



# 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

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## Abstract

*Layahima* Navás, 1912 is the most diverse antlion genus of the tribe Acanthoplectrini (Myrmeleontidae: Dendroleontinae) endemic to the Oriental region, currently comprising 12 species. However, the species diversity of this genus is still far from completely explored, and its larval stage is poorly known. Here, we describe four new species of *Layahima*, i.e., *L. haohani* sp. nov., *L. qilin* sp. nov., *L. pixiu* sp. nov., and *L. zhitengi* sp. nov., from Southwest China. Moreover, we describe the larval stages of three *Layahima* species, i.e., *L. chiangi* Banks, 1941, *L. lhoba* Zheng, Badano, Liu, 2023, and *L. yangi* Wan & Wang, 2006. The precise distribution of *L. chiangi*, whose type locality was previously unclear, has now been clarified to be exclusively restricted to the Nujiang dry hot river valley around Cawarong, Xizang. The phylogeny of *Layahima* by adding new species herein reported was inferred based on molecular data. The *L. zonata* group, once considered monophyletic, was recovered as paraphyletic within *Layahima*.

## Keywords

Myrmeleontoidea, taxonomy, phylogeny, larva, Oriental region

## 1. Introduction

*Layahima* Navás, 1912 is an Oriental antlion genus belonging to the tribe Acanthoplectrini, within the subfamily Dendroleontinae, currently comprising 12 species: *L. aspoekororum* Zheng, Badano & Liu, 2022 (Vietnam), *L. chiangi* Banks, 1941 (China), *L. contracta* (Walker, 1860) (India), *L. elegans* (Banks, 1937) (China), *L. lhoba* Zheng, Badano & Liu, 2022 (China), *L. melanocoris*

(Yang, 1997) (China and Vietnam), *L. monba* Zheng, Badano & Liu, 2022 (China), *L. nebulosa* Navás, 1912 (India, Nepal), *L. valida* (Yang, 1997) (China), *L. xinli-ae* Zheng, Badano & Liu, 2022 (China), *L. yangi* Wan & Wang, 2006 (China and Vietnam), and *L. zonata* (Navás, 1919) (Vietnam and Thailand) (Zheng et al. 2023; Oswald 2024). The adult of *Layahima* differ from other dendrole-

ontines by the comparatively short legs, the tibial spurs not reaching tarsomere 5, the broad and distally rounded wings with indistinct markings and without Banksian lines, the absence of pilula axillaris, the female gonocoxites 8 shaped as a pair of digitiform structures, and the female gonocoxites 9 with long stout blunt setae. Zheng et al. (2023) revised this genus based on molecular phylogeny, and reconstructed the biogeography of Acanthoplectrini, recovering *Layahima* as the most diverse genus of this tribe in the Oriental region. However, the species diversity of *Layahima* is still poorly explored in the Oriental region, especially in Southwest China. Moreover, the immature stages of *Layahima* are also poorly known, as the only existing account is an old record by Gravely and Maulik (1911) describing the larva of *L. contracta* (as *Myrmeleon*).

In the present study, we further investigate the species diversity of *Layahima*, describing four new species from Southwest China: *L. haohani* sp. nov., *L. qilin* sp. nov., *L. pixiu* sp. nov., and *L. zhitengi* sp. nov., and *L. qilin* sp. nov. which were discovered based on molecular and morphological comparisons between new available samples of *L. chiangi*, and the specimens previously identified as *L. chiangi* in Zheng et al. (2023). The new comparisons revealed that most of the specimens examined in Zheng et al. (2023) actually belong to a new species, i.e., *L. qilin* sp. nov. The accurate type locality of *L. chiangi* is further explored. Furthermore, the larval stages of *L. chiangi*, *L. lhoba*, and *L. yangi* are described, with observations on their morphology and ethology, confirming the *Layahima* affinity of the larva described by Gravely and Maulik (1911).

## 2. Material and methods

### 2.1. Institutional abbreviations

All specimens examined and mentioned herein are deposited in the following collections: **AMNH** American Museum of Natural History, New York, USA — **CAU** Entomological Museum, China Agricultural University, Beijing, China — **IZCAS** Institute of Zoology, Chinese Academy of Sciences, Beijing, China — **MNHN** Muséum National d'Histoire Naturelle, Paris, France — **MSNG** Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy — **ZCAU** Yuchen Zheng collection, China Agricultural University, Beijing, China

#### 2.1.1. Morphological comparisons

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. Habitus photos were taken by using Nikon® D850 digital camera with AF-S Micro Nikkor 105 mm 1/2.8G ED lens. Head, thorax and legs were photographed by

Nikon® D850 digital camera with Laowa® 25mm F/2.8 2.5–5.0× Ultra Macro lens. The photos of genitalia were taken using a Leica® DM2000 outfitted with Nikon® D850 digital camera.

Larvae of *L. chiangi*, *L. lhoba*, and *L. yangi* were preserved in 95% alcohol under –24°C. The larvae of *L. chiangi* were obtained from the eggs laid by females. All living larvae were placed in separate plastic bottles. We added dry paper towels to the bottle to serve as a climbing surface for the larvae. Rearing was carried out at room temperature (16–27°C). The 1st instar larvae were fed with undetermined species of springtails (Collembola: Poduromorpha: Neanuridae) and workers of *Reticulitermes speratus* (Kolbe, 1885) (Blattodea: Isoptera: Termitidae).

The classification system of Myrmeleontidae follows Machado et al. (2019). Terminology of wing venation mainly follows Breitkreuz et al. (2017), while that of wing fields follows Machado and Oswald (2020). Terminology of genitalia mainly follows Aspöck and Aspöck (2008), Badano et al. (2017a, b) and Zheng et al. (2022, 2023). Terminology of the antlion larval morphology follows Badano and Pantaleoni (2014a, b).

**Abbreviations of terms of wing venation:** C costa; Sc subcosta; RA radius anterior; RP radius posterior; MA media anterior; MP media posterior; CuA cubitus anterior; CuP cubitus posterior; A anal veins; BL Banksian line. Abbreviations of terms of male and female terminalia: ect ectoproct; gp gonapophysis; gst gonostylus; gx gonocoxite; pp pregenital plate; S sternum.

**Abbreviations of terms of larva:** 1t first tooth; 2t second tooth; 3t third tooth; Ms mesothoracic spiracle; Msp mesothoracic setiferous process; Do dolichaster; Ds digging setae; Op odontoid process.

#### 2.1.2. Sampling in phylogenetic analysis

Sampling for the molecular phylogenetic analysis is largely based on the specimens and data from Zheng et al. (2023). The additional samples in this paper include:

*Layahima chiangi* (voucher ID: LCXZC1, LCXZC2)

*L. haohani* sp. nov. (voucher ID: LYEYN1)

*L. pixiu* sp. nov. (voucher ID: LYUND, LYUNK)

*L. zhitengi* sp. nov. (voucher ID: LYUNNU)

*L. lhoba* (larva) (voucher ID: LHOXZL)

*L. yangi* (larva) (voucher ID: LYGXL)

Details of the sequenced samples are shown in Table S1.

## 2.2. DNA extraction, mitogenome sequencing, and assembly

The genomic DNA was extracted from the mesothoracic muscle of adult or larval specimens by using TIANamp Micro DNA Kit (TIANGEN, Beijing, China). For sequencing of the mitochondrial genomes, we constructed

a 350 bp paired-end sequencing library for each specimen and used Illumina NovaSeq platform to obtain 4 Gb of sequence data. Raw reads were trimmed of adapters using BWA (Burrows-Wheeler Aligner) software (Li and Durbin 2010). All specimens we sequenced were assembled mapping to the mitogenome as the reference sequence using Geneious Prime 2020 (Kearse et al. 2012), with the parameters set as follows: 95% minimum overlap identity, 4 maximum ambiguity, and a minimum overlap of 25 bp. Each mitochondrial contig was inputted into MITOS web service (Bernt et al. 2013) for initial mitogenome annotation. The resultant gene boundaries were checked by alignment with homologous genes of the published *Layahima* genes in Zheng et al. (2023). In the case of the larvae of *L. lhoba* and *L. yangi*, only the COI gene was sequenced. The COI barcodes were amplified using the primers COI1-R (5'-TAAACTTCTGGATGT-CCAAAAATCA-3') and COI4-F (5'-TGTA AACGACG-GCCAGTAACTAATARCCTTCAAAG-3') (Park et al. 2010; Lai et al. 2021). 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).

### 2.3. Phylogenetic analysis

The molecular dataset for the phylogenetic analysis was the sequence matrix concatenated by mitogenomes, gene fragments of COI and 16S rRNA, two nuclear genes (18S rRNA and 28S rRNA). The alignment of 13 protein-coding genes (PCGs) was based on amino acid sequences translated with invertebrate mitochondrial genetic codon table using MUSCLE (Edgar 2004) compiled in MEGA 7.0 (Kumar et al. 2016). The rRNAs and tRNAs were aligned using MAFFT 7.0 (Katoh and Standley 2013) under iterative refinement method incorporating the most accurate local (E-INS-i) pairwise alignment information. All alignments were concatenated using FASconCAT\_v1.0 (Kück and Meusemann 2010) for phylogenetic inference. We estimated the best partitioning scheme and model for our dataset with PartitionFinder 2 (Lanfear et al. 2017). The concatenated dataset was partitioned into five subsets, and GTR+I+G was selected as the best-fitting model for the present phylogenetic analysis (Table S2). Phylogenies were inferred using Bayesian inference (BI) and Maximum-likelihood (ML) methods. The BI analysis was conducted using MrBayes 3.2.6 (Ronquist et al. 2012) via the CIPRES web portal (Miller et al. 2010). The BI analysis contained four simultaneous Markov chain Monte Carlo (MCMC) runs of 50 million generations, and trees were sampled every 1,000 generations with a burn-in of 25%. Analyses terminated when the standard deviation of clade frequencies fell below 0.01, which indicates that stationarity had been reached. A majority-rule consensus tree was calculated with posterior probabilities for each node. The ML analysis was

performed in IQ-Tree web server (<http://iqtree.cibiv.univie.ac.at>) with 1000 bootstrap replicates, with substitution model set to auto, and the partition type set to edge-linked. Trees were visualized and edited with FigTree v1.4.4 (Rambaut 2019).

## 3. Results

### 3.1. Phylogenetic analysis

The ML and BI analyses resulted in phylogenetic trees with same topology (Fig. 1). The addition of the new samples to the dataset of Zheng et al. (2023) confirmed the monophyly of *Layahima*. However, the *Layahima zonata* group of the previous study was recovered as paraphyletic, and some nodes were recovered with low supports, e.g., node 1 (maximum likelihood bootstrap value/Bayesian posterior probabilities: 53/0.71), node 2 (41/0.66), and node 3 (56/0.89). The present result also supports the validity of the new species described herein, e.g., *L. qilin* sp. nov. is sister to *L. zhitengi* sp. nov. + *L. chiangi*, although *L. qilin* sp. nov. is morphologically similar to *L. chiangi*; *L. pixiu* sp. nov. is sister to *L. valida*, although *L. valida* is morphologically similar to *L. zhitengi* sp. nov.; and *L. haohani* sp. nov. is sister to the *L. elegans* group. Moreover, the larvae of *L. lhoba* and *L. yangi* are associated with the adults through molecular data.

### 3.2 Taxonomy

#### Family Myrmeleontidae Latreille, 1802

#### Subfamily Dendroleontinae Banks, 1899

#### Tribe Acanthoplectrini Markl, 1954

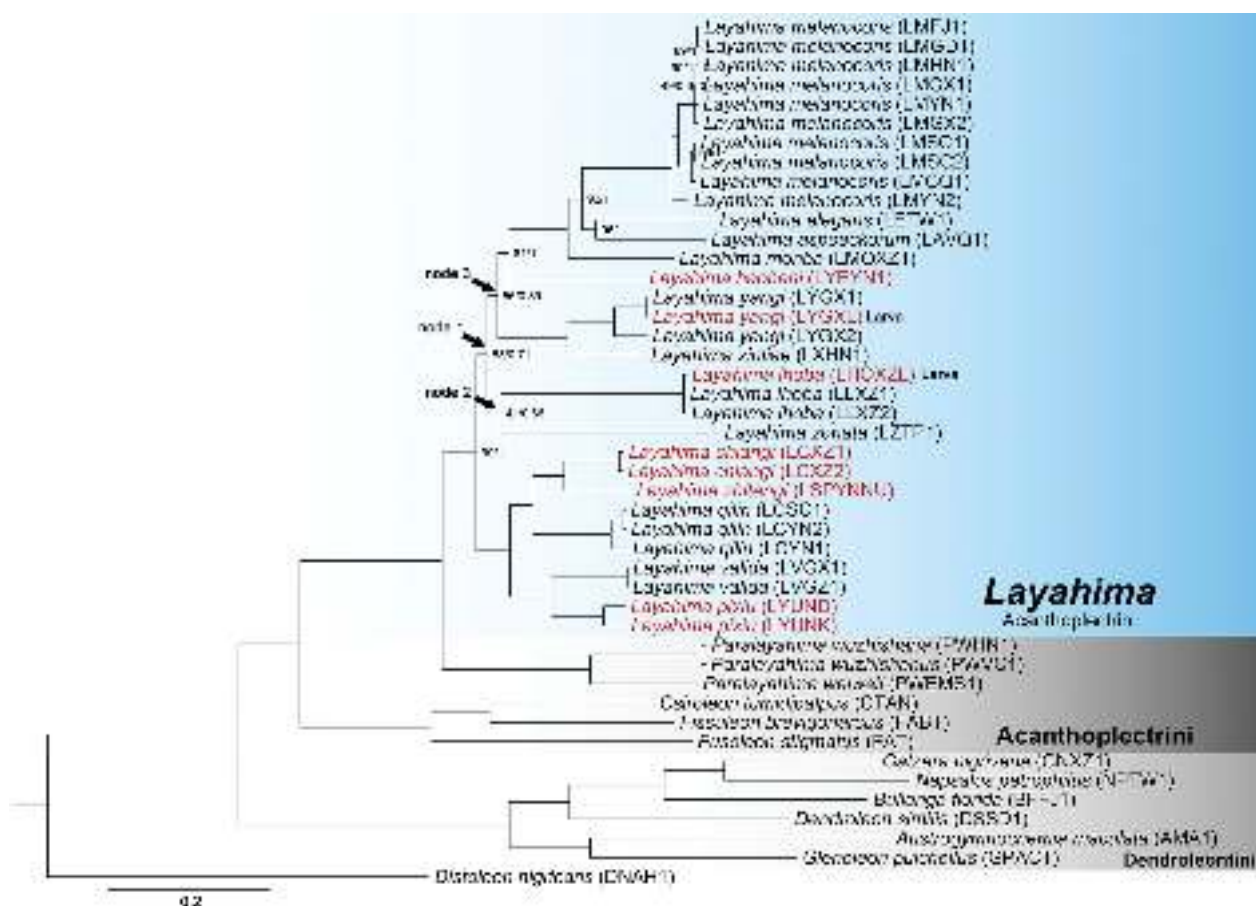
#### Genus *Layahima* Navás, 1912

*Layahima* Navás 1912: 36. Type species: *L. nebulosa* Navás, 1912, by original designation.

*Noues* Navás, 1919: 13; Stange 1976: 309 (as synonym). Type species: *Noues zonatus* Navás, 1919, by original designation.

*Asialeon* Yang 1997: 614; Stange 2004: 76; Wan et al. 2006: 35 (as synonym). Type species: *A. validus* Yang, 1997, by original designation.

**Diagnosis. Adult:** Frons wider than diameter of compound eye; vertex raised. Pronotum as long as wide. Legs short, as long as thorax at most; foreleg with femur nearly twice as long as coxa; maximum width of femur wider than that of tibia; tibial spurs slightly curved, not reaching tarsomere 5. Wings distally rounded. Forewing mediocubital area with some indistinct brown markings. Banksian lines absent. Male pilula axillaris absent. Male gonocoxites 9 as a pair of broad plates in posterior view, apex strongly sclerotized and scaly; gonocoxites 11 arched. Female ventral segment 8 forming an antrum, gonocox-



**Figure 1.** Phylogeny of Acanthoplectrini based on mitochondrial genomes and partial nuclear genes (18S rRNA and 28S rRNA). Topology is derived from the maximum-likelihood (ML) and Bayesian inference (BI) inferences. Numbers at nodes are maximum likelihood bootstrap values (left) and Bayesian posterior probabilities (right). Nodes without support values indicate that they were 100/1. Samples marked in red are newly added in this study.

ites 8 as a pair of digitiform structures; gonapophyses 8 various, absent in some species, nearly wide rectangular if present; digging setae on gonocoxites 9 long and blunt. — **Larva:** Body laterally covered with many blunt pale setae. Head wider than long. Dolichasters on anterior margin of clypeo-labrum thick, distally swollen and truncate. Ocular tubercles prominent. Distance between the first and second teeth on mandible longer than that between the second and third teeth. Pair of large spiracles present on laterodorsal abdominal segment 1. Odontoid process on abdominal segment 8 present. Abdominal sternum 9 ventrally with some tapered setae of uneven size; rastrum with four distal pair of tapered digging setae.

**Biology.** The known larvae of *Layahima* are not fossorial and do not camouflage under debris, living exposed under rocks or on tree trunks.

**Distribution.** China; India; Nepal; Thailand; Vietnam (Fig. 18).

**Remarks.** According to Zheng et al. (2023), *Layahima* lacks female gonapophyses 8. However, further examination demonstrated that the absence of gonapophyses 8 only occurs in the *L. elegans* species group, while this

character is present in most other species of the genus. Besides, unlike the related genus *Paralayahima* Zheng, Badano & Liu, 2023, the gonapophyses 8 of *Layahima* is broad and subrectangular, whereas the gonapophyses 8 of *Paralayahima* is thin and ribbon-like.

