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Source: Palaeodiversity, 16(1) : 125-134

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/pale.v16.a5

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A new coccid family, Adocimycolidae fam. nov. (Hemiptera: Coccomorpha), with extended hamulohalteres in Burmese (Myanmar) amber

George Poinar Jr. & Fernando E. Vega

Abstract

The present paper describes a male coccid (Hemiptera: Coccoidea) in mid-Cretaceous Burmese amber with the largest known hamulohalteres on any extant or extinct coccid. Aside from this character, the specimen has an unusual assortment of features, including a prolonged head with three cylindrical dorsal simple eyes in three rows joining laterally, a single ocellus dorsally placed at apex of a prolonged head, compound eyes in a ventro-lateral position and a 10-segmented antennae longer than body length. These features prohibit it from being assigned to any known extant or extinct family. Whether the large hamulohalteres on *Adocimycolus aarondavisii* gen. et sp. nov. are evidence of a plesiomorphic state of a lineage of Mesozoic Coccoidea that had fully developed metathoracic wings or could be a genetic mutation, is addressed.

K e y w o r d s : *Adocimycolus*; Adocimycolidae; Coccomorpha; hamulohalteres; male scale insect; Myanmar.

1. Introduction

Scale insects (Hemiptera: Coccoidea) are an ancient group, whose individuals show a range of morphological shapes and life histories. Over 8508 species are estimated to occur globally (Gullan & Cook 2007; ScaleNet https://scalenet.info/fams/). These small herbivores can be found today in many habitats, feeding on both the above and below ground stages of many plant groups, especially angiosperms, and sometimes causing serious crop damage (Comstock 1950; Gill 1993; Pellizzari & Germain 2010). The males and females are quite different, with the former supposedly living only a few days, having rudimentary or lacking mouthparts and normally possessing wings (Vinis & Kozár 1981 have reported on a wingless male scale insect species). Most sedentary females have well developed mouthparts and lack wings. In a few instances, scale insects, such as the ice plant scale, *Pulvinariella mesembryanthemi,* have been used as biological control agents against the introduced hottentot fig plant (*Carpobrotus edulus*) in California dunes (Poinar 2016).

Almost all of the natural sightings of extant coccids are females or the waxy protective structures they make, some of which appear as galls. Such structures also protect the nymphs that often accompany the sedentary females. Since the females are usually sedentary most of their lives, they are not as common as males in amber but some have been reported (Koteja & Zak-Ogaza 1988a, 1988b; Johnson et al. 2001; Koteja 2004; Gullan & Cook 2007; Vea & Grimaldi 2012, 2015; Wang et al. 2015; Poinar et al. 2020; Fig. 1; Table 1).

While the miniature adult males are rarely detected in nature, they are commonly found in amber since the wind currents blow them up against the sticky resin that acts as a trap. The early studies on coccid systematics were based mainly on the structure of the female mouthparts, sensilla and other morphological features (Koteja 1974a, 1974b, 2004) while later studies discussed the classification of male coccids (Theron 1958; Ghauri 1962; Giliomee 1967; Koteja & Poinar 2001; Koteja 2004; Gullan & Cook 2007; Koteja & Azar 2008; Vea & Grimaldi 2015; Poinar 2021).

Male scales are said to lack mouthparts (Ghauri 1962; Vea & Grimaldi 2015), but both Ghauri (1962) and Giliomee (1967) report mouth openings in these stages. While Ghauri (1962) considers these mouth openings "non-functional", some male scales, like the Burmese amber *Macrodrilus bostrychus* (Poinar 2021) and an undescribed member of the Weitschatidae (Koteja 2008) have mouthparts large enough to take in liquids and possibly even pollen grains (Poinar 2021). A male scale preserved in Burmese amber adjacent to a flower of *Tropidogyne lobodisca* could have been attracted to the large apical nectar disc in the center of the flower (Poinar & Chambers 2019; Fig. 2). This association suggests that some extinct male coccids could have visited flowers for nectar during their short existence. The presence of an anus in male scale insects (Ghauri 1962; Vea & Grimaldi 2015) suggests that there is a functional alimentary track.

The present study describes a male coccid in Burmese amber. The male specimen of *Adocimycolus aarondavisii* gen. et sp. nov. is quite unique by exhibiting the largest known hamulohalteres on a male scale insect. It is questioned whether these giant hamulohalteres are evidence of a plesiomorphic state of an Early Mesozoic lineage that had fully developed metathoracic wings or are the result of a genetic mutation.

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Fig. 1. The female scale insect, *Paleolepidotus macrocolus,* in Burmese amber. Note wax scales emerging from body (surrounding debris removed using Adobe Photoshop). – Scale: 0.9 mm. Accession # B-He-34 deposited in the Poinar Amber Collection maintained at Oregon State University.

2. Materials and methods

The specimen originated from the Noije Bum 2001 Summit Site mine excavated in the Hukawng Valley in 2001 and located southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E) in Myanmar. Based on paleontological evidence this site was dated to the late Albian of the Early Cretaceous (Cruickshank & Ko 2003), placing the age at 97 to 110 Mya. A study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Mya or at the Albian/Cenomanian boundary (Shi et al. 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar et al. 2007). Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 X. Classification and nomenclature follows that employed by Vea & Grimaldi (2015).

Table 1. List of scale insects from Burmese amber with distinguishing features that separate them from *Adocimycolus aarondavisii* gen. et sp. nov.

