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Review of the Oriental stick insect genus *Trachythorax* Redtenbacher, 1908 with two new species from Vietnam and comments on egg parasitism and morphological counteradaptations (Phasmida, Lonchodidae, Necrosciinae)

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Front cover: left: *Trachythorax albomaculatus* sp. nov., right: *Trachythorax auranticollis* sp. nov.
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Review of the Oriental stick insect genus *Trachythorax* Redtenbacher, 1908 with two new species from Vietnam and comments on egg parasitism and morphological counteradaptations (Phasmida, Lonchodidae, Necrosciinae)

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Abstract

The Oriental stick insect genus *Trachythorax* Redtenbacher, 1908 is diagnosed, compared to closely related taxa, and reviewed based on examination of type material, collection material and photographic records, including citizen science sourced data. Each species is discussed and two new species are described from Vietnam: *T. albomaculatus* sp. nov. from Kon Chu Rang National Park in Central Vietnam and *T. auranticollis* sp. nov. from Dong Nai Biosphere Reserve in Southern Vietnam. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov. is elevated to valid species, from status of subspecies of *T. maculicollis* (Westwood, 1848). *Trachythorax illaes* (Redtenbacher, 1908) stat. rev. comb. nov. is reinstated as a valid species from previous status of junior synonym of *T. maculicollis*. As a result the genus *Trachythorax* now contains 15 species. New distribution records are provided for several species including new country records: Thailand and Myanmar for *T. gohi* Brock, 1999, Sri Lanka for *T. illaes* Redtenbacher, 1908, Cambodia for *T. maculicollis*, India for *T. sparaxes* (Westwood, 1859) as well as Laos, Thailand, and Vietnam for *T. yunnanensis*. Distribution maps are provided for *T. albomaculatus* sp. nov., *T. auranticollis* sp. nov., *T. gohi*, *T. maculicollis* and *T. yunnanensis*. Egg morphology and egg deposition are described, discussed and illustrated for *T. maculicollis*, *T. albomaculatus*, *T. yunnanensis* and *T. illaes*, the three latter species for the first time. Morphological adaptations of eggs are compared to those observed in other closely related genera such as *Asceles* Redtenbacher, 1908, *Calvisia* Stål, 1875, *Korinnis* Günther, 1932, *Loxopsis* Westwood, 1859, *Marmessoidea* Brunner von Wattenwyl, 1893, *Sipyloidea* Brunner von Wattenwyl, 1893 and *Tagesoidea* Redtenbacher, 1908, and egg parasitism is hypothesized as a potential evolutionary driver. Egg parasitism by Hymenoptera: Chalcidoidea is documented for the first time in nature for *T. maculicollis* and *T. illaes*; it is hypothesized that several morphological characters are counteradaptations to the egg parasitism.

Keywords: Chalcidoidea, Global Taxonomy Initiative, ooparasitism, ootaxonomy, Phasmatodea

Introduction

The genus *Trachythorax* Redtenbacher, 1908 was described by REDTENBACHER (1908) to accommodate seven species: four that he described therein, *T. expallescens* Redtenbacher, 1908, *T. incertus* Redtenbacher, 1908, *T. planiceps* Redtenbacher, 1908 and *T. unicolor* Redtenbacher, 1908, as well as *Calvisia atrosignata* Brunner von Wattenwyl, 1893, *Phasma (Necroscia) maculicollis* Westwood, 1848 and *Necroscia sparaxes* Westwood, 1859. *Trachythorax* is distributed in Southeast Asia and currently comprises 11 species (BROCK *et al.*,

2021). *Trachythorax* is placed in the subfamily Necrosciinae Brunner von Wattenwyl, 1893 (family Lonchodidae Brunner von Wattenwyl, 1893) which contains 106 genera (BROCK *et al.*, 2021). Recent phylogenetic studies based on molecular data or oviposition technique have placed *Trachythorax* in a lineage together with *Korinnis* Günther, 1932, *Asceles* Redtenbacher, 1908, *Sipyloidea* Redtenbacher, 1893, *Diesbachia* Redtenbacher, 1908 and allies (BRADLER *et al.*, 2014; ROBERTSON *et al.*, 2018). The genus is characterized by the short tegmina and long alae (all species are capable of sustained flight), the strong sexual dimorphism with dwarfed males and the brightly coloured membrane between the pronotum and head (REDTENBACHER, 1908; GAO & LIANG, 2021). The eggs are adhesive and deposited in clusters; in most species, the capsule surface layer peels back except for the micropylar plate region, to form extensions radiating from the opercular collar (CLARCK-SELLICK, 1997). The eggs of *Trachythorax maculicollis* (Westwood, 1848) have been figured on several occasions in literature, mainly because of their aberrant appearance (CLIQUENOIS, 1999; BAXTER, 2002; BRADLER, 2015). However, until now, the function of the strange and diverse morphology of the eggs remained unexplained.

The identification of stick insect specimens collected during several expeditions in the framework of the Global Taxonomy Initiative projects “A step further in the entomodiversity of Cambodia” and “A step further in the entomodiversity of Vietnam” (CONSTANT *et al.*, 2018; CUMMING *et al.*, 2021), allowed the identification of four species of *Trachythorax* among which two appeared to be new to science. Captive breeding of three species allowed the observation and study of the eggs. This led us to a review of all the species of *Trachythorax* and to the gathering of data (involving citizen science participation through Facebook groups and iNaturalist) about their eggs and oviposition. Subsequently our attention on potential evolutionary drivers tied to the peculiar morphology of the eggs, including parasitism, led us to compare these adaptations in closely related taxa.

The present paper aims to describe and differentiate the two new species, propose a number of taxonomic changes for several other species and provide new distribution records and/or comments on all species of the genus. Additionally, a hypothesis for the peculiar and diverse egg morphology in *Trachythorax* spp. and allied taxa, and observations on egg parasitism, are discussed.

Material and methods

Due to their nocturnal behaviour, like most Phasmida, the specimens of *Trachythorax* were collected at night. A lightweight and waterproof Petzl MYO RXP head torch was used during collecting. The females were kept alive in a mesh pop up cage (Exo Terra explorarium™) for producing eggs. The female specimens were euthanized by an injection with 70% ethanol; males were euthanized in a killing jar with ethyl acetate (EtOAc) fumes. Specimens were then stored in airtight plastic “zip”-bags in wood chips (used in rodent cages) and sprinkled with ethyl acetate to prevent rotting and mould, and to keep the specimens flexible. The bags were frozen on arrival and the specimens mounted later.

The morphological nomenclature follows BRAGG (2001) and for the egg morphology we follow CLARK-SELLICK (1997, 1998).

In the descriptions, the colouration is described from dried specimens and from photographs of living insects.

The photographs of the wild specimens were taken with a Sony DSC-H300 camera, those of collection specimens, with a Canon 700D camera equipped with a Sigma 50 mm Macro lens, and those of the eggs with a Leica EZ4W stereo-microscope with an integrated camera, and

stacked with CombineZ software. Photographs were optimized with Adobe Photoshop CS3. Observations were done with a Leica MZ8 stereo-microscope. The distribution maps were produced with SimpleMappr (SHORTHOUSE, 2010).

Acronyms used for the collections:

ETHZ	=	Eidgenössische Technische Hochschule Zürich, Zurich, Switzerland
IEBR	=	Institute of Ecology & Biological Resources, Vietnamese Academy of Sciences, Hanoi, Vietnam
FH	=	Private collection of Frank Hennemann, Germany
MSNG	=	Museo Civico di Storia Naturale, Genoa, Italy
MNCS	=	Museo Nacional de Ciencias Naturales, Madrid, Spain
MMUE	=	Manchester Museum, Manchester University, UK
NHMUK	=	Natural History Museum, London, UK
NHMW	=	Naturhistorisches Museum Wien, Vienna, Austria
NKUM	=	Institute of Entomology, College of Life Sciences, Nankai University, Tianjin, China
MNHU	=	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
NTU	=	National Taiwan University, Taipei, Taiwan
OUM	=	Oxford University Museum of Natural History, Oxford, UK
RBINS	=	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RUPP	=	Royal University of Phnom Penh, Phnom Penh, Cambodia
VNMN	=	Vietnam National Museum of Nature, Hanoi, Vietnam.

Abbreviations:

B.S.:	Biological Station
B.R.:	Biosphere Reserve
N.P.:	National Park
N.R.:	Nature Reserve
W.S.:	Wildlife Sanctuary
PSF:	Phasmida species file (http://phasmida.speciesfile.org)
HT:	holotype
PT:	paratype
ST:	syntype.

Taxonomy

Family Lonchodidae Brunner von Wattenwyl, 1893
Subfamily Necrosciinae Brunner von Wattenwyl, 1893
Tribe Necrosciini Brunner von Wattenwyl, 1893

Genus *Trachythorax* Redtenbacher, 1908

Trachythorax REDTENBACHER, 1908: 507 [described]. Type species: *Phasma maculicollis* Westwood, 1859 by subsequent designation by BROCK (1995).

Trachythorax – SHIRAKI, 1935: 78 [recorded from Taiwan]. — BRADLEY & GALLIL, 1977: 183 [higher taxonomy]. — BROCK, 1995: 93 [recorded from Malaysia, designation of type species]. — SELLICK, 1997: 116 [egg structure]. — FRITZSCHE, 1999: 80 [recorded from Thailand]. — ZOMPRO, 2004: 322 [catalogued]. — OTTE & BROCK, 2005: 336 [catalogued]. — HENNEMANN

et al., 2008: 40 [recorded from China]. — CHEN & HE, 2008: 409 [key to Chinese species]. — MANDAL & YADAV, 2010: 21 [recorded from India]. — SEOW-CHOEN, 2017: 88 [recorded from Singapore]. — SEOW-CHOEN, 2018: 392 [recorded from Sumatra].

DIAGNOSIS. The genus *Trachythorax* differs from all other known genera of Necrosciinae by the following combination of characters:

- 1) Head and thorax smooth, back of head can be swollen to almost conical (Figs 5 F–G, 10 E, 12 E, 20 C–E, 27 D, 28 D–E, 31 C).
- 2) Inflatable and brightly coloured membrane between pronotum and head, usually the anterior margin of the pronotum has the same colouration (Figs 5 F–G, 14, 20 C–D, 24 B–C, 28 D).
- 3) Females have the mesonotum at best 2× longer than the pronotum.
- 4) Tegmina short, not reaching median segment; alae fully developed and allowing sustained flight, anal area never brightly coloured.
- 5) Subgenital plate of females spoon-shaped and notched apically; not reaching apex of abdomen (Figs 4 B–C, 13 B–C, 18 B–C, 27 F–G).
- 6) Anal segment of males with two distinct hooks posteroventrally (Figs 2 B–C, 11 B–C, 16 B–C).
- 7) Poculum very short, slightly flattened, not reaching base of vomer (Figs 2 B–C, 11 B–C, 16 B–C).
- 8) Vomer distinct, elongate triangular and up-curving, ending in a single spine (Figs 2 C, 11 C, 16 C).
- 9) Strong sexual dimorphism concerning size with male distinctly smaller than the females; body length of males maximum 60% of females (Figs 7 A–B, 11, 21 A, 25 C–D).
- 10) Posterior pole of the eggs glued to the surface of plants, sometimes with distinct specialisations on the opercular collar (Figs 6, 32).

The raised posterior portion of the mesonotum in females is a morphological character shared with the Southeast Asian Necrosciini genera *Calvisia* Stål, 1875 and *Loxopsis* Westwood, 1859. The conical head typical for the genus *Loxopsis* can also be found in several representatives of *Trachythorax* and in *Calvisia* (*Conocalvisia*).

SPECIES INCLUDED (15):

- Trachythorax albomaculatus* sp. nov.
- Trachythorax auranticollis* sp. nov.
- Trachythorax chinensis* (Redtenbacher, 1908)
- Trachythorax expallescens* Redtenbacher, 1908
- Trachythorax fuscocarinatus* Chen & He, 1995
- Trachythorax gohi* Brock, 1999
- Trachythorax illaesa* (Redtenbacher, 1908) stat. rev. comb. nov.
- Trachythorax incertus* Redtenbacher, 1908
- Trachythorax longialatus* Cai, 1989
- Trachythorax maculicollis* (Westwood, 1848)
- Trachythorax planiceps* Redtenbacher, 1908
- Trachythorax sexpunctatus* (Shiraki, 1911)
- Trachythorax sparaxes* (Westwood, 1859)
- Trachythorax unicolor* Redtenbacher, 1908
- Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov.

BIOLOGY. Species were found in different biotopes, ranging from mountain evergreen rainforests to dry and severely disturbed habitats. All species are capable of good flight. Most of the time when an adult female is observed, it is accompanied by the much smaller male, and females can easily fly transporting the attached males on their backs. Males also open their wings during flight in copulation.

DISTRIBUTION. Currently known from a wide range in South-east Asia: Sri Lanka, India, Bangladesh, Myanmar, Thailand, Vietnam, Cambodia, Peninsular Malaysia, Singapore, Indonesia (Sumatra and Java), southern China (including Hainan) and Taiwan.

NOTES. The taxonomy of the genus is currently poorly resolved with several taxa, e.g. *T. chinensis* (Redtenbacher, 1908) from China (Sichuan), *T. expallescens* Redtenbacher, 1908 from Sri Lanka, *T. fuscocarinatus* Chen & He, 1995 from Hainan, *T. incertus* Redtenbacher, 1908 from Vietnam (North Vietnam), *T. longialatus* Cai, 1989 from China (Sichuan) and *T. unicolor* Redtenbacher, 1908 from Java in need of revision and accurate re-description (see comments below), therefore a key to the species of *Trachythorax* is not included.

