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Two new genera of Cretaceous dustywings in amber from northern Myanmar (Neuroptera: Coniopterygidae)

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Abstract. Two new genera and species are added to the fauna of dustywings (Coniopterygidae) preserved in Upper Cretaceous (earliest Cenomanian) amber of northern Myanmar, doubling the described diversity from this deposit. One genus is of the subfamily Aleuropteryginae and described as ***Achlyoconis heptatrichia*** Engel, new genus and species. This species is noteworthy for the infumate and patterned wings and unique presence of seven prominent setae positioned on thickenings occurring along the length of the forewing media. ***Paranimboa litotes*** Engel, new genus and species, is representative of the subfamily Coniopteryginae and distinctive among Mesozoic groups for the unbranched Rs, among other traits. In addition, a peculiar larva preserved alongside the holotype of *P. litotes* is described. While having a prothoracic and head form similar to aleuropterygines as well as a labial palpus with only two palpomeres, diagnostic for Coniopterygidae, the antenna of the larva bears four articles rather than the two present in crown-group dustywings. A revised key to the genera of Cretaceous Coniopterygidae is provided.

INTRODUCTION

Coniopterygidae are the morphological outliers of the Neuroptera. Commonly referred to as dustywings owing to a distinctive waxy covering, these tiny insects have a characteristically reduced wing venation compared to their larger planipennian counterparts. Presently, there are 571 known species distributed throughout the

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world (Meinander, 1990; Sziráki, 2011; and various species described up to present), and where known they are predators of small arthropods such as mites, scale insects, or aphids. During the last quarter of a century, Coniopterygidae have been considered to be a comparatively derived family among the Hemerobiiformia (*e.g.*, Aspöck, 1992; Aspöck *et al*., 2001; Haring & Aspöck, 2004; Aspöck & Aspöck, 2008; Zimmermann *et al*., 2009). However, more recent investigations combining morphological and molecular data have largely resurrected the earlier notion of Withycombe (1924) that the family is more basal, indeed perhaps the most basal, among extant neuropteran families (Winterton *et al*., 2010). Such a phylogenetic placement implies considerable antiquity within the coniopterygoid lineage, albeit not necessarily so for crown-group coniopterygids or even dustywings as we circumscribe them based on extant species. Indeed, there were likely to have been any number of early stem-groups to the Coniopterygidae that were not as diminutive or concomitantly reduced in terms of wing venation. From available fossils that can be assigned to the Coniopterygidae as we conceive them, the family extends at least to the latest Jurassic (Meinander, 1975; Grimaldi & Engel, 2005). The Jurassic record for Coniopterygidae is based on an incomplete compression from Karatau in Kazakhstan, and while the diagnosis for the taxon is challenging, its placement as a dustywing is clear (Meinander, 1975). All remaining Mesozoic occurrences for the family are from the Cretaceous and found in amber, perhaps not surprising given the small size and comparatively soft bodies of dustywings (Table 1). Coniopterygidae are documented from most major amber deposits and undescribed taxa are known from the latest Albian of Spain (pers. obs.), and are likely to be recovered eventually from the fossiliferous Cretaceous resins of Canada and Alaska. Interestingly, the characteristic 'dusty' covering so apparent in modern species is rarely preserved in Cretaceous specimens, likely the result of its augmentation or dissolution in the resin and during diagenesis.

Two distinctive new genera of dustywings are here characterized from well-preserved males in the Upper Cretaceous amber of Myanmar, building upon earlier accounts of the fauna (Engel, 2004; Engel & Grimaldi, 2008). The two taxa considered are representative of the two principal subfamilies already recorded from the Cretaceous (the third subfamily, Brucheiserinae, is unknown as fossils). Although the attribution to subfamily of some Cretaceous dustywings is somewhat suspect owing to a blurring of distinctions between Coniopteryginae and Aleuropteryginae, the two taxa described herein correspond comparatively well to these groups except in the proximity of the origin of Rs and the relative positions of M and Cu_1 in the hind wing. These characters are fairly quantitative and tend to approximate each other in certain taxa, seemingly undermining their utility. The species are described, figured, and a revised key to the genera of Cretaceous Coniopterygidae is provided.

MATERIAL AND METHODS

Two well-preserved, male dustywings were identified among thousands of inclusions within Burmese amber in the James S. Zigras Collection, which through an agreement will be permanently deposited in the American Museum of Natural History, New York. The age and geological setting for the amber-bearing deposits of the Hukawng Valley are overviewed by Grimaldi *et al*. (2002), Cruickshank & Ko (2003), and Shi *et al*. (2012), the last of which has established a radiometric age estimate of approximately 98 Ma (or earliest Cenomanian, at the very start of the Late Cretaceous).

External morphological terminology used for the descriptions is adapted from that

Table 1. Described Mesozoic Coniopterygidae (updated from Engel & Grimaldi, 2007, 2008); daggers indicate extinct taxa; records come from amber deposits unless marked as compression fossils (*).