Scale insects described from Burmese amber	Family	Reference	Distinguishing features
Alacrena peculiaris	*incertae sedis*	Vea & Grimaldi 2015	Very long aedeagus; wing with alar notch
Albicoccus dimai	Albicoccidae	Koteja 2004	Antennae setae very short
Burmacoccus danyi	Burmacoccidae	Koteja 2004	Antennae setae shorter than segment width
Burmorthezia kotejai	Ortheziidae	Vea & Grimaldi 2012	Second stage nymph
Burmorthezia insolita	Ortheziidae	Vea & Grimaldi 2012	Second stage nymph
Gilderius eukrinops	Pseudococcidae	Vea & Grimaldi 2015	Antennae setae shorter than segment width; head round
Kozarius achronus	Kozariidae	Vea & Grimaldi 2015	Elongate penal sheath; 9-segmented antennae
Kozarius perpetuus	Kozariidae	Vea & Grimaldi 2015	Elongate penal sheath; compound eyes greatly protruding
Macrodrilus bostrychus	Macrodrilidae	Poinar 2021	Antennae lack bristles; long endophallus
Magnilens glaesaria	*incertae sedis*	Vea & Grimaldi 2015	Two segmented tarsi; large, protruding eyes
Marmyan barbarae	*incertae sedis*	Koteja 2004	Wings with distinct microtrichia
Mesophthirus engeli	Xylococcidae	Grimaldi & Vea 2021; Shcherbakov 2022	First stage nymph
Paleolepidotus macrocolus	*incertae sedis*	Poinar et al. 2020	Female scale insect
Pedicellicoccus marginatus	*incertae sedis*	Vea & Grimaldi 2015	Enlarged & bulbous pedicel; 9-segmented antennae
Pseudoweitschatus audebertis	Weitschatidae	Vea & Grimaldi 2015	Apical antennomeres with curved bristles
Rosahendersonia prisca	Coccidae	Vea & Grimaldi 2015	Hamulohalteres absent; antennae filiform, with hairlike setae not greater than width of antennomeres
Wathondara kotejai	Ortheziidae	Wang et al. 2015	Female scale insect

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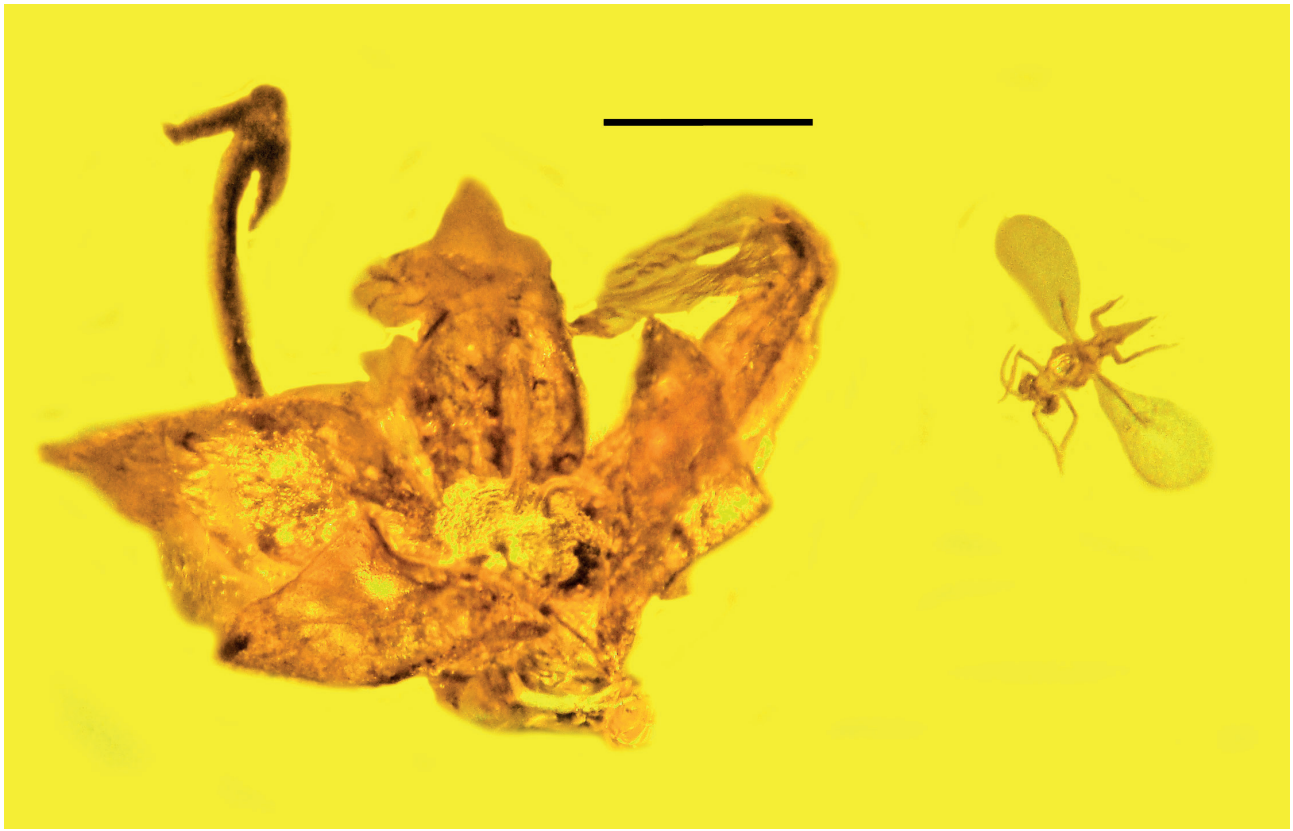

Fig. 2. A male coccid adjacent to the flower of *Tropidogyne lobodisca* in Burmese amber. Note large nectar dish in center of flower. – Scale: 0.9 mm. Accession # B-An-13 deposited in the Poinar Amber Collection maintained at Oregon State University.

