Dtsch. Entomol. Z. 73 (2) 2026, 333–362 | DOI 10.3897/dez.73.188790

PENSOFT

MUSEUM FÜR NATURKUNDE BERLIN

A revision of the antlion genus *Nuglerus* Navás, 1912 (Neuroptera, Myrmeleontidae, Dendroleontinae) from the Oriental region, including four new species and the first larval record of the genus

Yuchen Zheng[1], Davide Badano[2,3], Xingyue Liu[1]

1 *State Key Laboratory of Animal Biodiversity Conservation and Integrated Pest Management, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*

2 *Department of Life Sciences, University of Siena, Via Aldo Moro 2, I-53100 Siena, Italy*

3 *NBFC, National Biodiversity Future Center, Palermo, Italy*

https://zoobank.org/AC819DB4-9B84-4530-ADB8-16E23A550884

Corresponding author: Xingyue Liu (xingyue_liu@yahoo.com)

Academic editor: Susanne Randolf ♦ **Received** 15 February 2026 ♦ **Accepted** 1 July 2026 ♦ **Published** 27 July 2026

Abstract

Nuglerus Navás, 1912 is a rare Oriental genus of the antlion subfamily Dendroleontinae, previously including only three species: *N. maculatus* (Navás, 1915), *N. pustulatus* (McLachlan, 1867) and *N. scalaris* Navás, 1912. Based on the examination of types and additional material, together with COI barcode sequencing for some specimens, we revise here the taxonomy of *Nuglerus*. We treat *N. scalaris* **syn. nov.** as a junior synonym of the Sri Lankan species *N. pustulatus*; restore the Philippine species *N. insignis* Banks, 1939, **stat. rev.**, which was previously considered a junior synonym of *N. maculatus*; and transfer *Acratoleon dispar* Banks, 1934 endemic to Borneo (Malaysia) to *Nuglerus* as a new combination, i.e., *N. dispar* **comb. nov.** In addition, we describe four new species: *N. guimaraesae* Zheng, Badano & Liu, **sp. nov.** from southern India, *N. maizuqii* Zheng, Badano & Liu, **sp. nov.** from Malay Peninsula, *N. ruzzieri* Badano, Zheng & Liu, **sp. nov.** from Sulawesi (Indonesia), *N. shihongliangi* Zheng, Badano & Liu, **sp. nov.** from Bali (Indonesia). Moreover, we describe the larval morphology and ecology of *Nuglerus* for the first time. So far, *Nuglerus* comprises eight species, patchily distributed in tropical rainforests of the Oriental Region. We also provide a distribution map and an identification key for *Nuglerus* and discuss the affinities issues of this genus.

Key Words

Asia, integrative taxonomy, karst, Lacewing, larva, tropics

Introduction

Myrmeleontidae is a neuropteran family with a worldwide distribution, currently comprising four subfamilies (Ascalaphinae, Myrmeleontinae, Dendroleontinae, and Nemoleontinae), 303 genera, and ca. 2100 species (Machado et al. 2019; Oswald 2025). Several groups of Myrmeleontidae are associated with sandy habitats, and their larvae dig into sand or dried debris for hiding and prey capture (e.g., by building sandy pit-shaped traps) (Mansell 1999; Badano and Pantaleoni 2014), making antlions especially common and diverse in sandy environments. In forest habitats, sandy habitats are scarcer, yet myrmeleontid diversity in forests does not appear to be markedly lower. Besides exploiting the limited sand available in forests (Badano et al. 2018; Zheng and Liu 2020, 2023; Zheng et al. 2024a, 2024b), larvae of many forest species have evolved alternative habits, such as living in wet soil (e.g., Dendroleontinae, *Epacanthaclisis* Okamoto, 1910) (Matsumoto et al. 2016; Zheng et al. 2025a), in dry soil under rock overhangs (e.g., Nemoleontinae, *Ripalda* Navás, 1915)

Copyright *Yuchen Zheng et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

(Badano et al. 2018); leaf litter (e.g., Ascalaphinae, *Albardia* van der Weele, 1903) (Machado et al. 2021), on the surface of living plants (e.g., Ascalaphinae, *Haploglenius* Burmeister, 1839) (Ardila-Camacho and Jones 2012), tree holes (e.g., Dendroleontinae, *Dendroleon* Brauer, 1866; Nemoleontinae, *Glenurus* Hagen, 1866) (Miller and Stange 1983; Badano and Pantaleoni 2014; Tavares et al. 2025), or on rock surfaces (Myrmeleontinae, *Gnopholeon* Stange, 1970, *Jaffuelia* Navás, 1918, *Neulatus* Navás, 1912; Dendroleontinae, *Gatzara* Navás, 1915, *Nepsalus* Navás, 1914, and *Layahima* Navás, 1912) (Stange 1994; Zheng et al. 2022, 2024b, 2025b). Dendroleontinae is a myrmeleontid lineage adapted to forest environments. Most species of this subfamily have been recorded from humid forests in the Old World and North America (Ghosh 1984; New 1985; Mansell 1987, 1988; Stange 2004, 2008; Badano and Pantaleoni 2014; Krivokhatsky 2015; Wang et al. 2018; Machado and Oswald 2020; Zheng et al. 2022, 2023, 2024a, 2024b, 2025a, 2025b; Kim et al. 2025), with relatively fewer species occurring in semi-arid habitats in Central Asia (Krivokhatsky 1998), the Iberian Peninsula (Hölzel and Monserrat 2002), inland Australia (New 1985; Machado and Oswald 2020), and the Afrotropical region (Mansell 1985; Hölzel 2002; Zheng et al. 2025c). The present center of diversity of Dendroleontinae lies in the forests of the Oriental and Australian regions, where more than 170 species are known (Machado et al. 2019; Machado and Oswald 2020; Oswald 2025).

Nuglerus is a dendroleontine genus inhabiting the tropical rainforests of the Oriental region, currently including three valid species: *N. maculatus* (Navás, 1915), *N. pustulatus* (McLachlan, 1867), and *N. scalaris* Navás, 1912. All species were described based on a single specimen, and additional material has been rarely reported (Krivokhatsky 2015). The systematic position of *Nuglerus* has long been debated: it has been treated as a monogeneric subtribe Nuglerina within Dendroleontini (Stange 1976, 2004) or regarded as a separate tribe Nuglerini in the morphological phylogeny of Krivokhatsky (1998). However, all these treatments are exclusively based on morphological characters, and *Nuglerus* was not included in the phylogenomic analysis of Machado et al. (2019) due to the lack of specimens, in which it was provisionally placed in Dendroleontini (Dendroleontinae) pending further revision. This rare rainforest genus exhibits distinctive characters: the antennae are slender and long (longer than combined length of head and thorax), the poststigmal area of the wings bears thickened (or bulged) markings (i.e., the bulla), the hypostigmal cell is shorter than in most antlions (nearly twice as long as wide), and the anterior part of female gonocoxites 9 bears a setose plate. Nevertheless, the gently curved forewing 2A toward 3A, the presence of two hindwing presectoral crossveins at most, and the plate-like male gonocoxites 9 are typical traits of Dendroleontinae.

In this study, we present the first integrative taxonomic revision of *Nuglerus*, based on morphological examination and COI barcode data. This revision includes re-descriptions of known species, the proposal of a new synonym and a new combination, the restoration of a junior synonym, the description of four new species, and a record of larval stage. Moreover, we discuss the systematics, biology and distribution of *Nuglerus*.

Material and methods

Taxonomy

All specimens examined and mentioned herein are deposited in the following collections:

CBGP	Centre de Biologie pour la Gestion des Populations, Montpellier, France
IZCAS	Insect Collection of Institute of Zoology, Chinese Academy of Sciences, Beijing, China
MCZ	Museum of Comparative Zoology, Harvard, Cambridge, USA
MfN	Museum für Naturkunde, Bereich Zoologisches Museum, Berlin, Germany
MHNG	Muséum d'Histoire Naturelle de Genève, Geneva, Switzerland
MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum, London, UK
NHMW	Naturhistorisches Museum, Vienna (Wien), Austria
MSNG	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
RMNH	Naturalis Biodiversity Center, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
ZCAU	Yuchen Zheng collection, China Agricultural University, Beijing, China

The holotype of *Acratoleon flavum* Banks, 1934 (type information: "Salomons Ins. Shortlands Is. Ribbe." // "Acratoleon flavum type Bks" // "Acratoleon flavum Banks" // "Type" // "a14ed0" (MfN)) was examined for morphological comparison.

The types deposited in MCZ were from photographs obtained from MCZbase (holotype of *Nuglerus insignis* Banks: MCZ: Ent: 23020) (Harvard University, Museum of Comparative Zoology 2018).

Genitalia were prepared by clearing the apex of the abdomen with 20% KOH in 135 °C for seven minutes. After rinsing the KOH with distilled water, the apex of the abdomen was transferred to glycerin for further examination. Adult habitus and larval photos were taken using Nikon® D850 digital camera with AF-S Micro Nikkor 105 mm 1/2.8G ED lens. Head, thorax, and some genitalia were photographed by Nikon® D850 digital camera with Laowa® 25 mm F/2.8 2.5–5.0X Ultra Macro lens Photographs of some genitalia were taken using a Leica® DM2000 outfitted with Nikon® D850 digital camera.

The classification system of Myrmeleontidae follows Machado et al. (2019). Terminology of wing venation and

wing fields follows Breitkreuz et al. (2017) and Machado and Oswald (2020). Regarding the interpretation of genital segments 10–11 which is still controversial in Myrmeleontidae (Boudinot 2018; Marquez-López et al. 2024), we adopt the terminology previously widely used in studies of Myrmeleontoidea (Aspöck and Aspöck 2008; Badano et al. 2017a, 2017b; Zheng et al. 2023, 2024a), rather than the recently proposed terminology by Marquez-López et al. (2024).

Molecular comparisons

To facilitate species identification, we sequenced the barcode region of the cytochrome C oxidase subunit 1 (COI) gene for four ingroup specimens of *Nuglerus* and two specimens of *Layahima chiangi* Banks, 1941 as outgroups. The total genomic DNA of the samples was extracted from the mesothoracic muscle and legs of adults using the TIANamp Micro DNA Kit (TIANGEN®, Beijing, China). The COI barcodes were amplified using the primers COI1-R (5'-TAAACTTCTGGATGT-CCAAAAAAT-CA-3') and COI4-F (5'-TGTAAAACGACG-GCCAG-TAAACTAATARCCTTCAAAG-3') (Park et al. 2010; Lai et al. 2021, 2024). The thermal cycling program consisted of an initial denaturation at 95 °C for 5 min, followed by 39 cycles of 95 °C denaturation for 10 s, 52 °C annealing for 50 s, 65 °C extension for 1 min, and a final extension at 65 °C for 10 min. PCR products were sequenced bidirectionally by the PCR-based method in Sangon Biotech (Shanghai). Genetic distances (Table 2) of the COI barcode region were calculated using MEGA 6.0 (Tamura et al. 2013) with the Kimura 2 Parameter (K2P) model (Kimura 1980). The phylogenetic study included the following three analyses. Maximum likelihood (ML) analysis was performed with IQ-TREE (Nguyen et al. 2015). The DNA sequences of the COI barcode region of the present samples are deposited in GenBank. The accession numbers of the data used in this paper can be found in Table 1.

Results

Taxonomy

Family Myrmeleontidae Latreille, 1802
Subfamily Dendroleontinae Banks, 1899

Genus *Nuglerus* Navás, 1912

Nuglerus Navás, 1912: 245. Type species: *Nuglerus scalaris* Navás, 1912, by original designation.

Bofia Navás, 1915: 383. Type species: *Bofia maculata* Navás, 1915, by original designation. Synonymized by Banks 1931: 388.

Diagnosis. Adult: Antenna longer than combined length of head and thorax. Pronotum twice as long as wide. Mesoprescutum and mesonotum each anteriorly covered with a pair of tufts of long setae. Fore femur nearly as long as combined length of head and prothorax; fore tibia longer than combined length of head and prothorax. Basal tarsomere longer than combined length of tarsomeres 2–4, but shorter than combined length of tarsomeres 2–5. Poststigmal area of wings with thickened (slightly raised, Fig. 11C, D) markings. Forewing subcostal area with a continuous, regularly arranged series of spots and small dots; RP origin basal to MP and CuA fork; MP originates proximally to CuA fork. Hindwing normally with two presectoral crossveins. Only forewing anterior Banksian line present. Male pilula axillaris present. Miller's organ absent. Male gonocoxites 9 as a pair of plate-like structures; gonocoxites 11 wide and arched. Female with one pair of gonocoxites 8; anterior part of gonocoxites 9 with setose plate. **Larva:** Anterior margin of clypeo-labrum with a few short truncate dolichasters. Mandible not upturned. Some thoracic setiferous processes digitiform. Tuft of hair-like black setae on mesonotum absent. Odontoid process on ventral segment 8 absent. Segment 9 longer than wide, triangular in ventral view. Rastra and digging setae on segment 9 weakly developed.

Included species. *Nuglerus dispar* (Banks, 1934), comb. nov., *Nuglerus guimaraesae* Zheng, Badano & Liu,

Table 1. Molecular sampling information of the present analysis.

Species	Voucher ID	Material collected location	GenBank accession number	Remarks
Nuglerus maculatus	NMYB	CHINA: Yunnan, Xishuangbanna, Mengla County, Menglun Town, Mengxing Village, 600 m (ZCAU)	PZ155522	Sequencing data from present study
Nuglerus insignis	NUGIPHL1	THE PHILIPPINES: Palawan, Roxas (ZCAU)	PZ155524	Sequencing data from present study
Nuglerus insignis	NUGIPHL2	THE PHILIPPINES: Palawan, Roxas (ZCAU)	PZ155525	Sequencing data from present study
Nuglerus ruzzieri	NUG_IND	INDONESIA: Sulawesi, Pangia (MSNG)	PZ155523	Sequencing data from present study
Nuglerus maizuqii	NUGMAI	MALAYSIA: Pahang, downhill road from Bukit Fraser, 3°42'N, 101°46'E, 790 m (IZCAS)	PZ276962	Sequencing data from present study
Nuglerus shihongliangi	NUGSHI	INDONESIA: Bali Is., Buleleng, Pejarakan (IZCAS)	PZ276961	Sequencing data from present study
Layahima chiangi	LCXZ1	CHINA: Tibet, Nyingchi, Zayu County, Cawarong Township, Ridong, 1930 m (IZCAS)	PV083857	Obtained from Zheng et al. (2025b)
Layahima chiangi	LCXZ2	CHINA: Tibet, Nyingchi, Zayu County, Cawarong Township, Ridong, 1930 m (IZCAS)	PV083858	Obtained from Zheng et al. (2025b)

Table 2. The genetic divergences among specimens analyzed in this study.

	1	2	3	4	5	6	7
1. *Nuglerus maculatus* (NMYB)							
2. *Nuglerus insignis* (NUGIPHL1)	0.146						
3. *Nuglerus insignis* (NUGIPHL2)	0.144	0.012					
4. *Nuglerus ruzzieri* (NUG_IND)	0.098	0.141	0.141				
5. *Nuglerus maizuqii* (NUGMAI)	0.122	0.118	0.122	0.134			
6. *Nuglerus shihongliangi* (NUGSHI)	0.110	0.149	0.142	0.150	0.154		
7. *Layahima chiangi* (LCXZ2)	0.152	0.166	0.161	0.172	0.165	0.166	
8. *Layahima chiangi* (LCXZ1)	0.146	0.161	0.157	0.167	0.161	0.161	0.005

sp. nov., *Nuglerus insignis* Banks, 1939, stat. rev., *Nuglerus maculatus* (Navás, 1915), *Nuglerus maizuqii* Zheng, Badano & Liu, sp. nov., *Nuglerus pustulatus* (McLachlan, 1867), *Nuglerus ruzzieri* Badano & Zheng & Liu, sp. nov., *Nuglerus shihongliangi* Zheng, Badano & Liu, sp. nov.

Distribution. China, India, Indonesia, Malaysia, Sri Lanka, Thailand, the Philippines, Vietnam.

Biology. *Nuglerus* has only been recorded from tropical rainforests of the Oriental region. Larval biology can see the section of *N. maizuqii* sp. nov.

Key to species of *Nuglerus*

1 Thickened brown marking on poststigmal area semicircular (Figs 2A, 15A, F). Forewing radial, mediocubital, and cubital areas with many brown spots (Fig. 2A)..... *N. dispar* (Banks), comb. nov.
– Thickened brown marking on poststigmal area ovoid or circular. Forewing radial and cubital areas mostly hyaline..... 2
2 Vertex mostly dark brown (Figs 13C). Wings narrow; forewing maximum width shorter than 1/3 of forewing length (Figs 1F, 13A); rhegma indistinct (Figs 1F, 13A)..... *N. ruzzieri* Badano & Zheng & Liu, sp. nov.
– Vertex brown or yellowish brown, with some dark brown markings. Wings broad; forewing maximum width longer than 1/3 of forewing length; rhegma distinct..... 3
3 Vertex mostly yellowish brown, posteriorly with a discontinuous transverse dark brown band (Fig. 3B, C). Pronotum generally yellowish brown, with a few indistinct brownish markings (Fig. 3C)..... *N. guimaraesae* Zheng, Badano & Liu, sp. nov.
– Vertex yellowish brown, anteriorly and posteriorly with some dark brown markings. Pronotum with some distinct dark brown markings..... 4
4 Forewing mediocubital crossveins each with wide spots, about as long as wide; forewing cubital area basally with an oblique dark brown marking (Fig. 12A, C)..... *N. pustulatus* (McLachlan)
– Forewing mediocubital crossveins each with relatively narrow spots; marking on forewing basal cubital area relatively rounded..... 5
5 Wings marking distal to rhegma absent (Figs 4A, B, 5A, 15C, H)..... *N. insignis* Banks, stat. rev.
– Wings marking distal to rhegma present..... 6
6 Mesonotum mostly dark brown (Fig. 14C). Forewing radial area with many infuscations on veins (Figs 1G, 14A); thickened marking on poststigmal area circular and small (Figs 1G, 15N, S)..... *N. shihongliangi* Zheng, Badano & Liu, sp. nov.
– Mesonotum generally yellow or pale yellow with some dark markings. Forewing radial area mostly hyaline; thickened marking on poststigmal area ovoid and larger..... 7
7 Antenna dark brown (Fig. 7A). Pronotum without marking on anteromedial margin; mesoscutellum generally pale yellow (Fig. 7C). Fore- and mid-tarsomere 5 generally dark brown (Fig. 7A). Thickened marking on poststigmal area extending slightly into apical part of radial area (Figs 1E, 7A, 15E). Female gonocoxites 8 relatively wide and long (Fig. 7D, E)..... *N. maizuqii* Zheng, Badano & Liu, sp. nov.
– Non-swollen part of antennal flagellum basally and medially dark brown, distally yellowish brown (Fig. 6A). Pronotum with curved marking on anteromedial margin; yellowish mesoscutellum medially with a large dark brown marking (Fig. 6C). Fore- and mid tarsomere 5 generally pale yellow, distally dark brown (Fig. 7A). Thickened marking on poststigmal area extending distinctly into apical part of the radial area (Figs 1C, D, 6A, 15D)..... *N. maculatus* (Navás)

Nuglerus dispar (Banks, 1934), comb. nov.

Figs 2, 15A, F

Acratoleon dispar Banks, 1934: 571 (type locality: Malaysia: Sabah, Mt. Kinabalu, Lumu Lumu; holotype in NHMUK). New 2003: 175 (*Acratoleon*). Stange 2004: 124 (*Acratoleon*).

