

Cretaceous diversity of the relict genus *Alavesia* Waters and Arillo (Diptera: Empidoidea: Atelestidae)

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ABSTRACT

Alavesia has been known on the basis of five species in Late Cretaceous amber from Spain and Myanmar and two extant species from Namibia. Very recently, another extant species has been found in southern Brazil. Here we present a surprising diversity of *Alavesia* flies from the mid-Cretaceous of Myanmar (Late Albian-Early Cenomanian, ca. 99 Ma), including nine new species: *A. angusta*, sp. nov., *A. brevipennae*, sp. nov., *A. lanceolata*, sp. nov., *A. latala*, sp. nov., *A. longicornuta*, sp. nov., *A. magna*, sp. nov., *A. pankowskiorum*, sp. nov., *A. spinosa*, sp. nov., and *A. zigrasi*, sp. nov. The following new synonymy is proposed: *Nealavesia* Poinar and Vega, 2020 = *Alavesia* Waters and Arillo, 1999. Notes are provided on an unusual structure, leg furrows found on femora to varying degrees among species, sometimes on tibiae, as well as notes on swarming behavior. *Alavesia* has undergone extensive extinction, a finding that further supports the relict nature of this genus and helps to explain the distribution of the other four Recent genera of Atelestidae, found in south and north temperate regions. Relict arthropod taxa preserved in Burmese amber are briefly reviewed, which also are narrowly endemic to temperate regions today.

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INTRODUCTION

The dance fly genus *Alavesia* Waters and Arillo (fig. 12B) was originally erected for a species described from Peñacerrada amber (middle Albian–upper Aptian) collected in Álava Province, Spain (Waters and Arillo, 1999). A second species was described from amber collected in the El Caleyú outcrop (upper Albian) in Asturias Province, Spain (Peñalver and Arillo, 2007), and presence of the genus in amber from the mid-Cretaceous of Myanmar (Late Albian–Early Cenomanian) was reported by Grimaldi et al. (2002). Recently, three new species of *Alavesia* from Burmese amber were described (Poinar and Vega, 2020; Jouault et al., 2020; Zhang et al., 2020). Remarkably, two extant species of *Alavesia* were discovered and described from the Brandberg Massif in Namibia (Sinclair and Kirk-Spriggs, 2010). The Brandberg is a massive, ring-shaped granitic intrusion rising some 2000 m above the Namib Desert plains near the coast of southwestern Africa, formed approximately 130 Ma from rifting of the South Atlantic Ocean. Aside from *Alavesia*, the Brandberg supports a characteristic fauna of arthropods, including another living fossil group, Mantophasmatids (Klass et al., 2002). The summit plateau has winter rainfall and ephemeral pools but otherwise is dry; it supports a distinctive flora that includes some endemic succulents (Nordenstam, 1974). Just as remarkable is the very recent discovery of another living species of *Alavesia* in São Paulo state, Brazil, on the campus of the University of São Paulo, Ribeirão Preto. It was found in secondary, regrowth environment, near a small patch of old Dry Forest extension of the Atlantic Forest (Amorim et al., 2020).

Alavesia was originally tentatively assigned to the subfamily Ocydromiinae of the Hybotidae, sensu Chvála 1983, by Waters and Arillo (1999) and Peñalver and Arillo (2007). Sinclair and Kirk-Spriggs (2010) transferred *Alavesia* to the Atelestidae, having more detailed morphology (i.e., genitalia) as well as a phylogenetic context (Sinclair and Cumming, 2006). The small family Atelestidae currently contains 15 described Recent species in five genera, including *Alavesia* (table 1), and two subfamilies. Genera are each endemic to north or south temperate regions (southern South America, western North America, the Palearctic or Holarctic Regions), except for *Alavesia* in Namibia and Brazil. Relationships among extant genera of Atelestidae were analyzed by Sinclair and Kirk-Spriggs (2010), who found the relationships to be *Nemedina* (*Alavesia* (*Atelestus* (*Meghyperus* + *Acarteroptera*))). Hypotheses on the phylogenetic position of the family include it as a sister group to the Hybotidae (Sinclair and Cumming, 2006), or to the rest of the Empidoidea (Moulton and Wiegmann, 2007; Wahlberg and Johanson, 2018), and even to the entire Cyclorrhapha (Chvála, 1983). The two molecular studies involved two to five genes or gene fragments.

An unexpected, high diversity of *Alavesia* in Burmese amber provides additional evidence for the relict nature of the genus. *Alavesia* is a rather distinctive empidoid genus (having a large, broad, lamellate postpedicel, three-articled stylus, and wing venation with a distinctively diminutive cell dm and divergent M_{1+2} and M_4). The fossil record of the genus thus far occurs exclusively in Cretaceous amber. Given its obvious appearance, *Alavesia* would have been easily distinguished in compression fossils of Cretaceous or Cenozoic age, if at all preserved. In addition, it has not been found in the very large deposits of amber from the Baltic region and Cambay Basin of India (Eocene).

TABLE 1. Extant Taxa of the Family Atelestidae.

Genus	Species	Distributions
Subfamily Atelestinae		
Genus <i>Acarteroptera</i> Collin	<i>licina</i> Collin	Chile
	<i>recta</i> Collin	Chile
Genus <i>Alavesia</i> Waters and Arillo	<i>brandbergensis</i> Sinclair & Kirk-Spriggs	Namibia
	<i>aura</i> Sinclair & Kirk-Spriggs	Namibia
	sp.	São Paulo, Brazil
Genus <i>Atelestus</i> Walker	<i>dissonans</i> Collin	Europe
	<i>ibericus</i> Barták	Europe
	<i>pulicarius</i> (Fallén)	Europe, European Russia
	<i>turcicus</i> Barták	Europe
Genus <i>Meghyperus</i> Loew	<i>nitidus</i> Melander	USA: CA, ID, WA
	<i>occidens</i> Coquillett	USA: CA*
	<i>sudeticus</i> Loew	Europe, European Russia, Far-east Russia (Primorskiy Terr)**
Subfamily Nemedinae		
Genus <i>Nemedina</i> Chandler	<i>acutiformis</i> Carles-Tolrá	Spain, Turkey
	<i>alamirabilis</i> Chandler	Bulgaria, Hungary
	<i>zaitsevi</i> Sinclair & Shamshev	Kazakhstan

* Unidentified specimens from the United States: California, Montana, Oregon, Mexico (Baja California).

** Also undetermined specimens from Japan (Hokkaido).

MATERIAL AND METHODS

The source of Burmese amber for this study is material excavated from the Hukawng Valley of northern Myanmar (Burma) in Kachin State, dated to approximately 99 Ma (Albian-Cenomanian/ Early-Late Cretaceous boundary) using U-Pb isotopes of zircons in matrix adhering to amber nodules (Shi et al., 2012). Many of the natural, unprocessed pieces of amber are rounded, showing evidence of reworking, so it is possible that at least some of this amber has been reworked from slightly older deposits (Grimaldi and Ross, 2017). There is also in Myanmar Late Cretaceous (Campanian-aged) amber from Tilin, central Myanmar (Zheng et al., 2018), but this amber is not mined in appreciable quantities nor commercially marketed, the inclusions are distinctively compressed, and most (e.g., all AMNH) pieces were purchased prior to discovery of Tilin amber. Thus, there is no ambiguity concerning provenance. Grimaldi et al. (2002) reported undescribed species of *Alavesia* from Burmese amber, which were included in this study along with additional specimens.

Specimens are deposited in the American Museum of Natural History, Division of Invertebrate Zoology (with AMNH Bu prefix), which also houses specimens in the James Zigras Collection (JZC Bu prefix); and the U.S. National Museum of Natural History, Department of Paleobiology (USNM PAL prefix). AMNH material was purchased commercially between 1999 and 2016; USNM material was donated in 2018–2019 by the Pankowski family (see Acknowledgments).

Terms used for adult structures follow those of Cumming and Wood (2017). Virtually all the pieces required trimming and polishing to best observe critical structures, which followed the protocols in Nascimbene and Silverstein (2000). Trimming maximized a full view of a wing (parallel to the broadest surface), lateral view of the body (including full lateral view of the antenna), and ideally a close view of the male genitalia. In some cases the fly lay on an edge of the amber, which prevented any further preparation. Specimens will eventually be embedded in the synthetic resin EpoTek 301-2, to protect them against environmental exposure and deterioration. We did not use micro-CT scanning since many of the critical features were observed using light microscopy, and Burmese amber does not scan well using absorption-contrast CT.

For microscopic study at the AMNH, trimmed specimens were mounted and positioned in a small piece of dental wax on a microscope slide, with a drop of water or glycerine applied to the upper surface and then a glass coverslip. Illustrations of wings used a drawing tube on a Wild M5 stereomicroscope (up to 75 $\times$), or for smaller structures (i.e., antennae, genitalia, up to 175 $\times$), a Leitz GmbH stereoscope (Wetzlar Germany). Details of the genitalia were examined using a Nikon Eclipse E600 compound microscope with transmitted and reflected light, and Nikon EDWD (Extended Depth Working Distance) 20 $\times$ and 40 $\times$ Plan Fluor lenses (200–400 $\times$ total magnification). Photographs of many habitus views were taken with a Leica camera model DFC5400 using Leica Application Suite X. Photo montages were created using Zerene Stacker 1.04.

SYSTEMATICS

Alavesia Waters and Arillo

Alavesia Waters and Arillo, 1999: 60. Type species *Alavesia subiasi*[†] Waters and Arillo, by original designation.

Neoalavesia Poinar and Vega, 2020: 2. Type species *Neoalavesia hadroceria*[†] Poinar and Vega, by original designation, new synonymy.

NOTE ON SYNONYMY: The genus *Neoalavesia* is considered a junior synonym of *Alavesia*. The characters proposed by Poinar and Vega (2020) justifying their new genus (e.g., length of cell dm, apical curvature of CuA+CuP, slanting h crossvein, M₁₊₂ straight, length of R₁, shape of postpedicel) all fall within the present definition of *Alavesia* and identify only species differences. For this reason *Neoalavesia* is proposed as a new synonym of *Alavesia*.

DIAGNOSIS: Readily differentiated from all other empidoïd genera by the diminutive cell dm, M₁₊₂ and M₄ long, greater than half length of wing and widely divergent, postpedicel very

long and lanceolate (longer in males than females), stylus three-articled, legs with parallel rows of setulae, scutal chaetotaxy thickened; vein CuA straight, convex or arched to CuA+CuP.

GENERAL DESCRIPTION (updated from Sinclair and Kirk-Spriggs, 2010): *Male*. Dichoptic, frons broad (fig. 8A); inner margin of eye near antenna with shallow notch. Ocellar triangle slightly raised. Antenna (figs. 1, 8): postpedicel elongate, lanceolate to long triangular shape, tapered to apical point, micropubescent; stylus aristalike, terminal, 1/3 to 3× length of postpedicel (very long in males of two fossil species, which also have broadened apical “flags” on stylus), with 2 minute, ringlike basal articles. Proboscis (fig. 9): Short, labellum fleshy, with ~10 pseudotracheae per lobe; labrum well developed, lacking epipharyngeal blades; laciniae and hypopharynx well developed; palpus from short and paddlelike to long and digitate or spatulate.

Thorax: Anteprenotum without setulae; postpronotal lobe protruding (fig. 5), with short, stout setulae. Scutum moderately to strongly arcuate (figs. 12–17). Acrostichal setulae usually biserial (fig. 5), sometimes uniserial; dorsocentrals similar to acrostichals, minute, irregular, prescutellar dorsocentrals macrosetose; 2–5 notopleural setae, 1 stout supraalar seta, 1 stout postalar seta; 2–4 pairs marginal scutellar setae. Laterotergite bare. Legs: Length moderate, with distinct rows of setulae, mostly lacking large setae, except for subapical tibial setae. Fore- and mid femora slightly swollen, hind femur more strongly so; mid and hind femora with shallow longitudinal furrow, bare of setulae (fig. 11) on lateral or lateral + mesal surfaces; tibiae sometimes with such thin furrows (see below, Femoral Furrows). Tibiae slender, subequal in length to femur, foretibial gland absent; 1–2 stout apical setae present. Tarsi slender; pretarsal claws short, pulvilli small, padlike.

Wing (figs. 2–4, 10A): Hyaline to slightly tinted/infusate; with fine microtrichia over entire membrane. Pterostigma absent. Vein C terminating slightly beyond apex of M_{1+2} ; Sc apically evanescent, ending slightly before costal margin; Rs arising near or distant from level of humeral crossvein; R_1 ending at or slightly beyond midlength of wing; R_{2+3} shortly curved to C apically, ending closer to apex of R_1 than R_{4+5} ; R_{4+5} unbranched, slightly divergent to parallel to M_{1+2} ; cell dm very small, nearly or more than half length of basal cells, emitting two veins M_{1+2} and M_4 ; M_{1+2} and M_4 moderately to strongly divergent; CuA straight, curved, or sharply recurved; apex of cell cua truncate or acute. Anal lobe broad to very shallow, alula reduced.

Abdomen: Sclerites covered in distinct, short setae, posteromarginal setae slightly thicker on largest sclerites. Segments 1–5 broad, with remaining gradually narrowed. Tergum 8 very narrow, straplike, greatly prolonged laterally with triangular dorsomedial posterior extension. Sternite 8 greatly reduced, as pair of slender sclerites, weakened and partially folded at midlength; longer than sternite 7. Terminalia (figs. 6, 7; 10B): Symmetrical, unrotated, held posterodorsal to abdomen. Cercus small, flat, oval, and weakly sclerotized; hypoproct subtriangular. Epandrium U-shaped with dorsal bridge anterior to cerci. Surstylus subapical, commonly with small dorsal lobe at base. Hypandrium (in Recent species) short, divided into slender, straplike sclerites; anterolateral corner extending to articulate with epandrium. Postgonites caplike, joined or fused medially. Paired ventral apodemes extending anteriorly from postgonites; gonocoxal apodeme with slender rodlike process longer than hypandrium; ejaculatory apodeme

articulated at base of phallus (observed in Recent specimens). Phallus tubelike, arched and pointing ventrally; apex bifid in fossil species.

Female. Similar to male except postpedicel shorter; abdomen well sclerotized, tergites nearly twice as broad as long. Postabdomen (fig. 10C, D) weakly sclerotized, telescoping into segment 5. Tergites 6 and 7 reduced to pair of slender sclerites; sternites 6 and 7 rectangular, slender; tergite 10 absent; cercus well developed, pubescent, length about twice width. Spermathecal capsule spherical, darkly pigmented.