3. Systematic paleontology

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843

Infraorder Coccomorpha Chou, 1963

Superfamily Coccoidea Fallén, 1814

Family Adocimycolidae nov.

LSID: urn:lsid:zoobank.org:pub:C4E5F762-6029-4B5D-A214-D53B9CCA0120

Diagnosis: Based on the male holotype. Female characters unknown. Adocimycolidae fam. nov. differs from males of other coccoidid families by its enlarged hamulohalteres. In addition, the following combination of characters distinguishes Adocimycolidae fam. nov. from other coccoidid families: head prolonged, with three cylindrical dorsal simple eyes; single ocellus dorsally placed at apex of prolonged head; compound eyes with numerous ommatidia in ventro-lateral position at head tip, only slightly visible from above; ten-segmented antennae longer than body, with antennomeres longer than wide, flagellomeres multi-nodose, bearing erect black bristles much longer than width of flagellomeres, which lack satellite setae; legs elongate, foreleg with expanded trochanter; tarsi setose, ridged, one-segmented, bearing claws with digitules shorter than claw length; single tarsal digitule arising from outer distal tarsal margin. Forewings well-developed, with rounded tips and wide subcostal ridge extending to ¾ of the anterior wing margin and terminating in a faint pterostigma; cubital ridge arising from wing base, more than half wing length; wing membrane with a series of pseudo-veinlets composed of irregular planiform, prostrate scales arranged in broken rows extending out from margin of the wing membrane; microtrichia absent. Abdomen, with nine distinct segments, with extremely long tubular duct filaments arising from abdominal segments VII and VIII; anus membranous, distinct, penal sheath long, aedeagus short, slightly curved, anal lobes present. See also Table 1.

Type genus: *Adocimycolus* nov. (monotypic).

Genus *Adocimycolus* nov.

LSID: urn:lsid:zoobank.org:act:3317DD0C-A570-4DDF-AAE5-A4DAAFDB55BD

Etymology: Generic name from the Greek “adokimos” = false and the Greek “kolus” = leg, in regards to the extended left hamulohaltere that resembles a leg.

Type species: *Adocimycolus aarondavisii* gen. et sp. nov.

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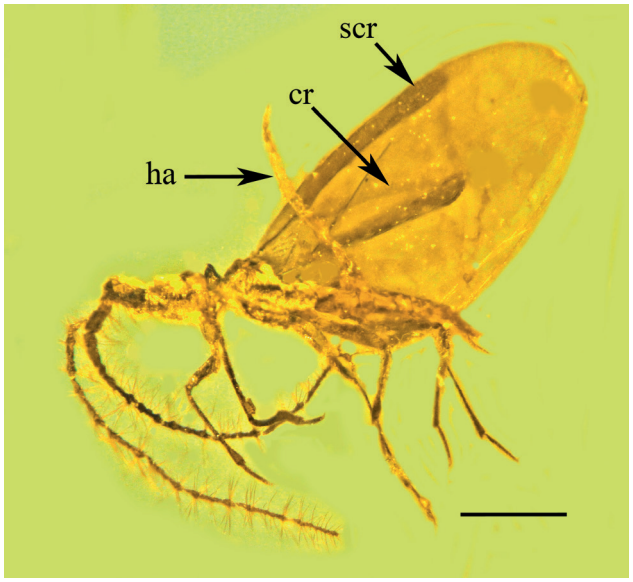

Fig. 3. Lateral view of entire holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. **cr** = cubital ridge, **ha** = left hamulohaltere, **scr** = subcostal ridge. – Scale: 0.5 mm.

Adocimycolus aarondavisii gen. et sp. nov.
Figs. 3–13

L S I D : urn:lsid:zoobank.org:act:E06AD30B-4ED8-4B40-A1D8-7CC285E26A98

E t y m o l o g y : The epithet is in honor of Aaron P. Davis, Senior Research Leader of Crops and Global Change at the Royal Botanic Gardens, Kew (UK), for his significant contributions to *Coffea* taxonomy, systematics, climate change resilience, sustainability, and crop development.

T y p e l o c a l i t y : Myanmar (Burma), state of Kachin, Noije bum 2001 Summit Site amber mine in the Hukawng Valley/ SW of Maingkhwan (26º 20´N, 96º 36´E).

D i a g n o s i s : As for family (monotypic).