***Trachythorax albomaculatus* sp. nov.**

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(Figs 1–9)

ETYMOLOGY. The species epithet is formed from “*albus*” (adj., Latin) meaning white, and “*maculatus*” (adj., Latin) meaning spotted. It refers to the characteristic white marking on the mesonotum of the females.

TYPE MATERIAL. VIETNAM: Holotype ♂: Gia Lai Prov., Kon Chu Rang N.R., 600–1200 m, 13–20.vii.2018, GTI Project, 14°28'28"N 108°32'27"E, Leg. J. Constant, J. Bresseel & X. Vermeersch, I.G.: 33.789 (RBINS).

Paratypes: (6♂♂, 5♀♀): 1♂, 1♀: same data as holotype (RBINS); 5♂♂, 4♀♀: same data as holotype, ex breeding B. Kneubühler 2018 (4♂♂, 3♀♀: RBINS; 1♂, 1♀: VNMN).

ADDITIONAL MATERIAL. Eggs: same data as holotype, B. Kneubühler 2018 (RBINS).

DIAGNOSIS & DIFFERENTIATION. Large and robust species. The combination of a large V-shaped white patch on the mesonotum and a yellow inflatable membrane between head and pronotum, immediately distinguishes the females from the other species. The male lacks any white and has an overall dark colouration with a yellow inflatable membrane behind the head. The males resemble those of *T. gohi* Brock, 1999 but lack the two conspicuous triangular markings on the posterior margin of the metanotum.

DESCRIPTION. Measurements: see Table 1.

MALE (Figs 1–2, 5 D–E, H).

Head: (Fig. 1 E–F) Indistinctly setose, otherwise smooth; more or less oval in shape and flattened dorsally. Back of head swollen and somewhat tapering; sides of head, occiput and posterior part of vertex black; dorsal portion beige with a small black marking between antennae, three small black spots between eyes with the median one being more distinct, and a pair of minute black points on vertex; beige colouration continuing posteriorly as a short mediolongitudinal line, not reaching occiput. Eyes strongly projecting hemispherically. Antennae longer than body; scapus slightly compressed dorsoventrally, black with pale lateral margins; pedicellus cylindrical; segment III distinctly narrower and longer than pedicellus; antennomeres filiform, variable in length towards apex. Antennae brown, with evenly spaced pale markings.

Thorax: (Fig. 1 C, E, 5 F) Slightly setose. Pronotum almost completely black, distinctly shorter than head. Prozona indistinctly widening towards the posterior with anterior margin concave and yellow; anterolateral angles somewhat pointed. Metazona longer than prozona, slightly broadening towards the posterior with few minute whitish granules on lateral margins; posterior margin rounded and with faint yellow colouration. Mesonotum more or less parallel-sided with lateral margins somewhat thickened, especially in posterior half; with predominantly dark colouration and hairs longer than on pronotum; with narrow mediolongitudinal carina ending in a small hump on posterior margin, anterior half of carina black and posterior half light brown; posterior half higher than anterior half in lateral view; posterior margin concave.

Wings: (Fig. 1 A–B, E) Tegmina short, light brown with black veins not reaching median segment and with definite hump anterolaterally; inner margins broadly rounded, overlapping medially; outer margins slightly concave; slightly rounded posteriorly. Alae well developed, projecting over posterior margin of tergum VII; costal area coloured like tegmina, anal area translucent brown-grey.

Legs: Brownish with evenly spaced pale bands and with very short hairs. Femora and tibiae with carinae not raised and indistinct, dorsolateral edges blackish except for pale bands; profemora indistinctly curved basally. Meso- and metafemora more or less the same length as corresponding tibiae. Basitarsi strongly elongate, claws small but acute.

Abdomen: (Fig. 2) Abdominal terga pale brown with several black longitudinal lines that are slightly thickening towards the posterior; terga II–V more or less of the same length; terga VI–VIII gradually shortening; terga VIII–X sub-equal in length. Anal segment slightly broadened with lateral margins rounded; posterolaterally with indistinct shallow notch; posterior margin slightly concave and posteroventral margin with pair of strong, short spines. Poculum small, cup-like, not reaching base of vomer (often deformed in dried specimens). Vomer distinct; body triangular with thickened lateral margins; posterior half strongly elongate and up-curving, apically acute.

Table 1. Measurements [mm] of *Trachythorax albomaculatus* sp. nov.

Length of	HT ♂	PT ♂♂	PT ♀♀
Body	46.5	49.3–51.9	89.8–94.4
Head	4.5	4.2–4.4	7.8–8.5
Pronotum	2.9	2.8–3.0	5.4–5.6
Mesonotum	5.3	4.8–5.5	7.9–8.5
Metanotum	4.5	5.0*	10.4–10.9
Median segment	3.3	3.7*	7.2–7.5
Tegmina	3.8	3.4–3.9	9.0–9.1
Alae	29.8	30.2–30.8	68.8–70.7
Profemora	12.7	12.8–13.6	17.1–17.2
Mesofemora	8.0	8.7–9.0	13.5–13.7
Metafemora	13.0	13.0–13.5	18.7–19.3
Protibiae	13.3	12.8–13.5	17.7–18.0
Mesotibiae	8.1	8.3–8.9	12.4–12.7
Metatibiae	13.7	13.6–14.0	18.3–18.5

* Only one paratype with open wings.

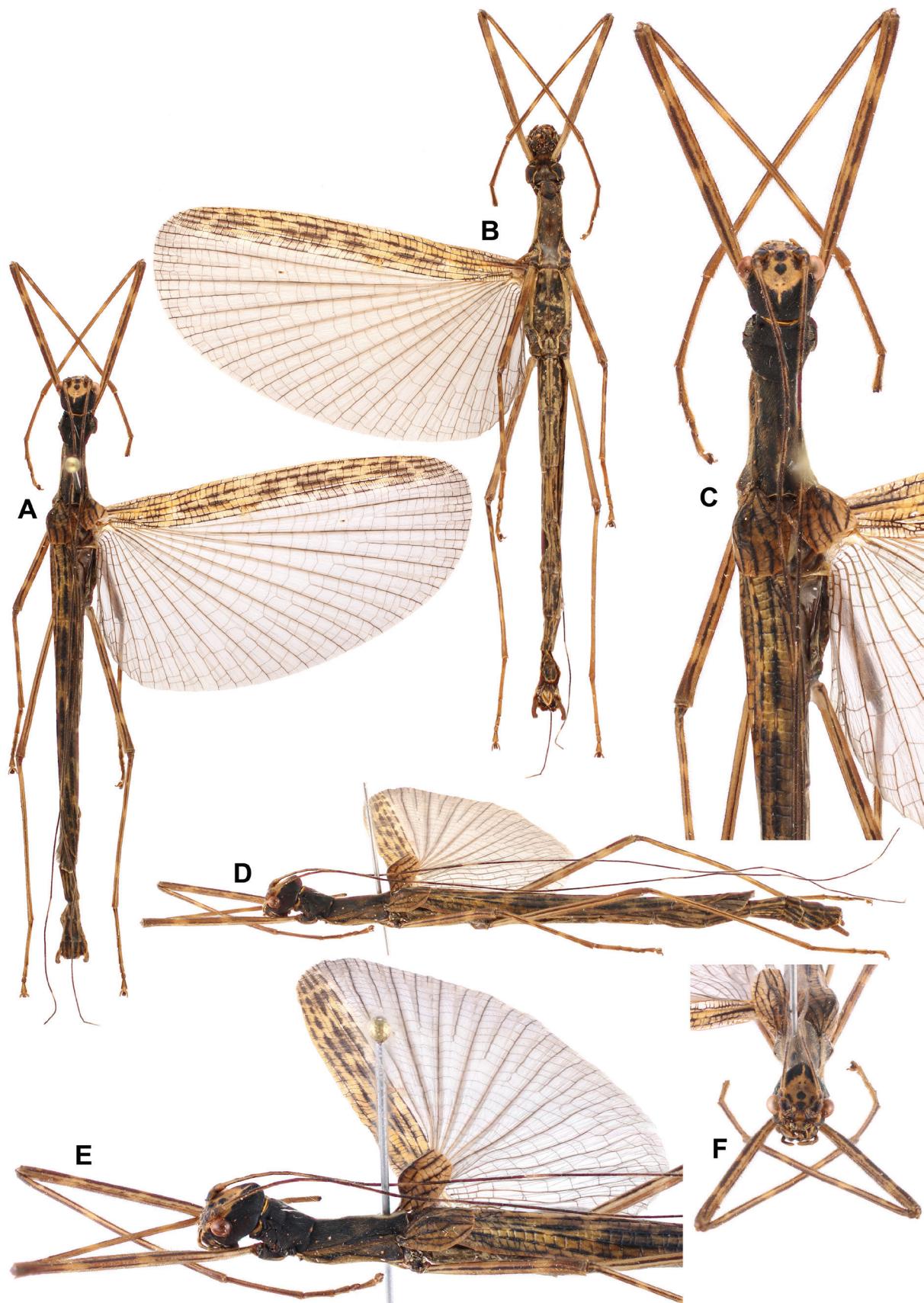


Fig. 1. *Trachythorax albomaculatus* sp. nov., holotype ♂ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head and thorax, dorsal view. D, habitus, lateral view. E, head and thorax, dorsolateral view. F, head dorsal, view.



Fig. 2. *Trachythorax albomaculatus* sp. nov., holotype ♂ (RBINS). A, terminalia, dorsal view. B, terminalia, lateral view. C, terminalia, ventral view.

FEMALE (Figs 3–4, 5 A–C, G).

Head: (Fig. 3 E–F) As in male, but back of head more elongate and almost conical, flattened dorsally. Sides of head, occiput and posterior part of vertex black. Dorsal portion beige, tapering towards the posterior, with a small black marking between antennae, three small black spots between eyes with median one more distinct and a pair of minute black points on vertex. Eyes black, circular in lateral view, strongly projecting hemispherically. Antennae as in males.



Fig. 3. *Trachythorax albomaculatus* sp. nov., paratype ♀ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head and thorax, dorsal view. D, habitus, lateral view. E, head and thorax, dorsolateral view. F, head anterodorsal, view.



Fig. 4. *Trachythorax albomaculatus* sp. nov., paratype ♀ (RBINS). A, terminalia, dorsal view. B, terminalia, lateral view. C, terminalia, ventral view.

Thorax: (Figs 3 C, E, 5 G) Pronotum as in male. Mesonotum black, with broad V-shaped white marking, reaching posterior margin; with a pair of distinct humps at about one third of its length, humps with black spot medially; first slightly widening towards the posterior, but slightly narrowing behind humps; mediolongitudinal carinae indistinct, at best with faint median line; portion behind humps higher than anterior portion in lateral view; posterior margin carinate and slightly raised.

Wings: (Fig. 3 A–B, E) Tegmina as in male. Alae coloured as in male, but distinctly longer, almost reaching apex of abdomen.

Legs: As in male.

Abdomen: As in male except for terminalia (Fig. 4). Terga VII–IX gradually shortening. Anal segment slightly longer than tergum VIII, broadened at base, tapering towards the posterior and with shallow notch apically. Sternum VII with praepercular organ visible in lateral aspect as a small posteromedian hump; in ventral view with subapical hump, followed by two short, slightly incurving, longitudinal ridges reaching end of segment; apical margin with transverse ridge. Subgenital plate fairly flat, with narrow mediolongitudinal carina; starting parallel-sided, broadening medially and later tapering towards the posterior; apex with shallow notch. Cerci straight, round in cross-section; projecting over apex of abdomen and with apices rounded.

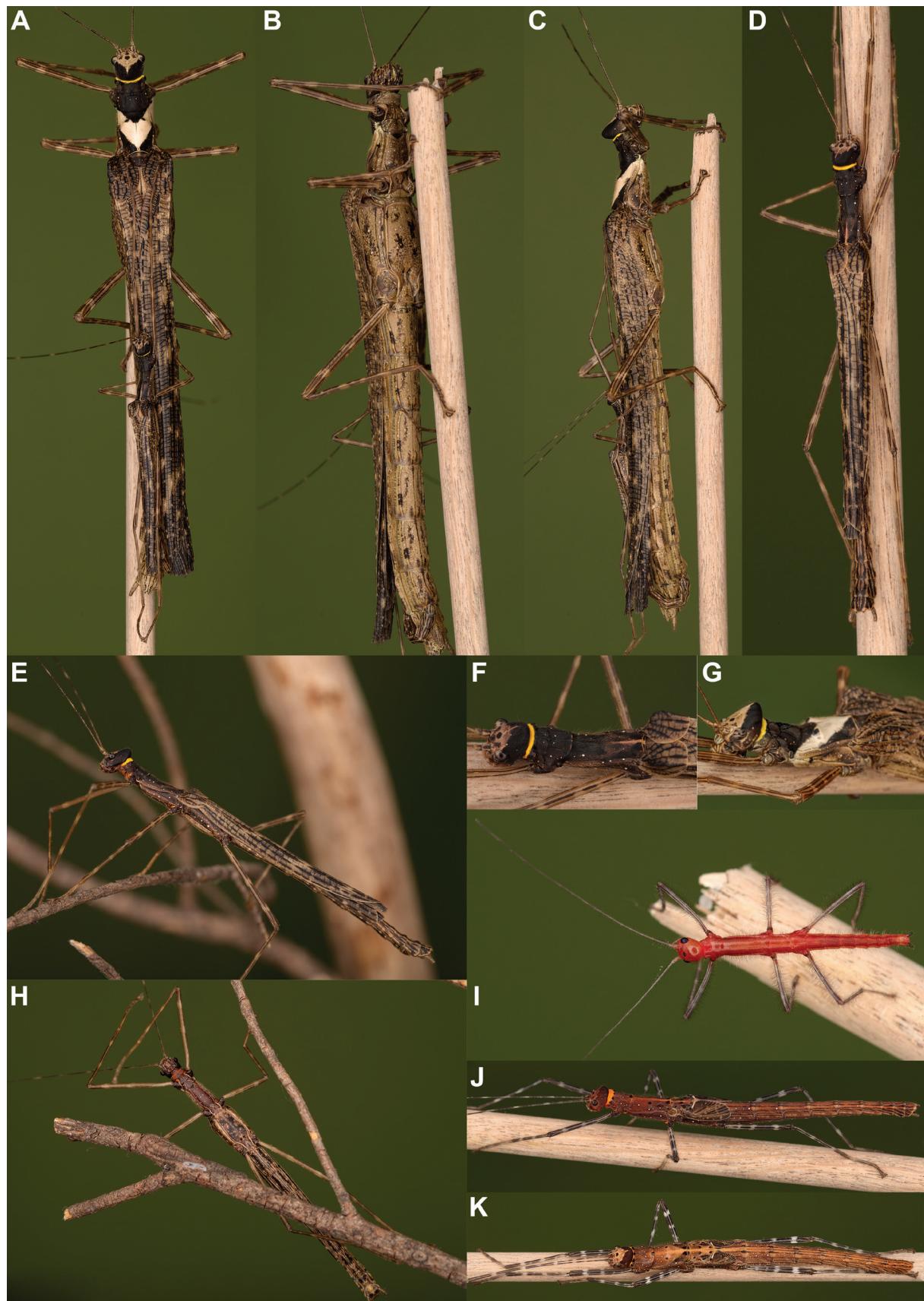


Fig. 5. *Trachythorax albomaculatus* sp. nov., in culture. A, mating pair, dorsal view. B, mating pair, ventral view. C, mating pair, lateral view. D, ♂, dorsal view. E. ♂, lateral view. F, ♂, head and thorax, dorsolateral view. G, ♀, head and thorax, dorsolateral view. H, ♂, ventral view. I, newly hatched nymph, dorsal view. J, subadult ♂ nymph. K, ♀ nymph.