Diagnosis. Vertex generally dark brown, medially and posteromedially with small yellowish-brown markings. Pronotum laterally with a pair of discontinuous slender dark lines and a pair of discontinuous wide dark stripes. Poststigmal area of wings with a semicircular thickened

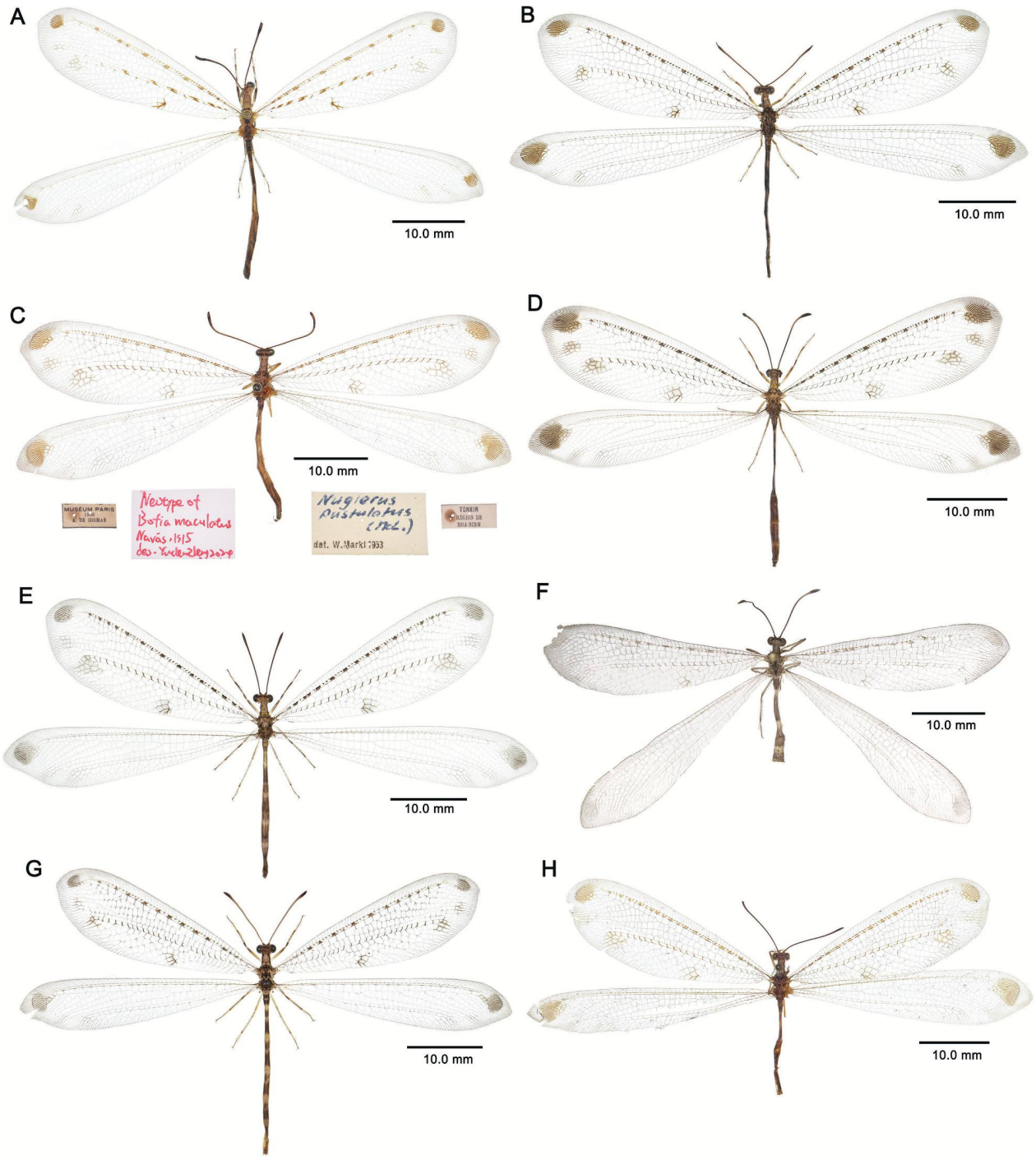


Figure 1. Habitus of *Nuglerus* spp., females. **A.** *N. guimaraesae* Zheng, Badano & Liu, sp. nov., holotype, Coimbatore (India); **B.** *N. insignis* Banks, 1939, stat. rev., Palawan (Philippines); **C.** Neotype of *Bofia maculata* Navás, 1915 (herein designate) (current name: *Nuglerus maculatus* (Navás, 1915)), Hoa Binh (Vietnam); **D.** *N. maculatus* (Navás, 1915), Yunnan (China); **E.** *N. maizuqii* Zheng, Badano & Liu, sp. nov., Pahang (Malaysia); **F.** *N. ruzzieri* Badano, Zheng & Liu, sp. nov., holotype, Sulawesi (Indonesia); **G.** *N. shihongliangi* Zheng, Badano & Liu, sp. nov., Bali Is. (Indonesia); **H.** *Nuglerus* sp., East Kalimantan (Indonesia).

brown marking. Forewing radial, mediocubital, and cubital areas with many brown spots. Hindwing rhegma and a marking distal to rhegma distinct.

Re-description. ***Head.*** Vertex generally dark brown, only medially and posteromedially with small yellowish-brown markings. Scape and pedicel mostly brown; non-swollen part of flagellum brown in the basal half, gradually yellow in the distal half, swollen part of flagellum dark brown (Fig. 2A, B). Scape surrounded by dark brown marking. Frons medially with short longitudinal dark brown stripe. Clypeus and labrum pale brown. Maxillary palpus pale brown. Labial palpus generally pale brown, distal palpomere fusiform and brown. Mandible brown with distal half dark reddish brown.

Thorax. Pronotum yellowish brown, with a lateral pair of discontinuous slender dark lines and a pair of

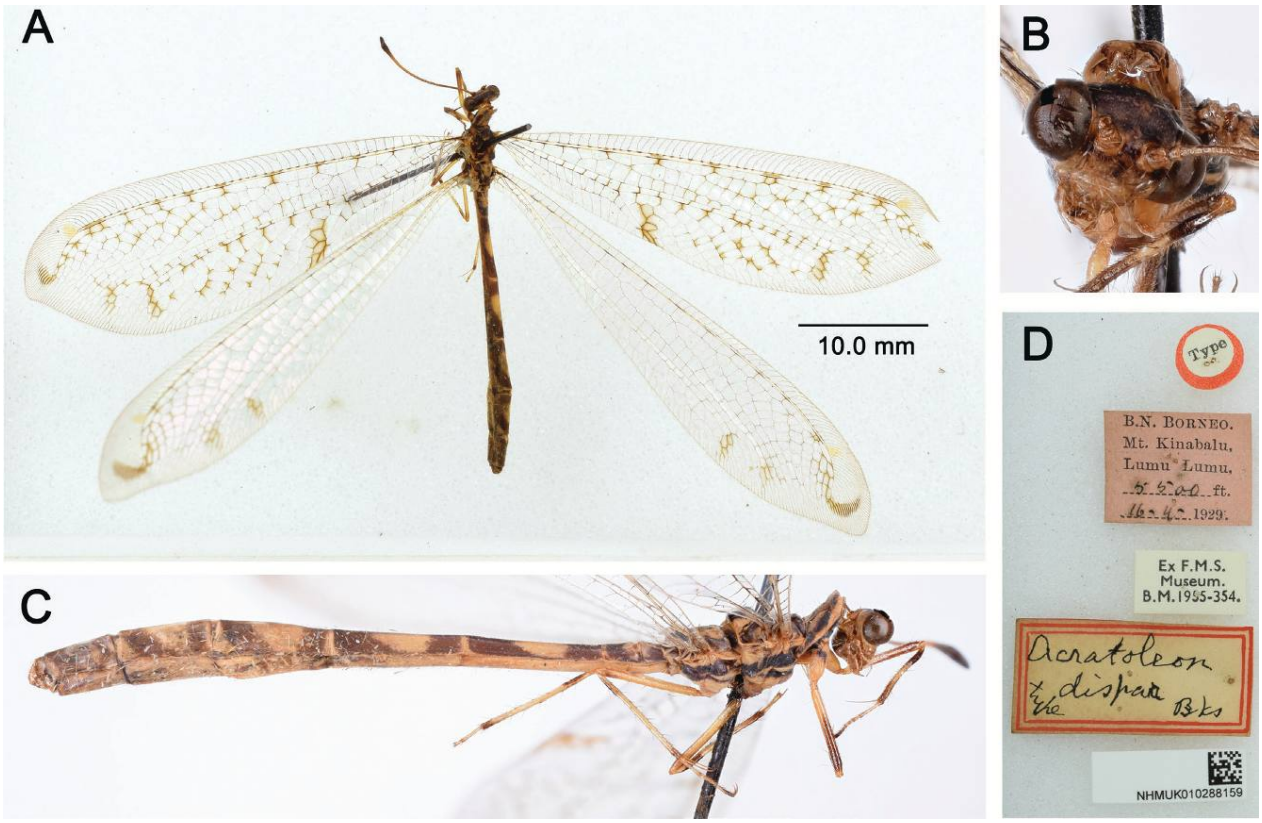


Figure 2. Holotype of *Acratoleon dispar* Banks, 1934 (current name: *Nuglerus dispar* comb. nov.), female, Sabah (Malaysia). **A.** Habitus; **B.** Head, frontal view; **C.** Body, lateral view; **D.** Labels. (Photos by Benjamin W. Price).

discontinuous wide dark stripes. Mesoprescutum generally dark brown; mesonotum generally dark brown with a few yellowish-brown spots; mesoscutellum dark brown, laterally with a pair of yellowish-brown markings. Metanotum medially yellowish brown, laterally dark brown; metascutellum dark brown, laterally with a pair of yellowish-brown spots. Pleurae yellowish-brown and black (Fig. 2A, C).

***Legs*.** Long and slender, with many setae. All tibial spurs long, distally curved; tarsomeres 1–4 generally pale yellow with distal part dark brown; tarsomere 5 basally pale yellow, distally dark brown, nearly as long as entire length of tarsomeres 2–4; pretarsal claws curved, reddish brown. Foreleg: coxa pale yellowish brown, basally with black spot; femur basally pale yellow, medially and distally dark brown; tibia pale yellow, basally and distally dark brown; tibial spurs reaching base of tarsomere 3. Midleg: Similar to foreleg. Hindleg: coxa generally pale yellowish-brown, black basally; femur generally pale yellow, with distal part dark brown; tibia pale yellow, basally and distally dark brown; tibial spurs reaching base of tarsomere 3; tarsomere 1 longer than that of fore- and midleg (Fig. 2C).

***Wings*.** Long with rounded apex. Forewing with anterior Banksian line. Pterostigma pale yellow. Poststigmal area with a semicircular thickened brown marking (Fig. 15A, F). Forewing shorter than hindwing. Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; radial, mediocubital, and cubital areas with many brown spots; rhegma as an oblique brown marking, distally with a smaller marking nearly fused to rhegma (Fig. 15A); cubital area basally with a distinct oblique dark brown marking; RP origin basal to MP and CuA fork; MP originates proximally to CuA fork; three presectoral crossveins present, with two biareolate cells; RP with nine branches. Hindwing distal radial area with some indistinct brown markings; rhegma as a brown marking, posteriorly with a brown marking (Fig. 15E); presectoral area with two to three crossveins (Fig. 2A).

***Abdomen*.** Tergum 2 anteriorly dark brown, posteriorly yellowish brown; tergum 3 anteriorly yellowish brown, posteriorly dark brown; terga 3–8 dark brown, each medially with a yellowish long ovoid marking (Fig. 2A, C). ***Male genitalia*.** Unknown. ***Female genitalia*.** With a pair of short digitiform gonocoxites 8 (Fig. 2C); other characters unexamined.

Type material. ***Holotype*** • ♀, Malaysia: "Type" // "B. N. BORNEO. Mt. Kinabalu, Lumu Lumu, 5500 ft. 16–4–1929." = Sabah, Ranau, Kinabalu Park, Kiau Gap View Monument, ca. 1700 m, 16.IV.1929 // "Ex F. M. S. Museum. B. M. 1955-354." // "Acratoleon dispar type Bks" // "NHMUK010288159" (NHMUK).

Distribution. Malaysia (Sabah).

Remarks. This species was originally assigned to *Acratoleon* Banks, 1915 (Nemoleontinae) (Banks 1939). The examination of the holotype revealed that it belongs to *Nuglerus* displaying all the diagnostic characters of

this genus. Moreover, we examined the holotype of *A. flavum* Banks, 1915, the type species of *Acratoleon*, from the Solomon Islands. In *A. flavum*, the forewing 2A bends at a sharp angle toward 3A, confirming that it is a member of Nemoleontinae and closely related to Protoplectrini from Australian Region. Therefore, *A. dispar* should be regarded as a species of *Nuglerus* (Dendroleontinae) and is here transferred to the latter under the new combination: *N. dispar* comb. nov.

This species can be readily distinguished from congeners by the semicircular thickened brown marking on the wing poststigmal area, and by the many brown spots on the forewing radial, mediocubital, and cubital areas.

Nuglerus guimaraesae Zheng, Badano & Liu, sp. nov.

https://zoobank.org/9579DDE8-3FE2-47BB-910D-3BD394791A6E

Figs 1A, 3, 15B, H

Diagnosis. Vertex yellowish brown, posteriorly with discontinuous transverse dark brown band. Pronotum generally yellowish brown, with few indistinct brownish markings. Mesoprescutum and mesonotum dark brown, each with a pair of yellowish-brown markings. Poststigmal area of wings with a circular thickened brown marking. Spots on forewing mediocubital crossveins wide, about twice as long as wide. Forewing and hindwing rhegma indistinct, marking distal to rhegma smaller. Female pregenital plate digitiform, sclerotized; anterior part of gonocoxites 9 with a linguiform setose plate.

Description. Size. Head width: 2.88–2.92 mm; forewing length: 30.21–31.82 mm; hindwing length: 31.45–32.92 mm.

***Head*.** Vertex yellowish brown, posteriorly with discontinuous transverse dark brown band. Scape dorsally dark brown, ventrally pale brown; pedicel dark brown; non-swollen part of flagellomeres dark brown medially, distally and basally yellowish brown, swollen part of flagellum dark brown, dorsally with a longitudinal brown stripe. Narrow dark brown marking around scape. Frons yellowish brown, medially with short longitudinal indistinct dark brown stripe. Clypeus and labrum pale yellowish brown. Maxillary palpus pale yellow. Labial palpus generally pale yellow, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Fig. 3B, C).

***Thorax*.** Pronotum generally yellowish brown, with a few indistinct brownish markings. Mesoprescutum and mesonotum dark brown, each with a pair of yellowish-brown markings and anteriorly covered with a pair of tufts of long setae; mesoscutellum dark brown, laterally with a pair of yellowish-brown stripes. Metanotum medially dark brown, laterally yellowish-brown; metascutellum dark brown. Pleurae yellowish-brown, with a wide dark brown stripe (Fig. 3C).

***Legs*.** Long and slender, with many setae. All tibial spurs long, distally curved; all tarsomeres basally pale yellow, distally dark brown; tarsomere 5 as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale yellow, anteriorly dark brown; femur basally pale yellow, medially and distally dark brown; tibia pale yellow, mediobasally and distally each with a dark brown marking; tibial spurs reaching base of tarsomere 3. Midleg: coxa pale yellow, other characters similar to foreleg. Hindleg: coxa pale yellow; femur mostly pale yellow, dorsally with a dark brown stripe; tibia pale yellow, distally dark brown; tibial spurs reaching distal part of tarsomere 2; tarsomere 1 longer than that of fore- and midleg (Fig. 3A).

***Wings*.** Long, apically rounded. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area with circular thickened brown marking (Fig. 15B, G). Forewing shorter than hindwing. Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; some mediocubital crossveins with brown spots nearly twice as long as wide; rhegma as an irregular brown marking, marking distal to rhegma smaller (Fig. 15B); cubital area basally with a distinct oblique brown marking; RP origin basal to MP and CuA fork; MP originates proximally to CuA fork; three to four presectoral crossveins present, with from one to three biareolate cells; RP with eight branches. Hindwing rhegma as an indistinct pale brownish marking, posteriorly with an indistinct oblique pale brownish marking (Fig. 15G); presectoral area with two crossveins (Figs 1, 3A).

***Abdomen*.** Tergum 2–3 generally dark brown; terga 3–8 dark brown, each medially with a yellowish ovoid marking (Fig. 1A). ***Male genitalia*.** Unknown. ***Female genitalia*.** Pregenital plate as a digitiform sclerotized structure. Gonocoxites 8 short digitiform. Anterior part of gonocoxites 9 with a linguiform setose plate. Gonocoxites 9 and ectoproct with many stout acicular digging setae. Ectoproct ovoid in lateral view (Fig. 3D, E).

Type material. ***Holotype*** • ♀, India: "SOUTH INDIA Coimbatore Dist. P. S. Nathan" // "MARUDAMALAI HILLS 1800 ft. XII. 1968" // "RMNH. INS. 1473967" (RMNH). ***Paratypes*:** • 1♀, same information as holotype, "RMNH. INS. 1473969" (RMNH); • 1♀, India: "South India (Madras State) Coimbatore, 1400 ft. –3–1977 Th. R. Susa, Nathan" // "coll. J. A. W. Lucas acq. 1984" // "RMNH. INS. 1473968" (RMNH).

Distribution. India (Tamil Nadu).

Etymology. This new species is dedicated to Ms. Monica Guimaraes Cruz, curator at RMNH, in recognition of her assistance to Yuchen Zheng in examining the RMNH collections, including facilitating the study of this new species.

Remarks. *Nuglerus guimaraesae* can be readily distinguished from congeners by the following characters: 1) pronotum largely yellowish brown; 2) thickened marking of poststigmal area circular and smaller than other species; 3) spots on forewing mediocubital crossveins broader than other species (about twice as long as wide); 4) female pregenital plate shaped as a digitiform sclerotized structure. This new species might be endemic to the tropical rainforests of the Western Ghats.

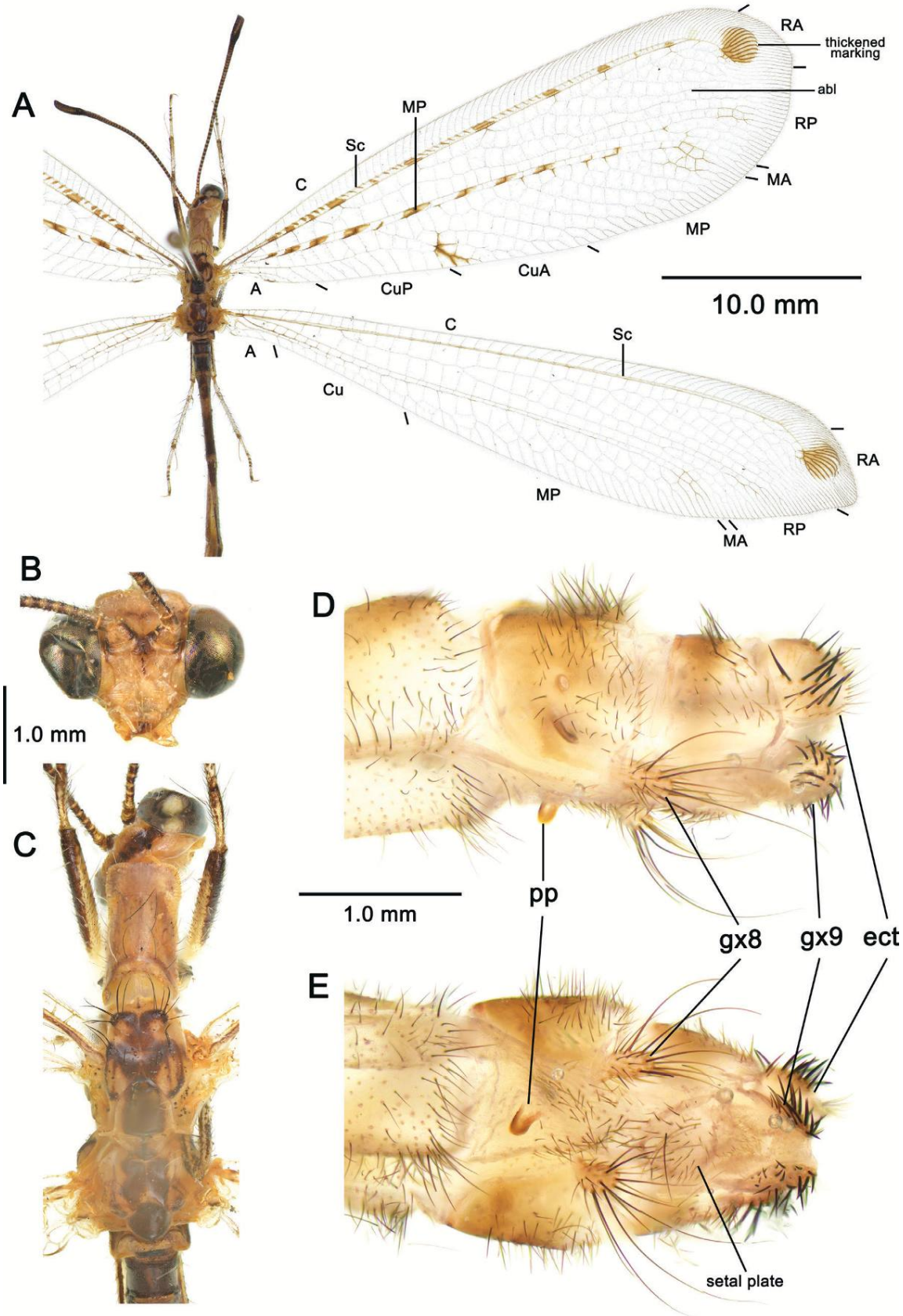


Figure 3. *Nuglerus guimaraesae* Zheng, Badano & Liu, sp. nov., holotype, female, Coimbatore (India). **A.** Habitus; **B.** Head, frontal view; **C.** Head and thorax, dorsal view; female terminalia (**D**, **E**): **D.** Lateral view; **E.** Ventral view. Abbreviations of terms of wing venation: A: anal veins; abl: anterior Banksian line C: costa; CuA: cubitus anterior; CuP: cubitus posterior; MA: media anterior; MP: media posterior; RA: radius anterior; RP: radius posterior; Sc: subcostal. Abbreviations of terms of terminalia: ect: ectoprocts, gx: gonocoxites, pp: pregenital plate.