### *Layahima chiangi* Banks, 1941

Figures 2A, B, 3, 4, 5A–E, 6, 7

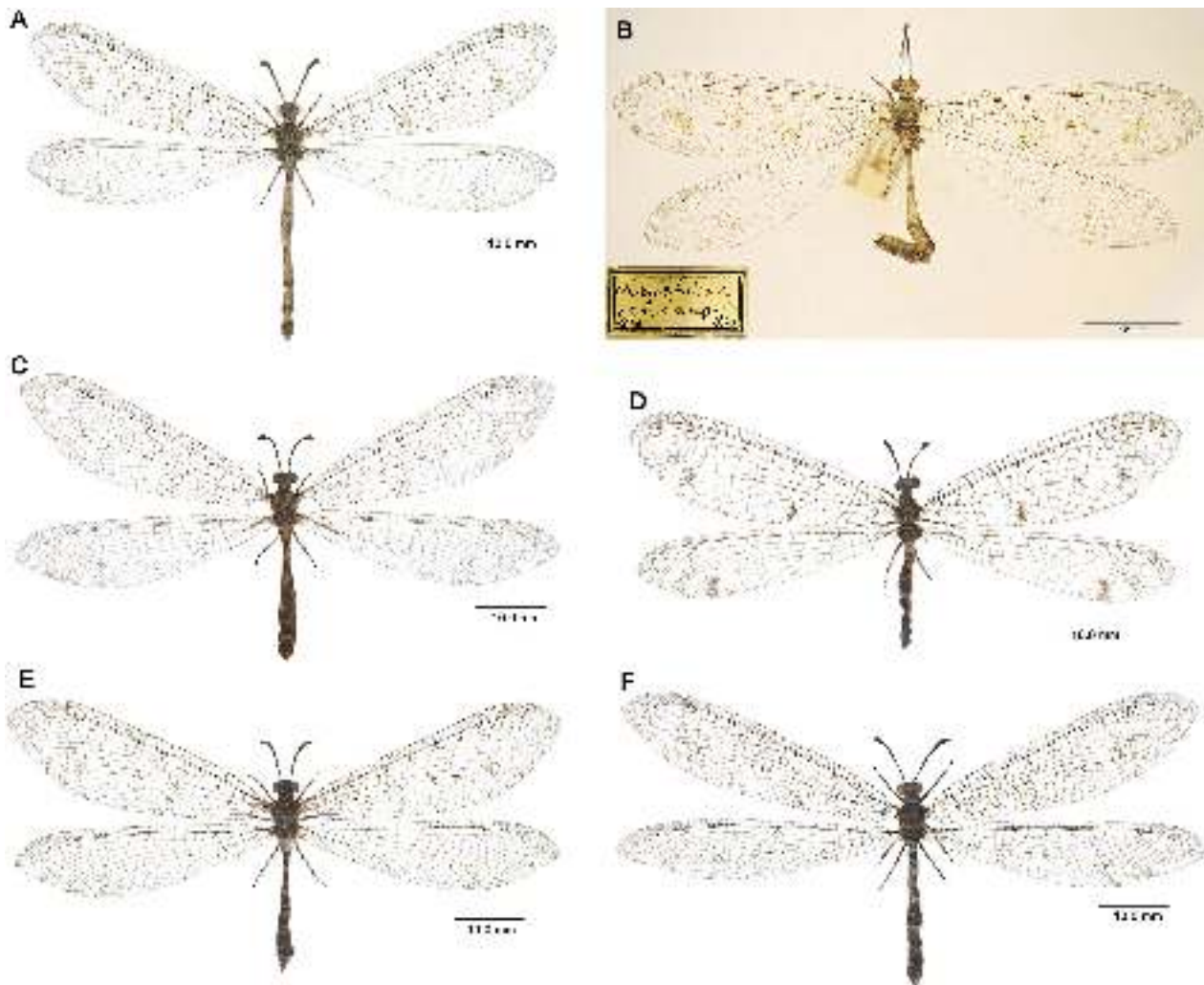
*Layahima chiangi* Banks 1941: 1 (type locality: China: Yunnan, “Loutsechiang”; holotype in AMNH). Stange 1976: 310 (*Layahima*). Stange 2004: 92 (*Layahima*). Wan et al. 2006: 38 (*L. qilin* sp. nov. misidentified as *L. chiangi*). Wang et al. 2018: 61 (*L. qilin* sp. nov. misidentified as *L. chiangi*). Zheng et al. 2023: 48 (*L. qilin* sp. nov. misidentified as *L. chiangi* but included type photo of the latter species).

**Diagnosis. Adult:** Body pale yellowish brown with some black and dark brown markings, parts with numerous black dots at base of setae. Both vertex and postgena each with a pair of distinct black spots (Fig. 3B, C). Frons and clypeus with six black spots (Fig. 3B). Pronotum medially with a black spot and laterally with four pairs of

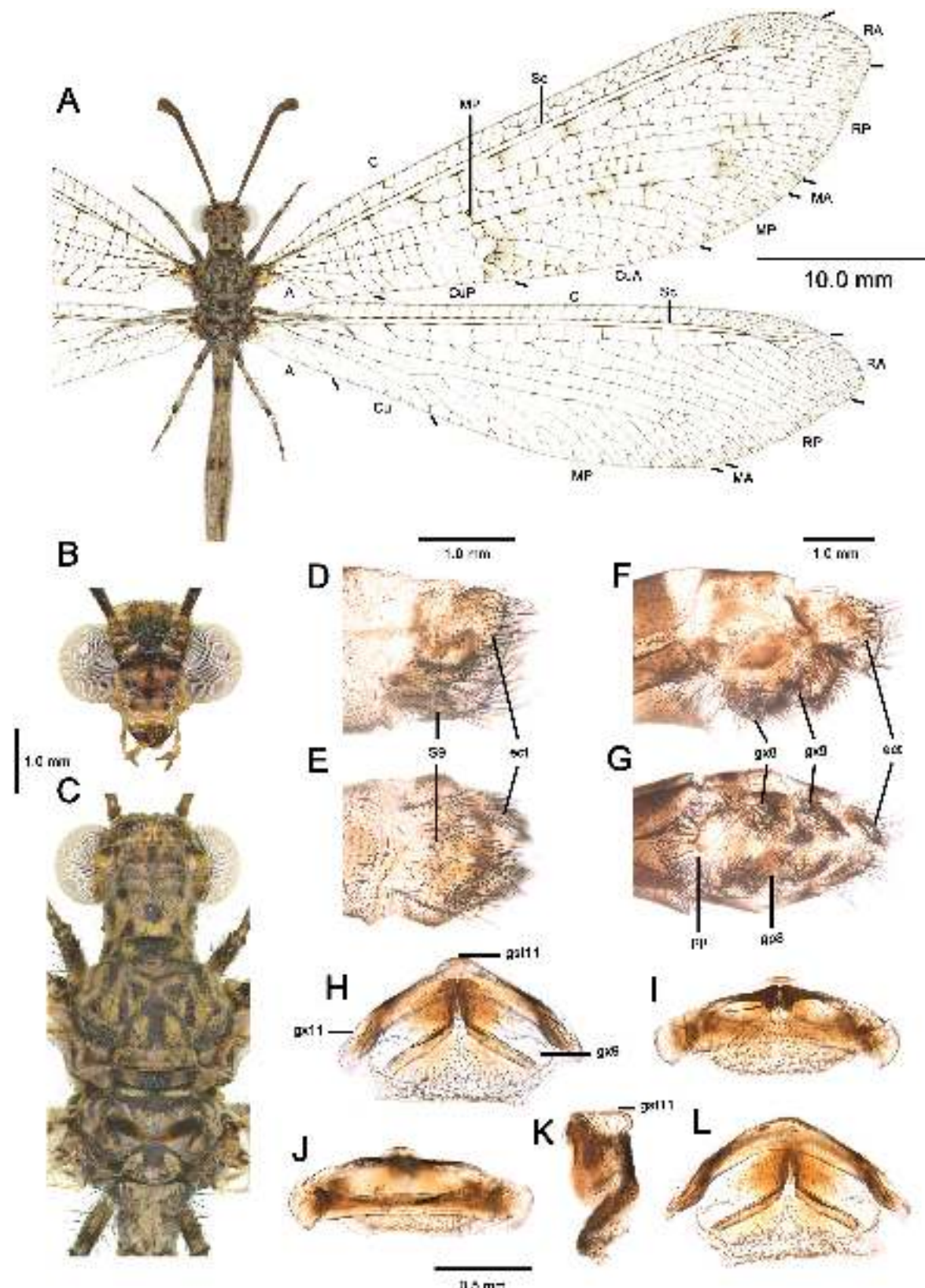
black spots. Forewing rhegma present as two indistinct brownish markings (Figs 3C, 5A–C). Male sternum 9 wide, posterior part narrowed and short (Fig. 3E); gonocoxites 9 as a pair of wide, oblate trapezoid plates, twice as wide as long; gonocoxites 11 are triangularly arched (Figs 3H–L, 5D). Female pregenital plate shaped as an indistinct tiny sclerite (Fig. 5E). Gonocoxites 8 short and wide, digitiform (Fig. 3F, G). — **1st instar larva:** Head generally brown and dark brown (Fig. 7A, B). Antenna short and robust. Thoracic setiferous processes tubercular; anterior mesothoracic setiferous processes larger than others (Fig. 7C). Abdomen greenish brown, with many dark markings; dorsal abdominal segment 1 with a pair of large transversal dark markings (Figs 6, 7D).

**Re-description of adult.** *Size.* Head width: 2.27–3.22 mm; forewing length: 28.11–32.24 mm; hindwing length: 28.08–32.20 mm. — **Head.** Vertex and postgena with a pair of dark brown spots. Scape mostly dark brown; pedicel pale yellowish brown with a dark brown circular marking; antenna mostly yellowish brown, non-swollen part of flagellomeres each basally dark brown, swollen

part of flagellum distally dark brown. A dark brown marking present around scapes, anteriorly concaved. Frons and clypeus with six black spots. Labrum pale yellow. Mandibles pale yellowish brown with distal half dark reddish brown. Maxillary palpus yellowish brown. Labial palpus generally yellowish brown, distal palpomere fusiform (Figs 3B, C, 5A–C). — **Thorax.** Pronotum medially with a black spot and laterally with four pairs of black spots. Mesoprescutum mostly black, anteriorly with a pair of pale yellowish-brown spots; mesonotum pale yellowish brown, with three pair of black stripes and a pair of black spots, pale yellowish-brown part with some black dots; mesoscutellum anteriorly black, mostly pale yellowish brown, variation present in different individuals. Metanotum pale yellowish brown and black; metascutellum dark brown, laterally with a pair of pale yellowish-brown spots. Pleurae pale yellowish-brown and black (Figs 3B, C, 5A–C). — **Legs.** Short, as long as thorax at most, with many black and pale setae. All tibial spurs slightly curved; tarsomeres each generally pale yellow with distal part dark brown; tarsomere 5 pale yellow, with distal part dark brown, nearly as long as entire length of tarsomeres



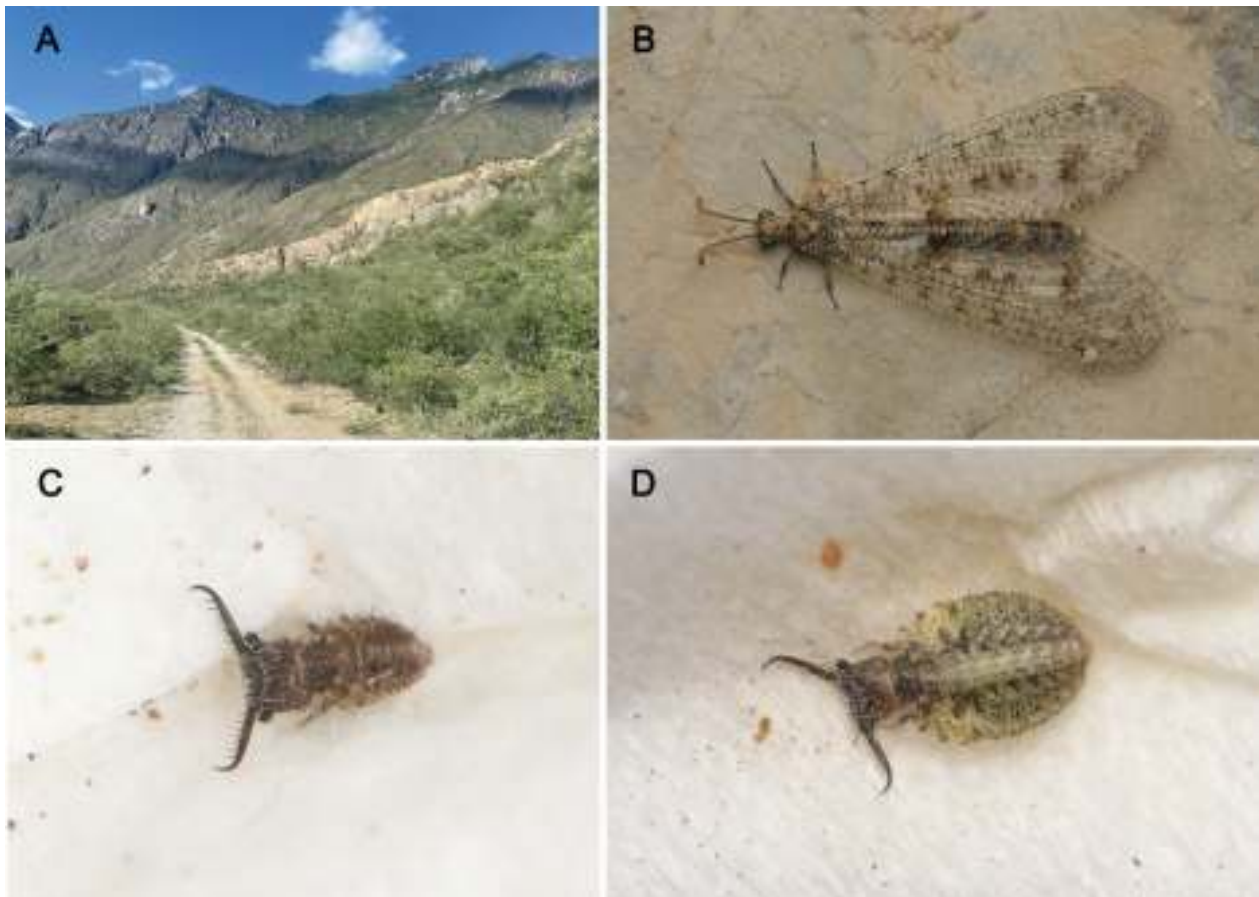
**Figure 2.** Habitus of *Layahima* spp. from China, adults: **A** *L. chiangi* Banks, 1941, male, Cawarong (Xizang); **B** *L. chiangi*, male, holotype (© D. Grimaldi from AMNH); **C** *L. qilin* sp. nov., male, holotype, Weixi (Yunnan); **D** *L. haohani* sp. nov., female, holotype, Puer (Yunnan); **E** *L. pixiu* sp. nov., female, holotype, Hutiaoxia (Yunnan); **F** *L. zhitengi* sp. nov., female, holotype, Fugong (Yunnan).



**Figure 3.** *Layahima chiangi* Banks, 1941, adult: **A** Habitus, female holotype; **B** head, frontal view; **C** head and thorax, dorsal view. **D**, **E** male terminalia: **D** Lateral view, **E** ventral view. **F**, **G** Female terminalia: **F** Lateral view, **G** ventral view. **H**–**L** Male genitalia: **H** Ventral view, **I** anteroventral view, **J** caudal view, **K** lateral view, **L** dorsal view.

