

Short communication

A new whitefly (Hemiptera, Sternorrhyncha, Aleyrodidae) in mid-Cretaceous Kachin amber, northern Myanmar

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ABSTRACT

Whiteflies (Aleyrodidae) are tiny hemipteran insects with specialized ontogeny and morphology. A new extinct taxon, *Paraburmoselis kachinensis* gen. et sp. nov., is erected herein based upon a fossil whitefly trapped in the mid-Cretaceous Kachin amber from northern Myanmar. *Paraburmoselis* gen. nov., as the fourth genus of the Mesozoic subfamily Bernaeinae, can be distinguished from its con-subfamilies by possessing a series of unique features: metatarsi with basitarsomere long, about 1.5 times as long as apical tarsomere; forewings with the wing membrane sclerotized and darkly coloured, peripheral membrane relatively thin, a peripheral vein distinct, and MP separated from MP+CuA almost at the same level as the bifurcation of R. In addition, the inconsistency of the reconstruction of aleyrodiform origin and evolutionary history inferred from different data types (i.e., morphology, molecular phylogenetics and palaeontology) is presented and briefly discussed.

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1. Introduction

The sternorrhynchan Infraorder Aleyrodomorpha Chou, 1963, collectively called whiteflies, is a lineage of hemipteran insects with small size and specialized ontogeny and morphology. Modern whiteflies undergo four larval stages in their life cycle, with the last preadult sessile instar as the so-called 'puparium' (Campbell et al., 1994; Shcherbakov, 2000; Martin, 2007; Drohojowska and Szwed, 2011; Szwed and Drohojowska, 2016). Winged whitefly adults are also typified by a series of remarkable morphological characteristics, which are unique within insects: integument commonly dusted with fine white wax powders produced by abdominal plates, anal dorsum with special structures comprising vasiform orifice and its operculum and lingula, and compound eyes usually subdivided into dorsal and ventral parts (Gill, 1990; Byrne and Bellows, 1991; Campbell et al., 1994; Shcherbakov, 2000; Drohojowska and Szwed, 2011).

Whiteflies are generally ascribed to the sole family Aleyrodidae Westwood, 1840 within the superfamily Aleyrodoidea. The monophyly of this family is well evidenced by morphological, molecular, anatomic and palaeontological data. The systematics of its subfamilies, however, remains controversial to date (Shcherbakov, 2000; Martin, 2007; Szwed and Drohojowska, 2016). One extinct subfamily (Bernaeinae Shcherbakov, 2000) and three modern subfamilies (Aleyrodinae Westwood, 1840, Udamoselinae; Enderlein, 1909; Aleurodicinae Quaintance and Baker, 1913) were recognized within Aleyrodidae. Nevertheless, some authors (Sampson, 1943; Shcherbakov, 2000) treated Aleurodicinae as the junior synonym of Udamoselinae; in contrast, some others (Schlee, 1970; Mound and Halsey, 1978) rejected the sub-familial position of Udamoselinae, and they argued that the monotypic genus *Udamoselis* should be regarded as *nomen dubium* due to its inadequate description on the basis of a single adult male specimen, which has subsequently never been located (Martin and Streito, 2003; Martin, 2007; Drohojowska and Szwed, 2015). Based on morphological characteristics of three new adult male *Udamoselis* individuals, Martin (2007) stated that Udamoselinae and Aleurodicinae are likely to be synonymous and Udamoselinae, as the older name, takes precedence over Aleurodicinae; but meanwhile, the author

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pointed out that this problem remains open due to absence of data on female and puparial specimens, which are vital to aleyrodid classification.

The extinct whitefly subfamily Bernaeinae was erected comprising some Mesozoic primitive whiteflies from the Upper Jurassic to lowermost Upper Cretaceous of Asia (Shcherbakov, 2000). Bernaeinae, as the hitherto known oldest representative of Aleyrodomorpha, bears a series of symplesiomorphic characteristics: head broad, eyes not subdivided, median ocellus retained, wings with complex venations, etc. Nevertheless, as stated by Shcherbakov (2000), no one apomorphic trait could be recognized, and so this subfamily is likely a paraphyletic group. Four genera were originally placed in Bernaeinae, including *Bernaesa* Schlee, 1970, *Burmoselis* Shcherbakov, 2000, *Juleyrodes*, Shcherbakov (2000), and *Heidea* Schlee, 1970 (Shcherbakov, 2000). The genus *Heidea*, however, was subsequently transferred to the subfamily Aleyrodinae by Drohojowska and Szwedo (2011) (Table 1).

