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A new genus of Empididae (Diptera) with enlarged postpedicels in mid-Cretaceous Burmese amber

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ABSTRACT

A new genus and species of Empididae (Diptera) in mid-Cretaceous Burmese amber is described as *Neolavesia hadroceria* gen. et sp. nov. in the subfamily Atelestinae. The male is characterised by its small size, unique wing venation with reduced cell dm and the greatly expanded postpedicels that may have been used as sexual attractants. A novel feature of the fossil is a small, elongate, glutinous structure containing numerous filiform, sperm-like bodies adjacent to the abdominal terminus.

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Diptera; Empididae;
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Introduction

Dance flies (Diptera: Empididae), also known as balloon flies, represent a cosmopolitan family of small to medium-sized flies that are predators of various arthropods. Their food habits are varied, and some are known to consume dead insects in spider webs while others ingest pollen and nectar from flowers. Some species are considered important in providing natural control of coccids (Hemiptera), mites (Acari), agromyzids (Diptera) and mosquitoes (Culicidae) (Steyskal and Knutson 1981).

The adults possess legs adapted for seizing prey. It is usually the foreleg that is raptorial; however, the middle and hind legs can also serve that function. The femora and tibia of such legs normally possess sharp, pointed spines on the inner surfaces. The size of these spines can vary considerably, from very small, as in the specimen described below, to large enough to penetrate the captured prey when the tibia and femur close against each other.

The common name, dance flies, refers to those species that collect in mating swarms; however, some species mate on vegetation or on the ground (Cumming and Sinclair 2009). Empidid larvae occur in a variety of terrestrial habitats, including damp soil, wood and dung, as well as in aquatic environments where they prey on larvae and pupae of black-flies (Simuliidae) and caddisflies (Trichoptera) (Steyskal and Knutson 1981).

In some groups, especially in the subfamily Empidinae, when males chose a mate to initiate copulation, they present a nuptial gift, which often is a prey item, secreted balloons or various inedible items. The nuptial gift may be the only proteinaceous food the females receive during their lifetime since they do not appear to be active predators (Steyskal and Knutson 1981). Swarming females may use their large wings, pinnate leg scales and eversible abdominal pleural sacs to attract males (Cumming 1994).

Mate choices may be actively made by females visiting male-dominated swarms (Cumming 1994). Thus, the new male specimen described below as *Neolavesia hadroceria* gen. et sp. nov., may have used its enlarged postpedicels to attract females, giving it

a mating advantage. The sexual selection behaviour of empidids makes them one of the most intriguing families of Diptera.

Materials and methods

The amber specimen originated from the Noiye Bum Summit Site mine in the Hukawng Valley, located southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E) in Myanmar (formerly known as Burma). The site has been dated to the late Albian of the Early Cretaceous (Cruickshank and Ko 2003), placing the age at 97–110 Mya. A more recent study estimated the age to be 98.8 ± 0.62 Mya or at the Albian/Cenomanian boundary (Shi et al. 2012). Nuclear magnetic resonance spectra and the presence of araucaroid wood fibres in amber samples from the Noiye Bum 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 a Nikon Optiphot compound microscope with magnifications up to 1000 X. Helicon Focus Pro X64 was used to stack photos and improve overall clarity and depth of field. Terms, including abbreviations for the wing venation, are based on works by Sinclair and Cumming (2006), Cumming and Sinclair (2009), and Hackston (2012). The fossil is well preserved and complete except for the missing tips of the mid and hind tarsi.

Results

Based on the studies of Sinclair and Kirk-Spriggs (2010) and Sinclair (2017), the fossil is assigned to the subfamily Atelestinae and of the various genera in the subfamily, shows most similarities to members of the genus *Alavesia* Waters and Arillo (1999). However, certain features of the wing venation and antennae are unique to the fossil and as such, it is described in a new genus that indicates affinities with the current genus *Alavesia*. Members of *Alavesia* were originally described from Late Cretaceous Spanish amber (Waters and Arillo 1999) and later from Lower Cretaceous Spanish amber (Peñalver and Arillo 2007). Two extant species were

described from Namibia in Southwest Africa (Sinclair and Kirk-Spriggs 2010).

