

# *Alavesia* Waters and Arillo—a Cretaceous-era genus discovered extant on the Brandberg Massif, Namibia (Diptera: Atelestidae)

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**Abstract.** Two new extant species of the fossil genus *Alavesia* Waters & Arillo (*A. brandbergensis* sp.n. and *A. daura* sp.n.) are described from the Brandberg Massif, Namibia. The genus is reassigned to the family Atelestidae (subfamily Atelestinae) on the basis of male terminalia (elongate gonocoxal apodemes, ventral apodemes, subapical surstylus), female terminalia (absence of tergum 10) and a three-articled stylus. This is the first record of Atelestidae from the Afrotropical Region. A genus-level phylogeny of the Atelestidae is resolved, in which *Alavesia* is the sister genus to the remaining genera of the Atelestinae. The biogeographic history of the genus is briefly discussed, as is the significance of this and other relict Diptera on the Brandberg.

## Introduction

Living fossils, being taxa that closely resemble fossil ancestors, have long fascinated biologists on account of their ancient history, apparent morphological stasis, and frequent geographic isolation. There are numerous and frequently cited examples of living fossils among the vertebrates, notably the coelacanth, lung fishes, tuatara and horseshoe crabs. Insect examples include the termite, *Mastotermes* Froggatt (Grimaldi & Engel, 2005), mymarommatid wasps and jurodid beetles.

We describe here the discovery of two extant species of the fossil dance fly genus *Alavesia* Waters and Arillo (Fig. 1), sampled on the Brandberg Massif, Namibia (21°13.5'S, 14°31.1'E) (Fig. 2). This series of extant species is clearly congeneric with *Alavesia*, on the basis of the distinct and broad lamellate postpedicel, three-articled stylus, and wing venation with a distinctive diminutive cell dm and divergent M<sub>1+2</sub> and M<sub>4</sub>.

Prior to its discovery on the Brandberg Massif, *Alavesia* was known only from Early to Late Cretaceous [112–89 Ma (million years ago)] amber inclusions. The genus was named originally for three specimens discovered in amber of Álava

(northern Spain) (Waters & Arillo, 1999), and subsequently an additional amber fossil species was described from El Caleyu (Spain) (Peñalver & Arillo, 2007) and an undescribed species is known from Burmese amber (Grimaldi *et al.*, 2002). The Brandberg has been highlighted previously as a refugium for living fossils by the discovery of the first living examples of the insect order Mantophasmatodea collected on the same expedition along with *Alavesia* in 2002 (Zompro *et al.*, 2003). Although numerous examples of present-day genera of flies are represented in Tertiary ambers (40–15 Ma), there are far fewer from Mesozoic fossils; such examples are mostly restricted to 'nematocerous' Diptera (Evenhuis, 1994). In the dance flies (Empidoidea), only one example is recorded (i.e. genus *Apalocnemis* Philippi), known from Santonian-aged (80–76 Ma) ambers of Canada (Grimaldi & Cumming, 1999). In all these cases, the extant genus was known initially from present-day species, and was subsequently identified in amber (e.g. the genus *Valseguya*) (Grimaldi & Engel, 2005), whereas *Alavesia* was based originally solely on fossil species.

*Alavesia* was tentatively assigned originally to the subfamily Ocydromiinae *sensu* Chvála 1983 by Waters & Arillo (1999). On the basis of these extant species and examination of the male and female terminalia, *Alavesia* is herein transferred from the family Hybotidae to the Atelestidae. This is the first record of Atelestidae from the Afrotropical Region.

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## Materials and methods

### Materials

Specimens were sampled using Malaise traps and yellow pans positioned over dry or episodic riverbeds at elevations of, or exceeding, 1750 m a.s.l. (above sea level), as part of a faunal inventory project undertaken in 1998 (Kirk-Spriggs & Marais, 2000) and in March 2002. These specimens were loaned from, or deposited in, the following institutions: Canadian National Collection of Insects, Ottawa, Canada (CNC); National Museum of Namibia, Windhoek, Namibia (NMNW).

All dissections were undertaken in glycerine, and tissues were cleared using hot 85% lactic acid. Terminology for adult structures principally follows that of McAlpine (1981), except in the case of the antenna, for which terms follow Stuckenberg (1999), and for wing venation, which follows Saigusa (2006) (as indicated in Fig. 4C). Homologies of the male terminalia follow those of Sinclair & Cumming (2006).

Label data for holotypes are cited exactly as they appear. A division slash (/) denotes the commencement of a new line; two division slashes (//), data on a further label. Additional information is included in [square] brackets.