Nuglerus insignis Banks, 1939, stat. rev.

Figs 1B, 4, 5, 15C, H

Nuglerus insignis Banks, 1939 (type locality: the Philippines: Los Baños, Mt. Makiling; holotype in MCZ). Baltazar 1990: 29 (*Nuglerus*). Stange 2004: 97 (*Nuglerus*). Synonymized by Krivokhatsky 2015: 700.

Diagnosis. Vertex anteriorly with slender dark brown band, posteriorly with a pair of fused round dark brown markings. Pronotum brown, with a median Y-shaped yellowish-brown marking, posterolaterally with a pair of long triangular yellowish-brown markings. Meso- and metanotum generally dark brown, with a few brown and yellowish-brown markings. Poststigmal area of wings with a round thickened dark brown marking, barely extending into radial area. Spots on forewing mediocubital crossveins narrow. Forewing and hindwing rhegma as an indistinct dark brown marking, marking distal to rhegma absent. Female pregenital plate as a small triangular sclerotization; anterior part of gonocoxites 9 with a rounded setose sclerotized plate.

Description. Size. Head width: 2.94–3.02 mm; forewing length: 31.78–32.12 mm; hindwing length: 33.11–33.95 mm.

Head. Vertex yellowish brown, anteriorly with a slender dark brown band, posteriorly with a pair of fused ovoid dark brown markings. Scape and pedicel dark brown; non-swollen part of all flagellomeres dark brown, distally yellowish brown, swollen part of flagellum dark brown. Scape surrounded by dark brown marking. Frons pale yellowish brown, with a short median longitudinal dark brown stripe. Clypeus and labrum pale yellowish brown. Maxillary palpus pale yellow. Labial palpus generally pale yellow, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Figs 4E, F, 5B, C).

Thorax. Pronotum brown, medially with a Y-shaped yellowish-brown marking, posterolaterally with a pair of long triangular yellowish-brown markings. Mesoprescutum and mesonotum each anteriorly covered with a pair of tufts of long setae; mesoprescutum dark brown, with a pair of yellowish-brown spots; mesonotum generally dark brown, lateral margin with a pair of longitudinal yellowish-brown stripes; mesoscutellum dark brown, anteriorly and posteriorly each with a pair of yellowish brown spots. Metanotum and metascutellum generally dark brown. Pleurae yellowish-brown, with a wide dark brown stripe (Figs 4F, 5C).

Legs. Long and slender, with many setae. All femora pale yellow, medially and distally brown; tibial spurs long, distally curved; tarsomeres each pale yellow, distally dark brown; tarsomere 5 about as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale yellow, anteriorly dark brown; tibia pale yellow, mediobasally and distally each with a brown marking; tibial spurs reaching middle of tarsomere 3. Midleg: coxa pale yellow, other characters

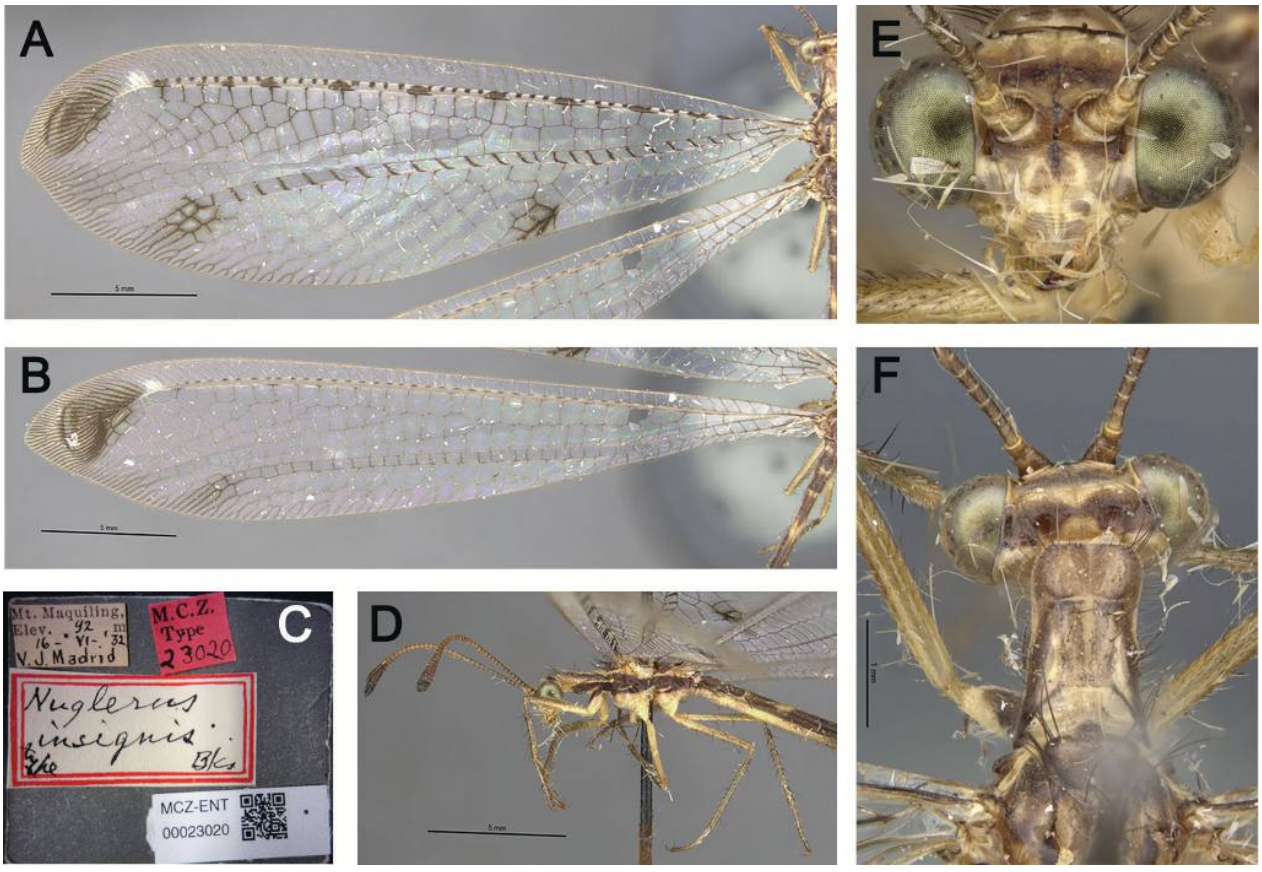


Figure 4. Holotype of *Nuglerus insignis* Banks, 1939, stat. rev., female, Los Baños (the Philippines). **A.** Forewing; **B.** Hindwing; **C.** Labels; **D.** Head and thorax, lateral view; **E.** Head, frontal view; **F.** Head and thorax, dorsal view. (Photos by Crystal A. Maier).

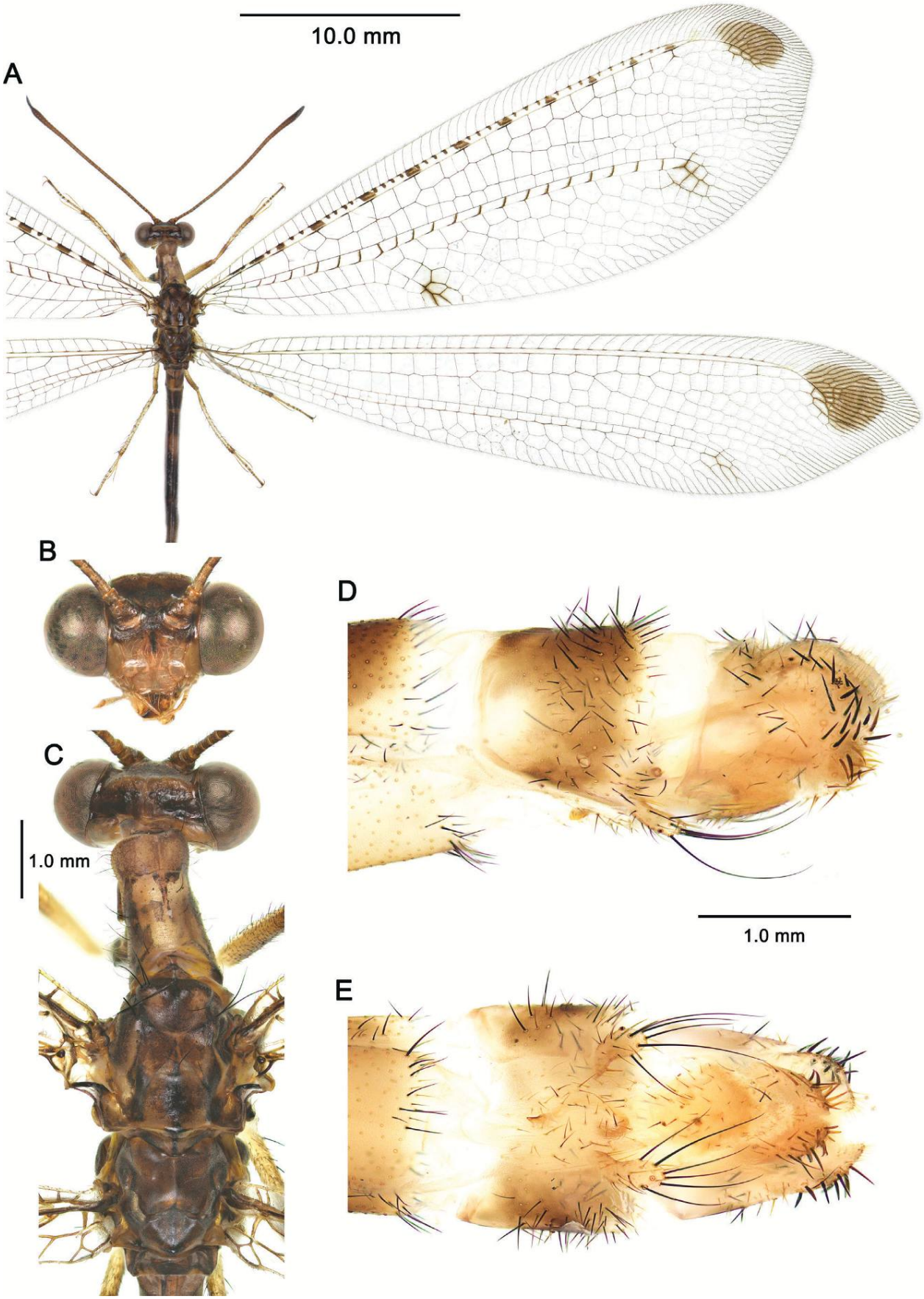


Figure 5. *Nuglerus insignis* Banks, 1939, stat. rev., female, Palawan (the Philippines). **A.** Habitus; **B.** Head, frontal view; **C.** Head and thorax, dorsal view; female terminalia (**D**, **E**): **D.** Lateral view; **E.** Ventral view.

similar to foreleg. Hindleg: coxa pale yellow; tibia pale yellow, distally brown; tibial spurs reaching base of tarsomere 3; tarsomere 1 longer than that of fore- and midleg (Figs 4D, 5A).

***Wings*.** Long ovoid. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area with an ovoid thickened dark brown marking, barely extending into radial area. Forewing shorter than hindwing (Fig. 15C, H). Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; mediocubital crossveins each with narrow spots; rhegma as an indistinct dark brown marking, without marking distal to rhegma (Fig. 15C); cubital area basally with a dark brown marking; RP origin basal to MP and CuA fork; MP originates proximally to CuA fork; three presectoral crossveins present, with from one to two biareolate cells; RP with seven to eight branches. Hindwing rhegma as an indistinct dark brown marking, without marking posterior to rhegma (Fig. 15H); presectoral area with two crossveins (Figs 1B, 5A).

***Abdomen*.** Tergum 2 anteriorly dark brown, posteriorly yellowish brown; tergum 3 dark brown; terga 4–8 dark brown, each medially with a yellowish ovoid marking (Fig. 1B). ***Male genitalia*.** Unknown. ***Female genitalia*.** Pregenital plate as a small triangular sclerotized structure. Gonocoxites 8 short digitiform. Anterior part of gonocoxites 9 with a rounded setose sclerotized plate. Gonocoxites 9 and ectoproct with many stout acicular digging setae. Ectoproct ovoid in lateral view (Fig. 5D, E).

Type material. ***Holotype*** • ♀, The Philippines: "Mt. Maquiling, Elev. 92, m 16–VI–32 V. J. Madrid" = Luzon, Los Baños, Mt. Makiling // "M.C.Z. Type 23020" // "Nuglerus insignis type Bks" // "MCZ-ENT 00023020" (MCZ).

Additional material examined. • 2♀, The Philippines: Palawan, Roxas (ZCAU).

Distribution. Philippines (Luzon, Palawan).

Remarks. Krivokhatsky (2015) treated *N. insignis* as a junior synonym of *N. maculatus*. However, based on our examination of the type material and further specimens, we treat *N. insignis* as a valid species. *N. insignis* is characterized by mesonotum mostly dark brown, thickened dark marking on poststigmal area of forewing barely extending into radial area, absence of marking distal to rhegma, and setose plate anterior to female gonocoxites 9 sclerotized. Instead, *N. maculatus* is distinguished by the mesonotum is mostly yellowish brown, the thickened dark marking on poststigmal area of forewing extending distinctly into apical part of radial area, presence of a dark brown marking distal to rhegma, and setose plate anterior to female gonocoxites 9 unsclerotized. These two species are also allopatric: *N. insignis* is distributed in the Philippine Islands, whereas *N. maculatus* occurs in Indochina. Moreover, our COI barcode results indicate that *N. insignis* and *N. maculatus* are clearly distinct species (Fig. 16). We therefore restore *N. insignis* **stat. rev.** as a valid species.

Nuglerus maculatus (Navás, 1915)

Figs 1C, D, 6, 15D, I

Bofia maculata Navás, 1915 (type locality: Vietnam: Tay Ninh (original)/ Hoa Binh (present); holotype lost, neotype in MNHN). Navás 1923: 38 (*Nuglerus*). Banks 1931: 388 (*Nuglerus*). Stange 1976: 301 (*Nuglerus*). New 2003: 179 (*Nuglerus*). Stange 2004: 97 (*Nuglerus*). Krivokhatsky 2015: 700 (*Nuglerus*).

Chinese common name. 硕斑泡蚁蛉.

Diagnosis. Vertex anteriorly with a dark brown band, posteriorly with a pair of fused ovoid dark brown markings. Pronotum yellowish brown, margins with a pair of long annular dark brown stripes. Mesonotum generally yellow, with a few dark brown markings; mesoscutellum yellow, with a median dark brown marking. Poststigmal area of wings with an ovoid thickened dark brown marking, extending distinctly into apical part of radial area. Spots on forewing mediocubital crossveins narrow. Forewing rhegma as a rounded dark brown marking, with a smaller rounded marking distal to rhegma. Hindwing rhegma and the marking distal to rhegma indistinct. Male gonocoxites 9 oblique sub-rectangular in ventral view (Krivokhatsky 2015). Female pregenital plate tiny, cone-shaped; anterior part of gonocoxites 9 with a sub-rectangular setose plate.

Re-description of adult. Size. Head width: 2.84–2.98 mm; forewing length: 28.46–31.22 mm; hindwing length: 29.76–32.74 mm.

***Head*.** Vertex yellowish brown, anteriorly with a dark brown band, posteriorly with a pair of fused ovoid dark brown markings. Scape and pedicel dark brown; non-swollen part of flagellum basally and medially dark brown, distally yellowish brown; swollen part of flagellum dark brown. Scape surrounded by dark brown marking. Frons pale yellowish brown, medially with short longitudinal dark brown line. Clypeus and labrum pale yellowish brown. Maxillary palpus pale yellow. Labial palpus generally pale yellow, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Fig. 6B, C).

***Thorax*.** Pronotum yellowish brown, margin with a pair of long annular dark brown stripes. Anterior part of both mesoprescutum and mesonotum with a pair of tufts of long setae; mesoprescutum yellow, anterolaterally and posteriorly each with a pair of dark brown markings; mesonotum generally yellowish brown, anterior and posterior margins with a pair of dark brown markings; mesoscutellum yellow, with a median dark brown marking. Metanotum generally dark brown, with a pair of yellowish-brown markings; metascutellum dark brown. Pleurae yellowish-brown, with a wide dark brown stripe (Fig. 6C).