Order: Diptera Linnaeus, 1758
Superfamily: Empidoidea
Family: Empididae Latreille, 1804
Subfamily: Atelestinae
Genus: *Nealavesia* gen. nov.

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Diagnosis

Small male fly with very short proboscis pointing slightly forward; eyes bare, occupying entire side of head, separated

on face; enlarged lanceolate-ovate postpedicel; wings hyaline, well developed with Rs originating proximal to level of humeral cross vein; Sc partly obscured at C; cell dm complete, separated from cell bm and emitting two unforked veins apically (M1 + 2 and CuA1); R4 + 5 unbranched; R1 meeting wing margin beyond mid wing; anal lobe somewhat expanded; legs long, foreleg with most raptorial features, located near head; fore femur somewhat thickened and spinose beneath.

Nealavesia hadroceria gen. et sp. nov.
(Figures 1–9).

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Figure 1. Lateral view of *Nealavesia hadroceria* gen. et sp. nov. in Burmese amber. Scale bar = 1.0 mm.



Figure 2. Lateral view of head and pronotum of *Nealavesia hadroceria* gen. et sp. nov. in Burmese amber. Arrow shows haltere. Arrowheads show postpronotal lobes. Scale bar = 55 μ m.

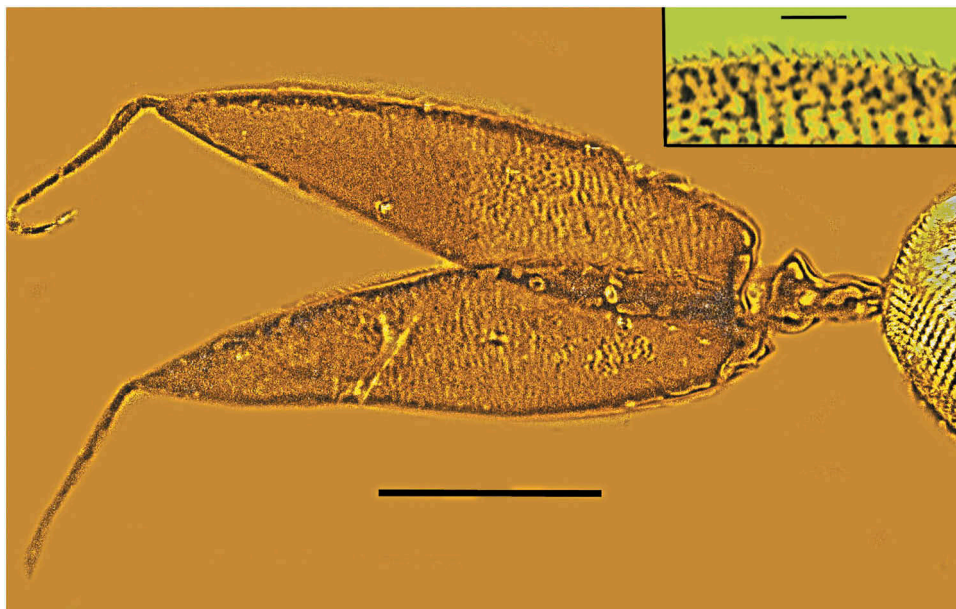


Figure 3. Large postpedicels of *Nealavesia hadroceria* gen. et sp. nov. in Burmese amber. Scale bar = 310 μ m. Insert shows a row of microscopic setae on the outer surface of the postpedicel. Scale bar = 88 μ m.



Figure 4. Dorsal view of head and pronotum of *Neopalavesia hadrocera* gen. et sp. nov. in Burmese amber. Upper arrow shows location of ocelli. Lower arrows show longitudinal setal bands. Scale bar = 277 μm .

Etymology. Generic name from the Greek ‘neo’ = new form, and the previously described genus *Alavesia*, thus showing recognised morphological similarities between the established and new genus.

Holotype. Accession no. B-D-1-73 deposited in the Poinar amber collection maintained at Oregon State University.