2–4; pretarsal claws curved, dark reddish brown. Foreleg: coxa pale yellow with a black spot; femur dorsally brown to dark brown, ventrally pale yellowish brown; tibia pale yellow with a dark anterior marking, distal part dark

brown; tibial spurs reaching base of tarsomere 3. Midleg: Coxa pale yellowish brown, black basally; femur mostly yellowish brown, distally dark brown; tibia pale yellow, with some black dots, distal part dark brown; tibial spurs

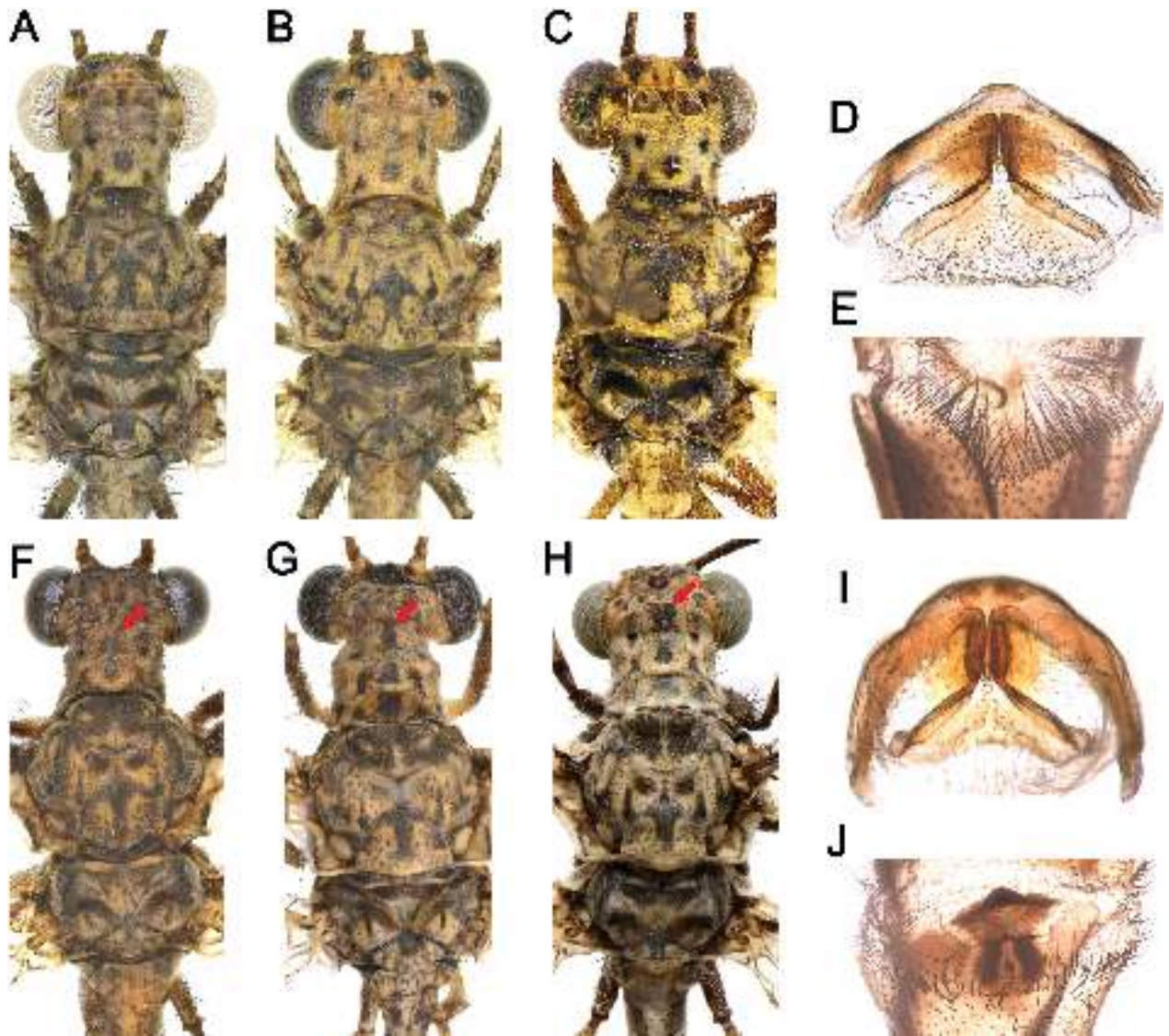


**Figure 4.** *Layahima chiangi* Banks, 1941, living photos and its habitat: **A** Habitat, Cawarong (Xizang), **B** living adult. **C** Newly hatched first instar larva. **D** Well-fed first instar larva (photos by Y. Zheng).

reaching basal of tarsomere 3. Hind leg: Coxa mostly pale yellowish brown, black basally; femur yellowish brown, with distal part dark brown; tibia pale yellow, distally dark brown; tibial spurs reaching tip of tarsomere 1; tarsomere 1 longer than that of fore- and midleg (Fig. 3A). — **Wings.** Mostly hyaline, distally rounded. Banksian lines absent. Pterostigma pale. Forewing slightly longer than hindwing. Forewing costal space with an indistinct brown spot proximal to pterostigma; subcostal area hyaline; radial area with some indistinct brown spots; medio-cubital area with a few indistinct brown spots; rhagma as two indistinct brown markings; cubital area with a basal indistinct dark brown marking; costal crossveins generally simple on basal 1/3 part, while distal 2/3 part each connect with a short oblique veins; RP originates proximally to MP fork; four to five presectoral crossveins present, with from two to three biareolate cells; RP with eight to nine branches. Hindwing rhagma indistinct; presectoral area with only one crossvein; RP originates anteriorly to MP fork (Figs 2A, B, 3). — **Abdomen.** Pale yellowish brown with some dark brown markings. Tergum 1 generally pale yellowish brown; tergum 2 with a dark brown marking; terga 3–8 each dark brown on posterior margin. — **Male genitalia.** Sternum 9 basal half wide, posterior part narrow, narrowed part as long as wide (Fig. 3E); gonocoxites 9 shaped as a pair of widely short trapezoid plates, twice as wide as long; gonocoxites 11 triangularly arched; gonostyli 11 slightly prominent (Figs 3H–L,

5D). Ectoproct slightly protruded (Fig. 3D). — **Female genitalia.** Pregenital plate weakly sclerotized. Gonocoxites 8 rounded, short digitiform; gonapophyses 8 rounded. Gonocoxites 9 with many tapered stout setae, slightly curved. Ectoproct rounded on distal margin (Fig. 3F, G).

**Description of 1st instar larva. Size.** Body length (excluding mandible): 2.13–3.22 mm; head length: 0.65–0.78 mm; head width: 0.69–0.82 mm; mandible length: 0.75–0.89 mm. — **Head.** Nearly rectangular in dorsal view, wider than long, generally brown and dark brown. Dolichasters thick, distally swollen and truncate, dark and pale, present on clypeo-labrum, dorsal head, and basal mandible. Dorsal head dark brown posteromedially and laterally. Ventral head mostly brown, lateral margin dark brown. Antenna short and robust, dark brown. Ocular tubercles well prominent. Mandible dark brown, basally with 3–4 interdental mandibular setae; first tooth shorter than second tooth; second tooth nearly as long as third tooth; two short interdental mandibular setae between first and second teeth; no seta between second and third teeth. Labial palpi dark brown (Figs 6A, B, 7A, B). — **Thorax.** Thoracic setiferous processes tubercular, with many pale setae and few dark setae. Pronotum dark brown and yellowish brown, with some dark and pale dolichasters. Mesothorax with spiracles present on short stout brown sclerotized tubercle; anterior process longer than posterior process. Metathorax medially with



**Figure 5.** Comparison of different individuals of *Layahima chiangi* Banks, 1941 and *L. qilin* sp. nov. **A–C, F–H** Head-thorax, dorsal view; **D, I** male genitalia, ventral view; **E, J** female pregenital plate, ventral view. Location (**A, B, D, E**) Cawarong (Xizang). **C** Holotype, type locality “Loutsechiang”, probably near to Cawarong (© D. Grimaldi from AMNH). **F** Holotype, type locality “Weixi, Zhonglu, Zhazidi” (Yunnan). **G, I** Batang (Sichuan). **H** Pantiange (Yunnan). **J** Baima-xueshan (Yunnan).

many dark dots; metathoracic setiferous processes equal in length (Figs 6A, 7C). — **Legs.** Pale brown, with many slender and short tapered setae (Fig. 6B, C). — **Abdomen.** Greenish brown, with many dark markings; dorsal abdominal segment 1 with a pair of large transversal dark markings. Abdomen dorsally covered with dark setae, laterally covered with pale setae. Sternum 9 ventrally with seven to eight tapered setae of uneven size; rastrum distally with four pair of tapered digging setae (Figs 6, 7D).

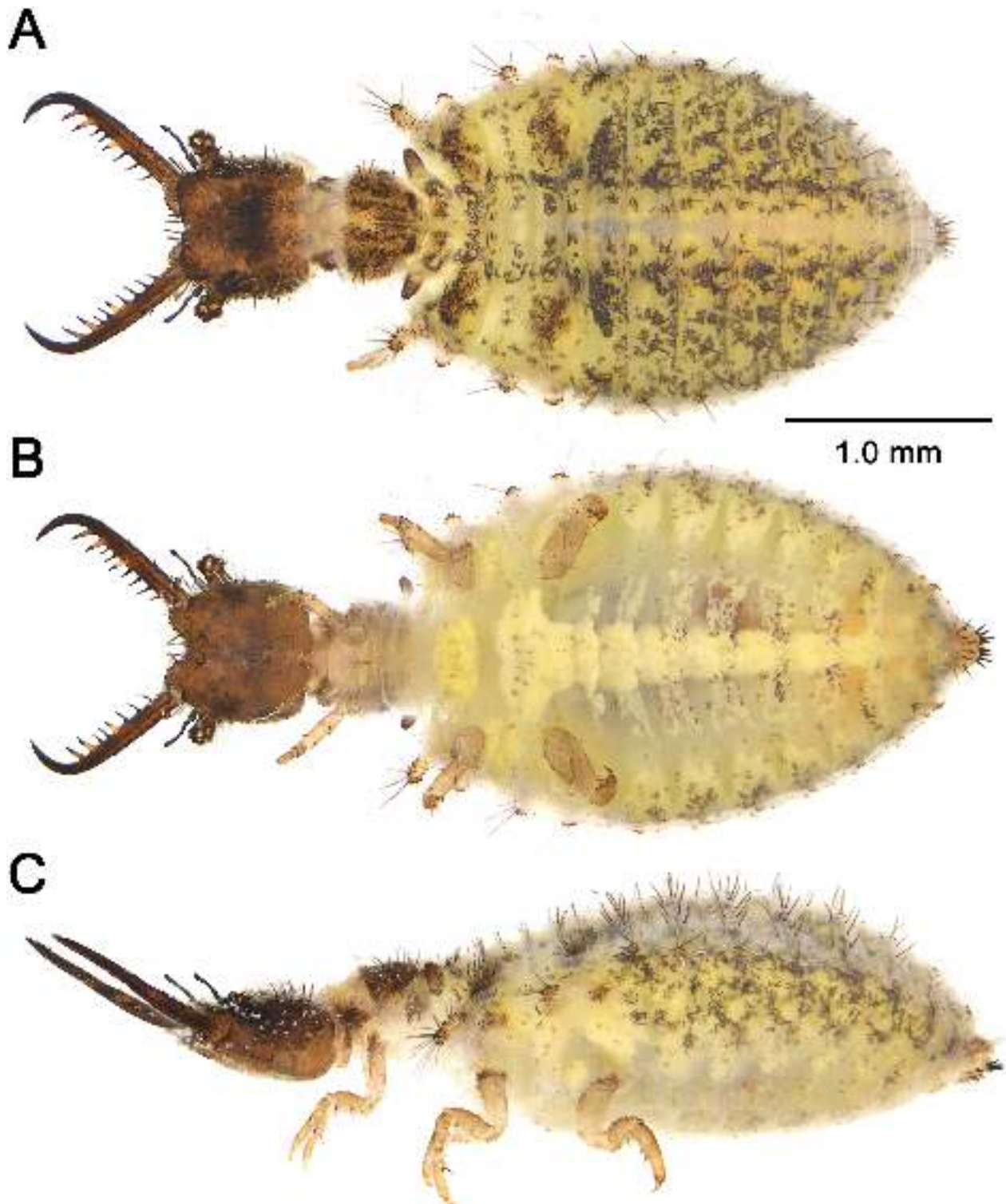
**Type material.** Holotype ♂, “Loutsechiang, Yunnan, China. Accession No. 24141”, the Nujiang dry hot river valley around the Cawarong region near Yunnan (AMNH).

**Additional material examined. Adult:** 18♂10♀, CHINA: Xizang, Nyingchi, Zayu County [察隅县], Cawarong Township [察瓦龙乡], Ridong [日东], 1930

m, 27–29.VI.2023, Yuchen Zheng (CAU). 4♂4♀, same information as above (IZCAS). 1♀, same locality as above, 1930 m, 11.VIII.2021, Xingyue Liu (IZCAS). 2♂1♀, same locality as above, 1900 m, 30.VII.2020, Yejie Lin (CAU). 1♂1♀, same locality as holotype (AMNH). 12♂, “Thibet” = [CHINA: Xizang], Coll. Lacroix (MNHN). — **Larva:** 5 1st larvae, hatched from the eggs, four preserved in 95% ethyl alcohol, one is still rearing, same locality as above, 27–29.VI.2023, Yuchen Zheng (IZCAS).

**Distribution.** China (Xizang) (Fig. 18).

**Biology.** The larvae were obtained from eggs laid by field-collected females, so their natural habitat remains unknown. In the artificial settings, the larvae showed a preference for the bare environment rather than burying under sand like most antlions. The larvae fed on termites



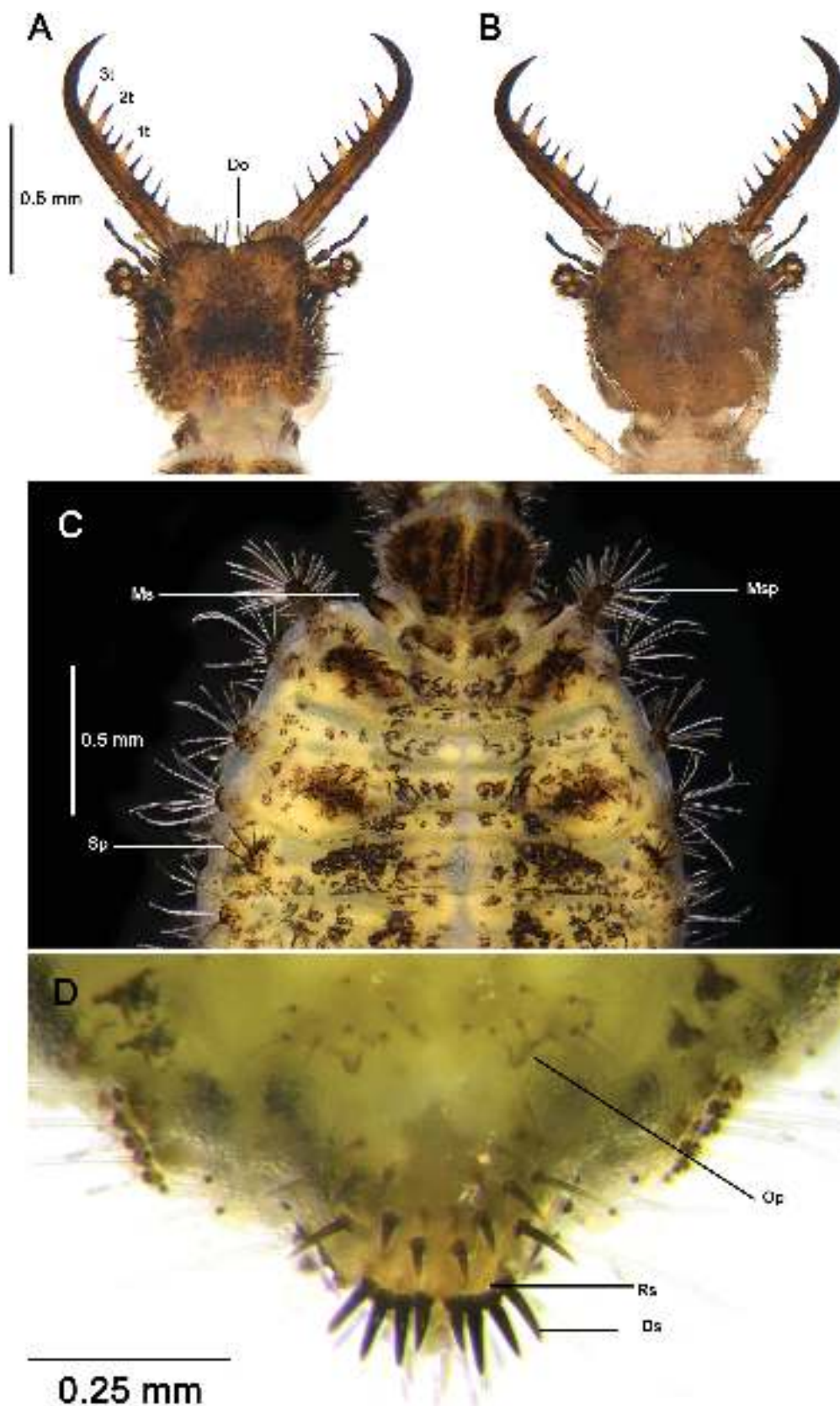
**Figure 6.** Habitus of *Layahima chiangi* Banks, 1941, first instar larva: **A** Dorsal view, **B** ventral view, **C** lateral view.

and springtails around them or crawling over their bodies, catching them with mandibles.

**Remarks.** This species is endemic to the Nujiang dry hot river valley near the Cawarong Region. According to Zheng et al. (2023), the absence of an anteromedial marking on pronotum of the holotype of *L. chiangi* is individual variability. However, a dozen specimens from Yunnan and western Sichuan preserved in CAU show some differences from the holotype, including the pres-

ence of the anteromedial markings, but the differences in all other characters are subtle. The type locality of *L. chiangi* is ambiguous (“Loutsechiang, Yunnan”, now called “Nujiang”, a watershed that throughs Xizang, Yunnan, Myanmar and Thailand), so it was not possible to locate the original collecting site, and the holotype and we can only refer to type photos for comparison.

Further collecting efforts in 2023 in the Nujiang dry hot river valley of Cawarong, Xizang, allowed to find further specimens of *L. chiangi*, which clarified the tax-



**Figure 7.** *Layahima chiangi* Banks, 1941, first instar larva: **A** Head, dorsal view; **B** head, ventral view; **C** thorax, dorsal view, on black background; **D** abdominal segments 8–9, ventral view.

onomic status of this species through genital comparisons and molecular analyses. The morphology of these specimens is consistent with the holotype of *L. chiangi*, confirming that the specimens from Yunnan and Sichuan

identified as this species in Zheng et al. (2023), belong to an undescribed taxon, i.e., *L. qilin* sp. nov.