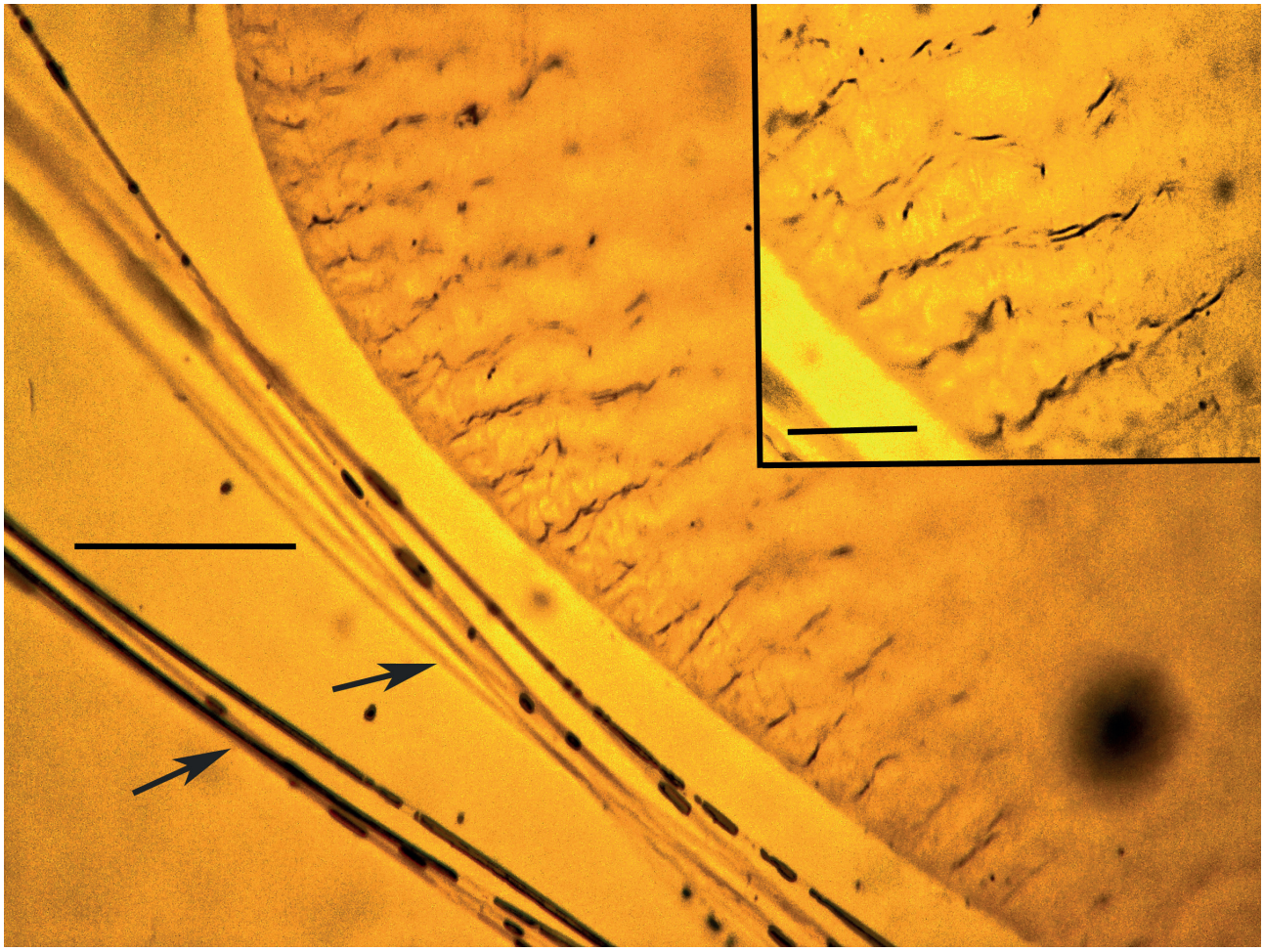

Fig. 4. Portion of wing membrane of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. Note broken rows of planiform scales extending inward from the wing membrane. Arrows show sets of wax filaments arising from abdominal segments 7 and 8. – Scale: 65 µm. Insert shows details of planiform setae in various positions. – Scale: 73 µm.

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Fig. 5. Ten-segmented antenna of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. Note protuberances and long spines on flagellomeres. – Scale: 0.3 mm.

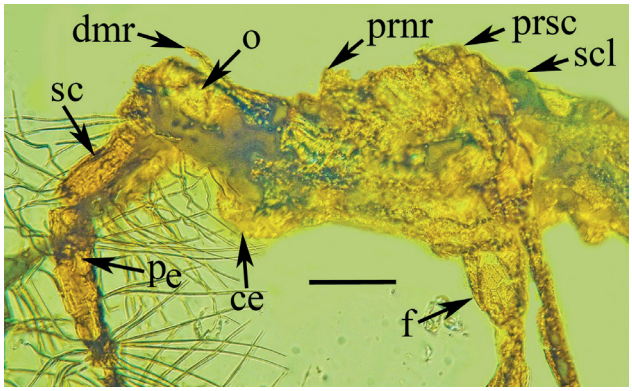

Fig. 6. Lateral view of head and thorax of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. **ce** = compound eye; **f** = foreleg; **dmr** = dorsal midcranial ridge; **o** = ocellus; **Pe** = pedicel; **prnr** = pronotal ridge; **prsc** = prescutum; **sc** = scape; **scl** = scutellum. – Scale: 146 µm.

LSID for publication: urn:lsid:zoobank.org:pub:C4E5F762-6029-4B5D-A214-D53B9CCA0120

Type material: Accession number B-He-42 deposited in the Poinar Amber Collection maintained at Oregon State University.

Description (Figs. 3–13): The specimen is complete except for the tips of the extended wax tails on abdominal segments VII and VIII.

