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New antlions (Insecta: Neuroptera: Myrmeleontidae) from the mid-Cretaceous of Myanmar and their phylogenetic implications

Xiumei Lu^a, Jiahui Hu^a, Bo Wang^{b,c}, Weiwei Zhang^d, Michael Ohl^e and Xingyue Liu^{a*}

^aDepartment of Entomology, China Agricultural University, Beijing 100193, China; ^bState Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China; ^cKey Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Science, Beijing 100101, China; ^dThree Gorges Entomological Museum, PO Box 4680, Chongqing 400015, China; ^eMuseum für Naturkunde, Berlin, Invalidenstraße 43, Berlin 10115, Germany

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Myrmeleontidae (antlions) is the most species-rich family of the holometabolous order Neuroptera. Evolutionary history of this diverse lacewing family remains largely unexplored. Here we report on three new genera and four new species of antlions from the mid-Cretaceous amber of Myanmar, namely *Allopteroneura burmana* Lu, Zhang & Liu gen. et sp. nov., *Phylloleon elegans* Lu, Wang & Liu gen. et sp. nov., *Phylloleon stangei* Lu, Ohl & Liu gen. et sp. nov. and *Nanoleon wangae* Hu, Lu & Liu gen. et sp. nov. A phylogenetic analysis of the Burmese amber antlions is performed based on morphological characters. The result shows that the antlion species presently described belong to different major clades across the phylogenetic tree, suggesting a diverse palaeofauna of this family from the mid-Cretaceous of Myanmar. The phylogenetic status of the extinct subfamily Araripeneurinae is also discussed.

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Keywords: Neuropterida; Myrmeleontidae; taxonomy; Burmese amber; Mesozoic

Introduction

Myrmeleontidae (antlions) is the most species-rich family of Neuroptera. Hitherto, more than 1700 extant species described in over 200 genera (Stange 2004; Badano *et al.* 2017b) have been described worldwide. Some antlion larvae are well known for catching prey by constructing pitfall traps in sandy soil. The adults of extant antlions can be characterized by the short and distally dilated antennae, the usually elongated wings, the absence of proximal subcostal crossveins, the presence of presectorial crossveins (absent in most Mesozoic species), and the subtriangular branching area of forewing CuA. Traditionally, Myrmeleontidae is considered to be the sister group of Ascalaphidae (Aspöck *et al.* 2001; Badano *et al.* 2017b; Michel *et al.* 2017), but some recent phylogenetic analysis based on genome-scale data suggested paraphyly of Myrmeleontidae, with only a part of antlion species together with Ascalaphidae assigned to form a monophylum (Wang *et al.* 2017; Winterton *et al.* 2018).

The origin of Myrmeleontidae dates back at least to the Lower Cretaceous based on the oldest antlion fossils

(i.e. *Choromyrmeleon othneius* Ren & Guo, 1996 and *Choromyrmeleon aspoecorum* Ren & Engel, 2008) from the Lower Cretaceous of China. Nevertheless, a much earlier origin of Myrmeleontidae during the Middle or Late Jurassic was estimated based on recent molecular divergence time estimates (Winterton *et al.* 2010, 2018; Wang *et al.* 2017). So far, 34 fossil antlion species in 15 genera are known from the Lower Cretaceous to the Miocene. Among them, 28 species are from the Lower Cretaceous of Brazil, while the remaining species come from the Lower Cretaceous of China and Mongolia, the mid-Cretaceous of Myanmar, and the Miocene of the Dominican Republic (see Supplemental Table 1).

Among the diverse palaeofauna of Neuroptera from the mid-Cretaceous of Myanmar, there is only one antlion species described, namely *Burmanaura minuta* Huang *et al.*, 2016. In this paper, we report on three new genera and four new species of Myrmeleontidae from the mid-Cretaceous Burmese amber, i.e. *Allopteroneura burmana* gen. et sp. nov., *Phylloleon elegans* gen. et sp. nov., *Phylloleon stangei* gen. et sp. nov. and *Nanoleon wangae* gen. et sp. nov. We conduct

*Corresponding author. Email: xingyue_liu@yahoo.com

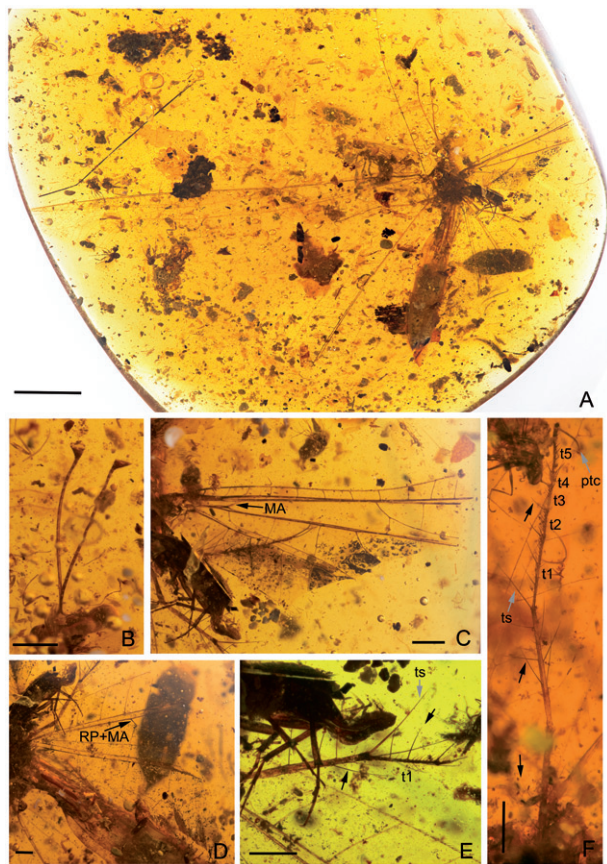


Figure 1. *Allopteroneura burmana* Lu, Zhang & Liu gen. et sp. nov., holotype EMTG BU-002082. **A**, photograph of habitus, dorsal view; **B**, photograph of antennae; **C**, photograph of proximal part of right forewing; **D**, photograph of proximal part of right hind wing; **E**, photograph of distal part of right hind leg; **F**, photograph of left hind leg. Abbreviations: ptc, pretarsal claw; ts, tibial spur; t, tarsomere. Black arrows in panels E and F indicate spinous setae on femur, tibia or tarsus. Scale bars: A = 5 mm, B–F = 1 mm.

a phylogenetic analysis combining fossil and extant antlions based on morphological data to infer the phylogenetic positions of these Burmese amber antlions. The new findings provide insight into a further understanding of the evolutionary history of Myrmeleontidae.

Material and methods

Material

The Burmese amber investigated here originated from the Hukawng Valley in Tanai Township, Myitkyina, District of Kachin State, Myanmar (see Kania *et al.* 2015, fig. 1). The age of this deposit has been investigated and dated to be ~99 Ma (earliest Cenomanian) by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi, G. H. *et al.* 2012).

The type specimens are currently housed in the Entomological Museum, China Agricultural University (CAU), Beijing, and will eventually be deposited in the Three Gorges Entomological Museum (EMTG), Chongqing, and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing (NIGP). Photographs and drawings were taken and made using a Zeiss SteREO Discovery V12 stereo microscope system. Terminology of wing venation generally follows Aspöck *et al.* (1980) and Kukalová-Peck & Lawrence (2004).

Abbreviations used for wing veins are: **A**, anal vein; **C**, costa; **Cu**, cubitus; **CuA**, cubitus anterior; **CuP**, cubitus posterior; **M**, media; **MA**, media anterior; **MP**, media posterior; **R**, radius; **RA**, radius anterior; **RP**, radius posterior; **ScA**, subcosta anterior; **ScP**, subcosta posterior; **cbr**, basal radial cell; **cir**, infra radial cell; **hc**, hypostigmal cell; **ps**, presectoral crossvein.

Phylogenetic analysis

For the ingroup taxa, we included all Mesozoic fossil genera of antlions except *Diegopteryx* from the Lower Cretaceous of Brazil (a monotypic genus lacking most characters herein coded due to poor preservation) (Martins-Neto & Rodriguez 2010) and representative genera (i.e. *Palpares* Rambur, *Stilbopteryx* Newman and *Myrmeleon* Linnaeus) of all three extant antlion subfamilies, i.e. Palparinae, Stilbopteryginae and Myrmeleontinae, following the classification system proposed by Stange (2004). We selected *Gumilla* Navás (Osmylidae) and *Norfolius* Navás (Nymphidae) as the out-group taxa. We also added an antlion-like genus, namely *Guyiling* Shi, Béthoux, Shih & Ren from Lower Cretaceous of China (familial placement unclear) in the analysis. This genus in general resembles Palaeoleontidae by the similar wing characters but has clubbed antenna (see Shi, C. *et al.* 2012). Two genera of Nemopteridae, i.e. *Roesleriana* Martins-Neto & Vulcano from the Lower Cretaceous of Brazil and *Pastranaia* Orfila, are included for testing the close relationship between Nemopteridae and Araripeneurinae *sensu lato* (or Araripeneuridae) presumed by Makarkin *et al.* (2018). The morphological characters used in the phylogenetic analysis comprise 26 adult characters (see Supplemental material). Unknown characters were coded as ‘?’, while the inapplicable characters were coded as ‘–’. The data matrix is given in Supplemental Table 2. All characters were treated as unordered and with equal weight. Analyses were performed using NONA ver. 2.0 (Goloboff 1993) with a heuristic search. Maximum trees to keep were set to 10,000 and the number of replications to 100. Character states were mapped on the strict consensus tree (MPT) using WinClada ver. 1.00.08 (Nixon 2002), showing only unambiguous changes.

Systematic palaeontology

Class **Insecta** Linnaeus, 1758

Order **Neuroptera** Linnaeus, 1758

Family **Myrmeleontidae** Latreille, 1802

Subfamily **Araripeneurinae** Martins-Neto & Vulcano, 1989a

Genus ***Allopteroneura*** Lu, Zhang & Liu gen. nov.

Type species. *Allopteroneura burmana* Lu, Zhang & Liu sp. nov.