### Cladistic analysis

Characters were scored for all six known genera of the Atelestidae and for three outgroup genera. A complete list of exemplars is provided in Table 1. Thirty-one characters were analysed in the cladistic analysis, including four multi-state characters (Table 2). All characters were treated as unordered, with multi-state characters considered as non-additive, and all characters were equally weighted. Character polarity was determined by rooting the tree with the three empidoid outgroups, which together were constrained to be paraphyletic in relation to the ingroup.

Parsimony analysis of the character state matrix (Table 3) was performed using the program PAUP\* version 4.0b10

(Swofford, 2002). A heuristic search with stepwise addition was implemented to find the most parsimonious trees using random addition sequence of taxa, tree-bisection-reconnection (TBR) branch swapping and 1000 random replications.

### *Alavesia* Waters & Arillo

(Figs 1, 3, 4)

*Alavesia* Waters & Arillo, 1999: 60.

Type-species *Alavesia*<sup>†</sup> *subiasi* Waters & Arillo, by original designation.

**Diagnosis.** This genus (e.g. Fig. 1) is readily differentiated from all other empidoid genera by the diminutive cell dm,  $M_{1+2}$  and  $M_4$  greater than half length of wing and widely divergent, postpedicel very long and lanceolate, stylus three-articled, legs with parallel rows of minute setulae.

**Re-description.** ♂. *Head*. Dichoptic, frons broad, divergent; eyes with sparse ommatrichia; inner margin near antennae with swallow notch. Ocellar triangle only slightly raised, ocellar bristles reduced. Frons broad, divergent, bearing some setulae. Antenna attached to middle of head; scape and pedicel subcylindrical, subequal in length; scape bare; pedicel with fringe of subapical setulae; postpedicel elongate, lanceolate, pubescent, tapered apically; stylus half to one-third length of postpedicel; arista-like stylus comprising three articles: two subcylindrical basal articles and elongate third article, bearing apical mechanoreceptor. Proboscis not dissected (inner components not examined). Length of proboscis, when exposed, about half length of eye height. *Thorax*. Prosternum broad, separate from proepisternum. Antepronotum lacking distinct setulae. Postpronotal lobe distinctly pronounced, bearing short stout setulae. Scutum strongly arcuate. Acrostichal setulae biserial; dorsocentral setulae similar to acrostichals, minute, irregular biserial, prescutellar bristles stout and long; 2 to 4 stout notopleural bristles; one stout postalar bristle. Scutellum with 2 to 4 marginal bristles. Laterotergite bare. Proepisternum with stout seta dorsal to coxa. *Legs*. Unmodified, of moderate length, with reduced setation. Fore coxae slightly longer than mid and hind coxae. Chaetotaxy forming distinct rows of setulae, mostly lacking prominent and outstanding bristles (except subapicals). Coxae with stout anterior and lateral setae. Fore and mid femora slightly swollen; hind femur more strongly swollen. Tibiae slender, subequal in length to femur; fore tibial gland absent; anteroapical and posteroapical combs absent on fore and hind tibiae, respectively; stout apical setae present. Tarsi, including hind first tarsomere, slender. Tarsal claws short; pulvilli pad-like. *Wing* (as in Fig. 4C). Hyaline, with fine microtrichia; short, stout basal costal seta present. Stigma absent. C terminating at or slightly beyond  $M_{1+2}$ ; Sc evanescent, ending well short of or slightly before costal margin; vein Rs arising near to or distant from level of humeral crossvein;  $R_1$  equally thickened along its entire length, ending beyond mid-length of wing;  $R_{2+3}$  shortly curved to C apically, ending closer to apex of

**Table 1.** List of exemplar taxa.

Taxon	Collection locality
<i>Acarteroptera recta</i> Collin	Las Trancas, Chile
<i>Alavesia</i> spp.	(See data in section below)
<i>Atelestus pulicarius</i> Walker	Slindon, West Sussex, England
<i>Meghyperus occidentis</i> (Coquillett)	Snow Creek, California, U.S.A.
<i>Meghyperus sudeticus</i> Loew	Zvenigorod, Russia
<i>Nemedina zaitsevi</i> Sinclair and Shamshev	Senek, Kazakhstan
Outgroup	
<i>Acarterus unicolor</i> Loew	Nieuwoudtville, Cape Prov., South Africa
<i>Iteaphila macquarti</i> Zetterstedt	Abisko, Sweden
<i>Empidadelpha propria</i> Collin	Lake Moana and Glitterburn, New Zealand

