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Revision of the genera *Thanmoia* Ramme, 1941 and *Paratoacris* Li & Jin, 1984 (Orthoptera: Acrididae: Oxyinae), with a proposal of a new generic synonym and a new combination

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Abstract. The genera *Thanmoia* Ramme, 1941 and *Paratoacris* Li & Jin, 1984 are revised based on the examination of type specimens of all species. As a result, the genus *Paratoacris* is synonymized with *Thanmoia* and a new combination is proposed: *Thanmoia reticulipennis* (Li & Jin, 1984) comb. nov. All five species are re-described and illustrated. A key to species is provided. *Thanmoia gustavi* Ramme, 1941 is recorded for the first time from China. Distribution patterns of species across Vietnam and China and the phylogenetic position of the genus *Thanmoia* are briefly discussed.

Keywords. Acrididae, Oxyinae, *Thanmoia*, *Paratoacris*, new synonym, new combination, distribution, new records, China, Vietnam.

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Introduction

Thanmoia Ramme, 1941 was established as a monotypic genus in the Oxyinae for *T. gustavi* Ramme, 1941. Hollis (1975) synonymized the genera *Annamacris* Willemse, 1957 and *Oxyacris* Willemse, 1957 with *Thanmoia* and transferred *Annamacris olivacea* Willemse, 1957 and *Oxyacris maculata* Willemse, 1957 (both from Vietnam) into *Thanmoia*. Storozhenko (1992) added a fourth species to *Thanmoia*, i.e., *T. ceracrifucosa* Storozhenko, 1992, based on a single male from Vietnam (Storozhenko 1992). In a recent review of *Thanmoia*, Storozhenko (2022) described the previously unknown female of *T. olivacea* Willemse, 1957, and provided an annotated checklist of the genus. All species of the genus *Thanmoia* were until now considered endemic to Vietnam.

The genus *Paratoacris* Li & Jin, 1984 was established as a monotypic genus for *P. reticulipennis* Li & Jin, 1984. The genus was endemic to China and closely related to *Toacris* (Li & Jin 1984). Except for records of the genus in some local faunas (Zheng 1993; Yin *et al.* 1996; Jiang & Zheng 1998; Li & Xia 2006), only few studies have been carried out on the genus *Paratoacris*. Based on complete mitogenome data, the phylogenetic position of *Paratoacris* was confirmed to lie in the subfamily Oxyinae and not in Catantopinae (Zeng *et al.* 2021). *Paratoacris reticulipennis* was described after a holotype male as well as one male and two female paratypes from the temperate region of Jinxiu, Guangxi in China. Except for the type locality, the species has also been found at an adjacent place, Guposhan, Hezhou, Guangxi, where the material was obtained for sequencing the mitogenome data (Zeng *et al.* 2021).

When studying the material collected in the last few years, it appeared that morphologically *P. reticulipennis* is extremely similar to *T. gustavi* and therefore should be assigned to *Thanmoia*. In this study, a brief revision of the genera *Thanmoia* and *Paratoacris* is made, the genus *Paratoacris* is synonymized with *Thanmoia*, *P. reticulipennis* is transferred to the genus *Thanmoia*, increasing the number of species in *Thanmoia* to five and expanding the distribution of *Thanmoia* from Vietnam to China. An updated key to all the species of the genus *Thanmoia* is presented.

Material and methods

This study is based on types of all species of the genera *Thanmoia* and *Paratoacris* as well as some additional material of *P. reticulipennis*, *T. gustavi* and *T. olivacea*. Photographs of the dried specimens and male genitalia were taken by the first author using a Nikon D600 digital camera or Leica DFC 5500 system, and the images were stacked using Helicon Focus ver. 6.0 (https://www.heliconsoft.com/heliconsoft-products/helicon-focus/). The photos of living individuals of *T. gustavi* were taken in the field by Jianhua Huang, and those of *T. ceracrifucosa* and *T. olivacea* were from iNaturalist (https://www.inaturalist.org/) and taken by Eugene Popov (https://www.inaturalist.org/observations/143176129), Do Ky Minh Hien (https://www.inaturalist.org/observations/166514248), Luan Mai Sy (https://www.inaturalist.org/observations/31116412) and Ober (https://www.inaturalist.org/observations/179127224), respectively. The terminology for morphology follows Uvarov (1966) and Storozhenko *et al.* (2015). The terminology of male genitalia follows Dirsh (1956), Hollis (1971) and Woller & Song (2017).

Abbreviations for morphological terms and measurements

The measurements generally used for grasshoppers are defined as below:

BL = body length, refers to the length from the apex of the fastigium to the apex of the subgenital plate
HFL = hind femur length, refers to the maximum distance from the base of the hind femur to the apex
PL = pronotum length, refers to the length from the anterior margin of the pronotum to the posterior margin
TL = tegmen length, refers to the length from the base of the tegmen to the apex

Institutional abbreviations

CSUFT = Insect collection of Central South University of Forestry & Technology, Changsha, China (curator: Jianhua Huang)
MfN = Museum für Naturkunde Berlin, Berlin, Germany (curator of Orthoptera collections: Birgit Jaenicke)
MNHN = Muséum national d'Histoire naturelle, Paris, France (curator of Orthoptera collections: Laure Desutter-Grandcolas)
NBC = Naturalis Biodiversity Center, Leiden, Netherlands (curator of Orthoptera collections: Luc Willemse)
SEM = Shanghai Entomological Museum, Chinese Academy of Sciences, Shanghai, China (curator: Haisheng Yin)
ZIN = Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia (curator of Orthoptera collections: A.V. Gorochov)

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Orthoptera Olivier, 1789
Superfamily Acridoidea MacLeay, 1821
Family Acrididae MacLeay, 1821
Subfamily Oxyinae Brunner von Wattenwyl, 1893

Genus ***Thanmoia*** Ramme, 1941

Thanmoia Ramme, 1941: 120.
Annamacris Willemse, 1957: 479 (type species: *Annamacris olivacea* Willemse, 1957, by original designation.
Oxyacris Willemse, 1957: 480 (type species: *Oxyacris maculata* Willemse, 1957, by original designation.
Paratoacris Li & Jin, 1984: 197, 203. **Syn. nov.**

Thanmoia – Willemse 1957: 483. — Hollis 1975: 207. — Otte 1995: 124. —Yin *et al.* 1996: 698. — Storozhenko 2022: 2–3.
Annamacris – Hollis 1975: 207 (synonymization).
Oxyacris – Hollis 1975: 207 (synonymization).
Paratoacris – Zheng 1993: 75. — Otte 1995: 326. —Yin *et al.* 1996: 519. — Jiang & Zheng 1998: 81. — Li & Xia 2006: 52. — Zeng *et al.* 2021: 733.

Type species

Thanmoia gustavi Ramme, 1941, by monotypy.

Diagnosis

Body medium-sized. Head shorter than pronotum; fastigium of vertex rounded pentagonal in dorsal view, without median carinula, slightly inclined forwards in lateral view; interocular distance broad, about 1.8–2.0 × as wide as frontal ridge between antennal sockets. Frontal ridge distinct, longitudinally sulcate throughout, with margins almost parallel; face reclinate in profile view; lateral facial keels curved. Eyes large and oval. Antennae filiform, longer than head and pronotum combined. Pronotum rugose or almost smooth, crossed by three transverse furrows, with anterior margin almost straight and posterior margin triangularly rounded; prozona distinctly longer than metazona; median carina vestigial; lateral carina absent; prosternal process conical and slender, with subacute or rounded apex. Mesosternal lobes broad, subsquare or trapezoidal; mesosternal interspace longer than wide. Both tegmina and hind wings fully developed or somewhat shortened; parallel veinlets in radial and median areas of tegmen absent. Hind femora slender, both dorsal and ventral median carinae smooth; ventral genicular lobes of hind knee with distinct apical spine. Hind tibiae apically expanded, outer apical dorsal spine absent or rarely very small. Hind tarsi short, not longer than half of hind tibiae; third segment (excluding claws) as long as two others together; arolium large, reaching apex of claws. Male: tenth abdominal tergite with weak furculae; supra-anal plate triangular, with median basal impression; cerci conical; subgenital plate short. Female: supra-anal plate elongated, triangular, with median basal impression; cerci conical; subgenital plate with triangular pointed apex. Ovipositor long, elongated; dorsal valves dentate only at apical quarter; ventral valves straight and dentate along their full length. Male genitalia: epiphallus bridge-shaped, symmetrical; bridge completely divided; oval sclerite present; valves of cingulum short and almost straight, left and right cingular valves separate, not fused dorso-medially to form a valvular plate to cover apical penis valves dorsolaterally (Fig. 4K) like in *Oxya hyla* Serville, 1831 (the type species of the genus *Oxya* Serville, 1831; see Hollis 1971: figs 6–10) and similar in this aspect to *O. chinensis* (Thunberg, 1815) (see Hollis 1971: figs 193–196); apical valves of penis shorter than valves of cingulum; basal valves of penis connected with apical ones by unbroken flexure.