In the present study, we erected a new genus and species on the basis of a whitefly fossil contained in mid-Cretaceous Kachin amber from northern Myanmar. Considering that some primitive features shown in the new taxon have been found in Bernaeinae, but not normally or never recorded in other three recent subfamilies, we tentatively assign the new genus to this extinct subfamily. Just for convenience of expression, we herein tentatively follow the traditional classificatory frameworks that Aleyrodidae is ordered into four subfamilies, as in a recent updated checklist presented by Martin and Mound (2007). However, it is noteworthy that the current taxonomic system of Aleyrodidae remains under controversy and might not necessarily reflect its natural division.

2. Material and methods

The new whitefly contained in a yellow and transparent amber piece was collected from Kachin Province, northern Myanmar (see locality in Chen et al., 2019: fig. 1) and deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, with specimen no. NIGP171162. As a significant window to mid-Cretaceous ecosystems, organic inclusions in Kachin amber have been studied for more than one century, and their diversity has increased dramatically in recent years (Cruickshank and Ko, 2003; Shi et al., 2012; Kania et al., 2015; Zheng et al., 2016). The age of Kachin amber is now considered as mid-Cretaceous on the basis of biostratigraphical evidence (Grimaldi et al., 2005), and is dated as earliest Cenomanian (98.79 ± 0.62 Ma) in a recent U–Pb zircon dating study (Shi et al., 2012).

To show details of the tiny insect more clearly, the amber piece was re-cut and polished, and then the specimen was checked, photomicrographed, and measured using the VHX 5000 digital

microscope platform, with incident and transmitted light used simultaneously. Illustrations of wings were prepared with image-editing software CorelDraw 12.0 and Adobe Photoshop CS3. Venational terminologies used herein are mainly followed Shcherbakov (2000), with slight modification: 1), MA is completely fused with R in Paraneoptera and so the independent median vein is treated as MP instead of M; 2), the first longitudinal vein on the clavus is treated as Pcu instead of A1 (Nel et al., 2012; Bourgoïn et al., 2015; Chen et al., 2018).

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:210776A2-3EC0-4A8C-A233-2F302B2FFED3.

3. Systematic palaeontology

Class **Insecta** Linnaeus, 1758

Order **Hemiptera** Linnaeus, 1758

Suborder **Sternorrhyncha** Amyot and Serville, 1843

Infraorder **Aleyrodomorpha** Chou, 1963

Family **Aleyrodidae** Westwood, 1840

Subfamily **Bernaestinae** Schlee, 1970

Genus ***Paraburmoselis*** gen. nov.

(urn:lsid:zoobank.org:act:0632E6AD-693B-4782-8D50-0E313D059A05)

Type species: *Paraburmoselis kachinensis* gen. et sp. nov.; here designated.

Etymology. The generic name is formed from 'para' and 'burmoselis', indicating that the genus is similar to the genus *Burmoselis* reported in Kachin amber.

Diagnosis. Head narrower than thorax; compound eyes large and produced. Pro- and mesotarsus with basitarsomere almost as long as apical tarsomere, and metatarsus with basitarsomere about 1.5 times as long as apical tarsomere. Abdomen stout, with ovipositor long. Forewings with membrane sclerotized and darkly coloured and peripheral membrane relatively thin; peripheral vein distinct; R+MP+CuA extremely short; R branching into R1 and Rs at about middle of wing length; Rs almost as long as stem R; MP+CuA forking at same level as bifurcation of R; MP with basal part present; Pcu relatively long and sinuous, occupying 0.6 of clavus. Hindwings with R and CuA separated at wing base; R with two terminal branches; CuA ending far away from wing margin; CuP residual, very short.

Paraburmoselis kachinensis gen. et sp. nov.

(urn:lsid:zoobank.org:act:0C6CA8F6-1146-4752-A4A4-7ADE545A46A7)

Figs. 1–4

Table 1
Mesozoic genera and species currently ascribed to the whitefly family Aleyrodidae.