**Table 2.** Characters used in the cladistic analysis of the Atelestidae.

1.	<i>Male eye contiguity</i> : holoptic (0); dichoptic (1)
2.	<i>Scape</i> : setose (0); bare (1)
3.	<i>Articulation beyond postpedicel (excluding apical receptor)</i> : two (0); three (1)
4.	<i>Postpedicel shape length</i> : tapered and elongate, equal to or greater than length of apical stylus (0); less than 2× length of stylus, ovate (1)
5.	<i>Epipharyngeal blades</i> : present (0); absent (1)
6.	<i>Male hind tibia shape</i> : slender, apex subequal to basal width (0); clavate, apex twice basal width (1)
7.	<i>Male hind first tarsomere shape</i> : slender, only slightly wider than width of remaining tarsomeres (0); dilated, more than twice width of remaining tarsomeres (1)
8.	<i>Costa termination</i> : circumambient (0); terminating at $M_{1+2}$ (1); terminating at $R_5$ (2)
9.	<i>Subcosta</i> : complete (0); incomplete (1)
10.	$R_{4+5}$ : branched (0); unbranched (1)
11.	<i>Cell br</i> : unmodified (0); modified by inclusion of $R_s$ (1)
12.	<i>Cell dm</i> : present (0); absent (1)
13.	<i>Cell dm size</i> : subequal to or larger than basal cells (0); shorter than basal cells (1)
14.	$M_{1+2}$ : branched (0); unbranched (1)
15.	$M_{1+2}$ branched distally: absent (0); present (1)
16.	<i>CuA curvature</i> : truncate (0); recurved (1); convex (2)
17.	<i>Alula type</i> : developed (0); reduced or absent (1)
18.	<i>Eighth abdominal tergum shape</i> : narrow or wide, but not produced posterolaterally (0); produced posterolaterally forming L-shaped sclerite in lateral view (1)
19.	<i>Ventral apodemes</i> : absent (0); paired (1); single (2)
20.	<i>Ejaculatory apodeme</i> : articulated with base of phallus (0); continuous with phallus (1)
21.	<i>Postgonites</i> : present (0); absent (1)
22.	<i>Postgonite form</i> : not sickle-shaped (0); sickle-shaped (1)
23.	<i>Gonocoxal apodemes</i> : short (0); greatly lengthened (1)
24.	<i>Hypandrium length</i> : long (0); short (1)
25.	<i>Epandrium shape</i> : U-shaped (0); semi-circular (1)
26.	<i>Epandrium apex</i> : tapered (0); rounded (1)
27.	<i>Surstylar position</i> : apical (0); subapical (1); subapical and internal (2)
28.	<i>Female tergum 10</i> : present (0); absent (1)
29.	<i>Female postabdomen</i> : telescopic (0); retracted into segment 4 or 5 (1)
30.	<i>Female postabdominal terga 6 and 7</i> : rectangular (0); paired and slender (1)
31.	<i>Spermathecal duct</i> : unpigmented (0); pigmented at termination to receptacle (1)

**Table 3.** Character state matrix for cladistic analysis of the Atelestidae.

Taxon	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	
<i>Acarteroptera recta</i>	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	2	1	1	1	0	0	1	1	1	1	1	2	1	1	0	0	
<i>Alavesia</i> spp.	1	1	1	0	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	1	0	
<i>Atelestus pulicarius</i>	0	1	0	1	1	1	0	1	1	1	0	1	–	1	0	2	1	1	0	1	0	0	1	1	0	0	2	1	1	1	0	
<i>Meghyperus occidentis</i>	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	2	1	1	1	0	0	1	1	1	1	1	2	1	1	0	1	
<i>Meghyperus sudeticus</i>	0	1	0	1	1	1	1	1	1	1	0	0	0	0	1	2	1	1	1	0	0	1	1	1	1	1	2	1	1	0	1	
<i>Nemedina zaitsevi</i>	0	1	0	0	1	0	0	1	1	1	1	1	–	1	0	2	0	0	0	0	1	–	1	1	0	0	0	1	0	0	0	
<i>Acarterus unicolor</i>	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Iteaphila macquarti</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Empidadelpha propria</i>	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Inapplicable characters are indicated by '–'.

$R_1$  then  $R_{4+5}$ ;  $R_{4+5}$  unbranched, slightly divergent to parallel to  $M_{1+2}$ ; cell dm very small, nearly half length of basal cells, emitting two veins  $M_{1+2}$  and  $M_4$  ( $=CuA_1$ );  $M_{1+2}$  and  $M_4$  strongly divergent; CuA straight; apex of cell cua ( $=cup$  or anal cell) truncate, length of cell subequal to cell bm; anal vein (CuP + CuA) distinctly curved subapically, arched to wing margin. Anal lobe broad, angle less than  $90^\circ$ ; alula reduced. *Abdomen*. Sclerites clothed in distinct short setae;

lacking longer posteromarginal setae. Segments 1–5 broad, remaining segments progressively narrowed. Tergum 8 very narrow, strap-like, greatly prolonged laterally with triangular dorsomedial posterior extension. Sternum 8 greatly reduced, forming pair of slender sclerites, weakened and partially folded near mid-length; longer than sternum 7. Abdominal plaques present (visible in macerated specimens). *Terminalia* (as in Fig. 3). Symmetrical, unrotated, held obliquely to abdomen