Holotype male: Small; body length, 1.9 mm; head with extension of dorsal midcranial ridge almost reaching apical edge of ocellus; head with dorsal median crest; antennae 2.1 mm, longer than body, with 8 nodulated flagellomeres; fleshy, capitate and satellite setae absent; no lateral extensions on segments; all antennomeres longer than wide; flagellomeres multi-nodose, bearing erect black bristles much longer than width of flagellomeres; length scape, 83 µm; width scape, 140 µm; length pedicel, 109 µm; width pedicel, 77 µm; length of flagellomeres: 1, 170 µm; 2, 290 µm; 3, 326 µm; 4, 307 µm; 5, 294 µm;

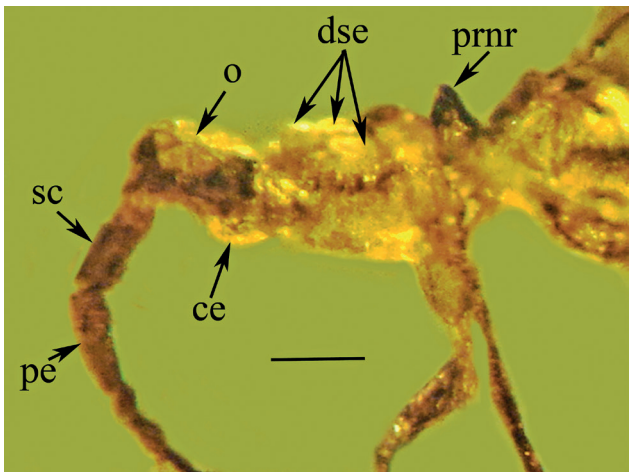

Fig. 7. Lateral view of head of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber (from a different angle and lighting than Fig. 8). **ce** = compound eye; **dse** = dorsal simple eyes; **o** = ocellus; **pe** = pedicel; **prnr** = pronotal ridge; **sc** = scape (spines on antenna removed using Adobe Photoshop). – Scale: 234 µm.

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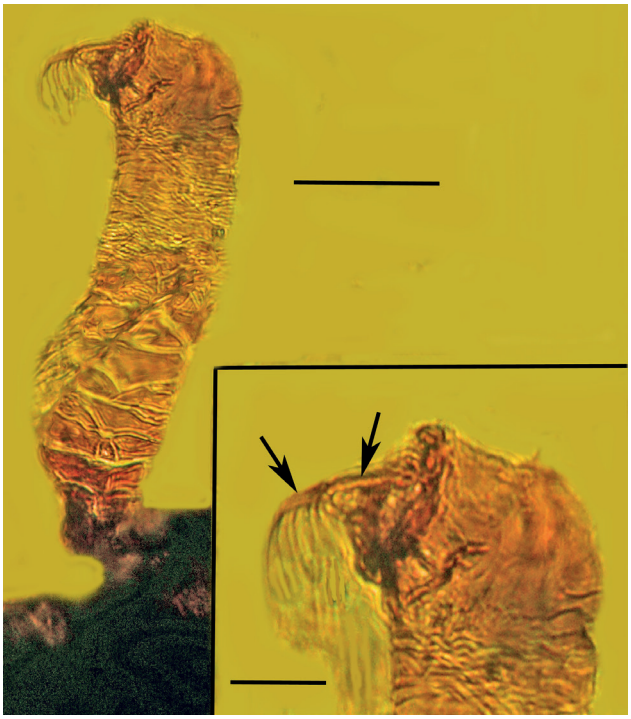
Fig. 9. Right hamulohaltere of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. – Scale: 82 µm. Insert shows two hami bearing cilia (arrows) at tip of hamulohalteres. – Scale: 54 µm.