*L. chiangi* is characterized by dark brown scape, pronotum lacking anteromedial marking, abdominal terga

with reduced dark markings, male sternum 9 short and posteriorly narrowed, male gonocoxites 9 twice as wide as long, male gonocoxites 11 triangularly arched, female pregenital plate weakly sclerotized, and shorter female gonocoxites 8. *Layahima qilin* sp. nov. differs in the pronotum with anteromedial marking, abdominal terga with wide dark markings, male sternum 9 elongate and posteriorly narrowed, male gonocoxites 9 as long as wide, female pregenital plate shaped as an anterior sclerotized prominent papilla and a posterior ridge-like prominence, and female gonocoxites 8 longer than that of *L. chiangi*.

We also shed new light on the type locality of *L. chiangi* with better precision. This species inhabits the unique habitat of the Nujiang dry hot river valley in Cawarong. This area represents an isolated “mountainous island”, surrounded by snow-capped mountains and monsoon rainforests, characterized by many endemic species, such as the spoon-winged lacewing *Sinonemoptera tibetana* Zheng & Liu, 2024 (Zheng and Liu 2024). Therefore, it is likely that the type locality of *L. chiangi* is the town of Cawarong or its environs, rather than Yunnan. All the examined specimens from the river valleys of belonged to *L. qilin* sp. nov. (Jinshajiang river valley and Lancangjiang river valley) and *L. pixiu* sp. nov. (Jinshajiang river valley). Finally, it is worth noting that the type locality of *L. chiangi* is labeled as “Yunnan” instead of “Xizang” or “Tibet”, because Cawarong Township is close to Gongshan County in western Yunnan Province, and both places are near the Nujiang River. Moreover, Cawarong was visited by European and American missionaries in the mid-19<sup>th</sup> early 20<sup>th</sup> centuries (Liu 2019), and they often collected insect specimens referring to the churches on the territory as geographic information, resulting in strongly biased locality data.

### *Layahima haohani* sp. nov.

<https://zoobank.org/DAA961C6-E549-4DB8-BA76-898DFD599988>

Figures 2D, 8

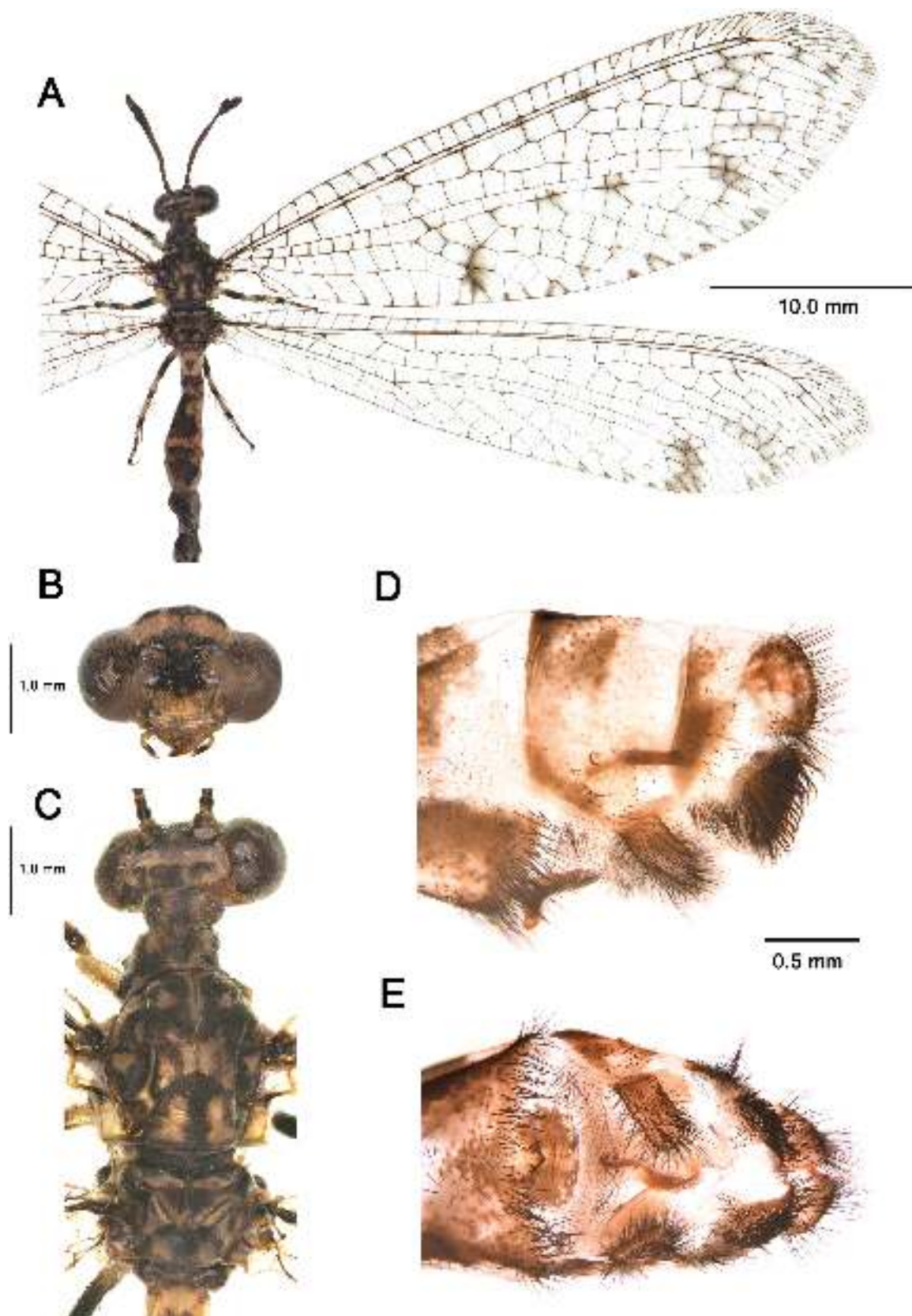
**Diagnosis. Adult:** Body pale yellow with dark markings. Vertex with three transversal black markings. Pronotum with three longitudinal black stripes, the middle one discontinuous, posterior margin mostly black (Fig. 8C). Forewing radial area distally with two indistinct dark brown markings, rhexma and basal cubital markings distinct. Hindwing radial area distally with an indistinct transversal dark brown stripe, marking of rhexma reaching wing margin (Figs 2D, 8A). Female pregenital plate shaped as a rounded sclerotized plate with a vertical prominence (Fig. 8D, E).

**Description. Size.** Head width: 2.12 mm; forewing length: 31.42 mm; hindwing length: 31.22 mm. — **Head.** Vertex pale yellow, with three transversal black markings. Scape mostly yellowish brown internally with a dark marking; pedicel mostly black; non-swollen part of flagellum brown, each flagellomere basally dark brown, swollen part of fla-

gellum mostly black. A dark brown marking present around scape, anteriorly protruded. Frons and clypeus pale yellow. Labrum brown. Mandibles pale yellowish brown with distal half dark reddish brown. Maxillary palpus mostly yellowish brown, distal margin with a dark brown marking. Labial palpus generally yellowish brown (Fig. 8B, C). — **Thorax.** Pronotum with three longitudinal black stripes, the middle one discontinuous, posterior margin mostly black. Mesoprescutum mostly black, medially with a pale yellowish stripe, laterally with a pair of pale yellowish spots; mesonotum, medially mostly pale yellow, laterally mostly black with two pair of pale yellowish spots, lateral margin pale yellow; mesoscutellum black with a pair of pale yellowish markings. Metanotum black and pale yellow; metascutellum black with a pair of pale yellowish spots. Pleurae pale yellow and black (Fig. 8C). — **Legs.** Short, as long as thorax at most, with many dark setae. All tibial spurs slightly curved; tarsomeres 1–2 pale yellow; distally brown, tarsomeres 3–4 black; tarsomere 5 pale yellow, distally black, nearly as long as entire length of tarsomeres 2–4; pretarsal claws curved, dark reddish brown. Foreleg: coxa pale yellow with a black spot; femur mostly pale yellow; tibia pale yellow, basally and distally black; tibial spurs reaching tip of tarsomere 3. Midleg: Coxa pale yellow, black basally; femur basally pale yellow, distally dark brown; tibia pale yellow, basally and distally black; tibial spurs reaching tip of tarsomere 3. Hind leg: Coxa mostly pale yellow; femur pale yellow basally, other part black; tibia pale yellow, medially and distally black; tibial spurs reaching base of tarsomere 2; tarsomere 1 longer than that of fore- and midleg (Fig. 8A). — **Wings.** Mostly hyaline, with some dark brown markings. Banksian lines absent. Pterostigma pale. Forewing slightly longer than hindwing, posterior margin rounded; costal space distally with a few indistinct brown dots; subcostal area with a few dark brown spots; radial area distally with two indistinct dark brown markings; rhexma dark brown; mediocubital area with four indistinct dark brown spots; cubital area basally with a dark brown marking; costal crossveins generally simple; RP originates proximally to MP fork; four presectoral crossveins present, with one biareolate cell; RP with five to six branches. Hindwing radial area distally with an indistinct transversal dark brown stripe, marking of rhexma reaching wing margin; presectoral area with only one crossvein; RP originating anteriorly to MP fork (Figs 2D, 8A). — **Abdomen.** Dark brown and pale yellow. Tergum 1 pale yellow medially with a subtriangular spot. Terga 2–8 mostly dark brown, each anterior and posterior margin pale yellow. — **Male genitalia.** Unknown. — **Female genitalia.** pregenital plate shaped as a rounded sclerotized plate with a vertical prominence. Gonocoxites 8 digitiform, slightly posterior curved; gonapophyses weakly sclerotized. Gonocoxites 9 with many tapered stout setae, slightly curved. Ectoproct slightly truncated (Fig. 8D, E).

**Type material.** Holotype ♀, CHINA: Yunnan, Puer, Yunxian Township [云仙乡], Mamu Village [骂木村], 980 m, 9.IV.2023 (IZCAS).

**Distribution.** China (Yunnan) (Fig. 18).



**Figure 8.** *Layahima haohani* sp. nov., adult: **A** Habitus, female, holotype; **B** head, frontal view; **C** head and thorax, dorsal view. **D, E** Female terminalia: **D** Lateral view, **E** ventral view.

**Etymology.** The new species is dedicated to Mr. Haohan Mao (毛昊涵), who helped us in obtaining the holotype of this rare species, also collecting many myrmeleontid specimens for us.

**Remarks.** The new species can be easily distinguished from other *Layahima* species by the markings on the body and wings, and the shape of female pregenital plate.

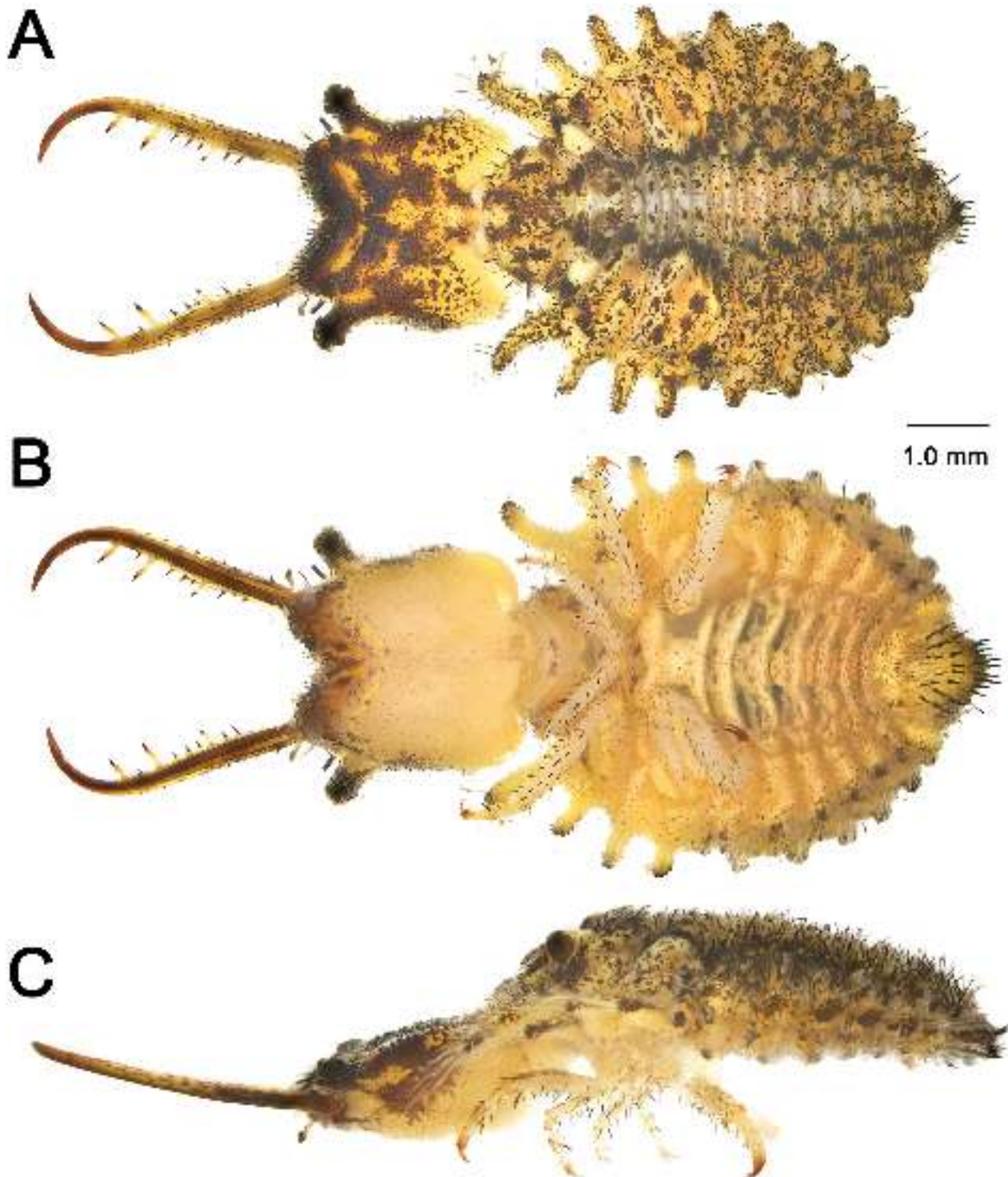
***Layahima lhoba* Zheng, Badano & Liu, 2022**

Figures 9, 10, 11A

*Layahima lhoba* Zheng et al. 2023: 56 (type locality: China: Xizang, Nyingchi, Bome County, Yiong Town, Tangmai Township, 2100 m, 6.VIII.2020, Yuchen Zheng; holotype in CAU).

**Diagnosis. Adult:** See Zheng et al. (2023). — **Larva:** Lateral body covered with many pale setae. Head pale yellow, medially with three pair of dark brown mark-

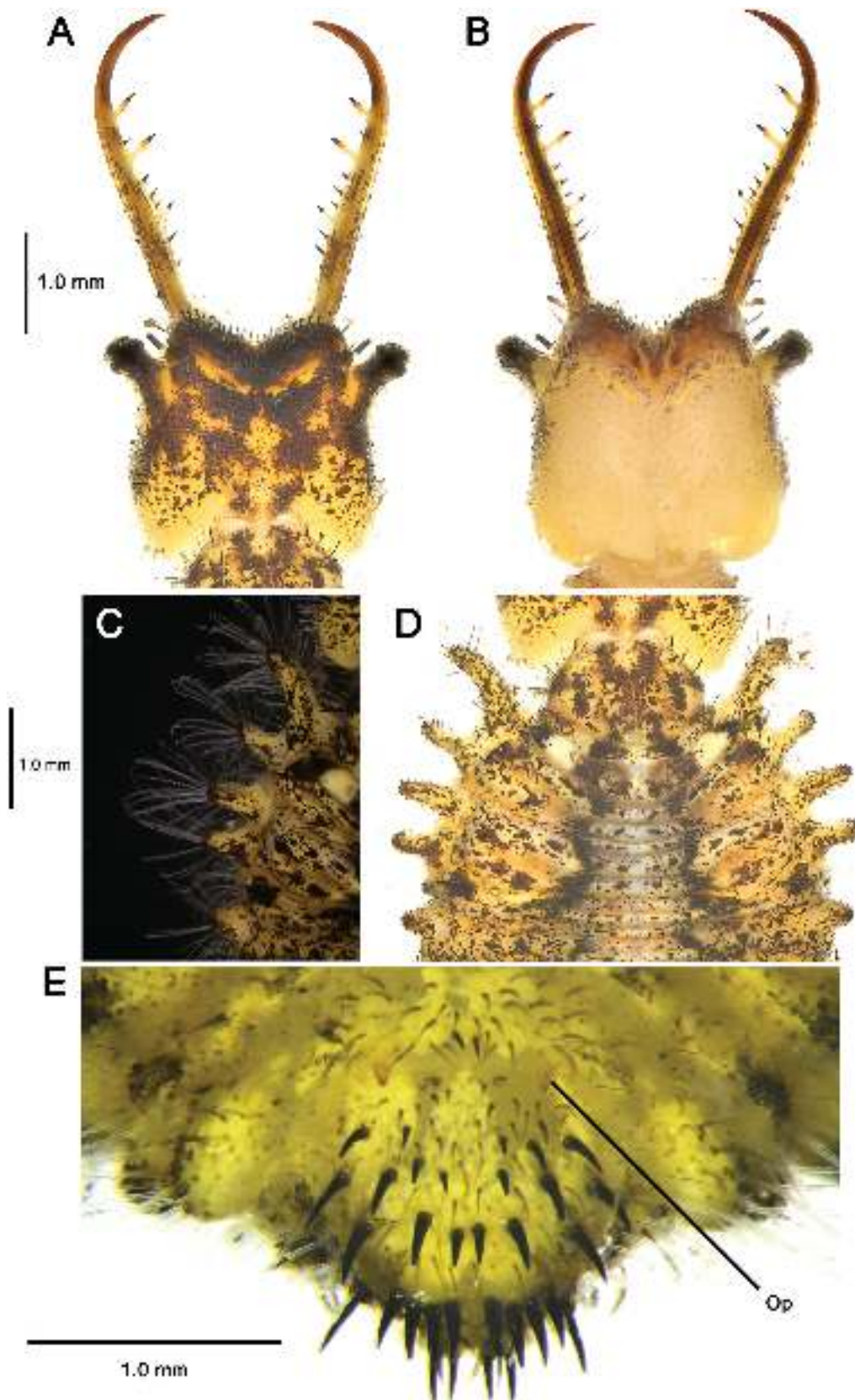
ings, laterally with a pair of dark brown stripes fused with the lateral markings in dorsal view. Dolichasters on clypeo-labrum dark and pale. Mandible mostly pale yellow, distally reddish brown. Three short interdental mandibular setae between first and second teeth; one seta between second and third teeth (Fig. 10A, B). Thoracic setiferous processes digitiform; anterior mesothoracic setiferous processes twice as long as others, curved; posterior mesothoracic setiferous processes nearly as long as others on metathorax. Meso- and metanotum, and dorsal abdominal medially pale, each segment with a pair



**Figure 9.** Habitus of *Layahima lhoba* Zheng, Badano & Liu, 2023, third instar larva: **A** Dorsal view, **B** ventral view, **C** lateral view.

of black markings (Fig. 10C, D). Abdomen with dozens black dots, abdominal setiferous processes tubercular (Fig. 9A, B). Segment 9 rastrum distally with five pair of tapered digging setae (Fig. 10E).