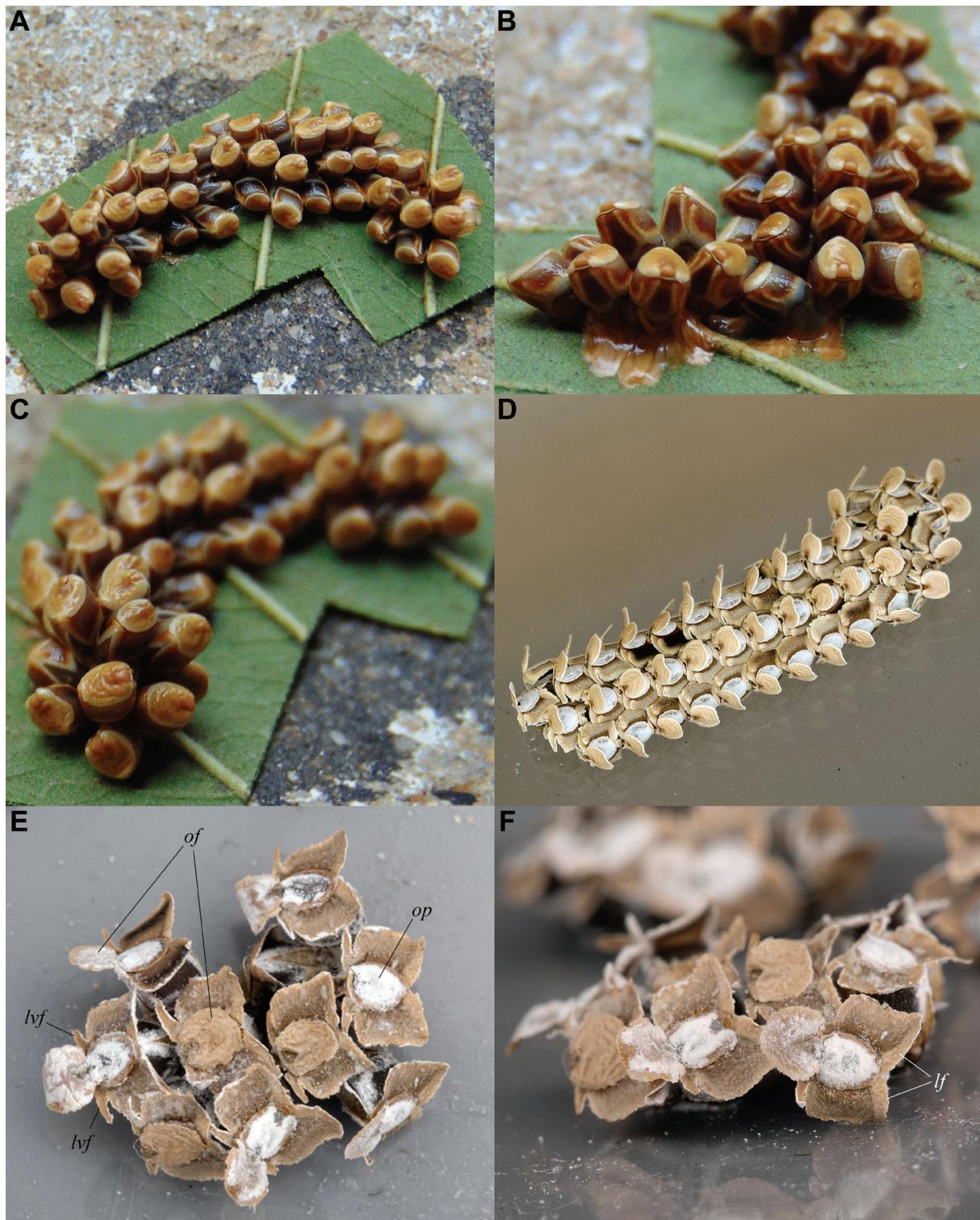


Fig. 6. *Trachythorax albomaculatus* sp. nov., eggs. A–C, freshly laid eggs by wild ♀ paratype (pics by J. Constant). D–F, eggs laid by ♀ paratype (pics by B. Kneubühler). D, egg clutch. E–F, anterior view.
 of = opercular flap; op = operculum; lf = lateral flap; lvf = lateroventral flap.

NYMPH (Fig. 5 I–K).

Newly hatched nymphs around 13mm in total length and strongly setose. Head and body bright orange red; eyes and cerci black. Head with dorsal round black spot at posterior margin of eyes; vertex with two depressions posteriorly. Legs setose and greyish with faint pale bands.



Fig. 7. *Trachythorax albomaculatus* sp. nov., in Kon Chu Rang Nature Reserve. A, mating pair, dorsal view. B, mating pair, dorsolateral view. C, ♀, head and thorax, dorsolateral view. D, mating pair in habitat.



Fig. 8. *Trachythorax albomaculatus* sp. nov., habitat in Kon Chu Rang Nature Reserve.

EGG (Fig. 6).

Measurements [mm]. Length: 3.6; width: 2.1; height: 2.1.

Egg capsule ovoid with posterior portion somewhat flattened laterally. Coronal collar slightly elongate (best visible in hatched eggs) with five flaps; flaps folded against capsule at the time of laying, unfolding with increasing dehydration; lateral flaps (*lf*) with ventral margin rounded, lateral margin more or less straight and dorsal margin somewhat more elongate; lateroventral flaps (*lvf*) distinctly smaller, elongate and narrowing towards the posterior; ventral flap invisible when the eggs are dry and only visible when dissecting egg clutch, narrow at base, slightly diverging towards apex. Ventral flap also uplifted from egg capsule after egg laying but obstructed by dorsal side of adjacent egg and covering its micropylar plate. Operculum oval with distinct round opercular flap (*of*) on ventral margin of opercular rim. In freshly deposited eggs, opercular flap folded onto the operculum (*op*), opening during dehydration process. After opening, silk-like secretion covering true operculum; similar silk-like material also found on flaps of coronal collar after unfolding from egg capsule. Micropylar plate more or less an elongate lozenge, with small micropylar cup almost medially; plate not covered with coronal flaps when freshly laid.

BIOLOGY (Figs 7–8). The species was collected in mountainous tropical evergreen rainforest, at medium altitude (600–1200 m). Only one pair and one male were observed in the field at night, resting on the leaves of a tree some 2–3 m above ground at the margin of the forest along a trail. The single male was disturbed from bushes at daytime. Males and females are able to fly and the female can fly with the male attached *in copula*, on her back.



Fig. 9. *Trachythorax* spp. distribution map.

In captivity (B. Kneubühler pers. comm., 2020), the species accepts *Euonymus* spp. (Celastraceae) as an alternative food plant. The females lay their egg clutches (one every 2–3 weeks) counting up to 30 eggs which hatch after about 4 months of incubation at 20–24°C. The nymphs of a single clutch will hatch over several days, at dawn or early morning but not during the night, and they often do not stay on the food plants at daytime.

The adult males and females show a characteristic defensive reaction when they feel disturbed or threatened: they bend the head ventrally, which reveals two membranous areas with a bright yellow warning colour (one between head and prothorax and one between pro- and mesothorax, the latter scarcely visible in the males). The species also has a defensive spray which is clear and has a slightly foul smell.

DISTRIBUTION. The species is currently only known from the type locality, Kon Chu Rang N.R., Gia Lai Province in Central Vietnam (Fig. 9).

***Trachythorax auranticollis* sp. nov.**

urn:lsid:zoobank.org:act:3F7D85C7-EB0B-4E62-A4BD-3B535E94ACE0
(Figs 9–14)

ETYMOLOGY. The species epithet is formed from “*aurantius*” (adj., Latin) meaning orange-coloured, and “*collum*” (noun, Latin) meaning neck. It refers to the characteristic bright orange anterior margin of the pronotum of this species.

TYPE MATERIAL. VIETNAM: Holotype ♂: Dong Nai Biosphere Res. 11°18'N 107°06'E, 25.vi–6.vii.2012, night collecting, Leg. J. Constant & J. Bresseel, I.G.: 32.161 (RBINS).

Paratype: 1 ♀: same data as holotype (RBINS).

COMMENT. Nymphs of this species were observed by the authors in Cat Tien N.P. (11°26'N 107°26'E) in July 2012.

DIAGNOSIS. Both sexes are immediately distinguishable from other species by the bright orange anterior margin of the pronotum. Overall brown insects with no distinct markings other than the orange margin. Hind wings reaching apex of abdomen in females and projecting over anterior margin of tergum VII in males. Fore femora almost straight.

DESCRIPTION. Measurements see Table 2.

Table 2. Measurements [mm] of *Trachythorax auranticollis* sp. nov.

Length of	HT ♂	PT ♀
Body	41.3	71.0
Head	3.4	6.8
Pronotum	2.3	4.5
Mesonotum	4.3	6.1
Metanotum	4.1	8.7
Median segment	3.1	5.5
Tegmina	3.4	7.6
Alae	25.2	56.7
Profemora	10.5	14.3
Mesofemora	7.6	11.8
Metafemora	10.7	15.8
Protibiae	10.3	14.6
Mesotibiae	7.2	10.3
Metatibiae	11.2	15.2

MALE (Figs 10–11, 14).

Head: (Figs 10 C, E, 14) Smooth, predominantly dark grey and slightly paler dorsally in living specimens; small black marking between antennae. Head capsule more or less oval in shape and dorsally flattened. Back of head swollen and broadly rounded. Eyes strongly projecting hemispherically. Antennae longer than body; scapus slightly compressed dorsoventrally, black with pale lateral margins; pedicellus cylindrical and slightly swollen; segment III distinctly narrower and longer than pedicellus; antennomeres filiform, dark grey, with evenly spaced pale markings.

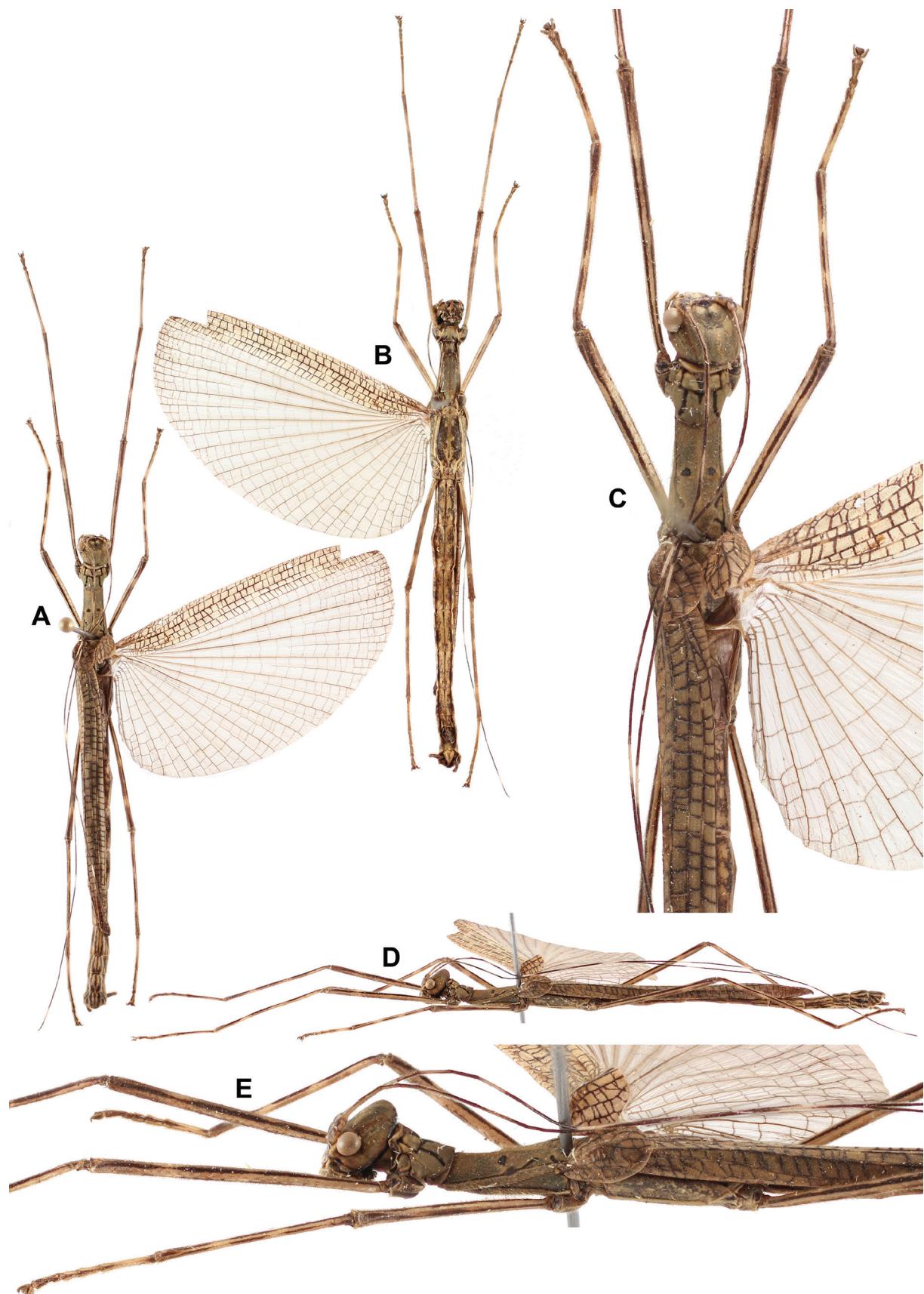


Fig. 10. *Trachythorax auranticollis* sp. nov., holotype ♂ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head and thorax, dorsal view. D, habitus, lateral view. E, head and thorax, dorsolateral view.