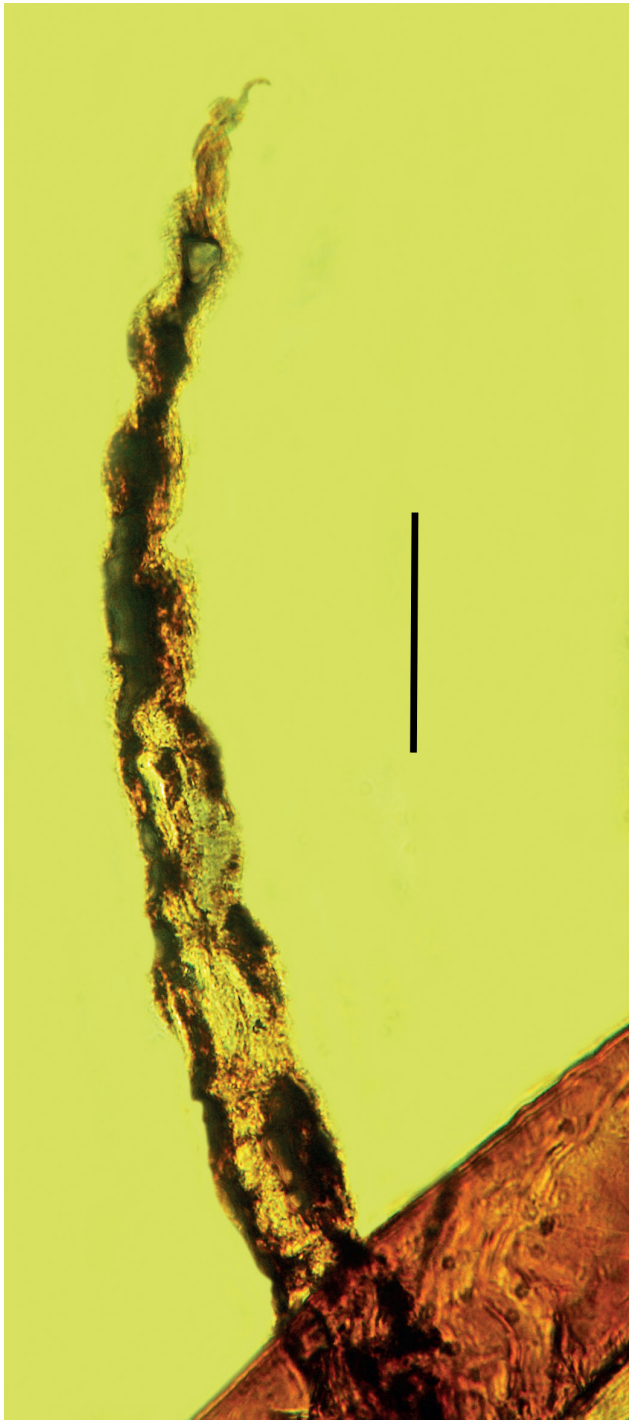


Fig. 8. Left hamulohaltere of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. Note segmented appearance and faint hamulus at tip. – Scale: 150 µm.

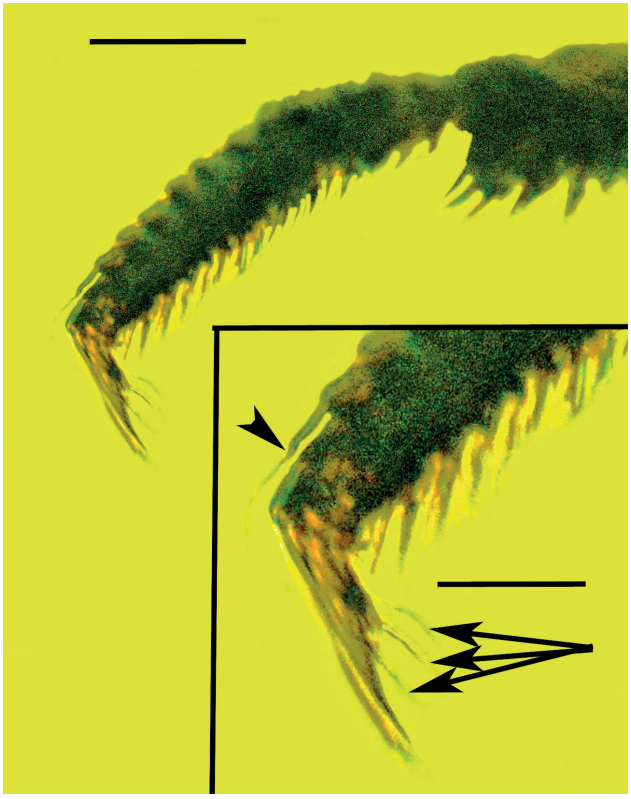


Fig. 10. Setose ridged tarsus of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. – Scale: 90 µm. Insert shows tarsal digitulae (arrows) arising from the inner base of the tarsal claw and a tarsal digitule (arrowhead) arising from the outer distal margin of the tarsus. – Scale: 40 µm.

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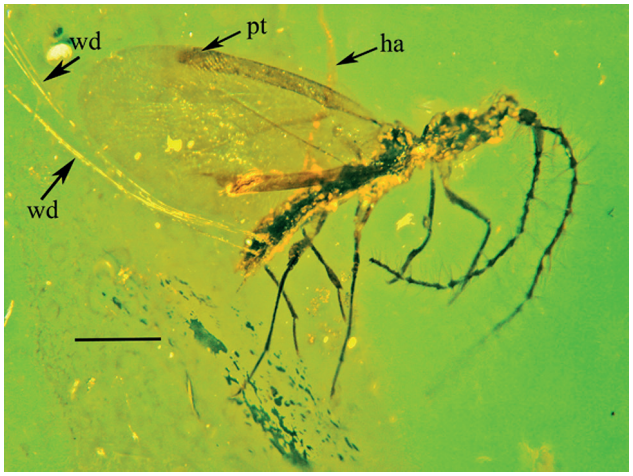

Fig. 11. Lateral view of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber under special lighting to show the elongate tubular wax ducts (**wd**) that surpass the body length and arise from abdominal segments VII and VIII. The left hamulohaltere (**ha**) and faint pterostigma (**pt**) are also noted. – Scale: 0.5 mm.

6, 294 µm; 7, 332 µm; 8, 307 µm; compound eyes large, round, ventral-lateral in position, only slightly protruding from head dorsally, 58 µm in diameter, with numerous ommatidia; ocellus large, flat, dorsally positioned on head apex; three cylindrical dorsal simple eyes on posterior head portion; neck constriction slight; pronotum with pronotal ridge and pronotal sclerite; length pronotum, 450 µm; prescutum flat in lateral view; prescutal ridge sclerotized; pronotal ridge triangular in lateral view; legs long, sub-equal to body length; forelegs walking type; tarsus separated from tibia; length procoxa, 112 µm; length first trochanter, 156 µm; length second trochanter, 192 µm; length profemur, 390 µm; protibia long, slightly swollen at tip, length protibia, 533 µm; length protarsus, 256 µm; single tarsus nodose, setose, slender, bearing single claw; claw length, 95 µm; two pairs of simple digitules at inner base of claw; ungual digitules do not protrude out of claw; small ventral expansion near middle of claw; single tarsal digitule arising from outer distal margin of tarsus; claw denticles absent; length second mesotrochanter, 185 µm; length mesofemur, 290 µm; length mesotibia, 625 µm; length mesotarsus, 270 µm; length first metatrochanter, 178 µm; length second metatrochanter, 106 µm; length metafemur, 220 µm; length metatibia, 605 µm; length metatarsus, 270 µm. Wing broad, tip rounded, length, 1.9 mm; ratio of wing to antenna = 0.9; length subcoastal ridge, 1.3 mm; subcostal