**Fig. 1.** *Alavesia daura* sp.n., female habitus. Scale bar: 0.5 mm. (Photograph: Henri Goulet).

in dried specimens. Cercus small, truncate apically in lateral view, oval in posterior view and weakly sclerotized; hypoproct subtriangular, microsetose. Epandrium U-shaped with dorsal bridge anterior to cerci. Surstylus subapical. Hypandrium short, divided into slender strip-like sclerites; anterolateral corner extending to articulate with epandrium. Postgonites present, cap-like, joined medially. Paired ventral apodemes extending anteriorly from postgonites. Gonocoxal apodeme with slender and greatly lengthened rod-like process, longer



**Fig. 2.** Mason Shelter on the plateau of the Brandberg Massif, Namibia, type-locality of *Alavesia brandbergensis* sp.n. and *A. daura* sp.n. Note the presence of ephemeral pools following periods of precipitation. (Photograph: Darren Mann).

than hypandrium; narrow in ventral view. Phallus tube-like, arched posteriorly. Ejaculatory apodeme articulated at base of phallus, posterior end broad and swollen.

♀. Similar to male, except in the following respects: Postpedicel shorter, subequal to apical stylus. Preabdomen well sclerotized, terga nearly twice as broad as long. Postabdomen (as in Fig. 4A,B) weakly sclerotized, retracted into segment 5. Intersegmental membrane posterior to tergum 5 broad, nearly subequal in length to tergum 5, with pair of pigmental vittae. Terga 6 and 7 reduced to pair of slender sclerites, connected anteriorly. Sterna 6 and 7 rectangular, one-third width of sternum 5. Tergum 8 square-shaped; sternum 8 longer than tergum, reduced to pair of slender sclerites. Tergum 10 absent. Cerci broad, pubescent, almost twice as long as wide. Spermathecal receptacle spherical, darkly pigmented.

#### *Alavesia brandbergensis* sp.n

(Fig. 3)

*Types.* Holotype, ♂, 'Namibia: BRANDBERG/Mason Shelter/21°04'39'S 14°05'43'E/05–14.iii.2002, 1750 m/A.H. Kirk-Spriggs & E./Marais/Malaise trap riverbed [printed, white card]/[HOLOTYPE/*Alavesia*/brandbergensis/Sinclair & Kirk-Spriggs [printed, red card]]' (NMNW). Paratype ♂, same data as holotype (CNC).

*Etymology.* The specific epithet *brandbergensis* refers to the type-locality: the Brandberg Massif, Namibia.

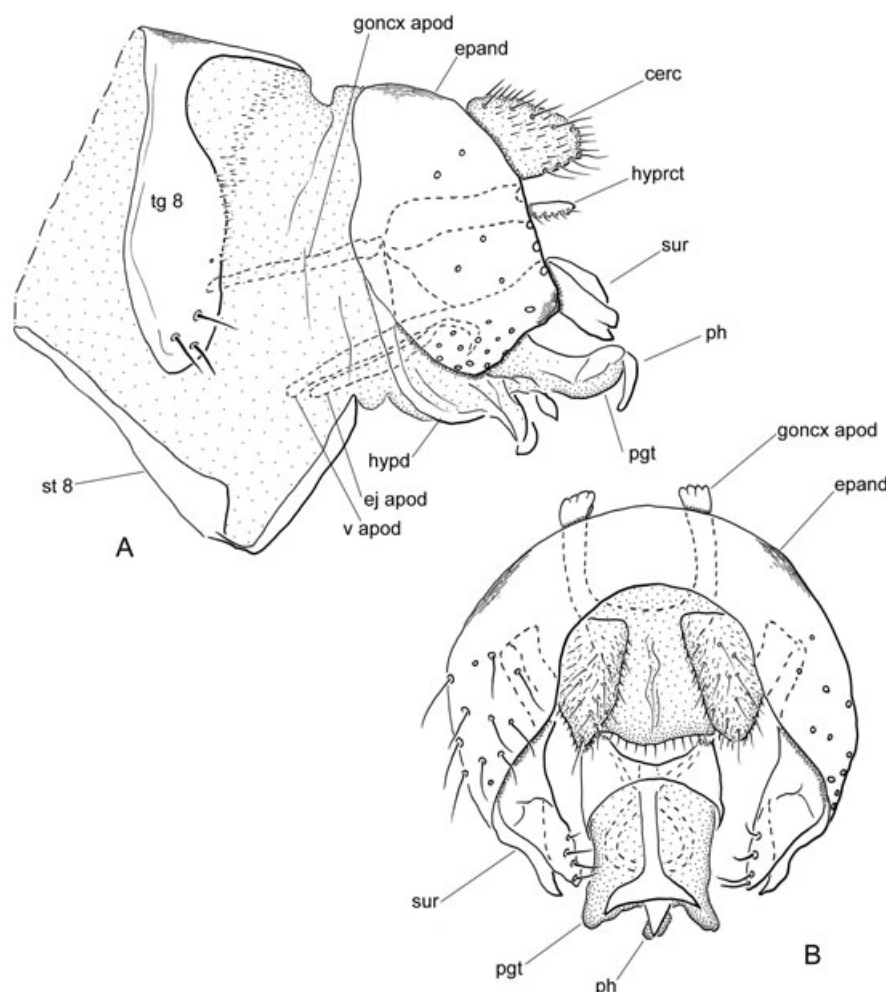
*Recognition.* This species is characterized by the pale yellow scape and pedicel, postpedicel subequal to length of scutum, and thorax and legs yellow.