JURASSIC**	
†*Juraconiopteryx* Meinander, 1975	
†*J. zherichini* Meinander, 1975	Kazakhstan (Oxfordian)*
CRETACEOUS	
†*Achlyoconis* Engel, n. gen.	
†*A. heptatrichia* Engel, n. sp.	Myanmar (Cenomanian)
†*Alboconis* Nel *et al*., 2005	
†*A. cretacica* Nel *et al*., 2005	Archingeay (Albian)
†*Apoglaesoconis* Grimaldi, 2000	
†*A. ackermani* Grimaldi, 2000	New Jersey (Turonian)
†*A. cherylae* Engel, 2002	New Jersey (Turonian)
†*A. luzzii* Grimaldi, 2000	New Jersey (Turonian)
†*A. swolenskyi* Grimaldi, 2000	New Jersey (Turonian)
†*Garnaconis* Perrichot & Nel in Perrichot *et al*., 2014	
†*G. dupeorum* Perrichot & Nel in Perrichot *et al*., 2014	Vendée (Santonian)
†*Glaesoconis* Meinander, 1975	
†*G. baliopteryx* Engel, 2004	Myanmar (Cenomanian)
†*G. cretica* Meinander, 1975	Taimyr (Santonian)
†*G. nearctica* Grimaldi, 2000	New Jersey (Turonian)
†*Libanoconis* Engel, 2002	
†*L. fadiacra* (Whalley, 1980)	Lebanon (Barremian)
†*Libanosemidalis* Azar *et al*., 2000	
†*L. hammanaensis* Azar *et al*., 2000	Lebanon (Barremian)
†*Paranimboa* Engel, n. gen.	
†*P. litotes* Engel, n. sp.	Myanmar (Cenomanian)
†*Phthanoconis* Engel, 2004	
†*P. burmitica* Engel, 2004	Myanmar (Cenomanian)

** Although Enderlein (1909) considered *Archiconiopteryx liasina* (Handlirsch) to be a Liassic dustywing, it is actually a sternorrhynchan as Handlirsch (1906) had asserted (Ansorge, 1996).

outlined by Meinander (1972), with numbers preceding abbreviations for longitudinal sectors indicating the particular abscissa (numbered from basal to apical). The apical portion of Sc_2 is fused to that of R_1, the latter seemingly terminating at or shortly beyond this fusion and prior to the wing margin (Withycombe, 1922). Thus, it is perhaps more appropriate to designate what is commonly referred to as the apical abscissa of Sc_2 as 'Sc_2+R_1'. However, pending more thoroughly elaborations of the course of the longitudinal sectors and vein identities across Coniopterygidae and all Neuroptera, the current standard terms are applied. The one exception pertains to the branches of Rs — these are considered simply as R_{2+3} and R_{4+5} (as is typical for Coniopterygidae, rather than as Rs_{1+2} and Rs_{3+4}, thereby easing comparison with other treatments of fossil dustywings), although prior to their separation the stem is simply denoted as Rs rather than as 'R_{2-5}'. Nonetheless, all of these branches are of the radial sector, so crossveins from these branches are considered collectively to be the rs-m series rather than simply 'r-m' (r-m is here reserved for crossveins between the stem of R and M). Microphotographs were taken with a Canon 7D digital camera and illuminated with a Xenon flash. Specimens were examined with an Olympus SZX-12 stereomicroscope and measurements were taken with the aid of an ocular micrometer.

SYSTEMATIC PALEONTOLOGY

Family Coniopterygidae Burmeister
Subfamily Aleuropteryginae Enderlein
Tribe Fontenelleini Carpentier & Lestage

Achlyoconis Engel, new genus

ZooBank: urn:lsid:zoobank.org:act:EFBD3231-BA4C-4A79-BC7E-B22FB5DD3FD8

TYPE SPECIES: *Achlyoconis heptatrichia* Engel, new species.

DIAGNOSIS: Antenna 27-articled (with 25 flagellomeres); scape about twice as long as wide. Forewing comparatively narrow; Sc_2 not curved anteriorly toward Sc_1; proximally R and M abut briefly but do not fuse; origin of Rs near wing midlength; Rs forked, with sc-rs meeting R_{2+3}; 2rs-m meeting R_{4+5} (not stem of Rs); $1R_{4+5}$ apically kinked; $2R_{4+5}$ superficially resembling branch of M; M with numerous distinctive thickenings bearing specialized setae (seven in total), series running proximally to near first branching in M; M trifurcate (three-branched: M_1, M_2, and M_{3+4}); Cu forked near wing base; separation between Cu_1 and Cu_2 on wing margin nearly twice that of marginal separation between M_{3+4} and Cu_1; cu_1-cu_2 present; two cu_2-a_1 crossveins; a_1-a_2 present. Hind wing Sc proximally with series of small, hamuli-like setae extending to slightly beyond tangent with Rs origin; sc-rs meeting R_{2+3} (rather than at or proximal to Rs fork); Rs origin near basal quarter of wing length; M and Cu parallel and separated by distinct membrane. Wing membranes hyaline, uniformly infumate, and with pattern of pigmented spots in forewing. Abdominal plicaturae present on segments 2–6.

ETYMOLOGY: The new generic name is a combination of the Greek terms *achlyos* (meaning, "darkness"; an allusion to the infumate wings) and *konis* (meaning, "dust"). The gender of the name is feminine.

Achlyoconis heptatrichia Engel, new species

ZooBank: urn:lsid:zoobank.org:act:8B9FFD60-B0C3-4638-B2A0-8CF9CFCC4FFB

(Figs. 1–2)

DIAGNOSIS: As for the genus (*vide supra*).