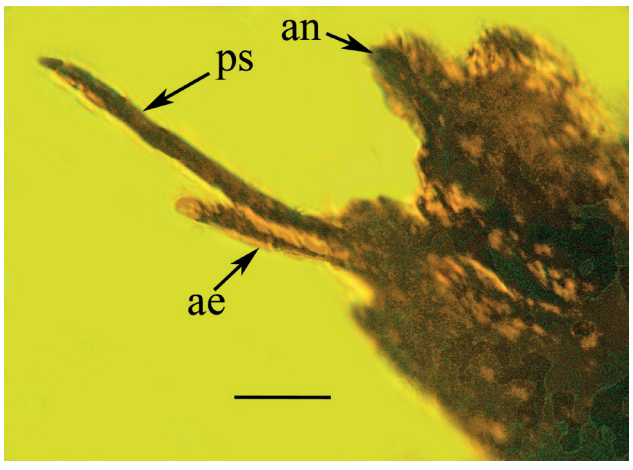

Fig. 12. Terminalia of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. **ae** = aedeagus; **an** = anus; **ps** = penial sheath. – Scale: 427 µm.

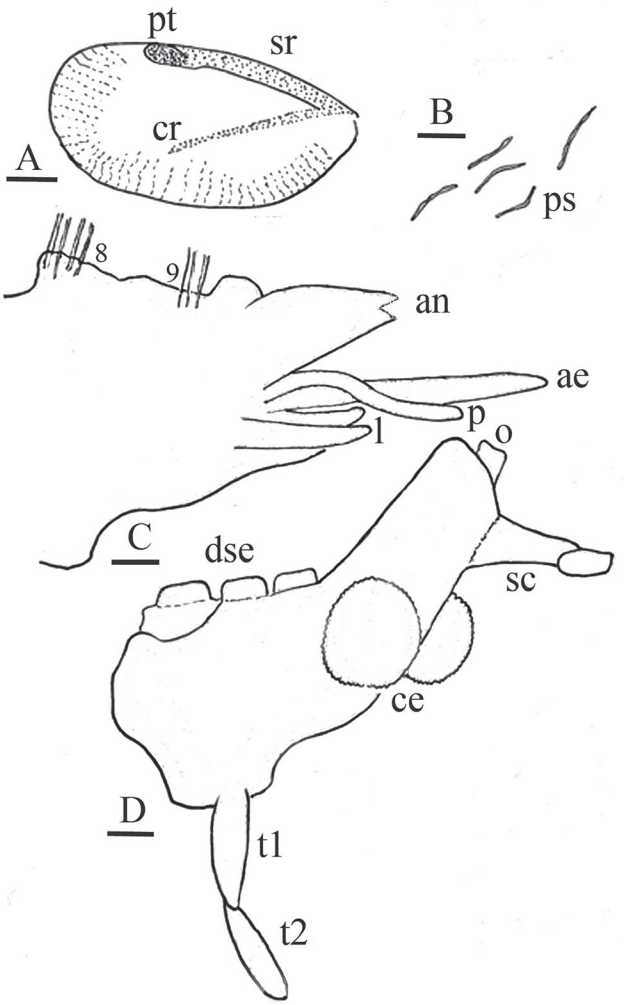

Fig. 13. Drawing of specific body parts of holotype of *Adocimycolus aarondavisii* gen. et sp. nov. in Burmese amber. **A:** Wing: cr = cubital ridge; sr= subcostal ridge; pt = pterostigma. – Scale: 320 µm. **B:** Planiform scales (ps) on wing membrane. – Scale: 32 µm, **C:** Terminalia: ae = aedeagus; an = anus; l = apical lobes; p = penal sheath; 8 = eighth abdominal segment with emerging wax filaments; 9 = ninth abdominal segment with emerging wax filaments. – Scale: 64 µm. **D:** Lateral view of head: ce = compound eyes; dse = dorsal simple eyes; o = ocellus; sc = scape; t1 = first trochanter; t2 = second trochanter. – Scale: 64 µm.

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ridge extending to ¾ of anterior wing margin, terminating in a faint pterostigma; cubital ridge faint, originating from near wing base, length 0.8 mm; no additional ridges observed; wing membrane with broken sub-parallel rows of planiform setae extending inward from margin; planiform setae longitudinally attached; from 12 µm to 18 µm in length, upright microtrichia absent; hamulohalteres large; length left hamulohaltere, 1 mm; ratio of wing to left hamulohaltere = 1.9; greatest width left hamulohaltere, 48 µm; length exposed portion of right hamulohaltere, 317 µm; greatest width right hamulohaltere, 70 µm; two hami bearing cilia protruding from apex of hamulohalteres. Abdomen nine-segmented, length 572 µm, greatest width, 315 µm; with anus and penial sheath on 9th segment; length aedeagus, 253 µm; width aedeagus, 16 µ; penial sheath elongate, length 158 µm; anal lobes present, only partially exposed; glandular pouches on abdominal segments VII and VIII producing five and six, respectively, extended wax tails.