*Description.* ♂. Scape and pedicel pale yellow, postpedicel brownish. Postpedicel greatly elongate, subequal to length of scutum; stylus subequal to length of postpedicel. Scutum and pleura yellow. Coxae, femora and tibiae yellow, hind tibia and tarsi of all legs increasingly dark apically. Halter knob dark, stem pale. Wing length: 2.2 mm.

Abdominal terga brown, sterna pale, yellowish. Terminalia (Fig. 3): cercus thinly sclerotized, setose; hypoproct with setulae. Epandrium U-shaped with broad dorsal bridge anterior to cerci; setae concentrated along ventrolateral margin. Surstylus subapical, not internal; subdivided into pair of pointed lobes; dorsal lobe with 3 to 4 setae along inner margin. Hypandrium divided into slender strip-like sclerites; anterolateral corner extending to articulate with epandrium; apex hook-like. Postgonites present, joined medially, membranous dorsally; paired ventral apodemes extending anteriorly from postgonites. Gonocoxal apodeme with slender and greatly lengthened rod-like process, longer than hypandrium; narrow in ventral view. Phallus tube-like, apex arched ventrally; ejaculatory apodeme articulated at base of phallus, posterior end broad and swollen.

♀. Unknown.





**Fig. 3.** *Alavesia brandbergensis* sp.n., male terminalia. (A) Lateral view; (B) dorsal view. Abbreviations: cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; goncx apod, gonocoxal apodeme; hypd, hypandrium; hypcrt, hypoproct; pgt, postgonite; ph, phallus; st, sternum; sur, surstylus; tg, tergum; v apod, ventral apodeme.

### *Alavesia daura* sp.n

(Figs 1, 4)

**Types.** Holotype, ♂, 'Namibia: BRANDBERG/Wasserfall-fäche at: 21°13.5'S 14°31.1'E/1980 m, 10–12.xi.1998/A.H. Kirk-Spriggs/10 yellow pan traps river [printed, white card]// HOLOTYPE/*Alavesia/daura*/Sinclair & Kirk-Spriggs [printed, red card]' (NMNW). Paratype ♀, Namibia, Brandberg, Mason Shelter, 21°04'39'S 14°05'43'E, 5–14.iii.2002, 1750 m, A.H. Kirk-Spriggs & E. Marais, MT [=Malaise trap] riverbed (NMNW).

**Etymology.** The specific epithet *daura* is derived from the indigenous Damara name *Dâures*, meaning 'burning mountain' (Kinahan, 2000).