Etymology. Specific epithet is from the Greek ‘hadros’ = well developed, and the Greek ‘keraia’ = horn-like projection, antenna.

Type locality. Myanmar (Burma), state of Kachin, Noiye Bum Summit Site amber mine in the Hukawng Valley, SW of Maingkhwan (26°20’N, 96°36’E).

Description

Body small, non-metallic, 2.2 mm long (not including antennae); antennae 1.4 mm long; scape short, tube-like; pedicel shorter than scape, globular; postpedicel expanded, 900 μm long; followed by a stylus composed of 2 minute articles and a long terminal article 420 μm in length; antenna emerging from middle of head between bare compound eyes occupying entire lateral surface of head; ocelli three, on top of head; pair of ocellar bristles present; proboscis very short, pointing slightly forward; thorax slender; pronotum with several raised longitudinal rows of short setae; postpronotal lobes short, protruding; wings hyaline, 2.8 mm in length and 1.1 mm at greatest width; humeral crossvein present; no trace of costal stigma; Rs originating basal to level of humeral crossvein; R4 + 5 and M1 + 2 unbranched; cell dm small, closed; cross vein dm-cu present; CuA1 straight; R1 meeting C at mid-wing; R2 + 3 ending closer to end of R1 than to end of R4 + 5; cell br not complete (branch of M absent); A1 vein strongly curved and fading at tip; anal lobe (AL) of wing expanded; halter small, with some short adjacent metapleura bristles; foreleg with raptorial spines, especially on femur; base of tibia with single-pointed spine and one or more pointed setae; terminalia positioned on dorsal side of tip of abdomen; curved phallus present; small, elongate, gelatinous deposit (length = 470 μm) adjacent to abdominal terminus contains clusters of narrow, elongate cells.

Comments

The genus *Alavesia* is distinguished from all other empidoid genera by the diminutive wing cell dm, veins M1 and M4 are longer than $\frac{1}{2}$ length of wing, a long, lanceolate postpedicel and a 3-segmented antennal stylus (Sinclair 2017).

However, in *Alavesia*, the wing cell dm is shorter than one half the length of cell bm, while in *Neoalavesia*, it is longer than $\frac{1}{2}$ the length of cell bm. In *Alavesia*, the CuA + CuP vein (corresponding to the A1 vein in *Neoalavesia*) has only a slight curve at the apex, meeting the wing margin at an angle of about 50 degrees, while in *Neoalavesia*, there is a distinct bend with the vein meeting the wing margin at about 90 degrees. Also, in *Alavesia*, h crossvein is straight, and M1 vein is broadly curved, while in *Neoalavesia* the h crossvein is clearly slanted and the M1 + 2 vein is nearly straight. In *Alavesia*, R1 meets the wing margin proximal to the midwing. In *Neoalavesia*, R1 meets the wing margin approximately at mid-wing. *Alavesia* has a slender, distinctly curved, lanceolate postpedicel covered with setae, while *Neoalavesia* has a straight, broad (oval-lanceolate) postpedicel devoid of setae. The thin epidermal layer of *Neoalavesia* contains some minute spines, mostly noticeable along the margins. The size, shape and ornamentation of the postpedicel of *Neoalavesia* quickly distinguishes it from males of other *Alavesia* species as well as from males of all known members of the Atelestidae (Sinclair 2017).

The above-mentioned differences in the wing venation and antennae are why the fossil was established as a new genus, but with affinities to the present genus *Alavesia*.

Discussion

Some biological features also support a separate genus for the Burmese fossil. In general, aerial swarms in Diptera are normally produced by males (Wilkinson and Johns 2005) while in empidids, it is common for males and females to swarm together and mate with each other. It is likely that the enlarged