***Legs*.** Long and slender, with many setae. All femora pale yellow, dorsally with a dark brown stripe; tibial spurs long, distally curved; tarsomeres each pale yellow, distally dark brown; tarsomere 5 about as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale yellow, anteriorly dark brown; tibia pale yellow, mediobasally with a brown marking, distally brown; tibial spurs reaching mid of tarsomere 3. Midleg: coxa

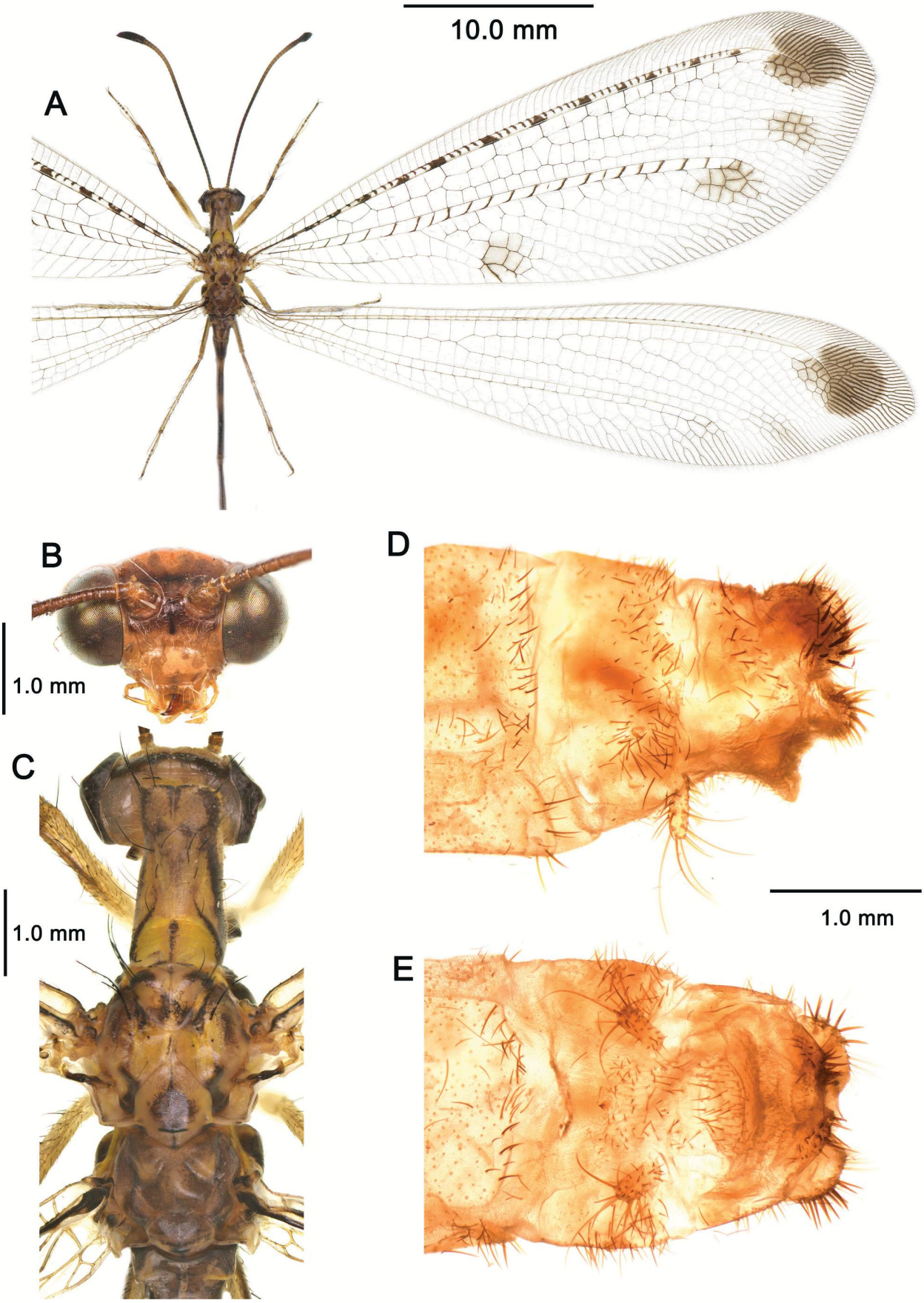


Figure 6. *Nuglerus maculatus* (Navás, 1915), female. **A.** Habitus, Yunnan (China); **B.** Head, frontal view, neotype, Hoa Binh (Vietnam); **C.** Head and thorax, dorsal view, Yunnan (China); female terminalia (**D, E**), Yunnan (China): **D.** Lateral view; **E.** Ventral view.

pale yellow, other characters similar to foreleg. Hindleg: coxa pale yellow; tibia pale yellow, distally brown; tibial spurs reaching base of tarsomere 3; tarsomere 1 longer than that of fore- and midleg (Fig. 6A).

***Wings*.** Long, with rounded apex. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area with an ovoid thickened dark brown marking, extending distinctly into apical part of the radial area (Fig. 15D, I). Forewing shorter than hindwing. Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; mediocubital crossveins each with narrow spots; rhegma as rounded dark brown marking, with a smaller rounded marking distal to rhegma (Figs 15D); cubital area basally with an indistinct rounded dark brown marking; RP origin basal to MP and CuA fork; MP basally not oblique, originates proximally to CuA fork; two to three presectoral crossveins present, with from one to two biareolate cells; RP with seven branches. Hindwing rhegma as an indistinct dark brown marking, with a slender indistinct marking distal to rhegma (Figs 15I); presectoral area with two crossveins (Figs 1C, D, 6A).

***Abdomen*.** Tergum 2 dark brown, medially with a pair of yellowish-brown spots; tergum 3 dark brown; terga 4–8 dark brown, each anterior margin with a yellowish marking; terga 4–6 each medially with a yellowish-brown spot. ***Male genitalia*.** Gonocoxites 9 oblique sub-rectangular in ventral view; rounded in latera view. Gonocoxites 11 widely arched. Ectoproct ovoid in lateral view (Krivokhatsky 2015). ***Female genitalia*.** Pregenital plate tiny coniform. Gonocoxites 8 short digitiform. Anterior part of gonocoxites 9 with a sub-rectangular setose plate. Gonocoxites 9 and ectoproct with many stout acicular digging setae. Ectoproct ovoid in lateral view (Fig. 6D, E).

Type material. ***Neotype*** • ♀, here designated, Vietnam: "TONKIN RÉGION DE HOA-BINH" // "MUSÉUM PARIS 1936 A. DE COOMAN" // "Neotype of Bofia maculatus Navás, 1915 des. Yuchen Zheng 2024" // "*Nuglerus pustulatus (McL.)* det. W. Markl 1953" (MNHN).

Additional material examined. • 3♀, same information as neotype (MNHN). • 2♀, China: Yunnan, Xishuangbanna, Mengla County [勐腊县], Mt. Kongmingshan [孔明山], 25.IX.1957, Lingchao Zang (IZCAS). • 1♀, China: Yunnan, Xishuangbanna, Mengla County, Menglun Town [勐仑镇], Mengxing Village [勐醒村], 600 m, 26.V.2023 (ZCAU). • 1♀, Thailand: Nakhon Ratchasima, Pak Chong District, Klang Dong, Station Suwan Farm. Env. 10 km Pak Chong, 27.IV.2000, Bruno Michel (CBGP). • 1♀, Thailand: "C. Siam 300m, Kwae Nor Riv Exp Ka Tha Lai 2–7.VI J.E. Jonkers 1946" = Kanchanaburi Province, Kwae Noi Basin, near Ka Tha Lai, Pan Paung River valley (RMNH).

Distribution. China (Yunnan), Vietnam (Bac Giang, Hoa Binh, Tay Ninh), Thailand (Nakhon Ratchasima, Kanchanaburi).

Remarks. *N. maculatus* is easily distinguished from the other species of *Nuglerus* by the pronotum and mesonotum being mostly yellowish brown, with a few dark markings present along the margins; and by the thickened marking on the forewing poststigmal area distinctly extending to the apex of the radial area.

Navás (1915) originally described this species from a single specimen from southern Vietnam and mentioned that this type was deposited in MNHG. However, when we contacted the curator of MNHG to locate this type, he informed us that the specimen is not deposited in MNHG and that there is no evidence that it was ever deposited there. Stange (1976, 2004) also indicated that the type of this species was lost. Moreover, the type information given by Krivokhatsky (2015) is clearly a translation of the original description rather than being based on his examination. Therefore, we designate another specimen from Vietnam in MNHN as the neotype (Fig. 1C).

Banks (1931) examined a specimen from the Malay Peninsula (Selangor) and identified it as "*N. maculatus*". We suspect that the record of Banks (1931) might refer to *N. maizuqii* sp. nov. rather than *N. maculatus*, based on the field sampling of YZ, although the possibility of another syntopic species cannot be excluded. We have also examined a specimen of *Nuglerus* from E. Kalimantan (material information: "E. Borneo Sangkoelirang Kaliorang V. 1937 J. W. Q. de Graaf" // "RMNH. INS. 1474026" (RMNH)) but missing terminalia (Figs 1H, 15O, T). This specimen differs from the typical *N. maculatus* and appears more similar to *N. insignis*. Krivokhatsky (2015: fig. 2) also examined a Sumatran specimen, which he identified as "*N. maculatus*", but it was severely damaged, and its wing markings were different from *N. maculatus* from Indochina. At present, we do not assign these Southeast Asian specimens (might also different species) to any species, waiting for new material from these areas to clarify their taxonomic affinities.

Nuglerus maizuqii Zheng, Badano & Liu, sp. nov.

https://zoobank.org/F8E72B5D-D274-414A-844F-885602BD431F

Figs 1E, 7–11, 15E, J

Diagnosis. Adult: Vertex anteriorly with an indistinct dark brown band, posteriorly with a dark brown band. Antenna dark brown. Pronotum pale yellow, lateral margin with a pair of dark brown stripes, medially with a few irregular and indistinct brownish markings. Mesonotum generally pale yellow, with a few dark brown markings; mesoscutellum mostly pale yellow. Fore- and mid tarsomere 5 dark brown. Poststigmal area of wings with ovoid thickened dark brown marking, extending slightly into apical part of radial area. Spots on forewing mediocubital crossveins narrow. Forewing rhegma as a rounded dark brown marking, with a smaller rounded marking distal to rhegma. Hindwing rhegma and marking distal to rhegma indistinct. Female pregenital plate tiny cone-shaped; gonocoxites 8 long digitiform. **Larva:** Head anteriorly with a curved transverse dark brown stripe, posteriorly with a pair of brown U-shaped markings in dorsal view; anteriorly with a pair of subtriangular dark brown markings in ventral view. Meso- and metathorax,

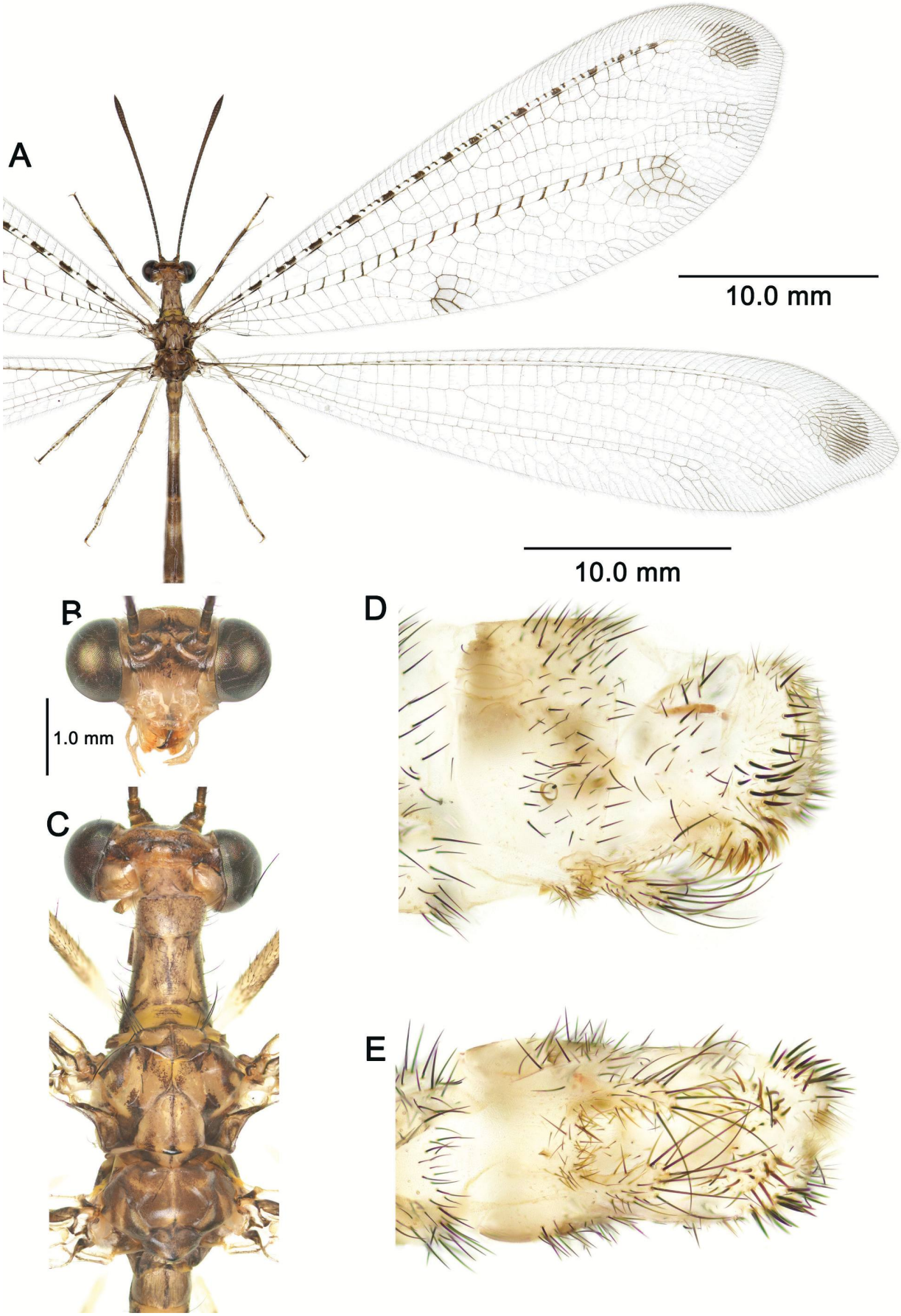


Figure 7. *Nuglerus maizuqii* Zheng, Badano & Liu, sp. nov., holotype, female, Pahang (Malaysia). **A.** Habitus; **B.** Head, frontal view; **C.** Head and thorax, dorsal view; female terminalia (**D, E**): **D.** Lateral view; **E.** Ventral view.

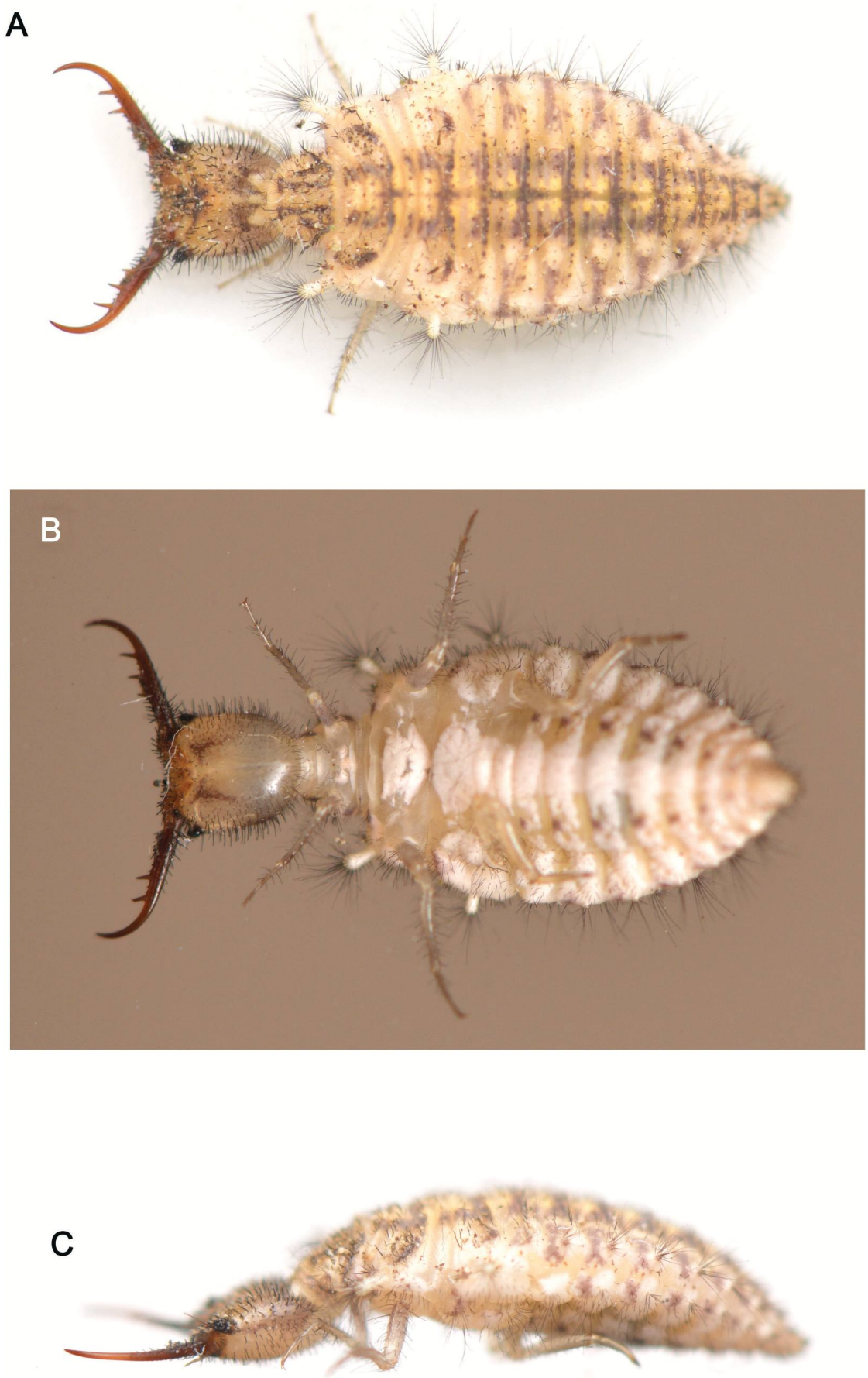


Figure 8. Habitus of *Nuglerus maizuqii* Zheng, Badano & Liu, sp. nov., 3rd instar larva, Pahang (Malaysia). **A.** Dorsal view; **B.** Ventral view; **C.** Lateral view.

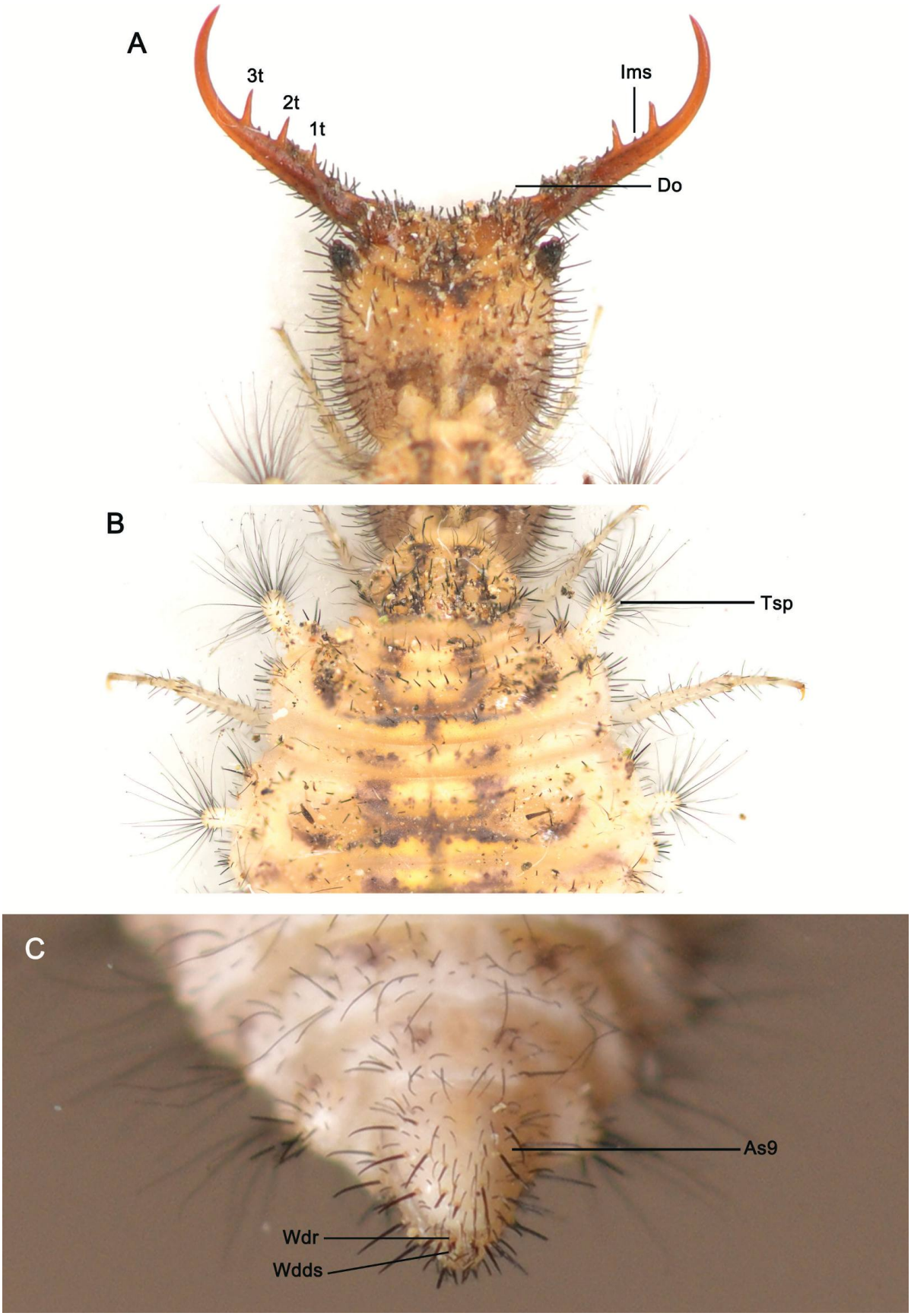


Figure 9. *Nuglerus maizuqii* Zheng, Badano & Liu, sp. nov., 3rd instar larva, Pahang (Malaysia). **A.** Head, dorsal view; **B.** Thorax, dorsal view; **C.** Terminal of abdomen, ventral view. Abbreviations of terms of larval characters: 1t: first tooth; 2t: second tooth; 3t: third tooth; Ims: interdental mandibular setae; Do: dolichaster; Tsp: thoracic setiferous processes; As9: abdominal segment 9; Wdr: weakly developed rastrum; Wdds: weakly developed digging setae.