Diagnosis. The new genus is characterized by the following combination of characters: (1) forewing elongated, leaf-like with acuminate apex (shared with *Cratoneura*, *Cratoalloneura* and *Phylloleon* gen. nov.; forewing relatively broader with rounded apical margin in other araripeneurine genera); (2) forewing costal space remarkably widened medially (shared with *Phylloleon* gen. nov.; feebly and gradually widened in other araripeneurine genera); (3) elongate infra radial cell (shared with *Araripeneura*, *Caririneura*, *Cratoneura*, *Cratoalloneura*; short in other araripeneurine genera); (4) MA diverging from RP greatly distad basal radial cell, with seven radial crossveins present before origin of MA from RP + MA (shared with *Cratoneura* and *Caldasia*, but with 5–10 radial crossveins in the former genus and over 10 in the latter genus; at or near basal radial cell in the other Araripeneurinae genera, with less than five crossveins); (5) forewing MP2 + CuA branches distinctly zig-zagged, with many curving crossveins between stem and branches of MP2 + CuA (straight and lacking aforementioned curving crossveins in other araripeneurine genera).

Etymology. From *allos* (Greek, meaning ‘different’), *pteros* (Greek, meaning ‘wing’) and *neuron* (Greek, meaning ‘nerve’, being as a frequent suffix of the genus-group name of Neuroptera). The name is an allusion to the abnormal wing shape of the species included in the genus. Gender feminine.

Remarks. The new genus belongs to Araripeneurinae *sensu lato* based on the distally dilated antennae, the presence of elongate hypostigmal cell, and the absence of forewing presectorial crossveins. Furthermore, the new genus is placed in the tribe Cratoalloneurini owing to the morphological similarity to *Cratoneura* Martins-Neto and *Cratoalloneura* Martins-Neto (Martins-Neto & Vulcano 1989a; Martins-Neto 1992a, 1994), and these genera share the leaf-like wings and many wing venational characters according to the phylogenetic analysis. However, *Allopteroneura* gen. nov. can be distinguished

from *Cratoalloneura* by the origin of forewing MA from RP + MA distantly apart from the basal radial cell. The new genus also differs from *Cratoneura longissima*, which is the type species of *Cratoneura*, by the zig-zagged forewing MP2 + CuA branches and relatively long forewing CuP.

It is noteworthy that three species of *Cratoneura* (i.e. *C. dividens*, *C. minor* and *C. pulchella*) are distinguished from *C. longissima* by having the zig-zagged forewing CuA branches and the relatively long forewing CuP (see Martins-Neto 1997, fig. 3A), both characters shared by *Allopteroneura* gen. nov. Therefore, these three *Cratoneura* species from the Lower Cretaceous of Brazil may belong to *Allopteroneura* gen. nov. or be separated from *C. longissima* as a distinct genus.

Allopteroneura burmana Lu, Zhang & Liu sp. nov.
(Figs 1, 2)

Diagnosis. As for the genus.

Material. Holotype, EMTG BU-002082, amber piece preserving a partly preserved adult of *Allopteroneura burmana*, together with several springtails, beetles, hymenoptera, dipterans, mites and spiders. It is polished in the form of a flattened rectangle cabochon, with length × width about 45.0 × 38.0 mm, height about 8.0 mm.

Etymology. The specific epithet ‘*burmana*’ refers to the occurrence of the new species in mid-Cretaceous Burmese amber. An adjective in the feminine gender.

Description. Body length 16.15 mm; head 0.61 mm long and 2.25 mm wide; distance between compound eyes 0.97 mm; diameter of compound eye 0.37 mm; antenna length 4.86 mm; prothorax 1.49 mm long and 0.87 mm wide; mesothorax 1.52 mm long and 2.14 mm wide; metathorax 0.99 mm long and 2.24 mm wide; preserved part of left forewing 27.99 mm long and 6.54 mm wide; preserved part of right hind wing 13.67 mm long and 6.22 mm wide; preserved part of abdomen 11.70 mm long.

Head orthognathous. Compound eyes large, semi-globular; diameter of eyes much shorter than distance between compound eyes. Antenna clubbed, nearly as long as length of head plus thorax; flagellomere about twice as long as wide.

Prothorax slightly widened posteriad, much longer but narrower than head; meso- and metathorax robust, metathorax almost as wide as mesothorax. Wings elongated, transparent and immaculate.

Forewing leaf-like, elongated, with narrow wing base and acuminate apex. Costal space quite narrow proximally, but strongly widened medially, and again slightly narrowed distad, with 37 preserved simple veinlets;

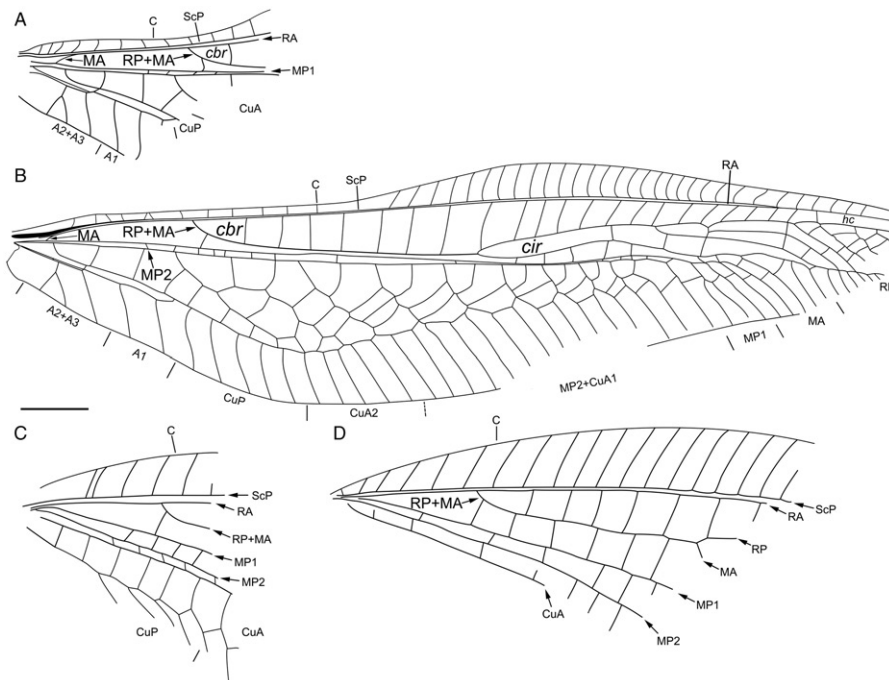


Figure 2. *Allopteroneura burmana* Lu, Zhang & Liu gen. et sp. nov., holotype EMTG BU-002082. **A**, line drawing of preserved part of right forewing; **B**, line drawing of preserved left forewing; **C**, line drawing of preserved part of right hind wing; **D**, line drawing of preserved part of left hind wing. Scale bar = 2 mm.

costal space much wider than subcostal space, but narrower than RA space. ScA absent; ScP and RA fused together before reaching to wing apex; subcostal crossveins absent. Presectorial crossveins absent. Hypostigmal cell incompletely preserved, but apparently long. RP+MA originating slightly distad wing base; RP and MA diverging almost from wing midpoint; RP pectinately branched from its mid-length, with a few crossveins allied as a longitudinal line; 22 crossveins present in RA space; infra radial cell thin and long. M proximally leaving a short oblique stem of MA that is fused with R near wing base; MA distally with five branches. MP1 long, almost straight for a long distance, distally slightly curved, with three branches. Base of MP2 (oblique vein) present proximad of initial branching point of MP2+CuA. CuA and CuP diverging near wing base; MP2+CuA pectinately branched from proximal 1/4, with 11 strongly zig-zagged branches, among which a series of curving crossveins are present and form eight subtrapezoidal cells with stem and branches of CuA; distal fork of branch of MP2+CuA nearly rectangular; CuP pectinately branched into five simple branches; six cua-cup crossveins present. A1 proximally parallel to but not fused into CuP, distally with two simple branches; A2+A3 short, proximally quite approximating and parallel to A1, with three branches.

Hind wing partly preserved. Costal space broad, much broader than that of forewing. Presectorial

crossveins absent. Seven crossveins present in RA space. MP diverging into MP1 and MP2 at wing base. CuP pectinately branched.

Legs slender and long; femora, tibiae and tarsi bearing several long spinous setae, which are much longer on tibiae (almost half-length of tibia) than those on femora and tarsi, tibial spurs slightly longer and stronger than tibial spinous setae, and slightly longer than tarsomere 1; numerous short spinous setae also present along tibiae and tarsi; tarsus slightly longer than tibia, 5-segmented, tarsomere 1 longest, tarsomeres 2 and 3 almost equal in length, tarsomere 4 shortest and only half-length of tarsomere 3, tarsomere 5 slightly shorter than tarsomere 1; paired simple pretarsal claws present, prolonged and distally curved, opposable on last tarsomere; arolium absent.

Abdomen slenderly elongate, almost $3/4 \times$ body length; anterior three segments much thinner than remaining segments. Genitalia not preserved.

Remarks. Considering the aforementioned morphological similarity between *Allopteroneura* gen. nov. and the three species of *Cratoneura*, the new species differs from *C. dividens*, *C. minor* and *C. pulchella* by the configuration of the forewing MP2+CuA branching area, particularly the presence of eight subtrapezoidal cells along its stem.

Genus *Phylloleon* Lu, Wang & Liu gen. nov.

Type species. *Phylloleon elegans* Lu, Wang & Liu sp. nov.

Diagnosis. The new genus is characterized by the following combination of characters: (1) forewing leaf-like with acuminate apex (shared with *Cratoneura*, *Cratoalloneura* and *Allopteroneura* gen. nov.; forewing broad with rounded apical margin in other araripeneurine genera); (2) forewing costal space remarkably widened medially (shared with *Allopteroneura* gen. nov.; feebly and gradually widened in other araripeneurine genera); (3) short infra radial cell (shared with most araripeneurine genera except for *Allopteroneura* gen. nov., *Araripeneura*, *Caririneura*, *Cratoneura* and *Cratoalloneura*); (4) MA diverging from RP greatly distad basal radial cell and also distad wing midpoint, with 5–8 radial crossveins between basal radial cell and origin of MA from RP+MA (not present in other araripeneurine genera); (5) initial branching point of forewing MP2+CuA slightly distad diverging point of RP+MA from R (shared with *Burmaneura*, *Choromyrmeleon*, and several araripeneurine genera, including *Cratopteryx*, and *Paracaririneura*; initial branching point of forewing MP2+CuA not distad diverging point of RP+MA from R in other araripeneurine genera); (6) 6–7 presectorial crossveins present in hind wing (shared with *Caririneura*; only one present in *Burmaneura* and *Nanoleon* gen. nov., but absent in other araripeneurine genera).