SPECIES COMPOSITION: The two species in Early Cretaceous amber from Spain, *Alavesia subiasi* Waters and Arillo and *A. prietoi* Peñalver and Arillo, exhibit all the diagnostic features of the living species. Distinctive features in both of these fossil species are: (1) the position of vein CuA, which is straight but strongly recurved, such that it is in line with crossvein m-cu or nearly so, and (2) veins R_{4+5} and M_{1+2} straight and parallel for their entire length. The species in Burmese amber with these features are *A. angusta*, sp. nov., *A. latala*, sp. nov., *A. longicornuta*, sp. nov., and *A. longistylata* Zhang and Wang. *Alavesia longicornuta* and *A. longistylata* are distinguished from the Spanish amber species by the very long stylus with apical flag. *Alavesia latala* has a distinctively broad wing. The wing of *Alavesia angusta* is quite similar to *A. prietoi*, in size (i.e., 1.4 and 1.5 mm, respectively), in the slender shape, and venation, including the slanted crossvein m-m. The postpedicel of *A. prietoi* is triangular and slightly broader (L/W 3.0), that of *A. angusta* is slender and fusiform (L/W 4.47).

The extant species from Namibia, *Alavesia brandbergensis* Sinclair and Kirk-Spriggs and *A. daura* Sinclair and Kirk-Spriggs, have a distinctively arched vein M_{1+2} that is widely divergent with M_4 , and cell dm is very small. Burmese amber species sharing these features are *A. brevipennae*, sp. nov., *A. myanmarensis*, and *A. pankowskiorum*, sp. nov., although in the last-named species there is significantly less arching. Of the seven species in Burmese amber where details of the male genitalia could be observed, all except one have a fringe of long setae on the distal margin of the ventral epandrial lamella and a slender, digitiform surstylus. The surstylus has at its base a slender or small dorsal lobe in *A. longistylata*, and *A. magna*, sp. nov. Like the Namibian species *A. brandbergensis*, the phallus in *A. longistylata*, *A. magna*, sp. nov., *A. pankowskiorum*, sp. nov., and *A. zigrasi*, sp. nov., is bent ventrad, but significantly longer in the fossil species and with a bifid, "feathered" apex. The male genitalia of *A. lanceolata*, sp. nov., and *A. spinosa*, sp. nov., are each unique and very different from other species in the genus, as described under those species.

FEMORAL FURROWS: In the course of this study it was noticed that some species and specimens possess a shallow longitudinal furrow along the lateral (sometimes medial) surface of the femora (especially mid and hind legs), and sometimes on the tibiae (fig. 11). The furrow readily appears to be an artifact of preservation, and in fact when the legs are slightly compressed or shrivelled the furrow is unapparent. However, the structure is certainly not preservational since in fully distended legs the furrow area is devoid of microsetae/setulae (which otherwise cover the rest of the femur), it is symmetrical between legs of the same pair, and there is often an even row of setulae bordering the furrow. Femoral furrows are well developed in *Alavesia longistylata*, *A. magna*, *A. pankowskiorum* and *A. zigrasi*, and are faint in *A. angusta* and *A. lanceolata*, suggesting

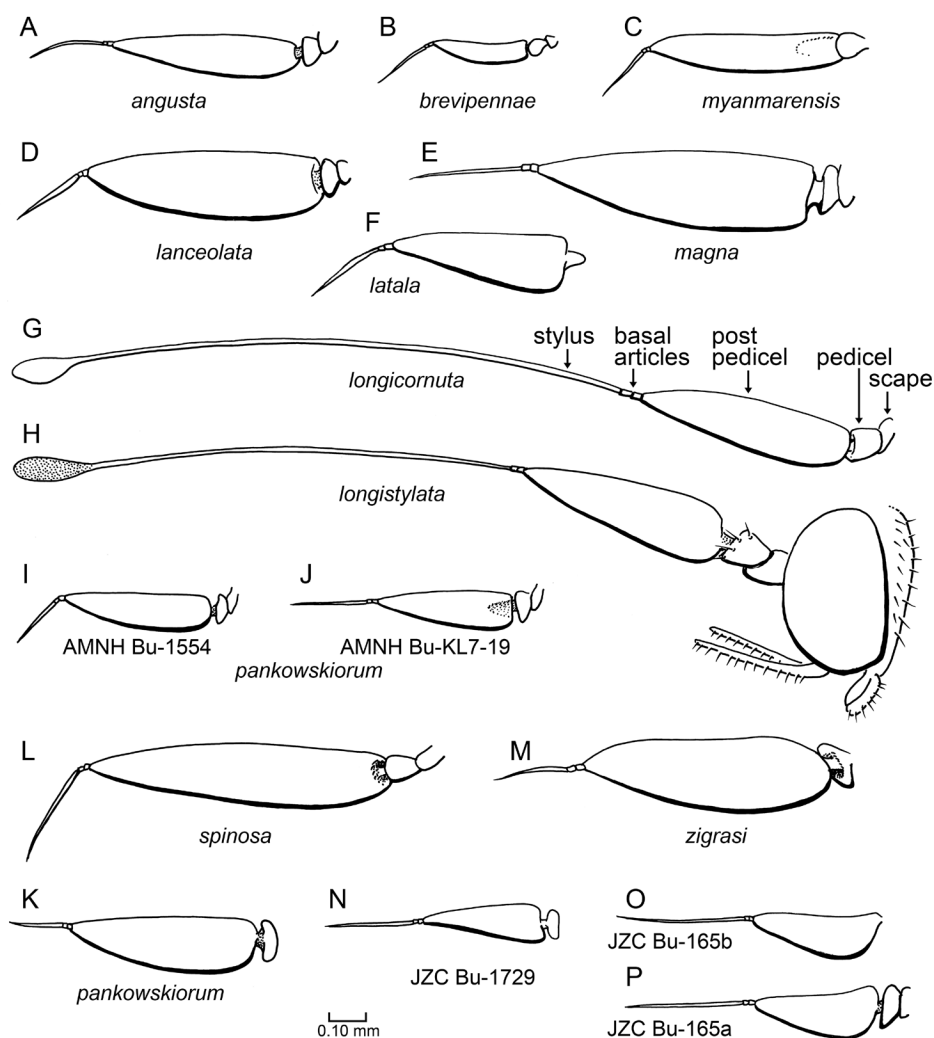


FIGURE 1. Antennae of Burmese amber *Alavesia* species, lateral views. All are males except N, O, P. Some antennae were reversed in direction for optimal comparison; *longicornuta* and *longistylata* are slightly reconstructed to account for curvature of the stylus. All are to the same scale. Specimen numbers: **A.** USNM PAL 726867. **B.** AMNH Bu-494. **C.** AMNH Bu-496. **D.** USNM PAL 726868. **E.** AMNH Bu-KL2-7. **F.** AMNH Bu-1476. **G.** JZC Bu-556 (AMNH). **H.** USNM PAL 726872. **K.** USNM PAL 726869. **L.** AMNH Bu-KL7-18. **M.** JZC Bu-282. **N.** Undetermined species. **O.** *A. zigrasi*. **P.** *A. zigrasi*.

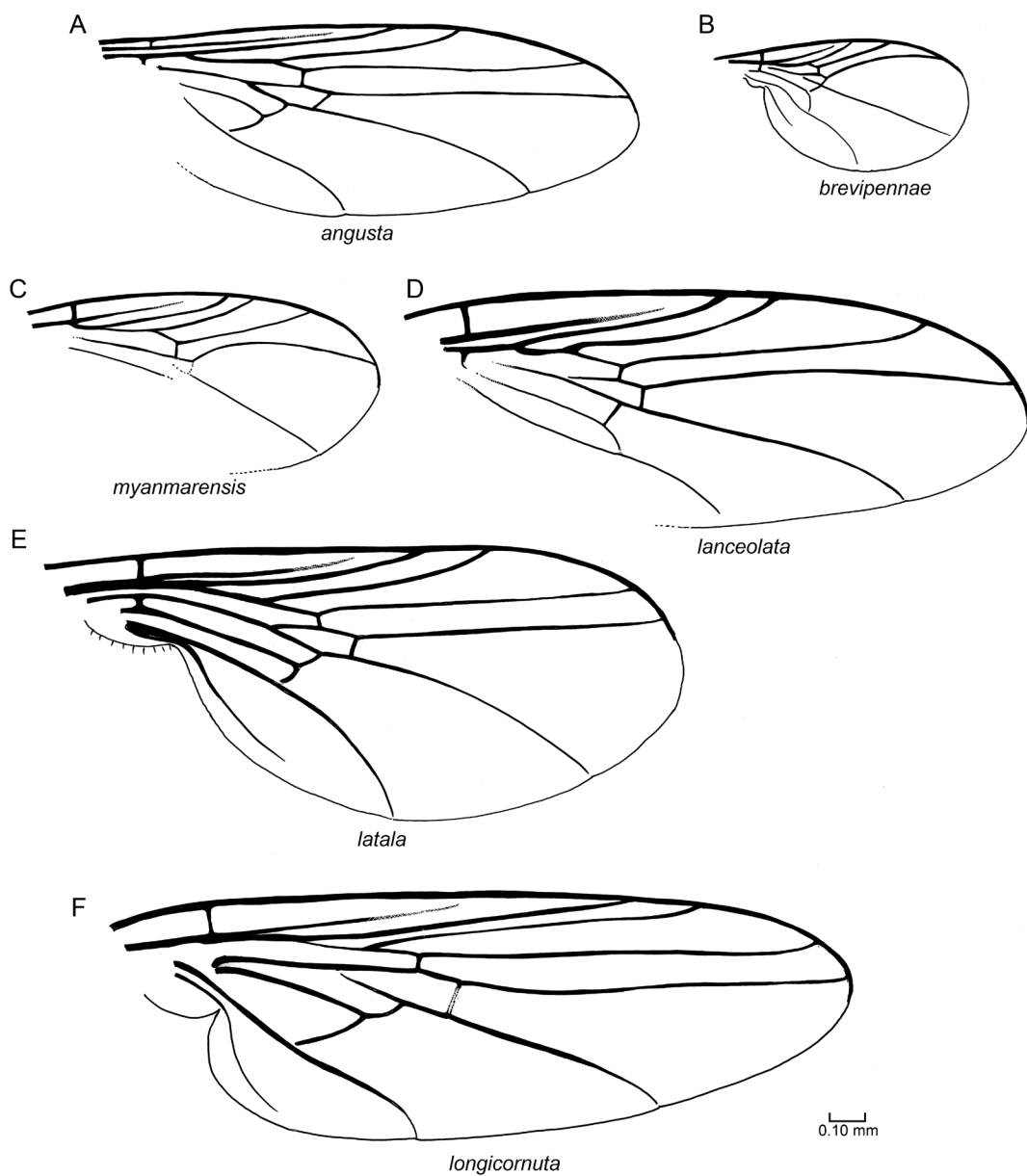


FIGURE 2. Wings of six species of *Alavesia* in Burmese amber. All are males, to the same scale. Specimens: A. USNM PAL 726867. B. AMNH Bu-494. C. AMNH Bu-496. D. USNM PAL 726868. E. AMNH Bu-1476. F. JZC Bu-556.

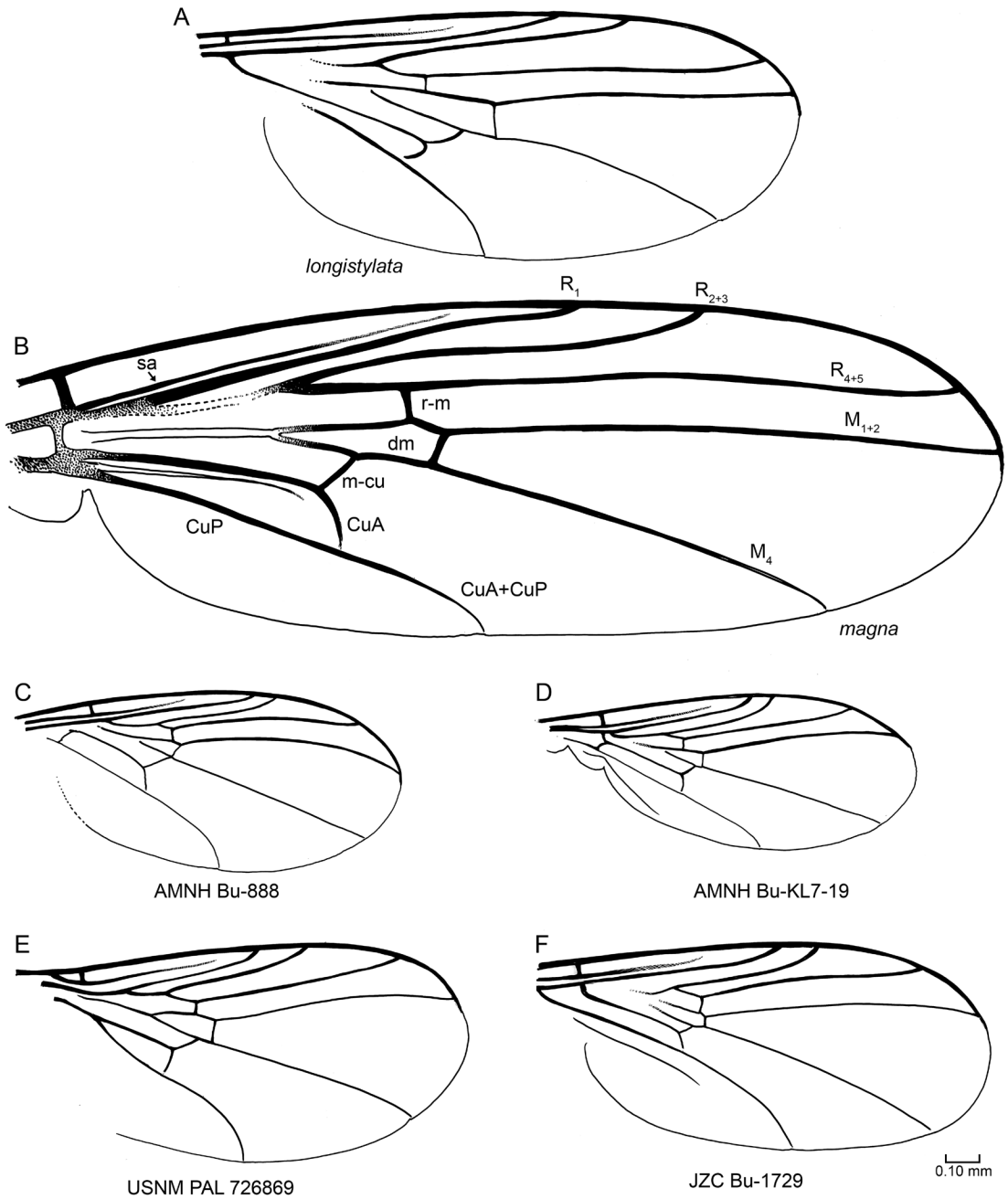


FIGURE 3. Wings of three species of *Alavesia* in Burmese amber. All are to the same scale. Specimens: A. USNM PAL 726872. B. USNM PAL 726873. C–E. *A. pankowskiorum*, see figure for specimen numbers. F. Undetermined species.