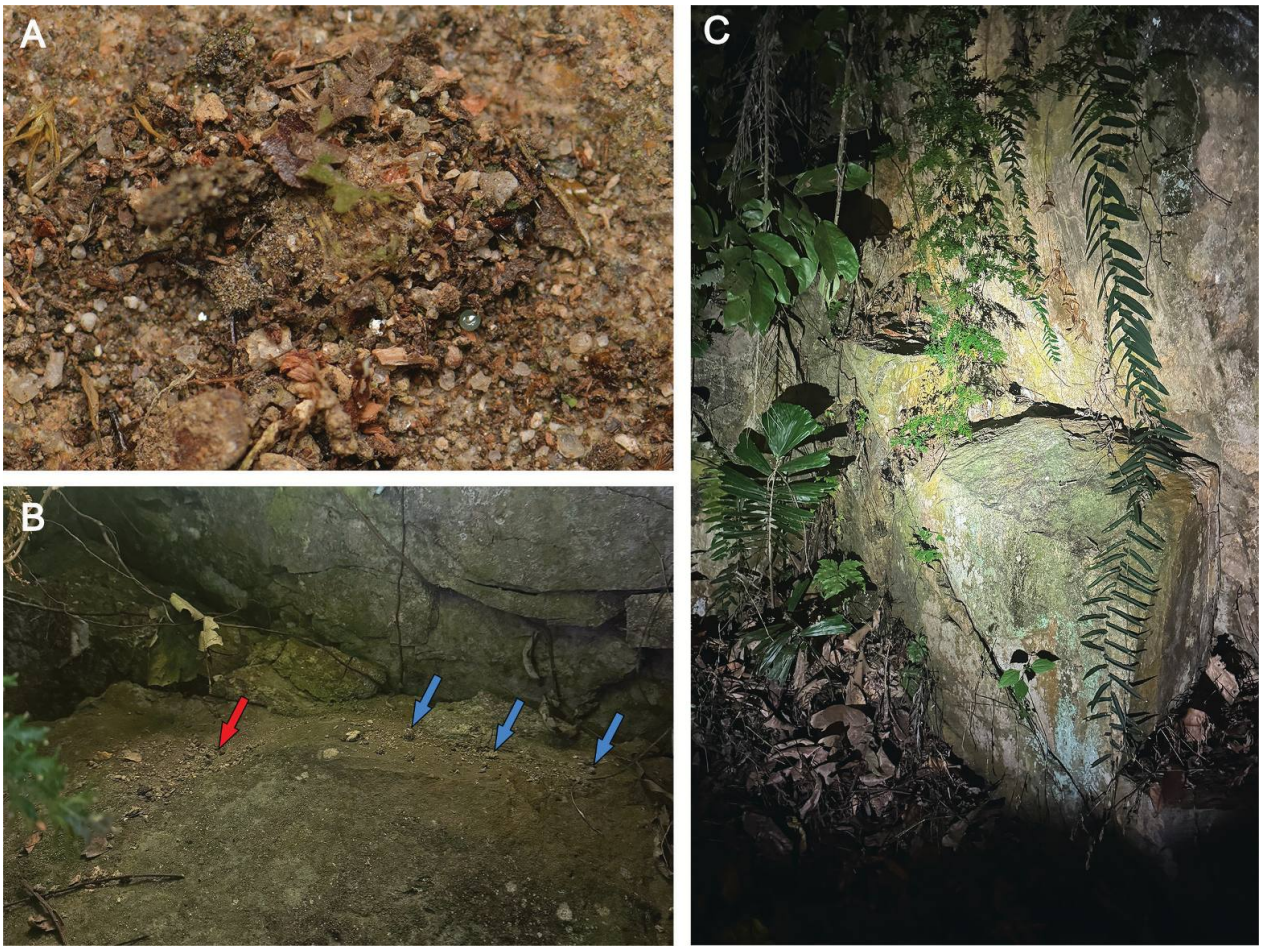


Figure 10. *Nuglerus maizuqii* Zheng, Badano & Liu, sp. nov., living larva and larval habitat, Pahang (Malaysia). **A.** 3rd instar larva in the microhabitat; **B.** Microhabitat (karst limestone platform), red arrow indicates the positions where the larvae was collected, blue arrows indicate the abandoned cocoons; **C.** THe overall environment of the larval habitat. (Photos by Yuchen Zheng).

and abdominal segments 2–8 each with a reversed arched dark brown band dorsally.

Description. Size. Head width: 2.70 mm; forewing length: 31.45 mm; hindwing length: 34.66 mm.

Head. Vertex anteriorly with an indistinct dark brown band, posteriorly with a dark brown band. Antenna dark brown. Scape surrounded by dark brown marking. Frons generally pale yellowish brown. Clypeus and labrum pale yellow. Maxillary palpus pale yellow. Labial palpus generally pale yellow, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Fig. 7B, C).

Thorax. Pronotum pale yellow, lateral margin with a pair of dark brown stripes, medially with a few irregular and indistinct brownish markings. Anterior part of both mesoprescutum and mesonotum with a pair of tufts of long setae; mesoprescutum dark brown, with a pair of large and fused yellowish markings; mesonotum generally pale yellow, anterior and posterior margins with a pair of dark brown markings, medially with a few irregular and indistinct brownish markings; mesoscutellum generally pale yellow. Metanotum generally dark brown, with two pairs of yellowish- brown markings; metascutellum dark brown. Pleurae yellowish-brown, with a wide dark brown stripe (Fig. 7C).

Legs. Long and slender, with many setae. All tibial spurs long, distally curved; tarsomere 5 about as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale yellow, anteriorly dark brown; femur generally brown, basally pale yellow; tibia dark brown, medially pale yellow; tibial spurs reaching base of tarsomere 3; tarsomeres 1–4 pale yellow, each dark brown distally, tarsomere 5 dark brown. Midleg: coxa pale yellow; femur pale yellow, distally brown; tibia pale yellow, basally with a dark brown marking, distally brown; other characters similar to foreleg. Hindleg: coxa pale yellow; femur pale yellow, externally brown; tibia pale yellow, distally brown; tibial spurs reaching base of tarsomere 3; tarsomeres 1–5 pale yellow, each dark brown distally; tarsomere 1 longer than that of fore- and midleg (Fig. 7A).

Wings. Long, with rounded apex. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area with an ovoid thickened dark brown marking, extending slightly into apical part of radial area (Figs 7A, 15E, J). Forewing shorter than hindwing. Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; mediocubital crossveins each with narrow spots; rhegma as rounded dark brown marking, with a smaller rounded marking distal to rhegma

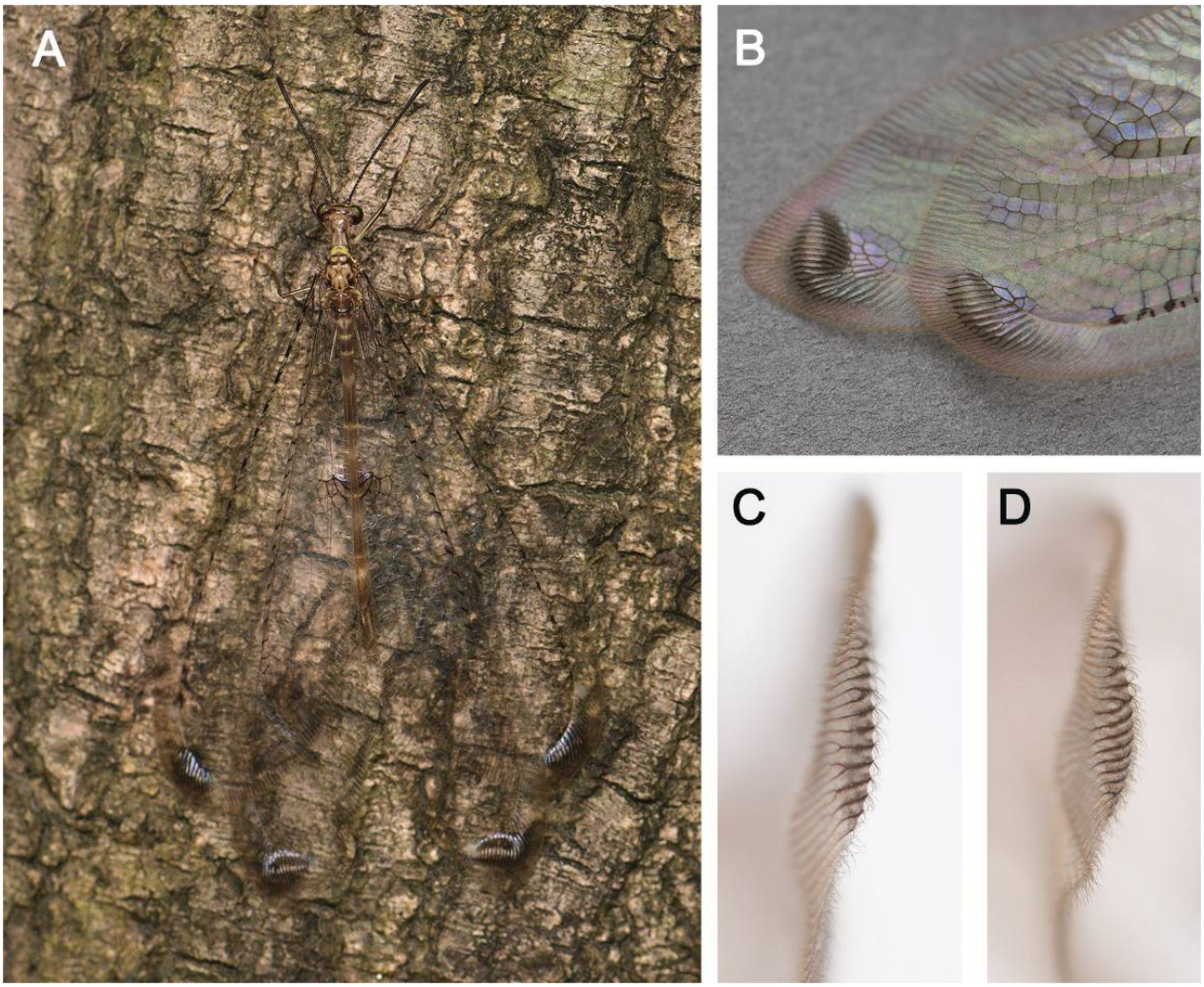


Figure 11. *Nuglerus maizuqii* Zheng, Badano & Liu, sp. nov., living adult, Pahang (Malaysia). **A.** Habitus; **B.** Distal wings of living adult; **C.** THickened markings on forewing poststigmal area, lateral view; **D.** Thickened markings on hindwing poststigmal area, lateral view. (Photos by Yuchen Zheng).

(Figs 7A, 15E); cubital area basally with an indistinct rounded dark brown marking; RP origin basal to MP and CuA fork; MP basally not oblique, originates proximally to CuA fork; three presectoral crossveins present, with from one biareolate cell; RP with seven branches. Hindwing rhegma as an indistinct dark brown marking, with a slender indistinct marking distal to rhegma (Figs 15J); presectoral area with two crossveins (Figs 1E, 7A).

***Abdomen*.** Tergum 2 dark brown, anterior and posterior margin pale yellow; terga 3–7 dark brown, each medially with a pale yellow marking. ***Male genitalia*.** Unknown. ***Female genitalia*.** Pregenital plate tiny coniform. Gonocoxites 8 long digitiform, curved. Gonocoxites 9 and ectoproct with many stout acicular digging setae. Ectoproct long fusiform in lateral view (Fig. 7D, E).

Description of 3rd instar larva. Size. Body length (excluding mandible): 8.24 mm; head length: 1.76 mm; head width: 1.54 mm; mandible length: 1.93 mm.

***Head*.** Nearly rectangular in dorsal view, longer than wide. Clypeo-labrum generally brown in dorsal view, medially with a dark brown marking; anterior margin barely concaved, with a row of dolichasters (Fig. 8A). Head pale yellow; in dorsal view, anteriorly with a curved transverse dark brown stripe, posteriorly with a pair of brown U-shaped markings, covered with many short stout setae (Figs 7A, 8A); in ventral view, anteriorly with a pair of subtriangular dark brown markings (Fig. 7B). Ocular tubercles black and small, slightly prominent. Antennae brown, filiform. Mandible not upturned (Fig. 7C), reddish brown, basally with around five interdental mandibular setae anterior to first tooth; first tooth present on nearly basal 1/3 part, shorter than second tooth; second tooth nearly as long as third tooth; 2 short interdental mandibular setae between first and second teeth; two short interdental mandibular setae between second and third teeth (Figs 7A, B, 8A). Labial palps pale.

***Thorax*.** Pronotum pale yellow, with a pair of long circular dark brown markings, dorsally with many short conical setae, anterolateral margin with long hair-like setae. Meso- and metathorax each with a reversed arched dark brown band. Mesothorax with spiracles present on short stout yellowish brown sclerotized tubercle; anterior

mesothoracic setiferous processes digitiform, posterior process reduced. Anterior metathoracic setiferous processes reduced, posterior process digitiform, shorter than anterior mesothoracic process. All setiferous processes distally with dense long slender setae (Figs 7A, B, 8B).

***Legs*.** Pale brown, with many slender setae (Fig. 7B, C).

***Abdomen*.** In dorsal view generally pale yellow, medially yellow, segments 2–8 each with a reversed arched dark brown band, lateral margin with a pair of transverse purple brown bands (Fig. 7A); in ventral view generally pale pink, segments 2–8 each with a pair of purple brown dots (Fig. 7B). Odontoid process absent. Segment 9 subtriangular, longer than wide; two pairs of tiny digging setae present on weakly developed rastra (Fig. 8C).

Type material. ***Holotype*** • 1♀, reared to adult, Malaysia: Pahang, downhill road from Bukit Fraser, 3°42'N, 101°46'E, 790 m, Yuchen Zheng, Zuqi Mai, Tianlang Lyu & Hongqu Tang (IZCAS).

Distribution. Malaysia (Pahang).

Biology. The larva was found on a karst limestone platform in the tropical rainforest (Fig. 9). Like the larvae of many Dendroleontinae (e.g., *Bullanga*, *Dendroleon*) (see Matsumoto et al. 2016; Zheng and Liu 2020; Zheng et al. 2024a), the larva of *N. maizuqii* covered itself in a shallow layer of dry sandy debris and ambushes prey. When removed from the sandy debris in which the larva was buried and exposed on the surface, the larva can move relatively quickly, pausing regularly as it moves.

The adult rests with its wings flattened against the substrate (Fig. 11); the adults may prefer to rest on wider surfaces such as barks or rocks, rather than on slender branches in the field.

Etymology. This new species is dedicated to Mr. Zuqi Mai [麦祖齐], who collected the holotype with the first author, in memory of their enjoyable time in the field.

Remarks. *N. maizuqii* from the Malay Peninsula is similar to *N. maculatus* from Indochina, but it can be distinguished by the coloration of the antenna, the markings on the pro- and mesonotum, the leg markings, and the length of the female gonocoxites 8.

Nuglerus pustulatus (McLachlan, 1867)

Figs 12, 15K, L, P, Q

Glenurus pustulatus McLachlan, 1867: 246 (type locality: Sri Lanka: “Ceylon”; holotype in NHMUK). Markl 1954: 196 (*Nuglerus*, misidentification). Stange 1976: 301 (*Nuglerus*). Stange 2004: 97 (*Nuglerus*). Krivokhatsky 2015: 702 (*Nuglerus*).

Nuglerus scalaris Navás, 1912 (type locality: “Brasil” (wrong location); holotype in NHMW). Banks 1941: 1 (*Nuglerus*). Stange 1976: 301 (*Nuglerus*). Ghosh and Sen 1977: 304 (*Nuglerus*). Bhattacharya and Dey 2000: 51 (*Nuglerus*). New 2003: 179 (*Nuglerus*). Stange 2004: 97 (*Nuglerus*). Krivokhatsky 2015: 703 (*Nuglerus*). syn. nov.

Diagnosis. Vertex anteriorly with dark brown band, posteriorly with a pair of fused large round dark brown markings. Pronotum dark brown, posteromedially with triangular yellowish-brown marking. Mesonotum medially dark brown, with a pair of yellowish-brown stripes; laterally yellowish-brown. Poststigmal area of wings with a rounded thickened dark brown marking, extending slightly into apical part of radial area. Spots on forewing mediocubital crossveins wide (about as long as wide); forewing cubital area basally with an oblique dark brown marking. Forewing rhegma as indistinct brown marking, with a smaller marking distal to rhegma. Female pregenital plate small, triangular; anterior part of gonocoxites 9 with sub-rectangular setose plate.

Re-description. Size. Head width: 3.04 mm; forewing length: 32.57 mm; hindwing length: 34.13 mm.

***Head*.** Vertex yellowish-brown, anteriorly with a dark brown band, posteriorly with a pair of fused large ovoid dark brown markings. Scape and pedicel pale brown ventrally, dark brown dorsally; flagellum generally dark brown. Scape surrounded by dark brown marking. Frons pale yellowish brown, medially with short longitudinal dark brown stripe, anterolaterally with a pair of dark brown dots. Clypeus and labrum pale yellowish brown. Maxillary palpus pale yellow. Labial palpus generally pale yellow, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Fig. 12E–G).

***Thorax*.** Pronotum dark brown, posteromedially with a triangular yellowish-brown marking. Both mesoprescutum and mesonotum with an anterior pair of tufts of long setae; mesoprescutum generally dark brown; mesonotum medially dark brown, with a pair of yellowish-brown stripes, laterally yellowish brown; mesoscutellum dark brown, lateral margins yellowish brown. Metanotum generally dark brown, with a pair of yellowish-brown spots, lateral margin yellowish brown; metascutellum dark brown. Pleurae yellowish-brown, with a wide dark brown stripe (Fig. 12G).

***Legs*.** Long and slender, with many setae. All tibial spurs long, distally curved; tarsomeres pale yellow, distally brown; tarsomere 5 about as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale yellow, anteriorly dark brown; femur pale yellow, distally dark brown; tibia pale yellow, basally with a brown marking, distally brown; tibial spurs reaching the middle of tarsomere 3. Midleg: coxa pale yellow, otherwise similar to foreleg. Hindleg: coxa pale yellow; femur generally pale yellow; tibia pale yellow, distally brown; tibial spurs reaching base of tarsomere 3; tarsomere 1 longer than that of fore- and midleg (Fig. 12J).