DESCRIPTION: ♂: Total length approximately 2.28 mm (as preserved); integument dark brown. Head longer than wide, with prominent compound eyes and narrow gena; frons well-sclerotized between antennal insertions; vertex prominent, domed, with sparse setae. Antenna with scape and pedicel stouter than flagellomeres, scape distinctly longer than pedicel, pedicel about as long as wide; flagellomeres each about as long as wide or slightly longer; first flagellomere no longer than second flagellomere; flagellomeres with numerous, minute, suberect setae. Terminal maxillary palpomere elongate hatchet-shaped, much longer and broader than preceding palpomeres; terminal labial palpomere elongate conical in shape. Legs slender; profemur shorter than and scarcely more swollen than meso- and metafemora; protibia shorter than meso- and metatibiae; tarsi pentamerous; basitarsus longest tarsomere, about as long as combined lengths of remaining tarsomeres; penultimate tarsomere (tarsomere IV) apically extended ventrally and bilobed; pretarsal claws short, simple; arolium absent. Abdomen large, broad, greatly tapering to narrow apical segments; plicaturae present on segments 2–6, particularly prominent on segments 2–4; broad ectoproct and short, circular gonocoxites IX; tergum X sclerotized and slightly projecting medi-

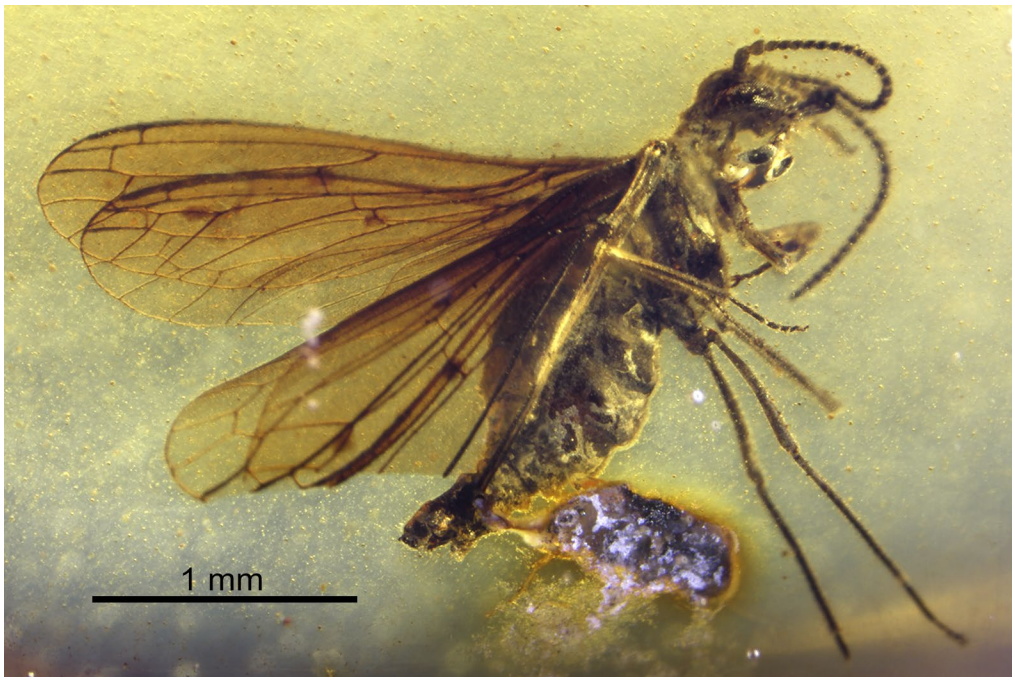

Figure 1. Holotype (AMNH JZC Bu-50) of *Achlyoconis heptatrichia*, new genus and species, in mid-Cretaceous amber from northern Myanmar.

ally; sternum IX arched medially; hypandrium narrow, slightly extended medially, with shallow medioapical concavity; gonarcus thin, apically sinuate; entoprocessus comparatively broad and short and medially meeting short penal sclerite.

Forewing length 2.43 mm, maximal width 0.93 mm; membrane hyaline, darkly infumate throughout, with pigmented spots located proximally around M_{1+2}, slightly distad M_{1+2}/M_{3+4} fork, around anterior portion of rs-m at contact with Rs, and around cu_1-cu_2; venation depicted in figure 2; two basal c-sc crossveins (= subcostal veinlets) in costal space, with 2c-sc only slightly distad divergence of stem of R; Sc largely parallel to costal margin; $1Sc_2$ basad sc-rs, separated by slightly more than $1Sc_2$ length; apical part of Sc_1 slightly arching toward $2Sc_2$, $2Sc_2$ straight; sc-rs contacting R_{2+3} distance beyond R_{2+3}/R_{4+5} fork less than sc-rs length; origin of Rs slightly proximal of wing midlength; Rs bifurcate apically; R_{2+3} extending apically from fork, $1R_{4+5}$ extending posteriorly, then kinked apically before meeting 2rs-m; two rs-m crossveins present; 1rs-m near wing midlength, posteriorly bordering specialized thickening in M; 2rs-m ($2r_{4+5}$-m_1) short, less than one-half length 1rs-m; stem of M briefly contacting stem of R near base of R, then diverging (obliquely) posteriorly to first thickening in M; M with series of seven thickenings bearing specialized setae, proximal four before 2m-cu_1, remaining three between 2m-cu_1 and M_{1+2}/M_{3+4} fork; M trifurcate, branching into M_{1+2} and M_{3+4} slightly distad apicalmost setal thickening in M, and M_1/M_2 fork situated slightly before transverse tangent with $1Sc_2$; M_1 connected to R_{4+5} by 2rs-m; M_1, M_2, and M_{3+4} rather evenly spaced along wing margin; M_{3+4} closer to apical termination of Cu_1 than to M_2; two m-cu crossveins; 1m-cu immediately proximal to R-M contact and Cu_1/Cu_2 divergence; 2m-cu (2m-cu_1) near wing midlength; Cu_1/Cu_2 fork near wing base, slightly basad R-M contact; one cu_1-cu_2 crossvein present, slightly basad and shorter than 2m-cu_1; two short, proximal cu_2-a_1 crossveins, first shortly beyond origin Cu_2,