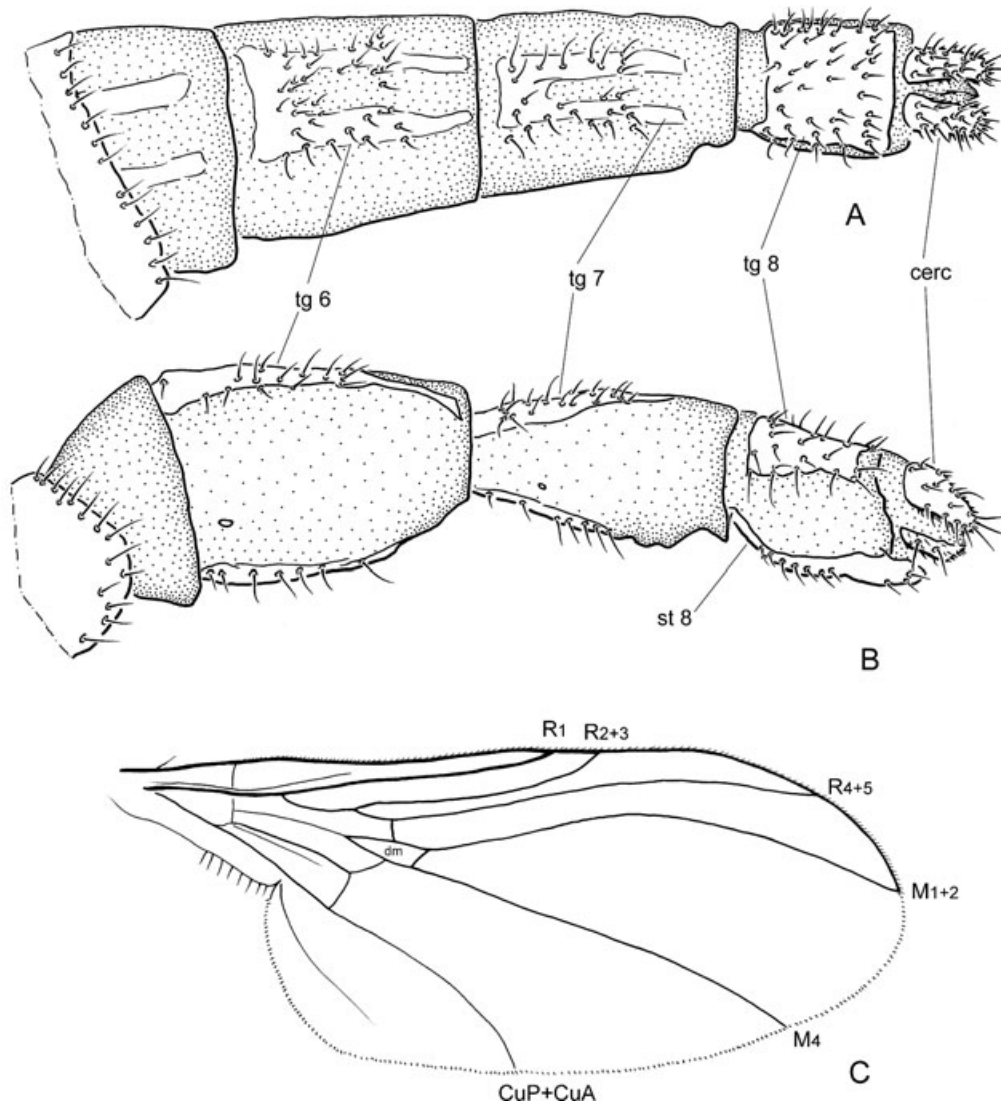
**Recognition.** This species is characterized by the dark antenna, male postpedicel shorter than length of scutum, thorax dark, and apex of hind femur and hind tibia (except base) dark.

**Description.** ♂. Antenna brown; postpedicel elongate, longer than height of head, more than twice length of apical stylus. Scutum and pleura dark brown, apex of postpronotal lobe slightly pale. Coxae, fore and mid femora and tibiae yellow, tarsi of all legs brown; apical third of hind femur dark; hind tibia brown, except extreme base pale. Halter knob predominantly pale, stem darker near base. Wing length: 1.9 mm.

Abdominal terga brown, sterna pale yellowish. Terminalia: lost in preparation (pencil sketch very similar to *A. brandbergensis* sp.n.).

Female similar to male except in the following respects: postpedicel shorter, stylus subequal to length of postpedicel. Postabdomen (Fig. 4A,B) as described under genus.

**Remarks.** The 1998 specimen was not available for the original provisional list of Empidoidea from the Brandberg Massif (Sinclair, 2000). The male terminalia unfortunately was lost during preparation.



**Fig. 4.** *Alavesia daura* sp.n., female terminalia. (A) Dorsal view; (B) lateral view; (C) wing. Abbreviations: cerc, cercus; CuP + CuA, anterior and posterior branches of cubitus; dm, discal medial; M, medial; R, radius; st, sternum; tg, tergum.

#### Key to extant species of *Alavesia*

1. Scape and pedicel pale yellow; male postpedicel subequal to length of scutum; thorax and legs yellow ..... *A. brandbergensis* sp.n.  
 –Antenna dark; male postpedicel shorter than length of scutum; thorax dark, apex of hind femur and hind tibia (except base) dark ..... *A. daura* sp.n.