Distribution

China, Vietnam.

Remarks

The type species of the genera *Thanmoia* and *Paratoacris* are *T. gustavi* and *P. reticulipennis*, respectively. Since *P. reticulipennis* is transferred to the genus *Thanmoia* as a new combination (see the remark under *T. reticulipennis*), the genus *Paratoacris* should accordingly be synonymized with *Thanmoia* according to Articles 23.1 and 23.3 of the Code of Zoological Nomenclature (ICZN 1999).

Composition

The genus consists of five species distributed in South China and Vietnam.

Key to the species of the genus *Thanmoia* Ramme, 1941

1. Hind tibia black 2
– Hind tibia bluish or red 3

2. Hind femur with an indistinct black band near the apex ..... ***T. reticulipennis*** (Li & Jin, 1984) comb. nov.
– Hind femur with a distinct black band near the apex ..... ***T. gustavi*** Ramme, 1941

3. Brachypterous, with tegmina and hind wings only reaching the fourth abdominal tergite; hind tibia and tarsus bluish or light bluish; hind femur without black band on outer surface .... ***T. maculata*** (Willemse, 1957)
– Macropterous, with tegmina and hind wings reaching the apex of the seventh to ninth abdominal tergites; hind tibia and tarsus red; hind femur with black bands on outer surface 4

4. Hind femur with three black bands, outer surface with large black spot near the base; basal part of hind wing bluish; male cercus with shallow excision at apex .. ***T. ceracrifucosa*** Storozhenko, 1992
– Hind femur with two black bands, outer surface without black spot near the base in female, but with a small blackish spot near the base in male; basal part of hind wing hyaline; male cercus with obtuse apex .....***T. olivacea*** Willemse, 1957

Thanmoia ceracrifucosa Storozhenko, 1992
Figs 1A–D, 5

Thanmoia ceracrifucosa Storozhenko, 1992: 27.

Thanmoia ceracrifucosa – Kim & Pham 2014: 57. — Storozhenko 2022: 4.

Type material

Holotype
VIETNAM • ♂; 20 km N of Kannak, Buon Luoi, Gia Lai Province; 21–30 Nov. 1998; A.V. Gorochov leg.; ZIN.

Redescription

Measurements (mm). BL: ♂ 24.5; PL: ♂ 4.7; TL: ♂ 17.6; HFL: ♂ 14.2.

Male
Body. Medium-sized, elongated, finely and more coarsely punctate.

Head. Large, shorter than pronotum; face reclinate in profile view, rugosely punctate; frontal ridge distinct, with lateral margins subparallel and somewhat thickened, percurrent to clypeal margin; lateral facial keels distinct, slightly curved; subocular furrow shallow and distinct; vertex convex; fastigium of vertex broad, not reaching beyond basal antennomere, with anterior margin rounded and obtuse, lateral margins nearly parallel, surface of fastigium somewhat concave and separated from vertex by shallow transverse impression. Antennae filiform, 27-segmented, reaching behind posterior margin of pronotum, with antennomeres elongate. Eyes long oval; interocular distance about twice as broad as basal antennomere; genae rugosely punctate.

Thorax. Pronotum longer than broad, more or less cylindrical with sides almost parallel; anterior margin almost straight, posterior margin triangularly rounded; median keel indistinct; both prozona and metazona punctate, first sulcus present only on disc, second and third both on disc and lateral lobes, second sulcus little before, third sulcus distinctly behind middle of pronotum; prozona 1.6 × as long as metazona, lateral lobe longer than high, central region of lateral lobe rugosely punctate, other parts of lobe coarsely punctate. Prosternal spine conical, nearly straight, with apex obtuse. Mesosternal lobes 1.2 × as broad as long, with interspace narrower than lobe, slightly widened posteriorly; metasternal lobes touching each other in middle.

Wings. Tegmina and hind wings well developed, almost reaching top of hind femur. Tegmen 5.7 × as long as wide, with apex rounded, anterior margin having small basal dilatation; anal vein reaching apical fourth. Wing elongate and relatively narrow, posterior margin slightly undulated.

Legs. Fore and mid legs normal. Hind femur relatively thick, 4.3 × as long as maximal width, with short attenuated apical part; upper median keels smooth, terminating into very small tooth; kneelobes with very sharp and distinct spine. Hind tibia straight, dilated apically, margins obtuse, with 10 inner and 9 outer spines, outer apical spine absent; inner spurs somewhat longer than outer ones. Hind tarsus short, not reaching hind tibia midlength, first joint with dilated margins, second joint distinctly shorter than first one, third joint shorter than two others together.

Genitalia. Supra-anal plate triangular, apex obtuse; disc with median basal sulcus and fine transverse sulcus in middle. Cercus conical, nearly straight, with apex subacute, reaching apex of supra-anal plate. Subgenital plate short, apical margin triangularly rounded.

Coloration. General coloration of male olivaceous green, ventral surface of body yellowish brown. Antennae with first antennomere green and blackish flagellum. Pronotum dark green with black sulci. Tegmen brown, anal area green. Hind wing pale bluish, apex and part of hind margin infumated. Fore and mid legs dark green. Hind femur yellow with three black bands on outer, upper and inner surfaces; knee reddish brown. Hind tibia red with blackish praegenicular ring; tibial spines red with black apex. Hind tarsus reddish.

Female

According to image of one living female (Fig. 1D), females similar to male. General coloration of females documented only with the photo of one living specimen (Fig. 1D), bright olivaceous green.

Distribution

Vietnam (Gia Lai Province).

Remarks

This species is known by a single male only. A photo of a living female is available in the present paper (Fig. 1D); unfortunately, this female has not been collected.

Thanmoia gustavi Ramme, 1941
Figs 1E–M, 4A–K, 5

Thanmoia gustavi Ramme, 1941: 120.

Thanmoia gustavi – Willemse 1957: 484. — Hollis 1975: 208. — Storozhenko 1992: 38; 2022: 4. — Otte 1995: 124. — Yin *et al.* 1996: 698. — Kim & Pham 2014: 57.

Type material

Holotype

VIETNAM • ♀; Than-Moi, Tonkin (former name for Lang Son Province); collecting date unspecified (recorded as "V. u. VI." in Ramme's (1941) original description); H. Fruhstorfer leg.; MfN.

Other material examined

VIETNAM • 1 ♀; Vinh Phuc Province, vicinity of Tam Dao; 900–1000 m a.s.l.; 9–18 Feb. 1990; A.V. Gorochov leg.; ZIN.