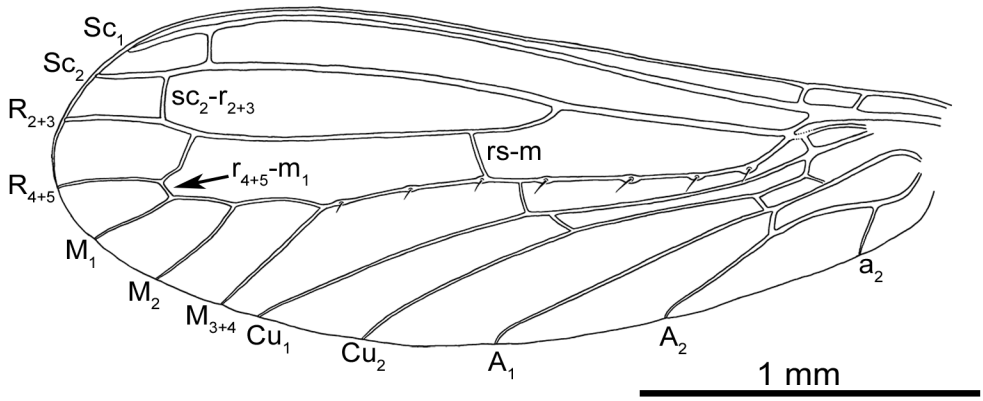

Figure 2. Forewing venation of holotype (AMNH JZC Bu-50) of *Achlyoconis heptatrichia*, new genus and species, with relevant vein elements labeled.

second slightly distad a_1-a_2; one slightly oblique a_1-a_2 crossvein present, slightly basad $2cu_2$-a_1; proximal portion of A_2 and hind margin connected by distinct a_2 crossvein; marginal fringes absent.

Hind wing length 2.15 mm, maximal width 0.80 mm, similar to forewing; origin of Rs slightly distad basal quarter of wing length; 1rs-m proximal, positioned beyond Rs origin by slightly more than 1rs-m length, nearly confluent with m-cu_1; M and Cu proximally running parallel and near to one another but with distinct membrane between, separation only slightly less than space between Rs and M at level of rs-m; a single m-cu crossvein present (no distal m-cu_1); one cu_1-cu_2 crossvein present, positioned proximal to m-cu_1 by slightly more than m-cu_1 length; cu_1-cu_2 slightly distad cu_2-a_1; marginal fringes absent.

♀: *Latet*.

HOLOTYPE: ♂, AMNH JZC-Bu50, in Upper Cretaceous (earliest Cenomanian) amber, near Tanai, Hukawng Valley, Kachin, northern Myanmar; deposited in the Zigras Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York. The holotype is currently segregated into its own block, but was originally part of a slightly larger fragment of amber that had as syninclusions two parasitoid wasps of *Burmaphron tridentatum* Engel & Grimaldi (Stigmaphronidae: these two individuals are new specimen records beyond those comprising the type series from Engel & Grimaldi, 2009) and a scatopsid fly (Scatopsoidea: Scatopsidae).

ETYMOLOGY: The specific epithet is a combination of the Greek terms *hepta* (meaning, "seven") and *trichos* (meaning, "hair"), and refers to the series of distinctive setae running along the forewing media.

Subfamily Coniopteryginae Burmeister
Tribe Coniopterygini Burmeister

Paranimboa Engel, new genus
ZooBank: urn:lsid:zoobank.org:act:2ED3B647-BD35-42BA-AC57-C4E7880E6A78

TYPE SPECIES: *Paranimboa litotes* Engel, new species.

DIAGNOSIS: Antenna 20-articled (with 18 flagellomeres) (24–31 articles in *Nimboa* Navás); scape slightly longer than wide. Forewing broad; two basal c-sc crossveins

present (one in *Nimboa*); Sc parallel with costal margin; Sc_1 and apical abscissa Sc_2 ($2Sc_2$) paralleling each other (*i.e.*, not arching toward each other); Rs originating at approximately basal third of wing length, abutting M proximally for short distance near origin, not forked apically (*i.e.*, Rs simple, as in *Nimboa*); one rs-m crossvein present, proximal to M fork (apical to M fork in *Nimboa*); M apically bifurcate (two-branched: M_{1+2} and M_{3+4}), without thickenings bearing distinctive setae; separation between M_{1+2} and M_{3+4} on wing margin greater than that of marginal separation between M_{3+4} and Cu_1 (separations approximately equal in *Nimboa*); cu_1-cu_2 present (absent in *Nimboa*); two cu_2-a_1 crossveins (one proximal in *Nimboa*). Hind wing similar to forewing. Wing membranes hyaline and clear, without pigmented spots. Abdominal plicaturae absent; male hypandrium protruding caudally.

Etymology: The new generic name is a combination of the Greek term *para* (meaning, "near") and *Nimboa* (the genus among coniopterygines to which the fossil has greatest superficial similarity). The gender of the name is feminine.

Paranimboa litotes Engel, new species

ZooBank: urn:lsid:zoobank.org:act:984B9C6F-1E3B-446E-9027-AF7B451C3C5D

(Figs. 3–4)

Diagnosis: As for the genus (*vide supra*).