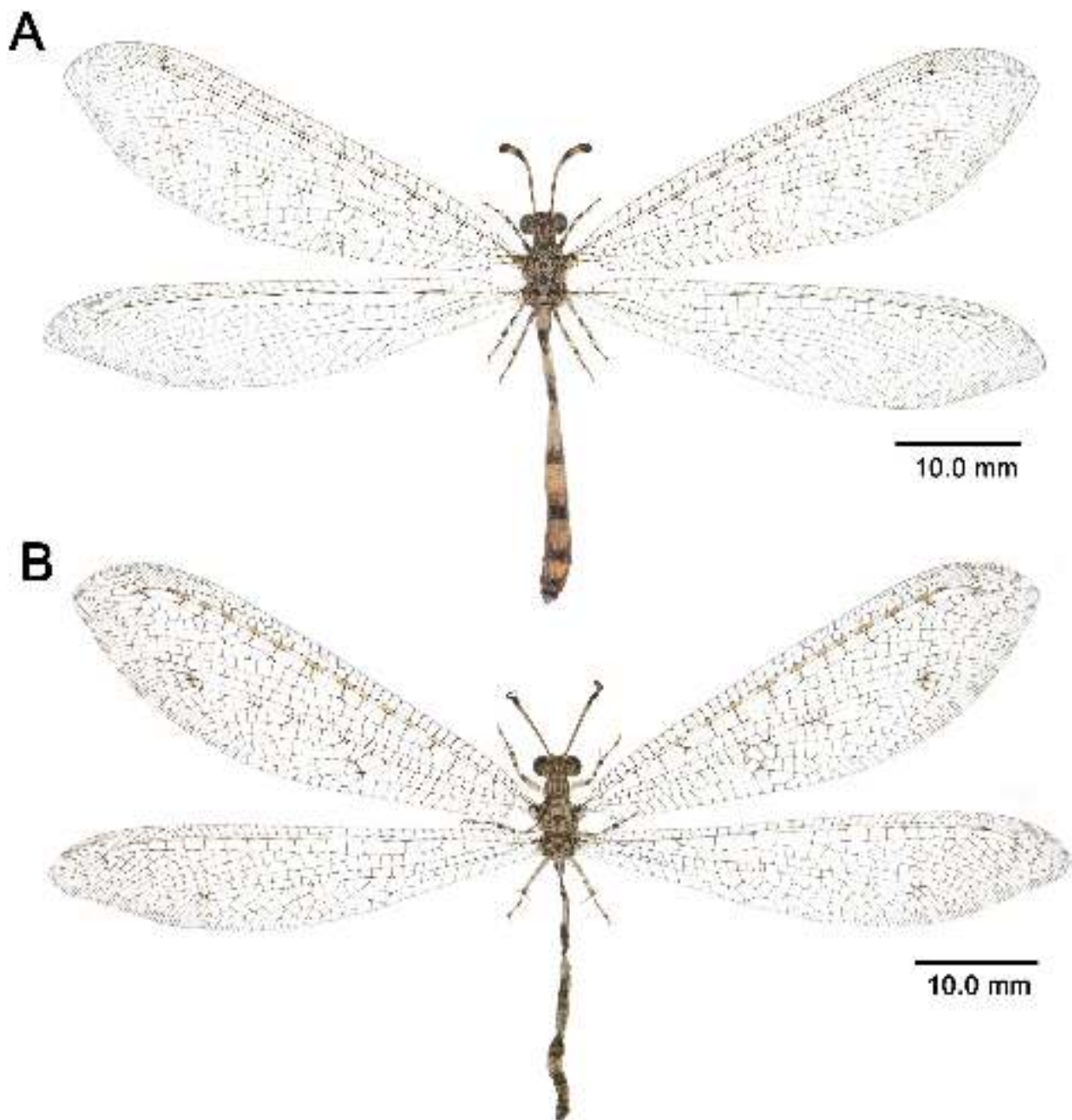
**Description of 3rd instar larva.** *Size.* Body length (excluding mandible): 4.32 mm; head length: 2.25 mm; head width: 2.27 mm; mandible length: 2.84 mm. Examined specimen discolored. — *Head.* Nearly rectangular in dor-



**Figure 10.** *Layahima lhoba* Zheng, Badano & Liu, 2023, third instar larva: **A** Head, dorsal view; **B** head, ventral view; **C** thorax, dorsal view, on black background; **D** thorax, dorsal view, on pale background; **E** abdominal segments 8–9, ventral view.

sal view, as long as wide, pale yellow and dark brown. Clypeo-labrum dark brown, with dark and pale dolichasters. Head pale yellow, medially with three pair of dark brown markings, laterally with a pair of dark brown stripes fused with the lateral markings in dorsal view, covered with pale setae laterally. Ventral head mostly pale yellow. Ocular tubercle prominent, ocular peduncle dark brown. Mandible mostly pale yellow with few irregular brown markings, distally reddish brown, basally with 3–4 interdental mandibular setae; first tooth shorter than second tooth; second tooth nearly as long as third tooth; three short interdental mandibular setae between first and second teeth; one seta between second and third teeth. Labial palp dark brown (Figs 9, 10A, B). — **Thorax.** Laterally with many pale setae. Thoracic setiferous processes digitiform, with dark brown

dots. Pronotum pale yellow, medially with a forked dark brown marking, laterally with a pair of arched dark brown markings, covered with many dark and pale setae. Mesothorax with spiracles present on short, sclerotized tubercle, mostly pale, distally dark brown; anterior mesothoracic setiferous processes twice as long as others, curved. Posterior mesothoracic setiferous processes nearly as long as others on metathorax. Meso- and metanotum medially pale, each with a pair of black markings (Figs 9, 10C, D). — **Legs.** Pale yellow, with many slender and short tapered setae (Fig. 9B, C). — **Abdomen.** Pale yellow with many dark brown markings. Dorsally covered with dense black setae, with dozens black dots; medially pale, each segment with a pair of black markings. Abdominal setiferous processes tubercular, distally dark brown. Lateral margin covered with pale



**Figure 11.** Habitus of adults of *Layahima* spp. associated with larvae: **A** *L. lhoba* Zheng, Badano & Liu, 2023; **B** *L. yangi* Wan & Wang, 2006.

setae. Ventrally generally pale yellow. Segment 9 dorsally with two pair of stout tapered setae; ventrally with 17 tapered setae of uneven size, the external row of setae largest, the internal row of setae smallest; rastrum distally with four pair of tapered digging setae; rastrum distally with five pair of tapered digging setae (Figs 9A, B, 10E).

**Type material.** Holotype ♂, China: Xizang, Nyingchi, Bome County, Yiong Town, Tangmai Township, 2100 m, 6.VIII.2020, Yuchen Zheng (CAU). Other type specimens were examined in Zheng et al. (2023).

**Additional material examined.** Larva. 3rd instar larva preserved in 95% ethyl alcohol, CHINA: Xizang, Nyingchi, Medog County [墨脱县], Ximo Bridge [西莫桥], 726m, 10.VII.2023, Zhiteng Chen (ZCAU).

**Distribution.** China (Xizang).

**Biology.** The only known larva of this species was found hiding under a rock by the collector looking for stoneflies (Plecoptera), who turned over a rock not far from the river while collecting stonefly nymphs.

### *Layahima pixiu* sp. nov.

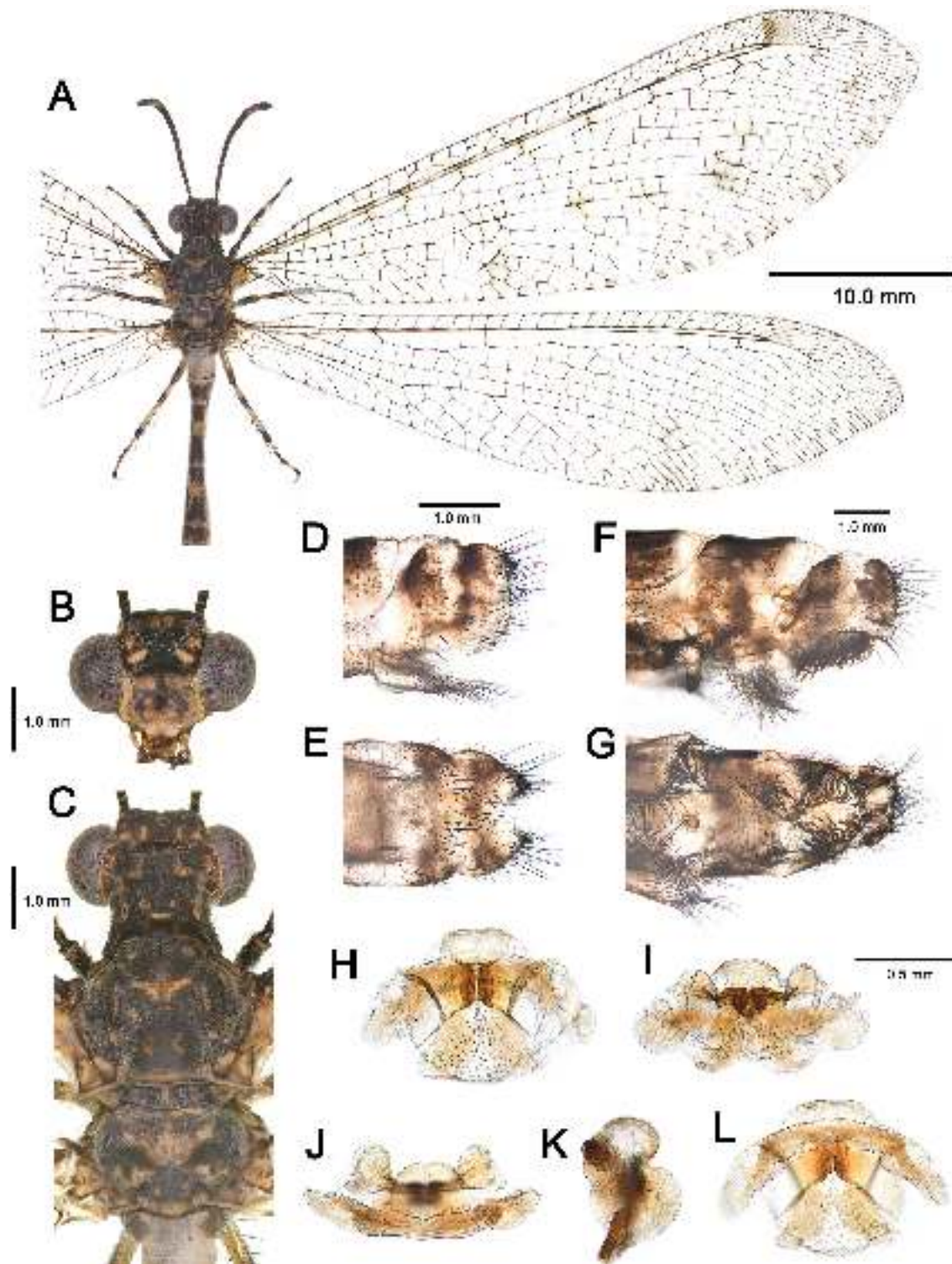
<https://zoobank.org/A507A628-4F72-4866-96E4-F3484462822A>

Figures 2E, 12

**Diagnosis. Adult:** Body black with some yellowish-brown markings. Vertex mostly black, anterior and posterior margins with a few yellowish-brown markings. Frons yellowish brown, with a crossed black marking (Fig. 12B, C). Pronotum mostly black, medially with four yellowish brown markings, laterally with a pair of curved yellowish-brown stripes, sometimes the middle markings connected with the lateral markings (Fig. 12B). Abdominal terga 3–7 black, each medially with a yellowish-brown marking and posterior margin yellowish brown (Fig. 2E). Male sternum 9 wide, posterior part narrowed and short (Fig. 12E); gonocoxites 9 externally swollen and protruded (Fig. 12H–L). Female pregenital plate shaped as a vertical prominence; gonocoxites 8 short and narrow, posteriorly curved (Fig. 12F, G).

**Description of adult. Size.** Head width: 2.68–3.12 mm; forewing length: 29.67–33.43 mm; hindwing length: 28.23–32.14 mm. — **Head.** Vertex mostly black, anterior and posterior margins with a few yellowish-brown markings. Scape and pedicel mostly dark brown; antenna mostly black, non-swollen part of flagellomeres each distally yellowish brown; swollen part of flagellum with a yellowish-brown marking. A dark brown marking present around the antennal scape, anteriorly slightly concaved. Frons yellowish brown, with a crossed black marking. Clypeus and labrum pale yellowish brown. Mandible pale yellowish brown with distal half dark reddish brown. Maxillary pal-

pus mostly dark brown, only segment 3 brown. Labial palpus generally yellowish brown, distal palpomere fusiform and dark brown (Fig. 12B, C). — **Thorax.** Pronotum mostly black, medially covered with short black setae, lateral margin with pale setae; medially with four yellowish brown markings, laterally with a pair of curved yellowish-brown stripes, sometimes the middle markings connected with the lateral markings. Mesoprescutum black with a pair of yellowish-brown spots; mesonotum black, medially with an inverted triangular yellowish brown marking, laterally with two pair of yellowish brown stripes and spots; mesoscutellum black, with a pair of yellowish brown spots, posterior margin yellowish brown. Metanotum black and yellowish brown; metascutellum mostly black, posterior margin yellowish brown. Pleurae mostly black (Fig. 12C). — **Legs.** Short, as long as thorax at most, with many black and pale setae. All tibial spurs slightly curved; tarsomere 1 pale yellow, tarsomere 2 pale yellow with distally black, tarsomeres 3–4 black; tarsomere 5 pale yellow with distally black, nearly as long as entire length of tarsomeres 2–4; pretarsal claws curved, dark reddish brown. Foreleg: coxa pale yellowish brown with a black spot; femur dorsally and ventrally black, laterally yellowish brown; tibia black, basally and medially with two pale yellow markings; tibial spurs reaching base of tarsomere 3. Midleg: Coxa pale yellowish brown with a black spot; femur mostly pale yellowish brown, distally dark brown; tibia black, basally and medially with two pale yellow markings; tibial spurs reaching base of tarsomere 3. Hind leg: Coxa pale yellowish brown with a black spot; femur mostly pale yellowish brown, distally dark brown; tibia pale yellow, mediobasally and distally black; tibial spurs reaching tip of tarsomere 1; tarsomere 1 longer than that of fore- and midleg (Fig. 12A). — **Wings.** Mostly hyaline, distally rounded. Banksian lines absent. Pterostigma pale. Forewing slightly longer than hindwing. Forewing costal space with a dark brown spot proximal to pterostigma; subcostal area with some indistinct brown spots; radial area with some indistinct brown spots; mediocubital area with a few indistinct brown spots; rhagma as two indistinct brown markings; cubital area with a basal indistinct dark brown marking; costal crossveins generally simple on basal 1/4 part, while distal 3/4 part each connect with a short oblique veins; RP originates proximally to MP fork; four to five presectoral crossveins present, with from two to four biareolate cells; RP with eight to nine branches. Hindwing rhagma as an indistinct brown marking reaching to posterior margin; presectoral area with only one crossvein; RP originates anteriorly to MP fork (Figs 2E, 12A). — **Abdomen.** Terga mostly black, with some yellowish-brown marking, sterna mostly yellowish brown. Tergum 1 generally pale; tergum 2 mostly dark brown; terga 3–7 black, each medially with a yellowish-brown marking and posterior margin yellowish brown (Fig. 2E). — **Male genitalia.** Sternum 9 wide, posterior part narrowed and short (Fig. 12E). Gonocoxites 9 shaped as a pair of trapezoid plates, externally swollen and protruded; gonocoxites 11 widely arched; gonostyli 11 rounded protruded in lateral view (Fig. 12H–L). Ectoproct rounded in posterior margin (Fig. 12D). — **Female genitalia.** Pregenital plate shaped as a vertical prominence. Gonocoxites 8 short and narrow,



**Figure 12.** *Layahima pixiu* sp. nov., adult: **A** Habitus, female holotype; **B** head, frontal view; **C** head and thorax, dorsal view. **D**, **E** Male terminalia: **D** Lateral view, **E** ventral view. **F**, **G** Female terminalia: **F** Lateral view, **G** ventral view. **H–L** Male genitalia: **H** Ventral view, **I** anteroventral view, **J** caudal view, **K** lateral view, **L** dorsal view.

digitiform, posteriorly curved; gonapophyses 8 indistinct and rounded. Gonocoxites 9 with many tapered stout setae, slightly curved. Ectoproct truncate on distal margin (Fig. 12F, G).