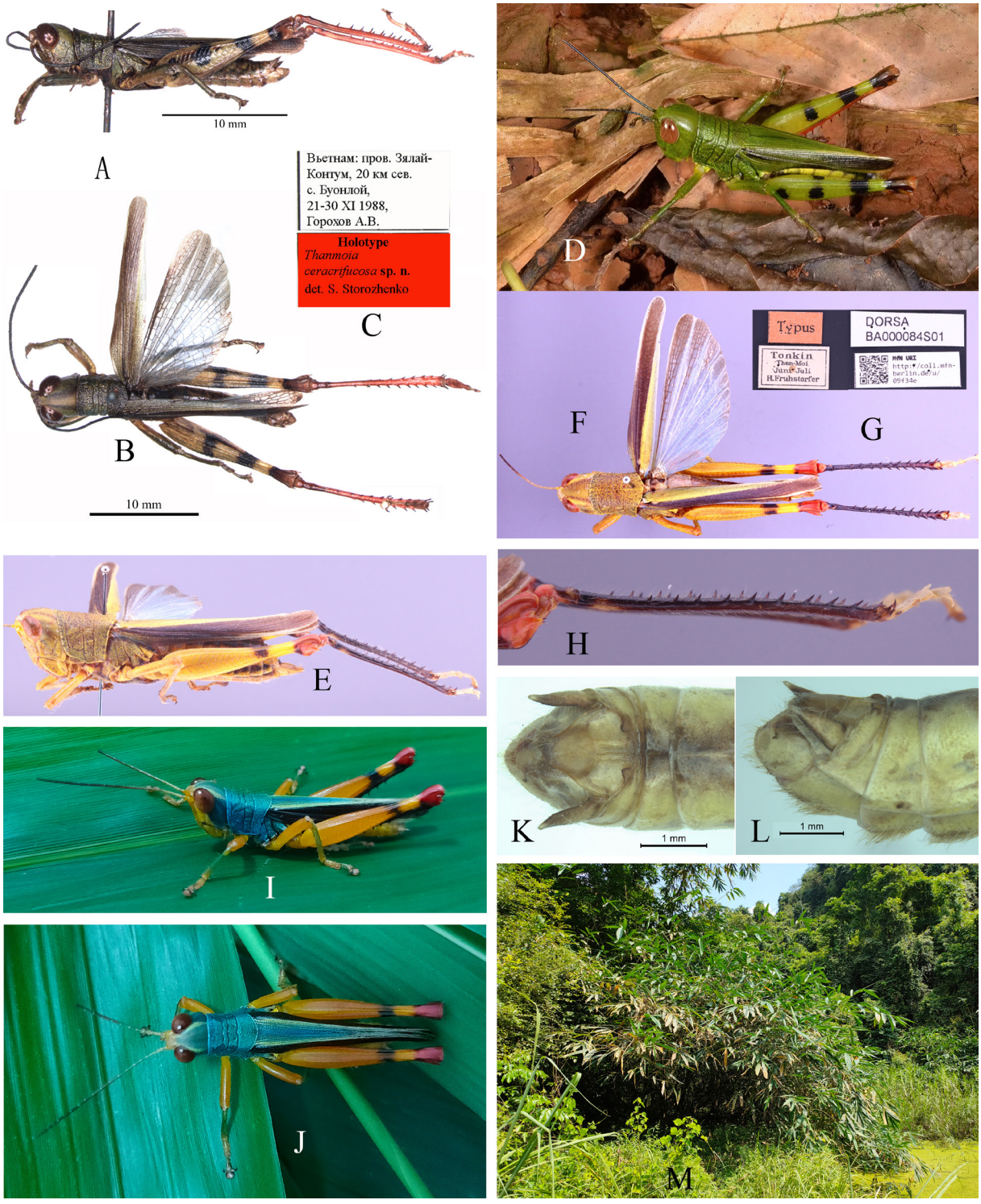

Fig. 1. A–D. *Thanmoia ceracrifucosa* Storozhenko, 1992. **A–C**. Holotype, ♂ (ZIN). **A–B**. Lateral and dorsal views. **C**. Labels. **D**. Living female from Vietnam, dorsolateral view (photo by Eugene Popov). – **E–L**. *T. gustavi* Ramme, 1941. **E–H**. Holotype, ♀ (MfN). **E**. Lateral view. **F**. Dorsal view. **G**. Labels. **H**. Hind tibia. **I–J**. Living male from Longjiang, Nonggang Natural Reserve, Guangxi, China, lateral and dorsal views. **K–L**. Living male, abdominal apex, dorsal and lateral views. **M**. Habitat of *T. gustavi* in Longjiang, Nonggang Natural Reserve, Longzhou, Guangxi, China.

CHINA • 1 ♂; Longjiang, Nonggang, Longzhou County, Guangxi; 22.47519149° N, 106.911604° E; 160 m a.s.l.; 30 Aug. 2024; Jianhua Huang leg.; CSUFT.

Redescription

Measurements (mm). BL: ♂ 24.9–25.6, ♀ 36.8–37.6; PL: ♂ 5.0–5.3, ♀ 8.0–8.2; TL: ♂ 18.3–18.8, ♀ 28.8–29.3; HFL: ♂ 15.1–15.6, ♀ 22.5–22.9.

Male

Body. Medium-sized, robust, finely and more coarsely punctate.

Head. Large, shorter than pronotum; face reclinate in profile view, finely rugosely punctate; frontal ridge very distinct, with lateral margins subparallel and somewhat thickened, percurrent to clypeal margin; lateral facial keels distinct, slightly curved; subocular furrow shallow and distinct; vertex convex; fastigium of vertex broad, not reaching beyond basal antennomere, with anterior margin broadly rounded, lateral margins short and nearly parallel, surface somewhat concave, and separated from vertex by shallow transverse impression. Antennae filiform, reaching behind posterior margin of pronotum, with antennomeres elongate. Eyes long oval; interocular distance twice as broad as basal antennomere; genae finely punctate or almost smooth, except along lower margin where there is rougher sculpturation.

Thorax. Pronotum longer than broad, more or less cylindrical with sides parallel; anterior margin rounded and somewhat thickened, posterior margin triangularly rounded and also somewhat thickened; median keel distinct but low; prozona punctate, metazona more finely punctate, first sulcus present only on disc, second and third both on disc and lateral lobes, second sulcus little before, third sulcus little behind middle; lateral lobe longer than high, lower margin ascending anteriorly from little behind middle and somewhat undulate, posterior part of lower margin practically straight, anterior and posterior margin straight, anterior angle obtusely rounded, posterior angle rectangularly rounded; submarginal sulcus present along anterior margin, indistinct however on disc; upper part of lateral lobe roughly and more finely punctate, with some irregular smooth spots. Prosternal spine conical, almost straight, with apex obtuse. Mesosternal lobes distinctly broader than long, with interspace narrower than the lobe, slightly widened posteriorly; metasternal lobes touching each other in middle.

Wings. Tegmina and hind wings well developed, reaching apex of hind femur. Tegmina with subparallel margins, apex rounded, anterior margin having a small basal dilatation; anal vein reaching apical fourth. Wing elongated and relatively narrow, posterior margin slightly undulated.

Legs. Fore and mid legs normal. Hind femur relatively thick, with short attenuated apical part; upper median keels smooth, terminating into very small tooth; knee lobes with very sharp and distinct spine. Hind tibia straight, somewhat dilated apically, margins obtuse, with 11–12 inner and 9 outer spines, outer apical spine absent; inner spurs somewhat longer than outer ones. Hind tarsus short, not reaching hind tibia midlength, second joint distinctly shorter than first one; third joint shorter than two others together; first joint with dilated margins.

Genitalia. Supra-anal plate triangular, apex obtuse; disc with median basal sulcus and fine transverse sulcus in middle. Cercus conical, almost straight, with apex subacute, reaching apex of supra-anal plate. Subgenital plate short, apical margin triangularly rounded. Epiphallus bridge-shaped, completely divided into two symmetric half, with pair of large and slender outer lophi and small pair of tooth-like inner lophi; ancorae small, apex curved; anterior and posterior projections broadly rounded; oval sclerites elongate. Phallic complex robust; basal valves of penis broad and apodemes long, slightly exceeding basal valves of penis; valves of cingulum short and nearly straight, left and right cingular valves separate,

not fused dorso-medially to form valvular plate to cover apical penis valves dorsolaterally (Fig. 4K); apical valves of penis shorter than valves of cingulum (Fig. 4A–K).

Coloration. General coloration olivaceous green, mixed with yellow. Antennae with basal antennomere yellow, pale green in basal half and brown or blackish brown in apical half. Head with face, mouthparts and lower part of genae yellowish green, antennal sockets yellow, labrum more light brown; vertex with lighter yellowish stripe behind each eye and series of light black spots inside of eyes along with yellow stripes. Pronotum green, mixed with dense dark green spots. Epimerum of meso- and metathorax green. Tegmen brown, anal area yellowish green, apical half of anterior margin and apical margin narrowly marginated with pale whitish band. Hind wing pale bluish, apex and part of hind margin infumate. Fore and mid legs yellow. Hind femur yellow, with incomplete blackish brown praegenicular ring; knee bright red, with black maculation at base; spine of knee lobe yellow with black tip. Hind tibia black with red condylus, sign of yellowish praegenicular ring at ventral surface of base, and somewhat more brownish black at apex; tibial spines black. Hind tarsus light olivaceous green or whitish. Sternum yellow with brownish longitudinal stripe on both sides; abdomen yellow, with dark brown band dorsally and on both sides.