Description: ♂: Total length approximately 1.47 mm (as preserved); integument preserved with dark reddish brown color, lighter on appendages. Head with prominent compound eyes; frons apparently sclerotized between antennal insertions; vertex prominent, high-domed, with sparse, minute setae. Antennal scape and pedicel stouter than flagellomeres, scape slightly longer than pedicel and each slightly longer than wide; flagellomeres each about twice as long as wide, although apical flagellomeres slightly shorter and tapering; first flagellomere slightly thicker than remaining flagellomeres, longer than second flagellomere; flagellomeres with sparse, minute setae. Terminal maxillary palpomere elongate, conical in shape, much longer and broader than preceding palpomeres; terminal labial palpomere similar to terminal maxillary palpomere. Legs slender; profemur slightly more swollen and shorter than meso- and metafemora; protibia much shorter than meso- and metatibiae; tarsi pentamerous; basitarsus longest tarsomere; probasitarsus slightly longer than succeeding protarsomere, about one-half combined length of remaining tarsomeres; meso- and metabasitarsi longer than probasitarsus, slightly shorter than combined lengths of succeeding tarsomeres; pretarsal claws minute, simple; arolium absent. Abdomen slender, with sparse, minute setae; plicaturae absent; left lateral portions of sterna apparently collapsed and obscured by thin, reflective bubble as preserved; details of terminalia difficult to discern — apparently with short, broad paramere tapered hypandrium, lighter in color than remaining portions of terga and sterna, and with short, broad paramere bluntly rounded apically; ectoproct rather broad, apicolaterally extended as short, semi-conical projections (latter perhaps corresponding to gonocoxites IX).

Forewing length 1.69 mm, maximal width 0.69 mm; membrane hyaline and clear, not infumate and without pigmented patterning; venation as in figure 4; two basal c-sc crossveins (= subcostal veinlets) in costal space; 2c-sc slightly distad tangent with origin of Rs; Sc parallel to costal margin; $1Sc_2$ distad r-rs; $2Sc_2$ paralleling Sc_1; origin of Rs at about one-third wing length; Rs abutting M briefly (proximally, slightly distad 1m-cu_1), length of contact about as long as 1m-cu_1; Rs simple, not sinuous proximally and not forking into R_{2+3} and R_{4+5}; Rs comparatively straight, terminating at wing apex; one

Figure 3. Holotype (AMNH JZC Bu-275) of *Paranimboa litotes*, new genus and species, in mid-Cretaceous amber from northern Myanmar.

r-rs crossvein present, basad $1Sc_2$ by slightly more than $1Sc_2$ length, and slightly distad rs-m by distance subequal to one-half distance of r-rs from $1Sc_2$; one rs-m crossvein present, meeting M slightly basad M_{1+2}/M_{3+4} fork, separated from fork by distance approximately equal to distance between rs-m and r-rs; M unmodified, without thickenings bearing specialized setae; M forking apically into M_{1+2} and M_{3+4}; two m-cu_1 crossveins present; 1m-cu_1 short, just proximal to contact of Rs and M; 2m-cu_1 well proximal to M_{1+2}/M_{3+4} fork, separated from fork by approximately 2.5 times its length; M_{3+4} and Cu_1 separation along wing much less than M_{1+2} and M_{3+4} separation on margin; Cu_1/Cu_2 fork near wing base; cu_1-cu_2 proximal to wing midlength, slightly distad $2cu_2$-a_1; Cu_1 and Cu_2 separation on wing margin narrow, less than M_{3+4} and Cu_1 separation; two cu_2-a_1 crossveins present; $1cu_2$-a_1 proximal, at proximal bend in Cu_2 after separation