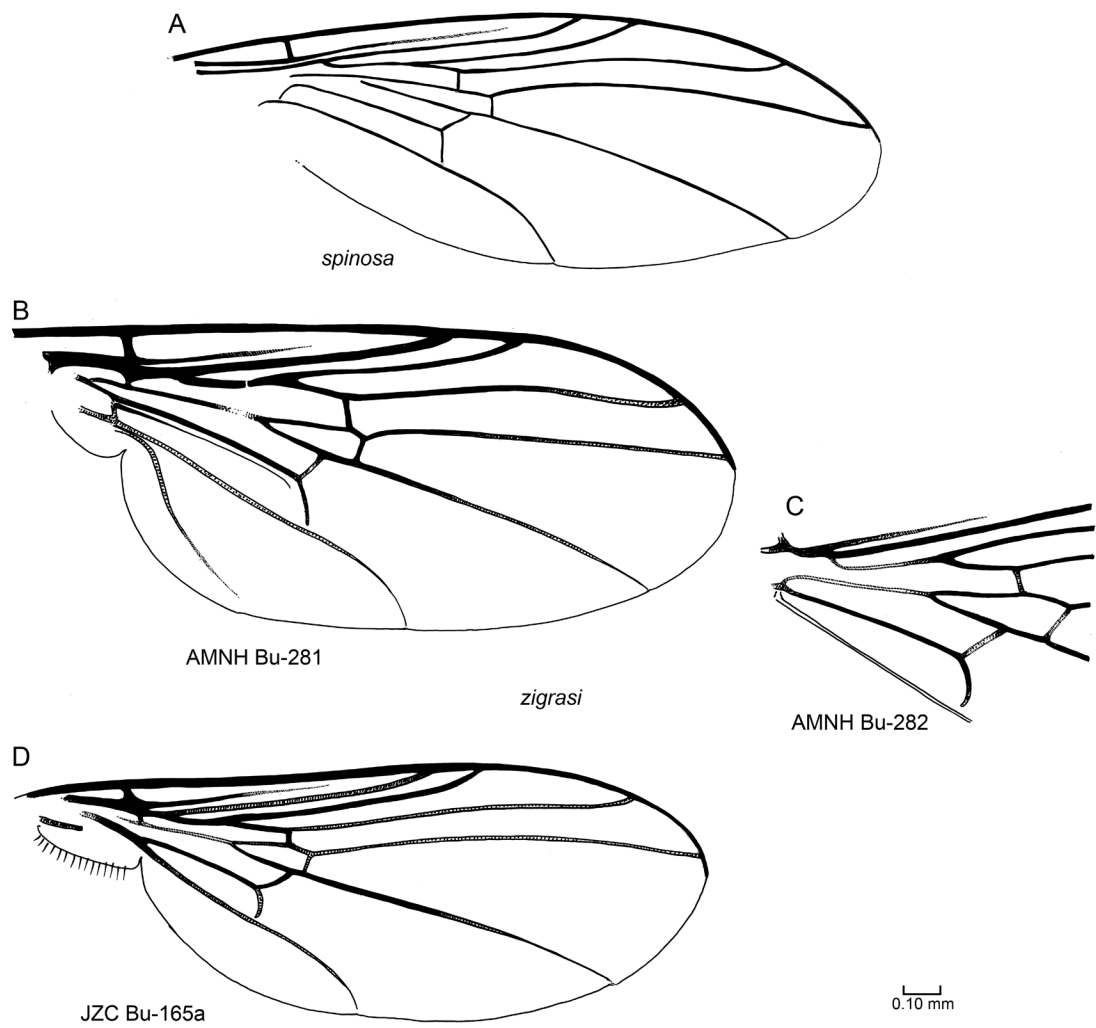


FIGURE 4. Wings of *Alavesia* spp. in Burmese amber. **A.** *A. spinosa*, AMNH Bu-KL7-18. **B–D.** *A. zigrasi*, showing some differences in venation among three specimens: **B.** male; **C.** male; **D.** female.

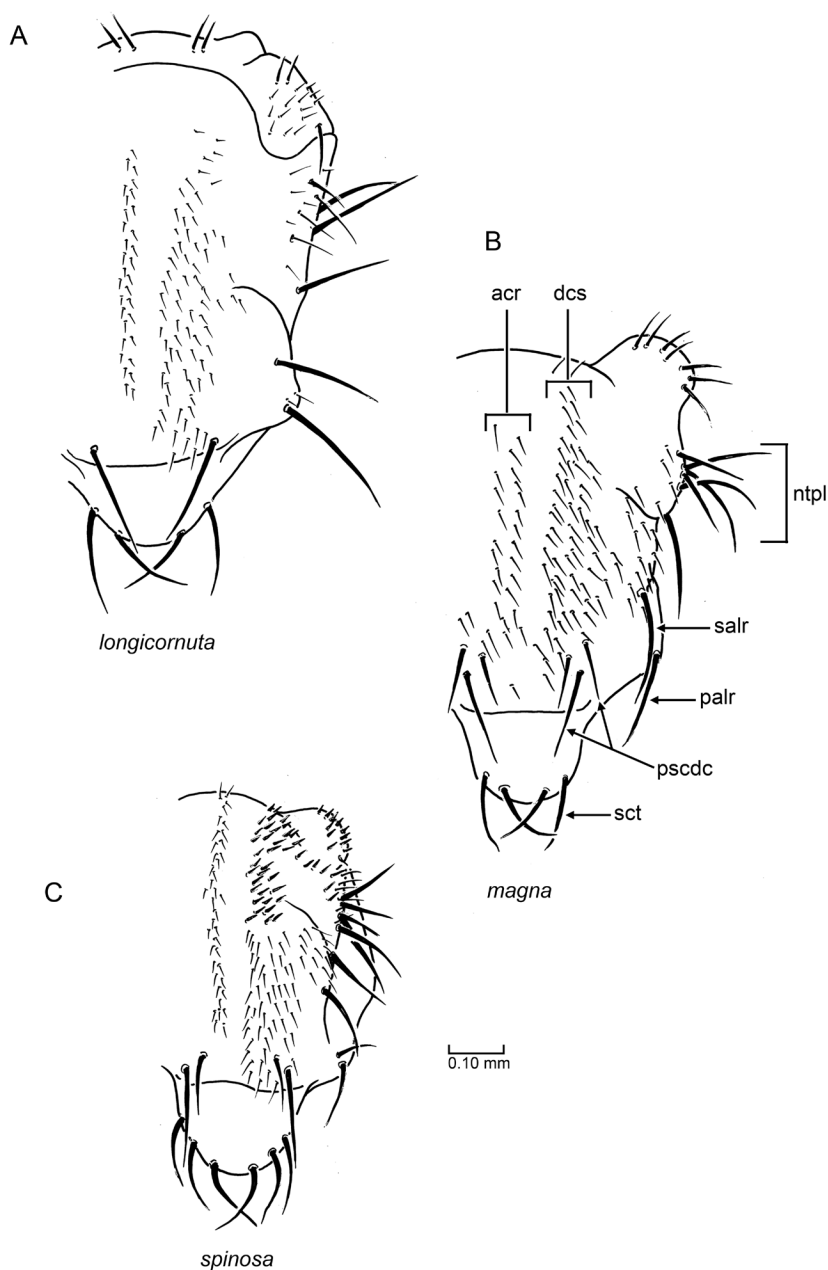


FIGURE 5. Thoraces of three species of *Alavesia* in Burmese amber, showing some of the differences in notal chaetotaxy. A. *A. longicornuta* (JZC Bu-556). B. *A. magna* (AMNH Bu-KL2-7). C. *A. spinosa* (AMNH Bu-KL7-18). All are to the same scale. Setal abbreviations: **acr**, acrostichals; **dcs**, dorsocentrals; **ntpl**, notopleurals; **palr**, postalar; **pscdc**, prescutellar dorsocentrals; **salr**, supraalar; **sct**, scutellars.

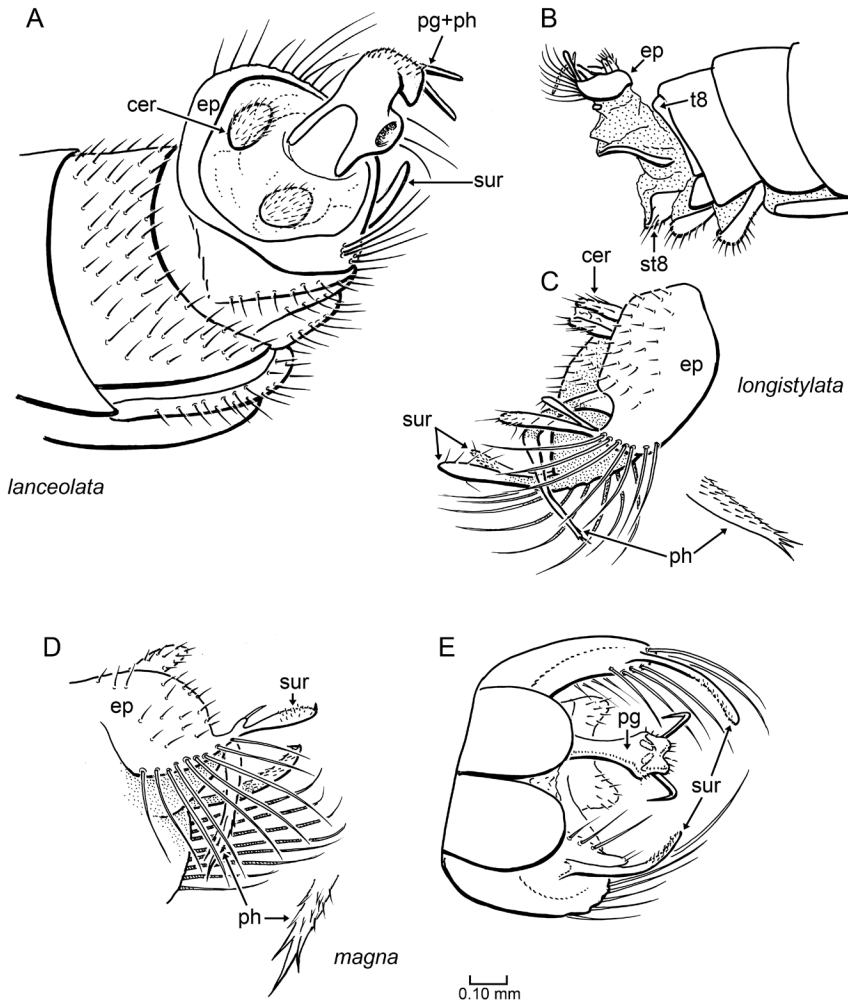


FIGURE 6. Male terminalia of three species of *Alavesia* in Burmese amber, shown in various views, to the same scale except for B. **A.** *A. lanceolata*, USNM PAL 726868, dorsolateral view. **B.** *A. longistylata*, USNM PAL 726872. **B.** Lateral view of abdominal apex. **C.** Epandrium and genitalia, posterolateral view. **D.** *A. magna*, AMNH Bu-KL2-7. **D.** Ventrolateral view. **E.** Dorsal view. Abbreviations: **cer**, cercus; **ep**, epandrium; **pg**, postgonite; **pg+ph**, postgonite + phallus (integrated); **ph**, phallus; **st8**, sternite 8; **sur**, sustylus; **t8**, tergite 8.

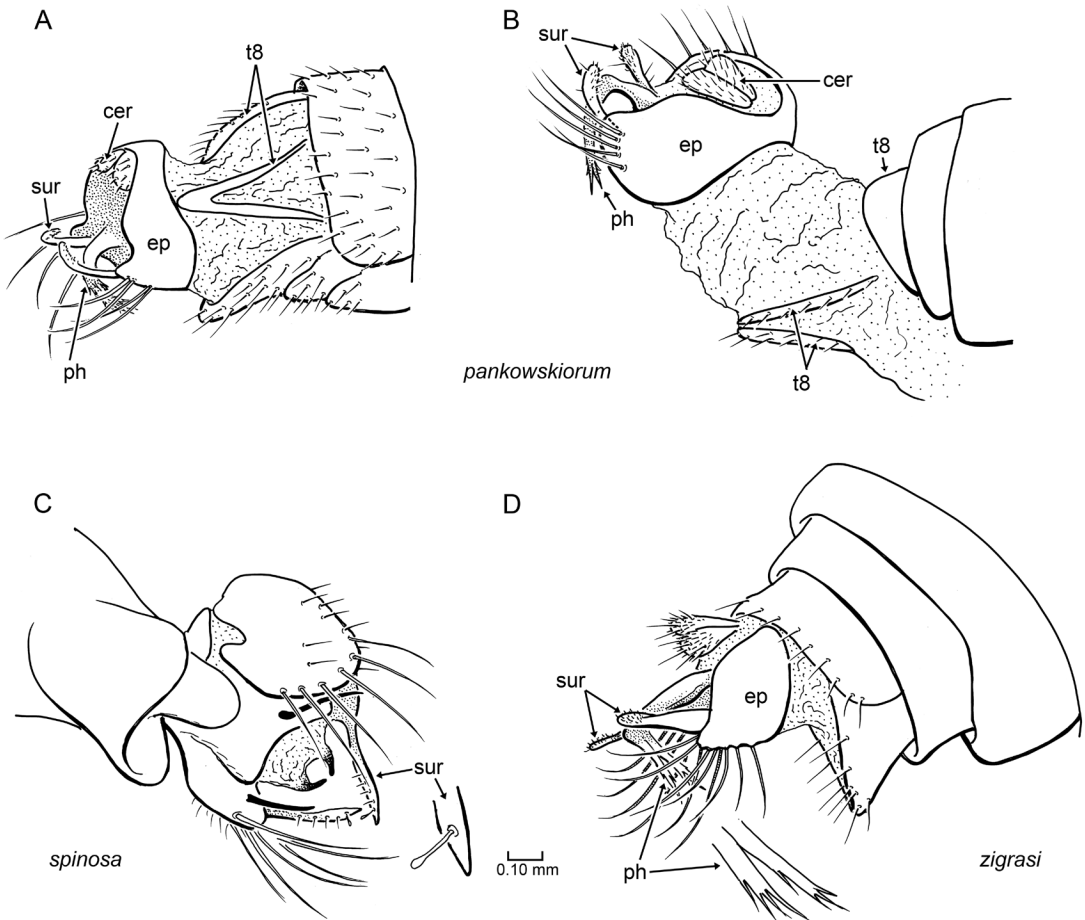


FIGURE 7. Male terminalia of three species of *Alavesia* in Burmese amber, shown in various views, to the same scale. **A.** *A. pankowskiorum*, AMNH Bu-KL7-19, lateral view. **B.** *A. pankowskiorum*, USNM PAL 726869, anterolateral view. **C.** *A. spinosa*, AMNH KL7-18, ventrolateral view, with detail of surstylus tip showing clavate setula. **D.** *A. zigrasi*, JZC Bu-281. For abbreviations see figure 6.

this may be a distinctive feature for *Alavesia*, or at least the Burmese amber species. Preservation of specimens in the other species may be insufficient to determine if the furrows are present or absent. Available living specimens have compressed legs due to air drying, but a longitudinal region devoid of setulae is apparent and likely represents a shallow furrow. The condition is Spanish amber species is unknown.