**Type material.** Holotype ♀, CHINA: Yunnan, Diqing, Shangri-La County [香格里拉县], Hutiaoxia Town [虎跳峡镇], Jiangbian Village [江边村], 1830 m, 25.V.2023,

Quanyu Ji (IZCAS). Paratypes: 1♀, same locality as above, 24.V.2023, Quanyu Ji (IZCAS); 1♂, CHINA: Sichuan, Garze, Muli County [木里县], Maidilong Township [麦地龙乡], Yalongjiang Town [雅砻江镇], Zhongpuzi Village [中埔子村], 18.V.2024, Hao Xun (CAU); 1♂, CHINA: Yunnan, Kunming, Luquan County [禄劝县], Shangshihuiyao [上石灰窑], 1860 m, 3.VII.2022, Zhixin Yang (IZCAS).

**Etymology.** The species name “*pixiu*” is derived from the Chinese mythological creature “Pixiu” (貔貅), which is a legendary animal known for its ability to attract wealth and protect against evil. According to the Chinese legend, the Pixiu only devours wealth (especially gold and silver treasures) and does not excrete, symbolizing wealth accumulation, not letting the loss of wealth. The Pixiu has a striking resemblance to both the mythical antlion, —associated with riches—and the real insect, known for not excreting at the larval stage. The name is treated as a noun in apposition.

**Distribution.** China (Sichuan, Yunnan) (Fig. 18).

**Remarks.** *L. pixiu* sp. nov. can be easily distinguished from other *Layahima* species by its mostly black body with reduced yellowish-brown markings, and the swollen and prominent external male gonocoxites 9. *L. pixiu* sp. nov. is distributed in some transition regions between the Mt. Hengduan Mountain and Ailaoshan Mountain ranges.

### *Layahima qilin* sp. nov.

<https://zoobank.org/7C38BC4E-7737-4A3A-AB70-B8BE45F87273>

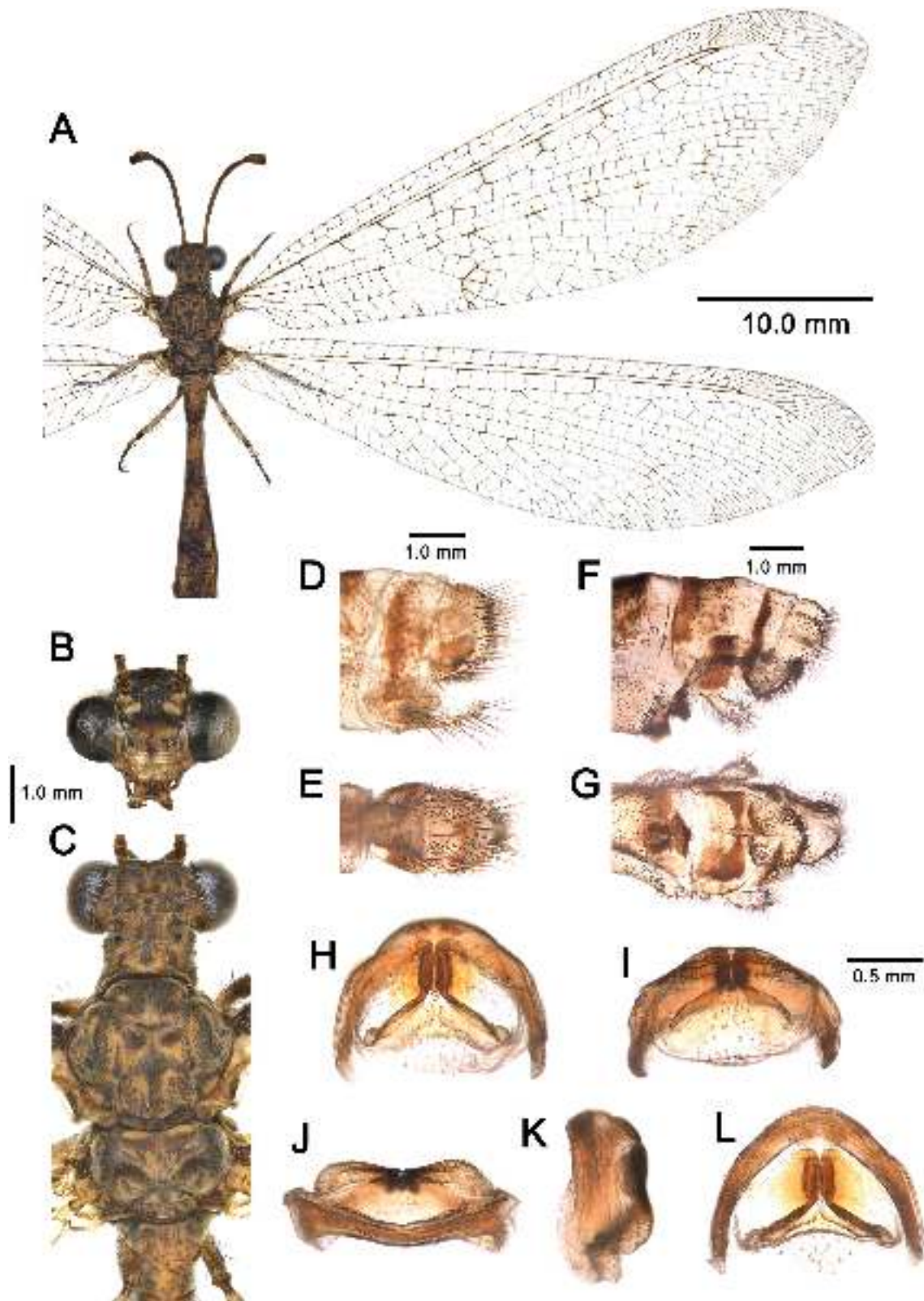
Figures 2C, 5F–J, 13

**Diagnosis. Adult:** Body pale yellowish brown with some black and dark brown markings, parts with numerous black dots at base of setae. Vertex anteriorly with four median small black spots, posteriorly with a pair of transversal black markings. Frons and clypeus mostly pale yellowish brown with a transversal stripe (Fig. 13B, C). Pronotum anteromedially with a dark brown marking, anteromedially with a pair of dark brown spots, medially with a dark brown spot, and laterally with four pairs of dark brown spots (Figs 5F–H, 13C). Male sternum 9 wide, posterior part narrowed and elongate (Fig. 13D, E); gonocoxites 9 are as long as wide. Female pregenital plate shaped as an anterior sclerotized papilla prominence and a posterior ridge-like prominence.

**Description of adult. Size.** Head width 3.09–3.31 mm; forewing length 27.45–32.35 mm; hindwing length 25.32–33.78 mm. — **Head.** Vertex anteriorly with four median small black spots, posteriorly with a pair of transversal black markings. Scape largely pale yellow, internal margin black; pedicel dark brown; flagellum mostly pale brown, each flagellomere brown basally. A dark brown marking present around scapes, anteriorly concaved. Frons and clypeus mostly pale yellowish brown with a transversal stripe. Labrum pale yellow. Maxillary palpus pale yellow. Labial palpus generally pale, distal flagellomere dark brown, fusiform. Mandible pale yellow with distal half dark reddish brown (Figs 5F–H, 13B, C). — **Thorax.** Pronotum anteromedially with a dark brown marking, anteromedially with a pair of dark brown spots, medially with a dark brown spot, and laterally with four pairs of dark brown spots. Mesoprescutum mostly black, anteriorly with a pair of pale yellowish-brown spots; mesonotum pale yellowish brown, with three pair of black stripes and a pair of black spots, pale yellowish-brown part with some black dots; mesoscutellum anteriorly black, mostly pale yellowish brown, variation present in different individuals. Metanotum pale yellowish brown and black; metascutellum mostly pale yellowish brown. Pleurae pale yellowish-brown and black (Figs 5F–H, 13C). — **Legs.** Short, as long as thorax at most, with many black and pale setae. All tibial spurs slightly curved; tarsomeres each generally pale yellow with distal part dark brown; tarsomere 5 pale yellow, with distal part dark brown, nearly as long as entire length of tarsomeres 2–4; pretarsal claws curved, dark reddish brown. Foreleg: coxa pale yellow with a black spot; femur dorsally brown to dark brown, ventrally pale yellowish brown; tibia pale yellow with a dark anterior marking, distal part dark brown; tibial spurs reaching base of tarsomere 3. Midleg: Coxa pale yellowish brown, black basally; femur mostly yellowish brown, distally dark brown; tibia pale yellow, with some black dots, distal part dark brown; tibial spurs reaching basal of tarsomere 3. Hind leg: Coxa mostly pale yellowish brown, black basally; femur yellowish brown, with distal part dark brown; tibia pale yellow, distally dark brown; tibial spurs reaching tip of tarsomere 1; tarsomere 1 longer than that of fore- and midleg (Fig. 13A). — **Wings.** Mostly hyaline, distally rounded. Banksian lines absent. Pterostigma pale. Forewing slightly longer than hindwing. Forewing costal space with an indistinct brown spot proximal to pterostigma; subcostal area hyaline; radial area with some indistinct brown spots; mediocubital area mostly hyaline; rhexma as two indistinct brown markings; cubital area with a basal indistinct dark brown marking; costal crossveins generally simple on basal 1/6 part, while distal 5/6 part each connect with a short oblique veins; RP originates proximally to MP fork; four to five presectoral crossveins present, with from two to three biareolate cells; RP with eight to nine branches. Hindwing rhexma indistinct; presectoral area with 1 crossvein; RP originates anteriorly to MP fork (Fig. 2D, 13A). — **Abdomen.** Pale yellowish brown with some dark brown markings. Tergum 1 generally pale yellowish brown; tergum 2 mostly dark brown; terga 3–8 each dark brown on posteromedial part (Fig. 2D). — **Male genitalia.** Sternum 9 wide, posterior part narrowed and elongate (Fig. 13E); gonocoxites 9 shaped as a pair of widely short trapezoid plates, as long as wide; gonocoxites 11 rounded arched; gonostyli 11 slightly prominent (Fig. 13H–L). Ectoproct slightly protruded (Fig. 13D). — **Female genitalia.** Pregenital plate shaped as an anterior sclerotized papilla prominence and a posterior ridge-like prominence; gonocoxites 8 slightly curved, short digitiform, with an anterior rounded depressed groove; gonapophyses 8 widely triangular. Gonocoxites 9 with many tapered stout setae, slightly curved. Ectoproct rounded on distal margin (Fig. 13F, G).

**Type material. Holotype** ♂, CHINA: Yunnan, Diqing, Weixi County [维西县], Zhonglu Township [中路乡], Zhazidi [扎子底], 1885 m, 6.VII.2022, Zhihao Qi (IZ-CAS). — **Paratypes:** 1♂1♀ CHINA: Sichuan, Garze,

**Type material. Holotype** ♂, CHINA: Yunnan, Diqing, Weixi County [维西县], Zhonglu Township [中路乡], Zhazidi [扎子底], 1885 m, 6.VII.2022, Zhihao Qi (IZ-CAS). — **Paratypes:** 1♂1♀ CHINA: Sichuan, Garze,



**Figure 13.** *Layahima qilin* sp. nov., adult: **A** Habitus, female holotype; **B** head, frontal view; **C** head and thorax, dorsal view. **D, E** Male terminalia: **D** Lateral view, **E** ventral view. **F, G** Female terminalia: **F** Lateral view, **G** ventral view. **H–L** Male genitalia: **H** Ventral view; **I** anteroventral view; **J** caudal view; **K** lateral view; **L** dorsal view.

Batang County [巴塘县], Suwalong Township [苏哇龙乡], 2410 m, 2.VII.2020, Yuezheng Tu & Di Li (IZ-CAS); 2♀, CHINA: Xizang, Qamdo, Markam County [芒康县], Yanjing Town [盐井乡], 2600 m, 7.VI.1976, Yinheng Han (CAU); 1♀, CHINA: Xizang, Qamdo,

19.IX.1982, Wang (CAU); 1♀, CHINA: Yunnan, Diqing, Deqen County [德钦县], Mt. Baimaxueshan [白马雪山], 23.VI.2020, Weidong Huang (CAU); 1♂1♀, CHINA: Yunnan, Diqing, Deqen County, Mt. Meilixueshan [梅里雪山], 22.VII.1982, Shuyong Wang (CAU); 1♀, CHINA:

Yunnan, Diqing, Deqen County, Xiaruo Township [霞落乡], 16.V.1976, Xiangqun Yuan (CAU); 3♂1♀, CHINA: Yunnan, Diqing, Deqen County, Yanmen Township [雁门乡], Cizhong Village [茨中村], 16–18.VI.2004, Hao Huang (CAU); 1♂ CHINA: Yunnan, Diqing, Weixi County, Pantiang Township [攀天阁乡], 9.VII.2010 (IZCAS); CHINA: Yunnan, Diqing, Weixi County, Yongchun Township [永春乡], Baipa [白帕], 2300 m, 1.VII.2023, Yuchen Zheng (CAU); 1♀, CHINA: Yunnan, Lijiang, Yulong County [玉龙县], Tacheng Township [塔城乡], 10.VII.2004, Hao Huang (CAU); CHINA: Yunnan, “Mekong” (Lancangjiang) valley, 35 km S Deqen, 3000 m, 14.VI.2000, Enrico Gallo (MSNG).

**Etymology.** This new species is named after the “Qilin” (麒麟), a mythical creature in Chinese mythology known for its kindness and auspiciousness. The name is treated as a noun in apposition.

**Distribution.** China (Sichuan, Xizang, Yunnan) (Fig. 18).

**Bio-ecology.** *L. qilin* sp. nov. is endemic to the middle elevations (1800–3000 m) of Shaluli and Mangkang mountain systems between Lanchangjiang and Jinshajiang River.

### *Layahima yangi* Wan & Wang, 2006

Figures 11B, 14–16

*Layahima yangi* Wan & Wang in Wan et al. 2006: 42 (type locality: China: Guangxi, Pingxiang; holotype in CAU). Wang et al. 2018: 66 (*Layahima*). Zheng et al. 2023: 58 (*Layahima*).

**Diagnosis. Adult:** See Zheng et al. (2023). — **Larva:** Head pale yellow, anteromedially with a pair of connected dark brown markings, and other part with many dark brown dots in dorsal view; lateral margin with a pair of oblique dark brown markings. Dolichasters on clypeo-labrum mostly pale. Mandible pale yellow with reddish brown markings. Basally with six to seven interdental mandibular setae; three short interdental mandibular setae between first and second teeth; one seta between second and third teeth (Fig. 15A, B). Thoracic setiferous processes long digitiform, meso- and metathorax each with anterior setiferous processes posteriorly curved, nearly twice as long as the posterior one. Mesothoracic posterior setiferous processes anteriorly curved (Fig. 15C). Abdomen rounded; setiferous processes short digitiform, processes on further posterior segment shorter; dorsally pale blue and pale yellow with many dark markings; ventrally without marking, green and pale yellow (Fig. 14A, B); Segment 9 dorsally with four digging setae, rastrum distally with four pair of tapered digging setae (Fig. 15D).

**Description of 3rd instar larva. Size.** Body length (excluding mandible): 10.20 mm; head length: 2.36 mm; head width: 2.58 mm; mandible length: 3.24 mm. — **Head.**

Nearly rectangular in dorsal view, wider than long, pale yellow with some dark markings. Clypeo-labrum dark brown, with pale dolichasters. Head pale yellow, anteromedially with a pair of connected dark brown markings, and other part with many dark brown dots in dorsal view; lateral margin with a pair of oblique dark brown markings; ventrally without marking. Antenna slender. Ocular tubercles well prominent, ocular peduncle dark brown. Mandible pale yellow with reddish brown markings; basally with six to seven interdental mandibular setae; first tooth shorter than second tooth; second tooth nearly as long as third tooth; three short interdental mandibular setae between first and second teeth; one seta between second and third teeth. Labial palps pale brown (Figs 14, 15A, B). — **Thorax.** Laterally with pale setae. Thoracic setiferous processes long digitiform. Pronotum pale yellow, medially with a pair of closed black stripes, laterally with irregular black markings. Mesothorax with spiracles present on short sclerotized tubercle, basally dark brown and pale yellow, distally pale, tip dark brown. Meso- and metanotum medially pale blue and laterally pale yellow, with many black markings; meso- and metathorax each with anterior setiferous processes posteriorly curved, mostly pale yellow, nearly twice as long as the posterior one; posterior setiferous processes mostly dark brown. Mesothoracic posterior setiferous processes anteriorly curved (Figs 14A, 15C). — **Legs.** Pale yellow, with many slender and short tapered setae (Fig. 14B, C). — **Abdomen.** Rounded, dorsally pale blue and pale yellow with many dark markings; ventrally green and pale yellow, without marking. A pair of large spiracles present on laterodorsal abdominal segment 1. Setiferous processes short digitiform, processes on further posterior segment shorter (Fig. 14A, B). Segment 9 dorsally with four digging setae; ventrally with seven tapered setae of uneven size, the external row of setae largest, the internal row of setae smallest; rastrum distally with four pair of tapered digging setae (Fig. 15D).