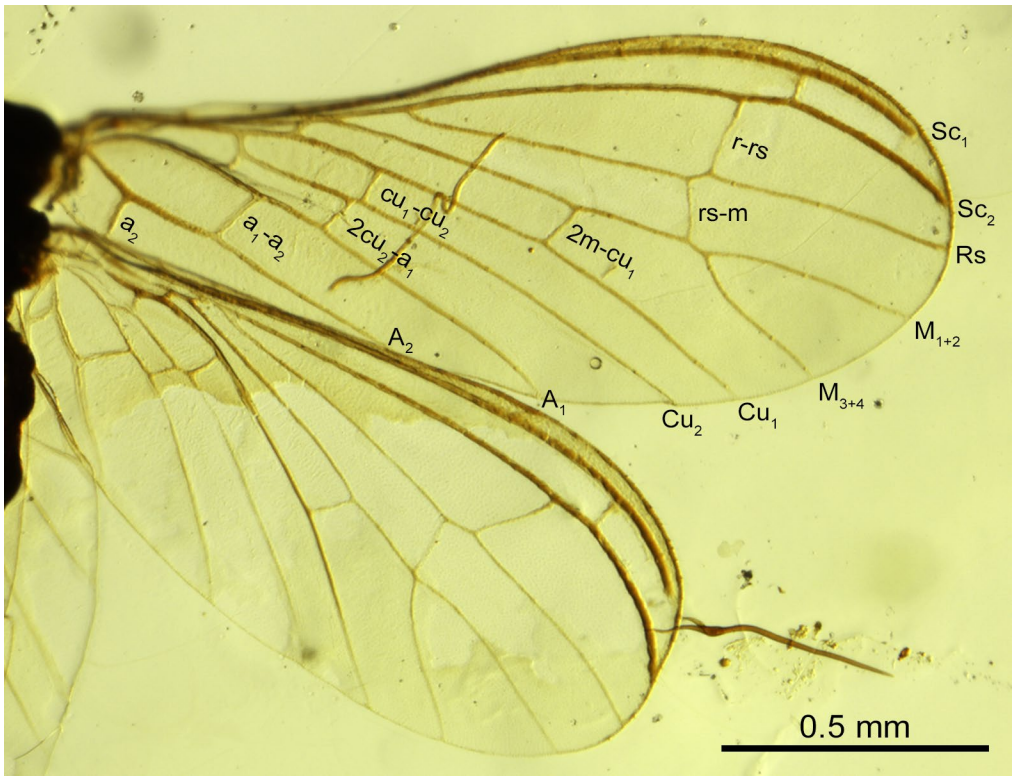

Figure 4. Wing venation of holotype (AMNH JZC Bu-275) of *Paranimboa litotes*, new genus and species, with important vein elements labeled on forewing.

from Cu_1, about as long as basal stem of Cu_2; $2cu_2$-a_1 situated near basal one-third of wing length; one a_1-a_2 crossvein present, positioned approximately halfway between $1cu_2$-a_1 and $2cu_2$-a_1; proximal half of A_2 and hind margin connected by long a_2 nearly orthogonal to A_2; marginal fringes absent.

Hind wing length 1.39 mm, maximal width 0.63 mm, similar to forewing, venation as in figure 4; apex of $2Sc_2$ more closely approximating Rs than in forewing; rs-m separated from r-rs by more than twice its posterior separation from M fork; marginal fringes absent.

♀: *Latet*.

Holotype: ♂, AMNH JZC-Bu275, in Upper Cretaceous (earliest Cenomanian) amber, near Tanai, Hukawng Valley, Kachin, northern Myanmar; deposited in the Zigras Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York. The holotype is in a small piece of amber with a wonderfully preserved and decidedly plesiomorphic-looking larva, but that despite its slender habitus and 4-articled antenna has only two labial palpomeres suggesting it might be a peculiar coniopterygid. Overlooking temporarily the traits peculiar to the fossil and differing from Coniopterygidae (albeit not approximating any other family owing to the two labial palpomeres), it is tempting to consider the adult and larva conspecific owing to their close proximity in a single piece of amber, but there is otherwise no real evidence to make such a conclusion. The larva is briefly and separately commented on below (*vide infra*).

ETYMOLOGY: The specific epithet is taken from the Greek term *litotes*, meaning, "simplicity", and refers to the comparatively simple wing venation.

Coniopterygid? Larva
(Figs. 5–6)

DESCRIPTIVE NOTES: **Larva:** Total length 1.49 mm; overall form slender, with sides of thorax and abdomen relatively parallel along length, tapering in width only slightly toward abdominal apex; few, elongate setae present laterally on head and each thoracic and abdominal segment, two such pairs of setae on head (one anteriorly near eyes, second posteriorly near temples), one pair each on thoracic segments, and two or three pairs on abdominal segments. Head about as long as wide, slightly tapering apically in dorsal view; eyes small, situated anterolaterally near antennal bases, diameter only slightly greater than antennal insertions, apparently with five ommatidia (exceedingly difficult to discern); antennae long (longer than mandibular-maxillary stylets), tetramerous, basal two articles similar in size and shape, each about 3 times as long as wide and slightly thicker than third article; third and fourth articles more elongate, with fourth article thinner than third article, apically bearing one fine seta; mandibular-maxillary stylets simple, without dentition, apically tapered to acute point, long (not greatly shortened as in Coniopteryginae and Brucheiserinae), comparatively straight (left stylets straight, right stylets slightly angled in apical third; right stylets slightly longer than left stylets; labial palpus dimerous, slender, and long, slightly shorter than mandibular-maxillary stylets; first labial palpomere longest, at least twice as long as second palpomere; second palpomere apparently with two, minute setae at apex. Prothorax about as wide as head, about twice as long as anterior width; mesothorax slightly wider than long; metathorax slightly longer than wide; legs short, with tibia-tarsus seemingly fused; pretarsal claws paired with minute empodium. Abdomen elongate, slightly longer than head and thorax combined; lateral margins of segments convex but without tubercles or scoli of any kind; apical segment blunt.

MATERIAL: Larva, AMNH JZC-Bu275, in Upper Cretaceous (earliest Cenomanian) amber, near Tanai, Hukawng Valley, Kachin, northern Myanmar; deposited in the Zigras Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

Key to Cretaceous Genera of Coniopterygidae
(Updated from Engel, 2004, and Perrichot *et al.*, 2014)

1. Media in forewing with three branches (M_1, M_2, and M_{3+4}) 2
—. Media in forewing with two branches (M_{1+2} and M_{3+4}) 5
2(1). Forewing without stiff setae on media 3
—. Forewing with stiff setae on media 4
3(2). Forewing $1R_{4+5}$ (*i.e.*, basal abscissa of R_{4+5}) more transverse, directed toward posterior of wing relative to $2R_{4+5}$ (*i.e.*, apical abscissa beyond distalmost rs-m), which is directed toward wing apex; antenna with 25 or more flagellomeres (25–30, where known) (Myanmar, New Jersey, Taimyr: Cenomanian–Santonian) ..... *Glaesoconis* Meinander
—. Forewing $1R_{4+5}$ obliquely directed toward wing apex, not strongly transverse, and instead completing a comparatively complete line with $2R_{4+5}$ to wing margin; antenna with less than 20 flagellomeres (Lebanon: Barre-

Figures 5–6. Primitive neuropteran larva preserved in AMNH JZC Bu-275. **5.** Relative positions of holotype male of *Paranimboa litotes*, new genus and species, and larva within the piece of amber. **6.** Expanded detail of larva in ventral view.

mian) ..... *Libanoconis* Engel

4(2). Forewing with two stiff setae proximally on media; R_{4+5} connected to M_{1+2} without crossvein; antenna with 21–23 flagellomeres; wing membranes hyaline and mostly clear (New Jersey: Turonian) ..... *Apoglaesoconis* Grimaldi

—. Forewing with numerous stiff setae present along media (Fig. 2); R_{4+5} connected to M_{1+2} by short rs-m crossvein (Fig. 2); antenna with 25 flagellomeres; wing membranes infumate (Myanmar: Cenomanian) ..... *Achlyoconis*, n. gen.

