

RESEARCH PAPER

New species and new data of the dragon lacewing genus *Nipponeurorthus* (Neuroptera: Nevrorthidae) from China

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Abstract. The genus *Nipponeurorthus* Nakahara, 1958 is an endemic group of the dragon lacewing family Nevrorthidae, currently comprising 13 species from China and Japan. However, due to their rareness in nature, the species and distribution of *Nipponeurorthus* from China are still poorly explored. Herein we describe five new species of *Nipponeurorthus* from the Chinese mainland, i.e., *N. ailao* sp. nov. (China: Yunnan), *N. flavipennis* sp. nov. (China: Guangxi), *N. kuanglu* sp. nov. (China: Jiangxi), *N. ningboensis* sp. nov. (China: Zhejiang), and *N. pallidipennis* sp. nov. (China: Jiangsu). We also redescribe *N. qinicus* Yang, 1999, which has been poorly documented since its original description. A molecular delimitation of the *Nipponeurorthus* species based on the DNA barcodes was performed. An updated key to the species of *Nipponeurorthus* is also provided.

Key words. Neuroptera, Osmyloidea, Nevrorthidae, new species, taxonomy, Oriental Region

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Introduction

The family Nevrorthidae (dragon lacewings) represents one of the major groups of aquatic Neuroptera, as a member of the superfamily Osmyloidea, currently comprising 21 extant species assigned to four genera (ASPÖCK et al. 2017, SAITO et al. 2024). Nevrorthidae exhibit a disjunct global distribution in three geographically isolated regions: the Mediterranean region, southeastern Australia and East Asia (ASPÖCK et al. 2017). *Nipponeurorthus* Nakahara, 1958 is an East Asian endemic genus, currently comprising 13 described species (ASPÖCK et al. 2017, SAITO et al. 2024). The species of *Nipponeurorthus* can be distinguished from other genera by the following characters: 1) wing membrane not leathery, 2) absence of enlarged male segment 7, and 3) complex of male gonocoxites, gonostyli and gonapophyses 11 with a small median fork (ASPÖCK et al. 2017). Notably, despite its scarcity in the wild, this genus shows a remarkably broad latitudinal range, with its distribution extending from southern Yunnan (China) in the south to southern Hokkaido (Japan) in the north (Fig. 1). So far, Japan has harbored the highest diversity of this genus, with seven species, all endemic to the country (SAITO et al. 2024). Notably, being different from the Mediterranean

genus *Nevrorthus* Costa, 1863 with all species ranges isolated from each other, many insular species of *Nipponeurorthus* are sympatric, particularly from the islands of Honshu, Amami Oshima, and Taiwan (ASPÖCK et al. 2017, SAITO et al. 2024). Adults of nevrorthid species usually stay in the canopy of forests beside small streams, and under the leaves of broadleaf plants (Figs 2E, F).

Considering the Chinese species of Nevrorthidae, the first two species were described from Taiwan by NAKAHARA (1958, 1966): *Nipponeurorthus fasciatus* Nakahara, 1958 and *N. multilineatus* Nakahara, 1966. The first nevrorthid species described from the Chinese mainland refers to *Nipponeurorthus qinicus* Yang, 1999 from Mt. Qinling in Shaanxi Province. *Nipponeurorthus tianmushanus* Yang & Gao, 2001 from Mt. Tianmushan in Zhejiang Province is the second described species from the Chinese mainland. However, these two species were poorly documented after their original description, and their primary types are probably lost. Besides, two additional species of *Nipponeurorthus* were described by LIU et al. (2014): *N. damingshanicus* Liu, H. Aspöck & U. Aspöck, 2014 from Guangxi and *N. furcatus* Liu, H. Aspöck & U. Aspöck, 2014 from Yunnan.



Here we describe five new species of *Nipponeurorthus* from the Chinese mainland: *N. ailao* sp. nov., *N. flavipennis* sp. nov., *N. kuanglu* sp. nov., *N. ningboensis* sp. nov., and *N. pallidipennis* sp. nov. In addition, we present a redescription of *N. qinicus* and a new distribution record of this species. A molecular delimitation of *Nipponeurorthus* species based on the DNA barcodes was performed.

Material and methods

Taxonomy. The specimens were examined using a Nikon SMZ745 stereo-microscope. Habitus photos were taken using a Canon® 5D Mark III with an MP-E 65mm f/2.8 1-5X Macro Lens with two Godox V850II flashes as light source. Genitalia were prepared by clearing the apex of the abdomen with 15% KOH at 135°C for 5 min, using an IKA® C-MAG HP4 heating table as heat source. After rinsing the KOH with distilled water, the apex of the abdomen was transferred to glycerin for further examination. The photographs of male genitalia were taken using a Leica® DM2000 outfitted with a Nikon® D850 digital camera. Zerene Stacker was used for image stacking. Distribution map was generated in QGIS. All images were modified and grouped into plates in Adobe Photoshop 2023.

Wing venation terminology generally follows ADAMS (1996) and BREITKREUZ et al. (2017). Venational abbreviations:

A – anal vein;
C – costa;
Cu – cubitus;
CuA – cubitus anterior;
CuP – cubitus posterior;
M – media;
MA – media anterior;
MP – media posterior;
RA – radius anterior;

RP – radius posterior;
RP1 – first (proximal-most) branch of RP;
RP2 – second (proximal-most) branch of RP;
Sc – subcostal.

Terminology of genitalia mainly follows ASPÖCK & ASPÖCK (2008), MARTINS et al. (2016), and WINTERTON & WANG (2016).

All specimens herein examined are deposited in the Entomological Museum, China Agricultural University, Beijing (CAU).

Sampling for phylogenetic analysis. The present sampling includes 14 species of *Nipponeurorthus* and two outgroup species of Osmylidae (*Heterosmylus wolonganus* Yang, 1992) and Sisyridae (*Sisyra nikkoana* (Navás, 1910)) (Table 1). A total of 42 samples were included, and 12 of them were newly sequenced in this study.

The genomic DNA was extracted from the mesothoracic muscle of adults by using TIANamp Micro DNA Kit (TIANGEN®, Beijing, China). Barcode region of COI was sequenced for each sample. Primers used for polymerase chain reaction (PCR) in this study are COI4-F (5'-TGTAACACGACGCCAGTAACTAATARCCTTCAAAG-3'), and COI4-R (5-TAAACTTCTGGATGTCCAAAAAATCA-3) from LAI et al. (2023).

All PCR products were sequenced in both directions using BigDye Terminator Sequencing Kit (Applied Bio Systems, San Francisco, CA) and ABI 3730XL Genetic Analyzer (PE Applied Biosystems) with two vector-specific primers and internal primers for primer walking. Thermal cycling was set as follows: 95°C for 30 s, 40 cycles of 95°C for 10 s, 52°C for 50 s (50°C for COI1-F/R), 65°C for 1 min, and final elongation at 65°C for 10 min.

Sequence assembly was performed in ContigExpress. Sequences were aligned using MUSCLE (EDGAR 2004) in

Table 1. Location information of the sampled *Nipponeurorthus* Nakahara, 1958 species and out-group taxa in molecular identification and GenBank ID of sequences used in this study.

Species	Voucher ID	Location information	GenBank ID	References
<i>N. damingshanicus</i>	NERGXDM	CHINA, Guangxi, Wuming, Mt. Damingshan	PX563155	this study
<i>N. qinicus</i>	NERSXYS	CHINA: Shaanxi, Yuncheng, Huangguan Reserve	PX563151	this study
<i>N. qinicus</i>	NERHNLY	CHINA: Henan, Luoyang, Deheng Town	PX563152	this study
<i>N. qinicus</i>	NERSXHY	CHINA: Shaanxi, Xian, Huyi district, Zhuque National Forest Park	PX563153	this study
<i>N. furcatus</i>	NERYNHLS	CHINA: Yunnan, Honghe, Lvchuan, Mt. Huanglian	PX563149	this study
<i>N. ailao</i> sp. nov.	NERYNAL	CHINA: Yunnan, Yuxi, Xiping, Ailaoshan N.N.R., Gasa Town, Shimenxia	PX563154	this study
<i>N. flavipennis</i> sp. nov.	NERGXHP	CHINA: Guangxi, Guilin, Lingui County, Huangsha Yao Ethnic Township, Huaping N.N.R., Anjiangping	PX563147	this study
<i>N. kuanglu</i> sp. nov.	NERJXLS	CHINA: Jiangxi, Jiujiang, Mt. Lushan	PX563159	this study
<i>N. ningboensis</i> sp. nov.	NERZJNB	CHINA: Zhejiang, Ningbo, Beilun district, Mt. Jiufeng	PX563148	this study
<i>N. ningboensis</i> sp. nov.	NERZJNB2	CHINA: Zhejiang, Ningbo, Beilun district, Mt. Jiufeng	PX563156	this study
<i>N. pallidimaculatus</i> sp. nov.	NERJSLY	CHINA: Jiangsu, Liyang, Shexijie	PX563150	this study
<i>N. pallidimaculatus</i> sp. nov.	NERJSLY2	CHINA: Jiangsu, Liyang, Shexijie	PX563157	this study
<i>N. pallidimaculatus</i> sp. nov.	NERJSLY3	CHINA: Jiangsu, Liyang, Shexijie	PX563158	this study
<i>Nipponeurorthus</i> spp.	-	JAPAN	LC745265.1– LC745300.1	SAITO et al. (2024)
<i>Sisyra nikkoana</i>	-	JAPAN	LC823820	SAITO et al. (2024)
<i>Heterosmylus wolonganus</i>	-	CHINA: Shanxi	KY491671	WINTERTON et al. (2017)

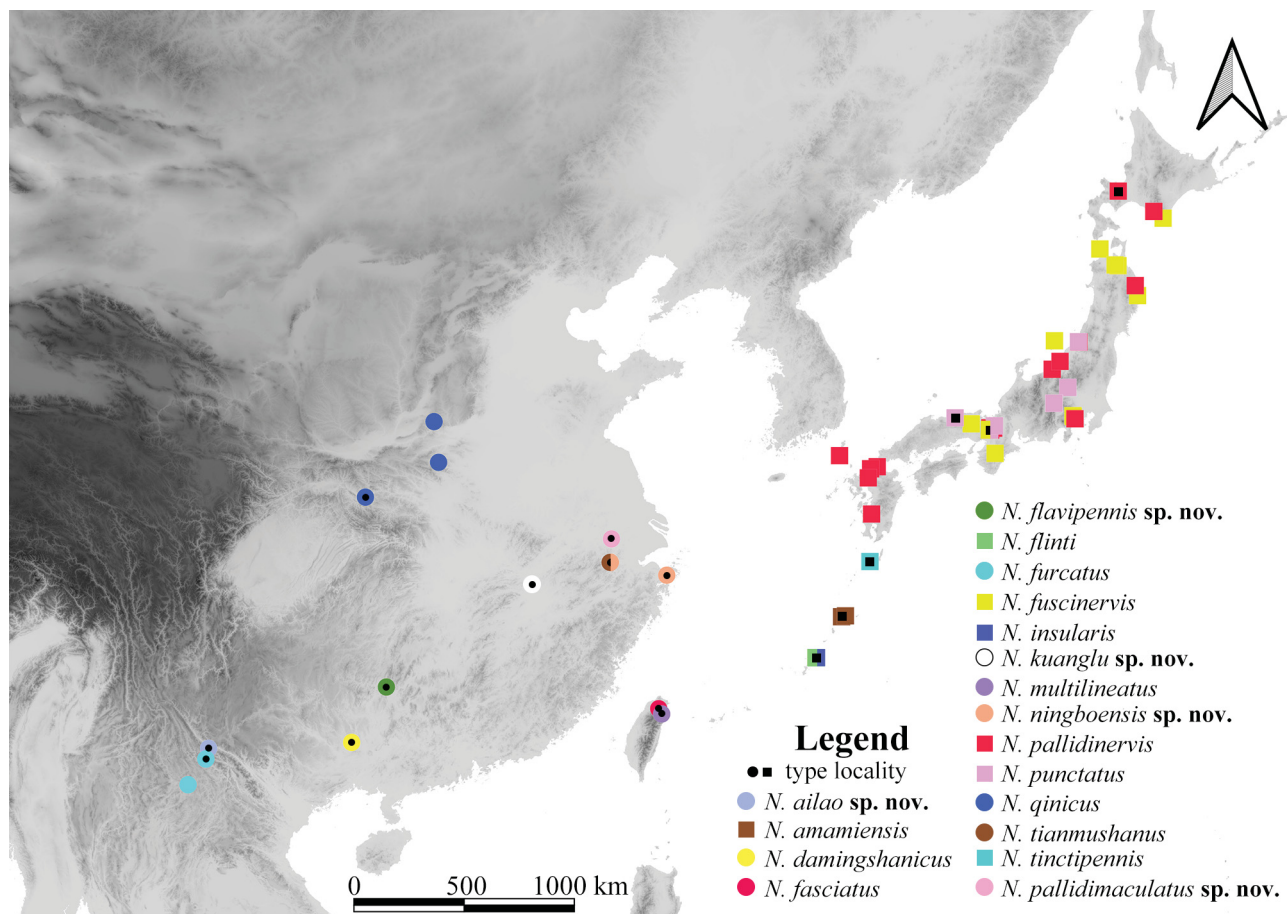


Fig. 1. Distribution map of the species of *Niponeurorthus* Nakahara, 1958.

MEGA 11. Genetic divergence was calculated with the Kimura 2-parameter (K2P) model (KIMURA 1980) in MEGA 11 (TAMURA et al. 2021) based on the DNA sequences of the COI barcode region.

Phylogenetic analysis. The Maximum Likelihood (ML) and Bayesian inference (BI) were performed based on the DNA sequences of the COI barcodes. The ML analysis was performed in IQ-Tree web server (<http://iqtree.cibiv.univie.ac.at/>) with 1000 bootstraps. Trees were visualized and edited with FigTree v1.4.4 (RAMBAUT 2019). The Bayesian inference (BI) analysis was performed using MrBayes 3.2.6 (RONQUIST et al. 2012), with the following settings: single Markov chain Monte Carlo (MCMC) simulation runs for 2 million generations, with a sample frequency of 1000. Analysis was terminated when the standard deviation of clade frequencies fell below 0.01, which suggested that stationarity had been reached.