#### Discussion

##### Phenology

Nothing is currently known regarding the biology of *Alavesia*. Specimens were sampled using a Townes-style

Malaise trap and yellow pans positioned over riverbeds at two localities on the upland plateau of the Brandberg, namely Mason Shelter and Wasserfallfäche. Sampling at Mason Shelter took place during and following periods of prolonged precipitation. As a result, the normally dry riverbeds sampled flowed for a period and were later filled with episodic pools of standing water (Fig. 2). Although sampling took place at Wasserfallfäche during a dry period, the sampling site was immediately below a series of granitic episodic pools, which contained standing water at the time. As extensive sampling elsewhere on the Brandberg did not yield additional specimens, it is likely that adult flight activity is highly seasonal and triggered by prolonged precipitation events, especially by periods in which ephemeral rivers are in spate and pools of standing water result.

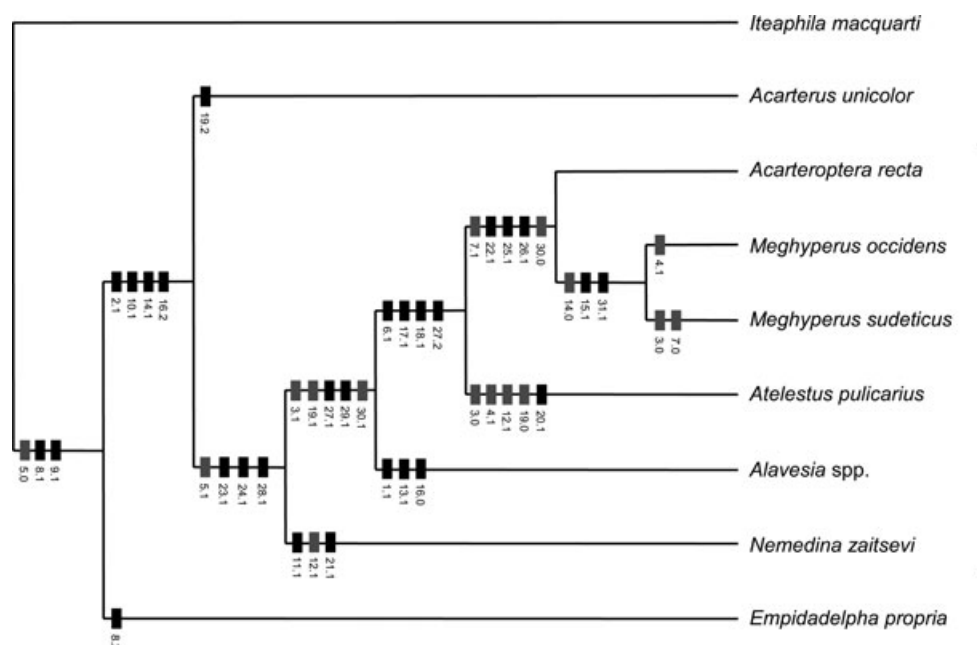
Hennig (1970) erected the subfamily Atelestinae for a group of three genera, namely: *Acarteroptera* Collin, *Atelestus* Walker, and *Meghyperus* Loew, assigned to the Ocydromioinea of the Empididae *sensu lato*. This lineage was elevated to familial status by Chvála (1983) and was regarded as the sister group to the Cyclorrhapha (Wiegmann *et al.*, 1993, for discussion). Currently the Atelestidae is considered either as the sister group to the remaining Empidoidea (Collins & Wiegmann, 2002; Moulton & Wiegmann, 2004, 2007), or as sister group to the Hybotidae (Sinclair & Cumming, 2006).

by Grimaldi & Cumming (1999)] (Sinclair & Cumming, 2006).

Wiegmann *et al.* (1993) tentatively proposed that the genus *Meghyperus* was paraphyletic in relation to *Acarteroptera*, where in nearly all trees illustrated in this work *M. occidentis* + *A. lacinia* and *M. sudeticus* + *Atelestus* were sister groups. The former group was supported on the basis of a three-articled stylus and the plesiomorphically prolonged postpedicel. In subsequent studies of molecular phylogenies, these relationships were either weakly supported or not congruent, or the taxon sampling was not sufficient to make comparisons (Collins & Wiegmann, 2002; Moulton & Wiegmann, 2004, 2007). Moulton & Wiegmann (2007) recommended that the Nearctic species of *Meghyperus* be transferred to *Acarteroptera* in order better to define genera.

In order to confirm placement of *Alavesia* within the Atelestidae and to determine its phylogenetic relationship within the family, a cladistic analysis was performed on the character state matrix (Table 2), which generated a single most parsimonious tree (Fig. 5), with tree length = 44; CI = 0.796; RI = 0.796; RC = 0.633. Many of the characters initially used by Wiegmann *et al.* (1993) were included, but these have been substantially redefined and definitions updated [Table 2 and see Sinclair (1995: 671) and Sinclair & Cumming (2006: 18) for discussion of the shortcomings in their scorings and characters].