Fig. 11. *Trachythorax auranticollis* sp. nov., holotype ♂ (RBINS). A, terminalia, dorsal view. B, terminalia, lateral view. C, terminalia, ventral view.

Thorax: (Figs 10 C, E, 14) Pronotum indistinctly setose and dark grey (light brown in preserved specimens) with some black markings, shorter than head with anterior margin distinctly concave and vividly orange coloured. Prozona slightly widening towards the posterior with anterolateral angles acute, anterior margin slightly thickened, followed by a narrow transverse black line, reaching sides of pronotum. Central transverse furrow between pro- and metazona black, not reaching sides of pronotum; anterior marking connected to central marking by short longitudinal black lines laterally. Metazona longer than prozona, slightly narrowing towards the posterior, with T-shaped black marking anteromedially and two oblique black markings sublaterally; posterior margin rounded and with faint orange colouration. Mesonotum more or less parallel-sided with predominantly dark grey colouration and hairs longer than on pronotum; with narrow mediolongitudinal carina and medially with a pair of indistinct elevations; posterior half slightly higher than anterior half in lateral view; laterally with narrow longitudinal black line; posterior half with four short, oblique black lines originating laterally.

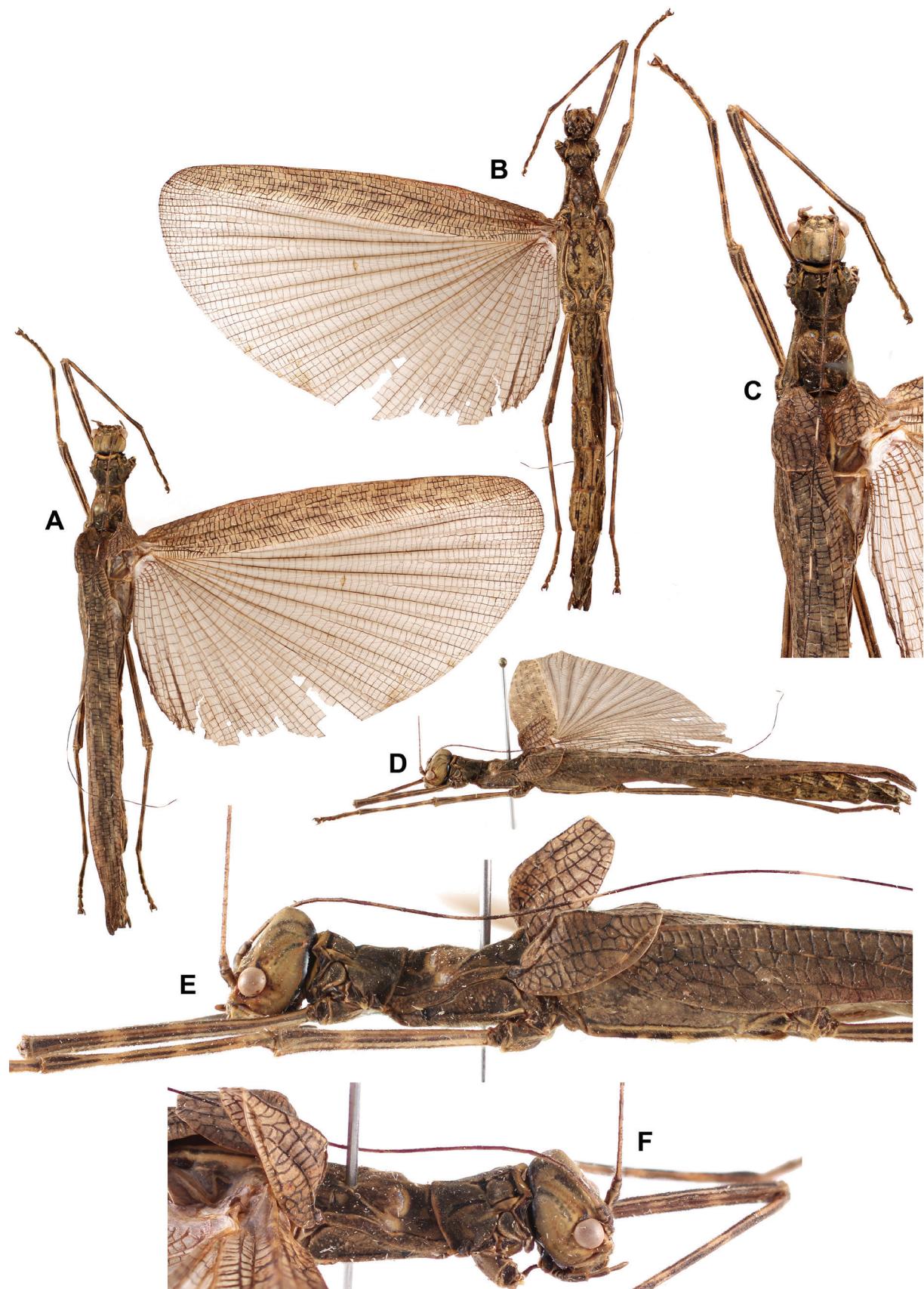


Fig. 12. *Trachythorax auranticollis* sp. nov., paratype ♀ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head and thorax, dorsal view. D, habitus, lateral view. E, head and thorax, lateral view. F, head and thorax, dorsolateral view.

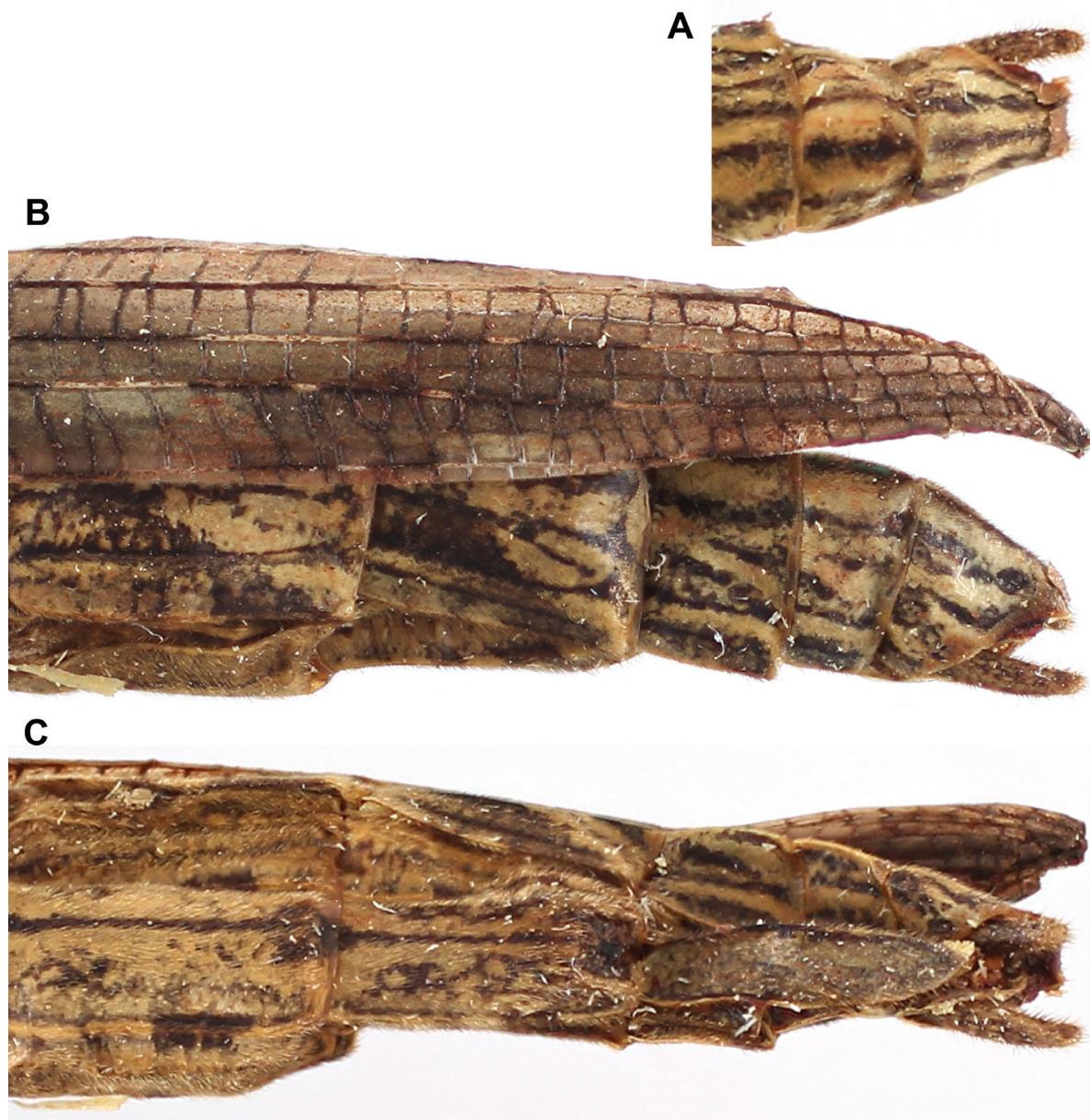


Fig. 13. *Trachythorax auranticollis* sp. nov., paratype ♀ (RBINS). A, terminalia, dorsal view. B, terminalia, lateral view. C, terminalia, ventral view.

Wings: (Fig. 10 A, B) Tegmina light brown with black veins, short, not reaching median segment. Small but definite rounded hump anterolaterally. Longitudinal veins and cross-veins distinct. Posterior margin rounded. Alae well developed; costal area coloured as tegmina; anal area infuscate, projecting over anterior margin of tergum VII.

Legs: Completely unarmed and brown, with distinct paler banding; carinae indistinct to absent and rounded. Femora more or less the same length as corresponding tibiae and with dorsolateral margins black. Basitarsi elongate, with small acute claws.

Abdomen: (Fig. 11) Median segment distinctly shorter than metanotum. All abdominal terga brown with narrow longitudinal black line centrally. Terga II–VI with some irregular black markings laterally, slightly shortening towards the posterior and parallel-sided. Tergum VII distinctly shorter than VI and slightly widening towards the posterior. Terga VIII–X the shortest segments of the abdomen with VIII about as long as anal segment and IX slightly longer than VIII.



Fig. 14. *Trachythorax auranticollis* sp. nov., mating pair, in Dong Nai Biosphere Reserve.

Terga VII–X with three longitudinal black lines with the sub-median lines broader than central lines; lateral margins also with irregular black markings. Anal segment wider than previous segment, with lateral margins rounded. Posterior margin concave laterally, convex centrally. Apex strongly curved downwards with two black, laterally flattened teeth near apex of vomer. Poculum gently rounded, scoop-shaped, not reaching base of vomer. Vomer distinct, elongate triangular with longitudinal furrow medially; posterior portion strongly up-curving, apex acute.

FEMALE (Figs 12–14).

Head: (Figs 12 C, E–F, 14) As in male, with back of head more elongate and somewhat tapering. Antennae as in males.

Thorax: (Figs 12 C, E–F, 14) Pronotum as in males. Mesonotum black, with broad heart-shaped paler marking reaching posterior margin; with a pair of humps at about one third of its length, the humps with black spot medially; at first slightly widening towards the posterior, but slightly narrowing behind humps; mediolongitudinal carinae indistinct, at best with faint median line; portion behind humps higher than anterior portion in lateral view; posterior margin carinate and somewhat raised. Black markings as in male.

Wings: (Fig. 12 A–B) Tegmina as in males. Alae coloured as in males, but distinctly longer, almost reaching apex of abdomen.

Legs: As in males.

Abdomen: (Fig. 14) Terga II–V about the same length; VI slightly shorter; VII distinctly shorter than VI; VII–IX gradually shortening. Anal segment about as long as tergum VIII, tapering towards the posterior and apically rounded. Sternum VII with praepercular organ in lateral view visible as small posterior hump; in ventral view with subapical hump medially, followed by two short, straight, longitudinal ridges reaching end of segment. Subgenital plate fairly flat with mediolongitudinal carina, more distinct in anterior half; apex with shallow notch. Cerci straight, round in cross-section and slightly projecting over apex of abdomen, with apices rounded.