Etymology. From *phyllos* (Greek, meaning ‘leaf’) and *leon* (Greek, meaning ‘lion’, being as a frequent suffix of the genus-group name of Myrmeleontidae). An allusion to the leaf-like forewing. Gender neutral.

Remarks. Placement of the new genus in Araripeneurinae *sensu lato* of Myrmeleontidae is mainly based on the distally dilated antennae, the presence of elongate hypostigmal cell, and the absence of forewing presectorial crossveins. The new genus resembles the genera belonging to the tribe Cratoalloneurini based on the elongated leaf-like wings and the wide costal space. However, *Phylloneura* gen. nov. can be distinguished from the other genera of Cratoalloneurini by the short forewing infra radial cell, the absence of the longitudinally directed outer gradate series of crossveins, the diverging point of forewing MP2+CuA distad origin of RP+MA, and the presence of 6–7 presectorial crossveins in hind wing. Notably, the new genus and *Paracaririneura* from the Lower Cretaceous of Brazil shares the short forewing infra radial cell that is widely apart from basal radial cell and the forewing

MP2+CuA with initial branching point relatively distad the origin of RP+MA, and it shares the presence of 6–7 hind wing presectorial crossveins with *Caririneura microcephala* (also from the Lower Cretaceous of Brazil). However, *Phylloleon* gen. nov. distinctly differs from the above taxa by the leaf-like forewings.

Phylloleon elegans Lu, Wang & Liu sp. nov.
(Figs 3–5)

Diagnosis. Generally same as for the genus. In addition, forewing more acutely produced distad, and fore- and hind wings almost equal in width.

Material. Holotype, NIGP168257, amber piece preserving a partly preserved adult female of *Phylloleon elegans*, together with a mayfly and some hymenopterans

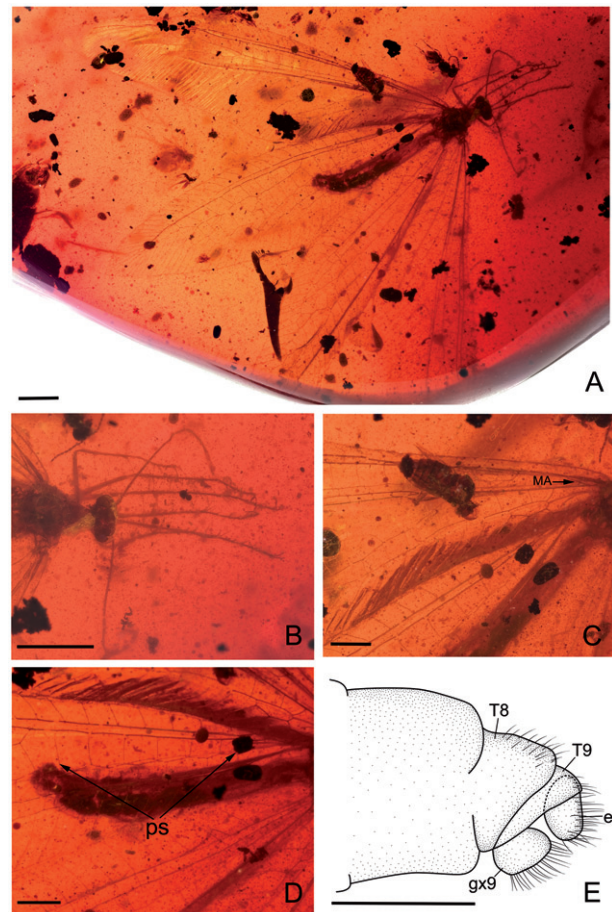


Figure 3. *Phylloleon elegans* Lu, Wang & Liu gen. et sp. nov., holotype NIGP168257. **A**, photograph of habitus, dorsal view; **B**, photograph of head and legs; **C**, photograph of proximal part of left forewing; **D**, photograph of proximal part of left hind wing **E**, line drawing of female genitalia, lateral view. Abbreviations: T, tergum; e, ectoproct; gx, gonocoxite. Scale bars: A–D = 2 mm, E = 1 mm.

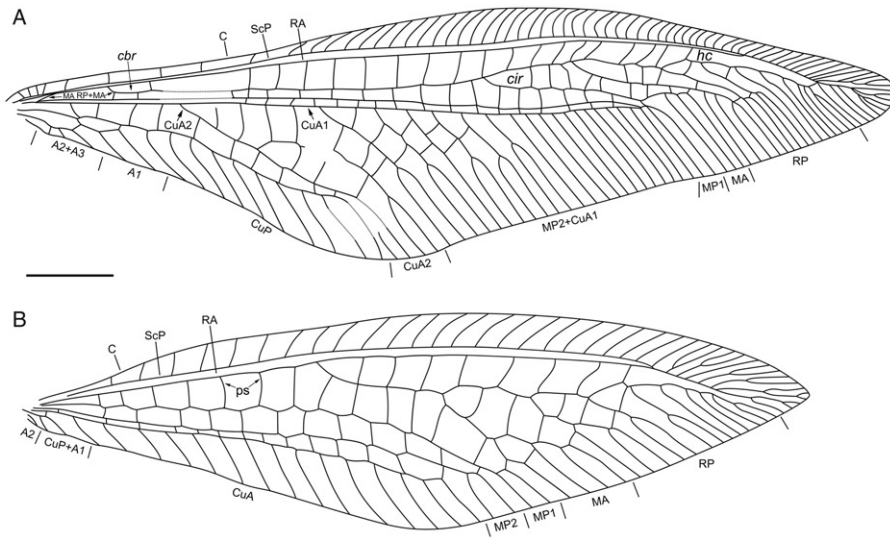


Figure 4. *Phylloleon elegans* Lu, Wang & Liu gen. et sp. nov., holotype NIGP168257. **A**, line drawing of left forewing; **B**, line drawing of left hind wing. Scale bar = 2 mm.

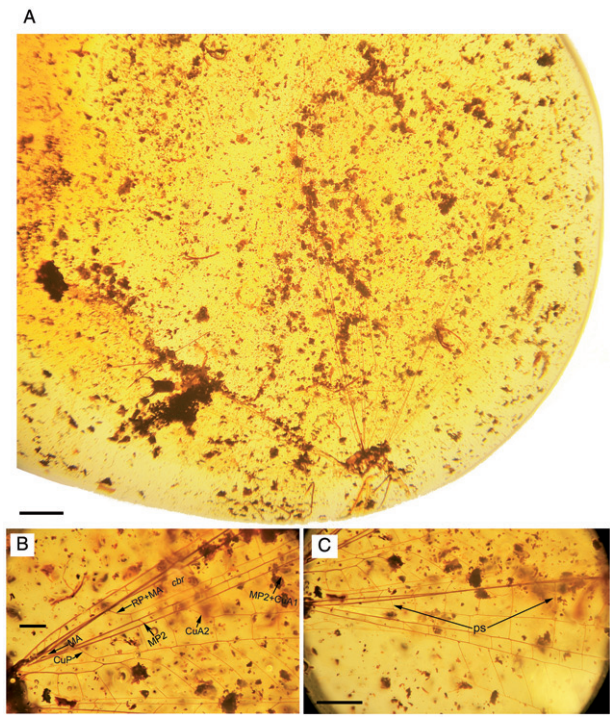


Figure 5. *Phylloleon elegans* Lu, Wang & Liu gen. et sp. nov., paratype NIGP168258. **A**, photograph of habitus; **B**, photograph of proximal part of left forewing; **C**, photograph of proximal part of left hind wing. Scale bars: A = 2 mm, B, C = 1 mm.

and dipterans. It is polished in the form of a flattened rhombus cabochon, with length × width about 58.0 × 40.0 mm, height about 1.0 mm. Paratype, NIGP168258, amber piece preserving a poorly preserved adult of *Phylloleon elegans*, and a psychopid larva. It is polished

in the form of a flattened subellipse cabochon, with length × width about 40.3 mm × 30.0 mm, height about 8.60 mm.

Etymology. The specific epithet *elegans* refers to elegant appearance of the new species. An adjective in the neuter gender.

Description. Body length 9.85 mm; head 0.56 mm long and 1.17 mm wide; distance between compound eyes 0.32 mm; antenna length 3.86 mm; prothorax 0.55 mm long and 0.54 mm wide; mesothorax 1.41 mm long and 1.30 mm wide; metathorax 0.49 mm long and 0.67 mm wide; forewing 17.60–20.37 mm long and 5.02–5.35 mm wide; hind wing 16.76–18.17 mm long and 4.76–5.01 mm wide; abdomen 7.46 mm long and 1.72 mm wide.

Head orthognathous, much wider than long. Compound eyes large, semi-globular; diameter of eyes much shorter than distance between compound eyes. Antenna slightly dilated distad, nearly as long as length of head plus thorax.

Prothorax slightly widened posteriad, much longer but narrower than head; meso- and metathorax robust, metathorax slightly smaller than mesothorax. Wings elongated, transparent and immaculate.

Forewing leaf-like, with narrow wing base and acuminate apex. Costal space quite narrow proximally, strongly widened medially, and again slightly narrowed distad, with over 60 veinlets. ScA absent; ScP and RA fused together, slightly bending and running to wing margin posteriad wing apex; subcostal crossveins absent. Presectorial crossveins absent. Hypostigmal cell long. RP + MA originating near wing base, and diverging into RP and MA distad midpoint of wing; 20 crossveins present in RA space; RP pectinately branched, with few

crossveins among anterior branches; infra radial cell short. M proximally leaving a short oblique stem of MA that is fused with R near wing base; MA distally with three branches. MP1 long, almost straight for a long distance, distally slightly curved, with three branches. Base of MP2 (oblique vein) present proximad initial branching point of MP2 + CuA. CuA and CuP diverging near wing base; MP2 + CuA pectinately branched from proximal 1/4 into 18 straightly directing branches, posterior six branches of MP2 + CuA1 mostly bifurcated distad, while remaining branches of MP2 + CuA1 simple, CuA2 long and deeply branched; CuP long, pectinately branched into 10 simple branches; nine cua-cup crossveins present. A1 short and zig-zagged, forked from its midpoint into two simple branches, connected with CuP by two short crossveins; A2 + A3 short, pectinately branched into three branches.