The results presented here indicate that *Nemedina* should be assigned as sister group to the remaining extant genera of the Atelestidae and represents the subfamily Nemedininae. *Alavesia* is sister group to the remaining genera of the



**Fig. 5.** Single most parsimonious cladogram produced by analysis of the data matrix (Table 3). Character distributions are shown by black hash marks for uniquely derived states and by grey hash marks for homoplasious states. Ingroup (Atelestidae) delimited by bracket.

Atelestinae, of which the subfamily is defined by the presence of a three-articled stylus (char. 3.1; secondarily lost in some *Meghyperus* and *Atelestus*), the presence of paired ventral apodemes (char. 19.1), surstylus subapical (char. 27.1), and female postabdomen retracted into segment 4 or 5 (char. 29.1). *Acarteroptera* and *Meghyperus* are sister genera by the presence of a dilated male hind first tarsomere (char. 7.1; secondarily lost in *M. sudeticus*), postgonite sickle-shaped (char. 22.1), epandrium semi-circular in shape (char. 25.1), and apex of epandrial lamellae rounded (char. 26.1). *Meghyperus* appears to be monophyletic (although based on a limited sample size), contrary to the view expressed by Wiegmann *et al.* (1993), based on the apically branched  $M_{1+2}$  (char. 15.1) and the pigmented spermathecal duct at the base of the receptacle (char. 31.1).

#### Fossil genera

*Atelestites senectus* Grimaldi & Cumming appears to be the stem group to *Acarteroptera*, *Atelestus* and *Meghyperus*, owing to its slender legs, and subapical and internal surstyli (Grimaldi & Cumming, 1999). This Lebanese amber fossil (Lower Cretaceous) bears a tripartite apex of the phallus (+postgonites?), which is similar to *Atelestus* and in some sense also to *Alavesia*. The form of the epandrium is similar to these two last-mentioned genera and not as derived as in *Acarteroptera* and *Meghyperus*, in which the epandrium is virtually semi-circular. *Atelestites*, however, has cell dm emitting three veins, a character not found in present-day Atelestidae.

*Dianafranksia fisheri* Coram, Jarzemboski & Mostovski has further been assigned to the Atelestidae and is based on a wing impression from Lower Cretaceous deposits in England (Coram *et al.*, 2000). The general appearance of the wing, with its stalked  $M_{1+2}$  and elongate anal cell, suggests that this species is an atelestine, possibly related to *Meghyperus*.

#### Biogeography

The Brandberg comprises a massive inselberg 650 km<sup>2</sup> in size, rising 1.8 km above the Namib peneplain. It consists of a granitic ring complex, which pre-dates the break-up of Gondwana and thus also the change in continental climatic and environmental conditions that prevailed during the Plio-Pleistocene (Kirk-Spriggs & Marais, 2000; Kirk-Spriggs & Stuckenberg, 2009). The extensive undulating upland plateau (c. 2000 m a.s.l.) exhibits a winter rainfall climate and associated flora. The significance of the Brandberg as a refugium for living fossils has been highlighted by the discovery of the first living examples of Mantophasmatodea (Zompro *et al.*, 2003). Gondwanan elements have been identified in the coleopterous family Cerambycidae (Adlbauer, 2000), and notable endemic species of Diptera on the Brandberg include the dolichopodid *Schistostoma brandbergense* (Shamshev &

Sinclair, 2006), the vermilionid *Leptyoma* (*Perianthomyia*) *monticola* (Stuckenberg, 2000), and the mythicomyiid genus *Hesychastes* (Evenhuis, 2001) and species *Psiloderoides dauresensis* (Kirk-Spriggs & Evenhuis, 2008). The discovery of *Alavesia* further serves to highlight the evolutionary significance of the Brandberg Massif. The thorny lacewings (Neuroptera: Rhachiberothidae), although not currently recorded from the Brandberg, have a similar distribution to *Alavesia*, restricted today to sub-Saharan Africa, but were widespread in the Cretaceous (Grimaldi & Engel, 2005).

The presence of fossil taxa of *Alavesia* in Spain and Burma and of extant species in southern Africa presents an interesting biogeographic scenario. This vicariant Laurasian–Gondwanan pattern suggests that *Alavesia* originated in an earlier geologic time in megacontinental Pangaea. The Burmese amber paleoenvironment is considered to be distinctly tropical (Grimaldi *et al.*, 2002), and climate change during the Tertiary, with colder temperatures in areas of low latitude, probably led to the extinction of these species of Laurasian origin.

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