BIOLOGY. The specimens were observed resting under leaves of small trees some 2–3 metres above the ground (Fig. 14), in tropical lowland rainforest.

DISTRIBUTION. Vietnam, Dong Nai Province, Dong Nai Biosphere Reserve and Cat Tien N.P. (Fig. 9).

Trachythorax yunnanensis Gao & Liang, 2021 stat. nov.

(Figs 9, 15–22)

Trachythorax maculicollis yunnanensis GAO & LIANG, 2021: 2 [described and figured].

MATERIAL EXAMINED. VIETNAM: (35♂♂, 23♀♀): 1♂, 1♀: Dak Nong Prov., Dray Sap. 12°29'45"N 107°54'47"E, 1–4.viii, 2019, GTI Project, Leg. J. Constant & J. Bresseel, I.G.: 34.048 (RBINS); 34♂♂, 22♀♀: same data, ex breeding T. Bollens 2020. (29♂♂, 17♀♀: RBINS; 5♂♂, 5♀♀: VNMN); eggs: same data, T. Bollens 2020. (RBINS).

LAOS: 1♂, 1♀: Province de Khammouane, rivière Hin Boun, Ban Nathan, Camp de l'Agame, Piège Malaise géant, bioqui: forêt de vallée, 17°59.733'N 104°49.395"E, 17–22.V.2012, IBCFL, Operation Canopée, radeau des cimes, H.P. Aberlenc leg. (RBINS).

PHOTOGRAPHIC RECORDS. THAILAND: 1♀ (Fig. 22 A–B): Surat Thani prov., Ban Chalok Lam, 9°46'57"N 100°00'22"E, 9.VII.2014, A. Giudici.

LAOS: 1♂, 1♀ (Fig. 22 C): Luang Prabang prov., Chompet district, Ban Charn Ti, Pha Tad Ke botanical gardens, 19°53'18"N 102°07'51"E, 12.V.2020, E. Jansen.

COMMENTS. The species was originally treated as a subspecies of *T. maculicollis* (Westwood 1848) by GAO & LIANG (2021), from which it was differentiated by the yellow colouration of the membrane between the pronotum and head in both sexes (Fig. 20 C–E) and the slightly shorter wings. Comparison of specimens (Figs 15–18) and eggs (Fig. 19) from Dak Nong Province in Central Vietnam matching the description provided by GAO & LIANG (2021) with ‘typical’ specimens of *T. maculicollis* from different localities throughout Vietnam, Cambodia and Thailand, show a distinctly more elongate anal segment in females of *yunnanensis* (Fig. 18) when compared to *T. maculicollis* (Fig. 28 F). Furthermore, captive breeding of both ‘*yunnanensis*’ from Dak Nong Province, Vietnam (Fig. 20) and of ‘typical *maculicollis*’ from Phnom Aural, Cambodia (Fig. 28 B–G) has shown that the colour of the membrane is a stable character that does not show any variation over the generations (BAXTER, 2002; T. Bollens, pers. comm., February 2021). Finally, considering the new records from Vietnam (Fig. 21), Thailand (Fig. 22 A–B) and Laos (Fig. 22 C) available for *yunnanensis*, it appears that its distribution overlaps that of *T. maculicollis* (Figs 9, 29). Based on this data, *T. yunnanensis* stat. nov. is here upgraded as a valid species instead of being a subspecies of *T. maculicollis*. For measurements of *T. yunnanensis* see Table 3.

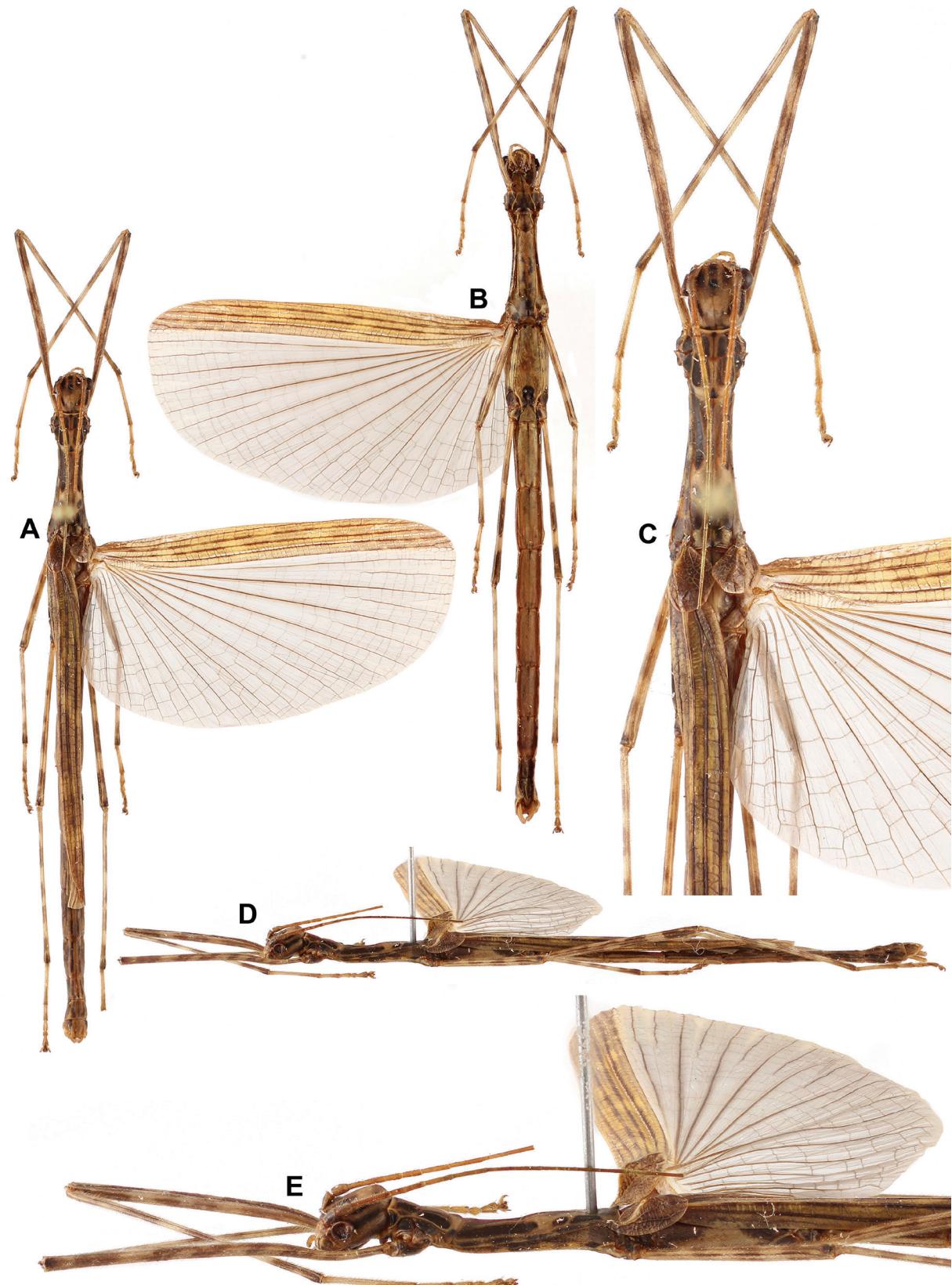


Fig. 15. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., ♂ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head and thorax, dorsal view. D, habitus, lateral view. E, head and thorax, dorsolateral view.



Fig. 16. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., ♂ (RBINS). A, terminalia, dorsal view. B, terminalia, lateral view. C, terminalia, ventral view.

Table 3. Measurements [mm] of *Trachythorax yunnanensis* from Dak Nong Province, Vietnam.

Length of	♂♂	♀♀
Body	44.1–45.0	79.2–89.4
Head	3.4–3.5	6.1–6.8
Pronotum	2.5–2.6	5.2–5.4
Mesonotum	5.6–5.9	8.3–9.3
Metanotum	5.8–6.3	
Tegmina	3.0–3.1	6.3–8.3
Alae	21.0–23.8	56.0–62.7
Profemora	9.7–11.8	17.4–19.2
Mesofemora	6.7–7.2	11.2–12.7
Metafemora	11.0–11.4	17.1–19.5
Protibiae	11.3–12.1	17.9–18.7
Mesotibiae	6.4–6.5	10.6–11.5
Metatibiae	11.1–11.3	17.5–18.0

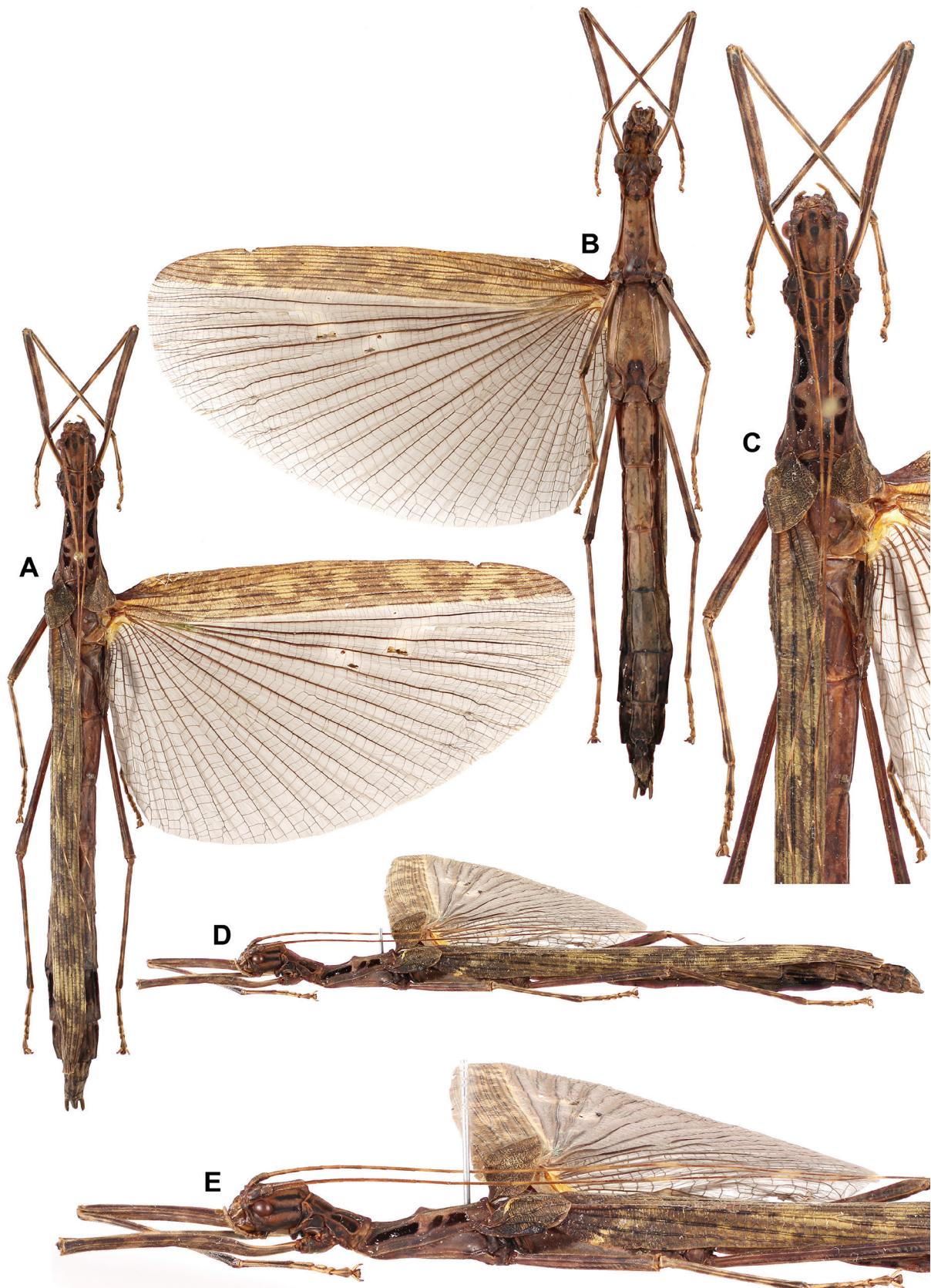


Fig. 17. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., ♀ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head and thorax, dorsal view. D, habitus, lateral view. E, head and thorax, dorsolateral view.



Fig. 18. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., ♀ (RBINS). A, terminalia, dorsal view. B, terminalia, lateral view. C, terminalia, ventral view.

SUPPLEMENTARY DESCRIPTION.

NYMPH (Fig. 20 F).

Newly hatched nymphs are much similar to those of *T. maculicollis* (Fig. 28 G). Setose and predominantly grey-brown. Head with black spot between eyes and between bases of antennae; anterior portion yellowish, posterior portion grey-brown; eyes black; antennae pale. Pronotum with minute black spots anterolaterally, posteromedially and near base of fore legs. Mesopleura with minute black marking. Legs with apex of femora and tibiae black, otherwise coloured like body.

BIOLOGY (Fig. 21). In Vietnam, the species was collected in tropical rainforest growing on volcanic soil, at medium altitude. Only one pair was observed in the field, at night, hanging from the leaves of a tree some 2–3 m above ground at the margin of the forest along a trail. Males and females are able to fly and the female can fly with the male attached to her back *in copula*.