Comments: Due to the small size and dark body of the fossil, it was not possible to determine certain fine morphological details, such as the presence or absence of thoracic and abdominal spiracles. Both hamulohalteres originate from the mesothorax where normal hamulohalteres are positioned. The left hamulohaltere is straight (Fig. 8) while the right hamulohaltere is angled forward and then bent backward (Fig. 9). The extended hamulohalteres separate *Adocimycolus aarondavisii* gen. et sp. nov. from all previously described fossil and extant male coccids (Comstock 1950; Ghauri 1962; Giliomee 1967; Koteja & Poinar 2001; Koteja 2004; Gullan & Cook 2007; Koteja & Azar 2008; Vea & Grimaldi 2015; Poinar 2021). Aside from the extended hamulohalteres, other distinguishing features separating *Adocimycolus* from previously described scale insects in Burmese amber are presented in Table 1. Due to its unique combination of characters, *Adocimycolus* could not be assigned to a current or extinct family. However, on the basis of its body shape and clusters of elongate setae on nodular antennae, *Adocimycolus* resembles the Lebanese amber coccid, *Hodgsonicoccus patefactus* Vea & Grimaldi (2015).

4. Discussion

Planiform scales, as on the wing membrane of *Adocimycolus aarondavisii* gen. et sp. nov., do not frequently occur on wing membranes of male scale insects (Ghauri 1962; Giliomee 1967; Hodgson 2020; Wu & Xu 2022). These wing scales, which differ from upright microsetae, appear as a series of broken veinlets radiating out from the wing margin. A closer examination shows that these planiform scales are closely appressed to the wing surface (Figs. 4, 13). These scales (which could be considered flattened setae) distinguish *Adocimycolus* from the archiococcids, a group defined as lacking wing setae (Hodgson 2020).

Reduced wings occur in several insect orders. Winged Diptera have only a single pair of functional wings attached to the mesothorax, while the metathoracic wings are represented by reduced stub-like appendages called halteres. These halteres are considered balancing or equilibrium organs since when removed, the power of flight is usually lost or greatly reduced (Wigglesworth 1965). The halter consists of a basal scabellum, a stalk-like pedicel and a terminal expanded knob-like capitulum. They contain hemolymph and at least one tracheole (Imms 1948).

In male Strepsiptera, it is the mesothoracic wings that are represented by halteres and if these are removed, the insects cannot fly (Wigglesworth 1965; Kogan & Poinar 2019). Present day aphids (Sternorrhyncha) have two pairs of wings. The hind pair are usually smaller than the front pair, but they are membranous and normally contain veins. However, in the mid-Cretaceous, there were aphid lineages whose mesothoracic wings were reduced to halteres (Poinar & Brown 2005, 2006).

Extant and extinct male scale insects have the metathoracic wings represented by reduced stub-like appendages called hamulohalteres. Such hamulohalteres are normally quite short and never extend above the body, which makes the extended hamulohalteres of *Adocimycolus* so unique. Whether they are evidence of a plesiomorphic state of some Early Mesozoic Coccoidea lineages that had fully developed metathoracic wings cannot be answered since such fossil specimens have not been found. Possibly these enlarged hamulohalteres represent a normal size for some males whose bodies became reduced over time (Comstock & Needham 1898).

The presence of two hami with cilia at the tip of the hamulohalteres indicates that these structures are truly overgrown hamulohalteres. The long, narrow left hamulohaltere of *Adocimycolus aarondavisii* sp. nov. bears a number of modulations (Figs. 3, 8), while the right hamulohaltere is flat and broad and could represent a deteriorated wing membrane (Fig. 9). Some members of the Ortheziidae also have long hamulohalteres but they do not exceed 315 µm so are much smaller than those of *Adocimycolus* (Vea 2014).

Another reason for their abnormal size is that these structures are the result of a genetic mutation since no present day or extinct male coccids have such a disparity between the hamulohalteres and mesothoracic wings. As Comstock (1950) commented regarding coccid morphology, "in nature, all gradations exist between the different types of structures and their development".

With both a mouth opening and an anus, it is possible that *Adocimycolus aarondavisii* gen. et sp. nov., has a functional alimentary canal. This would allow the species to ingest minuscule amounts of water or even floral nectar. A male scale insect adjacent to a flower of *Tropidogyne lobodisca* Poinar & Chambers (2019) characterized by having a large nectar disk (Fig. 2) suggests that some male coccoids may have consumed nectar as an energy source during their existence. The Burmese amber fossil *Adocimycolus aarondavisii* gen. et sp. nov., represents an extinct lineage with unique morphological characters. These features make it impossible to align it with any known fossil or extant family. This specimen provides yet another glimpse of mid-Cretaceous male scale insects,

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adding to our knowledge of the morphological diversity of Mesozoic Coccoidea.

Acknowledgements

We are grateful to Elizabeth Moll-Willard (Stellenbosch University, South Africa); Joanna Kalisz (University of Agriculture, Krakow, Poland); Xinyi Zheng (Guizhou University, People's Republic of China), and Chris J. Hodgson (The National Museum of Wales, Cardiff, UK) for providing scientific literature and J. H. Giliomee and another reviewer whose comments greatly improved the paper.

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Manuscript received: 5 February 2023, revised version accepted: 30 March 2023.

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