Results

Family Nevrorthidae Nakahara, 1915

Genus *Niponeurorthus* Nakahara, 1958

Niponeurorthus Nakahara, 1958: 25. Type species: *Niponeurorthus pallidinervis* Nakahara, 1958: 25, original designation.

Diagnosis. See ASPÖCK et al. (2017).

Included species and distribution. See the checklist in Table 2.

Species delimitation. The genetic distance of sampled species of *Niponeurorthus* was calculated based on the COI barcodes (Fig. 3). The genetic distance within *Niponeurorthus* ranges from 0.037 to 0.125; the lowest interspecific distance of 0.037 is between *N. pallidinervis* and *N. tinctipennis*. The intraspecific distance ranges from 0 to 0.026. The highest intraspecific distance of 0.026 is between the samples of *N. pallidinervis* from two locations in Honshu, rather than from Kyushu and Honshu.

Niponeurorthus qinicus Yang, 1999

Figs 2C, 4, 5, 6

Niponeurorthus qinicus Yang, 1999 in CHEN (1999: 105) [the CIP record for this book dates from 1998, while the publication edition was issued in 1999]; LIU et al. (2014: 230); ASPÖCK et al. (2017: 98).

Type material. NEOTYPE (here designated): ♂, CHINA: Shaanxi, Xi-an, Huyi district [鄂邑区], Zhuque National Forest Park [朱雀国家森林公园], 1560 m, 13.vii.2020, leg. Qiaoqiao Liu, Shiwen Xu and Zhaoyang Chen (CAU).

Additional material examined. 3 ♂♂, same as neotype; 1 ♂, CHINA: Shaanxi, Xian, Huyi district [鄂邑区], Zhuque National Forest Park [朱雀国家森林公园], 1590 m, 13.vii.2020, leg. Qiaoqiao Liu, Shiwen Xu and Zhaoyang Chen (CAU); 1 ♀, CHINA: Henan, Luoyang, Deheng Town [德亨镇], Tianshan Road [天山路], 955 m, 20.vii.2020, leg. Rongrong Shen, Jingyu Wu (CAU); 1 ♂, CHINA: Shanxi, Yuncheng, Huangguman Reserve [皇姑幔保护区], 1299 m, 23.vii.2020, leg. Xingyue Liu (CAU).

Diagnosis. Antennae pale, distal part of flagellum gradually darkened. Body pale. Wing spotless, colorless and hyaline. Longitudinal veinlets dark; forewing crossveins and basal

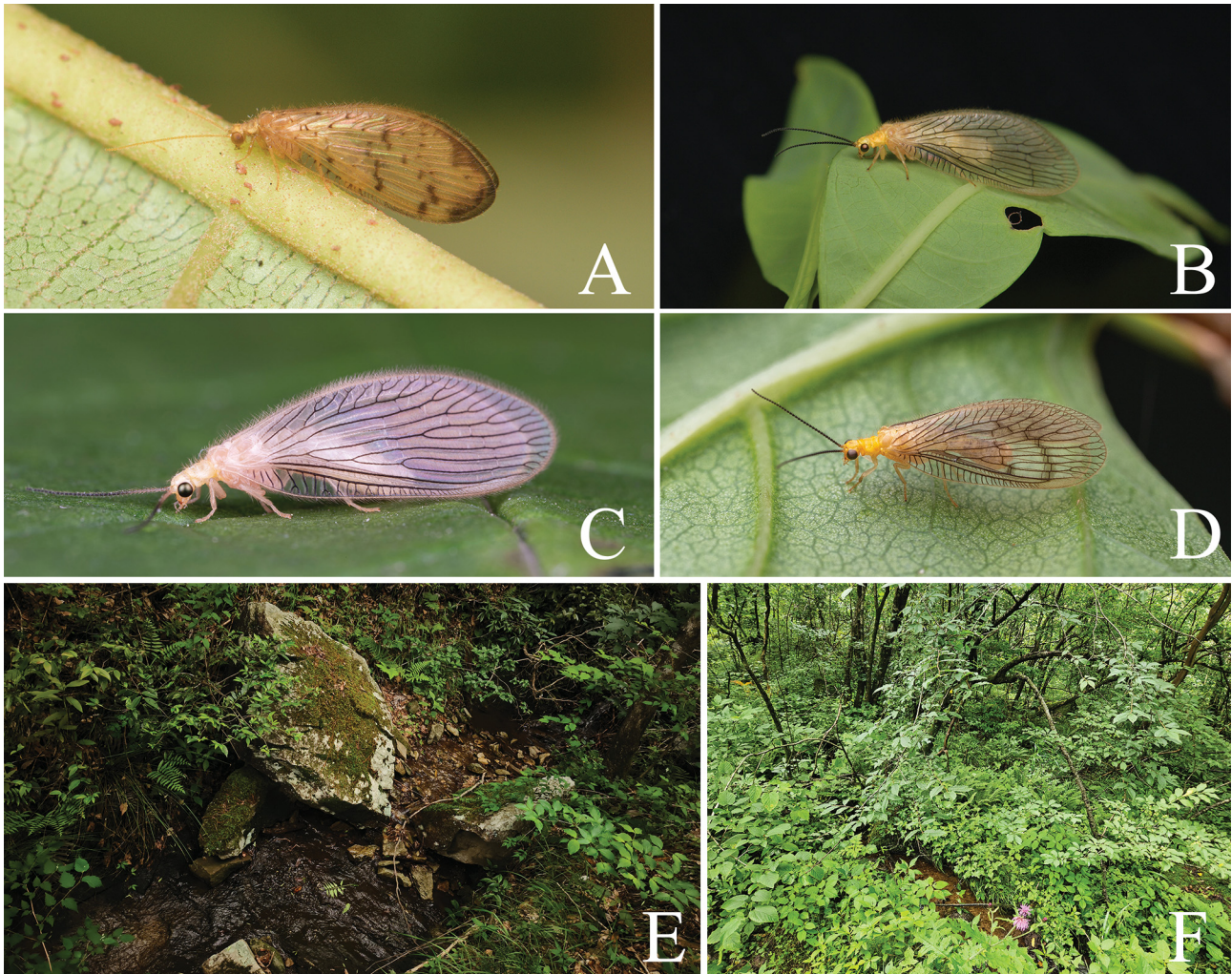


Fig. 2. A–D – living adults of *Nipponeurorthis* Nakahara, 1958: A – *N. furcatus* Liu, H. Aspöck & U. Aspöck, 2014; B – *N. ningboensis* sp. nov.; C – *N. qinicus* Yang, 1999; D – *N. pallidimaculatus* sp. nov. E – type locality of *N. kuanglu* sp. nov. F – habitat of *N. ningboensis* sp. nov. in Mt. Longwang. Photos: A, B – Yuchen Zheng; C – Rongzhen Xu, D – Zhenhao Ma, E – Yujie Zhao.

MA pale, indistinct; hindwing Cu and A pale, indistinct. Male gonocoxite 9 not bifurcated, robust on proximal half and strongly incurved on distal half, small hairy tubercles on inner surface absent. Complex of gonocoxite+gonostylus+gonapophysis 10 broad, subtriangular, distally with slenderly spinous projection.

Redescription. Body length 6.44 mm; forewing length 9.77 mm, hindwing length 8.98 mm.

Head pale. Compound eyes black. Antennae pale, distal part of flagellum gradually darkened. Mouthparts pale; mandibles yellow.

Thorax and legs pale, with yellowish setae.

Wings elliptical, colorless and hyaline, with pterostigmal area white (Fig. 4). Forewing immaculate, white stripe present along posterior margins. Longitudinal veins blackish brown, crossveins and basal MA pale, indistinct (Fig. 2C). Hindwing similar to forewing, veins paler, Cu and A pale, indistinct.

Abdomen pale. Male tergum 9 and sternum 9 fused into ring-like structure; tergum 9 anteriorly truncate and posteriorly broadly concave in dorsal view; sternum 9 posteriorly protruding medially. Gonocoxite 9 robust on

proximal half and strongly incurved on distal half. Gonostylus 9 as roundly tapered lobe and bearing spinous lobe. Ectoproct broad, directed posteriad, and subtrapezoidal and slightly concave on posterior margin in dorsal view. Complex of gonocoxite+gonostylus+gonapophysis 10 robust, subtriangular, distally with slenderly spinous projection. Gonocoxites 11 present as simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite (Fig. 5). Female tergum 8 relatively short, elongated ventrad, in lateral view posteroventral corner rounded. Fused gonocoxites 8 relatively longer than tergum 8, flatly and roundly plate-like. Gonapophyses 8 subtriangular, terminally flattened, basally covered by gonocoxites 8, lateral margin distinctly sclerotized, terminally truncate. Gonocoxite 9 foliate, almost vertically directed, with reduced, flat and ovoid gonostylus bearing tuft of hairs. Ectoproct subtrapezoidal in lateral view (Fig. 6).

Distribution. China (Henan, Shanxi, Shaanxi) (Yang in CHEN 1999, this paper).

Remarks. The holotype of this species should be deposited in CAU. However, we had examined all of the nevrorthid

Table 2. Checklist of *Niponeurorthus* Nakahara, 1958 species.

Species	Distribution
<i>N. ailao</i> sp. nov.	China: Yunnan (this paper)
<i>N. amamiensis</i> Saito & Hayashi, 2024	Japan: Amamioshima Island (SAITO et al. 2024)
<i>N. damingshanicus</i> Liu, H. Aspöck & U. Aspöck, 2014	China: Guangxi (ASPÖCK et al. 2017)
<i>N. fasciatus</i> Nakahara, 1958	China: Taiwan (ASPÖCK et al. 2017)
<i>N. flavipennis</i> sp. nov.	China: Guangxi (this paper)
<i>N. flinti</i> U. Aspöck & H. Aspöck, 2008	Japan: Okinawajima Island (SAITO et al. 2024)
<i>N. furcatus</i> Liu, H. Aspöck & U. Aspöck, 2014	China: Yunnan (ASPÖCK et al. 2017)
<i>N. fuscinervis</i> (Nakahara, 1915)	Japan: Hokkaido, Honshu, Sadogashima Island (SAITO et al. 2024)
<i>N. insularis</i> Saito & Hayashi, 2024	Japan: Okinawajima Island (SAITO et al. 2024)
<i>N. kuanglu</i> sp. nov.	China: Jiangxi (this paper)
<i>N. multilineatus</i> Nakahara, 1966	China: Taiwan (ASPÖCK et al. 2017)
<i>N. ningboensis</i> sp. nov.	China: Zhejiang (this paper)
<i>N. pallidinervis</i> Nakahara, 1958	Japan: Hokkaido, Honshu, Kyushu, Tsushima (SAITO et al. 2024)
<i>N. pallidipennis</i> sp. nov.	China: Jiangsu (this paper)
<i>N. punctatus</i> (Nakahara, 1915)	Japan: Honshu, Sadogashima Island (SAITO et al. 2024)
<i>N. qinicus</i> Yang, 1999	China: Henan, Shaanxi, Shanxi (CHEN 1999, this paper)
<i>N. tianmushanus</i> Yang & Gao, 2001	China: Zhejiang (ASPÖCK et al. 2017)
<i>N. tinctipennis</i> Nakahara, 1958	Japan: Yakushima Island (SAITO et al. 2024)

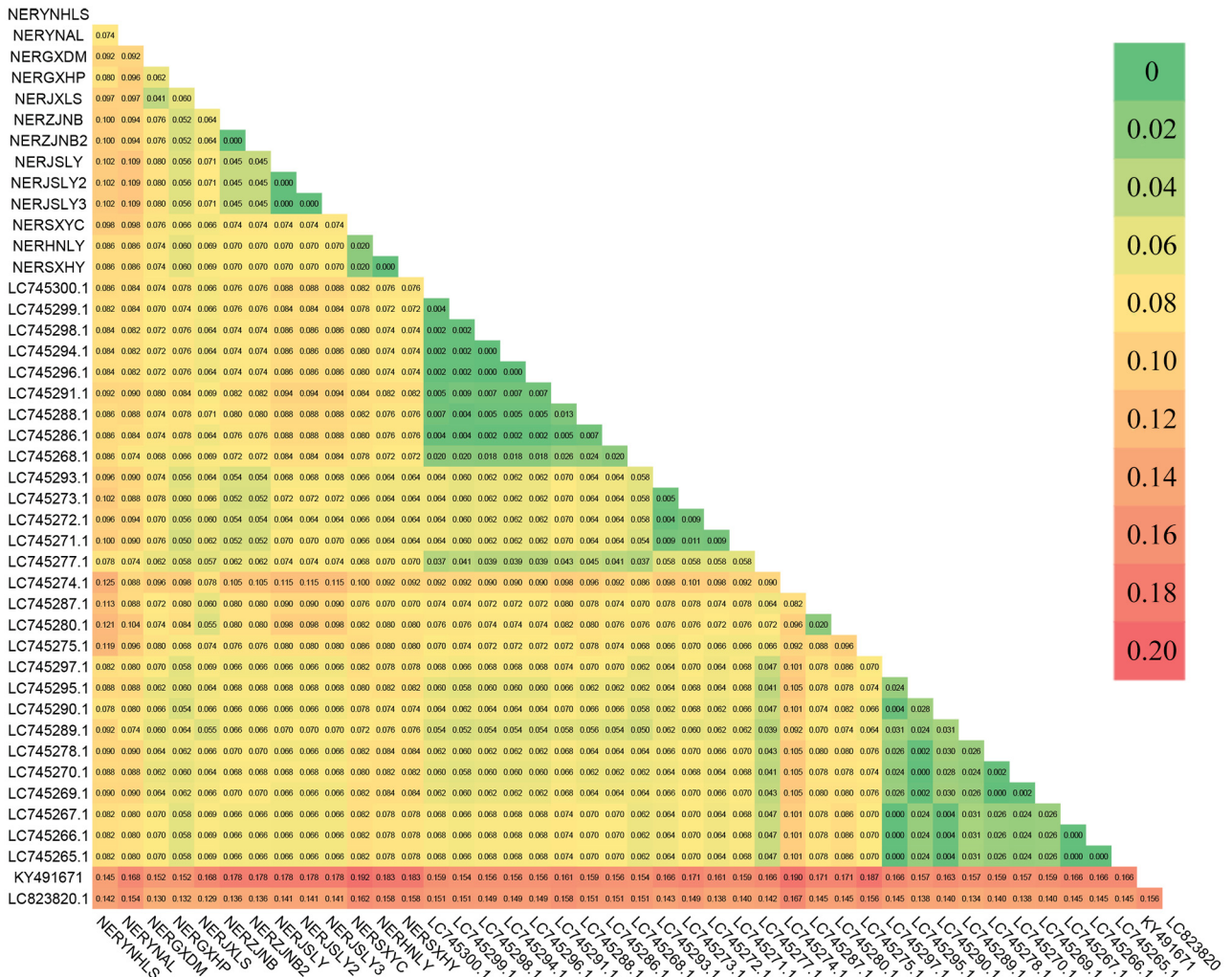


Fig. 3. The K2P genetic distance among the DNA barcodes (COI) of the species of *Niponeurorthus* Nakahara, 1958.