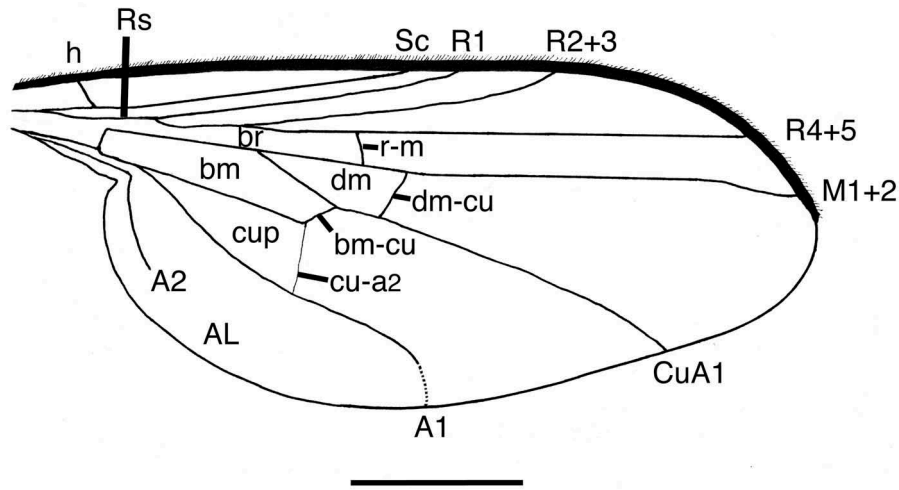


Figure 5. Wing venation of *Nealavesia hadroceria* gen. et sp. nov. in Burmese amber. Scale bar = 592 μ m.



Figure 6. Raptorial fore femur of *Nealavesia hadroceria* gen. et sp. nov. in Burmese amber. Arrowheads show spines on ventral surface of femur. Scale bar = 306 μ m.

postpedicels of *Nealavesia* were used to attract females since in some empidid lineages, females search male swarms for mates (Cumming 1994). Indication of attempted mating by *Nealavesia hadroceria* gen. et sp. nov. is a small, elongate, gelatinous deposit adjacent to the abdominal terminus (Figure 8). A close examination of the deposit reveals numerous narrow, elongate cells that resemble sperm (Figure 9). We suggest that this gelatinous structure is a spermatophore even though spermatophores have not previously been noted in members of the Empidoidea but are known to occur in other fly lineages (Wilkinson and Johns 2005).

In many species of lower Diptera and a few species of higher Diptera, sperm is transferred in spermatophores, essentially

packages of accessory gland secretions that enclose large numbers of sperm. Males that mate repeatedly could have a competitive advantage by depositing small, simple rapidly deployed, sac-like spermatophores. Many fly taxa that form mating aggregations, such as chironomids (Chironomidae), black flies (Simuliidae), tsetse flies (Glossinidae) and mosquitoes (Culicidae) transfer such spermatophores (Wilkinson and Johns 2005).

To our knowledge, *Nealavesia hadroceria* gen. et sp. nov. is the first complete description of an Empididae in Burmese amber. Cockerell (1917) described a possible Empididae in Burmese amber as *Burmitempis halteralis* Cockerell. However, the postpedicel of *B. halteralis* is only slightly longer than the combined length of the scape and pedicel and the length of the arista is almost 3 times



Figure 7. Genitalia of *Neolavesia hadroceria* gen. et sp. nov. in Burmese amber. Arrow shows phallus. Scale bar = 154 μm .