SPECIES IN BURMESE AMBER

Alavesia angusta, new species

Figures 1A, 2A, 12A

DIAGNOSIS: Postpedicel slender, fusiform, L/W 4.47; wing slender, L/W 2.8; M_{1+2} and R_{4+5} parallel for entire lengths; crossvein bm-cu at midlength of cell dm; crossvein dm-m slanted; CuA straight, directed to wing base, in line with crossvein m-cu; cell dm extending well beyond apex of cell cua.

DESCRIPTION: *Male.* **Coloration** not preserved. **Head:** Scape small, goblet-shaped; pedicel quadrate; postpedicel narrow, almost fusiform, L/W 4.47 (figs. 1A, 12A); stylus short, length $0.46\times$ the postpedicel, with 2 small basal articles. Palpus light, extended slightly beyond level of proboscis.

Thorax: Chaetotaxy: acrostichals fine, short, in biserial rows; dorsocentrals similar to acrostichals, ending in pair of long, fine prescutellars; 2 short postpronotal setae; 4 short, fine anterior notopleural setae, 2 large posterior notopleural setae; 1 postsutural supraalar seta; 1 finer postalar seta; 3 pairs scutellar setae, apical pair longest, upright, crossed for $\sim 0.5\times$ their length.

Legs: Forecoxa with many short setae on anterior surface. Forefemur with ventral row ~ 15 short, stiff setae. Tibiae with long, apical ventral seta. Hind tibia with dense dorsal row of setae, length about half width of tibia; posterior surface with fine, brushy setae.

Wing: Length 1.4 mm (fig. 2A); C terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} for entire lengths; crossvein r-m slightly distal to middle of cell dm; apex of M_4 slightly closer to M_{1+2} than to CuA+CuP; CuA strongly recurved, in line with bm-m; apex of cell cua truncate, cell cua shorter than cell bm; CuA+CuP slightly curved.

Abdomen: No longer than thorax; setae short, without differentiated posteromarginal setae. Segments 1–5 broad, other segments retracted into segment 5. Terminalia well preserved in holotype (not illustrated): Epandrium complete dorsally, U-shaped, with fringelike row of five long setae on ventral margin; cercus flat, broad, scalelike, meeting medially. Surstylus long, slightly curved (as in *A. magna*, sp. nov.); postgonites + phallus as for most other species: thicker at base, hook-shaped, bend in middle, phallus downturned.

TYPE MATERIAL: Holotype, male, USNM PAL 726867 (USNM).

ETYMOLOGY: The specific epithet is from the Latin *angustus* (narrow, slender), in reference to the narrow wing and cell cua.

Alavesia brevipennae, new species

Figures 1B, 2B, 8D, 12B, C

DIAGNOSIS: Tiny species (fig. 12B, C), wing length 0.75 mm; postpedicel 2.3× longer than aristalike stylus, slightly curved; wing shortened, rounded, and broad (L/W 1.75); M_{1+2} strongly arched, this vein and M_4 very divergent; CuA arched apically, CuA+CuP weakened, not reaching wing margin, M_4 closer to CuA+CuP than M_{1+2} .

DESCRIPTION: *Male.* **Coloration** not preserved. **Head:** Scape and pedicel quadrate, subequal in size and length. Postpedicel elongate, straplike, slightly curved, gradually tapered apically, 2.3× longer than stylus (fig. 1B). Stylus with two basal articles, short (fig. 8D), without apical flaglike expansion; length 0.32× that of postpedicel. Mouthparts very short; palpus short, not projecting.

Thorax: Chaetotaxy thickened, in numerous rows (not clearly visible): 2 anterior and 1 posterior postpronotal setae; 4 notopleural setae of variable lengths, 1 postsutural supraalar seta; 1 postalar seta; 2 pairs of scutellar setae.

Legs: Most setae thickened. Forecoxa with short erect anterior setae; anteroapical setae longer and stouter. Forefemur with anteroventral and posteroventral row of short setae. Mid and hind femora with anteroventral row of short setae. Mid and hind coxae with 2–3 stout lateral setae on apical half. Tibiae with biserial row of short, stout ventral setae; apex of tibiae with long, apical ventral seta; hind tibia with several dorsal setae, length about half width of tibia.

Wing (wing length 0.75 mm) (fig. 2B): shortened and rounded; costa terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} closely associated with M_{1+2} ; M_{1+2} arched, strongly divergent from R_{4+5} distally; cell dm very short, crossvein r-m nearly opposite apex of cell bm; M_4 straight to wing margin; apex of M_4 closer to CuA+CuP than M_{1+2} ; CuA arched; apex of cell cua convex, length of cell cua subequal to cell bm; CuA+CuP mostly straight, strongly curved subapically to wing margin.

Abdomen: Setae short, without distinct posteromarginal setae. Segments 1–5 broad. Terminalia and remaining segments damaged and partially obscured.

TYPE MATERIAL: Holotype, male, AMNH Bu-494 (AMNH).

ETYMOLOGY: The specific epithet is from the Latin *penna* (wing, feather) and *brevis* (short), referring to the shortened wing that characterizes this species.

Alavesia hadroceria (Poinar and Vega), new combination

Neoalavesia hadroceria Poinar and Vega, 2020: 2.

DIAGNOSIS: A large species (wing length 2.8 mm), distinguished by scape longer than pedicel; forefemur with row of long ventral setae; CuA straight, angled obliquely outward; R_{4+5} parallel to M_{1+2} slightly diverging at apices; CuA+CuP strongly arched on apical third.

REMARKS: No specimens of this recently described species were discovered or identified. The report of a gelatinous deposit or possible spermatophore attached to the tip of abdomen of the holotype (Poinar and Vega, 2020, figs. 1, 8) is merely an air bubble.

Alavesia lanceolata, new species

Figures 1D, 2D, 6A, 8A, 13A

DIAGNOSIS: A larger species (fig. 13A) (wing length 1.8 mm), male postpedicel broad and large (L/W 3.4 – 4.0), tapered on apical half, stylus short (0.35x L of postpedicel); 3 pairs of scutellar setae; M_{1+2} and R_{4+5} parallel for much of their length but slightly divergent at apex (parallel in *A. zigrasi*); crossvein dm-m clearly positioned beyond apex of cell bm; CuA arched apically (hybotidlike); female aristalike stylus slightly longer than postpedicel (female with similar CuA and thickened setae).

DESCRIPTION: *Male. Coloration* preserved: Frons and vertex dark brown. Pleura light including halter, except for anepisternum (which is light, fuscous brown, same color as scutum and dorsum of scutellum). Femora and tibiae light, tarsi dark. Tergites 1–5 dark, posterior ones light. **Head:** Scape short, pedicel quadrate, postpedicel broad and large (figs. 1D, 8A) (L/W 3.4–4.0), tapered on apical half, stylus short (0.35x L of postpedicel). Palpus very small; proboscis barely projecting beyond oral margin.

Thorax: Macrosetae thickened, acrostichals short, biserial; dorsocentral setae similar to acrostichals, ending in pair of long prescutellar dorsocentrals $>2\times$ length of preceding ones. Postpronotum with 1 small seta, barely larger than setulae; notopleural setae of graded lengths, 3 posterior ones largest; 1 postsutural supraalar seta; 1 postalar seta; 3 pairs scutellar setae, lateral pair $\sim 0.3\times$ length of apical pair, apical pair upright and crossed.

Legs: Forecoxa with short, decumbent setae on anterior surface. Forefemur with row of short, spinulelike setae on distal 2/3 of ventral surface; none on mid femur, a short distal row on hind femur. Foretibia with long, apical ventral seta; mid and hind tibiae with 2 such setae (1-2-2). Hind tibia with dense dorsal row of setae, lengths about 1/3 width of tibia; posterior surface with fine brush of setae.

Wing: Length 1.8 mm, slender, L/W 2.66 (fig. 2D). Vein C terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} but diverging at apices; crossvein r-m near middle of cell dm; apex of M_4 slightly closer to CuA+CuP than to M_{1+2} ; CuA arched, not aligned with bm-m; apex of cell cua acute, cell cua longer than cell bm; CuA+CuP slightly curved.

Abdomen: Shorter than thorax; setae short, little differentiated except for margins of sternites 2–5 with short, thick, spinulelike setae. Male terminalia distinctive (fig. 6A): Epan-drium short, ringlike, ventral lobe with relatively shorter setae $\sim 0.5\times$ length of epan-drium; posterior surface of terminalia extensively membranous, cerci small and separated by distance about equal to their diameter. Surstylus short, digitate, simple (no apparent dorsal lobe). Terminal median structure (postgonites + phallus) lobelike, very integrated, having small lateral lobe with central depression, apically microtrichose and with pair of downturned, spinelike apical lobes/setae.

TYPE MATERIAL: Holotype, male, USNM PAL 726868.

ETYMOLOGY: The specific epithet is named in reference to the broad, lanceolate postpedicel.

Alavesia latata, new species

Figures 1F, 2E, 13C

DIAGNOSIS: Wing short, broad, L/W 2.15, apex broadly rounded (fig. 13C); R_{4+5} and M_1 parallel for entire length; apex of CuA strongly recurved, anal lobe absent. Postpedicel triangular, L/W 2.48, arista 0.54× length of postpedicel.

DESCRIPTION: *Male.* **Coloration** not preserved. **Head:** Scape short, setose; pedicel slightly larger, quadrate, postpedicel an elongate triangle, lanceolate (fig. 1F), L/W 2.48; stylus relatively short, thick, 0.54× length of postpedicel, with two minute basal articles.

Thorax: Macrosetae thickened; acrostichals not fully visible; dorsocentrals ending in stout pair of long prescutellars; postpronotal lobe with 3 short setae; notopleurals not fully visible, but 3 well-developed ones visible; 1 postsutural supraalar seta, 1 postalar seta; 3 pairs scutellar setae, apical pair upturned and crossed, lengths ~2× that of lateral-most pair.

Legs: Forecoxa with dense setae on anterior surface. Forefemur with some fine ventral spinules, but complete distribution not visible; mid and hind femora with spinelike setae near apex only. Tibiae with long apical, ventral seta(e): 1-2-2. Hind tibia with dorsal row of ~6 thicker setae, lengths about half width of tibia; posterior surface with short brush of fine setulae.

Wing: Length 1.55 mm (fig. 2E), vein C terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} perfectly parallel to M_{1+2} ; crossvein r-m at middle of cell dm; apex of M_4 equidistant between M_{1+2} and CuA+CuP; CuP recurved, in line with bm-cu; apex of cell cua truncate; cell cua shorter than cell bm; vein A well developed but incomplete; anal lobe very narrow.

Abdomen: About same length as thorax; setation mostly not visible. Terminalia mostly not visible, but ventral margins of epandrium with fringe of long setae; surstyli very slender, digitiform.

TYPE MATERIAL: Holotype, male: AMNH Bu-1476. The fly is complete but preserved in turbid amber (fig. 13C), which obscures some details (i.e., of genitalia). Despite the preservation, the distinctive wing shape and venation allowed a reliable diagnosis of this species.

ETYMOLOGY: In reference to the broad wing, from Latin *latus* (broad) and *ala* (wing).

Alavesia longicornuta, new species

Figures 1G, 2F, 5A, 8F, 9C–D, 13D, 14A

DIAGNOSIS: Males of this species are distinctive, characterized by greatly lengthened arista-like stylus (figs. 13D, 14A) (2.9× length of postpedicel), bearing a light, apical flaglike expansion; elongate and flattened palpi; CuA strongly recurved, in line with m-cu; CuA+CuP sharply curved subapically to wing margin. Distinguished from males of *A. longistylata* by slightly longer stylus with a light (vs. dark) apical “flag,” broader palpus, longer and narrower wing; cell cua significantly thicker.

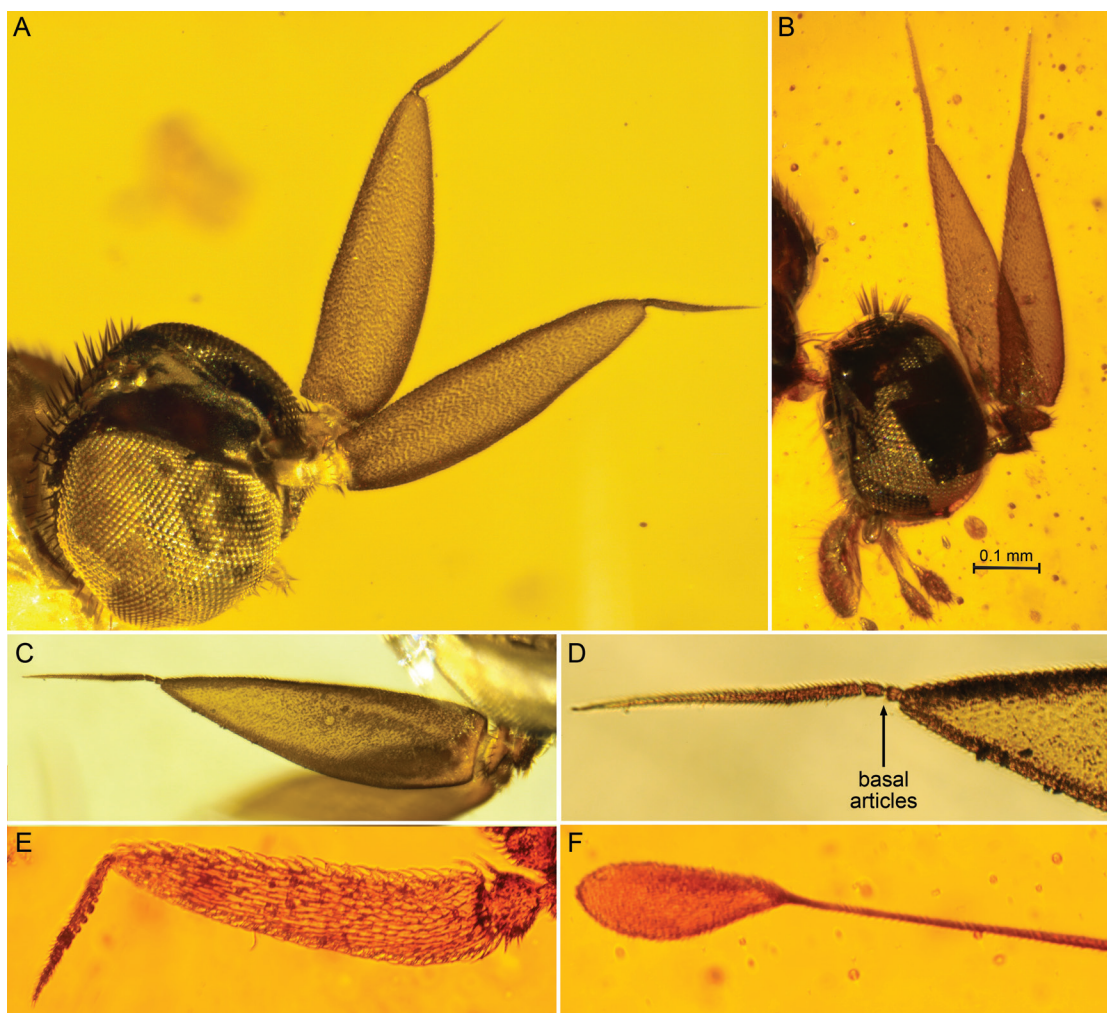


FIGURE 8. Heads and antennae of Burmese amber *Alavesia*. **A.** *A. lanceolata*, head and antennae, dorsolateral view, holotype, USNM 726868. **B.** *A. pankowskiorum*, head and antennae, lateral view, paratype, AMNH Bu-KL7-19. **C.** *A. magna*, left antenna, lateral view, holotype, AMNH Bu-KL2-7. **D.** *A. magna*, left antenna detail, lateral view, holotype, AMNH Bu-KL2-7. **E.** *A. brevipennae*, lateral view, AMNH Bu-494. Note the longer microtrichia on the postpedicel. **F.** *A. longicornuta*, holotype, stylus tip, lateral view, JZC Bu-556.