Hind wing costal space broad and slightly widened distad, with 30 veinlets. ScP and RA distally fused together, running to wing margin slightly posteriad wing apex; subcostal crossveins absent. RP + MA originating distad wing base, but slightly proximad midpoint of wing; eight crossveins present in RA space. Seven pre-sectorial crossveins present. MP1 zig-zagged, MP2 nearly straight, both of them bifurcated distally. CuA long, with stem running parallel to posterior margin, and pectinately branched into 15 simple and short branches. CuP + A1 very short, bifurcated; A2 simple, very weak; A3 absent.

Legs slender and long; tibiae and tarsi bearing several long spinous setae, these setae on tibia longer than those on tarsi, about $1/3 \times$ length of tibia; tibial spurs slightly longer than tarsomere 1; numerous short setae present along tibiae and tarsi; protarsus nearly as long as protibia, meso- and metatarsus about half length of meso- and metatibia, tarsomere 1 and tarsomere 5 nearly equal in length, but much longer than the other tarsomeres; paired simple pretarsal claws present, slender and distally curved, opposable on last tarsomere; arolium absent.

Abdomen slenderly elongate, about 0.7 times as long as body length, with anterior three segments slightly narrower than remaining segments. Female genitalia preserved; segment 8 much shorter than segment 7, strongly narrowed ventral in lateral view, but with ventral sclerites not clearly visible; tergum 9 about half length of tergum 8, slightly tapering ventrad in lateral view; gonocoxites 9 ovoid, bearing long setae along ventral margin; ectoprocts ovoid, slightly directed ventrad, with long setae; callus cerci not detected.

Phylloleon stangei Lu, Ohl & Liu sp. nov.

(Figs 6, 7)

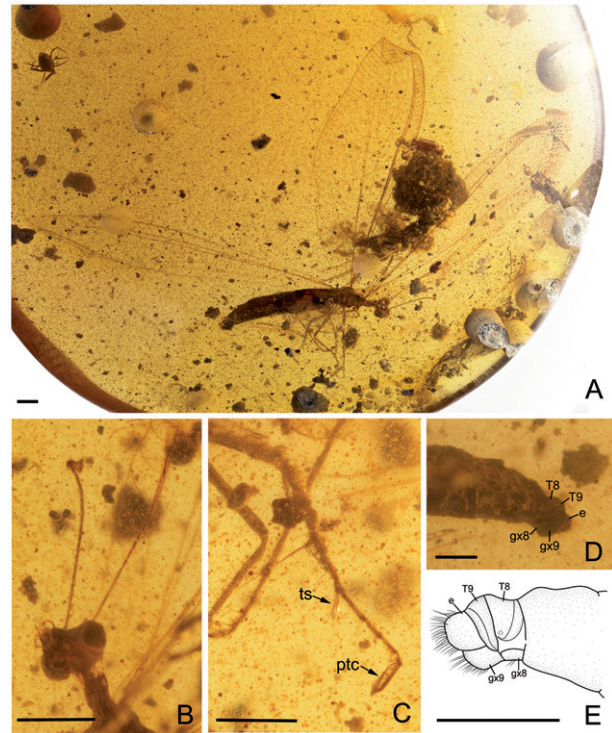


Figure 6. *Phylloleon stangei* Lu, Ohl & Liu gen. et sp. nov., holotype NIGP168259. **A**, photograph of habitus; **B**, photograph of head and antennae, ventral view; **C**, photograph of legs; **D**, photograph of genitalia; **E**, line drawing of genitalia, lateral view. Abbreviations: ptc, pretarsal claw; ts, tibial spur; T, tergum; e, ectoproct; gx, gonocoxite. Scale bars: A, B, D, E = 1 mm, C = 0.5 mm.

Diagnosis. Generally same as for the genus. Additionally, hind wing strongly narrowed, slightly longer and much more acutely produced than forewing.

Material. Holotype, NIGP168259, amber piece preserving a partly preserved adult female of *Phylloleon stangei*, together with a hymenopteran, a midge, a beetle, two pseudoscorpions, and a mite. It is polished in the form of a flattened round cabochon, with diameter about 30.0 mm, height about 5.0 mm.

Etymology. Dedicated to Dr Lionel A. Stange, one of the famous taxonomists of Myrmeleontidae.

Description. Body length 7.99 mm; head 0.53 mm long and 0.80 mm wide; distance between compound eyes 0.35 mm; antenna length 2.59 mm; prothorax 0.54 mm long and 0.27 mm wide; mesothorax 0.98 mm long and 0.89 mm wide; metathorax 0.51 mm long and 0.66 mm wide; forewing 12.68 mm long and 4.14 mm wide; hind wing 14.62 mm long and 2.12 mm wide; abdomen 5.73 mm long and 1.72 mm wide.

Head orthognathous, wider than long. Compound eyes large, semi-globular; diameter of eyes much shorter

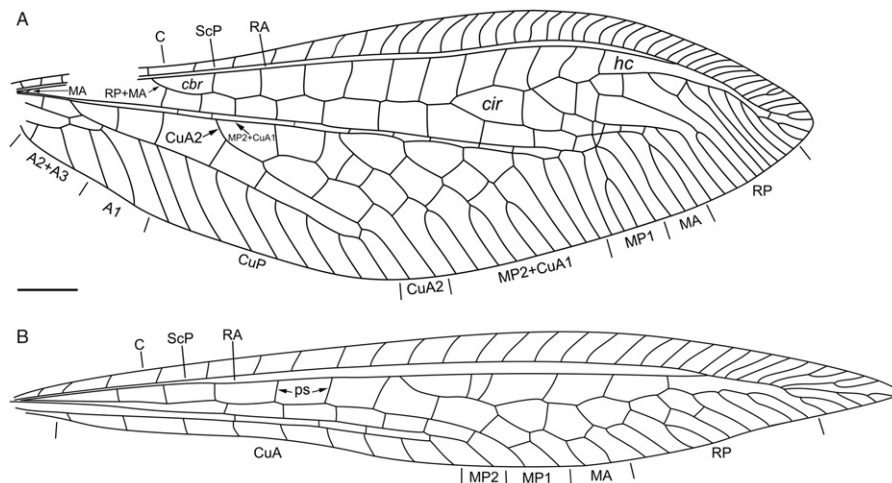


Figure 7. *Phylloleon stangei* Lu, Ohl & Liu gen. et sp. nov., holotype NIGP168259. **A**, line drawing of left forewing; **B**, line drawing of left hind wing. Scale bar = 1 mm.

than distance between compound eyes. Antenna nearly as long as length of head plus thorax, clubbed distad.

Prothorax much longer but narrower than head; meso- and metathorax robust, metathorax slightly smaller than mesothorax. Wings elongated, transparent and immaculate.

Forewing leaf-like, with narrow wing base and acuminate apex. Costal space quite narrow proximally, strongly widened medially, and again slightly narrowed distad, with *c.* 43 simple veinlets. ScA absent; ScP and RA fused together, slightly bending and running to wing margin posteriad wing apex; subcostal crossveins absent. Presectorial crossveins absent. Hypostigmal cell long. RP + MA originating near wing base, and diverging into RP and MA distad midpoint of wing; 11 crossveins present in RA space; RP pectinately branched into six branches, with few crossveins among these branches; infra radial cell short. M proximally leaving a short oblique stem of MA that is fused with R near wing base; MA distinctly curved posteriad at distal 1/3 and distally with three branches. MP1 long, almost straight for a long distance, distally distinctly curved, with two simple and one distally forked branches. CuA and CuP diverging near wing base; MP2 + CuA pectinately branched from proximal 1/3, with seven branches, posterior three branches of MP2 + CuA1 distally bifurcated, while remaining MP2 + CuA1 branches simple, CuA2 deeply forked; CuP pectinately branched into nine simple branches. A1 short and zig-zagged, bifurcated from its midpoint into two simple branches, connected with CuP by two short crossveins; A2 + A3 short, bifurcated.

Hind wing strongly narrowed, nearly half of forewing width, with acuminate apex. Costal space narrow, about three times as wide as subcostal space, with 28 veinlets, most of which are simple. ScP and RA fused together and straightly running to wing margin slightly posteriad

wing apex; subcostal crossveins absent. RP + MA originating from midpoint of wing; five crossveins present in RA space; RP and MA diverging slightly distad basal radial cell; RP pectinately branched into seven branches, with posterior two branches distally forked. MA distally bifurcated. Six presectorial crossveinlets present. MP1 and MP2 long, MP1 distally bifurcated, MP2 simple, space between them slightly broadened distad, with six crossveins. CuA pectinately branched into nine short simple branches; CuP and anal veins absent.

Legs slender and long; femur and tibia almost equal in length; tibiae and tarsi bearing several long spinous setae, these setae on tibiae longer than those on tarsi, about $1/6 \times$ length of tibia; tibial spurs slightly longer than tarsomere 1; numerous short setae present along tibiae and tarsi; tarsus much shorter than tibia, tarsomere 1 and tarsomere 5 nearly equal in length, but much longer than the other tarsomeres; paired simple pretarsal claws present, slender and distally curved, opposable on last tarsomere; arolium absent.

Abdomen slenderly elongate, about 0.7 times as long as body length. Female genitalia preserved; segment 8 much shorter than segment 7, with a broad ventral sclerite (putative gonocoxite 8); tergum 9 about $2/3 \times$ length of tergum 8, slightly tapering ventrad in lateral view; gonocoxites 9 ovoid, bearing long setae along ventral margin; ectoprocts nearly semicircular, much broader than gonocoxite 9, with long setae; callus cerci not detected.