Subfamily	Horizon and Locality	Taxon	Reference
Aleyrodinae	Lower Cretaceous; Central Lebanon	<i>Heidea cretacica</i> Schlee (1970); <i>Baetylus kahramanus</i> Drohojowska and Szwedo (2011)	Schlee (1970); Drohojowska and Szwedo (2011)
Aleurodicinae	Upper Cretaceous; Kachin, Myanmar Lower Cretaceous; Central Lebanon	' <i>Aleurodicus</i> ' <i>burmiticus</i> Cockerell (1919) <i>Gapenus rhinariatus</i> Drohojowska and Szwedo (2013); <i>Aretsaya therina</i> Drohojowska and Szwedo (2015); <i>Milqartis azari</i> Drohojowska and Szwedo (2015); <i>Shapashe aithiopa</i> Drohojowska and Szwedo (2015); <i>Yamis libanotos</i> Drohojowska and Szwedo (2015)	Cockerell (1919) Drohojowska and Szwedo (2013); Drohojowska and Szwedo (2015)
Bernaestinae	Upper Cretaceous; Kachin, Myanmar Lower Cretaceous; Central Lebanon Upper Jurassic or Lower Cretaceous; Mongolia Upper Jurassic; Kazakhstan	<i>Burmoselis evelynae</i> Shcherbakov (2000); <i>Paraburmoselis kachinensis</i> gen. et sp. nov. <i>Bernaesa neocomica</i> Schlee (1970) <i>Juleyrodes gilli</i> Shcherbakov (2000) <i>Juleyrodes visnyai</i> Shcherbakov (2000)	Shcherbakov (2000); this paper Schlee (1970) Shcherbakov (2000) Shcherbakov (2000)

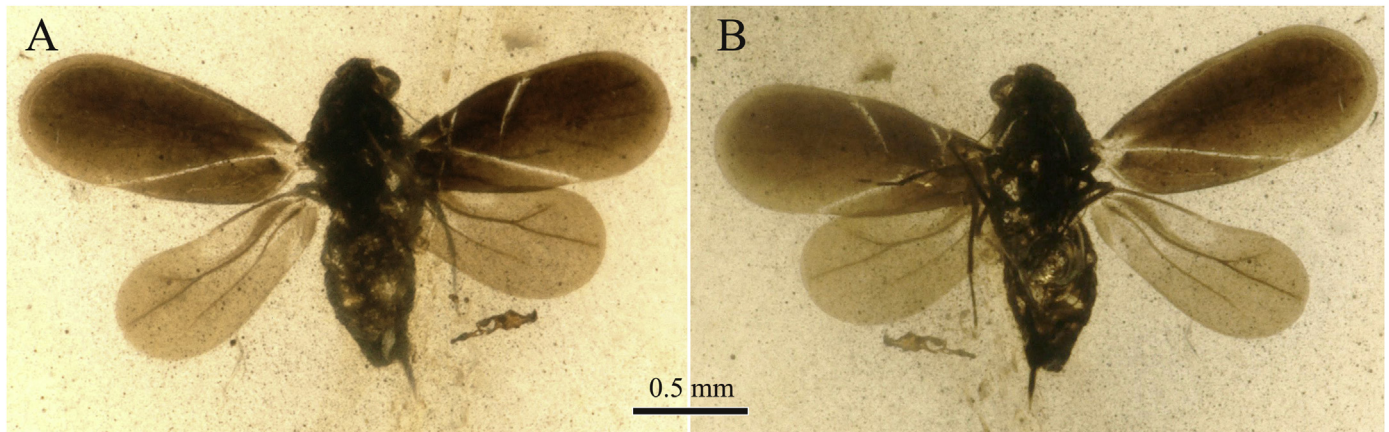


Fig. 1. Photographs of holotype of *Paraburmoselis kachinensis* gen. et sp. nov., NIGP171162. (A), laterodorsal view; (B), lateroventral view. All to scale.

Etymology. The specific epithet is after the region of Kachin Province in northern Myanmar, where the amber piece containing the new whitefly was collected.