Female

Similar to male, body slightly more robust. Valves of ovipositor straight, lamelliform, narrowed near apex, with upper and lower margins of lower valves finely dentate, and apex rounded truncate. Subgenital plate longer than broad, margins subparallel, posterior margin triangularly produced in middle. Ovipositor yellow.

Distribution

Vietnam (Lang Son and Vinh Phuc provinces), China (Longzhou County, Guangxi).

Remarks

This species is recorded for the first time from China. Apart from the holotype specimen, there is a female paratype deposited in the Natural History Museum Vienna and a male and two females from the type locality deposited in the National Museum of Natural Science, Madrid (Hollis 1975). The general coloration of the male individual collected in Longzhou, Guangxi, China is bright bluish and perfectly shows the intraspecific variation of this species in coloration.

Thanmoia maculata (Willemse, 1957)
Figs 2A–F, 5

Oxyacris maculata Willemse, 1957: 481.

Thanmoia maculata – Hollis 1975: 208. — Otte 1995:124. — Kim & Pham 2014: 57. — Storozhenko 2022: 4.

Type material

Holotype

VIETNAM • ♂; Nha Trang, Song Man; 1913; A. Krempf leg.; NBC.

Redescription

Measurements (mm). BL: ♂ 20.0; PL: ♂ 4.0; TL: ♂ 5.0; HFL: ♂ 13.5.

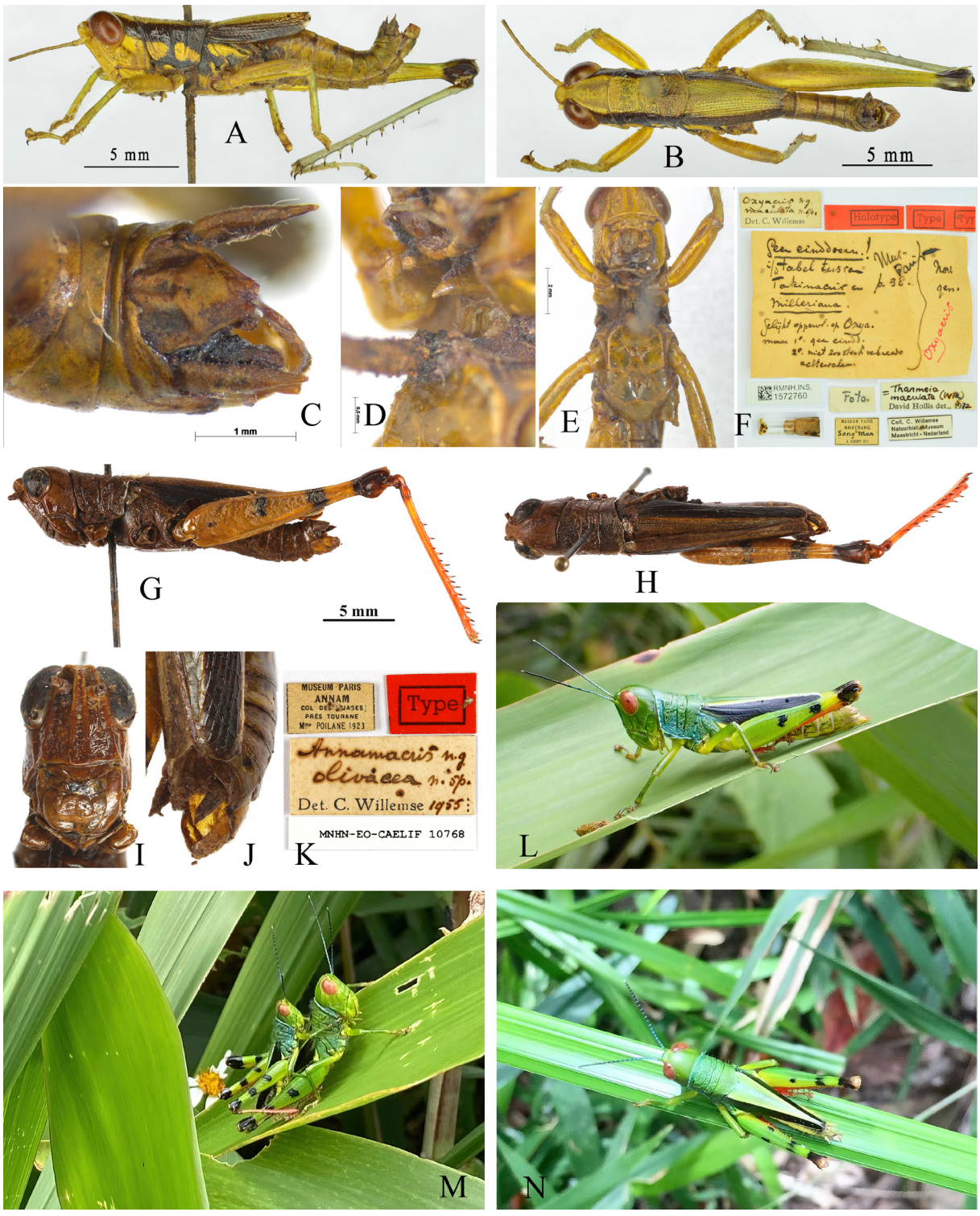

Fig. 2. A–F. *Thanmoia maculata* (Willemse, 1957), holotype, ♂ (NBC). **A**. Lateral view. **B**. Dorsal view. **C**. Abdominal apex, dorsolateral view. **D**. Prosternal process, ventrolateral view. **E**. Head and thorax, ventral view. **F**. Labels. – **G–N**. *T. olivacea* (Willemse, 1957). **G–K**. Holotype, ♂ (MNHN). **G**. Lateral view. **H**. Dorsal view. **I**. Head, frontal view. **J**. Abdominal apex, dorsolateral view. **K**. Labels. **L, N**. Living females from Vietnam, lateral and dorsal views (photos by Đỗ Kỳ Minh Hiển and Luan Mai Sy, respectively). **M**. Living copulating pair from Vietnam, lateral view (photo by Ober).

Male

Body. Medium-sized, slender, finely rugosely punctate.

Head. Frons reclinate and straight in profile view; frontal ridge distinct, percurrent to clypeal margin, with lateral margins parallel; lateral facial keels distinct and straight; vertex almost horizontal in profile view, dorsum smooth in the middle; fastigium of vertex inclined forwards, reaching little beyond eyes, separated from vertex by shallow impression, with anterior margin rounded, surface somewhat depress and finely rugose. Interocular distance about as broad as basal antennomeres. Antennae filiform, reaching base of hind femur, with antennomeres elongate. Eyes long oval, somewhat globose.

Thorax. Pronotum cylindrical, somewhat longer than head, with anterior margin rounded and posterior margin more triangularly rounded; disc finely rugosely punctured; median keel very low, somewhat indistinct, interrupted by transverse sulci; lateral keel absent; submarginal sulcus present only on lateral lobe, first transverse sulcus present only on disc, second and third transverse sulci present both on disc and lateral lobes, third transverse sulcus located far behind the middle; lateral lobe longer than high, coarsely punctured except for metazonal part, with some irregular smooth areas in upper part, lower margin from middle ascendant anteriorly and somewhat concave, anterior angle obtusely rounded, posterior angle rectangularly rounded, anterior margin straight, posterior margin almost straight. Prosternal spine conical with apex pointed; mesosternal lobes about as long as broad with inner margin rounded and interspace narrower than lobe; metasternal lobes contiguous near middle.

Wings. Tegmina short, only reaching little beyond base of hind femur, touching each other in middle, with margins gradually narrowing apically, apex rounded; hind wings very small, vestigial.

Legs. Fore and mid legs normal. Hind femur only slightly attenuated, not compressed, with upper median keel smooth, terminating into sharp tooth; lower knee lobes sharply pointed. Hind tibia slightly expanded apically, margins sharp, with 10 inner and 7 outer spines, outer apical spine absent. Hind tarsus short, with second joint much shorter than first one. Posterior margin of penultimate abdominal tergite interrupted in the middle, with small furcula on both sides.