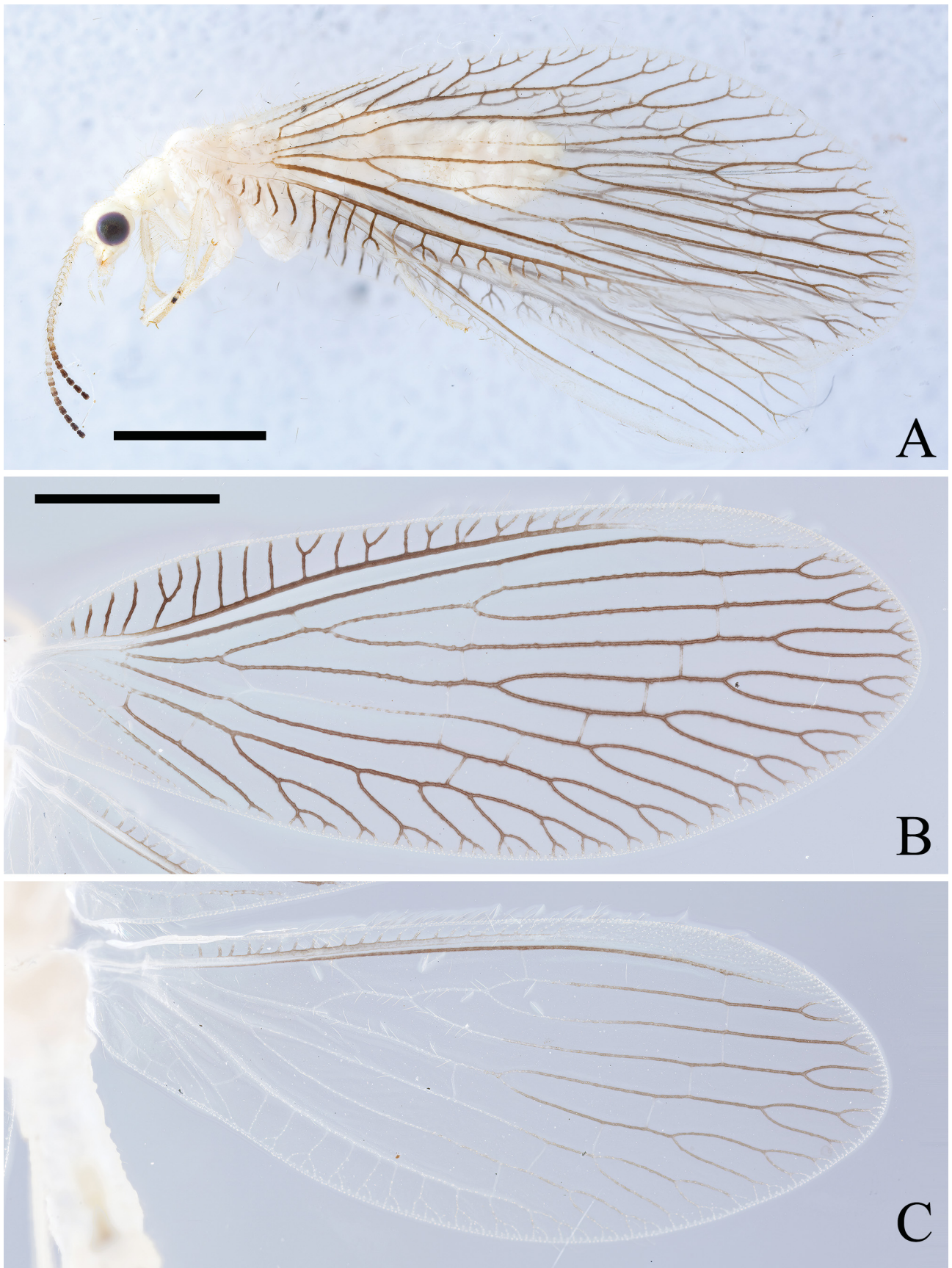


Fig. 4. Habitus of adult *Nipponeurorthus qinicus* Yang, 1999. A – lateral view; B – forewing; C – hindwing. Scale bar: 2 mm.

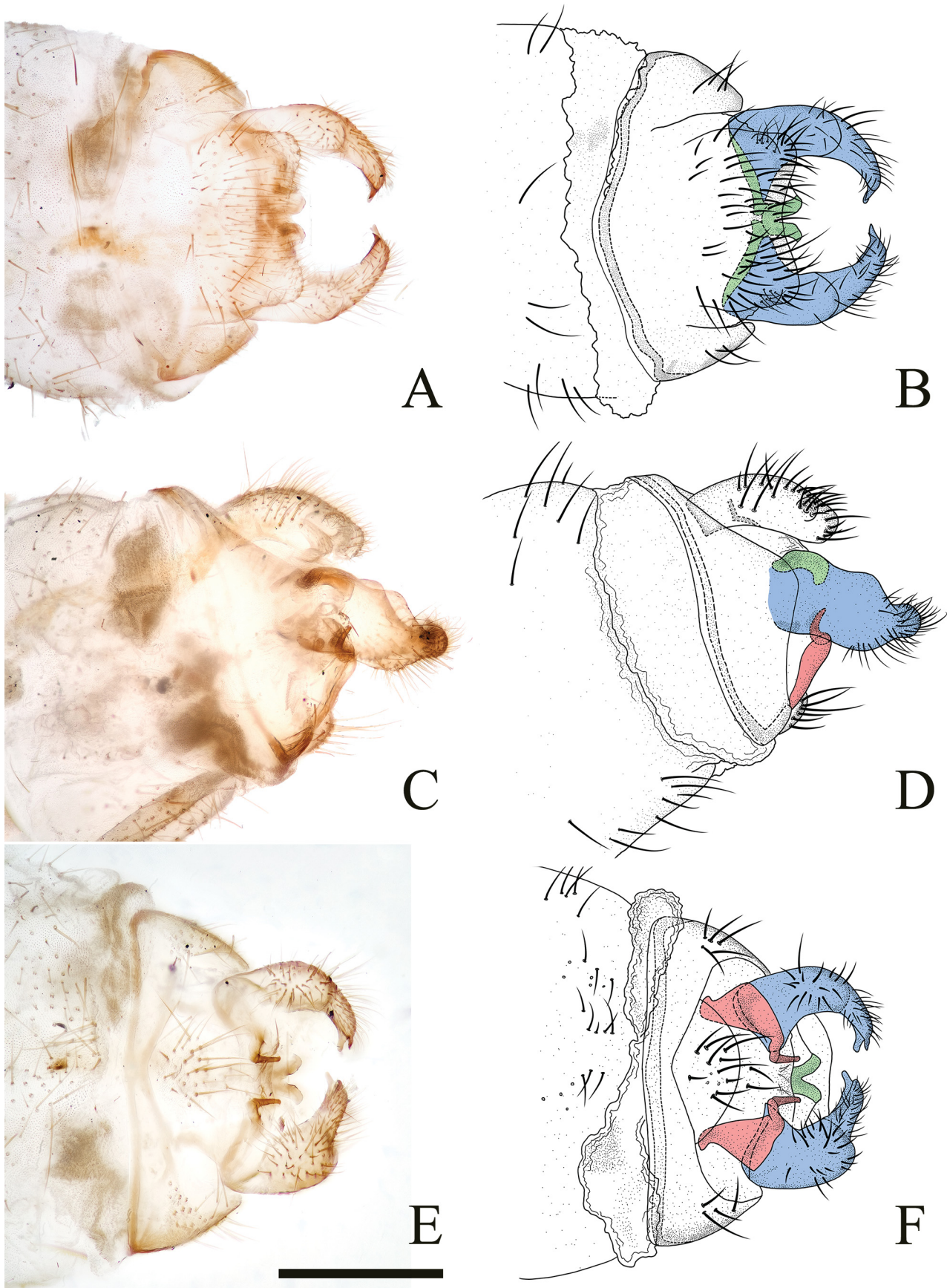


Fig. 5. Male genitalia of *Nipponeworthus qinicus* Yang, 1999. A, B – dorsal view; C, D – lateral view; E, F – ventral view. Scale bar: 0.5 mm. Colour scheme: blue (segment 9), red (segment 10) and green (segment 11).

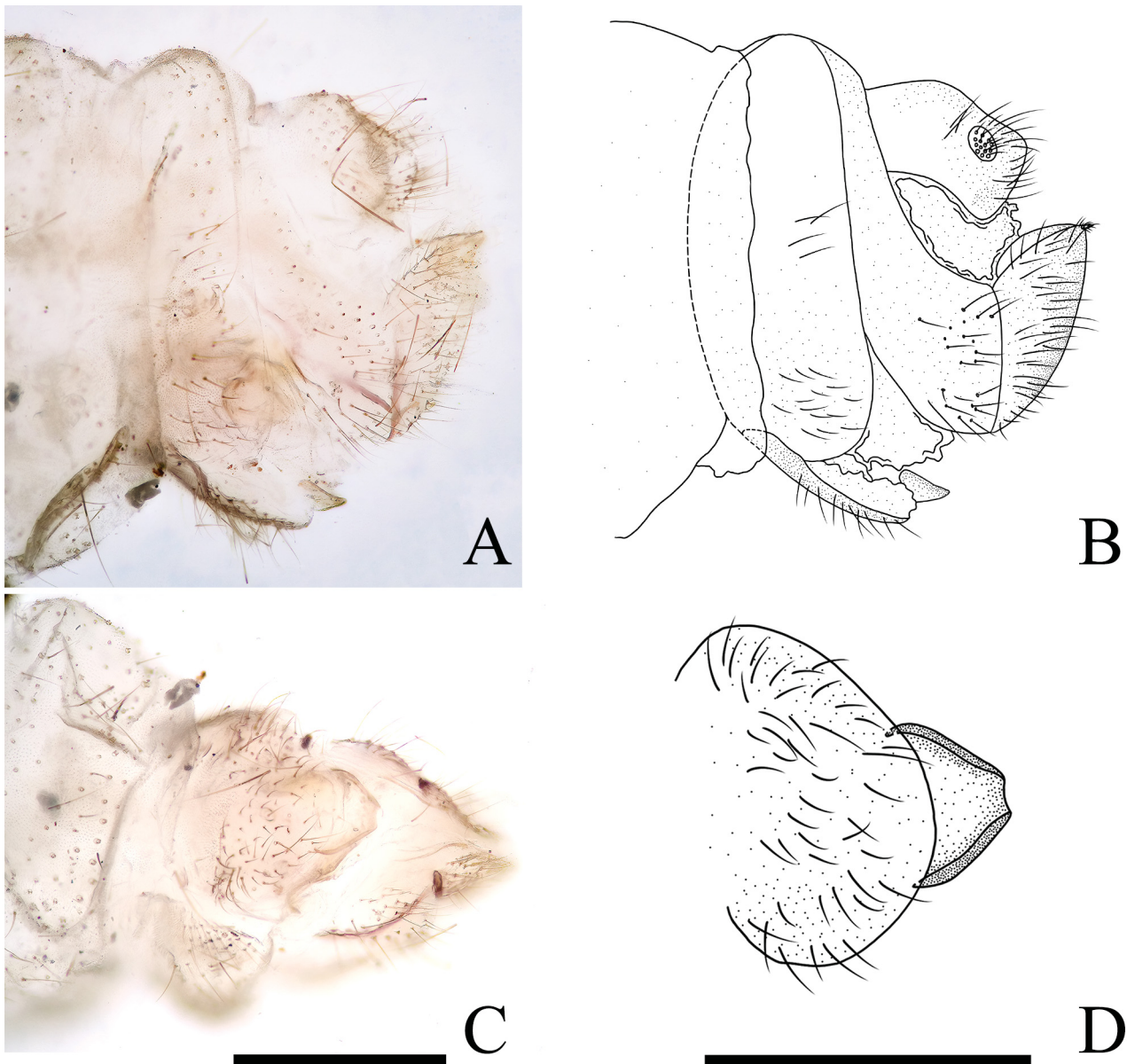


Fig. 6. Female genitalia of *Nipponeworthus qinicus* Yang, 1999. A, B – lateral view; C – ventral view; D – gonocoxite 8 and gonapophyses 8. Scale bar: 0.5 mm.

specimens in CAU and failed to find the holotype of this species (also mentioned in ASPÖCK et al. 2017). To fix the taxonomic concept of this species and provide a verifiable standard for its identity, a neotype is hereby designated. This species was originally from Ankang, Shaanxi, a locality in the Qinling Mountains (Yang in CHEN 1999). The presently examined specimens were collected from several localities in or near the Qinling Mountains. The morphological characters of these specimens fit well the original description of *N. qinicus*, i.e., basal part of antennae pale and gradually darken to the apex, immaculate wings, and hindwing veins basally pale. Thus, we identify these specimens as *N. qinicus* and designate a male specimen from Xi-an, Shaanxi (very close to original type locality) as the neotype of this species.

Nipponeworthus ailao sp. nov.

(Figs 7, 8)

Type material. HOLOTYPE: ♂, CHINA: Yunnan, Yuxi, Xinping, Ailaoshan N.N.R. [哀牢山国家级自然保护区], Gasa Town [嘎洒镇], Shimenxia [石门峡], 1937 m, 20.viii.2023, leg. Xingyue Liu (CAU). PARATYPE: 1 ♂, CHINA: Yunnan, Yuxi, Xinping, Ailaoshan N.N.R. [哀牢山国家级自然保护区], Gasa Town [嘎洒镇], Shimenxia [石门峡], 1937 m, 20.viii.2023, leg. Maozhi Wang (CAU).