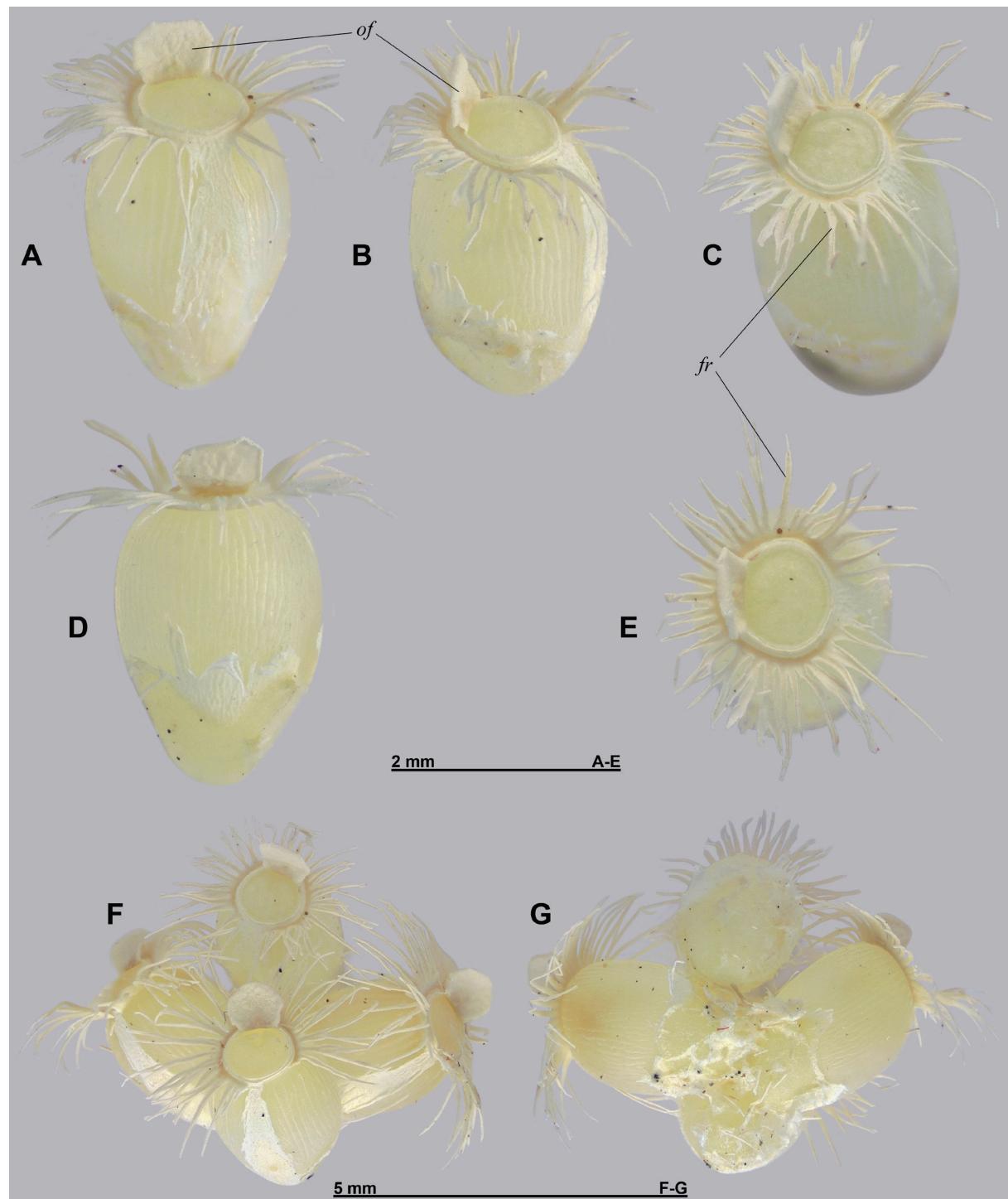


Fig. 19. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., eggs (RBINS). A, dorsal view. B, lateral view. C, anterolateral view. D, ventral view. E, anterior view. F–G, egg clutch. of = opercular flap; fr = frills.

In captivity (T. Bollens pers. comm., 2020), the species accepts *Euonymus* spp. (Celastraceae) as an alternative food plant. The females lay their egg clutches which hatch after about 2 months of incubation at 21–24°C. The nymphs of a single clutch will hatch over several days, at dawn or early morning, but not during the night, and they often do not stay on the food plants at daytime. The adult males and females show a characteristic defensive reaction when they feel disturbed or threatened: they bend the head ventrally, which reveals two membranous areas with a bright yellow to soft orange warning colour. The species also has a defensive spray which is clear and has a slightly foul smell.



Fig. 20. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., ex breeding. © Tim Bollens. A, ♂, dorsal view. B, ♀, dorsolateral view. C, ♂, head and thorax, dorsolateral view. D, ♂, head and thorax, dorsal view. E, ♀, head and thorax, dorsolateral view. F, newly hatched nymph.

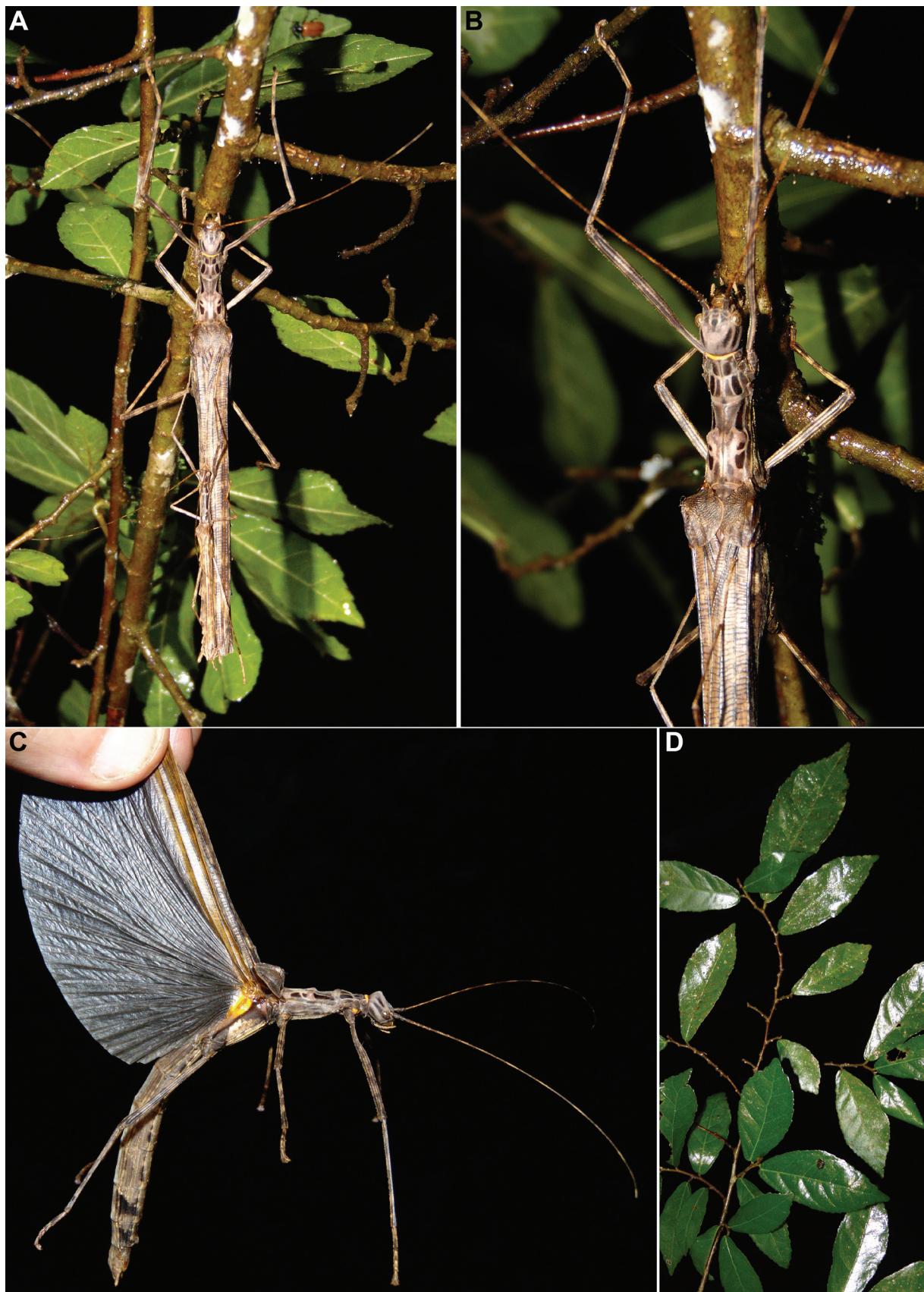


Fig. 21. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., in situ. A, mating pair, dorsal view. B, ♀, head and thorax, dorsal view. C, ♀, lateral view. D, host plant.

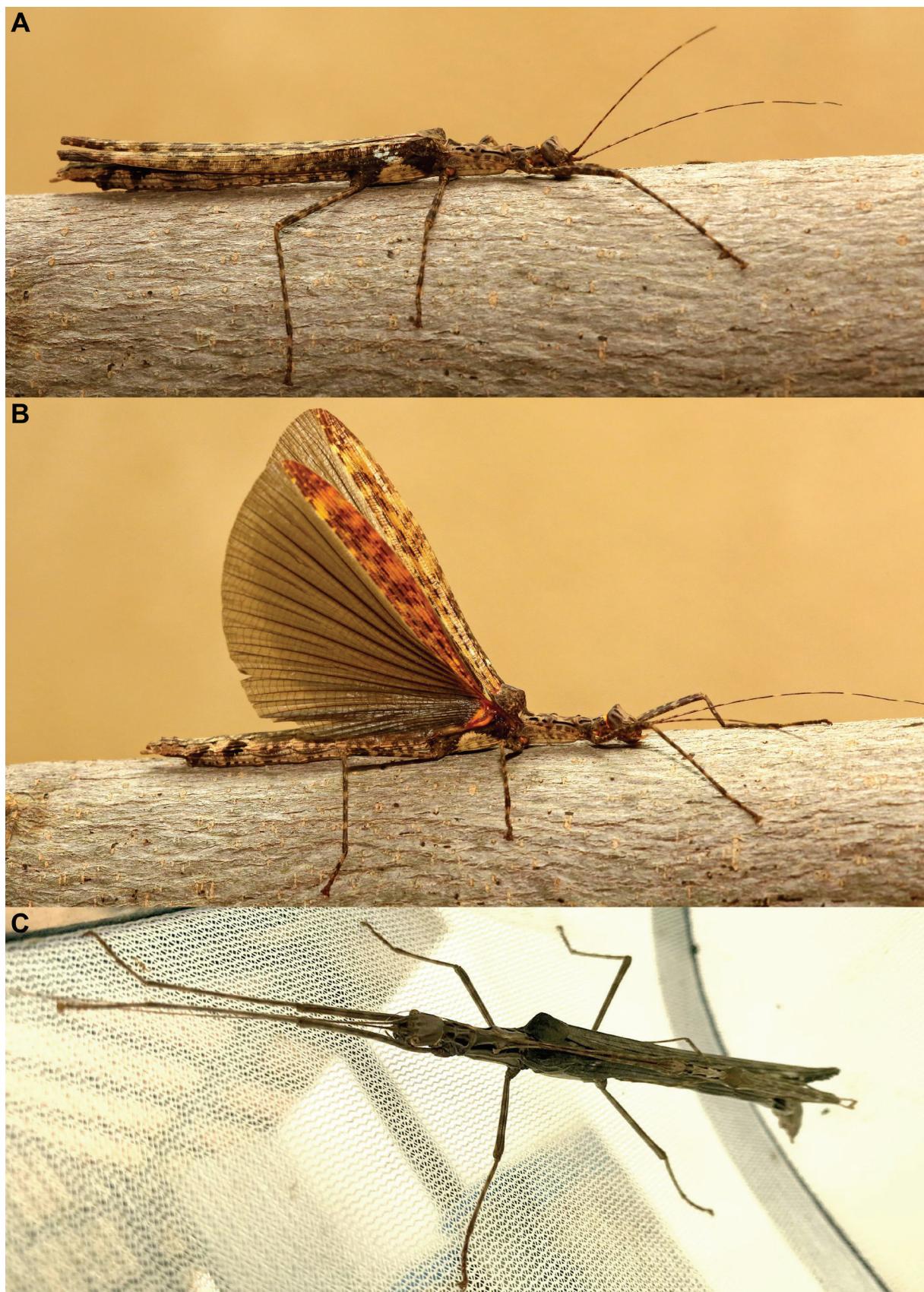


Fig. 22. *Trachythorax yunnanensis* Gao & Liang, 2021 stat. nov., A–B, ♀ from Prov. Surat Thani. © A. Giudici. C, ♂, ♀ from Luang Prabang Prov., Laos. © E. Jansen.

DISTRIBUTION. The species is currently known from China (Yunnan Province), Laos, Thailand (Surat Thani Province) and Vietnam (Dak Nong Province) (Fig. 9).

***Trachy thorax chinensis* (Redtenbacher, 1908)**
(Fig. 23 A)

Marmessoidea chinensis REDTENBACHER, 1908: 514 [described].

Marmessoidea chinensis – OTTE & BROCK, 2005: 193 [catalogued]. — ZOMPRO, 2005: 258 [catalogued, type data]. — CHEN & HE, 2008: 157 [in China]. — GAO & LIANG, 2021: 1 [in key to Chinese species].

Trachy thorax chinensis – SEOW-CHOEN, 2019: 86 [transferred to *Trachy thorax*].

TYPE MATERIAL. (examined from photographs on PSF – BROCK *et al.*, 2021) CHINA: HT ♀: Omi-Shan, West China, Kricheldorf S. (ZMHB).

PHOTOGRAPHIC RECORD. CHINA: ♂, ♀ in copula (Fig. 23A): Sichuan Prov., Luzhou, Gulin County, 28°13'48.6"N 105°46'07.7"E, 14.VIII.2021, iNaturalist user wangying <https://www.inaturalist.org/observations/91102094>.