5(1). Forewing crossveins r-rs and rs-m present; cu_1-cu_2 present or absent; R_{4+5} connected to M_{1+2} or M_1; m-cu_1 strongly basad bifurcation of M 6

—. Forewing crossveins r-rs, rs-m, and cu_1-cu_2 absent; R_{4+5} not connected to M; m-cu_1 near bifurcation of M (Myanmar: Cenomanian) .... *Phthanoconis* Engel

6(5). Rs branched (R_{2+3} and R_{4+5}); R_{4+5} connected to M_{1+2}; forewing $1Sc_2$ meeting or basad 'radial' crossvein (sc-rs) 7

—. Rs simple, not branched; Rs connected to M_1; forewing $1Sc_2$ strongly distad 'radial' crossvein (crossvein therefore r-rs as it originates prior to Sc_2-R_1 juncture; accordingly, sc-rs technically lacking) (Myanmar: Cenomanian) ..... *Paranimboa*, n. gen.

7(6). Forewing crossvein r-rs not meeting bifurcation of Rs (R_{2+3}/R_{4+5} divergence); rs-m, where known, greatly longer than $1R_{4+5}$; cu_1-cu_2 absent; antenna with 20 or fewer flagellomeres 8

—. Forewing crossvein r-rs meeting bifurcation of Rs; rs-m subequal to $1R_{4+5}$ (however, in hind wing rs-m is greatly longer than $1R_{4+5}$) cu_1-cu_2 present; an-

tenna with 24 flagellomeres (Lebanon: Barremian) .... *Libanosemidalis* Azar *et al*.

8(7). Forewing r-rs meeting Rs distinctly basad bifurcation R_{2+3}/R_{4+5} (*i.e*., connected to stem of Rs); only one crossvein between Rs and M; antenna with 17 flagellomeres (Vendée: Santonian) ..... *Garnaconis* Perrichot & Nel

—. Forewing r-rs meeting Rs strongly distad bifurcation R_{2+3}/R_{4+5} (*i.e*., connected to R_{2+3}); two crossveins between Rs and M; antenna with 20 flagellomeres (Archingeay: Albian) ..... *Alboconis* Nel *et al*.

DISCUSSION

The diversity of fossil Coniopterygidae has risen dramatically during the last 16 years, and, except for three species, the known Mesozoic taxa have all been described this century (Table 1). Currently, there are 15 Mesozoic and 16 Cenozoic species documented (Tables 1, 2). While the Cenozoic fossils correspond nicely with those traits of the various subfamilies and tribes as circumscribed on the basis of modern species, the genera from the Mesozoic do so less well. Indeed, it remains to be determined whether the Aleuropteryginae and its tribes, as well as the Coniopterygini, are monophyletic. Inclusion of the various Cretaceous genera that approximate Aleuropteryginae might render the subfamily even less natural — while some might be stem-group aleuropterygines, others could just as easily be stem groups to extant Coniopterygidae as a whole. Similarly, although *Paranimboa* best accords with Coniopterygini, the tribe seems to be largely defined on plesiomorphies, and such Cretaceous taxa could be stem groups to the tribe, the entire subfamily Coniopteryginae, or perhaps even to Coniopteryginae + Brucheiserinae. An analogous placement for *Phthanoconis* Engel along the coniopterygine stem is also possible. Extensive cladistic work remains to be undertaken within Coniopterygidae.

Despite the aforementioned difficulties in considering Cretaceous dustywing genera within modern tribes, the taxa may presently be placed heuristically and compared pragmatically with those modern species with which they have the greatest superficial similarity. The genus *Achlyoconis* is most similar to a group of exclusively Cretaceous genera in which M_{1+2} branches, thereby forming three terminal branches to M in the forewing. This distinctive trait is unknown among modern dustywings, and aside from the new genus is present in *Glaesoconis* Meinander, *Apoglaesoconis* Grimaldi, and *Libanoconis* Engel. *Libanoconis* and *Glaesoconis* lack the specialized thickenings bearing setae on the forewing media, while both *Apoglaesoconis* and *Achlyoconis* possess such setae. *Apoglaesoconis* have two such setae proximally on the media, similar to that of modern Aleuropteryginae, while *Achlyoconis* have a more numerous series of such specialized setae along the length of the media prior to its initial branching. Aside from the presence of such setae, *Achlyoconis* are further similar to Aleuropteryginae by the presence of abdominal plicaturae, the presence of two rs-m crossveins, and the more basal origin of Rs in the hind wing. Among aleuropterygines the wider placement of the proximal portions of M and Cu_1 in the hind wing is similar to that of the genera *Pseudoconis* Meinander and *Vartiana* Aspöck & Aspöck, whereas in most other Aleuropteryginae these veins are typically abutting each other, or nearly so. The distinctly sclerotized frons, presence of a cu_1-cu_2 crossvein, presence of two cu_2-a_1 crossveins, and position of sc-r on R_{2+3} are indicative of the tribe Fontenelleini, where the new genus is most similar to a group of genera allied to *Helicoconis* Enderlein, owing to the shorter scape (not greatly elongate as in *Spiloconis* Enderlein), and the superficial

Table 2. Described Cenozoic Coniopterygidae (updated from Engel & Grimaldi, 2007, 2008); daggers indicate extinct taxa; records come from amber deposits unless marked as compression fossils (*).