Diagnosis. Antennae pale yellow. Body pale yellow. Wings slightly yellowish. Veins yellowish; brown markings present on gradate crossveins, ra-rp crossveins, and distal branching points of most longitudinal veins. Male gonocoxite 9 not bifurcated, robust on proximal half and strongly incurved on distal half, small hairy tubercles present on inner surface. Complex of gonocoxite+gonostylus+gonapophysis 10 narrow, elongated; distally with slenderly

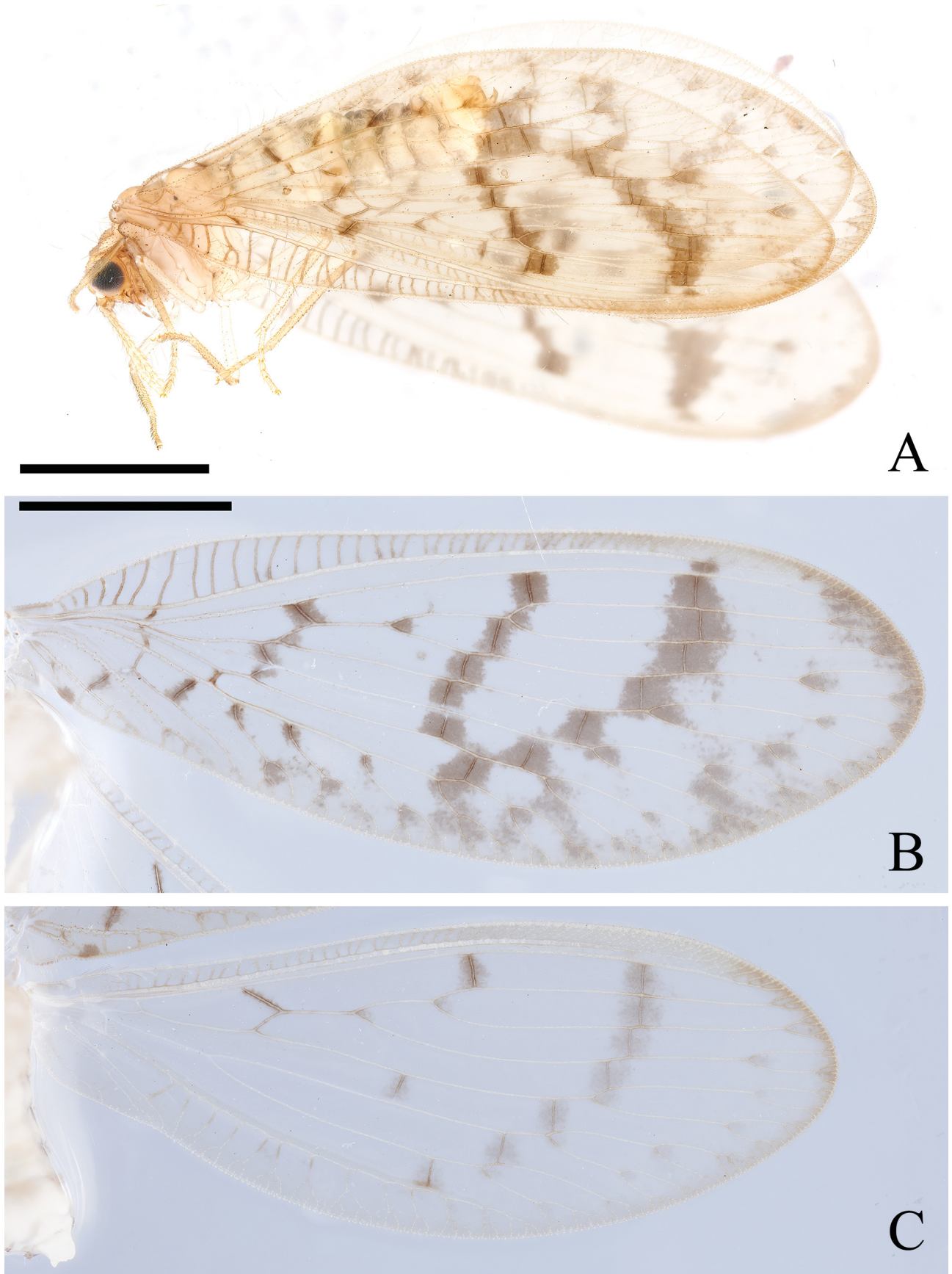


Fig. 7. Habitus of adult *Nipponeurorthus ailao* sp. nov. A – lateral view; B – forewing; C – hindwing. Scale bar: 2 mm.

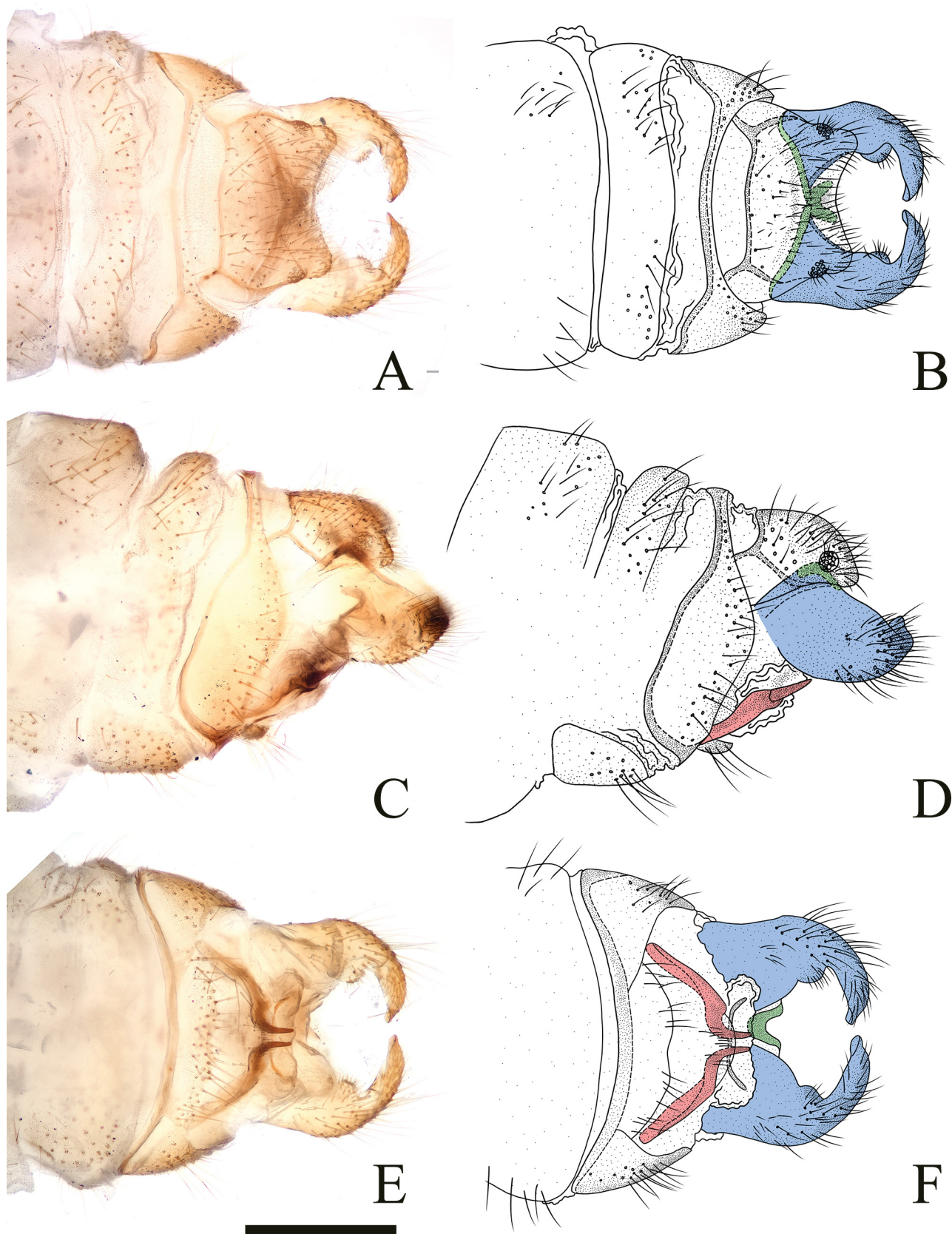


Fig. 8. Male genitalia of *Nipponeworthus ailao* sp. nov. A, B – dorsal view; C, D – lateral view; E, F – ventral view. Scale bar: 0.5 mm. Colour scheme: blue (segment 9), red (segment 10) and green (segment 11).

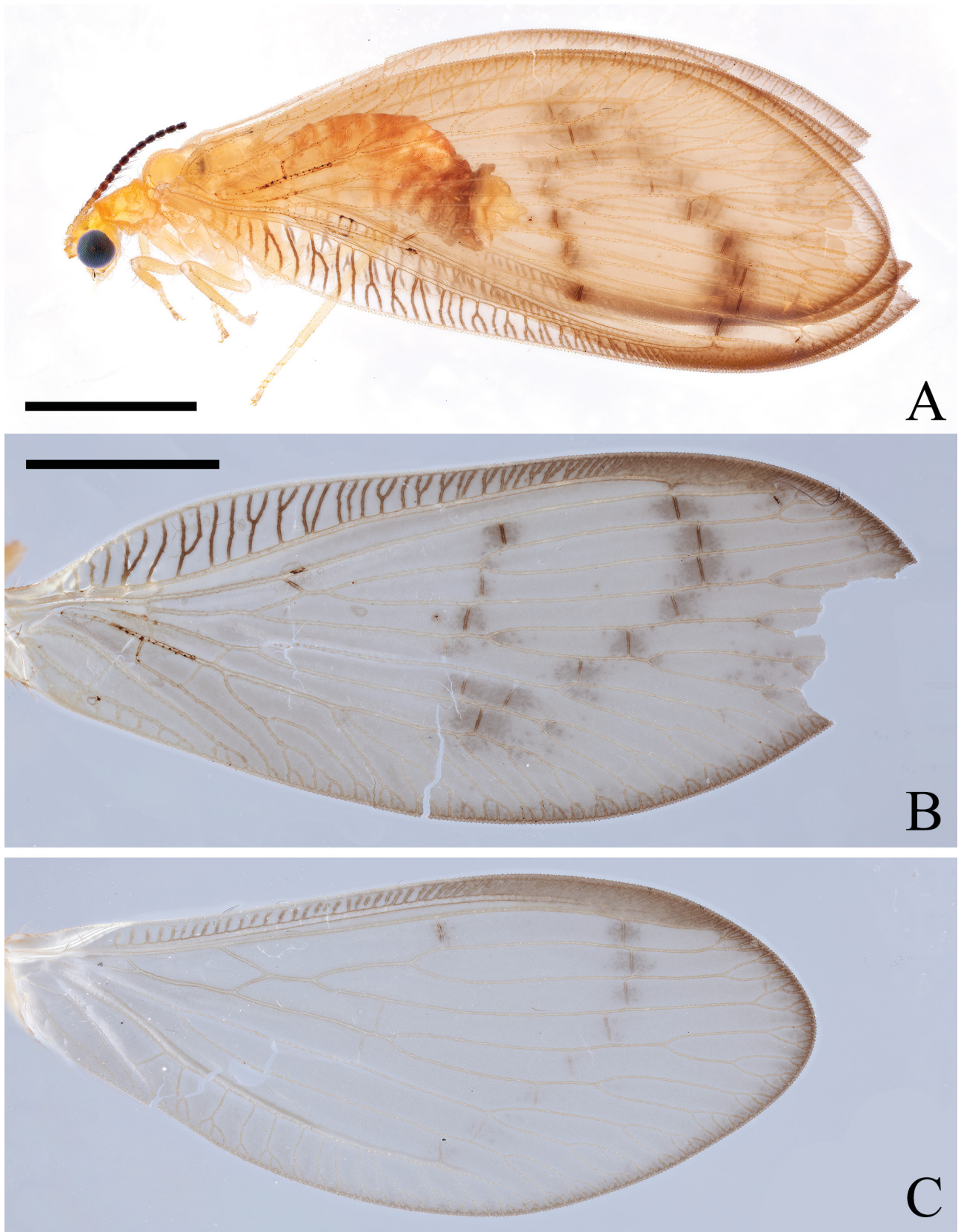


Fig. 9. Habitus of adult *Nipponeurorthus flavipennis* sp. nov. A – lateral view; B – forewing; C – hindwing. Scale bar: 2 mm.

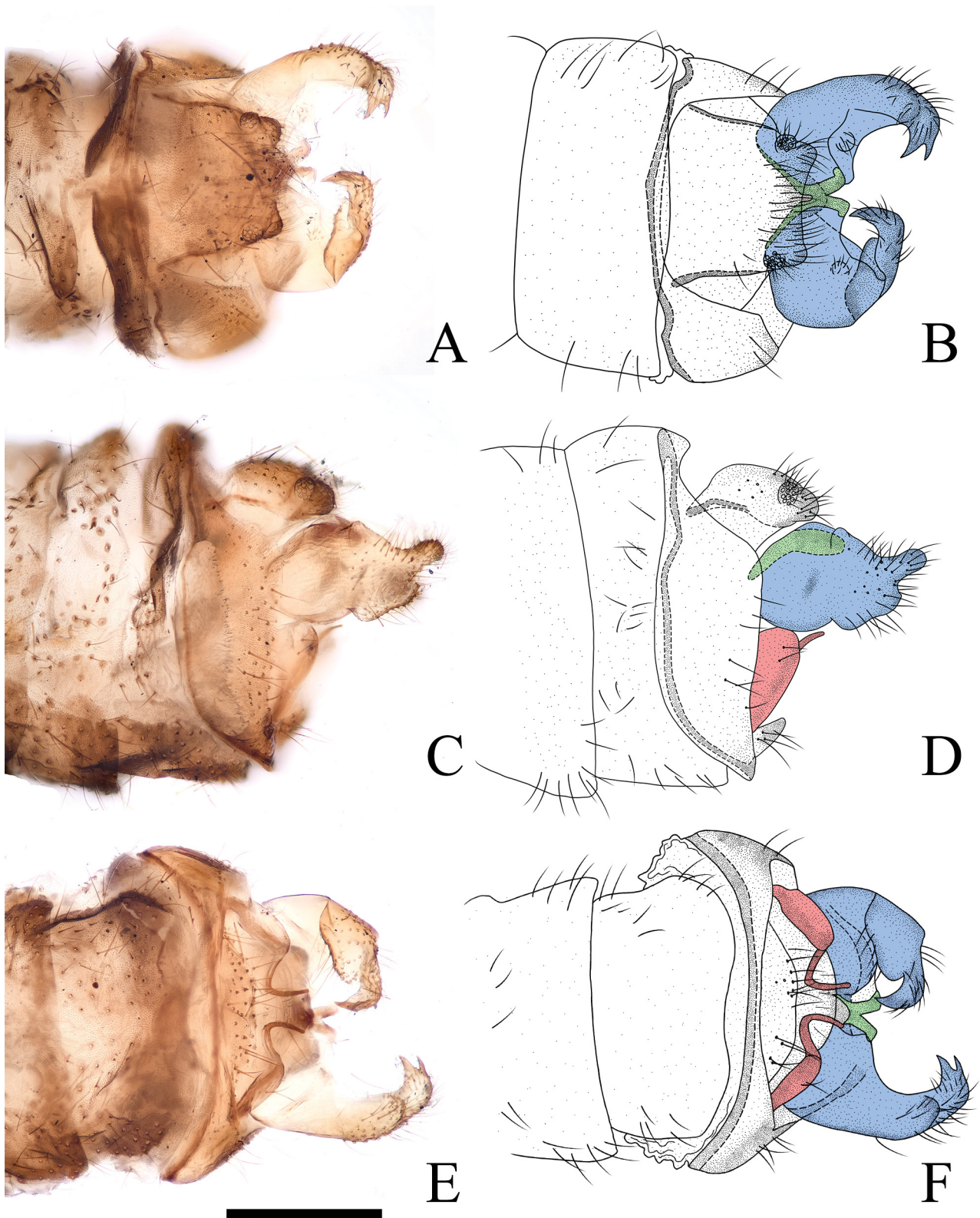


Fig. 10. Male genitalia of *Nipponeworthus flavipennis* sp. nov. A, B – dorsal view; C, D – lateral view; E, F – ventral view. Scale bar: 0.5 mm. Colour scheme: blue (segment 9), red (segment 10) and green (segment 11).

spinous projection, laterally bearing feebly sclerotized flat lobe; narrow, transverse, sclerotized area present.