FIGURE 9. Mouthparts of Burmese amber *Alavesia*. **A.** *A. zigrasi* head, lateral view, AMNH Bu-KL9-21. **B.** *A. zigrasi* (same specimen as A), mouthparts, showing labellum with pseudotracheae, labrum, hypopharynx. **C.** *A. longicornuta*, holotype, JZC Bu-556, showing setose palps. **D.** *A. longicornuta*, paratype, USNM PAL 726871, showing setose palps. **E.** *A. longistylata*, USNM PAL 726872, showing slender, setose palps.

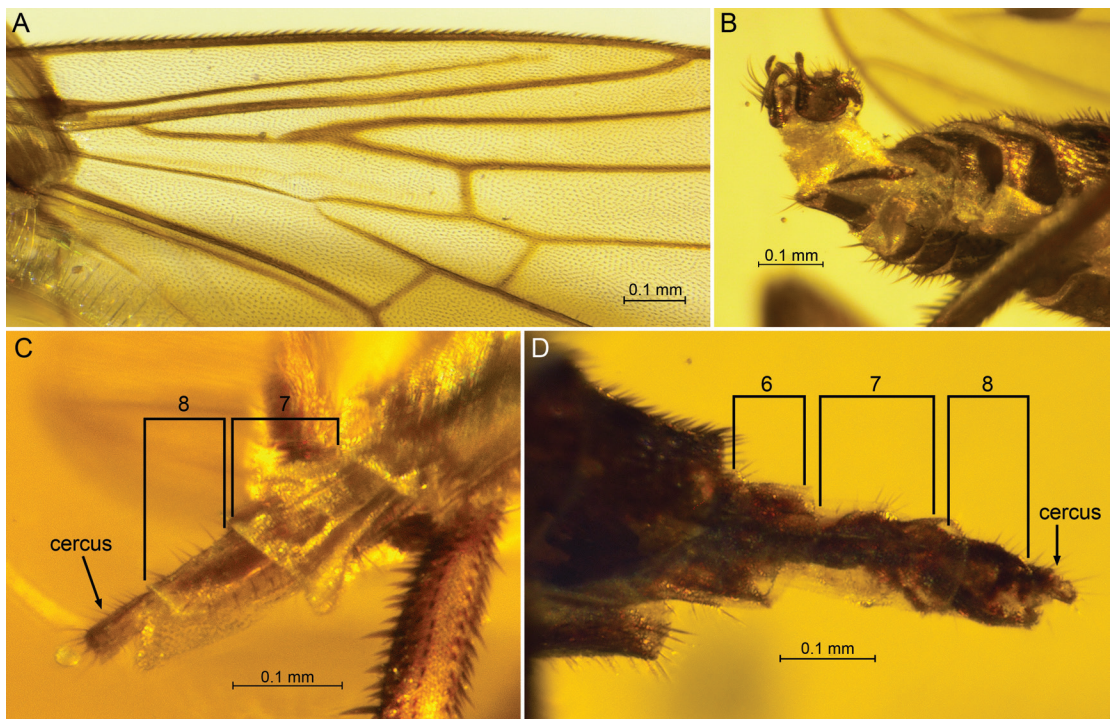


FIGURE 10. Features of *Alavesia* spp. **A.** *A. magna*, holotype, AMNH Bu-KL2-7, wing base. **B.** *A. pankowskiorum* male terminalia, right ventrolateral view, USNM PAL 726869. **C.** Female terminalia, *Alavesia* sp., lateral view, JZC Bu-1729. **D.** *A. zigrasi* female terminalia, lateral view, AMNH Bu-KL9-21.



FIGURE 11. Legs of *Alavesia* sp., showing the longitudinal furrows on the femora and tibiae (arrows). **A.** *A. longistylata*, fore and mid femora. **B.** *A. magna*, holotype, fore and mid femora, posterior surface. **C.** *A. magna*, holotype, hind tibiae. **D.** *A. pankowskiorum*, hind femur posterior/lateral surface, USNM PAL 726869. **E.** *Alavesia* sp., mid and hind femora, female, JZC Bu-1729. **F.** *Alavesia* sp., fore femur, posterior/lateral surface, same specimen as in E. **G.** *Alavesia* sp., right fore femur lateral surface, female, USNM PAL 726874.

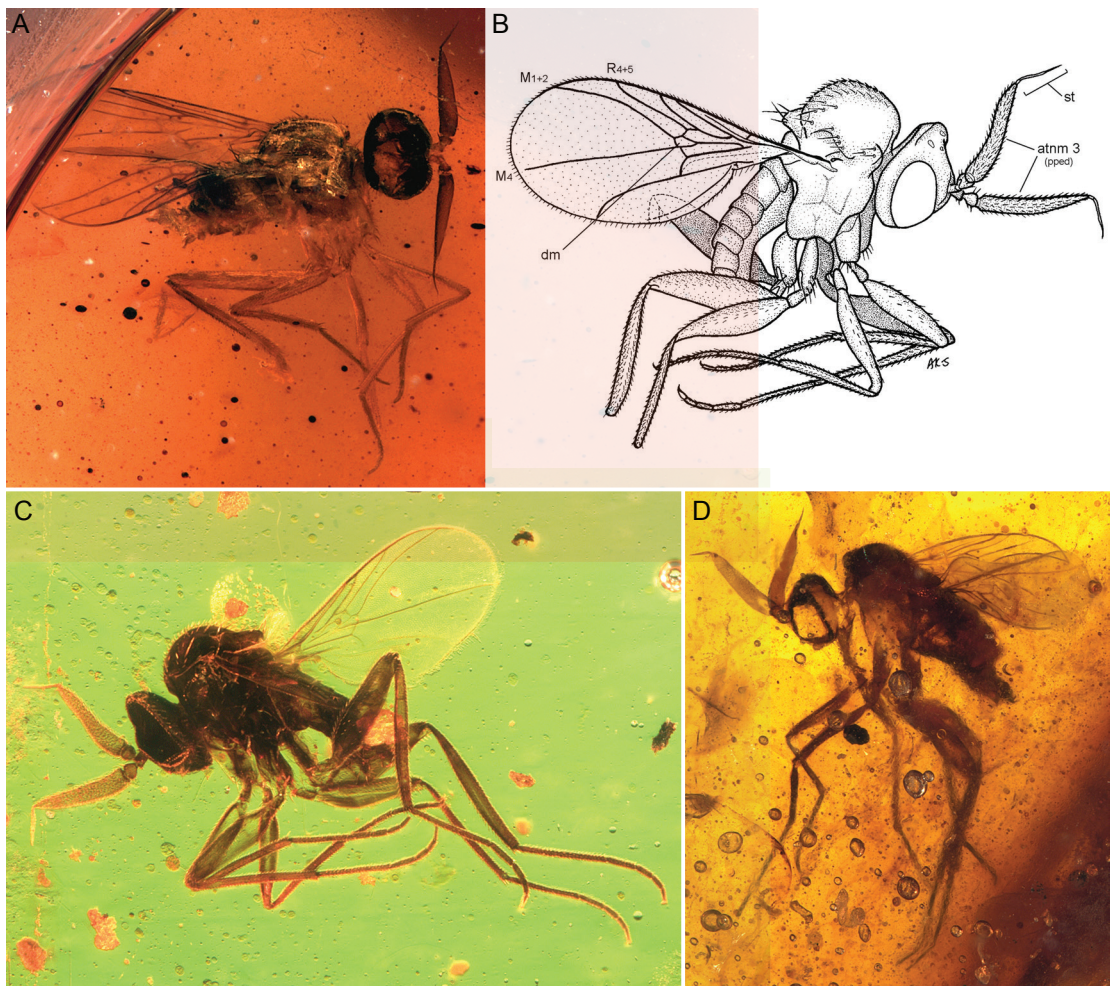


FIGURE 12. *Alavesia* spp. in Burmese amber. **A.** *A. angusta*, USNM PAL 726867. **B.** Drawing of *A. brevipennae*, AMNH Bu-494. **C.** Photomicrograph of *A. brevipennae*, AMNH Bu-494. **D.** *A. myanmarensis*, AMNH Bu-496.

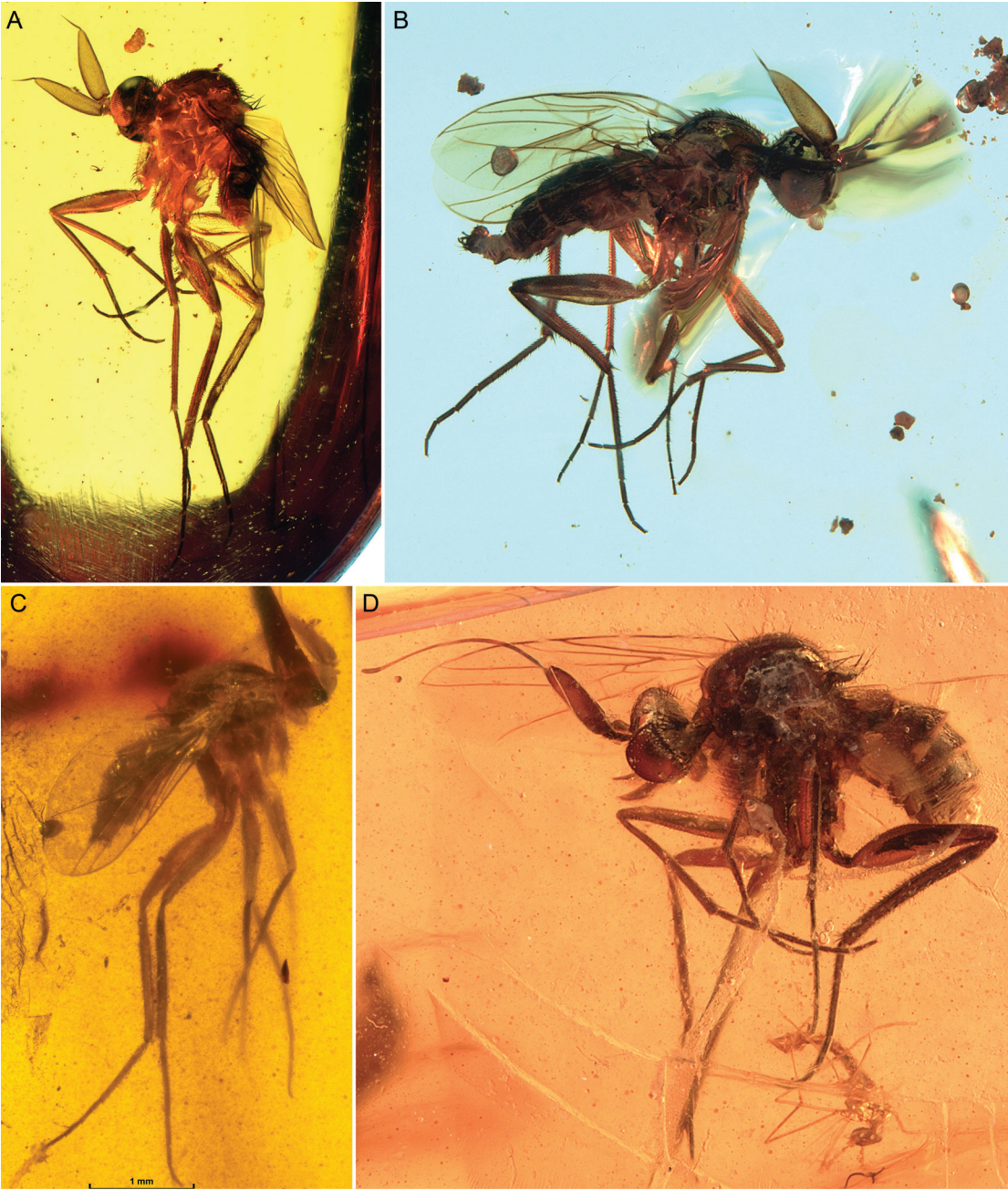


FIGURE 13. *Alavesia* spp. in Burmese amber. A. *A. lanceolata*, USNM PAL 726868. B. *A. pankowskiorum*, USNM PAL 726869. C. *A. latala*, holotype, AMNH Bu-1476. D. *A. longicornuta*, holotype, JZC Bu-556



FIGURE 14. *Alavesia* spp. in Burmese amber. A. *A. longicornuta*, paratype male, USNM PAL 726871. B, C. *A. longistylata*, USNM PAL 726872.

DESCRIPTION: *Male.* **Coloration**, except stylus, not preserved. **Head:** Scape and pedicel quadrate, scape longer than pedicel. Postpedicel greatly lengthened, L/W 4.0, tapered on apical two-thirds, longer than head height. Stylus with two small basal articles, with apical aristalike stylus 2.9× length of postpedicel (fig. 1G); apex of stylus with light, oval, flaglike flattened expansion (fig. 8F). Palpus bladelike (fig. 9C, D), flattened, projecting, strongly tapered, with fine setae ventrally, length about subequal to eye height.

Thorax: Chaetotaxy thickened (fig. 5A): biserial row of short acrostichal setae; dorsocentral setae similar to acrostichals, ending in pair of long prescutellar dorsocentral setae; 2 anterior and 1 posterior postpronotal setae; 4 anterior notopleural setae of variable lengths, 1 posterior notopleural seta; 1 postsutural supraalar seta; 1 postalar seta; 2–3 pairs of scutellar setae.

Legs: Forecoxa with short erect anterior setae. Femora with anteroventral row of short setae. Tibiae with long, apical ventral seta. Hind tibia with dorsal row of setae, length about half width of tibia; posterior face clothed with brush of fine setae.