Holotype. NIGP171162, a female adult insect with four wings outspread; housed in NIGP.

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 dark, 1.50 mm long; four wings outspread.

Head 0.11 mm long and 0.39 mm wide, narrower than thorax, with anterior margin smoothly convex. Compound eyes well developed, large and produced, not divided. Ocelli unclear. Antennae with 11 segments; flagellum about 0.66 mm long, slender, with basal two flagellomeres obviously thicker than others. Face not well preserved, with clypeus and rostrum obscure.

Thorax much longer and wider than head. Pronotum extremely narrow, 0.05 mm long in the middle line and 0.43 mm wide, chevron-shaped; anterior margin strongly convex anteriorly; posterior margin strongly concave, sub-parallel to anterior margin.

Mesopraescutum distinctly separated, 0.15 mm long and 0.17 mm wide; anterior margin somewhat rounded; posterior margin angled, delicately incised to mesoscutum. Mesoscutum slightly narrower than pronotum, broad, with anterior margin M-shaped; posterior margin smoothly rounded. Parapteron large, elongate. Tegulae obscure. Metascutum long and broad, 0.19 mm long and 0.16 mm wide, widest at its posterior angles; anterior margin slightly concave; lateral margins almost straight for anterior half, and smoothly curved outwards for posterior half; posterior margin strongly arched. Metascutellum and metapostnotum not well preserved, obscure. Prothoracic legs with femur relatively strong; tibia slenderer than femur; basitarsomere almost as long as apical tarsomere. Mesothoracic legs with tibia covered with some tiny setae, almost as long as protibia; tarsus with basitarsomere almost as long as apical tarsomere; tarsal claws tiny and sharp. Metathoracic legs with tibia covered with some tiny setae, slightly longer than pro- and mesotibia; tarsus with basitarsomere about 1.5 times as long as apical tarsomere; tarsal claws tiny and sharp.

Abdomen stout, bulging dorsally, widest near its middle. Pregenital abdomen largely membranous. Pygofer obviously truncate apically. Ovipositor extremely long, directed posteriorly, extending well beyond pygofer.

Forewings gradually widening apically, 1.31 mm long and 0.59 mm wide, with length/width ratio about 2.2. Wing membrane distinctly thickened (sclerotized) and darkly coloured. Costal area and clavus long and broad, nearly occupying 2/3rds of wing length. Peripheral vein present and sub-parallel to apical margin, with peripheral membrane light-coloured. Outer margin densely arranged with tiny setae. Costal margin nearly straight, thickened and carina-like. Apical margin rounded. Claval margin strongly arched, thickened. Stem R+MP+CuA extremely short, branching into R and MP at basal 0.15 of wing length. R long, nearly straight, branching into R1 and Rs at about middle of wing length. R1 smoothly curved, almost reaching peripheral vein. Rs almost as long as stem R, longitudinal, in prolongation of stem R, straight and with slightly curved anterior apically, reaching peripheral vein. MP+CuA forking almost at same level as bifurcation of R. MP sub-parallel to Rs, nearly straight, almost reaching peripheral vein, near wing apex. CuA much shorter than independent part of MP, slightly curved, in prolongation of stem MP+CuA. CuP straight and furrow-like. Pcu relatively long and sinuous, occupying 0.6 of clavus.

Hindwing shorter and narrower than forewing, 1.10 mm long and 0.51 mm wide, with length/width ratio about 2.2. Outer margin densely covered with tiny setae. Twelve long hairs visible on costal margin. Wing membrane slightly thickened, light-coloured, with costal area, basal part of area between stem R and CuA, and anal apex thin and transparent. Costal margin thickened and carina-like,