Description. Body length 4.82 mm; forewing length 8.05 mm, hindwing length 7.51 mm.

Head pale yellow. Compound eyes black. Antennae pale

yellow. Mouthparts yellow; mandibles yellowish brown.

Thorax and legs pale yellow, with yellowish brown setae; but tibiae relatively dark.

Wings elliptical, slightly yellowish, with pterostigmal area yellowish brown (Fig. 7). Forewing with distal and po-

sterior margins slightly brown; brown markings present on gradate crossveins, ra-rp crossveins, and distal branching points of most longitudinal veins. Veins yellowish. Hindwing similar to forewing, paler, fewer markings present.

Abdomen pale yellow, dorsally tinged with brown. Male tergum 9 and sternum 9 fused into ring-like structure; tergum 9 anteriorly truncate and posteriorly broadly concaved in dorsal view; sternum 9 posteriorly protruding medially. Gonocoxite 9 basally robust, and strongly incurved on distal half. Gonostylus 9 terminally flattened. Ectoproct broad, directed posteriad, and subtrapezoidal and concaved on posterior margin in dorsal view. Complex of gonocoxite+gonostylus+gonapophysis 10 narrow and elongated, distally with slenderly spinous projection, which laterally bears feebly sclerotized flat lobe; narrow, transverse, sclerotized area present. Gonocoxites 11 present as simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite (Fig. 8).

Differential diagnosis. This new species is closely related to *N. furcatus* in having similar markings on forewing and close distribution. However, it can be distinguished by the male gonocoxite 9. In *N. furcatus* the male gonocoxite 9 is bifurcated (not bifurcated in *N. ailao* sp. nov.).

Etymology. This new species is named after “Ailao” (哀牢), referring to the Ailao Mountain Range, the type locality of the new species, as well as an ancient kingdom and ethnic group historically associated with this region. Noun in apposition.

Distribution. China (Yunnan).

Nipponeurorthus flavipennis sp. nov.

(Figs 9, 10)

Type material. HOLOTYPE: ♂, CHINA: Guangxi, Guilin, Lingui County [临桂县], Huangsha Yao Ethnic Township [黄沙瑶族自治乡], Huaping N.N.R. [花坪国家级自然保护区], Anjiangping [安江坪], 1526 m, 31.v–4.vi.2023, leg. Guo Chen (CAU).

Diagnosis. Antennae basally yellow, most of flagellum darkened. Body yellow. Wings yellowish. Veins yellowish; indistinct brown markings present on gradate crossveins and crossveins on M and Cu area. Male gonocoxite 9 not bifurcated, round process present on medial dorsal margin, longitudinal robust process present on distal half of ventral margin, small hairy tubercles present on inner surface. Complex of gonocoxite+gonostylus+gonapophysis 10 broad, subtrapezoidal; distally with curved slenderly spinous projection, which dorsally bears sclerotized round plate.

Description. Body length 5.29 mm; forewing length 8.86 mm, hindwing length 8.53 mm.

Head yellow. Compound eyes black. Scape, pedicel and basal flagellum yellowish, rest of flagellum darkened. Mouthparts yellow; mandibles yellowish brown.

Thorax and legs pale yellow, with yellowish brown setae.

Wings elliptical, yellowish, with pterostigmal areas brown (Fig. 9). Forewing with distal and posterior margins brown; indistinct brown markings present on gradate crossveins and crossveins on M and Cu area. Veinlets yellowish, indistinct. Hindwing similar to forewing, paler,

fewer markings present.

Abdomen yellow, dorsally tinged with reddish brown. Male tergum 9 and sternum 9 fused into ring-like structure; tergum 9 anteriorly truncate and posteriorly broadly concaved in dorsal view; sternum 9 posteriorly protruding medially. Gonocoxite 9 robust, and strongly incurved on distal half, round process present on medial dorsal margin, longitudinal square process present on distal half of ventral margin, small hairy tubercles present on inner surface. Gonostylus 9 bifurcated, present as two spinous lobes. Ectoproct broad, directed posteriad, and subtrapezoidal and slightly concave on posterior margin in dorsal view. Complex of gonocoxite+gonostylus+gonapophysis 10 broad, subtrapezoidal; distally with curved slenderly spinous projection, which dorsally bears sclerotized round plate. Gonocoxites 11 present as simple, sclerotized band, laterally extending anteriad; gonostyli 11 present as posteriorly bifurcated sclerite (Fig. 10).

Differential diagnosis. This species can be easily distinguished from the other species of *Nipponeurorthus* by the unique yellowish wings. In *N. flavipennis* sp. nov., a longitudinal robust process is present on distal half of ventral margin of the male gonocoxite 9, and complex of the male gonocoxite+gonostylus+gonapophysis 10 is broad and subtrapezoidal, a curved slenderly spinous projection is present distally, which dorsally bears a sclerotized round plate.

Etymology. The species name is a composed Latin adjective *flavipennis* (-is, -e) meaning “having yellow wings”.

Distribution. China (Guangxi).

Nipponeurorthus kuanglu sp. nov.

(Figs 11, 12, 13)

Type material. HOLOTYPE: ♂, CHINA: Jiangxi, Jiujiang, Mt. Lushan [庐山], 1044 m, 24.v.2025, leg. Yujie Zhao (CAU). PARATYPE: 1 ♀, CHINA: Jiangxi, Jiujiang, Mt. Lushan [庐山], Lushan Botanical Garden [庐山植物园], 1000–1300 m, 12.vi.2025, leg. Youfeng Peng (CAU).

Diagnosis. Antennae pale. Body pale. Wings colorless and hyaline. Veinlets pale yellow. Black markings present on most crossveins and distal branching points of most longitudinal veins. Male gonocoxite 9 not bifurcated, small hairy tubercles present on inner surface. Complex of gonocoxite+gonostylus+gonapophysis 10 slender, basally bearing triangular lateral angle; distally with slenderly and twistedly spinous projection, which is apically rounded.

Description. Body length 5.5 mm; forewing length 8.2 mm, hindwing length 7.8 mm.

Head pale. Compound eyes black. Antennae pale. Mouthparts pale; mandibles yellow.

Thorax and legs pale yellow, with yellowish brown setae.

Wings elliptical, colorless and hyaline, with pterostigmal areas indistinct (Fig. 11). Forewing with black markings present on most crossveins and distal branching points of most longitudinal veins; veinlets pale yellow. Hindwing similar to forewing, markings paler.

Abdomen pale, dorsally tinged with reddish brown. Male tergum 9 and sternum 9 fused into ring-like structure; tergum 9 anteriorly truncate and posteriorly broadly concaved in dorsal view; sternum 9 posteriorly protruding medially. Gonocoxite 9 robust, and strongly incurved on distal half,

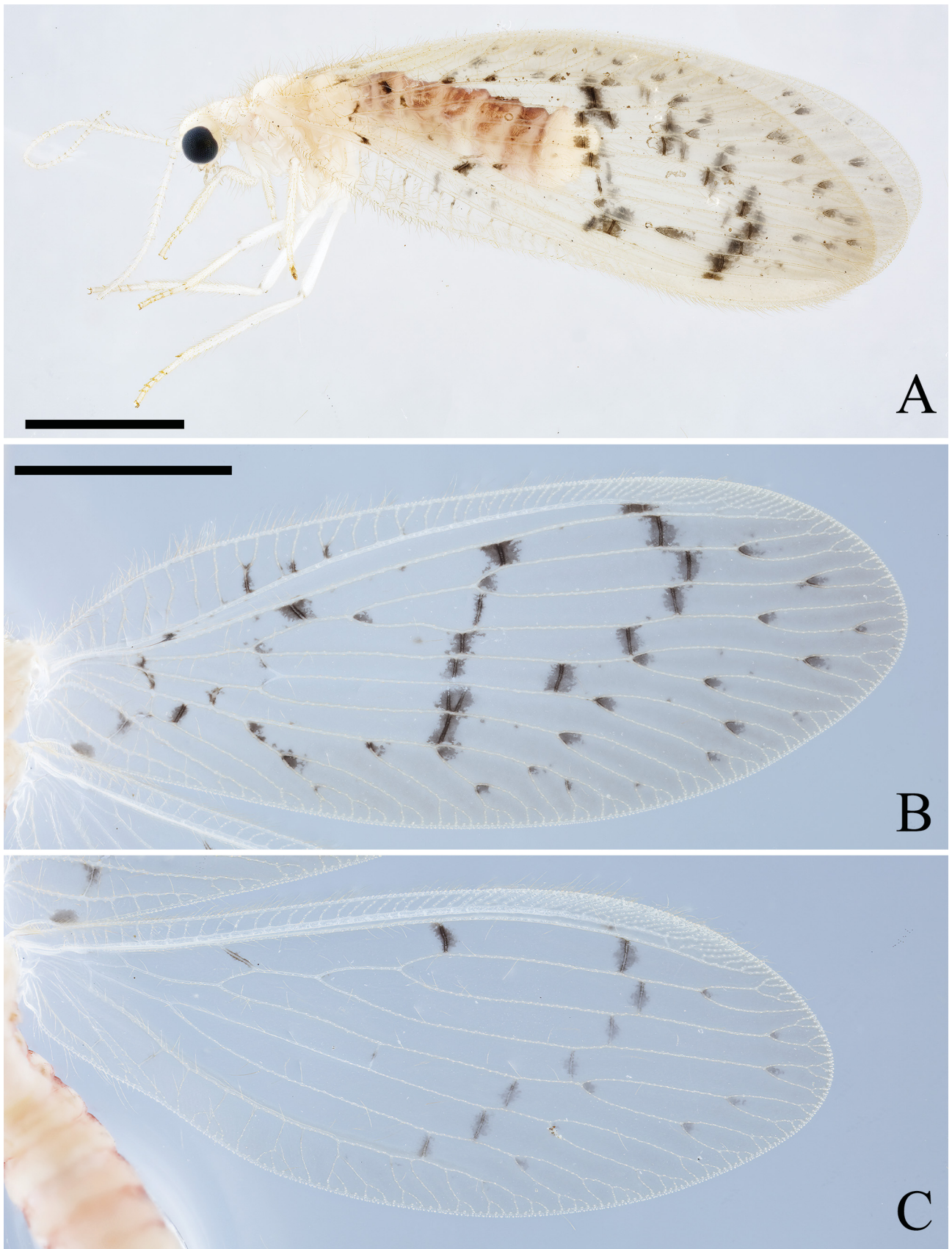


Fig. 11. Habitus of adult *Nipponeurorthus kuanglu* sp. nov. A – lateral view; B – forewing; C – hindwing. Scale bar: 2 mm.