***Wings*.** Long, apically rounded. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area of wings with a round thickened dark brown marking, extending slightly into apical part of the radial area (Fig. 15K, L). Forewing shorter than hindwing. Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; mediocubital crossveins each with wide spots, about as long as wide; rhegma as indistinct brown marking, with a smaller marking distal to rhegma; cubital area basally with an oblique dark brown marking; RP origin basal to MP

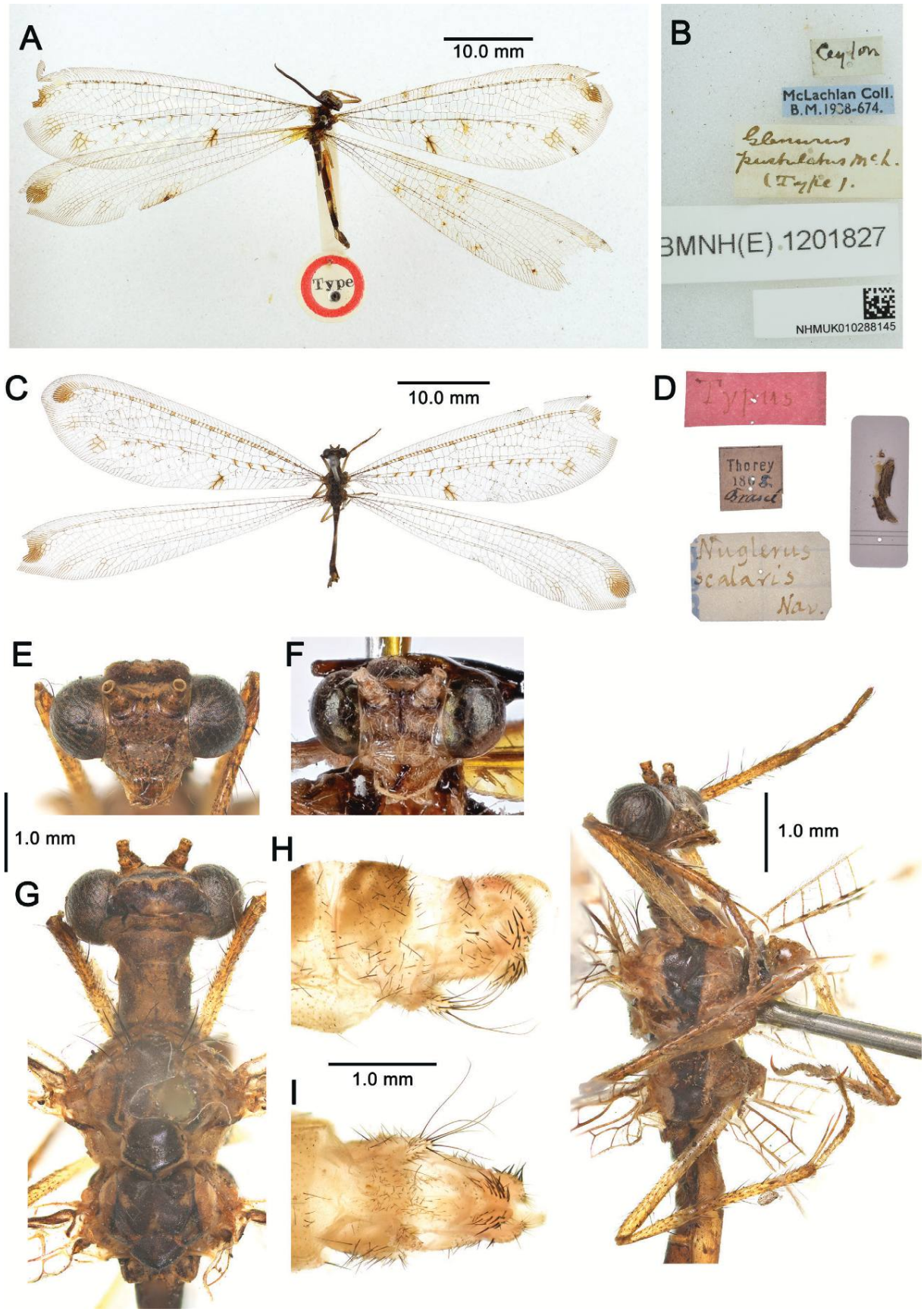


Figure 12. *Nuglerus pustulatus* (McLachlan, 1867), female. **A, B, F.** Holotype of *Glenurus pustulatus* McLachlan, 1867, Sri Lanka; **C, D, E, G–J.** Holotype of *Nuglerus scalaris* Navás, 1912, with wrong type locality ("Bresil") (now junior synonym of *N. pustulatus*); **A, C.** Habitus; **B, D.** Labels; **E, F.** Head, frontal view; **G.** Head and thorax, dorsal view; female terminalia (**H, I**): **H.** Lateral view; **I.** Ventral view; **J.** Head and thorax, lateral view.

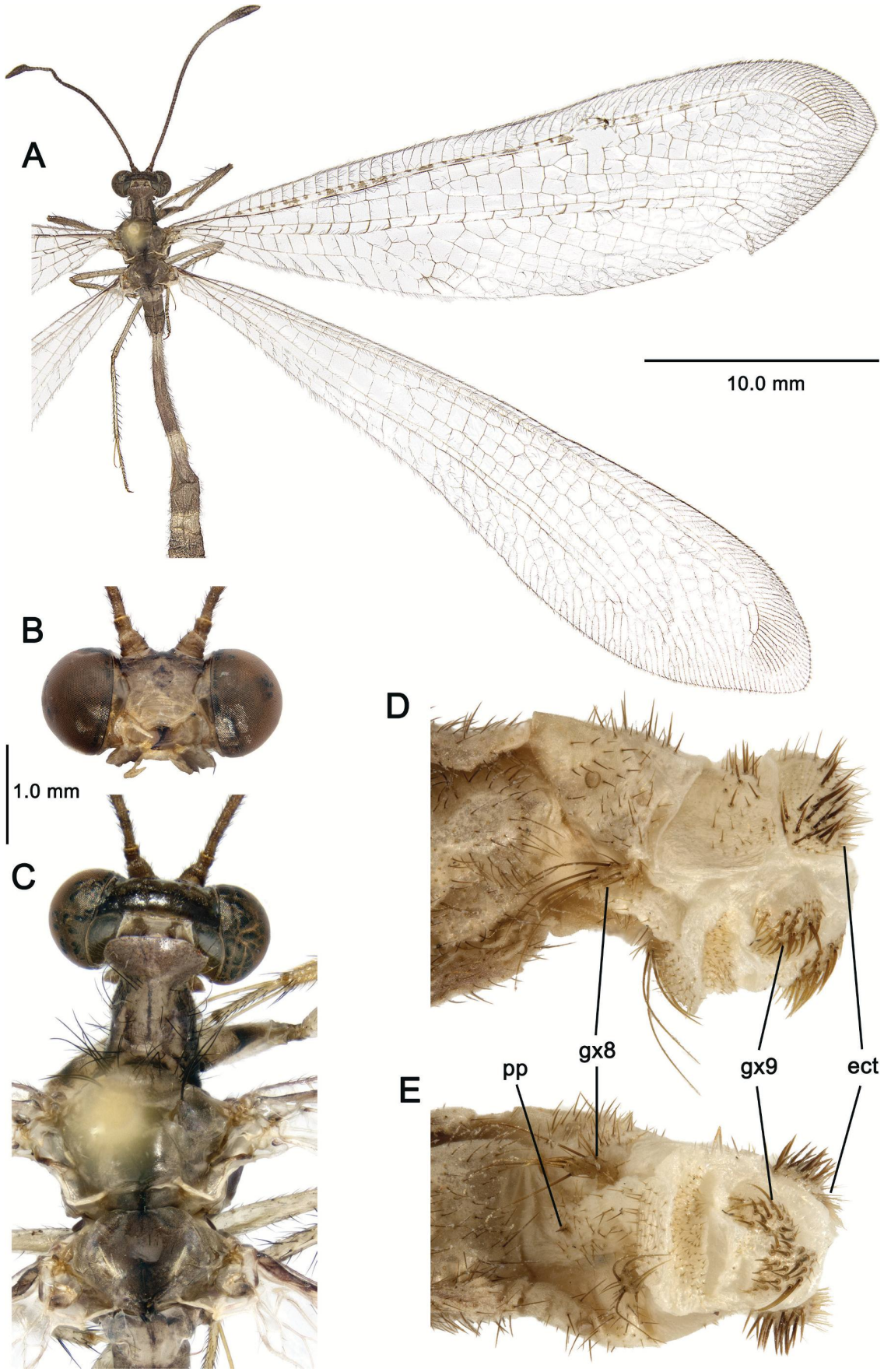


Figure 13. *Nuglerus ruzzieri* Badano, Zheng & Liu, sp. nov., holotype, female, Sulawesi (Indonesia). **A.** Habitus; **B.** Head, frontal view; **C.** Head and thorax, dorsal view; female terminalia (**D, E**): **D.** Lateral view; **E.** Ventral view. Abbreviations of terms of terminalia: ect: ectoprocts, gst: gonostylus, gx: gonocoxites, pp: pregenital plate.

and CuA fork; MP basally not oblique, originates proximally to CuA fork; two to three presectoral crossveins present, with from one biareolate cell; RP with seven to eight branches. Hindwing rhegma as an indistinct oblique brown marking, with a slender indistinct marking distal to rhegma (Fig. 15P, Q); presectoral area with two crossveins (Fig. 12A, C).

***Abdomen*.** Terga 2–3 generally dark brown, medially with a pair of yellowish-brown spots; tergum 3 dark brown; terga 4–5 dark brown, each with a median yellowish-brown spot (Fig. 12A, C, D). ***Male genitalia*.** Unknown. ***Female genitalia*.** Pregenital plate tiny triangular. Gonocoxites 8 short digitiform. Anterior part of gonocoxites 9 with a sub-rectangular setose plate. Gonocoxites 9 and ectoproct with many stout acicular digging setae. Ectoproct narrow ovoid in lateral view (Fig. 11H, I).

Type material. ***Holotype*** • ♀, Sri Lanka: "Ceylon" // "McLachlan Coll. B. M. 1938-674" // "Glenurus pustulatus McL. (Type)." // "BMNH (E) 1201827" // "NHMUK010288145" (NHMUK). Holotype of *Nuglerus scalaris* Navás, 1912 ♀, "Thorey 1808 Brasil" // "Typus" // "*Nuglerus scalaris* Nav." (NHMW).

Distribution. Sri Lanka.

Remarks. Navás (1912) described *N. scalaris* from "Bresil" (i.e., Brazil) (Fig. 11D), but this species does not occur in the New World, and the type locality is clearly erroneous, as implied by the original label of McLachlan's collection. This mistake was already pointed out by Banks (1931), Stange (1976, 2004), and Krivokhatsky (2015), who all agreed that this species is distributed in Sri Lanka. Based on our comparison of the types of *N. scalaris* and *N. pustulatus*, we found that their body and wing markings are identical (Figs 12, 15K, L, P, Q). Therefore, we treat *N. scalaris* syn. nov. as a junior synonym of *N. pustulatus*. This species is similar to *N. maculatus*, but can be reliably distinguished by the darker mesonotum, the broader spots on the forewing mediocubital area, and the oblique markings on the forewing cubital area.

Nuglerus ruzzieri Badano, Zheng & Liu, sp. nov.

https://zoobank.org/244334C9-A078-4107-8AA3-18B78F5EF201

Figs 1F, 12, 14M, R

Diagnosis. Vertex dark brown, darker posteriorly. Pronotum pale brown, with a narrow median dark line. Mesonotum brown, darker medially. Poststigmal area of wings with a faint brown marking not extending into apical part of radial area. Spots on forewing mediocubital crossveins narrow. Forewing and hindwing rhegma indistinct, distal marking to rhegma absent. Female pregenital plate small, narrowly triangular, pointed; anterior part of gonocoxites 9 with rectangular setose plate.

Description. Size. Head width: 2.6 mm; forewing length: 30.15 mm; hindwing length: 30.34 mm.

***Head*.** Vertex brown, darker, posterior margin darker. Scape and pedicel brown, external sides slightly darker; flagellum brown. Frons yellowish brown, with median darker marking. Clypeus and labrum yellowish brown. Maxillary palpus pale yellow. Labial palpus yellowish brown, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Figs 13B).

***Thorax*.** Pronotum brown, with a median narrow dark line, a pair of short medio-lateral dark bands and lateral margins dark brown; pronotum with long black setae. Both mesoprescutum and mesonotum with anterior tufts of long black setae; mesoprescutum brown, with median dark marking; mesonotum brown; mesoscutellum brown, lateral margin brown. Metanotum and metascutellum brown, darker medially. Pleurae brown, with a dark brown stripe (Fig. 13A–C).

***Legs*.** Long and slender, with many setae. All tibial spurs long, distally curved; tarsomeres pale brown; tarsomere 5 about as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale brown, anteriorly brown; femur pale brown, slightly darker distally; tibia pale brown; tibial spurs reaching mid of tarsomere 3. Midleg: similar to foreleg. Hindleg: similar to foreleg, paler; tibial spurs reaching base of tarsomere 3; tarsomere 1 longer than that of fore- and midleg (Fig. 13A).

***Wings*.** Long but relatively narrow, apically rounded. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area of wings with a faint dark marking, not extending into radial area (Fig. 15M, R). Forewing shorter than hindwing. Forewing costal space hyaline; subcostal area with regularly arranged series of spots and small dots; mediocubital crossveins each with narrow marking at crossveins; rhegma as small indistinct brown marking; cubital area basally with faint brown marking; RP origin basal to MP and CuA fork; MP basally not oblique, originating proximally to CuA fork; presectoral area with three crossveins; RP with seven branches. Hindwing rhegma small, indistinct (Fig. 15M, R); presectoral area with two crossveins (Figs 13A).

***Abdomen*.** Terga 2–5 brown, anteriorly paler (Figs 13A). ***Male genitalia*.** Unknown. ***Female genitalia*.** Pregenital plate small, narrowly triangular, apically pointed. Gonocoxites 8 short, digitiform. Anterior part of gonocoxites 9 with a sub-rectangular setose plate. Gonocoxites 9 and ectoproct with many stout acicular digging setae. Ectoproct narrow, ovoid in lateral view (Fig. 13D, E).

Type material. ***Holotype*** • ♀, Indonesia: North Sulawesi, Pangia / 01/2013 (MSNG).

Distribution. Indonesia (Sulawesi).

Etymology. The new species is named after the Italian entomologist Enrico Ruzzier, who brought this interesting specimen to the attention of the authors. The specific epithet is a noun in the genitive case.

Remarks. The type specimen appears to be freshly emerged, and the body coloration is likely not definitive, although the general pattern is clearly recognizable. Nevertheless, the genetic distance from other congeners is congruent with its status as a new species (Fig. 16) and, also considering the biogeographical relevance of the finding, we considered it necessary to describe it within the context of the present genus revision, pending further

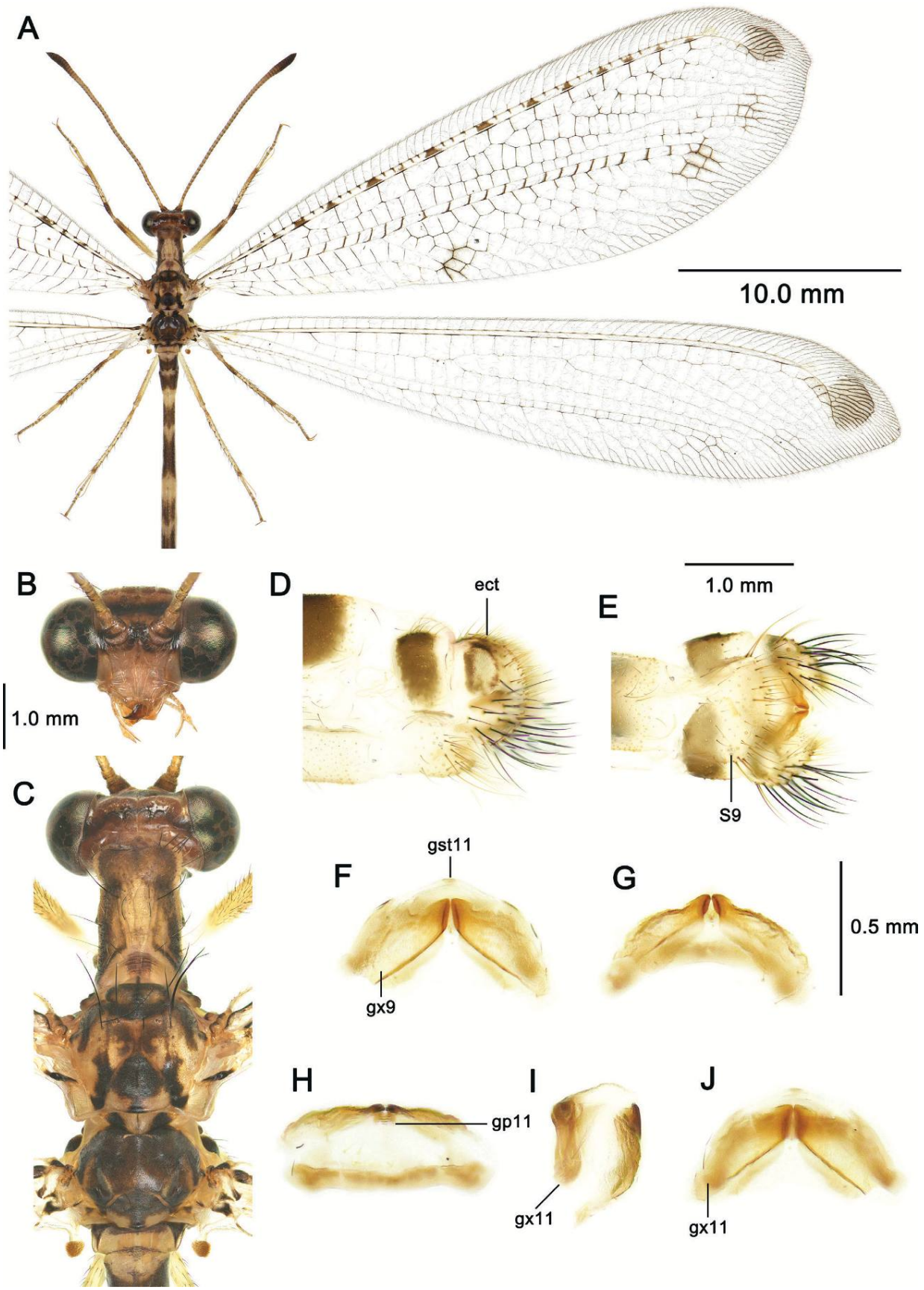


Figure 14. *Nuglerus shihongliangi* Zheng, Badano & Liu, sp. nov., holotype, male, Bali Is. (Indonesia). **A.** Habitus; **B.** Head, frontal view; **C.** Head and thorax, dorsal view; male terminalia (**D, E**): **D.** Lateral view; **E.** Ventral view; male genitalia (**F–J**): **F.** Ventral view; **G.** Anteroventral view; **H.** Caudal view; **I.** Lateral view; **J.** Dorsal view. Abbreviations of terms of terminalia: ect: ectoprocts, gst: gonostylus, gx: gonocoxites, gp: gonapophyses, S9: sternum 9.