Wing: Length 2.2 mm (fig. 2F), costa terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} until near wing margin; crossvein r-m opposite near middle of cell dm; apex of M_4 at equal distance between M_{1+2} and CuA+CuP; CuA straight, turned toward wing base, aligned with bm-m; apex of cell cua truncate, length of cell cua shorter than cell bm; CuA+CuP mostly straight, sharply curved subapically to wing margin.

Abdomen: Setae short, without distinct posteromarginal setae. Segments 1–5 broad, remaining segments retracted with segment 5. Terminalia obscured by bubble.

TYPE MATERIAL: Holotype, male, JZC Bu-556 (AMNH). Paratype: USNM PAL 726871 (1 male, USNM).

ETYMOLOGY: The specific epithet is from the Latin *cornutus* (“horned, bearing horns”), in reference to the elongate aristalike stylus.

Alavesia longistylata Zhang and Wang

Figures 1H, 3A, 6B–C, 9E, 11A, 14B–C

Alavesia longistylata Zhang and Wang in Zhang et al., 2020.

DIAGNOSIS: Like *A. longicornuta*, sp. nov., males characterized by greatly lengthened aristalike stylus (2× length of postpedicel) (fig. 14B, C), bearing an apical, flaglike expansion; palpi elongate, narrow, projecting; CuA strongly recurved, cell cua truncate; M_{1+2} and R_{4+5} parallel. Differences with *A. longicornuta* given in diagnosis of that species.

REDESCRIPTION: *Male.* **Coloration**, except stylus, not preserved. **Head:** Scape and pedicel quadrate, subequal in size and length. Postpedicel greatly lengthened (fig. 1H), L/W 3.3, tapered throughout, longer than head height. Stylus with two small basal articles, apical aristalike stylus 2× length of postpedicel; apex of stylus with darkened, flaglike flattened expansion, twice width of apex of postpedicel. Palpus slender and elongate, tapered apically (fig. 9E), length about

two-thirds as long as eye height; ventral edge with short, erect setulae; apex with several longer, curved setulae.

Thorax: Chaetotaxy thickened: uniserial row of short acrostichal setae; dorsocentral setae similar to acrostichals, ending in pair of long prescutellar dorsocentral setae; 1 anterior and 1 posterior postpronotal seta; 4 anterior notopleural setae of variable lengths, 1 posterior notopleural seta; 1 postsutural supraalar seta; 1 postalar seta; 1 pair of apical scutellar setae.

Legs: Forecoxa with short erect anterior setae; anteroapical setae longer and stouter. Femora (fig. 11A) with anteroventral row of short setae. Mid and hind coxae with 2–3 stout lateral setae on apical half. Tibiae with biserial row of short, stout ventral setae; apex of tibiae with long, apical ventral seta; hind tibia with dorsal row of setae, length about half width of tibia.

Wing: Length 1.9 mm (fig. 3A), costa terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} , slightly divergent near wing margin; crossvein r-m opposite near middle of cell dm; apex of M_4 equal distance between M_{1+2} and CuA+CuP; CuA straight, strongly recurved; apex of cell cua truncate, length of cell cua shorter than cell bm; CuA+CuP mostly straight, curved subapically to wing margin.

Abdomen: Setae short, without distinct posteromarginal setae. Segments 1–5 broad, remaining segments retracted with segment 5. Terminalia (fig. 6B, C): cercus finely setose; truncate apically. Epandrium U-shaped with broad dorsal bridge anterior to cerci; row of ~7 long setae along posteroventral margin, half length of epandrium. Surstylus very narrow and elongate, digitiform, projecting nearly vertically from epandrium, slightly shorter than apical epandrial setae; surstylus having thinner, shorter dorsal lobe. Phallus slender, sclerotized projection; strongly bent subapically with apex arched ventrally, tip microsetulose.

MATERIAL EXAMINED: Male, USNM PAL 726872.

Alavesia magna, new species

Figures 1E, 3B, 5B, 6D–E, 8C–D, 10A, 11B–C, 15A–B

DIAGNOSIS: One of two largest species of genus (fig. 15A, B), wing length 3.0 mm; wing linear, long and slender, L/W 2.97; R_{4+5} and M_{1+2} entirely parallel; apex of CuA not recurved; postpedicel slender, L/W 3.45. Male genitalia: surstylus very slender, digitiform, with small dorsal lobe bearing stiff, short seta; postgonites+phallus long, phallus downcurved, minutely feathered at tip.

DESCRIPTION: Coloration: Yellowish portions of body: palpus, labellum, much of coxae (also with light brown portions), stem of halter, proximal halves of femora, tergites 6–8; remaining areas light to dark brown (fig. 15A, B). Female paratype slightly darker (preservational artifact?). Wing lightly tinted yellowish on costal half. **Male. Head:** Scape short, caplike; pedicel

FIGURE 15. *Alavesia* spp. in Burmese amber. **A.** *A. magna*, holotype, AMNH Bu-KL2-7. **B.** *A. magna*, paratype female, USNM PAL 726873. **C.** *A. pankowskiorum*, piece with holotype, AMNH Bu-1554. **D.** *A. pankowskiorum* holotype, AMNH Bu1554a. **E.** *A. pankowskiorum*, paratype male, piece with holotype, AMNH Bu-1554b. **F.** *A. pankowskiorum*, paratype male, AMNH Bu-KL7-19.



short, caplike, with distal ring of setulae. Postpedicel large, lanceolate (fig. 1E), tapered in distal half, L/W 3.45; stylus of moderate length, $0.45 \times$ L postpedicel, with 2 minute basal articles (fig. 8C, D). Palpus very small; labellum bulbous, with ~ 7 –8 pseudotracheae.

Thorax: Macrosetae thickened (fig. 5B); acrostichals very fine, small, in irregular biserial rows; dorsocentral setae slightly larger than acrostichals, gradually longer posteriad, ending in pair of long prescutellar setae (longest setae on thorax). Two postpronotal setae (slightly larger than setulae); 8 notopleural setae of variable lengths, 3 posterior ones longest; 1 postsutural supraalar seta; 1 postalar seta; 2–3 pairs of scutellar setae, apical pair largest, crossed at midlength.

Legs (fig. 11B, C): Forecoxa with short, erect setae on anterior surface, longer ones apically. Forefemur with anteroventral row of ~ 40 small, spinulelike setae; short row of such setae near apices of mid and hind femora. Tibiae with long, apical ventral setae: 1–2–2. Hind tibia with 2 dorsolateral rows of thicker setae, lengths $\sim 0.7 \times$ width of tibia; posterior surface with slight brush of finer setae.

Wing: Length 3.0 mm (figs. 3B, 10A). Vein C terminating slightly beyond M_{1+2} ; Sc nearly touching costal margin; R_{4+5} entirely parallel to M_{1+2} , both very straight, crossvein r-m at apical $1/3$ of cell dm; apex of M_4 about equidistant between M_{1+2} and CuA+CuP; CuA arched; apex of cell cua acute, cell cua longer than cell bm; CuA+CuP virtually straight.

Abdomen: Longer than thorax; setae short, no differentiation of posteromarginal setae on tergites or sternites. Segments 1–4 very broad (2 very large), remaining segments much smaller, partially retracted. Terminalia (fig. 6D, E): observable dorsally and laterally. Epandrium complete dorsally, with setulae and marginal fringe of ~ 8 –10 long, fine setae on ventral margin. Surstylus long, slender, digitate, with small dorsal lobe bearing small spinelike seta, apically with minute toothlike apical seta that points inward; mesal surface of surstylus with microtrichia. Postgonites highly integrated, projecting posteriad; phallus abruptly bent ventrad, apex bifid and finely feathery. Female terminalia telescoping; cerci exposed and deflexed downward.

TYPE MATERIAL: Holotype male AMNH Bu-KL2-7. Paratype, female USNM PAL 726873.

ETYMOLOGY: In reference to the body size, being one of the largest of all the Burmese amber species, along with *A. longicornuta*.

Alavesia myanmarensis Jouault, Ngô-Muller, and Nel

Figures 1C, 2C, 12D

Alavesia myanmarensis Jouault, Ngô-Muller, and Nel in Jouault et al., 2020: 205.

Alavesia n. sp. Grimaldi et al., 2002: 59, fig. 40a, b.

DIAGNOSIS: A short species (fig. 12D) with a short cell dm and strongly curved and divergent M_{1+2} . Differs from *A. brevipennea* by larger size (wing length: 1.1 mm vs. 0.75 mm); M_4 arched; postpedicel straplike, tapered on apical fourth, length of stylus to postpedicel 0.32.

REDESCRIPTION: *Male.* **Coloration** not preserved. **Head:** Scape and pedicel quadrate, subequal in size and length. Postpedicel elongate, straplike (fig. 1C), L/W 5.5, tapered on apical fourth; stylus short, $0.32 \times$ length of postpedicel, with two basal articles, without apical flaglike expansion. Mouthparts very short; palpus short, not projecting.

Thorax: Chaetotaxy thickened, in numerous rows (not clearly visible); postpronotum and notopleuron damaged; 1 postalar seta; 2 pairs of scutellar setae.

Legs: Most setae thickened. Forecoxa with short erect anterior setae; anteroapical setae longer and stouter. Forefemur with anteroventral and posteroventral row of short, slender setae. Mid and hind coxae with 2–3 stout lateral setae on apical half. Tibiae with biserial row of short, stout ventral setae; apex of tibiae with long, apical ventral seta; hind tibia with several dorsal setae, length about half width of tibia.

Wing: Length ~1.1 mm (base obscured) (fig. 2C): Costa terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_1 distinctly preapically arched to costa; R_{4+5} closely associated with M_{1+2} , divergent apically; M_{1+2} strongly curved and divergent from R_{4+5} distally; cell dm short, crossvein r-m nearly opposite apex of cell bm; M_4 arched to wing margin; apex of M_4 closer to CuA+CuP than M_{1+2} ; veins at base of wing difficult to observe.

Abdomen: Setae short, without distinct posteromarginal setae. Segments 1–5 broad. Terminalia with paired, subapical sickle-shaped projections, probably surstyli.

MATERIAL EXAMINED: Male, AMNH Bu-496 (AMNH).

REMARKS: The male terminalia of this species was described in detail by Zhang et al. (2020).

Alavesia pankowskiorum, new species

Figures 1I–K, 3C–F, 7A–B, 8B, 10B, 15C–F

DIAGNOSIS: Relatively small species (fig. 15C–F), wing length 1.0 to 1.4 mm. Males with postpedicel lanceolate to slightly narrow-triangular L/W 4.3–3.4x, arista ~0.43× length of postpedicel; cell cua slightly acute to truncate; M_{1+2} and R_{4+5} parallel (but slightly curved), diverging slightly at wing margin; M_{1+2} and M_4 widely divergent; acrostichals in uniserial (vs. biserial) row; 2 (vs. 3) pairs scutellar setae.

DESCRIPTION: *Male.* **Coloration:** notum, abdominal tergites, terminalia evenly light brown, without bold markings; legs and postpedicel lighter. **Head:** Scape elongate, about as long as width of broadest portion of pedicel. Postpedicel lanceolate to slightly narrow-triangular, gradually and evenly tapered (fig. 1I–K), L/W 4.3–3.4x; stylus ~0.43× length of postpedicel, with two basal articles. Palpus short and narrow (fig. 8B).

Thorax: Macrosetae thickened; acrostichals fine, short, in uniserial row; dorsocentral setae similar to acrostichals, ending in pair of long prescutellar dorsocentral setae; 1 anterior and 1 posterior postpronotal seta; 4 anterior notopleural setae of variable lengths, 1 posterior notopleural seta; 1 postsutural supraalar seta; 1 postalar seta; 2 pairs of scutellar setae.

Legs: Forecoxa with short erect anterior setae; anteroapical setae longer and stouter. Forefemur with anteroventral row of short, spinulelike setae; shorter rows near apex of mid and hind femora. Mid and hind coxae with 2–3 stout lateral setae on apical half. Tibiae with biserial row of short, stout ventral setae; apex of tibiae with long, apical ventral seta(e): (1-2-2). Hind tibia with dorsal row of stout setae, length about half width of tibia.

Wing: Length 1.0–1.4 mm (fig. 3C–F). Costa terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} , diverging slightly near wing margin, veins straight

to slightly or obviously curved; crossvein r-m at midlength to apical quarter of cell dm; M_4 straight to wing margin; apex of M_4 approximately equidistant between M_{1+2} and CuA+CuP; M_{1+2} and M_4 widely divergent; CuA slightly convex; apex of cell cua slightly convex to virtually truncate, length of cell cua slightly shorter than cell bm; CuA+CuP mostly straight, slightly curved subapically to wing margin. Anal vein present; anal lobe very narrow.

Abdomen: Setae short, posteromarginal setae of tergites and sternites hardly differentiated. Segments 1–5 broad, remaining segments retracted with segment 5. Terminalia (fig. 7A,B): cercus finely setose; truncate apically. Epandrium U-shaped with broad dorsal bridge anterior to cerci; long setae along posterior margin, half length of epandrium. Surstylus very narrow and elongate, projecting nearly vertically from epandrium, as long as apical epandrial setae. Phallus slender, sclerotized projection; strongly and evenly (vs. abruptly) bent subapically, hooklike, with apex arched ventrally, apex minutely feathered, probably bifid. Female terminalia like that of *Alavesia* sp. (JZC Bu-1729: fig. 10C) and *A. zigrasi* (AMNH Bu-KL9-21: fig. 10D).

TYPE MATERIAL: Holotype, male, AMNH Bu-1554 (other 2 males, 2 females paratypes). Paratypes, male AMNH Bu-888; male AMNH Bu-KL7-19; male USNM PAL 726869.

ETYMOLOGY: The specific epithet is named in honour of Pankowski family who donated several specimens used in this study.

Alavesia spinosa, new species

Figures 1L, 4A, 5C, 7C, 17A

DIAGNOSIS: Wing moderately slender (fig. 17A), L/W 2.88, with distinctly narrowed apex; R_{4+5} and M_{1+2} slightly curved; bm-cu and CuA nearly symmetrical; cell dm long and slender. Postpedicel very large, L/W 4.88, lanceolate. Male genitalia with pair of thick, spinelike setae just anterior to bases of surstyli.

DESCRIPTION: *Male. Coloration* partially visible, much of cuticle with layer of air. Mesoscutum and scutellum dark tan/light brown; postpedicel brown; pleura brown at least in center, perhaps more; halter knob light brown; tarsi entirely dark brown, tibiae and femora lighter; tergites 1–4 dark brown, others yellowish; wing completely hyaline. **Head:** Scape slender, longer than pedicel; pedicel small, quadrate, setose; postpedicel long, lanceolate (fig. 1L), L/W 4.88; stylus relatively short, $0.39\times$ length of postpedicel, with 2 minute basal articles.