Remarks. The new species differs from the congeneric species *Phylloleon elegans* by the forewing with less protruded apex and the strongly narrowed and acutely protruded hind wing. In the latter species, the forewing is slightly longer than hind wing, with apex much more

protruded, and the hind wing is broad, nearly as wide as forewing. In addition, *P. stangei* has much fewer forewing MP2 + CuA1 branches than *P. elegans*.

Considering the strongly narrowed hind wing and the presence of six presectorial crossveins, the new species appears also similar to *Caririneura microcephala* from the Lower Cretaceous of Brazil. However, the new species can be distinguished from *C. microcephala* by the leaf-like forewing, with strongly broadened costal space and produced wing apex, and by the presence of more crossveins between RA and RP + MA as well as between RP + MA and MP1 in the forewing.

Subfamily *incertae sedis*

Genus *Nanoleon* Hu, Lu & Liu gen. nov.

Type species. *Nanoleon wangae* Hu, Lu & Liu sp. nov.

Diagnosis. The new genus is characterized by a series of combinational characters: (1) forewing RP + MA diverging from RA well distad wing base (shared by *Burmaneura* and pseudonymphine genera; near wing base in araripeneurinae genera); (2) one forewing presectorial crossvein present (forewing lacking presectorial crossveins in Araripeneurinae and Pseudonymphinae; forewing with three or more presectorial crossveins in other antlion subfamilies); (3) one hind wing presectorial crossvein present (shared by *Caririneura*, *Burmaneura* and many extant antlion species; absent in most species of Araripeneurinae and Pseudonymphinae); (4) initial branching point of forewing MP2 + CuA slightly distad diverging point of RP + MA from RA (shared by *Burmaneura*, *Choromyrmeleon*, and the pseudonymphine genera, but almost at the same level in most araripeneurinae genera); (5) CuA2 short (shared by *Burmaneura*, *Choromyrmeleon*, the pseudonymphinae genera, and all extant antlions; long in Araripeneurinae).

Etymology. From *nanos* (Greek, meaning 'small') and *leon* (Greek, meaning 'lion', being as a frequent suffix of the genus-group name of Myrmeleontidae). An allusion to the small size of the species included in the genus. Gender neutral.

Remarks. The placement of *Nanoleon* in Myrmeleontidae is undoubted considering the short and clubbed antenna as well as the presence of presectorial crossveins in both wings, but the subfamilial affiliation of the new genus is still unclear. The presence of only one presectorial crossvein in both fore- and hind wings is rarely found in Myrmeleontidae. The result of present phylogenetic analysis suggests its closer relationship with extant antlions. Notably, the new genus possesses the forewing CuP distally fused with A1, which is an important

diagnostic character of the subfamily Myrmeleontinae. However, *Nanoleon* lacks the sensory hair on pro- and mesofemora, and it has relatively long pretarsal claws, apparently being different from the species of Myrmeleontinae.

Nanoleon wangae Hu, Lu & Liu sp. nov.

(Figs 8–10)

Diagnosis. As for the genus.

Material. Holotype, NIGP168260, amber piece preserving a partly preserved adult female of *Nanoleon wangae*. It is polished in the form of a flattened subequilateral triangular cabochon, with length × width about 43.0 × 32.4 mm, height about 42.8 mm. Paratype, NIGP168261, amber piece preserving a nearly complete adult female of *Nanoleon wangae* and a beetle. It is polished in the form of a flattened subelliptical cabochon, with length × width about 28.5 mm × 21.0 mm, height about 3.87 mm.

Etymology. The new species is dedicated to Prof Xinli Wang, who has made great contributions to the taxonomy of Myrmeleontidae from China, and also helped the last author of this paper in various ways for many years.

Description. Body length 7.36–8.44 mm; head 0.62–0.90 mm long and 1.45 mm wide; distance between compound eyes 0.41 mm; diameter of compound eyes 0.60–0.78 mm; antenna length 1.73 mm; prothorax 0.74 mm long, 0.34 mm wide; forewing 10.17–10.97 mm long and 3.12–3.95 mm wide; hind wing 9.90–10.09 mm long and 2.33–2.36 mm wide; abdomen 5.09–5.73 mm long and 0.5–1.19 mm wide.

Head orthognathous, subtriangular. Compound eyes large, semi-globular; diameter of compound eye slightly longer than distance between compound eyes. Antenna slightly shorter than combined length of head and thorax, dilated at distal 1/4. Mouthparts with parts of maxillae and labium discernible; maxilla with galea slightly broadened and rounded distad; maxillary and labial palpi, each with terminal segment tapering distad.

Prothorax short and slender; meso- and metathorax robust. Wings transparent, immaculate.

Forewing elongated, gradually broadened distad. Costal space rather narrow, about 2.5 times as wide as subcostal space, but distinctly widened from pterostigmal area, with 34 veinlets, most of which are simple. ScA absent; ScP and RA fused together at distal 1/4 of wing, slightly bending and running to wing margin posteriad wing apex; subcostal crossveins absent. One presectorial crossvein present. Five crossveins in RA space

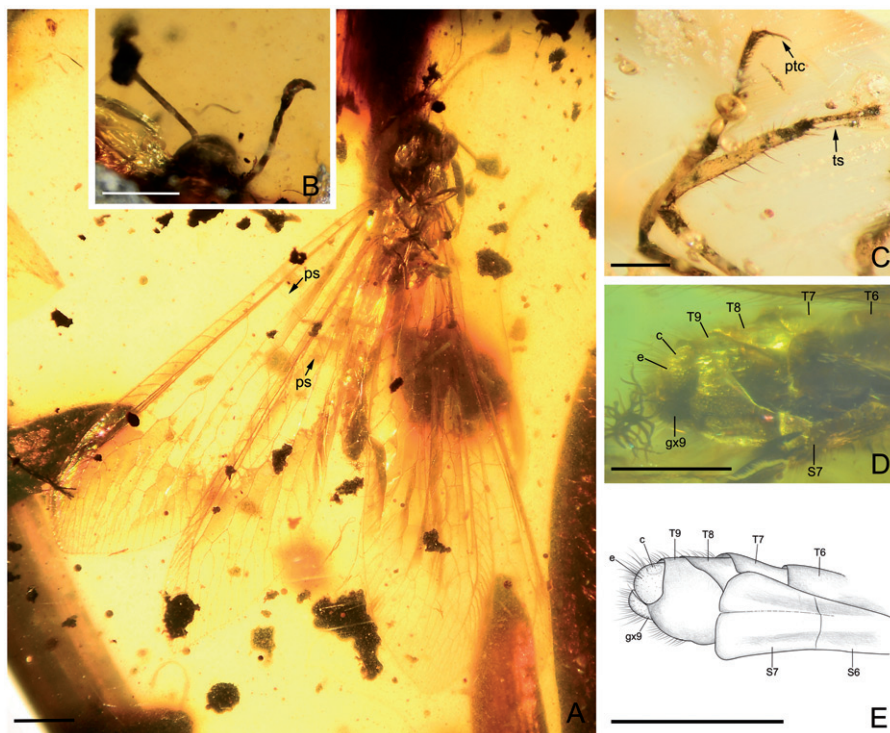


Figure 8. *Nanoleon wangae* Hu, Lu & Liu gen. et sp. nov., holotype NIGP168260. **A**, photograph of habitus, ventral view; **B**, photograph of antennae; **C**, photograph of hind leg; **D**, photograph of genitalia; **E**, line drawing of genitalia. Abbreviations: T, tergum; c, callus cercus; e, ectoproct; gx, gonocoxite. Scale bars: A, B, D = 1 mm, E = 0.5 mm, C = 0.2 mm.

present. Hypostigmal cell long. RP+MA diverging from RA well distad wing base, nearly at proximal 1/3 of wing, with seven pectinate branches and most of them forked distally; infra radial cell short; two short series of gradate crossveins present. MA leaving a short oblique stem near wing base; diverging point of MA from RP+MA not far beyond diverging point of RP+MA from RA, with only one crossvein on radial space between these two diverging points. MP1 long, straight, distally trifurcated; base of MP2 (oblique vein) untraceable. CuA and CuP diverging near wing base; MP2+CuA pectinately branched from midpoint, with seven branches; posterior two branches of MP2+CuA1 bifurcated distally; CuA2 slightly shorter than first branch of MP2+CuA1, medially forked. CuP with a short stem discernible, distally fused with A1, with six simple branches; A2 bifurcated, arcuately curved posteriad; A3 simple, strongly arched toward wing margin.

Hind wing elongated, much narrower than forewing, with wing base strongly narrowed, and with wing apex slightly narrowed and feebly excavated along distal margin. Costal space widened from pterostigmal area, with 23 veinlets, most of which are simple. ScP and RA fused together at distal 1/5 of wing, running to wing margin slightly posteriad wing apex, with a few marginally forked veinlets; subcostal crossveins absent.

RP+MA diverging from RA near proximal 1/3 of wing; five crossveins present in RA space; one presectorial crossvein present. MA trifurcated distally. MP1 with only a marginal fork, MP2 pectinately branched into 6–7 single branches; seven crossveins present between MP1 and MP2. CuA stem running parallel to posterior margin, pectinately branched into three simple branches; CuP and anal veins fused together, leaving three short simple branches.

Legs relatively short and stout, densely setose; femur slightly longer than tibia, without sensory hair; tibia with sparsely spaced long spinous setae, tibial spurs present, almost straight; tarsus much thinner and shorter than tibia, 5-segmented; tarsomere 1 long, but slightly shorter than combinational length of remaining tarsomeres; tarsomere 2–4 short, almost equal in length; paired pretarsal claws present, slenderly elongate, and curved distally, seemingly not opposable on last tarsomere.

Abdomen slenderly elongated, almost $2/3 \times$ body length. Female genitalia preserved; tergum 8 much shorter than tergum 7; gonocoxites 8 not discernible; tergum 9 strongly broadened ventrad in lateral view; gonocoxites 9 small, with arcuate ventral view, bearing long setae; ectoprocts nearly semicircular in lateral view, with large ovoid callus cerci.