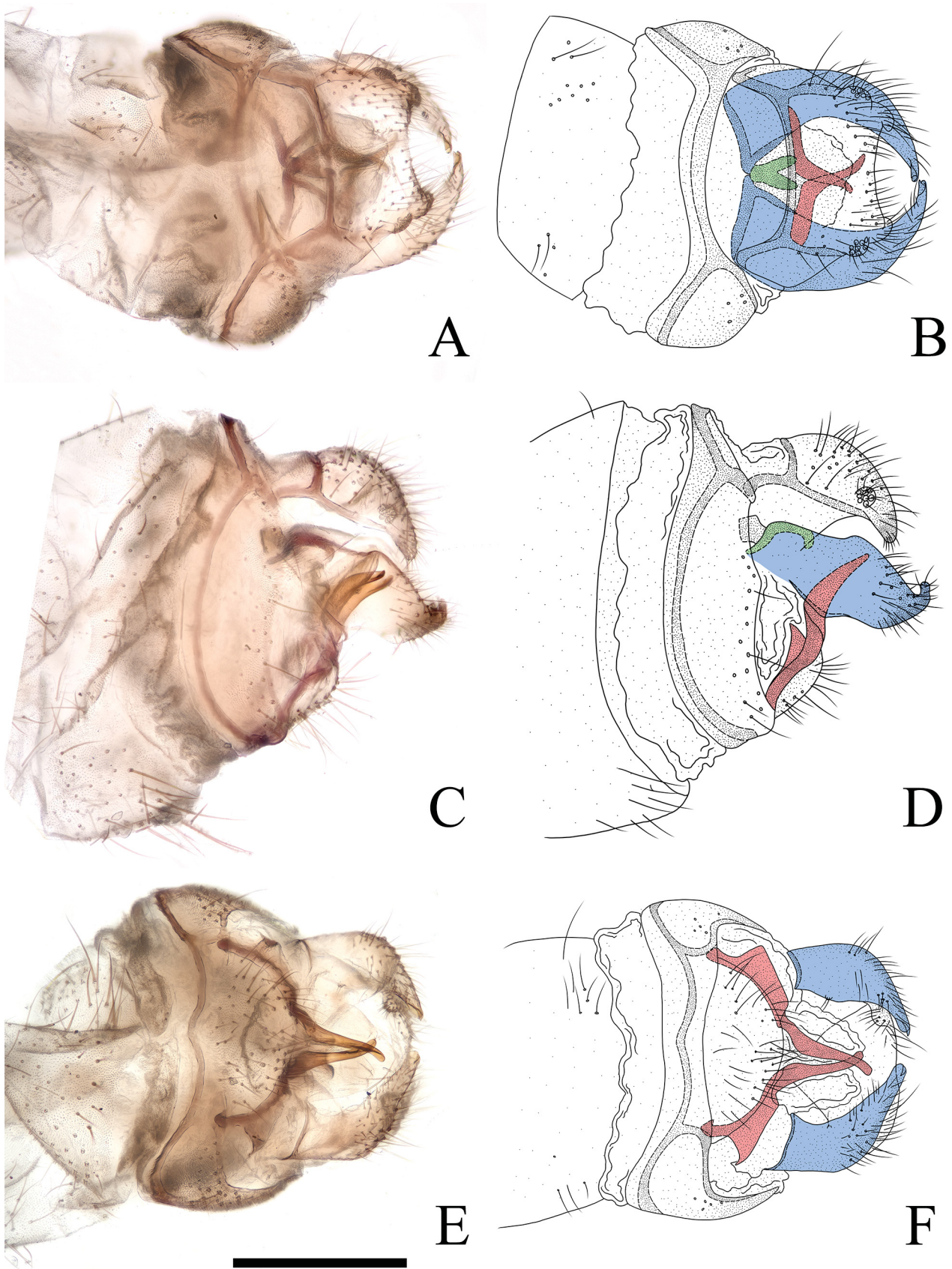


Fig. 12. Male genitalia of *Niponeurorthus kuanglu* sp. nov. A, B – dorsal view; C, D – lateral view; E, F – ventral view. Scale bar: 0.5 mm. Colour scheme: blue (segment 9), red (segment 10) and green (segment 11).

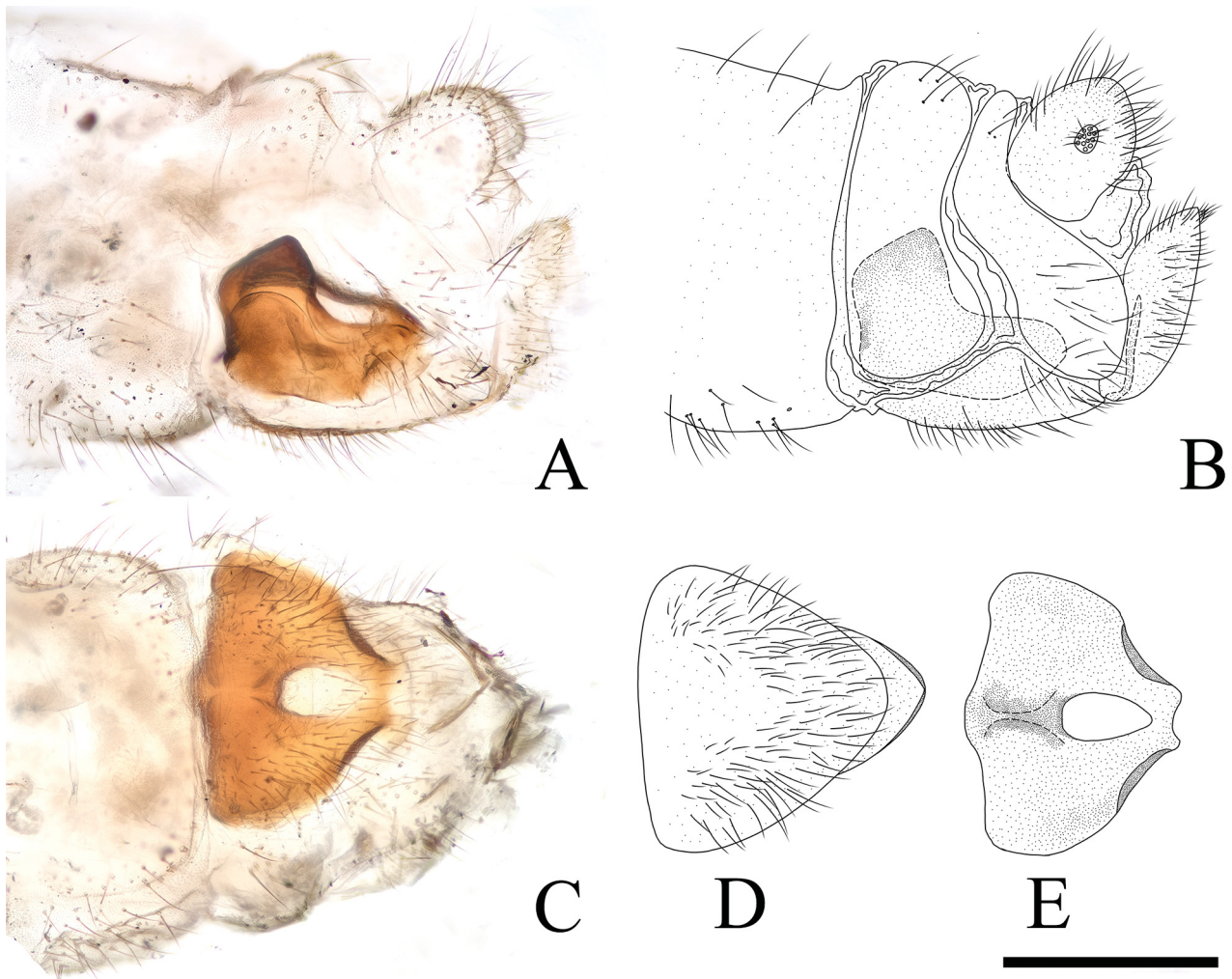


Fig. 13. Female genitalia of *Nipponeworthus kuanglu* sp. nov. A, B – lateral view; C – ventral view; D – gonocoxite 8 and gonapophyses 8; E – bursa copulatrix. Scale bar: 0.5 mm.

small hairy tubercles present on inner surface. Gonostylus 9 bifurcated distally, present as two small spinous lobes. Ectoproct broad, lateral margin convex, posterior margin concaved medially; posterolateral corner protruding into digitiform process and curved ventrad. Complex of gonocoxite+gonostylus+gonapophysis 10 slender, basally bearing triangular lateral angle; distally with slenderly and twistedly spinous projection, which is apically rounded. Gonocoxites 11 present as simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite (Fig. 12). Female tergum 8 relatively short, elongated ventrad, in lateral view posteroventral corner rounded. Fused gonocoxites 8 relatively longer than tergum 8, being plate-like flat and rounded subtriangular. Gonapophyses 8 subtriangular, apically sharp, basally covered by gonocoxite 8, lateral margin distinctly sclerotized, terminally truncate. Gonocoxite 9 foliate, almost vertically directed, with reduced, flat and ovoid gonostylus bearing tuft of hairs. Bursa copulatrix well sclerotized, subtriangular in ventral view, terminally flattened, posterolateral margins curved ventrad; basally protruding dorsad, posterior half with oval hole. Ectoproct round in lateral view (Fig. 13).

Differential diagnosis. The new species is closely related to *N. tianmushanus* and *N. damingshanicus* in having similar wing markings and male genitalia. However, it can be distinguished from *N. tianmushanus* by the following characters: in *N. kuanglu* sp. nov., the antennae are entirely pale (dark distally in *N. tianmushanus*). In *N. kuanglu* sp. nov., numerous black markings are present on most distal branching points of most longitudinal veins (absent in *N. tianmushanus*). In *N. kuanglu* sp. nov., the brown stripe along forewing posterior margins is absent (present along the forewing distal and posterior margins; in *N. tianmushanus* and *N. damingshanicus*). In *N. kuanglu* sp. nov., the markings on wings are dark (brownish in *N. damingshanicus*). In *N. kuanglu* sp. nov., the bursa copulatrix is subtriangular with a dorsal protrusion at the base (divided basally and lacking dorsal protrusion in *N. damingshanicus*).

Etymology. This new species is named after “Kuanglu” (匡庐), referring to the Lushan Mountain Range, the type locality of the new species. Noun in apposition.

Distribution. China (Jiangxi).



Fig. 14. Habitus of adult *Niponeurorthus ningboensis* sp. nov. A – lateral view; B – forewing; C – hindwing. Scale bar: 2 mm.

***Niponeurorthus ningboensis* sp. nov.**

(Figs 2B, 14, 15, 16)

Type material. HOLOTYPE: ♂, CHINA: Zhejiang, Ningbo, Beilun district [北仑区], Mt. Jiufeng [九峰山], 190 m, 16.iv.2021, leg. Danyang Zhou (CAU). PARATYPES: 2 ♂♂ 1 ♀, same as holotype (CAU).

Additional material examined. CHINA: ZHEJIANG: Hangzhou, Mt. Longwang, 1100 m, 12.vi.2025. All specimens were utilized for DNA sequencing and could not be deposited as voucher specimens.

Diagnosis. Antennae basally pale yellow, flagellum brown. Body pale yellow. Wings spotless, colorless and hyaline. Veinlets brown, crossveins distinct; hindwing basal longitudinal veinlets pale, indistinct. Male gonocoxite 9 not bifurcated, small hairy tubercles present on inner surface. Complex of gonocoxite+gonostylus+gonapophysis 10 relatively broad, subtrapezoidal; distally with slenderly spinous projection curved at right angles. Female gonocoxites 8 subtriangular, gonapophyses 8 subtriangular, basally covered by gonocoxite 8, lateral margins distinctly sclerotized.

Description. Body length 4.47 mm; forewing length 7.75 mm, hindwing length 7.32 mm.

Head pale yellow. Compound eyes black. Scape pale yellow, pedicel yellowish brown, flagellum brown. Mouthparts pale; mandibles yellow.

Thorax and legs pale yellow, with yellowish brown setae.

Wings elliptical, colorless and hyaline, with pterostigmal areas white (Fig. 14). Forewing spotless and colorless, veinlets dark, basal MA pale. Hindwing similar to forewing, basal longitudinal veinlets pale, indistinct.

Abdomen pale. Male tergum 9 and sternum 9 fused into ring-like structure; tergum 9 anteriorly truncate and

posteriorly broadly concaved in dorsal view; sternum 9 posteriorly protruding medially. Gonocoxite 9 robust, and strongly incurved on distal half, small hairy tubercles present on inner surface. Gonostylus 9 bifurcated, present as two spinous lobes. Ectoproct broad, lateral and posterior margin convex medially, and with posterolateral corner protruding into process. Complex of gonocoxite+gonostylus+gonapophysis 10 relatively broad, subtrapezoidal; distally with slenderly spinous projection curved at right angles. Gonocoxites 11 present as simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite (Fig. 15). Female tergum 8 relatively short, elongated ventrad, in lateral view posteroventral corner rounded. Fused gonocoxites 8 relatively longer than tergum 8, flatly and rounded subtriangular plate-like. Gonapophyses 8 subtriangular, terminally flattened, basally covered by gonocoxite 8, lateral margins distinctly sclerotized, terminally truncate. Gonocoxite 9 foliate, almost vertically directed, with reduced, flat and ovoid gonostylus bearing tuft of hairs. Ectoproct round in lateral view (Fig. 16).

Differential diagnosis. The new species is closely related to *N. qinicus* in having similar spotless wings. However, it can be distinguished from *N. qinicus* by the following characters: in *N. qinicus* the crossveins are pale and indistinct, and the process on posterolateral corner of male ectoproct is absent (crossveins brown and distinct, process present in *N. ningboensis* sp. nov.).

Etymology. The species name refers to the type locality, Ningbo, of the new species; adjective.

Distribution. China (Zhejiang).

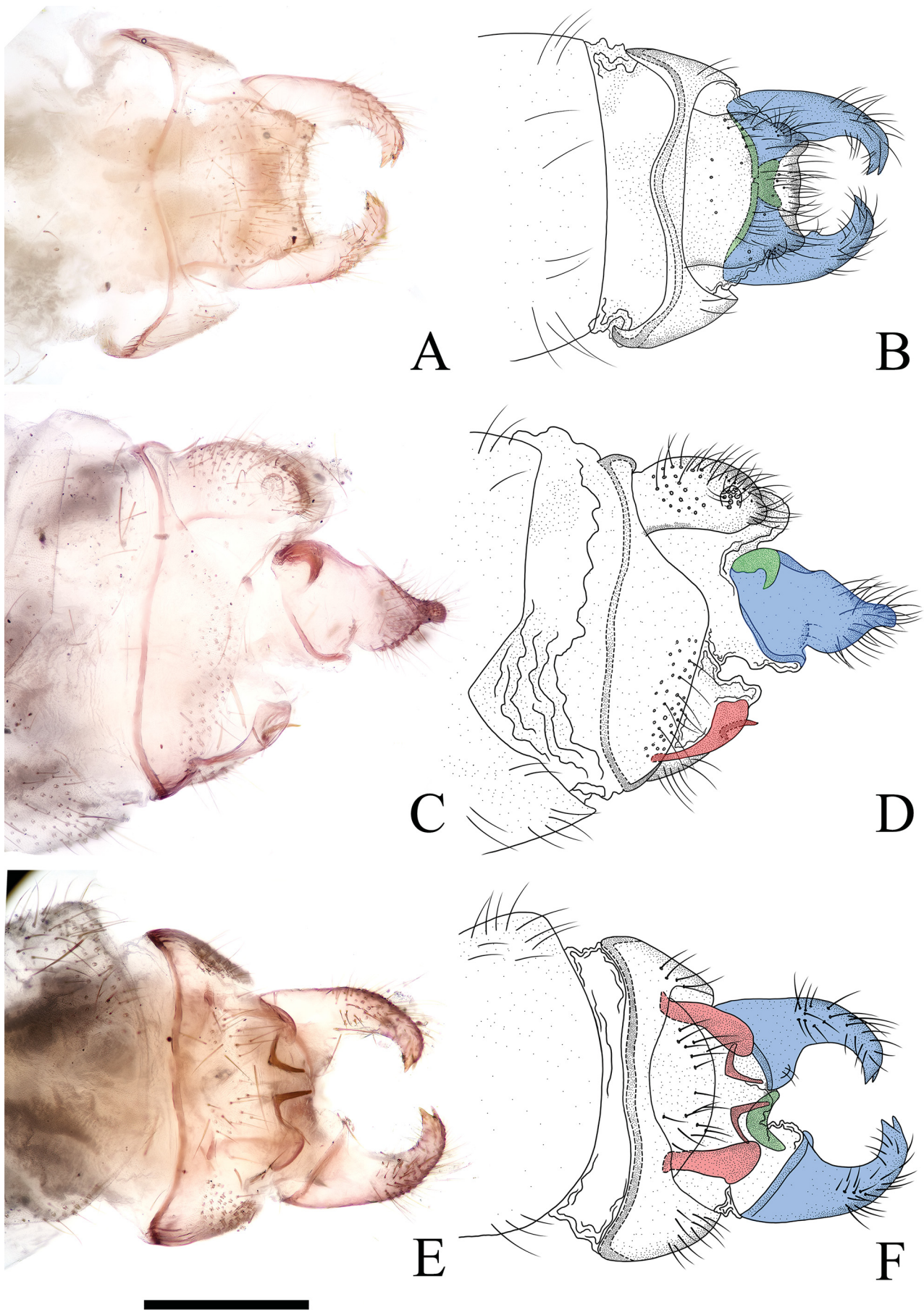


Fig. 15. Male genitalia of *Nipponeworthis ningboensis* sp. nov. A, B – dorsal view; C, D – lateral view; E, F – ventral view. Scale bar: 0.5 mm. Colour scheme: blue (segment 9), red (segment 10) and green (segment 11).