COMMENTS. Surprisingly REDTENBACHER (1908) described this species in the genus *Marmessoidea* Brunner von Wattenwyl, 1893 although he described the genus *Trachy thorax* Redtenbacher, 1908 in the same publication. The author differentiated both genera in his key to the Necrosciini by the presence (*Trachy thorax*) or absence (*Marmessoidea*) of a pair of blunt humps on the mesonotum. *Trachy thorax chinensis* (Redtenbacher, 1908) also shows a pair of mesonotal humps, though being less pronounced. The type-locality Omi-Shan (currently Emei Shan) is located in Northwest Sichuan, China. A second species, *Trachy thorax longialatus* Cai, 1989 (Fig. 27), was also described from Sichuan, with its type locality about 125 km to the north. At the time of publication, CAI (1989) was probably unaware of the species *chinensis* as it was omitted from the list of *Trachy thorax* species from China that the author provided, and the species was only later transferred to *Trachy thorax* by SEOW-CHOEN (2019). GAO & LIANG (2021) differentiated *T. chinensis* from *T. longialatus* by the presence of black spots on the head in the former species. The holotype of *T. chinensis* is actually of a darker colouration than the holotype of *T. longialatus*, but no relevant differences in morphological characters could be observed when comparing images of the type specimens.

Direct comparison of the type material of both taxa combined with the examination of more recent material from Sichuan Province will allow to confirm or refute the possible synonymy between the two species. An illustration of a live specimen is provided here for the first time (Fig. 23 A).

DISTRIBUTION. China: Sichuan Province (REDTENBACHER, 1908).

***Trachy thorax expallescens* Redtenbacher, 1908**

Trachy thorax expallescens REDTENBACHER, 1908: 508 [described].

Trachy thorax expallescens – OTTE & BROCK, 2005: 336 [catalogued].

MATERIAL EXAMINED. TYPE MATERIAL. (examined from photographs on PSF – BROCK *et al.*, 2021) SRI LANKA: HT ♀: Nord-Ceylon, Coll. Bolivar (MNCN).

COMMENTS. The female holotype was never examined by REDTENBACHER (1908) as he stated “I only know this species from Brunner’s notes”. The specimen’s colouration is strongly faded and the mesonotum is slightly more than two times the length of the pronotum, a feature not found in any other species of *Trachy thorax*. In *T. sparaxes* (Westwood, 1859), another species

from Sri Lanka, the mesonotum is 2x the length of the pronotum. REDTENBACHER (1908) distinguished this species from *T. sparaxes* by the globose head. However, the specimen was mounted with the head in a strange position and a detailed examination of the holotype or the study of conspecific material is necessary to fully clarify the generic attribution of the species.

DISTRIBUTION. Sri Lanka (REDTENBACHER, 1908).

***Trachythorax fuscocarinatus* Chen & He, 1995**

(Fig. 23 B)

Trachythorax fuscocarinatus CHEN & HE, 1995: 197, figs 1–4 [described and figured].

Trachythorax fuscocarinatus – CHEN & HE, 1996: 664, figs 3–4 [description of male]. — OTTE & BROCK, 2005: 336 [catalogued]. — BROCK *et al.*, 2016: 181 [catalogued, type data]. — HENNEMANN *et al.*, 2008: 41 [catalogued]. — CHEN & HE, 2008: 180; fig. 145 [in China, illustrated]. — HO, 2016: 328 [catalogued, in Hainan]. — GAO & LIANG, 2021: 1 [in key to Chinese species].

PHOTOGRAPHIC RECORD. CHINA: ♀ (Fig. 23 B): Hainan, Jianfengling, 12.III.2013, F. Seow-Choen.

COMMENTS. An illustration of a live specimen from the type locality is provided here for the first time (Fig. 23 B).

DISTRIBUTION. China, Hainan Island (CHEN & HE, 2008).

***Trachythorax gohi* Brock, 1999**

(Figs 9, 24)

Trachythorax gohi BROCK, 1999: 122, fig. 81 [described and figured].

Trachythorax gohi – SEOW-CHOEN, 2000: 34, plate 87 [in Malaysia, figured]. — OTTE & BROCK, 2005: 336 [catalogued]. — BROCK *et al.*, 2016: 181 [catalogued, type data].

MATERIAL EXAMINED. TYPE MATERIAL. (examined from photographs on PSF – BROCK *et al.*, 2021) MALAYSIA: HT ♀: Peninsular Malaysia, Gunung Jerai, Kedah, 1987, D. Goh (NHMUK).

ADDITIONAL MATERIAL. (examined from photographs provided by Frank Hennemann) MYANMAR: Tenasserim, leg. Lemann, 18.III–16.IV.1996, FH 0306 - 1 (FH).

PHOTOGRAPHIC RECORDS. THAILAND: 2♀♀, 1♀ nymph (Fig. 24 A–B, D): Surat Thani Province, Phanom District, Khlong Sok, Khao Sok N.P., C. Hübner; 1♂ (Fig. 24 C); same data as preceding, 26.iii.2012, L. Day; mating pair: Narathiwat Province, Waeng District, 5.VII.2021, iNaturalist user Khonkhinaoi <https://www.inaturalist.org/observations/85908458>.

COMMENTS. *Trachythorax gohi* was described based on a single female by BROCK (1999). The species is here recorded for the first time from Thailand. Both sexes of the species were photographed in Khao Sok National Park, revealing the unknown male (Fig. 24 C). It is quite similar to *T. albomaculatus* sp. nov., however, *T. gohi* can be distinguished by (1) the two black, longitudinal stripes behind the eye; (2) females lacking the conspicuous white V-shaped patch on the mesonotum which is chocolate-brown instead; (3) both sexes have the mesonotum with a distinct black, triangular marking on the posterolateral angles, contrasting with the rest of the mesonotum.

DISTRIBUTION. Myanmar (Tenasserim), Northern peninsular Malaysia, Southwestern Thailand (Fig. 9).



Fig. 23. A, mating pair of *Trachythorax chinensis* (Redtenbacher, 1908) in Luzhou, Sichuan Province, China.
© Wangying. B, female of *Trachythorax fuscocarinatus* Chen & He, 1995 in Jianfengling, Hainan, dorsal view.
© F. Seow-Choen.

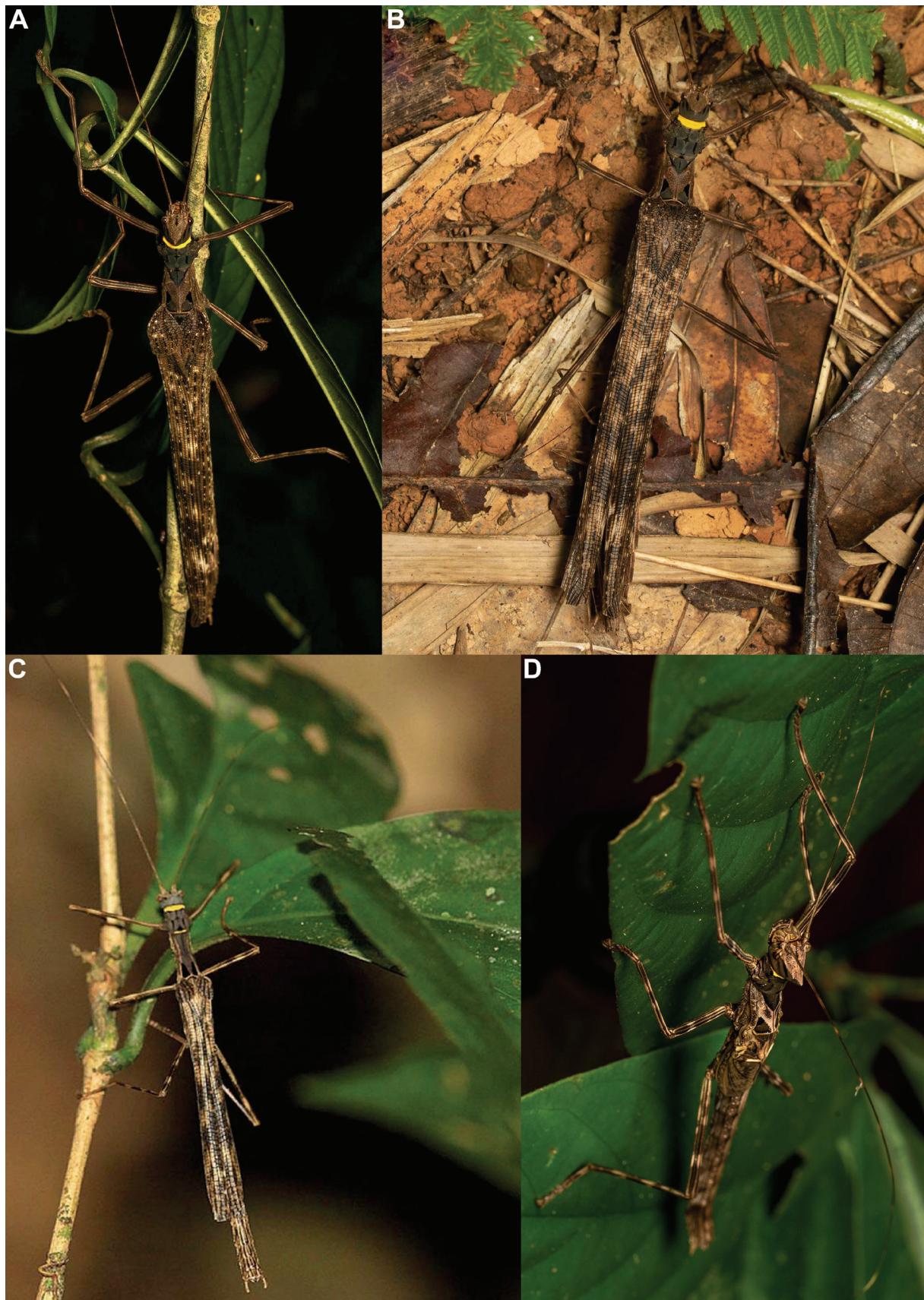


Fig. 24. *Trachythorax gohi* Brock, 1998 in Khao Sok N.P., Thailand. A–B, ♀, dorsal view. C, ♂, dorsal view. D, ♀ nymph. A–B, D. © C. Hübner. C. © L. Day.

***Trachythorax illaesa* (Redtenbacher, 1908) stat. rev. comb. nov.**
(Figs 25–26)

Necroscia illaesa REDTENBACHER, 1908: 564 [described].

Trachythorax maculicollis – BROCK & DELFOSSE, 2005: 52 [Pantel collection, synonymy]. — OTTE & BROCK, 2005: 336 [catalogued]. — SEOW-CHOEN, 2017: 88 [as synonym of *maculicollis*]. — DELFOSSE *et al.*, 2019: 205 [catalogued].

MATERIAL EXAMINED. TYPE MATERIAL. (examined from photographs – Fig. 25 A) INDIA: HT ♂: Shenbagan., VIII.00, N°3 P. Decoly, MNHN-EO-PHAS800 (MNHN).

PHOTOGRAPHIC RECORDS. INDIA: 1 ♂ (Fig. 25 B): Karnataka State, Mangalore, IX.2018, Jitesh Pai; mating pair (Fig. 25 E): Karnataka State, Puttur, X.2018, Abhijith A.P.C.; mating pair (Fig. 25 F) and eggs: Karnataka State, Agumbe, X.2020, Vishwanath Gowda; eggs: Maharashtra state, Mumbai, Nagla trail, 2018, Prajwal Ullal; mating pair and eggs (Figs 25 D, 26): Maharashtra State, Amboli, 2016 & 2020, Varad B. Giri.

SRI LANKA: mating pair (Fig. 25 C): Matale, Laggala-Pallegama, 13.IV.2018, iNaturalist user Pieterprins <https://www.inaturalist.org/observations/37204645>.

COMMENTS. *Necroscia illaesa* was described based on a single male by REDTENBACHER (1908). BROCK & DELFOSSE (2005) synonymised the species under *Trachythorax maculicollis*. The holotype male (Fig. 25 A) differs considerably from the male of *T. maculicollis*. It lacks the conspicuous pattern on the pro- and mesonotum (by which it also differs from *T. yunnanensis*), has a yellow membrane between the head and pronotum and has a conspicuous mediolongitudinal black line on the mesonotum. Thus, it is hereby reinstated as a valid species with the new combination *Trachythorax illaesa* stat. rev. comb. nov. The species was previously only known from male specimens, but photographic records of mating pairs and eggs have revealed the female and the egg deposition method (Figs 25 C–F, 26 A).

SUPPLEMENTARY DESCRIPTIONS

FEMALE

Females much resemble males and have a light brown ground colour. The head has a pair of small black spots between the eyes followed by a short mediolongitudinal line; sides of head with black postocular stripe. Pronotum with anterior margin yellow and with a black spot anteromedially; prozona with a pair of black elongate stripes submedially: metazona as prozona: posterior margin with black spot medially. Mesonotum with distinct black mediolongitudinal line not reaching the posterior margin; anterior half with a pair of elongate black markings submedially; strong anteroapical carina parallel to posterior margin followed by a distinct red transverse crescent. Wings brown with dark and lighter mottling, almost reaching the apex of the abdomen in females. The legs are banded light and dark brown, bands less distinct in males.

EGGS (Figs 26 B–D, 32 C–E).

The eggs of *T. illaesa* are deposited in groups with the specialised structures of the opercular collar folded against the capsule (Fig. 26 A–B); they fold open shortly after egg laying to form an almost completely sealed egg-case (Fig. 26 C–D). Egg capsule ovoid, with polar area glued to other eggs or to a surface. Opercular collar with two large lateral trapezoidal flaps and two small triangular lateroventral flaps. Lateral margins of flaps paler and distinctly toothed. Operculum more or less oval with rounded tubercle subcentrally (Fig. 26 C–D).

DISTRIBUTION. Southeast India (Karnataka and Maharashtra states), Sri Lanka.