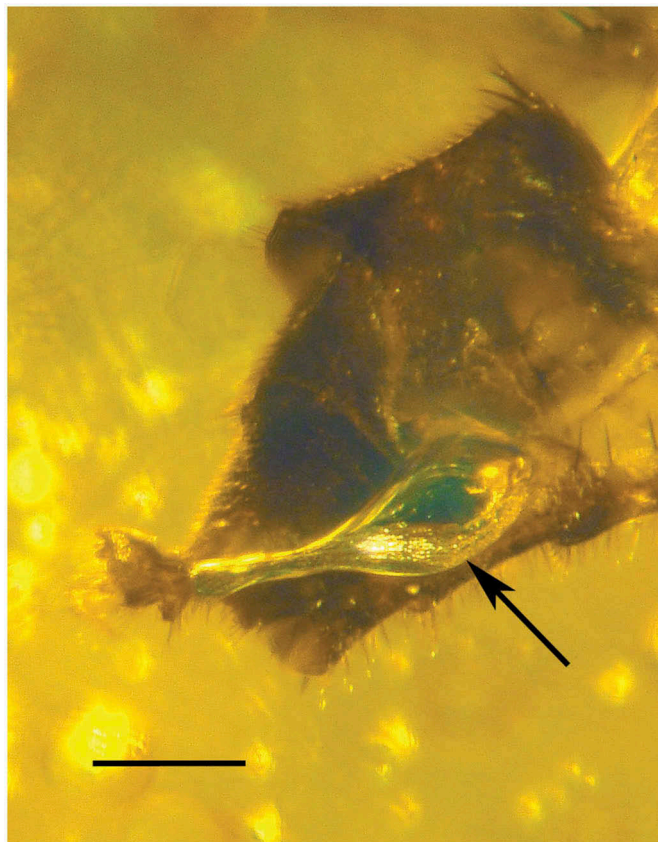


Figure 8. Elongate, gelatinous deposit (arrow) adjacent to abdominal terminus of *Neolavesia hadroceria* gen. et sp. nov. in Burmese amber. Scale bar = 200 μm .

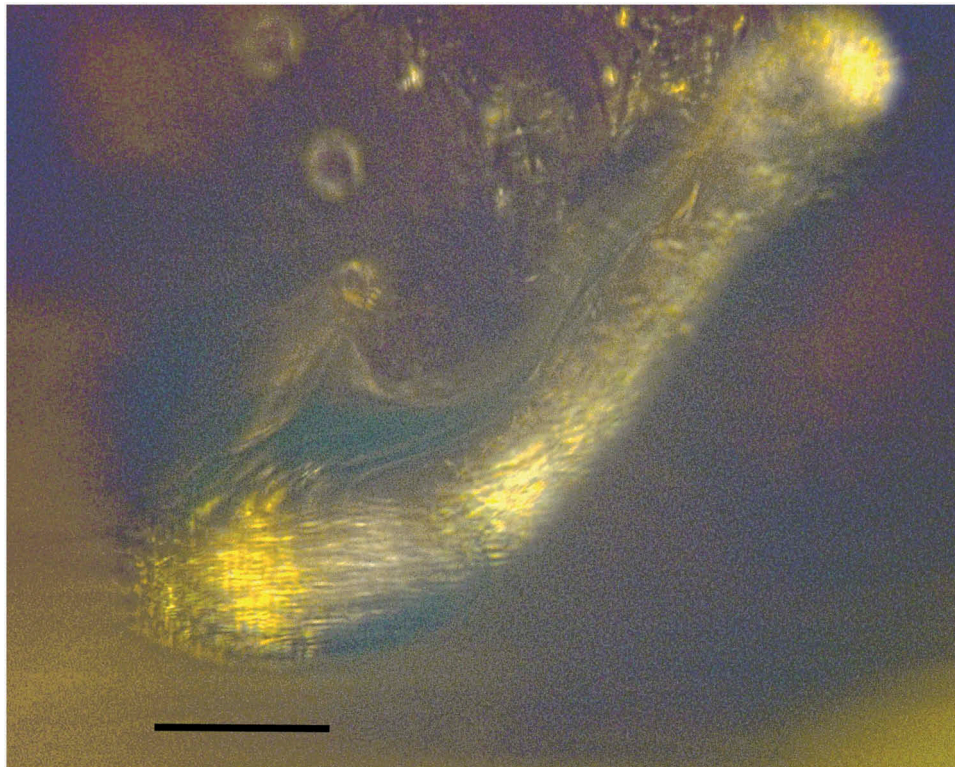


Figure 9. Clusters of narrow, elongate cells in gelatinous deposit adjacent to abdominal terminus of *Nealavesia hadroceria* gen. et sp. nov. in Burmese amber. Scale bar = 87 μ m.

the length of the postpedicel. These features as well as the wing venation clearly separate *Burmitempis* from *Nealavesia*. Several other empidids, including a possible representative of the genus *Alavesia*, were noted in Burmese amber, however they were never described (Grimaldi et al. 2002).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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