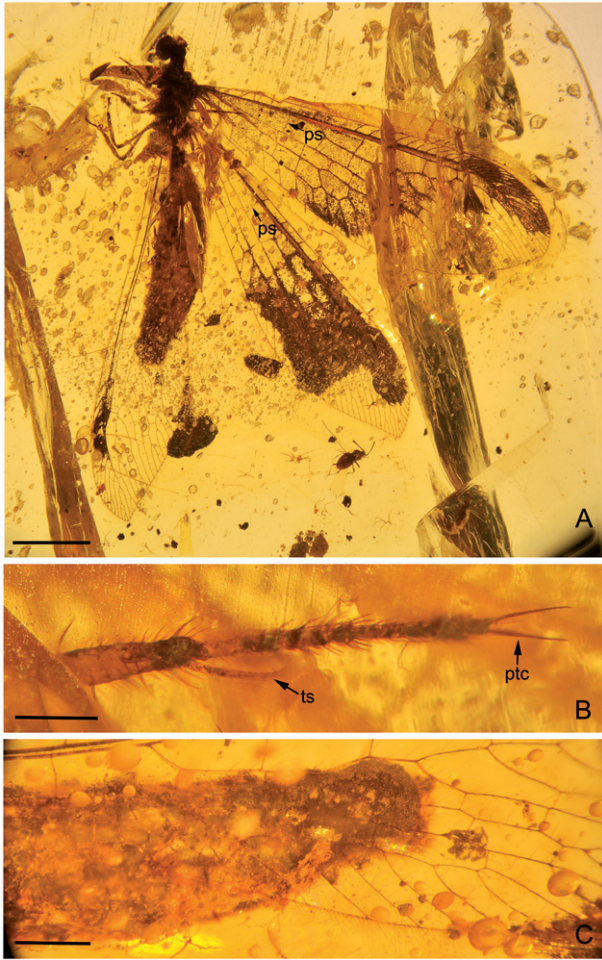


Figure 9. *Nanoleon wangae* Hu, Lu & Liu gen. et sp. nov., paratype NIGP168261. **A**, photograph of habitus; **B**, photograph of left mid leg; **C**, photograph of genitalia. Abbreviations: ptc, pretarsal claw; ts, tibial spur. Scale bars: A = 2 mm, B = 0.2 mm, C = 0.5 mm.

Results

The heuristic search in NONA yielded four most parsimonious trees (MPT) (length = 54, consistency index = 57, retention index = 82). The strict consensus tree is shown in [Supplemental Figure S1](#). The deep-level phylogenetic relationships are poorly resolved. Particularly, the genera of Nemopteridae are not clustered, probably due to the large proportion of missing data in *Paracroce*, which is known as only an incomplete forewing (Ponomarenko 1992). By deleting *Paracroce*, we re-analysed the dataset with the same method. The heuristic search yielded two MPTs (length = 54, consistency index = 57, retention index = 82) ([Fig. 12](#)). The strict consensus tree of these two MPTs is shown in [Figure 13](#). The result was improved considering the recovered monophyletic clade including the nemopterid genera. Most antlion genera constitute two

main clades, except *Choromyrmeleon*, whose phylogenetic position is unresolved. The phylogenetic position of the antlion-like genus *Guyiling* is also unclear.

The first main clade of antlions consists of most genera of Araripeneurinae. Its monophyly is supported based on the trapezoidal forewing prehypostigmal cell (char. 7:1), the pectinately branched forewing MA (char. 10:1), the closely spaced forewing MA and MP2 + CuA (char. 12:1), the deeply forked forewing CuA2 (char. 14:1), the long forewing CuA2 (char. 16:1), and the hind wing strongly tapering distad (char. 20:1). Within this clade, *Cratopteryx* was recovered to be at relatively basal position, while the remaining genera form a monophylum based on the absence of forewing oblique vein (char. 19:2). Most genera except *Paracaririneura* are grouped together based on the diverging point of forewing CuA2 proximad origin of RP + MA (char. 15:1).

Allopteroneura gen. nov. and *Phylloleon* gen. nov. from the mid-Cretaceous of Myanmar were recovered to form a monophyletic lineage together with *Cratoneura* and *Cratoalloneura* from the Lower Cretaceous of Brazil, supported by the distally strongly narrowed forewing (char. 4:1), the proximally strongly narrowed forewing costal space (char. 5:1), and the presence of longitudinally directed outer gradate series of crossveins (char. 8:1). *Caldasia* was assigned to be the sister group of the preceding lineage based on the hind wing costal space wider than that of forewing (char. 22:1) and the arched hind wing costal margin (char. 23:1). The phylogenetic positions of *Araripeneura* and *Caririneura* are not resolved.

The second main clade of antlions comprises three genera of the extinct subfamily Pseudonymphinae, two Burmese amber genera (i.e. *Burmaneura* and *Nanoleon* gen. nov.), and all extant genera, representing Stilbopteryginae, Palparinae and Myrmeleontinae. Autapomorphy of this clade refers to the forewing oblique vein present distad initial branching point of CuA (char. 19:1). Within this clade, the two Burmese amber genera (i.e. *Burmaneura* and *Nanoleon* gen. nov.) were assigned to be grouped with the three extant genera, i.e. *Palpares*, *Stilbopteryx* and *Myrmeleon*, based on the presence of hind wing presectorial crossveins (char. 25:1). *Nanoleon* gen. nov. has a closer relationship to these extant genera by the presence of forewing presectorial crossveins (char. 18:1). The phylogenetic relationships concerning the three genera of Pseudonymphinae, i.e. *Bleyeria*, *Blittersdorffia* and *Pseudonymphes*, are not resolved.

Discussion

Myrmeleontidae is the most species-rich lacewing family, which has been diversified in all zoogeographical

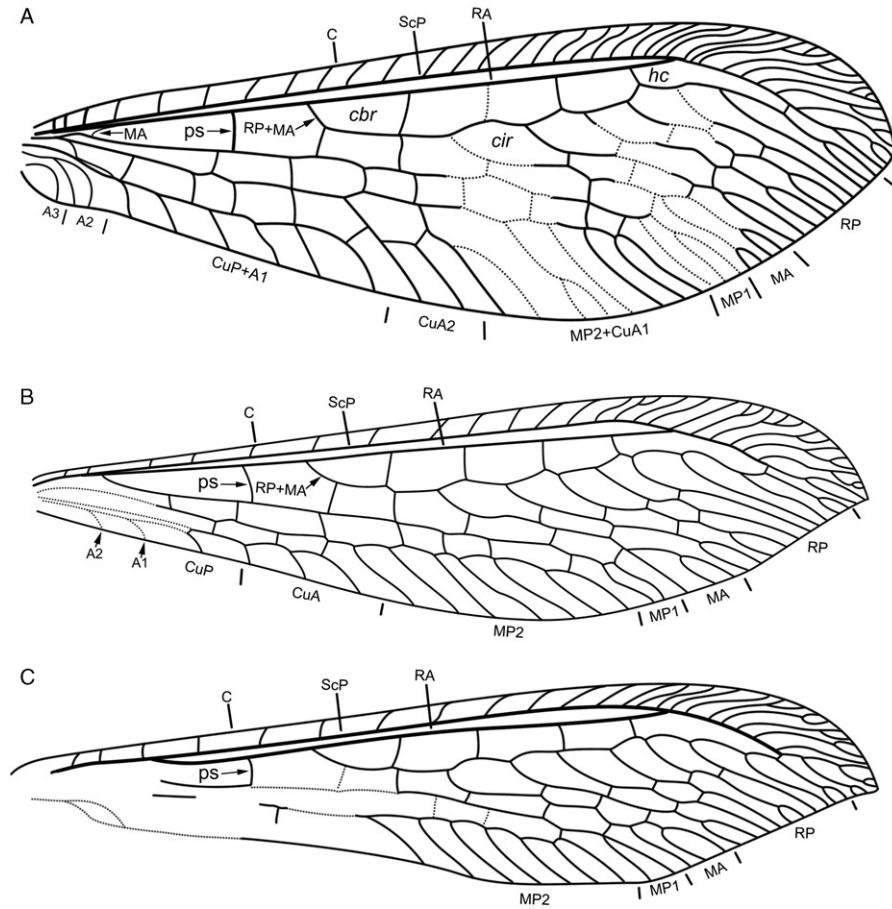


Figure 10. *Nanoleon wangae* Hu, Lu & Liu gen. et sp. nov., paratype NIGP168261. **A**, line drawing of left forewing; **B**, line drawing of left hind wing; **C**, line drawing of right hind wing. Scale bar = 2 mm.

regions. However, most of the fossil records of antlions are known from the Cretaceous, particularly from the Lower Cretaceous of the Crato Formation in Brazil. In other Cretaceous deposits with rich insect fossils, such as Yixian Formation of China and Baissa of Russia, antlion fossils are very rare. The present finding of four new antlion species from the mid-Cretaceous of Myanmar is remarkable and provides important evidence for further understanding the evolutionary history of this family.

The new Burmese amber antlions display diversified morphological characters. *Allopteroneura* gen. nov. and *Phylloleon* gen. nov. possess leaf-like forewings. Although some extant antlion species of Dendroleontini also have leaf-like wings (New 2003), the shape of forewing costal space in *Allopteroneura* gen. nov. and *Phylloleon* gen. nov. is distinctly different from that in extant species. Among the species of *Allopteroneura* gen. nov. and *Phylloleon* gen. nov., however, the hind wings are different in shape. Particularly, in *P. stangei* sp. nov. the hind wing is strongly narrowed. Moreover, the presence/absence and the number of presectorial

crossveins, which is a useful character for distinguishing antlion species, greatly vary among Burmese amber antlions. Considering the leg morphology, *Allopteroneura* gen. nov. and *Phylloleon* gen. nov. possess long pretarsal claws that are opposable on the last tarsomere. This feature is shared by some extant species of Dendroleontini and Nemoleontini (Stange 2004). Notably, *Allopteroneura* gen. nov. also has extremely long spinous setae on tarsi, while this feature is absent in extant antlions (see Fig. 11). The female genitalia of these Burmese amber antlions are generally similar to that of extant antlions, but the thickened digging setae that are present in most extant antlion species are absent in the new species.