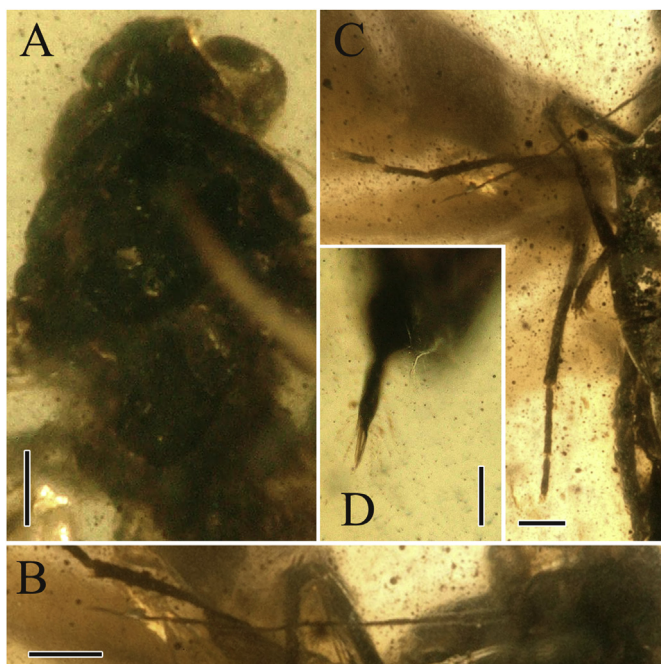


Fig. 2. Body structures of holotype of *Paraburmoselis kachinensis* gen. et sp. nov., NIGP171162. (A), head and thorax in laterodorsal view; (B), right antenna; (C), right thoracic legs; (D), pygofer and ovipositor. Scale bars = 0.1 mm.



Fig. 3. Left wings of holotype of *Paraburmoselis kachinensis* gen. et sp. nov., NIGP171162. (A), forewing; (B), hindwing; (C), enlarged claval margin of forewing and costal margin of hindwing. Scale bars = 0.1 mm.

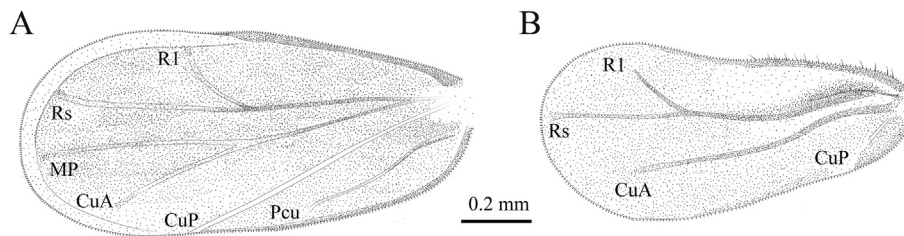


Fig. 4. Line drawings of wings of holotype of *Paraburmoselis kachinensis* gen. et sp. nov., NIGP171162. (A), forewing; (B), hindwing. All to scale.

arched at base, and then nearly straight. Apical margin rounded. R and CuA separated at wing base. Stem R thick, bifurcating into R1 and Rs at basal 0.62 of wing length, with wing membrane around it distinctly thickened and darkly pigmented. R1 short, oblique, ending far away from wing margin. Rs nearly straight, longitudinal, in prolongation of stem R, almost reaching apical margin and close to wing apex, about twice as long as R1 and half as long as stem R. MP absent. CuA long and slightly sinuous, ending far away from wing margin; basal part thickened and darkly pigmented. CuP residual, very short, ending far away from wing margin.

4. Discussion

Bernaestinae, with a series of symplesiomorphies, is the hitherto known oldest representative of Aleyrodomorpha: Aleyrodidae (Shcherbakov, 2000; Drohojowska and Szwed, 2015). The new genus is ascribed to the subfamily on the following morphological imaginal characteristics: the head relatively broad with compound eyes rounded and entire, antennae 11-segmented; the ovipositor long and directed posteriorly; forewings with costal margin thickened, venation complex with MP retained (Shcherbakov, 2000).

The new genus possesses some unique features, which discriminate it from all known bernaestines: metatarsi with basitarsomere long, about 1.5 times as long as apical tarsomere; forewings with wing membrane sclerotized and darkly coloured, peripheral membrane relatively thin, peripheral vein distinct, and MP separated from MP+CuA almost at the same level as bifurcation