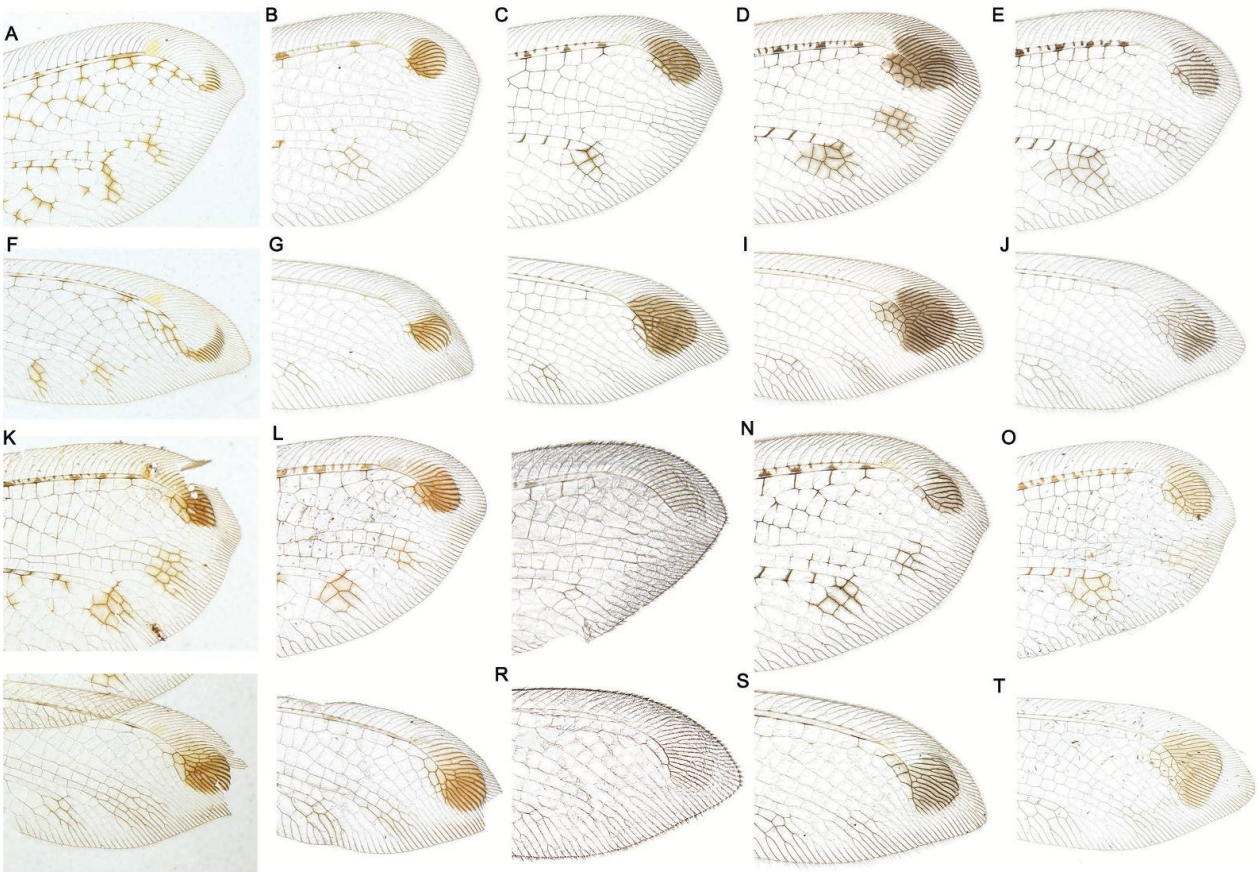


Figure 15. Distal wings of *Nuglerus* spp., females. **A–E, K–O.** Forewing; **F–J, P–T.** Hindwing; **A, F.** Holotype of *Acratoleon dispar* Banks, 1934 (current name: *Nuglerus dispar* comb. nov.), Sabah (Malaysia); **B, G.** *N. guimaraesae* Zheng, Badano & Liu, sp. nov., holotype, female, Coimbatore (India); **C, H.** *N. insignis* Banks, 1939, stat. rev., Palawan (the Philippines); **D, I.** *N. maculatus* (Navás, 1915), Yunnan (China); **E, J.** *N. maizuqii* Zheng, Badano & Liu, sp. nov., Pahang (Malaysia); **K, P.** Holotype of *Glenurus pustulatus* McLachlan, 1867, Sri Lanka (current name: *N. pustulatus*); **L, Q.** Holotype of *Nuglerus scalaris* Navás, 1912, with wrong type locality ("Bresil") (current status: a junior synonym of *N. pustulatus*); **M, R.** *N. ruzzieri* Badano, Zheng & Liu, sp. nov., holotype, Sulawesi (Indonesia); **N, S.** *N. shihongliangi* Zheng, Badano & Liu, sp. nov., holotype, Bali Is. (Indonesia); **O, T.** *Nuglerus* sp., E. Kalimantan (Indonesia).

research in Sulawesi and neighboring islands. *N. ruzzieri* can be distinguished from its congeners by the following combination of characters: 1) vertex dark brown; 2) pronotum light brown with narrow median stripe; 3) Fore- and hindwings narrower than in congeners; 4) marking of postigmal area small, faint and not extending into the radial area; 5) rhegma faint in forewing and absent in hindwing; 6) female pregenital plate small, narrowly triangular and apically pointed. It is possible that in a fully mature specimen the wing markings would be more contrasted, but they are clearly less extended than in other species of *Nuglerus*.

Nuglerus shihongliangi Zheng, Badano & Liu, sp. nov.

https://zoobank.org/E7CFC085-2D23-4D73-BDBC-5A34E3F9DD46

Figs 1G, 14, 15N, S

Diagnosis. Vertex brown, posteriorly with a continuous transverse dark brown band. Pronotum pale yellow, laterally with a pair of long and wide dark brown stripes, anteriorly fused, posteriorly with a pair of slender curved dark brown lines fused with the lateral stripes. Mesonotum pale yellow with many dark brown markings. Metanotum generally dark brown. Poststigmal area of wings with a circular thickened dark brown marking, barely extending into radial area. Forewing radial area with many infuscations on veins. Spots on forewing mediocubital crossveins narrow. Forewing and hindwing rhegma as an indistinct dark brown marking, with a smaller rounded marking distal to rhegma. Male gonocoxites 9 as long rhombus in ventral view.

Description. Size. Head width: 2.75 mm; forewing length: 29.46 mm; hindwing length: 30.55 mm.

Head. Vertex brown, posteriorly with a continuous transverse dark brown band, anteriorly with a transverse dark brown band. Scape dark brown; pedicel yellowish brown; non-swollen part of all flagellomeres brown, distally pale yellow, swollen part of flagellum generally dark brown. Scape surrounded by dark brown marking. Frons pale yellowish brown. Clypeus and labrum pale yellowish brown. Maxillary palpus pale yellow. Labial palpus

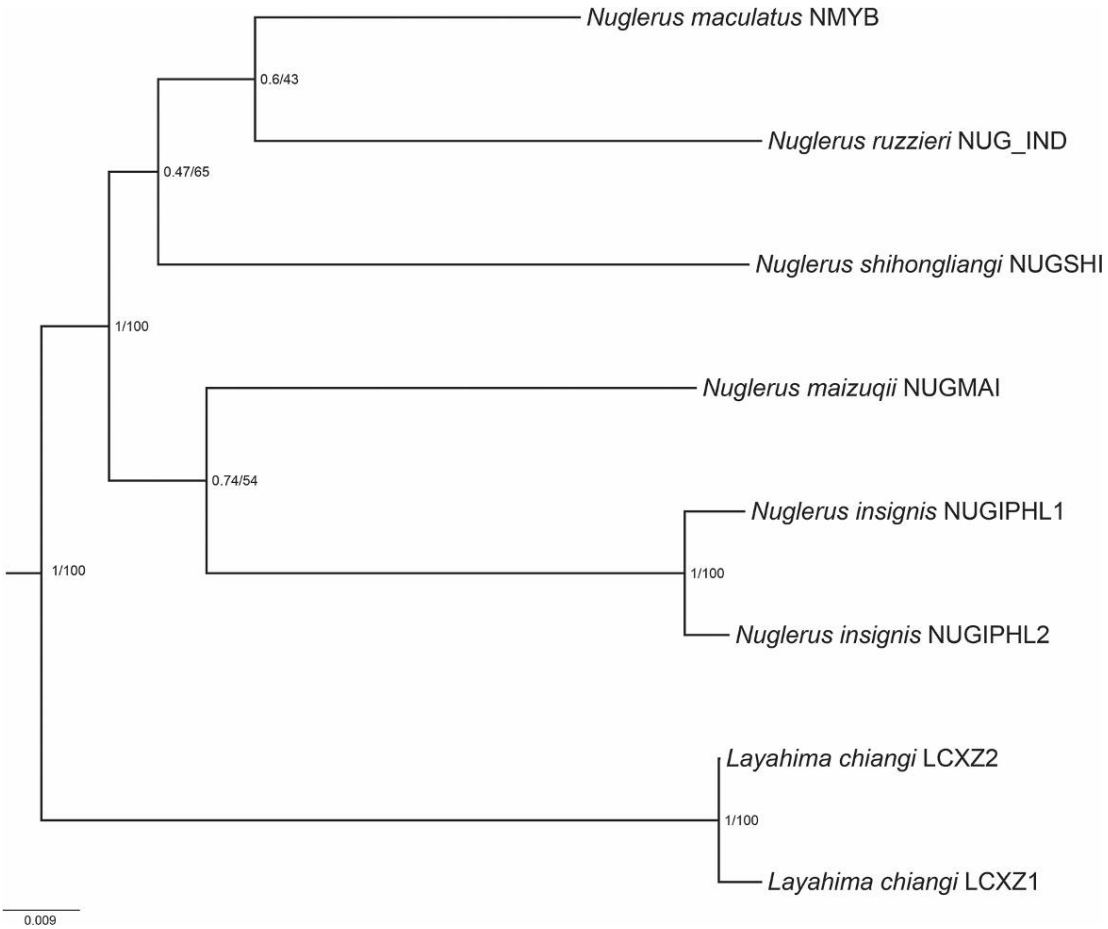


Figure 16. Molecular phylogeny of *Nuglerus* and selected species of Myrmeleontidae based on COI barcoding sequence data. Tree topologies are identical among the Maximum Likelihood inference (ML) / Neighbour-joining analyses (NJ).

generally pale yellow, distal palpomere fusiform. Mandible brown with distal half dark reddish brown (Fig. 14B, C).

Thorax. Pronotum pale yellow, laterally with a pair of long and wide dark brown stripes, anteriorly fused, posteriorly with a pair of slender curved dark brown lines fused with the lateral stripes. Mesoprescutum and mesonotum each anteriorly covered with a pair of tufts of long setae; mesoprescutum dark brown, with a pair of pale yellowish spots; mesonotum generally pale yellow, anteriorly with an arched dark brown marking, medially with a pair of curved brown markings, posteriorly with a pair of longitudinal dark brown stripes; mesoscutellum dark brown, posteriorly with a pair of pale yellowish markings. Metanotum generally dark brown; metascutellum dark brown, posteriorly with a pair of pale yellowish markings. Pleurae yellowish-brown, with a dark brown stripe (Fig. 14B, C).

Legs. Long and slender, with many setae. All tibial spurs long, distally curved; tarsomeres each pale yellow, distally dark brown; tarsomere 5 about as long as entire length of tarsomeres 2–4; pretarsal claws curved, brown. Foreleg: coxa pale yellow, anteriorly dark brown; femur pale yellow, distally dark brown; tibia pale yellow, basally dark brown, distally brown, with some dark dots; tibial spurs reaching middle of tarsomere 3. Midleg: coxa pale yellow; femur pale yellow, distally brown; other characters similar to foreleg. Hindleg: coxa pale yellow; femur pale yellow, distally brown; tibia pale yellow, distally brown; tibial spurs reaching base of tarsomere 3; tarsomere 1 longer than that of fore- and midleg (Figs 14A).

Wings. Long ovoid. Forewing with anterior Banksian line. Pterostigma pale. Poststigmal area with a circular thickened dark brown marking, barely extending into radial area. Forewing shorter than hindwing (Fig. 15N, S). Forewing costal space hyaline; subcostal area with a continuous, regularly arranged series of spots and small dots; radial area with many infuscations on veins; mediocubital crossveins each with narrow spots; rhegma as an indistinct dark brown marking, with a smaller rounded marking distal to rhegma (Fig. 15N); cubital area basally with a dark brown marking; RP origin basal to MP and CuA fork; MP originates proximally to CuA fork; three presectoral crossveins present, with a biareolate cell; RP with seven branches. Hindwing rhegma as an indistinct brown marking, with a marking posterior to rhegma (Fig. 15S); presectoral area with two crossveins (Figs 1G, 14A).

Abdomen. Tergum 2 dark brown, posterior margin pale yellow; terga 3–7 dark brown, each pale yellow on anterior and posterior margin, medially with a yellowish arrow-shaped marking (Figs 1G, 14A). ***Male genitalia.*** Sternum 9 subrectangular, distal margin rounded in ventral view. Gonocoxites 9 as long rhombus in ventral view, internally curved in anteroventral view, truncate in lateral

view. Gonocoxites 11 wide arched, half as long as wide; gonapophysis 11 tiny (14D–J). ***Female genitalia.*** Unknown.

Type material. ***Holotype*** • ♂, Indonesia: Bali Is., Buleleng, Pejarakan, 8°08'S, 114°33'E, 20 m, Hongliang Shi & Ganyan Yang (IZCAS).

Distribution. Indonesia (Bali Is.).

Biology. The holotype of this new species was collected in coastal tropical rainforest.

Etymology. This new species is named in honor of Dr. Hongliang Shi [史宏亮], a coleopterologist and one of the collectors of the holotype, in recognition of his support for this study.

Remarks. This new species can be reliably distinguished from other species by the markings on the vertex, pronotum, and mesonotum, and the presence of infuscations on the veins of the forewing radial area.

Molecular identification

The COI interspecific genetic divergence (Fig. 16) among the five species of *Nuglerus* ranges from 0.098 to 0.149 (Table 2). The intraspecific genetic divergence between the two specimens of *N. insignis* is 0.012 (Table 2).

Discussion

The first discovery of the larva of *Nuglerus* is quite important from a phylogenetic point of view. Larvae of Myrmeleontidae often preserve abundant morphological, ethological, and ecological information (Mansell 1999; Badano et al. 2017c; Zheng et al. 2022, 2024b), making the larval stage important for investigating the evolutionary history of different lineages and species diversification. Larval morphology also constitutes an important source of evidence for understanding relationships among lineages: in the absence of molecular phylogenetic data, it can provide a reasonable basis for inferring systematic position, and it will serve as an important data source of morphological information for future molecular phylogenetic studies. At present, based on adult and larval morphology, the assignment of this genus to Dendroleontinae is relatively uncontroversial, but its systematic position within the subfamily remains uncertain. Machado et al. (2019) also mentioned that, due to the lack of molecular sampling, *Nuglerus* could only be provisionally treated as a member of Dendroleontini, pending further revision. Based on our larval record (Figs 8, 9), several key larval characters are consistent with the diagnosis of Dendroleontini (Badano and Pantaleoni 2014; Matsumoto et al. 2016; Zheng and Liu 2020; Zheng et al. 2022; Zheng et al. 2024a, 2024b): the absence of the odontoid process on segment 8, the relatively elongate abdominal segment 9 (longer than wide), and the reduced rastrum and digging setae on abdominal segment 9. However, some features of *Nuglerus* are typical of Acanthoplectrini but absent in Dendroleontini (Machado and Oswald 2020; Zheng et al. 2023, 2025a, 2025b): *Nuglerus* lacks Miller's organ, its fore femur is shorter than the combined length of the head and pronotum, and the larval mandible is not upturned. Moreover, the long tufts of setae on the mesonotum of *Nuglerus* are very similar to those of *Paralayahima* Zheng, Badano & Liu, 2023 (Zheng and Liu 2021; Zheng et al. 2023); and the setose plate on anterior part of gonocoxites 9 is also present in Australian Acanthoplectrini (as "ventromedial plate" in Machado and Oswald 2020). These characters seem to suggest that *Nuglerus* is likely to be a transitional lineage between Acanthoplectrini and Dendroleontini. A comprehensive molecular phylogeny of Dendroleontinae will help reveal the systematic position of *Nuglerus*, thereby allowing a clearer understanding of the evolutionary history of this subfamily.

The larva of *N. maizuqii* sp. nov. was found on karst limestone in a tropical rainforest (Fig. 9). This habitat likely provides the larva with stable shade, temperature, and humidity, and the rock surface is rich in moss, lichens, and salts, which also attract many invertebrates to this microhabitat. Such conditions can increase the possibility of prey capture by *Nuglerus* larvae. Extensive quarrying of karst limestone from Indochina to the Malay Peninsula in recent decades has likely affected the populations of *Nuglerus*. As in many species endemic to karst habitats, *Nuglerus* probably faces similar ecological threats (Clements et al. 2006). On the other hand, observations on the larval biology of *Nuglerus* may also help explain the distribution pattern of the genus (Fig. 17). If species of *Nuglerus* are restricted to karst limestone habitats within tropical rainforests, desertification, mountain barriers, and island formation may have contributed to divergence within the genus, limited faunal exchange, and shaped the present diversity pattern. Only two species of *Nuglerus* have so far been recorded from the tropical rainforests of South Asia, one from the southern Western Ghats and the other from Sri Lanka (Fig. 17). The wide semi-arid savanna environments of the Indian subcontinent are unsuitable for *Nuglerus* and have therefore limited exchange between South and Southeast Asian lineages of *Nuglerus*. Although tropical rainforest and karst limestone habitats are widespread across Indochina and the Malay Peninsula, *Nuglerus* species from these two regions have also diverged (Fig. 17). This pattern might be related to the Isthmus of Kra, a biogeographic transition area long regarded as an important factor in the divergence of related taxa between Indochina and the Malay Peninsula (Dejtaradol et al. 2015; Hinckley et al. 2023). Southeast Asian islands are the most species-rich region for *Nuglerus*. At present, four described species and at least two unidentified species have been recorded from this area (Fig. 17). Island isolation, together with the more fragmented karst limestone habitats, likely facilitated the divergence among the insular Southeast Asian species of *Nuglerus*. However, all of these hypotheses require further testing through detailed biogeographic analyses. Future sampling of fresh material will be important for reconstructing the historical biogeography of

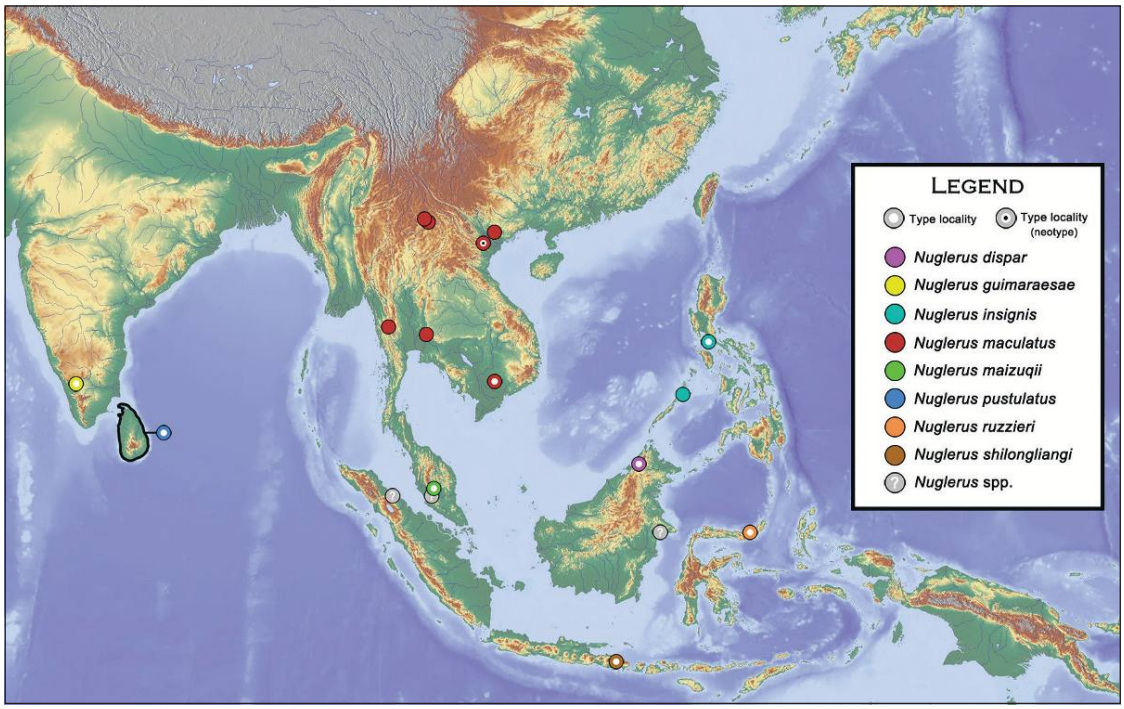


Figure 17. Distribution map of the species of *Nuglerus* Navás, 1912. *Nuglerus* spp. refers to unidentified specimens, which may represent different species.

this genus and for further investigating the ecology of this rare tropical rainforest antlion genus, thereby providing baseline data for the conservation of karst fauna.