Systematic status of Araripeneurinae *sensu lato*

Most known antlions from Cretaceous belong to the extinct subfamily Araripeneurinae, which was originally established by Martins-Neto & Vulcano (1989a). Martins-Neto (2002) raised Araripeneurinae to be a family, i.e. Araripeneuridae, proposing three autapomorphies: the forewing MA with more than five branches,



Figure 11. Distal part of legs of extant antlions. **A, B**, photographs of fore- and hind leg of *Stilbopteryx walker* Kimmins. **C, D**, photographs of fore- and hind leg of *Palpares radiates* Rambur. **E, F**, photographs of fore- and hind leg of *Acanthaclisis baetica* (Rambur). **G, H**, photographs of fore- and hind leg of *Cymothales* sp. **I, J**, photographs of fore- and hind leg of *Myrmecaelurus* sp.

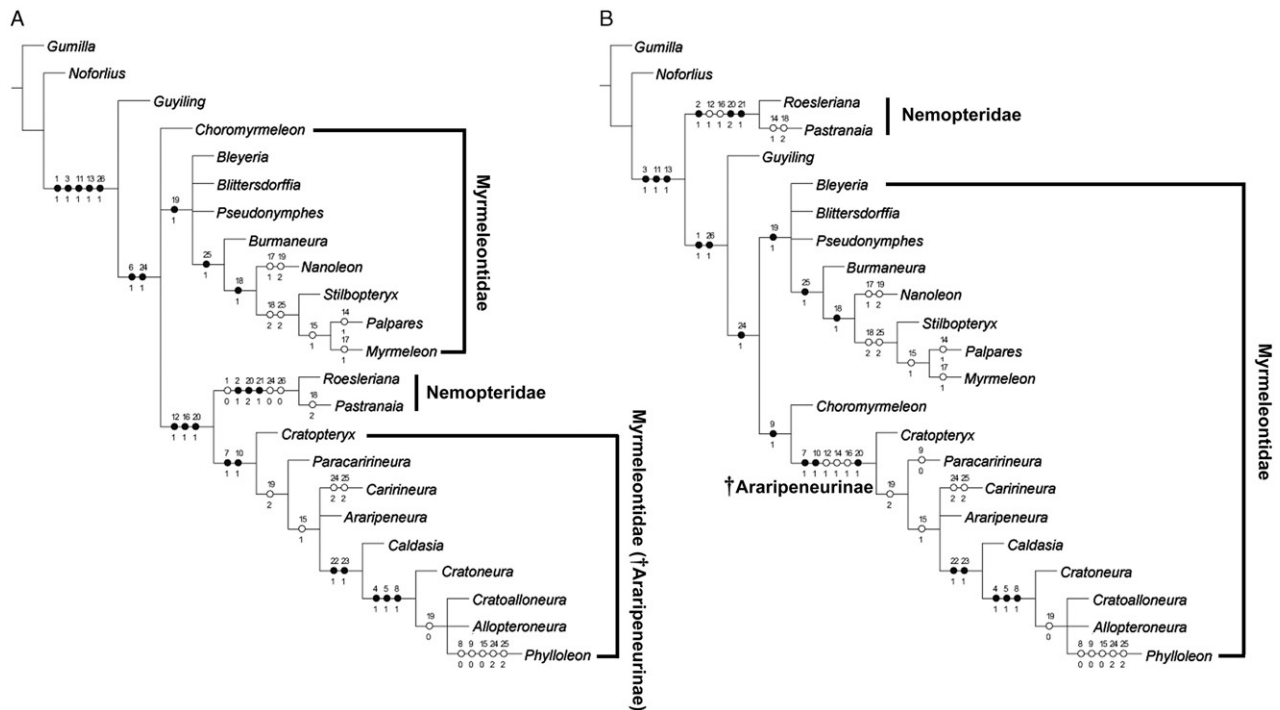


Figure 12. Two most parsimonious trees yielded from the dataset without *Paracroce*. **A**, topology represents the Araripeneurinae was assigned to be the sister group of Nemopteridae; **B**, topology represents the Nemopteridae was assigned to be the sister group of all remaining ingroup taxa, including Araripeneurinae, other Myrmeleontidae and other antlion-like genera.

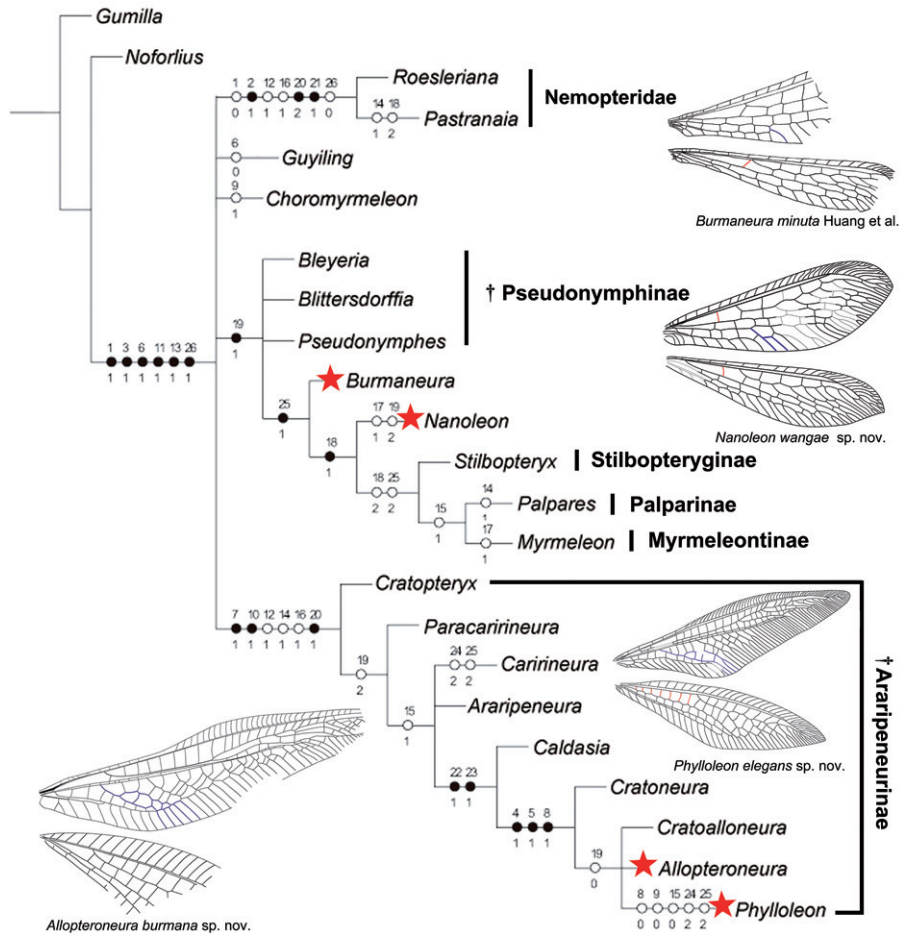


Figure 13. Phylogeny of extinct and extant Myrmeleontidae. Topology represents the strict consensus tree of the two most parsimonious trees yielded from the dataset without *Paracroce*. Unambiguous morphological character state changes are shown on the tree with a black circle as the homologous state and a white circle as the homoplasious state. Red star indicates the genus from the Burmese amber. Wing venations of all Burmese amber antlion genera are presented, with presectorial crossveins (red) and forewing CuA2 (blue) highlighted. Wing venation of *Burmaneura minuta* is modified from Huang *et al.* (2016).

the absence of forewing presectorial crossveins, and the trapezoid prehypostigmal cell. According to the classification of Martins-Neto (2002) and Martins-Neto & Rodrigues (2010), the Araripeneuridae comprises two subfamilies, i.e. Araripeneurinae *sensu stricto* (*Araripeneura*, *Caririneura*, *Caldasia*, *Cratoneura* and *Cratoalloneura*) and Cratopteryginae (*Cratopteryx* and *Diegopteryx*). However, a few genera originally placed in Araripeneurinae (Martins-Neto & Vulcano 1989a, b, 1997; Martins-Neto 1992a, 1998), i.e. *Pseudonympes*, *Blittersdorffia* and *Bleyeria*, are considered to form an independent subfamily, i.e. Pseudonympinae (Martins-Neto 1992b). Although some characters were proposed to support the familial status of Araripeneuridae and to define the aforementioned three subfamilies (see Martins-Neto 1992b, 2002; Martins-Neto & Rodrigues 2010), convincing autapomorphies of these taxa are very few.

Considering the autapomorphies proposed for Araripeneuridae (Martins-Neto 2002), first, the forewing MA with more than five branches is actually variable among species within this family. For example, in *Araripeneura* and *Caririneura* the forewing MA possesses many fewer branches. Second, the absence of forewing presectorial crossveins is a plesiomorphic state in Neuroptera. Thus, it appears inappropriate and unnecessary to separate Araripeneuridae as a different family from Myrmeleontidae based solely on the trapezoid forewing prehypostigmal cell.

Makarkin *et al.* (2018) presented a systematic reappraisal of Araripeneuridae and deemed its familial status. Unfortunately, no autapomorphies of Araripeneuridae are found in Makarkin *et al.* (2018). The arguments for separating Araripeneuridae as an independent family from Myrmeleontidae in Makarkin *et al.* (2018) are confined to

the wing characters. Makarkin *et al.* (2018) considered that the wings of Araripeneuridae are entirely dissimilar to most Myrmeleontidae because the forewing CuP is not fused with A1, the base of forewing MP2 (oblique vein) is located proximad initial branching point of MP2 + CuA, and the absence of pilula axillaris on the base of hind wing in males. However, as mentioned in Makarkin *et al.* (2018), all these character states in Araripeneuridae are plesiomorphic. Thus, it just suggests that Myrmeleontidae *sensu* Makarkin *et al.* (2018) is a relatively advanced group by having a series of apomorphic characters in comparison with Araripeneuridae, and it cannot be refuted that Araripeneuridae represents a stem group within Myrmeleontidae in a broad sense.