Thorax: Macrosetae thickened (fig. 5C); acrostichals small and fine, in biserial rows; dorsocentrals similar to acrostichals, ending in pair of long prescutellar setae plus 3 smaller macrosetae per side. Postpronotal setae only slightly larger than acrostichals; 5 notopleural setae of variable lengths; 1 postsutural supraalar seta; 1 postalar seta; 3 pairs scutellar setae, apical pair upright, crossed at tips, only slightly larger than lateralmost scutellars.

Legs: Forecoxa setose on anterior surface, longer at apex; forefemur with anteroventral row of ~ 30 short, spinulelike setae along length of femur; mid and hind femora with such setae only near apex. Tibia with long, apical ventral seta(e): 1-2-2. Hind tibia with short dorsal row of 3–4 thick setae, lengths $\sim 0.7\times$ width of tibia, posterior surface with brush of fine setulae.

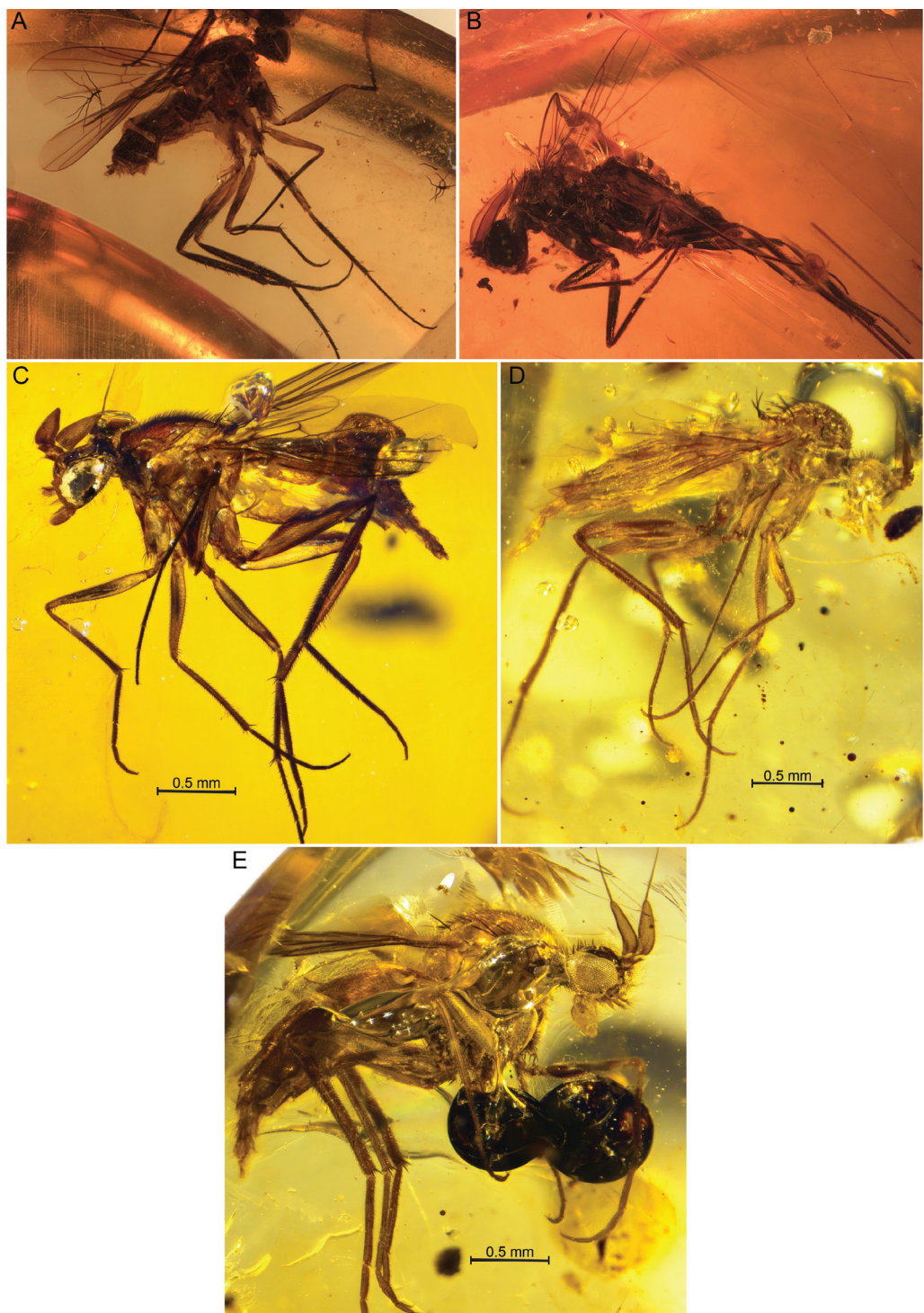


FIGURE 16. *Alavesia zigrasi* in Burmese amber. A. Holotype, JZC Bu-281. B. Male paratype, JZC Bu-282. C. Female paratype, AMNH Bu-KL9-21. D. Female paratype, JZC-165a. E. Female paratype, JZC Bu-165b.

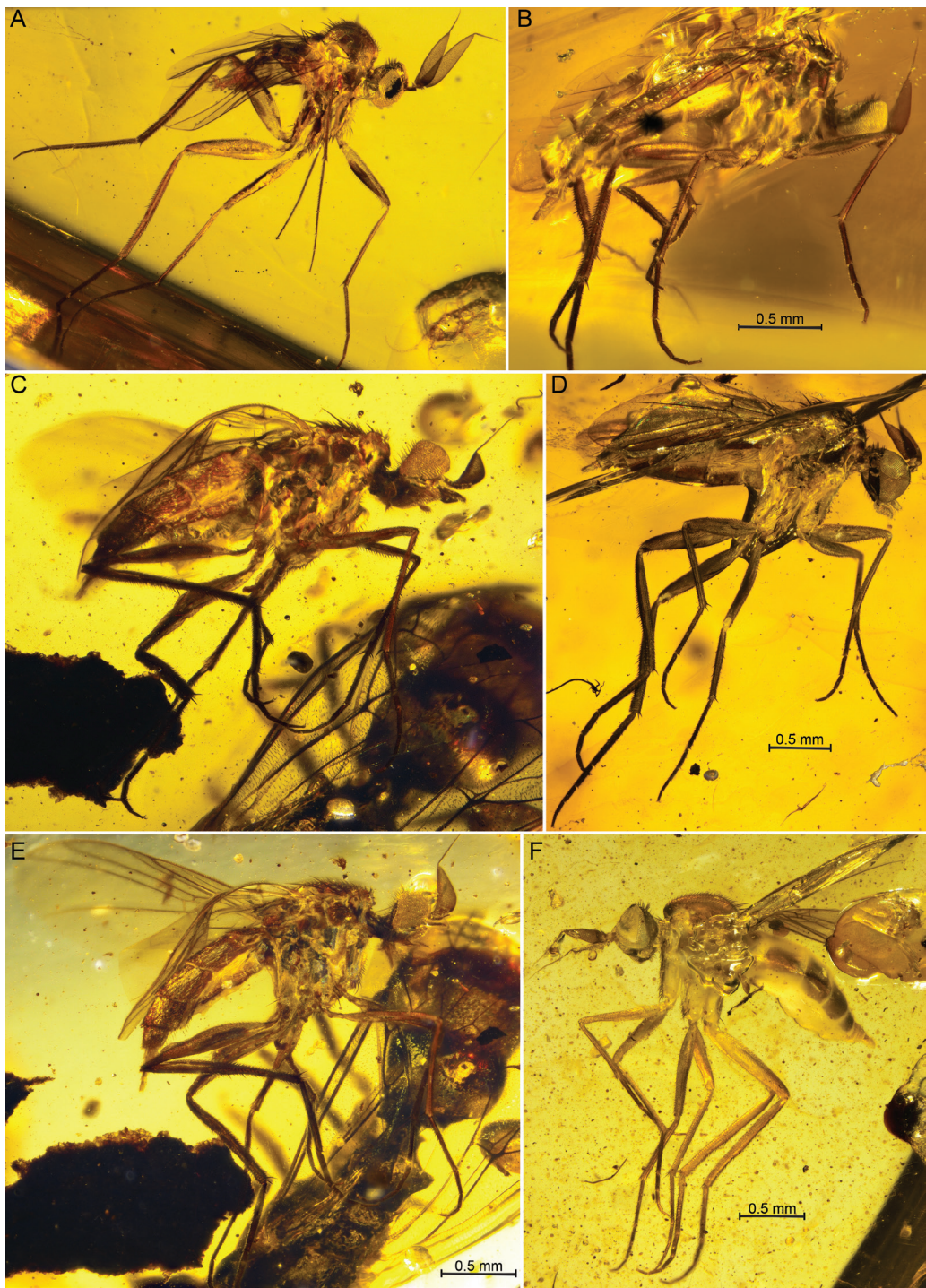


FIGURE 17. *Alavesia* spp. in Burmese amber. B–F are all females unidentified to species. A. *A. spinosa* holotype, AMNH Bu-KL7-18. B. JZC Bu-1729. C. USNM PAL 726870. D. USNM PAL 726874. E. USNM PAL 726870. F. USNM PAL 726875.

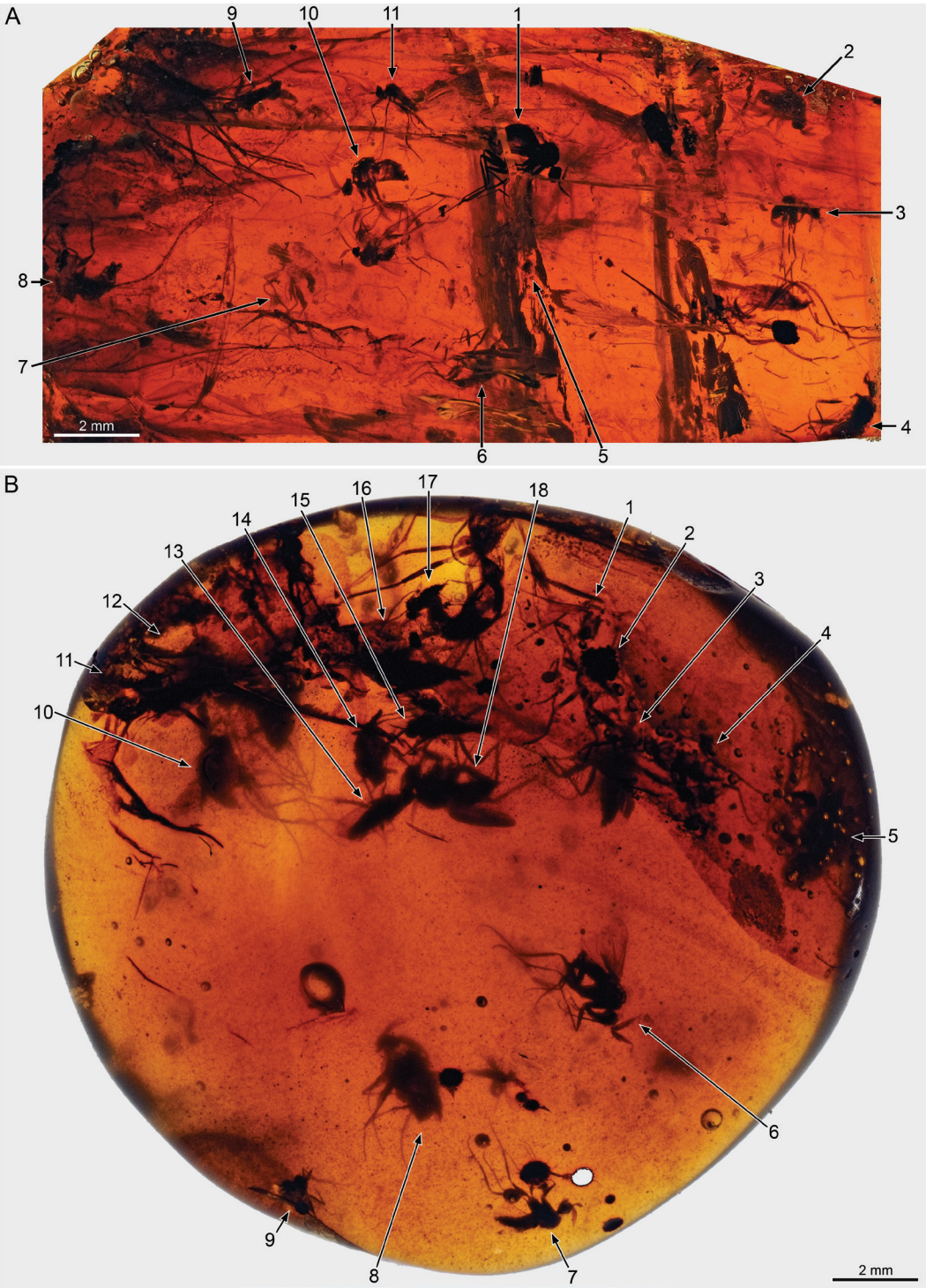


FIGURE 18. Two pieces of Burmese amber with small swarms of *Alavesia*. Numbers indicate *Alavesia* individuals. See text for descriptions and interpretations. **A.** AMNH Bu-177. **B.** AMNH Bu-KL15.

Wing: Length 1.7 mm (fig. 4A), vein C terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} but diverging at apices, both veins slightly curved (not straight); crossvein r-m at distal third of cell dm, cell long and slender; apex of M_4 slightly closer to M_{1+2} than to CuA+CuP; CuA not aligned with bm-m; apex of cell cua acute, cell cua almost symmetrical with cell bm; CuA+CuP bent slightly in middle.

Abdomen: Slightly longer than thorax. Setae short, with little differentiation; sternites 2–4 with slightly thicker, short setulae on posterior and lateral margins. Terminalia (fig. 7C): Epan-drium short, broad, dorsally complete, with some setulae and fringe of 5–6 long, fine setae on ventral margins. Cercus small. Surstylus long, slender, digitate, with medial row of 5 fine setulae, apical setula clavate. Phallus short, bifid. Genitalia uniquely with pair of stout, large, spine-like setae near bases of surstyli.

TYPE MATERIAL: Holotype, male: AMNH KL7-18. The fly is in excellent condition, preserved in clear yellow amber with many microscopic details visible.

ETYMOLOGY: The specific epithet is from the Latin *spinosus* (thorny), in reference to the pair of thick, spinelike setae on the male terminalia.

Alavesia zigrasi, new species

Figures 1M, 4B–C, 7D, 9A–B, 10D, 16

DIAGNOSIS: Large species (fig. 16), wing 2.1 mm; M_{1+2} and R_{4+5} parallel; cell dm extending well beyond apex of cell cua; crossvein br-m at two-thirds of cell dm; CuA arched apically.