of R. In addition, it differs from *Juleyrodus* Shcherbakov, 2000 from the Upper Jurassic of Kazakhstan and the Upper Jurassic or Lower Cretaceous of Mongolia in having forewings much narrower basally than apically, with the costal margin nearly straight, the claval margin smoothly curved, and the bifurcation of both R and MP+CuA at the middle of the wing length; from *Bernaesia* Schlee, 1970 from Lower Cretaceous Lebanese amber in having much narrower head than thorax, 11-segmented antennae, and more complex forewing venation; and from *Burmoselis* Shcherbakov, 2000 from the Kachin amber in having a stout abdomen with maximum width near its middle, and forewings with R+MP+CuA extremely short, Rs almost as long as stem R, MP with basal part present, and Pcu ending far away from wing base and occupying 0.6 of clavus. Cockrell (1919) described the first whitefly '*Aleurodicus burmiticus*' from Burmese amber. Shcherbakov (2000) doubted its generic assignment but confirmed its subfamily placement. The new genus and species can be easily distinguished from this taxon in possessing a stout abdomen widest near its middle, and forewings with the wing membrane sclerotized, a peripheral vein distinct, the costal margin thickened, and the venation complex.

So far, 14 species in 13 genera belonging to Aleyrodidae have been reported from the Upper Jurassic to lowermost Upper Cretaceous of Asia based on adult specimens (Table 1), and some adults and puparia from the Lower Cretaceous of Lebanese, Purbeck and Weald of England, and Montsec in Spain, which are still undescribed (Shcherbakov, 2000; Drohojowska and Szwed, 2011). The extinct subfamily Bernaestinae has been reported from the Upper Jurassic of Central and Northeast Asia, Lower Cretaceous of Lebanon

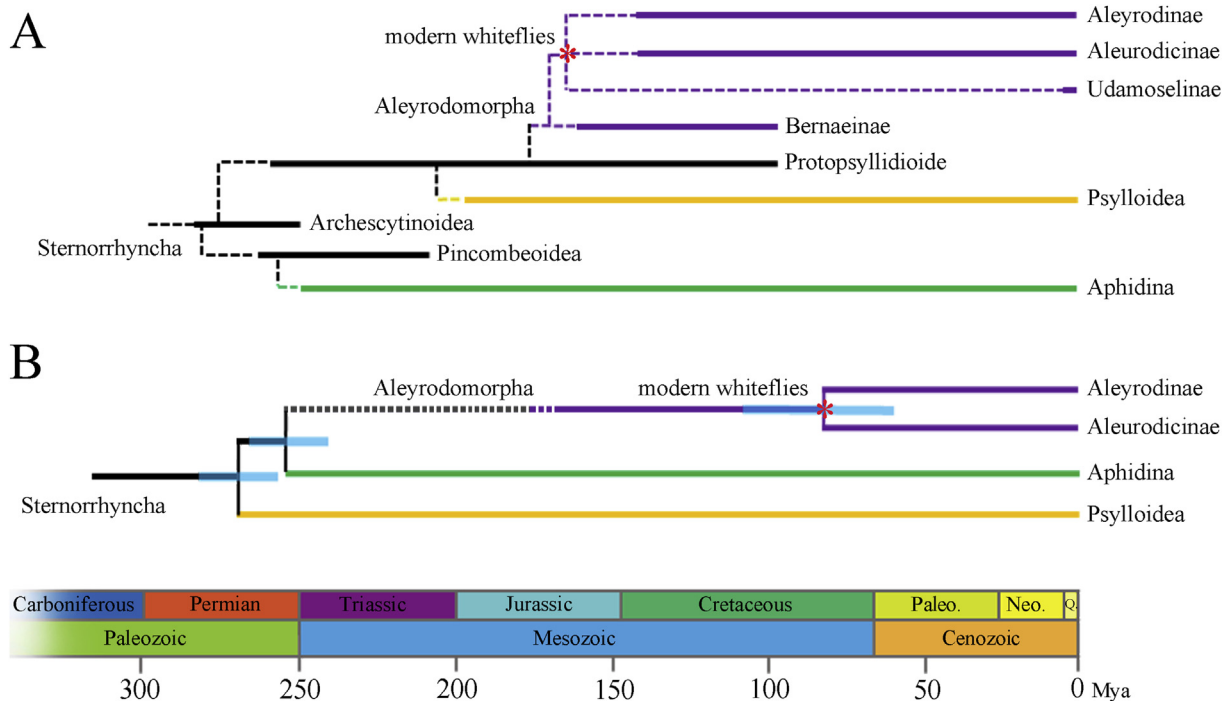


Fig. 5. Phylogeny and divergence time estimates of Sternorrhyncha with emphasis on Aleyrodomorpha. (A), chronogram based on fossil and morphological data, modified from Shcherbakov (2000) and Drohojowska and Szwedlo (2015); (B), chronogram based on mitochondrial phylogenomic PCGRNA dataset with bars on nodes indicating their 95% mean confidence intervals, modified from Li et al. (2017). Abbreviations: Paleo., Paleogene; Neo., Neogene; Q., Quaternary.