Acknowledgements

We are also grateful to Ms. Mónica Guimarães Cruz and Mr. Max Caspers for assisting Yuchen Zheng with photographing the specimens in RMNH. We thank Dr. Hongliang Shi and Dr. Ganyan Yang for providing an important specimen. We sincerely thank Mr. Zuqi Mai for assisting with the sequencing of some specimens. Yuchen Zheng is especially grateful to Mr. Zuqi Mai, Dr. Hongqu Tang, and Mr. Tianlang Lyu for their help during fieldwork, and for the memorable time spent with them in the field. We would like to express our sincere gratitude to Bruno Michel for his help in examining a *N. maculatus* in CBGP. We are grateful to Dr. Benjamin W. Price for sharing the type photos of *N. dispar* and *N. pustulatus* in NHMUK. We greatly appreciate Dr. Susanne Randolf, Mr. Harald Bruckner, and Dr. Ulrike Aspöck for assisting us in examining the holotype of *N. scalaris* in NHMW. We appreciate Dr. Crystal A. Maier for sharing the type photos of *N. insignis* on MCZbase. We sincerely thank Dr. Kuiyan Zhang, Ms. Hong Liu, and Dr. Jun Chen for assisting Yuchen Zheng with examining the specimens in IZCAS. We sincerely thank Dr. André Nel for assisting Yuchen Zheng with photographing the specimens in MNHN. We appreciate Dr. John Hollier for his assistance in clarifying the status of the *Nuglerus* material in the MHNG collections. We also appreciate Dr. Hongyu Li, Ms. Stefanie Krause, and Dr. Michael Ohl for sharing the type photos of *Acratoleon flavum* in MfN. We thank Mr. Yuezheng Tu for his help with the submission. Finally, we are grateful to Dr. Susanne Randolf, Dr. Renato Jose Pires Machado, and Dr. Leon Tavares for critically reading and editing the draft of this paper. We are also grateful to the Museum für Naturkunde (Berlin) for its generous support in covering the publication charges.

References

Ardila-Camacho A, Jones JR (2012) A new species of *Haploglenius* Burmeister, 1839 (Neuroptera: Ascalaphidae) from the Colombian Orinoquía. Zootaxa 3268: 40–46. https://doi.org/10.11646/zootaxa.3268.1.4

Aspöck U, Aspöck H (2008) Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). Systematic Entomology 33: 97–127. https://doi.org/10.1111/j.1365-3113.2007.00396.x

Badano D, Pantaleoni RA (2014) The larvae of European Myrmeleontidae (Neuroptera). Zootaxa 3762: 1–71. https://doi.org/10.11646/zootaxa.3762.1.1

Badano D, Aspöck H, Aspöck U, Haring E (2017a) Eyes in the dark … Shedding light on the antlion phylogeny and the enigmatic genus *Pseudimares* Kimmins (Neuropterida: Neuroptera: Myrmeleontidae). Arthropod Systematics & Phylogeny 75: 535–554. https://doi.org/10.3897/asp.75.e31923

Badano D, Aspöck H, Aspöck U (2017b) Taxonomy and phylogeny of the genera *Gymnocnemia* Schneider, 1845, and *Megistopus* Rambur, 1842, with remarks on the systematization of the tribe Nemoleontini (Neuroptera, Myrmeleontidae). Deutsche Entomologische Zeitschrift 64: 43–60. https://doi.org/10.3897/dez.64.11704

Badano D, Aspöck U, Aspoeck H, Cerretti P (2017c) Phylogeny of M yrmeleontiformia based on larval morphology (N europterida: N europtera). Systematic Entomology 42: 94–117. https://doi.org/10.1111/syen.12200

Badano D, Miller R, Stange LA (2018) Rediscovery and revision of the antlion genus *Ripalda* Navás within a phylogeny of Nemoleontini (Neuroptera, Myrmeleontidae). Invertebrate Systematics 32: 933–949. https://doi.org/10.1071/IS18022

Baltazar CR (1990) An Inventory of Philippine Insects. I. Orders Neuroptera, Strepsiptera, Siphonaptera, Trichoptera & Diptera. University of the Philippines at Los Baños, Laguna, Philippines, 703 pp.

Banks N (1931) Some neuropteroid insects from the Malay Peninsula. Journal of the Federated Malay States Museums 16: 377–409.

Banks N (1934) Supplementary neuropteroid insects from the Malay Peninsula, and from Mt. Kinabalu, Borneo. Journal of the Federated Malay States Museums 17: 567–578.

Banks N (1939) Neuropteroid insects from the Philippines. Philippine Journal of Science 69: 133–145.

Banks N (1941) Some new and interesting Neuroptera in the American Museum of Natural History. American Museum Novitates 1143: 1–5.

Bhattacharya DK, Dey SR (2000) A checklist of Neuroptera (Insecta) of Western Himalaya, India. Transactions of the Zoological Society of East India 4: 49–52.

Boudinot BE (2018) A general theory of genital homologies for the Hexapoda (Pancrustacea) derived from skeletomuscular correspondences, with emphasis on the Endopterygota. Arthropod Structure & Development 47: 563–613. https://doi.org/10.1016/j.asd.2018.11.001

Brauer F (1866) Reise der Österreichischen Fregatte Novara um die Erde: in den Jahren 1857, 1858, 1859, unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. In: von Scherzer K (Ed.) Zoologischer Theil, Bd. 2, No. 4 (Neuroptera). K. Gerold, Wien, 104 pp.

Breitkreuz LCV, Winterton SL, Engel MS (2017) Wing tracheation in Chrysopidae and other Neuropterida (Insecta): a resolution of the confusion about vein fusion. American Museum Novitates 3890: 1–44. https://doi.org/10.1206/3890.1

Burmeister HCC (1839) Handbuch der Entomologie. Zweiter Band [=Vol. 2 (of 2)], Besondere Entomologie. Zweite Abtheilung [=Part 2], Kaukerfe. Gymnognatha. (Zweite [=2nd] Hälfte; vulgo Neuroptera). Theod. Chr. Friedr. Enslin, Berlin, 1050 pp.

Clements R, Sodhi NS, Schilthuizen M, Ng PK (2006) Limestone karsts of Southeast Asia: imperiled arks of biodiversity. Bioscience 56: 733–742. https://doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.CO;2

Dejtaradol A, Renner SC, Karapan S, Bates PJ, Moyle RG, Päckert M (2015) Indochinese-Sundaic faunal transition and phylogeographical divides north of the Isthmus of Kra in Southeast Asian Bulbuls (Aves: Pycnonotidae). Journal of Biogeography 43: 471–483. https://doi.org/10.1111/jbi.12662

Ghosh SK (1984) Contribution to the taxonomical studies of Neuroptera (Suborder Planipennia) from eastern India. 1. Family Myrmeleontidae. Records of the Zoological Survey of India, Miscellaneous Publications, Occasional Paper 52: 1–63.

Ghosh SK, Sen S (1977) Check-list of Indian Planipennia (Order Neuroptera). Records of the Zoological Survey of India 73: 277–326.

Hagen HA (1866) Hemerobidarum Synopsis synonymica. Stettiner Entomologische Zeitung 27: 369–462. https://doi.org/10.26515/rzsi/v73/i1-4/1977/161921

Hinckley A, Hawkins MT, Maldonado JE, Leonard JA (2023) Evolutionary history and patterns of divergence in three tropical east Asian squirrels across the Isthmus of Kra. Journal of Biogeography 50: 1090–1102. https://doi.org/10.1111/jbi.14598

Hölzel H (2002) Neuroptera collected by the German Yemen expeditions 1996, 1998 und 2000 (Neuroptera: Chrysopidae, Hemerobiidae, Berothidae, Mantispidae, Nemopteridae, Myrmeleontidae, Ascalaphidae). Esperiana 9: 129–146.

Hölzel H, Monserrat VJ (2002) *Tricholeon relictus* nov. sp. -- ein neuer europäischer Ameisenlöwe (Neuropterida: Neuroptera: Myrmeleontidae). Linzer Biologische Beitrage 34: 1151–1154.

Kim J-s, Ahn N-h, Kim S-r (2025) A taxonomic review of the family Myrmeleontidae Latreille (Neuroptera, Myrmeleontiformia) from the Korean peninsula, highlighting the conservation value of this family. Zookeys 1262: 97–174. https://doi.org/10.3897/zookeys.1262.163194

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111–120. https://doi.org/10.1007/BF01731581

Krivokhatsky VA (1998) Additions to the knowledge of the genus *Epacanthaclisis* Okamoto, 1910 (Neuroptera: Myrmeleontidae). Journal of Neuropterology 1: 37–54.

Krivokhatsky VA (2015) Description of the male of *Nuglerus maculatus* (Navás, 1915) with comments on the composition of the genus *Nuglerus* Navás, 1912 (Neuroptera, Myrmeleontidae). Entomological Review, Leningrad 94: 698–704. https://doi.org/10.1134/S0013873815070106

Lai Y, Liu Y-h, Liu X-y (2021) Elevational Diversity Patterns of Green Lacewings (Neuroptera: Chrysopidae) Uncovered with DNA barcoding in a biodiversity hotspot of southwest China. Frontiers in Ecology and Evolution 9: 1–14. https://doi.org/10.3389/fevo.2021.778686

Lai Y, Li K-y, Liu X-y (2024) Comprehensive DNA barcode reference library and optimization of genetic divergence threshold facilitate the exploration of species diversity of green lacewings (Neuroptera: Chrysopidae). Insect Science 31: 613–632. https://doi.org/10.1111/1744-7917.13254

Machado RJP, Oswald JD (2020) Morphological phylogeny and taxonomic revision of the former antlion subtribe Periclystina (Neuroptera: Myrmeleontidae: Dendroleontinae). Zootaxa 4796: 1–322. https://doi.org/10.11646/zootaxa.4796.1.1

Machado RJP, Gillung JP, Winterton SL, Garzon-Orduña IJ, Lemmon AR, Lemmon EM, Oswald JD (2019) Owlflies are derived antlions: anchored phylogenomics supports a new phylogeny and classification of Myrmeleontidae (Neuroptera). Systematic Entomology 44: 418–450. https://doi.org/10.1111/syen.12334

Machado RJP, Oliveira SS, Lopes WR, Pujol-Luz JR (2021) Description of the larva and updated distribution of *Albardia furcata* van der Weele (Neuroptera: Myrmeleontidae). Revista Brasileira de Entomologia 65: e20210061. https://doi.org/10.1590/1806-9665-RBENT-2021-0061

Mansell MW (1985) The ant-lions of southern Africa (Neuroptera: Myrmeleontidae). Introduction and genus *Bankisus* Navás. Journal of the Entomological Society of Southern Africa 48: 189–212.

Mansell MW (1987) The ant-lions of southern Africa (Neuroptera: Myrmeleontidae): genus *Cymothales* Gerstaecker, including extralimital species. Systematic Entomology 12: 181–219. https://doi.org/10.1111/j.1365-3113.1987.tb00195.x

Mansell MW (1988) The Myrmeleontidae (Neuroptera) of southern Africa: Genus. *Tricholeon* Esben-Petersen. Neuroptera International 5: 45–55.

Mansell MW (1999) Evolution and success of antlions (Neuropterida: Neuroptera: Myrmeleontidae). Stapfia 60: 49–58.

Markl W (1954) Vergleichend-morphologische Studien zur Systematik und Klassifikation der Myrmeleoniden (Insecta, Neuroptera). Verhandlungen der Naturforschende Gesellschaft in Basel 65: 178–263.

Marquez-López Y, Martins CC, Guevara-Chumacero LM, Ramíez-Ponce A, Contreras-Ramos A (2024) Comparative morphology of male genitalia in antlions (Insecta, Neuroptera, Myrmeleontidae), with emphasis on owlflies (Ascalaphinae) and a possible structural evolutionary scenario. Journal of Morphology 285: 1–31. https://doi.org/10.1002/jmor.21701

Matsumoto R, Kikuta Y, Yoshitomi H (2016) Larvae of three Japanese species of Myrmeleontidae (Neuroptera). Japanese Journal of Systematic Entomology 22: 101–108.

McLachlan R (1867) New genera and species, &c., of neuropterous insects; and a revision of Mr. F. Walker's British Museum Catalogue of Neuroptera, part ii. (1853), as far as the end of the genus *Myrmeleon*. Journal of the Linnean Society of London, Zoology 9: 230–281.

Miller RB, Stange LA (1983) The ant-lions of Florida. *Glenurus gratus* (Say) (Neuroptera: Myrmeleontidae). Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Entomology Circular 251: 1–2.

Navás L (1912) Myrméléonides (Ins. Névr.) nouveaux ou peu connus. Annales de la Société Scientifique de Bruxelles 36: 203–248.

Navás L (1914) Myrméléonides (Ins. Névr.) nouveaux ou critiques [I]. Annales de la Société Scientifique de Bruxelles 38(pt. 2): 229–254.

Navás L (1915) Neurópteros nuevos o poco conocidos (Cuarta [IV] serie). Memorias de la Real Academia de Ciencias y Artes de Barcelona 11: 373–398.

Navás L (1918) Insectos chilenos. Boletín de la Sociedad Aragonesa de Ciencias Naturales 17: 212–230.

Navás L (1923) Insecta orientalia. I Series. Memorie dell'Accademia Pontifica dei Nuovi Lincei, Rome 6: 29–41.

New TR (1985) A revision of the Australian Myrmeleontidae (Insecta: Neuroptera). II. Dendroleontini. Australian Journal of Zoology, Supplementary Series 105: 1–170. https://doi.org/10.1071/AJZS106

New TR (2003) The Neuroptera of Malesia. Fauna Malesiana. Vol. 4. Brill, Leiden, 204 pp. https://doi.org/10.1163/9789004474611

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

Okamoto H (1910) Die Myrmeleoniden Japans. Wiener Entomologische Zeitung 29: 275–300. https://doi.org/10.5962/bhl.part.23335

Oswald JD (2025) Lacewing Digital Library: Neuropterida Species of the World. https://lacewing.tamu.edu/SpeciesCatalog/Main [accessed 14 December 2025]

Park D-s, Suh S-j, Oh H-w, Hebert PDN (2010) Recovery of the mitochondrial COI barcode region in diverse Hexapoda through tRNA-based primers. BMC Genomics 11: 423. https://doi.org/10.1186/1471-2164-11-423

Stange LA (1970) Revision of the ant-lion tribe Brachynemurini of North America (Neuroptera: Myrmeleontidae). University of California Publications in Entomology 55: 1–192.

Stange LA (1976) Clasificacion y catalogo mundial de la tribu Dendroleontini con la redescripcion del genero *Voltor* Navás (Neuroptera: Myrmeleontidae). Acta Zoológica Lilloana 31: 261–320.

Stange LA (1994) Reclassification of the New World antlion genera formerly included in the tribe Brachynemurini (Neuroptera: Myrmeleontidae). Insecta Mundi 8: 67–119.

Stange LA (2004) A systematic catalog, bibliography and classification of the world antlions (Insecta: Neuroptera: Myrmeleontidae). Memoirs of the American Entomological Institute 74: 1–565.

Stange LA (2008) A new species of the genus *Dendroleon* Brauer from Mexico (Neuroptera: Myrmeleontidae). Insecta Mundi 54: 1–9.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. Molecular Biology and Evolution 30: 2725–2729. https://doi.org/10.1093/molbev/mst197

Tavares LG, Marquez-López Y, Zheng Y-c, Machado RJ, Contreras-Ramos A (2025) Picture-winged antlions, the *Glenurus* Hagen (Neuroptera: Myrmeleontidae) from Mexico and Central America: key, redescriptions and description of two new species. Taxonomy 5: 68. https://doi.org/10.3390/taxonomy5040068

van der Weele HW (1903) Description of a new genus and species of holophthalmous Ascalaphidae. Notes from the Leyden Museum 23: 234–236.

Wang X-l, Zhan Q-b, Wang A-q (2018) Fauna Sinica. Vol. 68 (Insecta, Neuroptera, Myrmeleontoidea). Science Press, Beijing, 285 pp.

Zheng Y-c, Liu X-y (2020) First description of immature stages of the antlion *Bullanga florida* (Navás, 1913) (Neuroptera, Myrmeleontidae, Dendroleontini). Zootaxa 4858: 394–404. https://doi.org/10.11646/zootaxa.4858.3.5

Zheng Y-c, Liu X-y (2021) A spectacular new antlion species of the subfamily Dendroleontinae (Neuroptera: Myrmeleontidae) from Malaysia. Zoological Systematics 46: 289–299. https://doi.org/10.11865/zs.2021403

Zheng Y-c, Liu X-y (2023) A revision of the Oriental antlion genera *Indoleon* Banks, 1913, *Indophanes* Banks, 1940 and *Yunleon* Yang, 1986 (Neuroptera: Myrmeleontidae: Nemoleontinae). Zootaxa 5239: 41–78. https://doi.org/10.11646/zootaxa.5239.1.2

Zheng Y-c, Hayashi F, Price BW, Liu X-y (2022) Unveiling the evolutionary history of a puzzling antlion genus *Gatzara* Navás (Neuroptera: Myrmeleontidae: Dendroleontinae) based on systematic revision, molecular phylogenetics, and biogeographic inference. Insect Systematics and Diversity 6: 4. https://doi.org/10.1093/isd/ixac007

Zheng Y-c, Badano D, Liu X-y (2023) Systematic revision, molecular phylogeny and biogeography of the antlion tribe Acanthoplectrini (Neuroptera: Myrmeleontidae: Dendroleontinae), with emphasis on the Oriental lineage. Systematic Entomology 48: 40–68. https://doi.org/10.1111/syen.12561

Zheng Y-c, Hayashi F, Matsumoto R, Liu X-y (2024a) The antlions of the *Dendroleon pupillaris* group (Neuroptera, Myrmeleontidae, Dendroleontinae), with description of three new species from China. Journal of Asia-Pacific Entomology 27: 102181. https://doi.org/10.1016/j.aspen.2023.102181

Zheng Y-c, Tu Y-z, Mai Z-q, Badano D, Liu X-y (2024b) The Asian rock-dwelling antlions *Gatzara* Navás, 1915 and *Nepsalus* Navás, 1914 (Neuroptera: Myrmeleontidae): new advancements in systematics, biogeography and life history. Invertebrate Systematics 38: IS24010. https://doi.org/10.1071/IS24010

Zheng Y-c, Badano D, Aspöck U, Aspöck H, Hayashi F, Liu X-y (2025a) Revision of the antlion genus *Epacanthaclisis* Okamoto, 1910 (Neuroptera: Myrmeleontidae: Dendroleontinae). Zootaxa 5657: 1–100. https://doi.org/10.11646/zootaxa.5657.1.1

Zheng Y-c, Tu Y-z, Badano D, Liu X-y (2025b) New insights into diversity and evolution of the Oriental antlion genus *Layahima* Navás, 1912 (Neuroptera: Myrmeleontidae), with description of new species and new larvae from China. Arthropod Systematics & Phylogeny 83: 543–571. https://doi.org/10.3897/asp.83.e145082

Zheng Y-c, Aspöck U, Aspöck H, Liu X-y (2025c) *Cymothales manselli* sp. nov.: an unexpected new antlion species widely distributed in the Afrotropics (Neuroptera: Myrmeleontidae: Dendroleontinae). Zootaxa 5642: 301–316. https://doi.org/10.11646/zootaxa.5642.4.1

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

This research was supported by the National Natural Science Foundation of China (No. 32370484), the Initiative Scientific Research Program (2024IOZ0108), Institute of Zoology, Chinese Academy of Sciences, the 2115 Talent Development Program of China Agricultural University, the China Scholarship Council, and the National Animal Collection Resource Center, China.

Author contributions

All authors have contributed equally.

Author ORCIDs

Y. Zheng https://orcid.org/0000-0003-2397-2008
D. Badano https://orcid.org/0000-0001-9715-3107
X. Liu https://orcid.org/0000-0002-9168-0659

Data availability

All of the data that support the findings of this study are available in the main text.