**Type material.** Holotype ♀, CHINA: Guangxi, Chongzuo, Pingxiang City [凭祥市], 16.V.1963, Chikun Yang (CAU). Other type specimens were examined in Zheng et al. (2023).

**Additional material examined. Larva:** 1 3rd instar larva, CHINA: Guangxi, Guilin, Lingchuan County [灵川县], Sanjie Town [三街镇], 18.IV.2024, Haofei Fan (ZCAU).

**Distribution.** China (Guangxi); Vietnam (Hoa Binh) (Fig. 18).

**Bio-ecology.** The only known larva of this species was found anchored on a vertical limestone surface, with its body attached to green mosses (Fig. 16). This behavior resembles that of some owlfly larvae (e.g., *Puer* Lefèbvre, 1842) (Badano & Pantaleoni, 2014b), and some antlion larvae (*Gatzara* Navás, 1915, *Nepsalus* Navás, 1914, and *Jaffuelia* Navás, 1918) (Zheng et al. 2022, 2024; Stange et al. 1994, 2003).

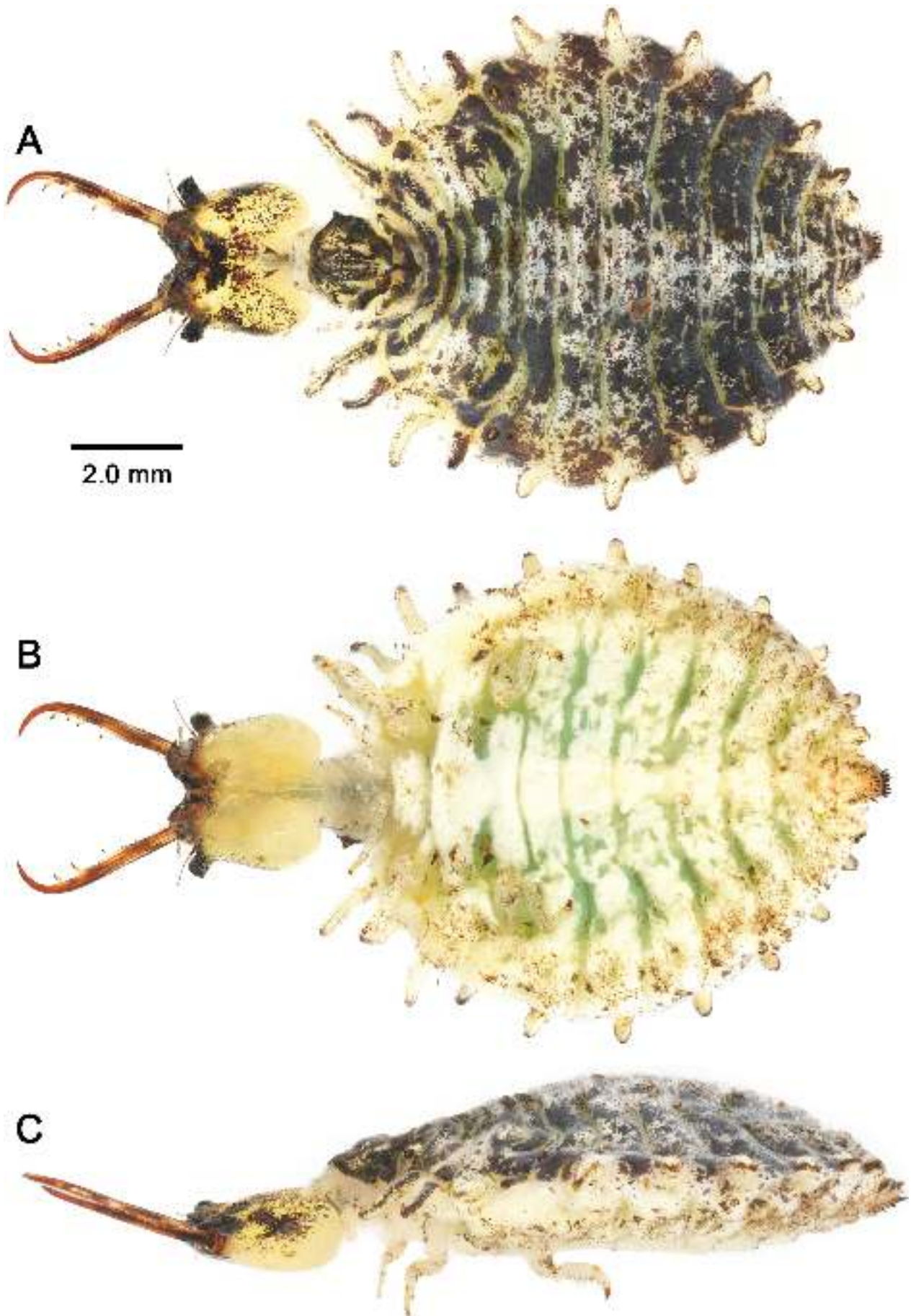
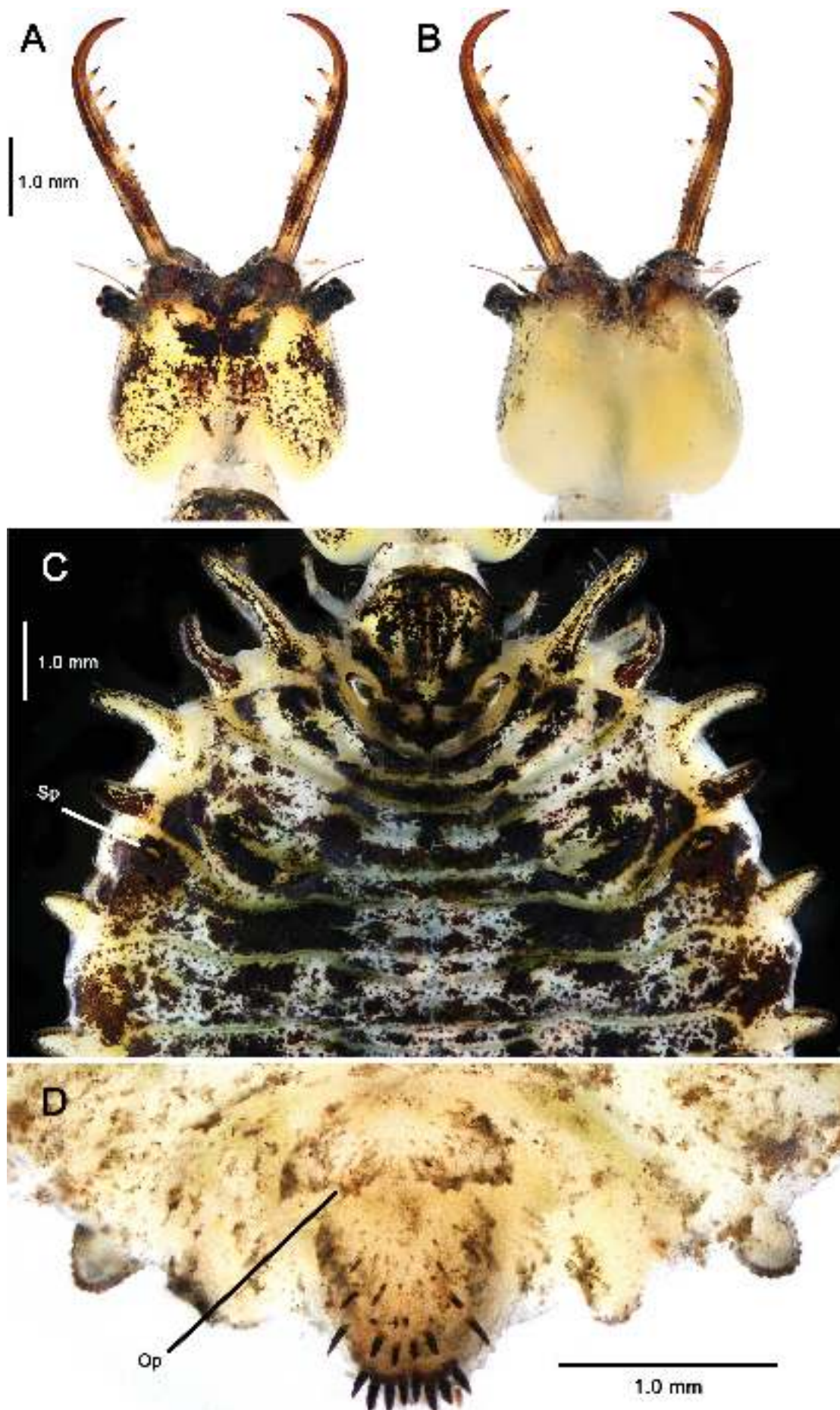
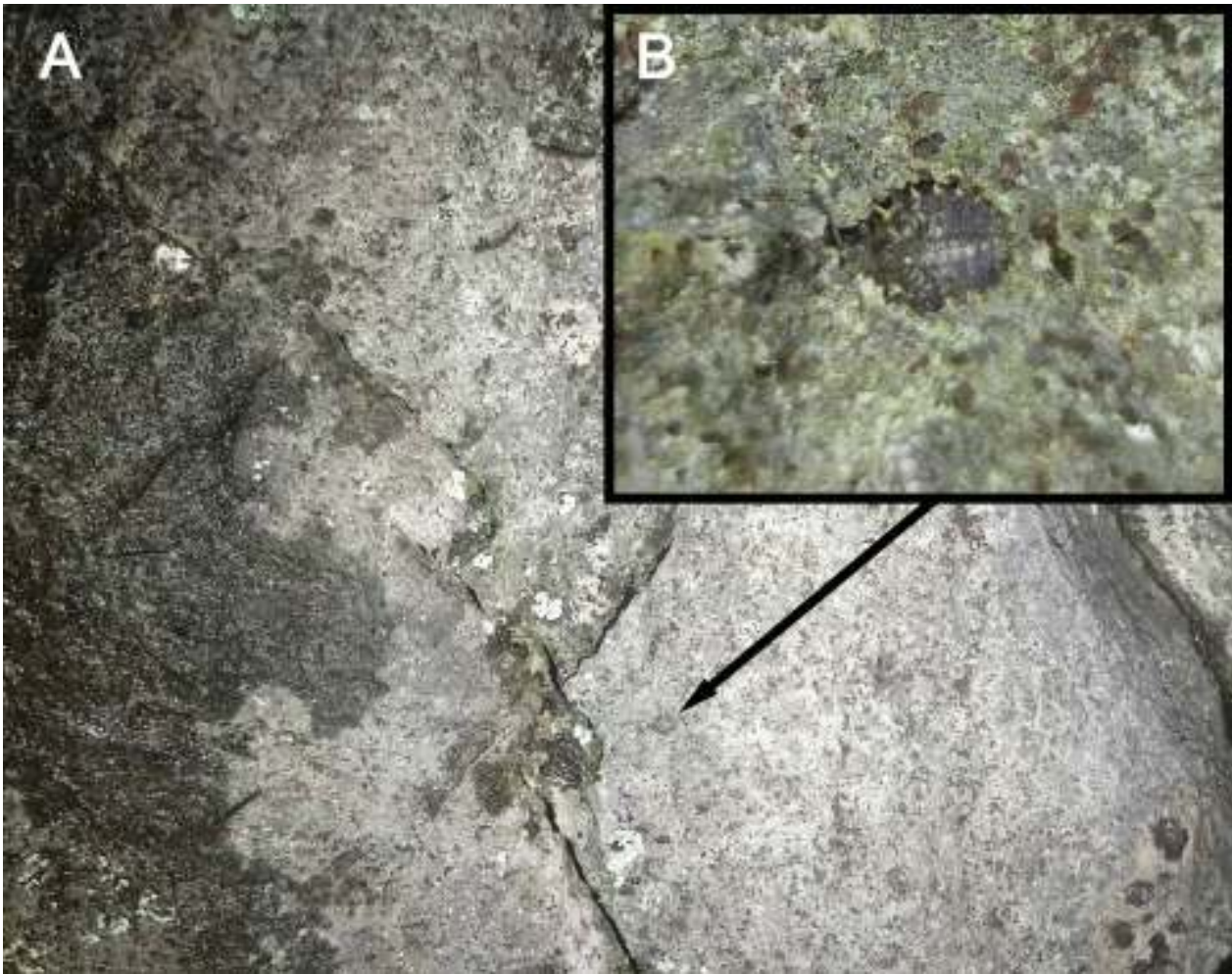


Figure 14. Habitus of *Layahima yangi* Wan & Wang, 2006, third instar larva: A Dorsal view, B ventral view, C lateral view.



**Figure 15.** *Layahima yangi* Wan & Wang, 2006, third instar larva: **A** Head, dorsal view; **B** head, ventral view; **C** thorax, dorsal view, on black background; **D** abdominal segments 8–9, ventral view.



**Figure 16.** Living third larva of *Layahima yangi* Wan & Wang, 2006: **A** Habitat, limestone in Guilin (Guangxi); **B** Living 3rd larva on the limestone surface (photos by Haofei Fan).

### *Layahima zhitengi* sp. nov.

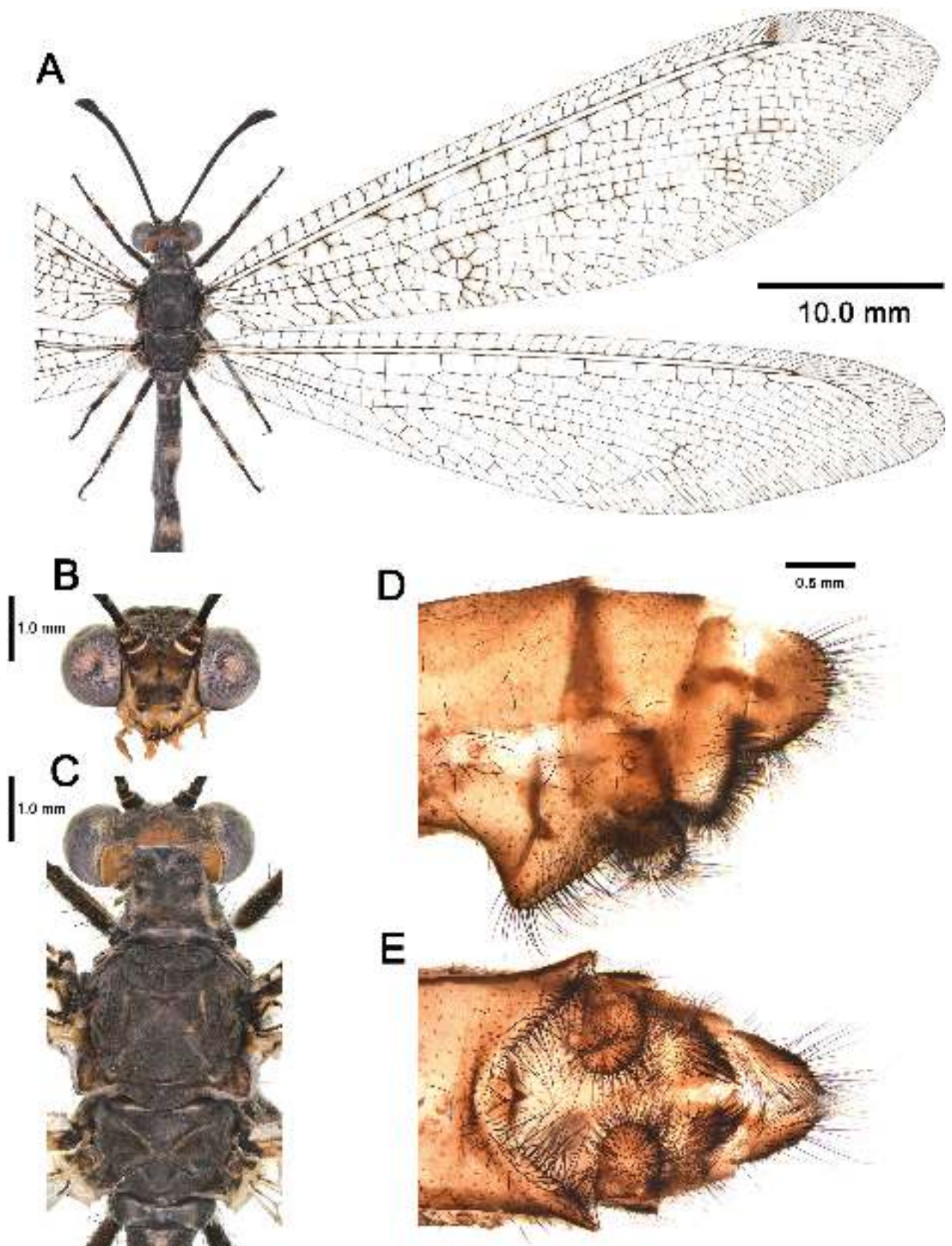
<https://zoobank.org/D57DDADF-2133-449F-90CE-62BC-DED1D7DE>

Figures 2F, 17

**Diagnosis.** Body generally dark grey. Posterior margin of vertex and postgena orange. Pronotum with a pair of “F” shaped pale yellowish markings. Mesonotum with a few pale yellowish markings (Fig. 17C). Forewings long, narrow, nearly four times as long as maximum width, with dense indistinct markings (Figs 2F, 17A). Abdomen mostly dark grey, terga 1 and 3–5 each medially with a pale yellowish marking (Fig. 2F). Female pregenital plate shaped as a sclerotized cone; gonocoxites 8 wide, thumb-shaped (Fig. 2D, E).