and lowermost Upper Cretaceous of Myanmar (Schlee, 1970; Shcherbakov, 2000; this study). The recent subfamilies Aleurodicinae and Aleyrodinae have been also well documented in Cretaceous Lebanese and Burmese amber (Cockerell, 1919; Schlee, 1970; Drohojowska and Szwedlo, 2011, 2013, 2015). Udamoselinae, however, remains undescribed from Mesozoic strata and to its living representatives are two species attributed into its type genus known only from four male adults (Enderlein, 1909; Martin, 2007). Shcherbakov (2000) stated that some undescribed udamoselines occur in Lebanese amber. Considering that the author also proposed to restore the subfamily Udamoselinae in the broad sense (including Aleurodicinae) in this paper, the 'udamoselines' mentioned in Shcherbakov (2000) are likely members of the Aleurodicinae and were described by Drohojowska and Szwedlo (2013, 2015).

The hitherto known oldest aleyrodomorphan, as representatives of Bernaeinae, is from the Late Jurassic of Central and Northeast Asia, and the origin of this sternorrhynchan lineage is inferred to be slightly earlier based on its available fossil evidence, morphological traits and presumptive systematic position: Psyllomorpha, Aleyrodomorpha and their ancestral group Protopsyllidoidea comprise a monophyletic group, as a sister group to Aphidina (Coccidomorpha and Aphidomorpha) plus its ancestral group Pincombeoidea, and Aleyrodomorpha derived from Protopsyllidoidea in the Early to Middle Jurassic (Fig. 5; Shcherbakov, 2000; Shcherbakov and Popov, 2002; Drohojowska and Szwedlo, 2011, 2015). Molecular phylogenetics is considered as a robust test of taxonomic classification and evolutionary relationships (Chen et al., 2011). Unfortunately, just a few molecular studies have been focused on the phylogeny of high level relationships of Sternorrhyncha or within Aleyrodomorpha (e.g., Campbell et al., 1994; Thao et al., 2004). Recently, some phylogenomic analyses of the order Hemiptera also included some sternorrhynchan taxa (Cui et al., 2013; Li et al., 2017; Wang et al., 2017; Johnson et al., 2018). Compared to palaeontological inferences, these studies provide us with a different

scenario: all these studies indicated that Psyllomorpha and Aleyrodomorpha did not compose a monophyletic lineage; molecular dating analyses suggested that ancient aleyrodomorphs might originate as early as in the Paleozoic (Li et al., 2017; Wang et al., 2017; Johnson et al., 2018); in the chronogram of Li et al. (2017) with multiple aleyrodid taxa included, Aleurodicinae (represented by *Aleurodicus dugesii*) and Aleyrodinae (represented by *Bemisia tabaci*, *B. afer*, *Aleurochiton aceris* and *Trialeurodes vaporariorum*) likely separated in the Late Cretaceous.

5. Conclusions

The systematics of whiteflies is unusually based almost solely on the immature puparium, with imaginal characteristics unknown for most living taxa (Shcherbakov, 2000; Martin, 2007; Drohojowska and Szwedlo, 2011). The situation now greatly embarrasses the reconstruction of the origin and early evolutionary history of Aleyrodomorpha, because the taxonomic frameworks of its living related lineages (i.e., Aphidina and Psyllomorpha) as well as extinct Sternorrhyncha including Mesozoic whiteflies are mainly on the basis of imaginal traits. The conflict between palaeontological and molecular data further exacerbates the chaos of our knowledge on the evolution and taxonomy of Aleyrodomorpha. The problem likely remains unresolved until data on adult characters of the three living subfamilies, molecular phylogeny, as well as extinct stem groups (e.g., Bernaeinae) have been greatly updated.

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