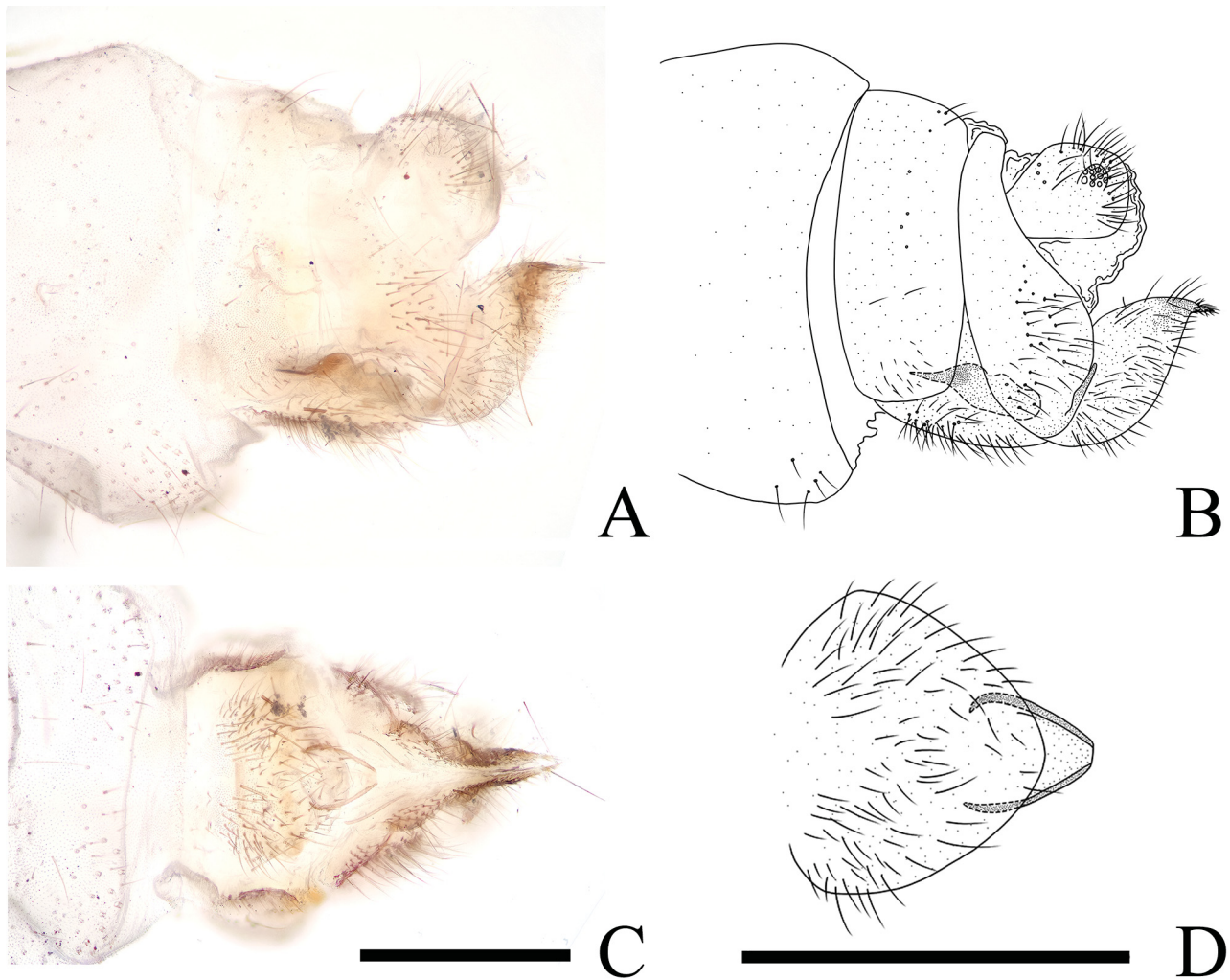


Fig. 16. Female genitalia of *Niponeurorthus ningboensis* sp. nov. A, B – lateral view; C – ventral view; D – gonocoxite 8 and gonapophyses 8. Scale bar: 0.5 mm.

***Niponeurorthus pallidimaculatus* sp. nov.**

(Figs 2D, 14, 15)

Type material. HOLOTYPE: ♂, CHINA: Jiangsu, Liyang, Shenxijie [深溪芥], 150 m, 9.vi.2022, leg. Zhishun Song, Siyuan Xu and Haoyu Zhu (CAU). PARATYPES: 9 ♂♂, same as holotype (CAU).

Diagnosis. Antennae basally yellowish brown, rest of flagellum darkened. Body pale yellow. Wing colorless and hyaline. Veinlets pale brown, crossveins distinct. Indistinct pale brown markings present on outer gradate crossveins. Male gonocoxite 9 not bifurcated, medially robust and strongly incurved on distal half, small hairy tubercles present on inner surface. Complex of gonocoxite+gonostylus+gonapophysis 10 broad, oval; distally with slender spinous projection curved at right angle.

Description. Body length 4.22 mm; forewing length 7.81 mm, hindwing length 6.65 mm.

Head pale yellow. Compound eyes black. Scape yellow, pedicel yellowish brown, flagellum brown. Mouthparts pale; mandibles yellow.

Thorax yellow and legs pale, with yellowish brown setae.

Wings elliptical, colorless and hyaline, with pterostigmal areas white (Fig. 17). Forewing colorless, indistinct pale brown markings present on outer gradate crossveins. Veinlets pale brown. Hindwing similar to forewing, basal longitudinal veinlets pale, indistinct.

Abdomen pale, dorsally tinged with dark brown. Male tergum 9 and sternum 9 fused into ring-like structure; tergum 9 anteriorly truncate and posteriorly broadly concave in dorsal view; sternum 9 posteriorly protruding medially. Gonocoxite 9 medially robust and strongly incurved on distal half, small hairy tubercles present on inner surface. Gonostylus 9 bifurcated, present as two spinous lobes. Ectoproct broad, posterior margin convex medially, two processes present posterolaterally. Complex of gonocoxite+gonostylus+gonapophysis 10 broad, oval; distally with slender spinous projection curved at right angle. Gonocoxites 11 present as transverse, sclerotized band, which is fused with apodeme of gonocoxite 9, shaping X-shaped structure; gonostyli 11 present as posteriorly bifurcated sclerite, distally twisted (Fig. 18).

Differential diagnosis. This new species is similar to *N. tianmushanus* according to its original description.

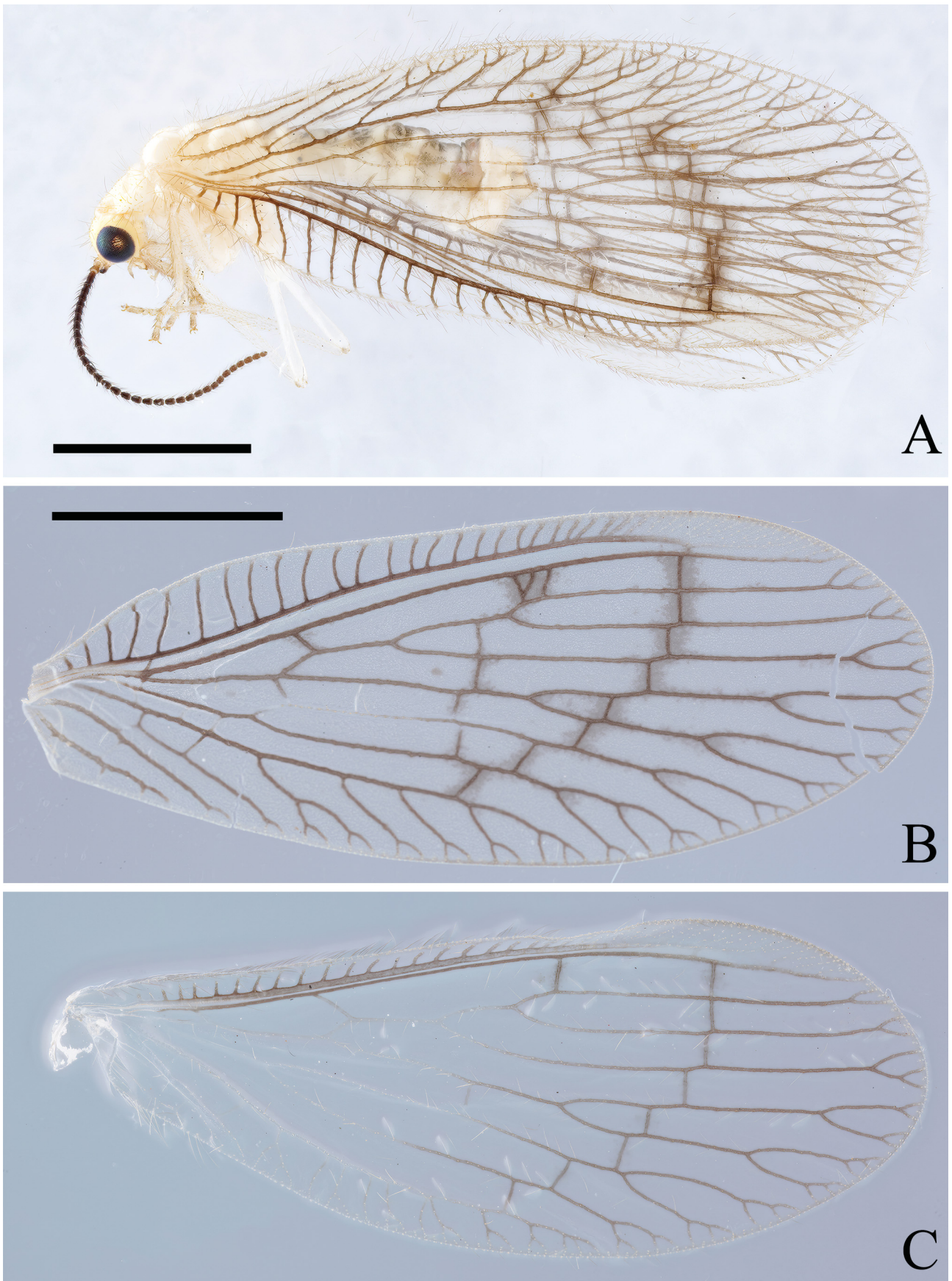


Fig. 17. Habitus of adult *Nipponeurorthus pallidimaculatus* sp. nov. A – lateral view; B – forewing; C – hindwing. Scale bar: 2 mm.

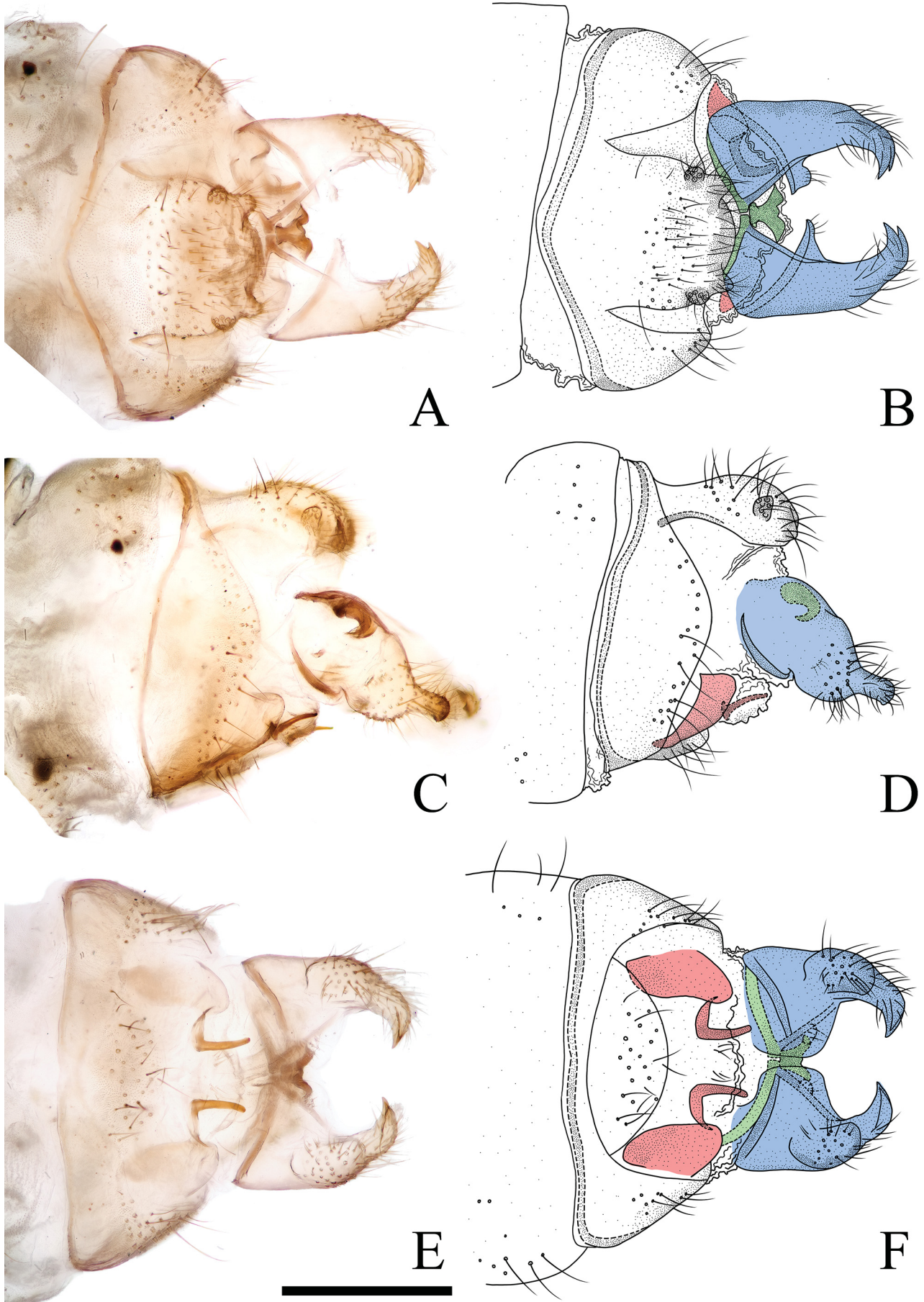


Fig. 18. Male genitalia of *Nipponeworthus pallidimaculatus* sp. nov. A, B – dorsal view; C, D – lateral view; E, F – ventral view. Scale bar: 0.5 mm. Colour scheme: blue (segment 9), red (segment 10) and green (segment 11).