Genitalia. Supra-anal plate triangular, with apex subacute, small median sulcus at base and depression on both sides of this sulcus. Cercus conical, broad at base and pointed at apex, reaching beyond supra-anal plate. Subgenital plate short, apical margin triangularly pointed.

Coloration. General coloration yellow with green. Antennae with basal joints light olivaceous green, darker and brownish black from middle to apex. Face and mouthparts yellow; vertex greenish; postocular band black, continued along sides of pronotum to tegmen; genae with distinct clear yellow spot below postocular band, and short blackish streak below eye; lower part of genae greenish yellow. Pronotum with greenish disc, narrow yellow stripe on both sides bordering from above black postocular band; lateral lobe black, with two irregular large yellow spots below postocular band, and first of these spots occupying anterior angle of lateral lobe, remaining part of lower margin black. Epimerum of pro-, meso- and metathorax black with small yellow spot. Sternum yellowish. Tegmina black, with anal area greenish. Fore and mid legs with yellow femora, tibiae light olivaceous green, tarsi from below somewhat reddish. Hind femur yellow, outer area somewhat greenish, knee blackish brown, knee lobes bluish. Hind tibia bluish, spines with black tips. Hind tarsus light bluish. Abdomen yellowish brown, with dark stripe on both sides.

Female

Unknown.

Distribution

Vietnam (Khanh Hoa Province).

Remarks

This species is known only from a single male.

Thanmoia olivacea (Willemse, 1957)
Figs 2G–N, 5

Annamacris olivacea Willemse, 1957: 480.

Thanmoia olivacea – Hollis 1975: 208. — Otte 1995: 124. — Kim & Pham 2014: 57. — Storozhenko 2022: 6.

Type material

Holotype

VIETNAM • ♂; Annam, Col des Nuages, near Tourane; 1923; Mme Poilane leg.; MNHN.

Other material examined

VIETNAM • 1 ♀; Bach Ma National Park, Hua Thien Hue Province; 22–23 Sep. 2008; V.G. Bezborodov leg.; ZIN.

Redescription

Measurements (mm). BL: ♂ 24.0, ♀ 29.8; PL: ♂ 5.0, ♀ 7.0; TL: ♂ 13.0, ♀ 17.0; HFL: 15.5, ♀ 18.5.

Male

Body. Medium-sized.

Head. Elongated in frontal view, somewhat rugose; frontal ridge narrow, complete, almost reaching clypeus. Face in lateral view reclinate; frontal ridge almost straight. Eyes large, oval; vertical diameter of eye 1.7 × as long as subocular furrow. Antennae filiform, surpassing posterior margin of pronotum.

Thorax. Pronotum long, somewhat rugose, crossed by three transverse furrows; prozona 1.6 × as long as metazona. Mesosternal lobes subsquare, 1.3 × as wide as long; mesosternal interspace narrow, 2.5 × as broad as long.

Wings. Tegmina touching each other in resting position, reaching 9th abdominal tergite, with rounded apex. Hind wings in resting position as long as tegmina.

Legs. Hind femora slender, 4.8 × as long as their maximal width. Hind tibiae with 8 outer and 9 inner dorsal spines including very small outer apical spine. Tympanum large, oval.

Genitalia. Supra-anal plate triangle, elongate; median longitudinal sulcus shallow. Cerci conical with pointed apex, exceeding apex of supra-anal plate. Subgenital plate triangular in dorsal view with apex bluntly rounded.

Coloration. Body olivaceous green. Face and genae olivaceous brown, anterior margin of clypeus blackish. Vertex dark olivaceous green. Pronotum with general coloration. Sternum yellowish brown. Antennae black. Tegmen blackish brown; anterior margin at base and at apex more or less hyaline,

anal area green, with olivaceous green stripe along upper (posterior) margin and narrow yellow stripe between black and green parts. Hind wing hyaline, apex and posterior margin infumated. Fore and mid legs olivaceous yellow or green. Hind femur yellow with black praegenicular ring; outer surface with blackish spot near middle continuing on upper area and part of inner area, sometimes with small blackish spot near base in male but absent in female; knee black, with ventral genicular lobes yellowish green or reddish brown, spines of knee lobes reddish brown. Hind tibia red, with two small black spots at base, spines red with black tips. Hind tarsus red or yellowish red. Abdomen yellowish brown; tergites yellow with black marks.

Female

Similar to male, but body larger in size. Eyes with vertical diameter 1.2 × as long as subocular furrow. Antennae 26-segmented, prozona 1.8 × as long as metazona. Mesosternal lobes 1.1 × as wide as long; mesosternal interspace 2.7 × as wide as long. Hind femora 4.4 × as long as their maximal width. Subgenital plate elongated with posterior margin triangular. Dorsal valves of ovipositor as long as lower ones. Ovipositor greenish brown.

Distribution

Vietnam (Thien Hue Province).

Thanmoia reticulipennis (Li & Jin, 1984) comb. nov.
Figs 3A–R, 4L–Q, 5

Paratoacris reticulipennis Li & Jin, 1984: 198, 203.

Paratoacris reticulipennis – Zheng 1993: 75. — Otte 1995: 326. — Jiang & Zheng 1998: 81. — Li & Xia 2006: 53.

Type material

Holotype

CHINA • ♂; Dayao Mountains, Jinxiu County, Guangxi Province; 17 Sep. 1981; Tianshan Li leg.; 14523515; SEM.

Paratype

CHINA • 1 ♀; Guanyin Mountains, Jinxiu County, Guangxi Province; 900 m a.s.l.; 18 Sep. 1981; Gentao Jin and Fuliang Li leg.; 14514001; SEM.

Other material examined

CHINA • 1 ♀; Hekou, Jinxiu County, Guangxi Province; 600 m a.s.l.; 12 Jun. 2006; Jianhua Huang leg.; CSUFT • 1 ♀; Hekou, Dayaoshan, Jinxiu County, Guangxi Province; 545 m a.s.l.; 24 Sep. 2011; Ruigang Yang leg.; CSUFT • 1 ♂; Jinxiu County, Guangxi Province; 16 Sep. 2021; Chunfu Feng leg.; private collection of Jin-Chen Yang • 1 ♀; Jinxiu County, Guangxi Province; 31 Jul. 2022; Chunfu Feng leg.; private collection of Jin-Chen Yang • 1 ♂; Guposhan, Hezhou City, Guangxi Province; 1000 m a.s.l.; 11 Jul. 2009; Tailin Yu leg.; CSUFT • 1 ♀; Guposhan, Hezhou City, Guangxi Province; 29 Jul. 2013; Guohao Lin leg.; CSUFT • 1 ♀; Jinshi Town, Xing'an County, Guangxi Province; 1000 m a.s.l.; 20 Aug. 2000; Jianhua Huang leg. CSUFT • 1 ♀; Jinshi Town, Xing'an County, Guangxi Province; 29 Aug. 2000; Jianhua Huang leg.; CSUFT • 2 ♂♂, 1 ♀; Heishiding, Fengkai County, Zhaoqing City, Guangdong Province; 8 Jul. 2014; Chengli Liu leg.; CSUFT • 2 ♀♀; Gudoushan, Beifengshan Forest Park, Taishan City, Guangdong Province; 22.224968° N, 112.968806° E; 16 Jul. 2024; Wenqing Lv leg.;