Makarkin *et al.* (2018) further claimed that Araripeneuridae and Nemopteridae are more closely related by sharing many forewing character states, e.g. the MP2 (oblique vein) located proximad the initial branching point of MP2 + CuA, the MP1 close to anterior trace of MP2 + CuA, the MP2 + CuA space broad, the deeply forked CuA2, and the presence of three fully separated similarly configured anal veins (A1 deeply forked; A2 and A3 short, simple and closely spaced at a crossvein between them). Among these character states, three states seem to be apomorphic and included in our phylogenetic analysis, i.e. the closely spaced MP1 and MP2 + CuA, the broad MP2 + CuA space, and the deeply forked CuA2, while the others are plesiomorphic. However, the closely spaced forewing MP1 and MP2 + CuA is also present in Myrmeleontidae and Ascalaphidae (see Aspöck *et al.* 1980, fig. 213, F. 259). The broad MP2 + CuA space seems to be related to the large-sized forewing and can be found also in antlions with broad forewing, such as *Palpares* (see Aspöck *et al.* 1980, fig. 211) and *Glenoleon* Banks (see New 1985, fig. 805). In Araripeneuridae and Nemopteridae the broad MP2 + CuA is just another indication of long forewing CuA2. In our phylogenetic analysis, however, these three apomorphic character states were not assigned confidently as the synapomorphies of Araripeneuridae + Nemopteridae.

The two MPTs yielded from our dataset show different schemes on the relationships among Araripeneuridae, Nemopteridae and Myrmeleontidae (Fig. 12); Nemopteridae was assigned to be the sister group either of Araripeneuridae or of all remaining ingroup taxa, which include Araripeneuridae, Myrmeleontidae and other antlion-like genera. Therefore, at present we cannot refute any one of the two equivalent results from the phylogenetic analysis.

Makarkin *et al.* (2018) mentioned that Araripeneuridae superficially resemble Myrmeleontidae in general appearance and by their short, apically dilated

antennae, but they claimed that the similarity of Araripeneuridae with Myrmeleontidae is convergent. However, no evidence was provided to support such convergent morphological similarity in Makarkin *et al.* (2018). In extant Myrmeleontidae and Ascalaphidae the clubbed antenna is the most important and obvious diagnostic character. Recent molecular phylogenetic studies (Wang *et al.* 2017; Winterton *et al.* 2018) corroborated that Myrmeleontidae and Ascalaphidae constitute a monophyletic group, but also suggested that these two families themselves are not monophyletic respectively and possibly better integrated into a single family. Nevertheless, the clubbed antenna still stands as an autapomorphy to support the monophyly of the group comprising Myrmeleontidae and Ascalaphidae. So far, besides Myrmeleontidae and Ascalaphidae, the clubbed antenna is only known in Araripeneuridae and some other antlion-like genera (e.g. *Choromyrmeleon* and *Guyiling*) amongst fossil lacewing families. In one of the two MPTs generated herein the clubbed antenna was assigned to be a synapomorphic character of all antlion or antlion-like genera.

The tibial spur is another important character, which however was not considered by Makarkin *et al.* (2018). In Myrmeleontidae and Ascalaphidae the tibial spur is well developed, usually being prolonged, thickened, or strongly curved. However, in Nymphidae, Babinskaiidae and Nemopteridae the tibial spur is less modified or reduced. In the Burmese amber species of Araripeneuridae the tibial spur is strongly elongated. Unfortunately, the feature of tibial spur in the other araripeneurid species is barely known due to the poor preservation on compression fossils.

Conclusively, the familial status of Araripeneuridae and its sister group relationship with Nemopteridae cannot be confidently verified based on present evidence. Although the wings possess plenty of important characters for taxonomy of fossil Neuroptera, solely using wing characters, especially those similar but not synapomorphic character states, to infer the phylogenetic relationships among fossil lacewings is very problematic (see Liu *et al.* 2017) as they underwent intense adaptations and usually contain homoplasies, parallelisms and reversals (Kukalová-Peck 2008). The male genitalia could be helpful to resolve the present problem in Araripeneuridae. In Ascalaphidae and Myrmeleontidae, the male gonocoxites 9 and 11 are strictly associated into a complex, which appears to be an important autapomorphy of Ascalaphidae + Myrmeleontidae (Aspöck & Aspöck 2008; Badano *et al.* 2017a). In Nymphidae, Nemopteridae and Babinskaiidae, these gonocoxites are independent and distinct sclerites (Aspöck & Aspöck 2008; Lu *et al.* 2017). Thus, the male genital characters

of Araripeneuridae are valuable for clarification of its systematic status. However, no male of Araripeneuridae has been found. Therefore, we prefer to retain the subfamilial status of Araripeneurinae *sensu lato* (= Araripeneuridae) under Myrmeleontidae.

Phylogenetic positions of Burmese amber antlions

Our results generally corroborate the close relationships among *Araripeneura*, *Caririneura*, *Caldasia*, *Cratoneura* and *Cratoalloneura*, which form the Araripeneurinae *sensu stricto* by Martins-Neto (2002). The two Burmese amber genera, *Allopteroneura* gen. nov. and *Phylloleon* gen. nov., were recovered as a monophyletic group together with these genera. The elongate forewing infra radial cell was assigned to be the autapomorphy of this lineage according to Martins-Neto (2002). Instead, the diverging point of forewing CuA2 proximad origin of RP + MA is the autapomorphy of this lineage recovered in our analysis.

Martins-Neto (2002) also established a tribe, Cratoalloneurini, including *Cratoneura*, *Cratoalloneura* and *Caldasia*. Autapomorphies of this tribe recovered by Martins-Neto (2002) comprise the notably long and narrow hypostigmal cell, the multi-branched MP1 with more than five secondary branches, the CuA2 origin distad the RP + MA origin in the forewing, and the hind wing costal space broader than that in the forewing. *Allopteroneura* gen. nov. and *Phylloleon* gen. nov. are merged into this tribe in our analysis based on the hind wing costal space broader than forewing costal space (char. 22:1) and the arched and convex hind wing costal margin (char. 23:1). Considering the characters defining Cratoalloneurini in Martins-Neto (2002), the long and narrow hypostigmal cell is actually not distinct in all genera of Cratoalloneurini. In *Phylloleon elegans* sp. nov. the forewing hypostigmal cell is relatively short. Moreover, in *Phylloleon* gen. nov. the forewing MP has much fewer branches than the other genera of this tribe, and the forewing CuA2 originates proximad the RP + MA origin. As such, these characters were not assigned to be the autapomorphies of Cratoalloneurini in our analysis. Thus, based on only hind wing characters as the tribal diagnosis, the phylogenetic status of the tribe Cratoalloneurini is doubtful.

The closer relationship among *Burmaneura*, *Nanoleon* gen. nov. and extant antlions is another noteworthy issue. *Burmaneura* was originally placed in Araripeneurinae by the absence of presectorial crossveins (Huang *et al.* 2016). However, the presence of a presectorial crossvein in hind wing supports that *Burmaneura* appears to be closer to *Nanoleon* gen. nov. and extant antlions. Although the presence of presectorial crossveins

can be found in several myrmeleontoid families besides Myrmeleontidae, such as Babinskaiidae and Nemopteridae, according to the present phylogeny of antlions, it can be inferred that the presence of forewing presectorial crossveins is a derived condition within Myrmeleontidae and had been gained in some Cretaceous antlions, with the number of these crossveins increased in extant antlions. Nevertheless, the character evolution of hind wing presectorial crossveins is more complicated, and the presence of these crossveins can be found in heterogenous genera, e.g. *Caririneura*, *Phylloleon* gen. nov., *Burmaneura*, *Nanoleon* gen. nov. and the extant antlions.

Makarkin *et al.* (2018) considered that *Burmaneura* probably belongs to Pseudonymphinae. The presently reconstructed phylogeny in general supports that *Pseudonymphes*, *Blittersdorffia* and *Bleyeria* of Pseudonymphinae are closer to extant antlions rather than Araripeneurinae. However, the monophyly of Pseudonymphinae is not recovered in our analysis, being consistent to the paraphyly of Pseudonymphinae proposed in Makarkin *et al.* (2018). Martins-Neto (1992b) proposed the diagnosis of this subfamily, including the short antenna with enlarged apex, the unforked forewing MA, the RP + MA origin far from wing base, the absence of presectorial crossveins, the small cubital area, and the subparallel condition of MP, CuA and CuP at their pre-forking area. However, none of these characters are present in these three genera, and some characters, such as the branching condition of forewing MA, are actually highly variable amongst these three genera. Martins-Neto (2002) recovered the absence of forewing Banksian line as the autapomorphy of Pseudonymphinae. However, the absence of forewing Banksian line can be found in many distantly related antlion lineages. Therefore, the myrmeleontid affinity of *Burmaneura* and *Nanoleon* gen. nov. is undoubted, but these two genera cannot be assigned to any of the known subfamilies of Myrmeleontidae.

Lastly, the immature stages of the Burmese amber antlions should be mentioned. So far, there is no immature stage, e.g. the larva, described and assigned to Myrmeleontidae from the Burmese amber. However, a number of larvae, with interesting debris-carrying behaviour, are reported and identified to be Ascalaphidae from the Burmese amber (Wang *et al.* 2016). Hitherto, no adult of Ascalaphidae has yet been found from the Burmese amber based on our examination of huge number of amber pieces including lacewings. Thus, considering the close relationship between Ascalaphidae and Myrmeleontidae, and considering the comparable number of diverse antlion adults, we predict

that at least some of the ascalaphid larvae reported in Wang *et al.* (2016) might belong to Myrmeleontidae.

Conclusions

The palaeofauna of Myrmeleontidae from the mid-Cretaceous of Myanmar is the second richest one after that from the Lower Cretaceous of Brazil. The palaeofaunal similarity of Myrmeleontidae between the mid-Cretaceous of Myanmar and the Lower Cretaceous of Brazil is remarkable. It raises the question whether the antlion species from the mid-Cretaceous of Myanmar had been diverged from their common ancestor in Brazil as a Gondwanan origin. More exploration of fossil antlions from other Mesozoic deposits is important. Furthermore, additional new findings of antlions from the Burmese amber are promising and will provide more evidence to unravel the evolutionary history of Myrmeleontidae and its allied families.

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Supplemental material

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