taphonomical and preservative factors, and so this morphological trait should be further confirmed by checking more fossil material.

Although the infraorder Dipsocoromorpha is one of the most basal clades of Heteroptera (Schuh, 1979; Wheeler et al., 1993; Wang et al., 2016; Li et al., 2017), its Mesozoic record is extremely limited relative to other heteropteran infraorders (Perrichot et al., 2007). Up to now, most recorded and all described Mesozoic dipsocoromorphs belong to Schizopteridae: Hypselosomatinae (Perrichot et al., 2007; Azar and Nel, 2010; Poinar and Brown, 2015; this study), one of the ancient lineages within Dipsocoromorpha (Weirauch and Štys, 2014). Five Mesozoic monotypic genera, recorded in the Lower to mid-Cretaceous of France, Lebanon and Myanmar, together with new genus reported herein, have been attributed to Hypselosomatinae, suggesting that this subfamily was widespread in the Laurasian land mass with high taxonomic and morphological disparity in the Cretaceous. The hitherto known Mesozoic hypselosomatines (males and females) share some ancient morphological characteristics, such as the tegmen being macropterous, not elytrous, with thick and complex venation, and compound eyes large, but smaller than usual in this subfamily (Azar and Nel, 2010). Meanwhile, these litter bugs evolved some remarkably uncommon traits, such as ocelli touching the compound eyes (*Kachinia cretacea* gen. et sp. nov.), tegmen with independent R very long and fused with M1 apically (*Libanohypselosoma popovi* Azar and Nel, 2010), and head much narrower than thorax and abdomen (*Lumatibialis burmitis* Poinar, 2015).

5. Conclusions

Amber affords exceptional preservation of insects and other microorganisms (Chen et al., 2016), thus, it is unsurprising that as tiny insects with a size commonly 1–2 mm (Weirauch and Fernandes, 2015), most reported fossil dipsocoromorphs were trapped in amber and described from amber pieces (Perrichot et al., 2007). The fossils of Dipsocoromorpha are scarce relative to other true bug lineages perhaps due to their small size as well as cryptic habits (Perrichot et al., 2007). Our findings add the palaeodiversity of this tiny bug group, suggesting that they likely has been widespread by the late Mesozoic.

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