DESCRIPTION (based on holotype): *Male. Coloration* of holotype well preserved; body almost entirely dark brown, including pleura and halter. Coxae mostly yellowish, dark area on distal portion of anterior surface. Forefemur yellowish, basal 2/3 of mid and hind femora yellowish, apices brown. Tibiae and tarsi dark brown. Wing slightly tinted, trailing edge lighter. All tergites dark, including epan-drium; cerci light.

Head: Scape barely observable; pedicel short, conelike. Postpedicel large, broad (fig. 1M), L/W 3.22. Stylus short, L 0.36× length of postpedicel, with two small basal articles. Palpus broad, rounded apically; labellum with at least 10 pseudotracheae (fig. 9A, B).

Thorax: Macrosetae very thickened; acrostichals robust, in biserial rows; dorsocentral setae similar to acrostichals, ending in 2 pairs long prescutellars (posterior pair longest); 1 anterior and 1 posterior postpronotal seta; notopleural setae of variable lengths (3 most posterior ones thick and long); 1 postsutural supraalar seta; 1 postalar seta; 3 pairs scutellar setae, lateral pair 0.6× L apical pair.

Legs: Forecoxa with short, erect setae on anterior surface, 5–6 of them thick. Forefemur with anteroventral row of short, spinulelike setae; short row of such setae near apices of mid and hind femora. Tibiae with long apical ventral setae: 1-2-2. Hind tibia with dense dorsal row of setae, length about half width of tibia, plus row of ~6 larger, spinelike setae (length slight less than tibial width); posterior surface of hind tibia with fine, brushy setulae.

Wing: Length 2.1 mm (fig. 4B, C), vein C terminating slightly beyond M_{1+2} ; Sc nearly reaching costal margin; R_{4+5} parallel to M_{1+2} ; crossvein r-m at distal third of cell dm; apex of

M_4 slightly closer to M_{1+2} than to $CuA+CuP$; CuA oblique, slightly arched, not aligned with $bm-m$, apex of cell cua acute, cell cua longer than cell bm ; apex of $CuA+CuP$ slightly curved at apex. Vein A well developed.

Abdomen: Slightly longer than thorax, setae short, spinulelike setae on posterior and lateral margins of sternites 2–5. Segments 1–5 broad, others retracted into segment 5. Terminalia unique (fig. 7D): Epandrium dorsally incomplete, long fringe of ~8 setae on ventral margin. Cercus small; surstylus straight (curved slightly inward), projecting backward, thicker than in other species. Phallus flexed anteroventrad, apex bifid and minutely feathered.

TYPE MATERIAL: Holotype, male JZC Bu-281. The left antenna and distal half of the right foreleg lost. Paratypes, three females (AMNH Bu-KL9-21, JZC Bu-165a, JZC Bu-165b), JZC Bu-282 (male), genitalia not well preserved; coloration not preserved, body with some compression; differs from holotype by venation (fig. 4C): $r-m$ at middle of cell dm , $bm-m$ and $m-cu$ slanted, CuA strongly arched.

ETYMOLOGY: The specific epithet is named in honour of James Zigras, from whose collection these and other fossil specimens originate.

Undetermined Specimens

Four pieces of Burmese amber in the AMNH contain specimens that are difficult to identify to species, based on inadequate preservation. All except AMNH KL7-7 were found in a large batch of unprocessed amber (Grimaldi et al., 2002). A significant portion of Burmese amber contains arthropod inclusions that are too distorted by compression for definitive identification; since these usually contain many fine fractures, such pieces are rarely sold commercially, a source of the fossils that will skew the natural abundances of inclusions. The undetermined *Alavesia* species are reported here for the sake of completeness.

AMNH Bu-129: Possibly male; postpedicel long, slender; R_{4+5} curved, quite divergent from M_1 ; CuA arched, not recurved. Amber turbid, fractured; specimen crumpled. Syninclusions: Psychodidae, female empidoid (?*Neoturionius*).

AMNH Bu-769: Male, very poor preservation, identifiable as *Alavesia* on basis of very distinctive antennae. Left wing preserved but most venation not visible; CuA recurved. Piece with many fine fractures; fly is partial and crumpled. Syninclusions: particulate debris; undetermined larva.

AMNH Bu-957: Like *A. brevipennae* a tiny species, postpedicel microtrichose and lanceolate (tapered for entire length), stylus microtrichose; R_{4+5} slightly arched, quite divergent with M_1 . Unlike in *A. brevipennae* CuA is recurved (vs. acute). Head is deformed, but mouthparts well preserved and visible. Syninclusions: stellate trichomes, 2 fine feather barbs with very fine, short barbules.

AMNH KL7-7: A piece that contains 2 males and 1 female of possibly *A. myanmarensis*. Species of average size; male postpedicel large, lanceolate; R_{4+5} arched, M_1 slightly arched, CuA arched (not recurved). Syninclusions indicate a ground-dwelling assemblage: Staphylinid beetle, cecidomyiid midge, 5 mites, soil particles, 3 leaflets (with parallel venation), a thrips, and a male coccoid.

The following undetermined females of *Alavesia* species are reported here for the sake of completeness: JZC Bu-1729 (AMNH) (figs. 1N, 3F, 10C, 11E–F, 17B); USNM PAL 726870

(USNM) (fig. 17C, E); USNM PAL 726874 (USNM) (figs. 11G, 17D); and USNM PAL 726875 (USNM) (fig. 17F).

KEY TO MALES OF BURMESE AMBER FOSSIL SPECIES OF *ALAVESIA*

1. Aristalike stylus greatly lengthened, at least twice length of postpedicel, with apical expansion or flag (fig. 1G, H)2
- Aristalike stylus shorter than postpedicel, without modified apex3
2. Palpus narrow and elongate (figs. 9E, 14C); apical aristalike stylus $2\times$ length of postpedicel; apical flag darkened (figs. 1H, 14B, C)*A. longistylata*
- Palpus flattened and elongate (fig. 9C, D); aristalike stylus more than $2.9\times$ length of postpedicel; apical flag light colored (figs. 8F, 13D)*A. longicornuta*, sp. nov.
3. Cell dm very short, crossvein dm-m opposite apex of cell bm (figs. 2B, C, 3C)4
- Cell dm longer, crossvein dm-m clearly positioned beyond apex of cell bm6
4. M_{1+2} strongly arched towards R_{4+5} (fig. 2B, C)5
- M_{1+2} gradually arched to wing margin (fig. 3C) *Alavesia pankowskiorum*, sp. nov. [in part]
5. Smaller size (wing length: 0.75 mm); postpedicel slightly curved and gradually tapered apically (fig. 1B)*Alavesia brevipennae*, sp. nov.
- Larger size (wing length: 1.1 mm); postpedicel straight and tapered on apical fourth (fig. 1C) ..
Alavesia myanmarensis
6. M_{1+2} and R_{4+5} divergent apically (figs. 2D, 3D–F, 4A, B)7
- M_{1+2} and R_{4+5} nearly parallel apically (figs. 2A, E, 3B)10
7. Wing with distinctly narrowed apex; cell dm long and slender (fig. 4A)
Alavesia spinosa, sp. nov.
- Wing with rounded apex; cell dm short and expanded apically (figs. 2D, 3D–F, 4B)8
8. Wing less than 1.5 mm (fig. 3D–F); postpedicel narrow lanceolate to narrow triangular (fig. 1I–K) *Alavesia pankowskiorum*, sp. nov. [in part]
- Wing more than 1.5 mm (figs. 2D, 4B); postpedicel large and broad (fig. 1D, M)9
9. Wing length 1.8 mm (fig. 2D) *Alavesia lanceolata*, sp. nov.
- Wing length 2.1 mm (fig. 4B)*Alavesia zigrasi*, sp. nov.
10. Scape longer than pedicel*Alavesia hadroceria*
- Scape shorter than pedicel11
11. CuA recurved, aligned with apex of cell bm (fig. 2A, E); wing short (less than 2.0 mm), narrow or rounded12
- CuA arched distally, extending beyond cell bm (fig. 3B); wing very long (3.0 mm), narrow and linear *Alavesia magna*, sp. nov.
12. Wing apex pointed (fig. 2A); postpedicel narrow and fusiform (fig. 1A); stylus length $0.46\times$ postpedicel *Alavesia angusta*, sp. nov.
- Wing apex broadly rounded (fig. 2E); postpedicel elongate triangle (fig. 1F); stylus length $0.54\times$ postpedicel *Alavesia latala*, sp. nov.

Swarms

Three pieces of amber contain multiple individuals of *Alavesia*, indicating these to be partial or entire swarms (fig. 18).

AMNH Bu-177 (fig. 18A): A roughly rectangular piece 20×11 (L/W) $\times 7.5$ mm thick, with several natural margins preserved; embedded in EpoTek resin (which clarifies viewing the inclusions). The amber is dark and contains four concentric flow lines, which, with shape of the piece indicate that it is a 20 mm section of an original resin runnel that flowed down a tree trunk. All 11 *Alavesia* individuals in the piece are male but appear to belong to two species: *A. brevipennae* (distinctive for its small size and unique curvature of antennae) and a species that is ~30% larger. The piece could not be sectioned for closer viewing because of the multiple inclusions, and preservation is suboptimal, so species identification is uncertain. Syninclusions are two Mycetophilidae (Diptera), one Scydmaenidae and one Staphylinidae (Coleoptera), one adult thrips (Thysanoptera), portion of an adult hemipteran, and seven legs from the left side of a centipede. The mycetophilid nearest the surface seems snagged on fine, twisted fibers (no doubt spider silk), but none of the *Alavesia* seem snagged. A runnel with internal flows and a surface-dwelling arthropod (the centipede) indicates this amber occurred on the vertical surface of a tree trunk. The flies were almost certainly swarming very close to a tree.

AMNH Bu-KL15 (fig. 18B): A roughly circular piece 18–20 mm in diameter, 5 mm thick, lenticular in overall shape; composed of dark, turbid amber. Piece contains 18 *Alavesia* individuals (14 males, 4 females), of either *A. myanmarensis* or *A. pankowskiorum* (preservation precludes definitive identification). They all seem to be the same species based on a uniform body size. The flies face different directions. Three flies are preserved just as casts on the surface of an internal flow, the darkened core suggesting some weathering prior to later flows. Syninclusions are a partial male aculeate wasp (probably an ant), and a tiny brachyceran fly (possibly *Chimeromyia*).

AMNH Bu-1554 (fig. 15C). This piece contains the type specimen of *Alavesia pankowskiorum* (a male), as well as four other individuals of *Alavesia*, all or most of which are males. Piece has been sectioned for better viewing.

The relative abundance of the genus in amber might suggest a trunk association, with more chance to be engulfed by resin. The swarms are not necessarily mating aggregations, especially given the two species in one piece. Mating swarms are typically mostly males, into which a few females enter for mating. The dichoptic eye condition of males of *Alavesia* could support that these are mating aggregations, whereas a holoptic male eye condition is a modification generally viewed as indicative of aerial mating swarms. Aggregations could also be based on feeding sites, landmarks, and appropriate microenvironments in a forest, such as a patch of sunlight on a tree trunk.

DISCUSSION AND CONCLUSIONS

Recent discoveries of fossil and living species demonstrate that caution is required when interpreting biogeographic distributions, particularly for poorly sampled organisms like small flies. For more than a century it was assumed, for example, that the distribution of the small basal cyclorrhaphan family Opetiidae was exclusively Palearctic, but recently the family was discovered in Chile (Amorim et al., 2018). *Alavesia* is another excellent

TABLE 2. Relict Arthropod Taxa in Burmese Amber.

Genus/Genera	Order: Family	Present Distribution
<i>Afrarchaea</i>	Araneae: Archaeidae	S Africa, Madagascar, Australia
<i>Burmomerope</i>	Mecoptera: Meropeidae	SW Australia, S Brazil, NE North America
<i>Hilarimorphites</i>	Diptera: Apystomyiidae	California
<i>Burmapsilocephala</i>	Diptera: Apsilocephalidae	SW U.S., Chile
<i>Cretaseguya</i>	Diptera: Valseguyidae	SE Australia
<i>Paleopetia</i> , <i>Proironia</i>	Diptera: Ironomyiidae	E Australia
various genera	Raphidioptera	Paleartic, W North America
various genera	Neuroptera: Rhachiberothidae	S Africa
<i>Kronostephanus</i>	Hymenoptera: Stephanidae: Schlettereriinae	E Asia, W North America

example, a group first discovered in amber from Laurasia, then found alive in southern Africa and South America. This history of discovery is very similar to that of the order Mantophasmatodea, first known in Eocene Baltic amber, then 15 extant species were discovered in southern Africa, originally on the Brandberg Massif (Picker et al., 2002; Klass, 2002, 2003). With an adult length of about a centimeter, these apterous insects are not exactly inconspicuous.

Despite the uncertainty in geographic sampling, there are some consistent patterns among relicts that have extinct relatives preserved in Burmese amber (table 2): (1) The groups are quite old (at least Cretaceous), and usually phylogenetically basal within their respective orders, suborders, or families. (2) There are few living species. (3) They are narrowly endemic and often highly disjunct, little doubt because of widespread extinction. (4) Endemism appears to be restricted to south temperate and north temperate regions and areas: southern Africa, Australia, southern South America, California, etc. There are no examples of relicts from fully tropical areas.

The primary question is this: why do these relict taxa persist in temperate regions? The classical explanation (reviewed in Grimaldi and Engel, 2005) is that older, less competitive taxa are forced to biogeographic margins that are cool to seasonally cold or arid (or both), away from wet tropical areas where plant productivity is very high, but niches are packed and inter-specific interactions like competition, predation, and parasitism are intense. This is a subject requiring study. Range contractions may have occurred in the Late Cretaceous as the paleoclimate cooled, or even in the late Eocene and Oligocene, after the globally tropical conditions of the late Paleocene and early Eocene.

The family Atelestidae is clearly a relict group whose diversity and distributions have been substantially culled by extinctions. *Atelestites* Grimaldi and Cumming, known from Lebanese amber, is the earliest representative of the family. Despite its primitive venation, the male terminalia suggest affinities to *Atelestus* Walker (Grimaldi and Cumming, 1999; Sinclair and Kirk-Spriggs, 2010). There are three living species of *Nemedina* Chandler (in Bulgaria, Spain, Turkey, Hungary, and Kazakhstan) (table 1), one species in Baltic amber (Sinclair and Arnaud, 2001), and five genera with nine species in Cretaceous ambers from Canada, Lebanon, and New Jersey

(Grimaldi and Cumming, 1999), as well as undescribed species in Burmese amber. Unlike Nemediinae, the Cretaceous *Alavesia* are quite similar to the living species, possessing virtually all the same synapomorphies of the genus, and it was not a rare group in the Burmese amber forest. Moreover, the distributions of the three other atelestid genera, *Acarteroptera* Collin, *Atelestus*, and *Meghyperus* Loew, in Chile, Eurasia, and western North America (table 1), fit the temperate relict pattern, and strongly suggests that there has been substantial extinction in these genera as well.

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