**Description.** *Size.* Head width: 3.08 mm; forewing length: 34.23 mm; hindwing length: 34.42 mm. — **Head.** Mostly dark grey. Vertex dark grey, posterior margin orange. Postgena orange. Antenna mostly black. Frons with a pair of indistinct curved pale yellowish markings. Clypeus anteriorly dark brown, posteriorly pale. Labrum yellowish brown, with some yellowish-brown setae. Maxillary and labial palpus yellowish brown. Mandibles pale yellowish

brown with distal half dark reddish brown (Fig. 17B, C). — **Thorax.** Pronotum mostly dark grey, with a pair of “F” shaped pale yellowish markings, with some dark and pale setae. Mesoprescutum and mesoscutellum mostly dark grey; mesonotum with a few pale yellowish markings. Metanotum and metascutellum mostly dark grey. Pleurae dark grey (Fig. 17C). — **Legs.** Short, as long as thorax at most, with many black and pale setae. All tibial spurs slightly curved; tarsomere 1 basally pale yellow with distally dark brown, tarsomeres 1–4 generally black, tarsomere 5 pale yellow with distally black, nearly as long as entire length of tarsomeres 2–4; pretarsal claws curved, pale yellowish brown. Foreleg: Coxa yellowish brown; femur mostly dark brown; tibia black, basally and medially with two pale yellow markings; tibial spurs reaching tip of tarsomere 2. Midleg: Coxa pale yellowish brown with a black spot; femur mostly dark brown; tibia black, basally and medially with two pale yellow markings; tibial spurs reaching base of tarsomere 3. Hind leg: Coxa pale yellowish brown with a black spot, femur mostly dark brown; tibia black, basally and medially with two pale yellowish markings; tibial spurs reaching base of tarsomere 2; tarsomere 1 longer than that of fore- and midleg (Fig. 17A). — **Wings.** Long, narrow. Banksian lines absent. Pterostigma pale. Forewing nearly four times as long as maximum width, with dense indistinct



**Figure 17.** *Layahima zhitengi* sp. nov., adult: **A** Habitus, female, holotype; **B** head, frontal view; **C** head and thorax, dorsal view. **D, E** Female terminalia: **D** Lateral view, **E** ventral view.

markings; costal space with a dark brown spot proximal to pterostigma; costal crossveins generally simple on nearly basal half, while nearly distal half each connected by a short oblique vein; RP originates proximally to MP fork; four to

five presectoral crossveins present, almost with biareolate cells; RP with 10 branches. Hindwing nearly 3.5 times as long as maximum width; riegma indistinct; presectoral area with only one crossvein; RP originates anteriorly to MP fork

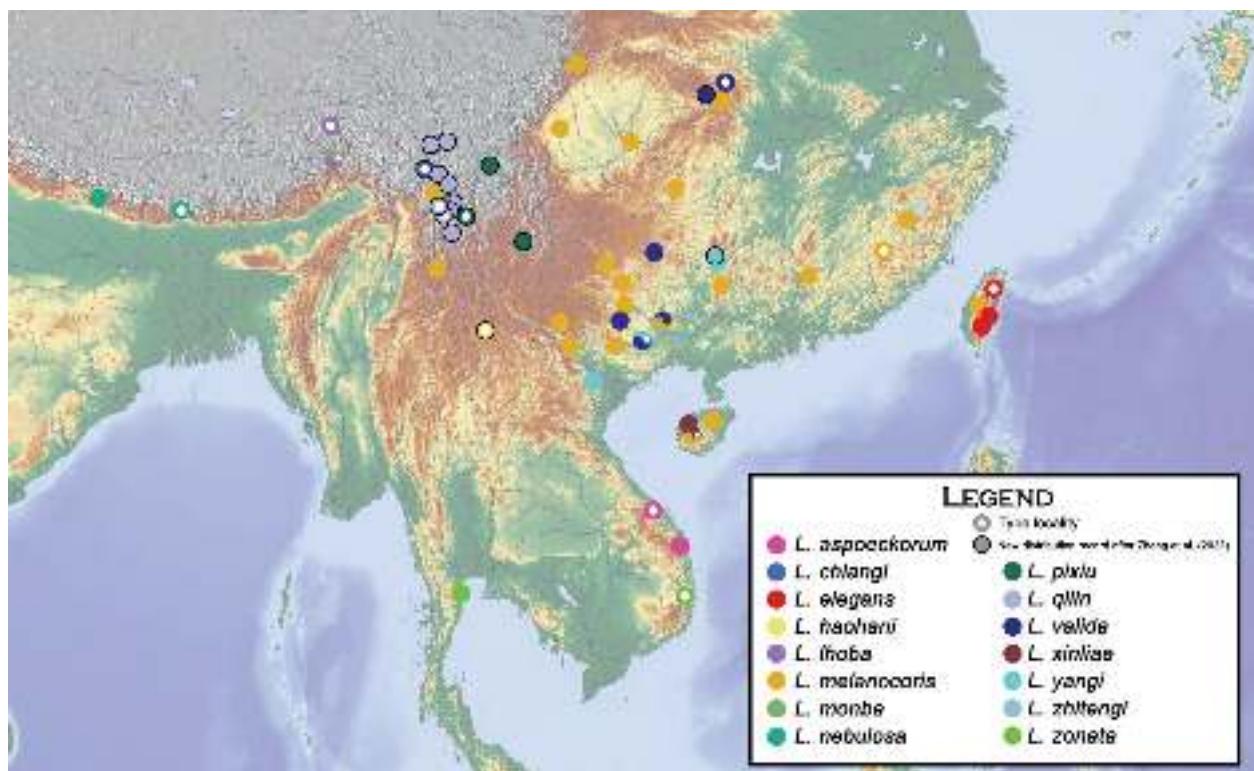


Figure 18. Distribution map of *Layahima* spp.

(Figs 2F, 17A). — **Abdomen.** Mostly dark grey, terga 1 and 3–5 each medially with a pale yellowish marking (Fig. 2F). — **Male genitalia.** Unknown. — **Female genitalia.** Pregenital plate shaped as a vertical prominence. Gonocoxites 8 wide, thumb-shape; gonapophyses 8 indistinct and rounded. Gonocoxites 9 with many tapered stout setae, slightly curved. Ectoproct rounded on distal margin (Fig. 2D, E).

**Type material.** Holotype ♀, CHINA: Yunnan, Nujiang, Fugong County [福贡县], Haizha [害扎], 1200 m, 2.VII.2022, Zhiteng Chen (IZCAS).

**Etymology.** The new species is dedicated to the plecopteran researcher Dr. Zhiteng Chen (陈志腾), who donated us the holotype of this new species and a larva of *L. lhoba*.

**Distribution.** China (Yunnan) (Fig. 18).

**Remarks.** This new species is similar to *L. valida* (Yang, 1997), which occurs in South and Central China. Both species are dark grey and have long, narrow wings. However, *L. zhitengi* sp. nov., is characterized by orange posterior vertex, mesonotum with few pale yellowish markings, abdomen with some pale yellowish spots, female pregenital plate shaped as a vertical prominence, and female gonocoxites 8 thumb-shaped; while *L. valida* differs in the entirely dark grey vertex, mesonotum, and abdomen, female pregenital plate shaped as a pair of strongly sclerotized subtriangular plates, and female gonocoxites 8 narrowed and digitiform.

**Key to species of *Layahima* based on adult characters after Zheng et al. (2023)**

- 1 Body mostly dark grey, with a few pale markings.....2
- 1' Body black, yellow, pale yellow, yellowish brown or pale yellowish brown with many markings .....3
- 2 Vertex entirely dark grey; lateral pale markings on pronotum smaller; mesonotum entirely dark grey; abdomen entirely dark grey; female pregenital plate shaped as a pair of strongly sclerotized subtriangular plates, and gonocoxites 8 narrowed and digitiform .....*L. valida* (Yang, 1997)
- 2' Vertex posterior part orange; lateral pale markings on pronotum larger; mesonotum with a few pale markings; abdomen with some pale yellowish spots; female pregenital plate shaped as a vertical prominence, and gonocoxites 8 thumb-shaped ..... *L. zhitengi* sp. nov.
- 3 Body bright yellow or bright pale yellow with dark markings; forewing subcostal area with dark brown dashes...4
- 3' Body pale yellowish brown or dull pale yellowish brown with markings; forewing subcostal area without or with faint dashes.....8
- 4 Body yellow; mesoprescutum yellow with a pair of black spots; mesonotum medially yellow, laterally with a pair of black markings.....5

- 4' Body pale yellow; mesoprescutum black with a pair of pale yellowish spots; mesonotum medially with a M-shaped black marking.....6
- 5 Frons medially slightly depressed at black marking; mesoscutellum yellow, posteromedially with a triangular black marking; abdominal tergites 3–8 each generally yellow, posterior margin black; male sternite 9 flat, gonocoxites 9 present as a pair of transversal trapezoid plates, gonocoxites 11 medial tubercle absent; female gonocoxites 8 broad.....*L. melanocoris* (Yang, 1997)
- 5' Frons medially prominent at median black marking; mesoscutellum yellow, laterally with a pair of black markings; abdominal tergites 3–8 generally black, anteriorly each with an arched yellow marking; male sternite 9 slightly bent upward, gonocoxites 9 present as a pair of short plates with internal margin rounded, gonostylus 11 present as a tubercle in lateral view; female gonocoxites 8 slender.....*L. monba* Zheng, Badano & Liu, 2022
- 6 Forewing with an indistinct dark brown marking near the hypostigmal cell, a marking on basal cubital area distinct; female pregenital plate shaped as a rounded sclerotized plate with a vertical prominence.....*L. haohani* sp. nov.
- 6' Forewing without marking near the hypostigmal cell, a marking on basal cubital area indistinct; female pregenital plate shaped as a tiny coniform prominence.....7
- 7 Pronotum medially mostly dark brown; tarsomere 5 distally dark brown; rhexma on forewing present as two brown markings, rhexma on hindwing present as a large curved brown marking; female gonocoxites 8 broad.....*L. aspoekorum* Zheng, Badano & Liu, 2022
- 7' Pronotum medially mostly pale yellow; all tarsi pale yellow; rhexma on forewing present as an irregular dark brown marking, rhexma on hindwing present as a dark brown spot; female gonocoxites 8 slender.....*L. elegans* (Banks, 1937)
- 8 Forewing costal crossveins mostly simple; forewing subcostal area with a series of pale brownish dots.....9
- 8' Forewing with crossveins on distal half of costal area connected by oblique veinlets; forewing subcostal area transparent or with a series of brownish markings.....10
- 9 Pale yellowish-brown part of body immaculate; vertex with three dark brown spots anteriorly; femur and tibia with dark brown stripes; wings distally narrow.....*L. contracta* (Walker, 1860)
- 9' Pale yellowish-brown part of body with numerous black dots; vertex with a dark brown marking medially; femur and tibia with many dark brown dots; wings distally broad.....*L. nebulosa* Navás, 1912
- 10 Clypeus with a pair of black spots; hindwing poststigmal area with a brown spot.....*L. zonata* (Navás, 1919)
- 10' Clypeus without a pair of black spots; hindwing poststigmal area without marking.....11
- 11 Thorax generally black with some small yellowish-brown spots.....*L. pixiu* sp. nov.
- 11' Thorax generally pale yellowish brown with some dark markings.....12
- 12 Vertex with a pair of distinct dark spots; pronotum lateromedially with two pairs of dark spots.....13
- 12' Vertex with three spots at least; pronotum lateromedially with a pair of longitudinal dark stripes.....14
- 13 Pronotum anteromedially without spot; male sternum 9 short and posteriorly narrowed, gonocoxites 9 twice as wide as long, gonocoxites 11 triangularly arched; female pregenital plate weakly sclerotized.....*L. chiangi* Banks, 1941
- 13' Pronotum with anteromedial marking; male sternum 9 elongate and posteriorly narrowed, gonocoxites 9 as long as wide; female pregenital plate shaped as an anterior sclerotized prominent papilla and a posterior ridge-like prominence.....*L. qilin* sp. nov.
- 14 Swollen part of flagellum basally and distally black, medially pale yellowish brown; female gonocoxites 8 extending ventrad.....*L. lhoba* Zheng, Badano & Liu, 2022
- 14' Swollen part of flagellum black; female gonocoxites 8 extending distad.....15
- 15 Frons posteromedially pale yellowish brown; pronotum posteromedially with a black marking and mediolaterally with three pairs of black spots, pale yellowish brown part with some dots; mesoscutellum mostly black; tarsomeres 3–4 generally pale yellowish brown; wings broad.....*L. xinliae* Zheng, Badano & Liu, 2022
- 15' Frons generally dark brown; pronotum medially with three longitudinal black stripes, pale yellowish brown part without dots; mesoscutellum pale yellowish brown, anteromedially with a dark brown trident-shaped marking; tarsomeres 3–4 generally dark brown; wings narrow.....*L. yangi* Wan & Wang, 2006

## 4. Discussion

### 4.1. Larval stage of *Layahima* and phylogenetic implication

Unlike other neuropteran families, larval morphology and behavior of Myrmeleontidae have significant taxonomic and systematic value (Stange and Miller, 1990).

The larva of the Indian species *Layahima contracta* is one of the first non-European antlion larvae thoroughly described (Gravely and Maulik, 1911). However, the description of Gravely and Maulik (1911) only contains hand-drawn illustrations of larva and pupa, and lacks any image of the adult, raising doubts on the identification as *Layahima*. The discovery of the larvae of three *Layahima* species (*L. chiangi*, *L. lhoba*, and *L. yangi*) from China allows to confirm the assignment of the larva described

by Gravely and Maulik (2011) to *Layahima*, although the species identification remains uncertain.

The *Layahima* larvae exhibit unique characters (see Diagnosis of the genus) and behaviors among the genera with larval records in the Old World, especially among the representatives of Dendroleontinae. The larvae of *Layahima* are active, climbing on rock surfaces or tree trunks, in contrast to the Asian dendroleontine genera *Nepsalus* Navás, 1914 and *Gatzara* Navás, 1915, which have a largely immobile life-mode, restricted to rock covered with dust lichen (Zheng et al. 2022, 2024). The behavior of *Layahima* is similar to that of many owlflies (Ascalaphinae: Ascalaphini, Haplogleniini, and Ululodini) (Badano and Pantaleoni 2014b; Machado et al. 2021) and some New World antlion genera *Gnopholeon* Stange, 1970, and *Jaffuelia* Navás, 1918 (Myrmeleontinae: Brachynemurini) (Stange 1994, 2003). The larvae of *Layahima* differ from the other known larvae of Dendroleontinae, with the exception of *Epacanthaclisis* Okamoto, 1910, by the presence of developed odontoid process and rastra with digging setae. These differences may reflect the phylogenetic relationships between Acanthoplectrini and Dendroleontini, although the larval stages of all Australian genera of Acanthoplectrini are still unknown. Moreover, the larvae of *Epacanthaclisis* also have well-developed odontoid process and rastra, suggesting a potential affinity with Acanthoplectrini, which will be tested in near future.

## 4.2. Interspecific phylogeny of *Layahima*

After adding new samples, the *L. zonata* group was recovered to be paraphyletic but not monophyletic as recovered in Zheng et al. (2023) (Fig. 1). However, the other species group of *Layahima*, the *L. elegans* group, as defined in Zheng et al. (2023), still remains to be monophyletic in presently inferred phylogeny. Based on morphological characters, the species of the *L. zonata* group share a same wing character (i.e., forewing costal crossveins connected by oblique veinlets on the distal half), while all species of the *L. elegans* group have the forewing costal crossveins barely connected by oblique veinlets, being an opposite state to that of the *L. zonata* group. Thus, following the present topology, the reduction of interlinking veinlets between forewing costal crossveins may be apomorphic, while the opposite state in the *L. zonata* group may be plesiomorphic. Nevertheless, it should be noted that the supports in the nodes referring to the species of the *L. zonata* group in the present and previous results (Zheng et al. 2023) are not strong. Therefore, the interspecific phylogeny of *Layahima* should be reinvestigated by using larger genomic data. Moreover, two remarkable Indian species *L. contracta* and *L. nebulosa*, which are missing in present study, should be sampled in future analysis because these two species exhibit transitional characters between both species groups, i.e., the presence of simple forewing costal crossveins barely connected by oblique veinlets, and the pale yellowish-brown body coloration.

## 4.3. Diversity and distribution of *Layahima*

The four new species herein described are all found from Southwest China. As the *Layahima* larvae typically rely on rocky environments, geographical isolation and habitat partition may act as important driving forces for the diversification of this genus. For example, concerning the distribution of the species from the Hengduan Mountains, *L. chiangi* is endemic to the dry hot river valley along the Nujiang River around Cawarong; *L. zhitengi* **sp. nov.** is only recorded in the Gaoligong mountain range along the Nujiang River; *L. qilin* **sp. nov.** is found only in the Mangkang and Yunling mountain ranges between the Lancangjiang and Jinshajiang Rivers; and *L. pixiu* **sp. nov.** is recorded in the Shaluli mountain range to the east of the Jinsha River, extending to the northern section of the Ailaoshan mountain range (Fig. 18). Thus, diversification of these species might have been related to the remarkably diverse landforms and microhabitats of the Hengduan mountain range. Judging from the present distribution of *Layahima* (Fig. 18), there are still large gaps in Indochina where further species are expected to be discovered, considering its similar diversity of landforms and microhabitats to that of the Hengduan mountain range.

## 5. Declarations

**Data availability statement.** The data that support the findings of this study are openly available in GenBank. Accession numbers for all gene fragments are listed in Table S1.

## 6. Acknowledgements

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## Supplementary Material 1

### Tables S1, S2

**Authors:** Zheng Y, Tu Y, Badano D, Liu X (2025)

**Data type:** .docx

**Explanation notes:** **Table S1.** Sampling information of the present phylogenetic analysis. — **Table S2.** The best-fitting partitioning scheme for phylogenetic analyses.

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