†*Archiconiocompsa* Enderlein, 1910	
†*A. prisca* Enderlein, 1910	Baltic & Ukraine (Eocene)
†*Archiconis* Enderlein, 1930	
†*A. electrica* Enderlein, 1930	Baltic (Eocene)
Coniopteryx Curtis, 1834	
†*C. antiquua* Engel & Grimaldi, 2007	Dominican Republic (Miocene)
†*C. enderleini* Meunier, 1910a**	Togo copal (Pleistocene)
†*C. timidus* (Hagen in Pictet-Baraben & Hagen, 1856)	Baltic (Eocene)
†*Gallosemidalis* Nel *et al*., 2005	
†*G. eocenica* Nel *et al*., 2005	Paris (Eocene)
†*Geroconiocompsa* Engel, 2010	
†*G. ostara* Engel, 2010	Baltic (Eocene)
†*Heminiphetia* Enderlein, 1930	
†*H. fritschi* Enderlein, 1930	Baltic (Eocene)
Hemisemidalis Meinander, 1972	
†*H. kulickae* Dobosz & Krzemiński, 2000	Baltic (Eocene)
†*H. sharovi* Meinander, 1975	Baltic (Eocene)
†*Pararchiconis* Nel, 1990	
†*P. quievreuxi* Nel, 1990	Alsace (Oligocene)*
Semidalis Enderlein, 1905	
†*S. copalina* Meunier, 1910b**	Malagasy copal (Pleistocene)
Spiloconis Enderlein, 1907	
†*S. eominuta* Grimaldi & Engel in Grimaldi *et al*., 2013	India (Eocene)
†*S. glaesaria* Meinander, 1998	Dominican Republic (Miocene)
†*S. oediloma* Engel & Grimaldi, 2007	Dominican Republic (Miocene)
Neoconis Enderlein, 1930	
†*N. paleocaribis* Grimaldi & Engel in Grimaldi *et al*., 2013	Dominican Republic (Miocene)

** It is possible that these species described from copal are conspecific with extant taxa, merely representing subfossil occurrences.

resemblance of $2R_{4+5}$ to an anterior branch of the media. From all of these genera, however, the trifurcate media immediately distinguishes *Achlyoconis*. Fontenelleini may consist of the more plesiomorphic groups of Aleuropteryginae hence the resemblance between the Cretaceous genus and some members of this tribe.

The genus *Paranimboa* is most similar in wing venation to the coniopterygine *Nimboa*, an uncommon group of approximately seven species found at diverse localities ranging from Spain to Afghanistan, and southward to South Africa and India (Meinander, 1972, 1990). Among their many traits, *Nimboa* are unique among extant Coniopterygini for the possession of a simple Rs in both wings, as is the case for the Cretaceous fossil. *Paranimboa* differ in the shorter flagellum (18 flagellomeres in *Paranimboa* versus 22–29 flagellomeres in *Nimboa*), the two basal c-sc crossveins (one in *Nimboa*), the placement of rs-m proximal to the fork in M (apical in *Nimboa*), the two cu_2-a_1 crossveins (one in *Nimboa*), the presence of a cu_1-cu_2 crossvein (absent in *Nimboa*), and the broader terminal separation between M_{1+2} and M_{3+4} relative to that between M_{3+4} and Cu_1 (these approximately equal in *Nimboa*).

The larva included in the same amber piece as the holotype of *P. litotes* and briefly described above is certainly peculiar. Its minute size and the presence of only two labial palpomeres are certainly consistent with Coniopterygidae, and not with other fami-

lies in the order. The form of the head and prothorax is reminiscent of Aleuropteryginae, as both Coniopteryginae and Brucheiserinae have more pronouncedly triangular heads that are reduced in length posterior to the eyes, have the eyes more laterally projecting, have the stylets reduced such that they scarcely exceeding the labral apex, and have the prothorax enlarged. In stark contrast to all modern Coniopterygidae, however, the antennae have four articles, rather than the two antennal articles characteristic of the family, and overall the body is slenderer than in most modern species. If this is a dustywing larva, then it is decidedly plesiomorphic relative to the known larvae of extant Coniopterygidae and the tetramerous antennal form would tend to suggest that this particular larva is of a stem-group species.

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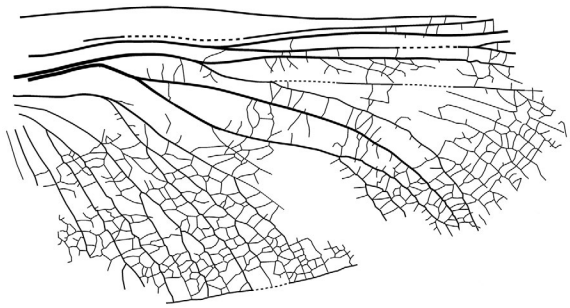

Pharciphyzelus lacefieldi Beckemeyer & Engel, 2011

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