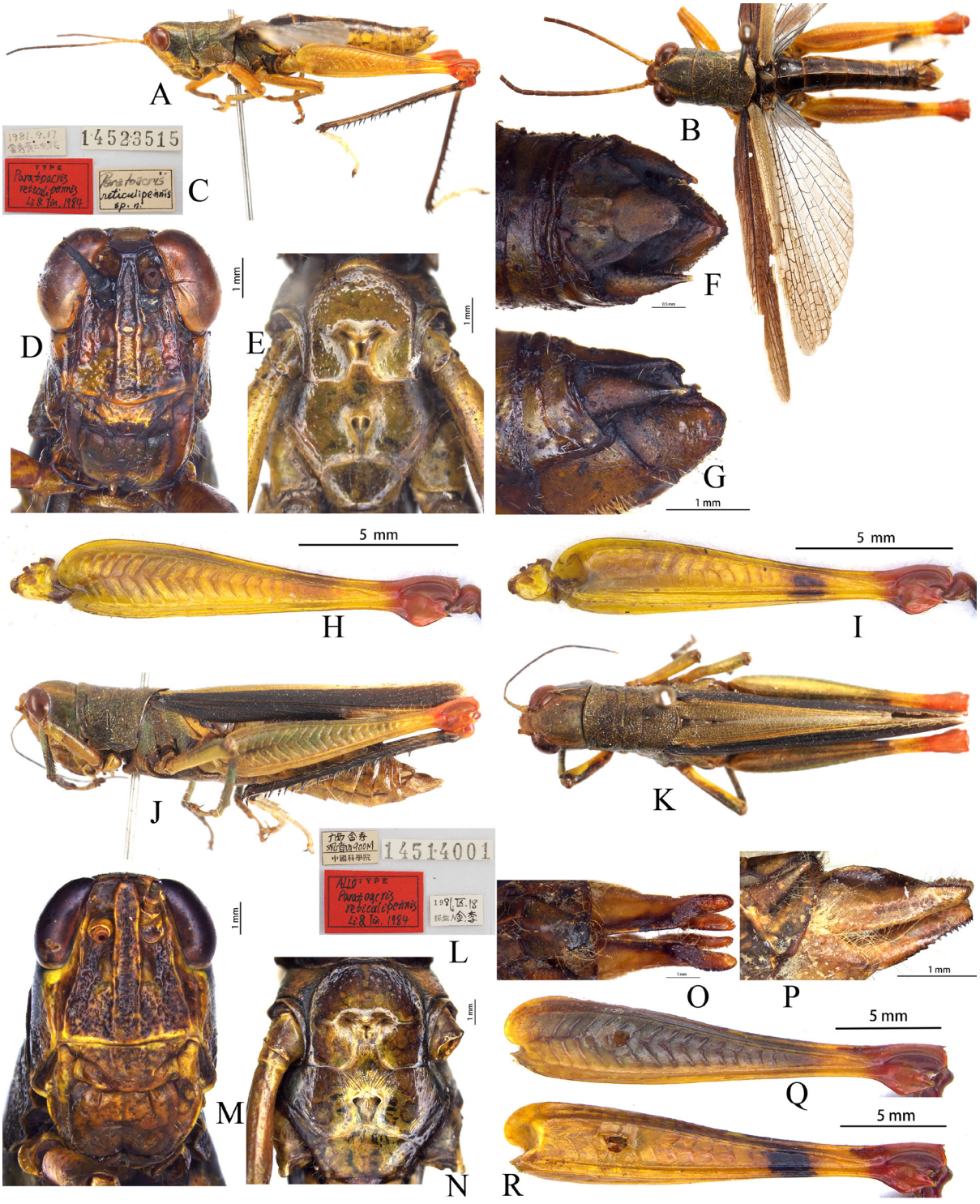

Fig. 3. *Thanmoia reticulipennis* (Li & Jin, 1984) comb. nov. **A–I**. *Paratoacris reticulipennis*, holotype, ♂ (14523515; SEM). **A**. Lateral view. **B**. Dorsal view. **C**. Labels. **D**. Head, frontal view. **E**. Meso- and metasterna, ventral view. **F**. Abdominal apex, dorsal view. **G**. Same, lateral view. **H**. Outer surface of hind femur. **I**. Inner surface of hind femur. **J–R**. *P. reticulipennis*, paratype, ♀ (14514001; SEM). **J**. Lateral view. **K**. Dorsal view. **L**. Labels. **M**. Head, frontal view. **N**. Meso- and metasterna, ventral view. **O**. Abdominal apex, dorsal view. **P**. Same, lateral view. **Q**. Outer surface of hind femur. **R**. Inner surface of hind femur.

CSUFT • 1 ♀; Dajiangyuan, Dupangling Nature Reserve, Daoxian County, Hunan Province; 17 Aug. 2019; Xiang Zeng leg.; CSUFT.

Redescription

Measurements (mm). BL: ♂ 25.0–26.0, ♀ 31.6–36.5; PL: ♂ 5.0–5.4, ♀ 7.0–8.0; TL: ♂ 18.0–18.9, ♀ 20.0–24; HFL: ♂ 14.5–15.7, ♀ 15.0–19.8.

Male

Body. Medium-sized.

Head. Punctured and rugose, large but shorter than pronotum. Fastigium obtuse rounded, median keel indistinct, lateral foveola absent. Face oblique in profile view; fontal ridge distinct, longitudinally sulcate throughout, with lateral margin nearly parallel; lateral facial keels curved. Interocular distance broad, twice as broad as frontal ridge between antennal sockets. Eyes oval, with longitudinal diameter about 1.5 × as long as horizontal diameter. Antennae filiform, slightly exceeding base of hind femora; length of median joints about 4 × as long as width.

Thorax. Pronotum punctured and rugose, cylindrical, with anterior margin curved, posterior margin obtusely rounded; median keel and three transversal sulci distinct, lateral keel absent; prozona about 1.6 × as long as metazona. Lateral lobe of pronotum with posterior margin oblique backward, posterior and lower margin undulated. Prosternal spine conical with sharp apex. Interspace of mesosternal lobes narrow, with its length 3 × its minimum width; lateral lobes of metasternum contiguous with each other posteriorly. Tegmina and hind wings well developed.

Wings. Tegmina subcoriaceous, exceeding abdominal apex, not reaching apex of hind femur, without parallel veinlets in radial and median areas.

Legs. Hind femora slender, with upper median keels smooth and spined at apex; lower knee lobes with apical spine. Hind tibia without or with extremely small outer apical spine.

Genitalia. Terminal abdominal tergite with pair of small furculae in middle of posterior margin. Supra-anal plate triangular, with short longitudinal sulcus in middle. Cerci conical. Subgenital plate short and conical, apex slightly obtuse. Epiphallus bridge-shaped, completely divided into two symmetric half, with pair of large and slender outer lophi and small pair of tooth-like inner lophi; ancorae small, apex curved; anterior and posterior projections broadly rounded; oval sclerites elongate. Phallic complex robust; basal valves of penis broad and apodemes long, slightly exceeding basal valves of penis; valves of cingulum short and nearly straight, left and right cingular valves separate, not fused dorso-medially to form valvular plate to cover apical penis valves dorsolaterally; apical valves of penis shorter than valves of cingulum.

Coloration. Body greenish brown variegated with yellow, or bright blue in some fresh individuals. Head greenish brown and frons yellowish brown. Eyes brown. Occiput with pair of fine yellow longitudinal stripes. Antennae yellowish brown in base, pale yellow apically and remaining section gradually becoming black. Pronotum greenish brown. Tegmina almost opaque, anal area yellow, and rest part dark brown. Hind wings pellucid, with base dusty blue, outer margin brown. Hind femora yellow, with distinct black patch on inner surface near knees and indistinct black maculation on outer surface near knees; knees red. Hind tibiae dark brown; tarsi yellowish. Abdomen with dorsum dark brown, with dark brown maculation in lateral, and rest yellow.