However, these two species can be distinguished by the following characters: in *N. tianmushanus*, a brown stripe is present along the distal margins of forewing, and the processes on male ectoproct are directed posteroventrad (brown stripe absent, processes directed posteriad in *N. pallidimaculatus* sp. nov.).

Etymology. The specific name is a composed Latin adjective *pallidimaculatus* (-a, -um) (= pale-spotted) referring to the pale brown markings on the forewing in the new species.

Distribution. China (Jiangsu).

Key to species of *Nipponeurorthus*

- 1 Forewing with a brown stripe along distal margin. 2
- Forewing without any marking along distal margin. ... 7
- 2 Wings distinctly yellowish. ... *N. flavipennis* sp. nov.
- Wings colorless. 3
- 3 Male gonocoxite 9 bifurcated (LIU et al. 2014: fig. 9).
..... *N. furcatus* Liu, H. Aspöck & U. Aspöck, 2014
- Male gonocoxite 9 not bifurcated. 4
- 4 Male ectoproct with posterolateral corners strongly protruding into a pair of digitiform processes (LIU et al. 2014: Fig. 4); distal parts of male gonocoxite+gonostylus+gonapophysis 10 blade-like and crossing each other at mid-length (LIU et al. 2014: fig. 4).
.. *N. damingshanicus* Liu, H. Aspöck & U. Aspöck, 2014
- Male ectoproct with posterolateral corners feebly produced; distal parts of male gonocoxite+gonostylus+gonapophysis 10 not crossing each other. 5
- 5 Forewing with brownish markings distal to outer series of gradate crossveins (NAKAHARA 1958: Plate 8-2; Fig. 4B). 6
- Forewing without brownish markings distal to outer series of gradate crossveins (YANG & GAO 2001: fig. 1). *N. tianmushanus* Yang & Gao, 2001
- 6 Male gonocoxite 9 with small hairy tubercles on inner surface; male gonocoxite 9 robust, without round process on ventral surface (Figs 8A, B).
..... *N. ailao* sp. nov.
- Male gonocoxite 9 without small hairy tubercles on inner surface; male gonocoxite 9 narrow, with a round process distally on ventral surface (ASPÖCK et al. 2017: figs 9a, b). *N. fasciatus* Nakahara, 1958
- 7 Male gonocoxite 9 distally bifurcated or trifurcated. ... 8
- Male gonocoxite 9 distally simple. 12
- 8 Forewing with dark markings. 9
- Forewing without any dark marking. 11
- 9 Forewing only with brown markings on most crossveins and branching points of most longitudinal veins (NAKAHARA 1958: Plate 2-1); a digitiform process present on ventral surface of male gonocoxite 9 (SAITO et al. 2024: figs 9B, C). 10
- Forewing with blackish brown markings along most longitudinal veins on distal half and costal crossveins on proximal half (NAKAHARA 1966: Plate 4-2); a robust process present on ventral surface of male gonocoxite 9 (NAKAHARA 1966: figs 20, 21; ASPÖCK et al. 2017: figs 11a, b). *N. multilineatus* Nakahara, 1966
- 10 Male gonocoxite 9 basally broad (SAITO et al. 2024: fig. 9C). *N. insularis* Saito & Hayashi, 2024

- Male gonocoxite 9 basally narrow (ASPÖCK et al. 2017: fig. 12a). *N. punctatus* (Nakahara, 1915)
- 11 Male gonocoxite 9 distally bifurcated into a slender, acutely pointed gonostylus 9 and an obtuse ventral lobe (ASPÖCK & ASPÖCK 2008b: fig. 3).
..... *N. flinti* U. Aspöck & H. Aspöck, 2008
- Male gonocoxite 9 distally trifurcated into a slender, acutely pointed gonostylus 9 and two obtuse lobes (NAKAHARA 1958: fig. 4a; ASPÖCK et al. 2017: figs 10d, e). *N. fuscineris* (Nakahara, 1915)
- 12 Forewing with markings on outer gradate crossveins. 13
- Forewing without markings on outer gradate crossveins. 14
- 13 Forewing with distinct black markings on outer gradate crossveins; most distal branching points of most longitudinal veins with black markings (Fig. 11); posterolateral corner of male ectoproct protruding into a digitiform process and curved ventrad (Fig. 12).
..... *N. kuanglu* sp. nov.
- Forewing with indistinct brown markings on outer gradate crossveins; distal branching points of most longitudinal veins without markings (Fig. 17); posterolateral corner of male ectoproct weakly developed (Fig. 18). *N. pallidipennis* sp. nov.
- 14 Crossveins indistinct (Figs 2C, 4); flagellum pale gradually darkened toward apex (Fig. 4).
..... *N. qinicus* Yang, 1999
- Crossveins distinct; flagellum entirely yellow or dark brown. 15
- 15 Forewing with yellowish brown markings (SAITO et al. 2024: fig. 6B).
..... *N. amamiensis* Saito & Hayashi, 2024
- Forewing without markings. 16
- 16 Forewing with longitudinal veins almost yellow (NAKAHARA 1958: Plate 9-2, SAITO et al. 2024: fig. 5A); male gonocoxite+gonostylus+gonapophysis 10 as separate structures (ASPÖCK et al. 2017: fig. 11h, SAITO et al. 2024: fig. 7D). *N. pallidinervis* Nakahara, 1958
- Forewing with longitudinal veins entirely brown (NAKAHARA 1958: Plate 9-2; SAITO et al. 2024: fig. 5B, 9B); male gonocoxite+gonostylus+gonapophysis 10 fused. 17
- 17 Flagellum yellow (SAITO et al. 2024: fig. 5B); male gonocoxite+gonostylus+gonapophysis 10 slender, distal parts robust and short (SAITO et al. 2024: fig. 9A).
..... *N. tinctipennis* Nakahara, 1958
- Flagellum dark brown (Fig. 2B); male distal parts of male gonocoxite+gonostylus+gonapophysis 10 broad, subtrapezoidal, distally with a slenderly spinous projection curved at right angle (Fig. 18C).
..... *N. ningboensis* sp. nov.

Discussion

Ulrike ASPÖCK (2004) assumed that *Austroneurorthus* Nakahara, 1958, and partly also *Nipponeurorthus*, show a coastal distribution pattern. However, this hypothesis has been challenged by subsequent discoveries of numerous nevrorthid species from the Chinese mainland

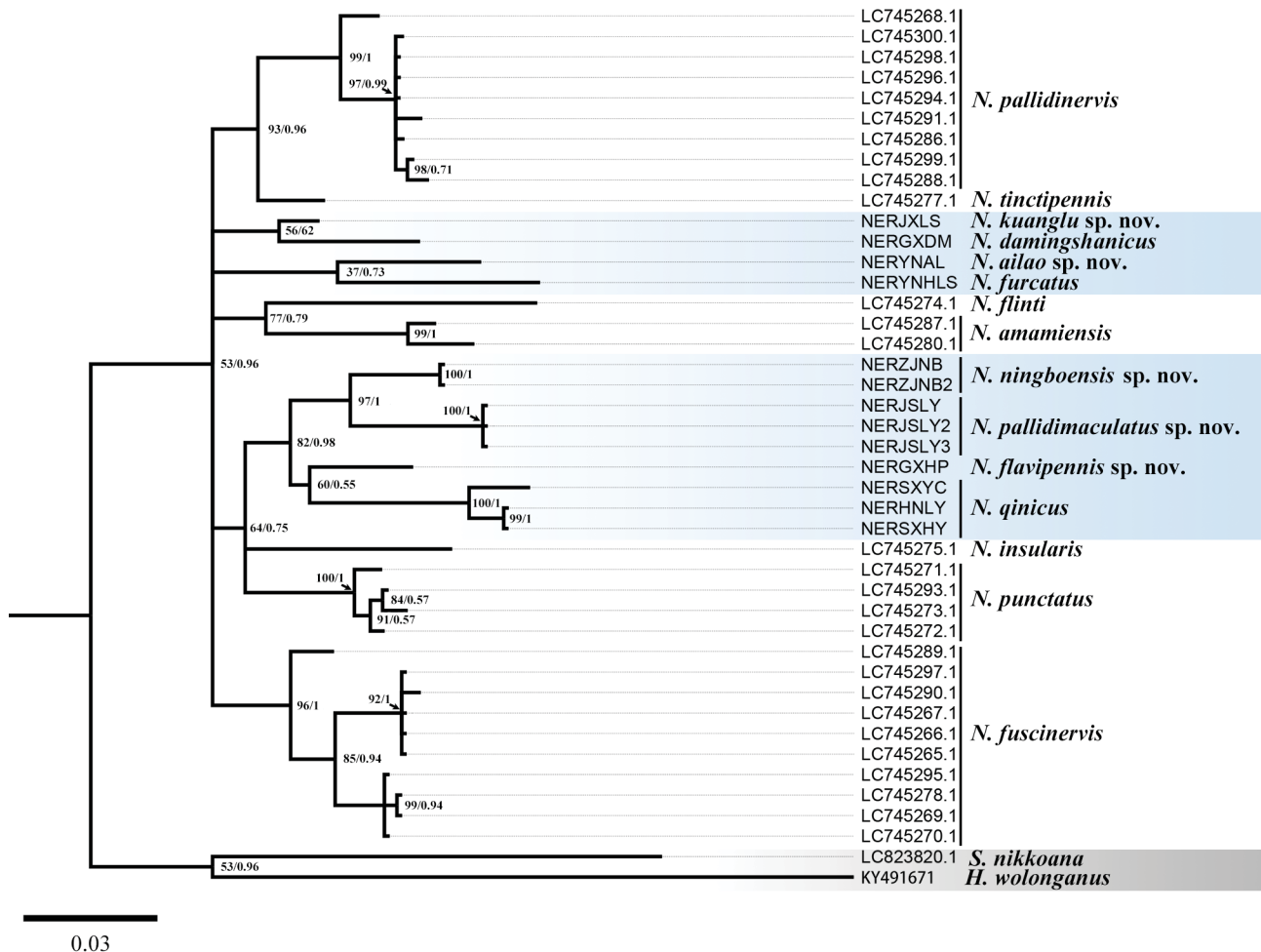


Fig. 19. Interspecific phylogeny of *Nipponeurorthus* Nakahara, 1958. Numbers at nodes are maximum likelihood bootstrap values (left) and Bayesian posterior probabilities (right). Chinese species marked in blue and out group marked in grey.

(ASPÖCK et al. 2017). Our new findings further confirm that the *Nipponeurorthus* species can be distributed in the mainland far from the coastal areas. Currently, the species of *Nipponeurorthus* only occur in China and Japan, while the distribution patterns between mainland and insular species distinctly differ. All mainland species, i.e., those from the Chinese mainland, are allopatric, and there is no area with two or more species co-occurring. However, some species from the Taiwan and the Japanese archipelago are sympatric (Fig. 1).

Based on COI barcodes, the species of *Nipponeurorthus* herein analyzed could be clearly delimited. However, the interspecific relationships among most species were not well resolved, probably due to the limited informative sites from the barcode sequences (Fig. 19). According to the present results, the Chinese species, i.e., *N. flavipennis* sp. nov., *N. qinicus*, *N. ningboensis* sp. nov., and *N. pallidimaculatus* sp. nov., together with the Japanese species *N. insularis* and *N. punctatus*, form a monophyletic lineage. Two species from Yunnan were assigned to be sister groups to each other. The Chinese species *N. damingshanicus* and *N. kuanglu* sp. nov. were also recovered as sister groups. For the other Japanese species, *N. amamiensis* and *N. flinti* from the Ryukyus are sister groups, and *N. tinctipennis* and *N. pallidinervis* are also sister groups. It is notable that the

mainland species and insular species do not respectively form monophyletic lineages, whereas some mainland and insular species are phylogenetically closer. Besides, it is also noteworthy that those species with distinct wing marking patterns and those with immaculate wings are not clearly divided from each other. Thus, our result demonstrates that the biogeographical history and the evolution of wing marking patterns are complex. To fully clarify the evolutionary history of this genus, future phylogenomic studies with complete taxon sampling are required.

Conclusions

This study provides important new data on the diversity and distribution of the little-known lacewing family Nevrorthidae from East Asia. It is clear that the species diversity of *Nipponeurorthus* from the mainland of East Asia is richer than previously thought. A distinct allopatric distribution in the mainland species of *Nipponeurorthus* is remarkable and it suggests that more species of this genus occur and remain undescribed in many mountainous areas in mainland China, and possibly in northern Indochina as well. To understand the diversification history of this enigmatic aquatic lacewing group it is critical to recover the phylogeny of *Nipponeurorthus*.

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