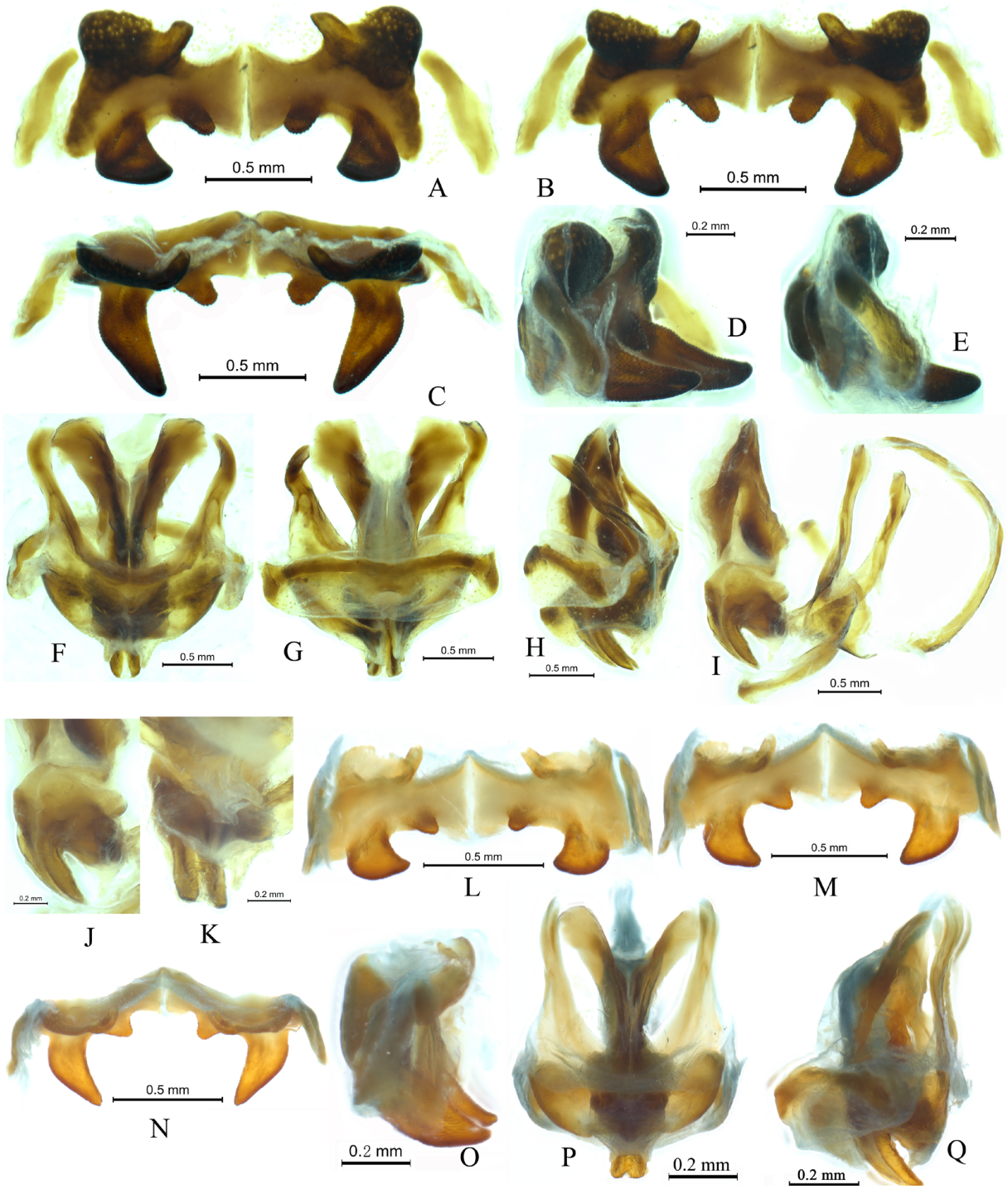

Fig. 4. Male genitalia. **A–K**. *Thanmoia gustavi* Ramme, 1941 (CSUFT). **A–E**. Epihallus, dorsal, dorsofrontal, frontal, dorsolateral and lateral views, respectively. **F–K**. Phallic complex, dorsal, ventral and lateral views, respectively. – **L–Q**. *T. reticulipennis* (Li & Jin, 1984) comb. nov. **L–O**. Epiphallus, dorsal, dorsofrontal, frontal and lateral views, respectively. **P–Q**. Phallic complex, dorsal and lateral views, respectively.

Female

Similar to male but larger and more stout. Antennae exceeding posterior margin of pronotum but not reaching base of hind femora. Metasternum with lateral lobes separate from each other. Ovipositor valves long and slender; dorsal valves ensiform, with serration in upper margin of apex; ventral valves falciform, with serration throughout lower margin. Other features same as males.

Distribution

China (Guangxi, Guangdong, Hunan).

Remarks

In terms of external morphology, *P. reticulipennis* is very similar to *T. gustavi* except for the black patch on the outer surface near the knee, which is distinct in *T. gustavi* but indistinct or even absent sometimes in *P. reticulipennis*. Since *P. reticulipennis* completely agrees with the generic diagnosis of the genus *Thanmoia*, we transfer *P. reticulipennis* from *Paratoacris* to *Thanmoia* as a new combination, *T. reticulipennis* (Li & Jin, 1984) **comb. nov.**

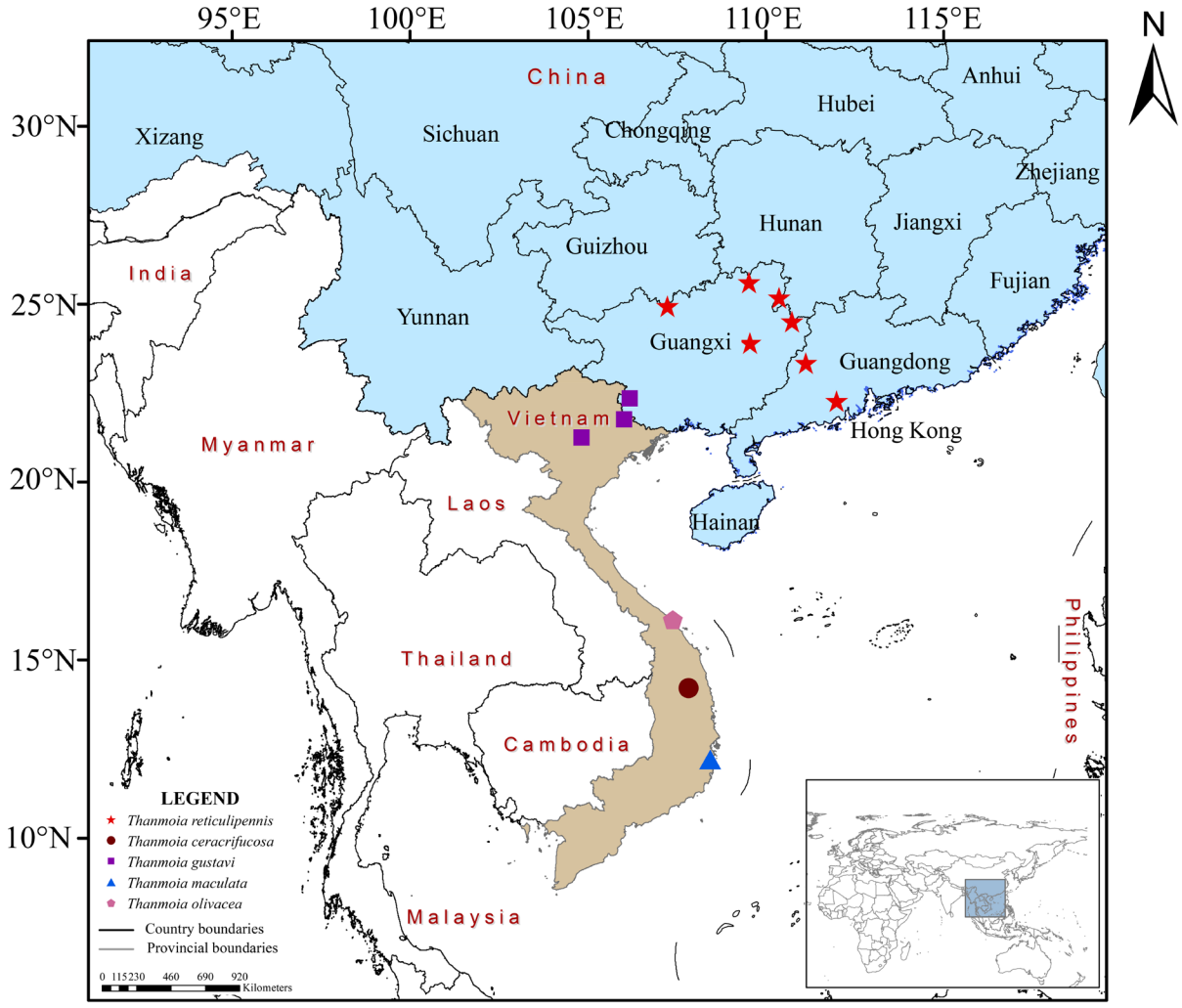

Fig. 5. Distribution map of the species in the genus *Thanmoia* Ramme, 1941. The ground map is downloaded from the website GADM (https://gadm.org/index.html), a data base freely available for academic use and other non-commercial use.

Discussion

Distribution pattern of the species of the genus *Thanmoia* Ramme, 1941

Up to now, five species have been assigned to the genus *Thanmoia*, distributed from the central part of South Vietnam to Southeastern China (Fig. 5). All five species are known by a few specimens, which could mean that the population size in all species of the genus *Thanmoia* may be small, making it difficult to find them in the field, or that their ecological requirements are not known today. This results in an extremely low number of records for all species, especially for *T. ceracrifucosa* and *T. maculata*, both of which are only known from the holotype male so far (Storozhenko 2022). The distribution patterns of the five *Thanmoia* species are mutually exclusive (Fig. 5). *Thanmoia ceracrifucosa*, *T. maculata* and *T. olivacea* are found in Central Vietnam, *T. gustavi* in North Vietnam and South China near the boundary between China and Vietnam, and *T. reticulipennis* occurs in south and east Guangdong, central and north Guangxi as well as south Hunan, China. No distributional overlap occurs between any of the species.

Where did the genus originate? How did such a disjunct distributional pattern evolve? Disjunct distribution has been recorded in alpine groups distributed in temperate regions, such as *Stenobothrus cotticus* Kruseman & Jeekel, 1967 found in the southwestern Alps and southwestern Bulgaria (Berger *et al.* 2010), the species of *Podisma* Berhold, 1827 from the Iberian Peninsula (Ortego *et al.* 2022) and the narrow-endemic Iberian species of *Omocestus* Bolivar, 1878 (Tonzo & Ortego 2021). The present highly fragmented distribution of the alpine and montane species is thought to derive from the range shifts caused by cyclic climatic oscillations during the Pleistocene. A warming climate leads to shifts in distribution ranges to higher latitudes and altitudes. Consequently, cold-adapted alpine species can be trapped in interglacial Holocene refugia on high mountain summits if they fail to expand their ranges to the north (Berger *et al.* 2010). However, as the species of *Thanmoia* occur at low altitudes in tropical or subtropical regions, their disjunct distribution seems difficult to be explained using the hypothesis of range shifts shown by alpine and montane species. The hypothesis of ecological speciation in the tropics may provide an alternative explanation for species diversification in tropics, unless the present distribution pattern reflects only the lack of distribution knowledge about these species. Ecologically mediated selection contributes to genetic divergence both in the presence or absence of geographic isolation between populations and is considered an important driver of speciation (Beheregaray *et al.* 2015). In addition, many of the warm temperate and tropical Oxyinae are associated with wet forest environments. Therefore, there is another possibility that the present day disjunct distribution of species of *Thanmoia* might be largely explained by historical deforestation and loss of habitat. To unveil the mechanism of speciation in the genus *Thanmoia*, accurate estimates of the time for species divergence based on molecular evidence is needed.

Phylogenetic position of the genus *Thanmoia* Ramme, 1941

Robust phylogeny is fundamental to evolutionary research. While the females of *Thanmoia* share the specific ornamentation of the ovipositor valves with representatives of the subfamily Incolacridinae Tinkham, 1940, which is assumed to point to a similar substrate for oviposition rather than phylogenetic relationship (Storozhenko 2021), the genus *Thanmoia* undoubtedly belongs to the tribe Oxyini of the subfamily Oxyinae Brunner von Wattenwyl, 1893 (Acrididae) based on the symmetrical male genitalia with completely divided epiphallus, the conical prosternal spine, the narrow mesosternal interspace, the smooth dorsal and ventral median carinae of the hind femora, the distinct spine on the ventral genicular lobes of the hind knee, the hind tibiae being expanded apically, and the outer apical dorsal spine of the hind tibiae being absent or very small (Storozhenko 2022). However, the relationship of *Thanmoia* with other members of the subfamily Oxyinae and the phylogeny of the species within *Thanmoia* are still unknown. The only molecular data of the genus *Thanmoia* for the moment is the complete mitogenome of *T. reticulipennis* (Zeng *et al.* 2021). The phylogenetic reconstruction based on this complete mitogenome data shows that *Thanmoia* has its closest relationship with the genera *Fer* Bolivar, 1918 and *Oxytauchira*

Table 1. Mitogenomes of the subfamily Oxyinae available in NCBI so far.

Species	Accession number	Reference
Caryanda neoelegans Otte, 1995	NC_036750 (= MF095791)	Yuan *et al.* (2019)
C. xinpingensis Hu *et al.* (2017)	NC_030165 (= KU375571)	Hu *et al.* (2017)
Caryandoides hunanica Zeng et al. (2021)	NC_053659 (= MT916718)	Zeng *et al.* (2021)
Fer nigripennis Zheng & Xie, 2007	NC_053658 (= MT916717)	Zeng *et al.* (2021)
Gesonula punctifrons (Stål, 1861)	PP157623, NC_046411(= MN046214)	Hou & Li (2024); Chang *et al.* (2020a)
Lemba yunnana Ma & Zheng, 1994	OQ270623	Sun *et al.* (2023)
Longchuanacris curvifurculus Mao, Ren & Ou, 2007	NC_036994(= MF989227)	Hu *et al.* (2018)
L. macrofurcula Zheng & Fu, 1989	OQ270621	Sun *et al.* (2023)
Oxya adentata Willemse, 1925	MK903571	Chang *et al.* (2020b)
O. agavisa Tsai, 1931	NC_045883 (= MH718849)	Li *et al.* (2020)
O. chinensis (Thunberg, 1815)	NC_010219 (= EF437157)	Zhang & Huang (2008)
O. hainanensis Bi, 1986	NC_045928 (= MH718848), MN083185	Li *et al.* (2020); Chang *et al.* (2020a)
O. hyla Serville, 1831	NC_032076 (= KX673203)	Song *et al.* (2016)
O. intricata (Stål, 1861)	KP313875	Dong *et al.* (2016)
O. japonica (Thunberg, 1815)	NC_043773 (= MF125299)	Li *et al.* (2020)
O. ningpoensis Chang, 1934	OQ205199	Sun *et al.* (2023)
Oxytauchira aurora (Brunner von Wattenwyl, 1893)	OQ270618	Sun *et al.* (2023)
Oxytauchira brachyptera Zheng, 1981	NC_046570 (= MN046216), MT916721	Chang *et al.* (2020a); Zeng *et al.* (2021)
Oxytauchira flange Mao, Ren & Ou, 2011	NC_053745 (= MT920116)	Zeng *et al.* (2021)
Oxytauchira ruficornis (Huang, 1985)	NC_080529 (= OQ282993)	Sun *et al.* (2023)
Thanmoia reticulipennis (Li & Jin, 1984) comb. nov.	NC_053660 (= MT916720)	Zeng *et al.* (2021)
Pseudoxya diminuta (Walker, 1871)	NC_025765 (= KM244694)	Tang et al. (2014)

Ramme, 1941 (Zeng *et al.* 2021). However, in contrast with the 230 valid species belonging to 38 genera of the subfamily Oxyinae (Cigliano *et al.* 2024), this phylogeny was reconstructed using a very limited sampling strategy in which only 8 genera and 11 species were involved. At present, 25 mitogenomes representing 10 genera and 22 species of the subfamily Oxyinae are available in NCBI (Table 1), and more will be sequenced and uploaded in the near future. We believe that, with the addition of more genera and species into the phylogenetic inference, the topology of the phylogenetic tree will certainly more and more approach the actual phylogeny of the subfamily Oxyinae.

Species of the genus *Thanmoia* exhibit a slightly abundant diversity in several morphological characters. For example, the color of the hind tibiae is reddish in *T. ceracrifucosa* and *T. olivacea*, bluish in *T. maculata*, and black in *T. reticulipennis* and *T. gustavi*, the tegmen is fully developed in *T. gustavi*, *T. ceracrifucosa* and *T. reticulipennis* (macropterous), but slightly shortened in *T. olivacea*, and distinctly reduced in *T. maculata* (brachypterous), the outer surface of the hind femur has three black dots (including the praegenicular ring) in *T. ceracrifucosa*, only two black dots in *T. olivacea*, only the praegenicular ring in *T. gustavi* and *T. reticulipennis*, but no maculation in *T. maculata*. How did these characters evolve in the genus *Thanmoia*? The evolutionary mechanism of these morphological characters in *Thanmoia* will be elucidated only if a robust phylogeny of the genus is reconstructed.

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