Fig. 25. *Trachythorax illaesae* (Redtenbacher, 1908) stat. rev. comb. nov. A, HT ♂, dorsal view and labels. © MNHN. B, ♂, Karnataka State, Mangalore, IX.2018. © Jitesh Pai. C–F, mating pairs. C, Matale, Laggala-Pallegama, Sri Lanka. 3.iv.2018. © Pieter Prins, iNaturalist, observations/37204645. D, Maharashtra State, Amboli, 2020. © Varad Giri. E, Karnataka State, Puttur, X.2018. © Abhijith APC. F, Karnataka State, Agumbe, X.2020. © Vishwanath Gowda.



Fig. 26. *Trachy thorax illaesae* (Redtenbacher, 1908) stat. rev., comb. nov., Maharashtra State, Amboli, 2016.
© Varad Giri. A, egg laying ♀ with ♂ attached. B, freshly laid eggs. C–D, eggs after 10 hours.

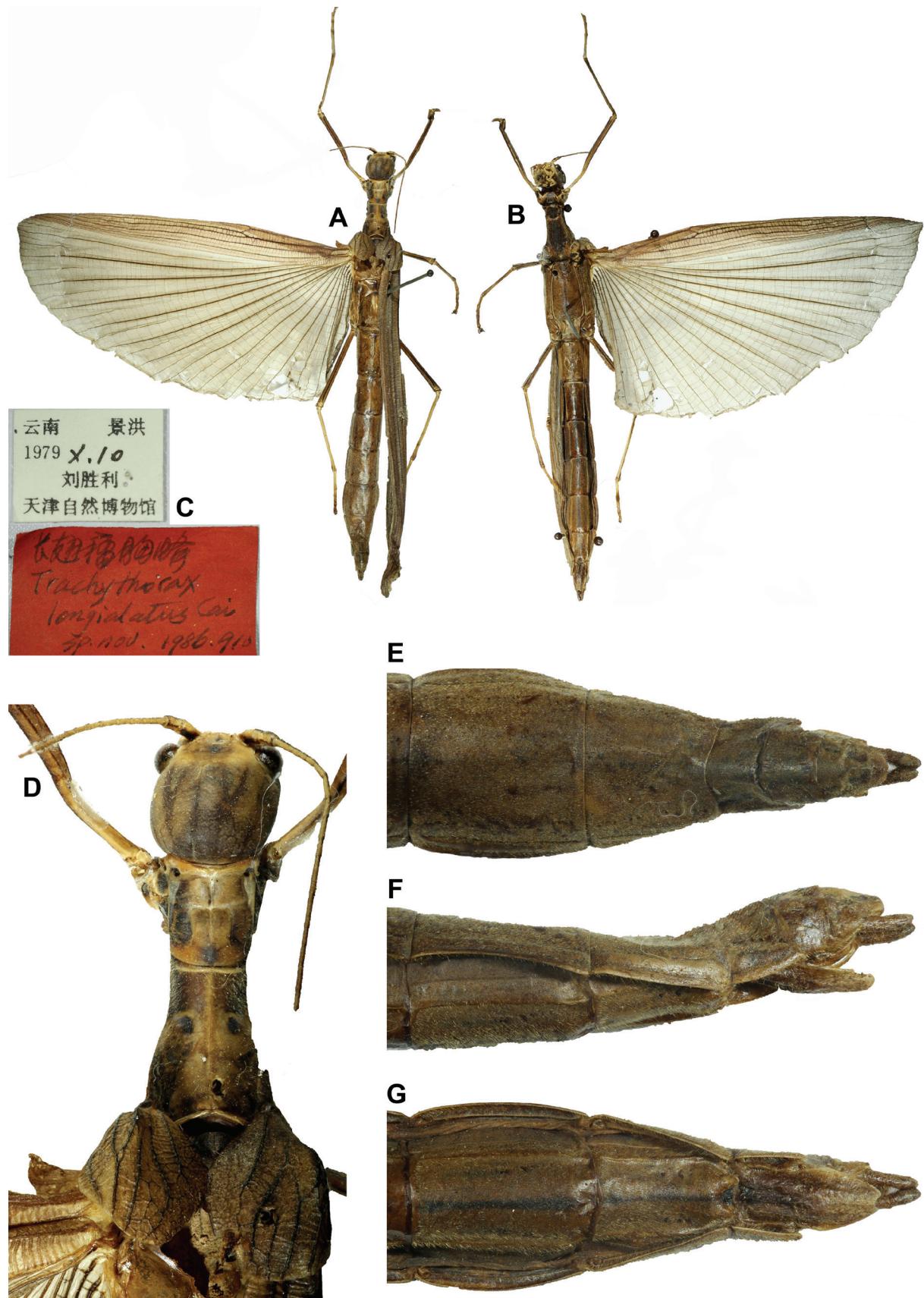


Fig. 27. *Trachythorax longialatus* Cai, 1989, HT ♀. A, habitus, dorsal view. B, habitus, ventral view. C, labels. D, head and thorax, dorsal view. E, terminalia, dorsal view. F, terminalia, lateral view. G, terminalia, ventral view. © NKUM.

***Trachythorax incertus* Redtenbacher, 1908**

Trachythorax incertus REDTENBACHER, 1908: 508 [described].

Trachythorax incertus – BROCK, 1998: 34 [type data]. — OTTE & BROCK, 2005: 336 [catalogued].

MATERIAL EXAMINED. TYPE MATERIAL. (examined from photographs on PSF – BROCK *et al.*, 2021) VIETNAM: HT ♀: Tonkin, Than-Moi, Juni-Juli, H. Frühstorfer (NHMW).

COMMENTS. Currently still only known from a single female from Than-Moi (or Thanh Moi), in North Vietnam (21°38'N, 106°32'E) (SCHILEYKO, 2011). The type-locality is close to Ba Be N.P. The species is morphologically close to *T. chinensis* Redtenbacher, 1908 and *T. longialatus* Cai, 1989; more material is necessary to correctly differentiate this species from congenerics. It can be differentiated from *T. albomaculatus* sp. nov and *T. auranticollis* by the pink membrane between the pronotum and the head and by the distinct dark spots on the pronotum.

***Trachythorax longialatus* Cai, 1989**
(Fig. 27)

Trachythorax longialatus CAI, 1989: 322, figs 1–5 [described and figured].

Trachythorax longialatus – OTTE & BROCK, 2005: 336 [catalogued]. — HENNEMANN *et al.*, 2008: 41 [catalogued]. — CHEN & HE, 2008: 181; fig. 146 [in China, illustrated]. — GAO & LIANG, 2021: 1 [in key to Chinese species].

MATERIAL EXAMINED. TYPE MATERIAL. (examined from photographs – Fig. 27) CHINA: HT ♀: Sichuan, Guanxian County, 15.VIII.1980, Wu Wenbling (NKUM).

COMMENTS. See comment under *Trachythorax chinensis* (Redtenbacher, 1908).

***Trachythorax maculicollis* (Westwood, 1848)**
(Figs 28–29)

Phasma (Necroscia) maculicollis WESTWOOD, 1848: 77, plate 38: 2 [described and figured].

Calvisia atrosignata BRUNNER VON WATTENWYL, 1893: 85, plate 3: 27 [described and figured].
Synonymised by SEOW-CHOEN (2017).

Marmessoidea conspersa REDTENBACHER, 1908: 515 [described]. Synonymised by SEOW-CHOEN (2017).

Necroscia maculicollis – WESTWOOD, 1859: 155 [redescribed].

Calvisia maculicollis – KIRBY, 1904: 369 [catalogued]. — REHN, 1904 [recorded from Thailand].

Trachythorax maculicollis – REDTENBACHER, 1908: 508, plate 26: 3 [redescribed, transferred to *Trachythorax*]. — SCHULTEN, 1995: 60, fig. 32 [rearing]. — SELLICK, 1998 [egg structure]. — CLIQUENNOIS, 1999: 52 [recorded from Bangladesh], figs 18–19 [female and mating pair], 23 [egg]. — BAXTER, 2002: 89 [rearing, egg]. — OTTE & BROCK, 2005: 336 [catalogued]. — HARMAN, 2012: 16 [origin of culture stocks]. — BROCK *et al.*, 2016: 181 [catalogued]. — MAOSHENG, 2016: 143 [in Singapore]. — SEOW-CHOEN, 2017: 88, figs 74–75 [in Singapore]. — SEOW-CHOEN, 2018: 392, figs 306–309 [in Sumatra].

Trachythorax maculicollis maculicollis – GAO & LIANG, 2021: 1 [as subspecies, in key to Chinese species].

Trachythorax atrosignatus — REDTENBACHER, 1908: 504 [redescribed, transferred to *Trachythorax*]. — VANSCHUYTBROECK & COOLS, 1981: 10 [material in RBINS collection, in Vietnam, Thailand & Java]. — CAI, 1989: 323 [in China]. — BROCK, 1998: 16 [type data]. — BROCK, 1999: 121, fig. 180 [as valid species]. — OTTE & BROCK, 2005: 336 [catalogued]. — CHEN & HE, 2008: 179 [in China].

Trachythorax atrosignata — HENNEMANN *et al.*, 2008: 40 [in China].

Marmessoidea conspersa — BROCK, 1998: 23 [type data, lectotype, synonym of *T. atrosignata*].

ADDITIONAL MATERIAL. CAMBODIA: 2♂♂, 2♀♀: Kampong Speu, Phnom Aural W.S., nr. Srae Ken vill., 10–14.V.2018, 200–400m, 11°59'N 104°08'E, GTI project, leg. J. Constant & P. Limbourg, I.G.: 33.732 (RBINS); 3♂♂: ex breeding Tim Bollens, 2018: Kampong Speu, Phnom Aural W.S., nr. Srae Ken vill., 10–14.V.2018, 200–400m, 11°59'N 104°08'E, GTI project, leg. J. Constant & P. Limbourg, I.G.: 33.732 (RBINS); 5♂♂, 5♀♀: ex breeding Tim Bollens, 2019: Kampong Speu, Phnom Aural W.S., nr. Srae Ken vill., 10–14.V.2018, 200–400 m, 11°59'N 104°08'E, GTI project, leg. J. Constant & P. Limbourg, I.G.: 33.732 (3♂♂, 3♀♀: RBINS; 1♂, 1♀: RUPP; 1♂, 1♀: VNMN); 1♂: Koh Kong prov., Tatai, 11°35'13"N 103°05'50"E, 27.VII.2016, day collecting, Leg. G. Chartier (RBINS); 2♂♂, 1♀: Mondulkiri Prov., Keo Seima Wildlife Sanctuary nr O Pam station, 12°11'39"N 107°01'01"E, 14–24.XI.2018, leg. J. Constant, I.G.: 33.919 (RBINS).

VIETNAM: 10♂♂: Nge An Province, Pu Mat National Park, 18°59'N 104°40'E, 4-9.VII.2017, night collecting, GTI project, leg. J. Constant & J. Bresseel, I.G.: 33.498 (RBINS); 3♂♂: Dong Nai Biosphere Res. 11°18'N 107°06'E, 25.vi–6.vii.2012, night collecting, Leg. J. Constant & J. Bresseel, I.G.: 32.161 (RBINS); 5♂♂, 1♀: VinhPhuc pr., Melinh B.S., 21°23'38"N 105°42'56"E, 30.VI–1.VII.2015, night collecting, Leg. J. Constant & J. Bresseel, I.G.: 33.092 (RBINS); 1♂, 1♀: Con Dao N.P., Con Son Isl., 08°41'30"N 106°38'00"E, 17–24.VI.2012, day collecting, Leg. J. Constant & J. Bresseel, I.G.: 32.161 (RBINS); 1♂, 2♀♀: Tonkin, Than Moi, Juni–Juli, H. Fruhstorfer (RBINS); 14♀♀: Than Moi, Tonkin, 2–3000, IV–V, H. Rölle, Berlin, S.W.11, ex. coll. Le Moult (RBINS); 1♂, 5♀♀: Than Moi, Tonkin, ex. coll. Le Moult, I.G. 18.487 (RBINS); 4♂♂, 9♀♀: Annam, Phuc-Son, nov.–dez., H. Fruhstorfer (RBINS); 1♀: Chapa, Tonkin, Collection Le Moult, Naturaliste Paris (RBINS).

THAILAND: 1♂, 1♀: Loei prov., Na Haeo, 16.V.2003, Leg. J. Constant & K. Smets (RBINS); 1♂, 1♀: Bangkok, P. Rolin (RBINS).

PHOTOGRAPHIC RECORDS. CAMBODIA: mating pair (Fig. 28 A): Kampot, 10°36'N 104°10'E, 12.III.2009, R. Overtoom.

INDIA: mating pair: Assam, Karimganj, Dosdewa forest trail, 24°21'10"N 92°20'41"E, 11.IV.2020, iNaturalist user rejoicegassah <https://www.inaturalist.org/observations/44459807>.

MALAYSIA: mating pair: Kelantan, Kota Bharu, 6°06'16"N 102°15'05"E, 4.III.2021, iNaturalist user izzati1 <https://www.inaturalist.org/observations/70554087>.

DIAGNOSIS. The type-species of *Trachythorax* with males much smaller than females and characterised by the pattern on the head, pro- and mesonotum and by the peculiar pink inflatable membrane between the pronotum and the head (this last feature not always visible in dried specimens). Head with a pair of black spots between the eyes followed by a median black spot dorsally; behind the eye with two longitudinal black stripes. Pronotum with prozona with a pair of elongate oval black spots; metazona with four elongate oval black spots, median pair often less distinct than outer pair. Mesonotum with a lateral black stripe in the anterior half; posterior half with two markings laterally, anterior one small and more or less oval, posterior one distinctly bigger and slightly elongate. Females with a pair of humps almost medially on the mesonotum.

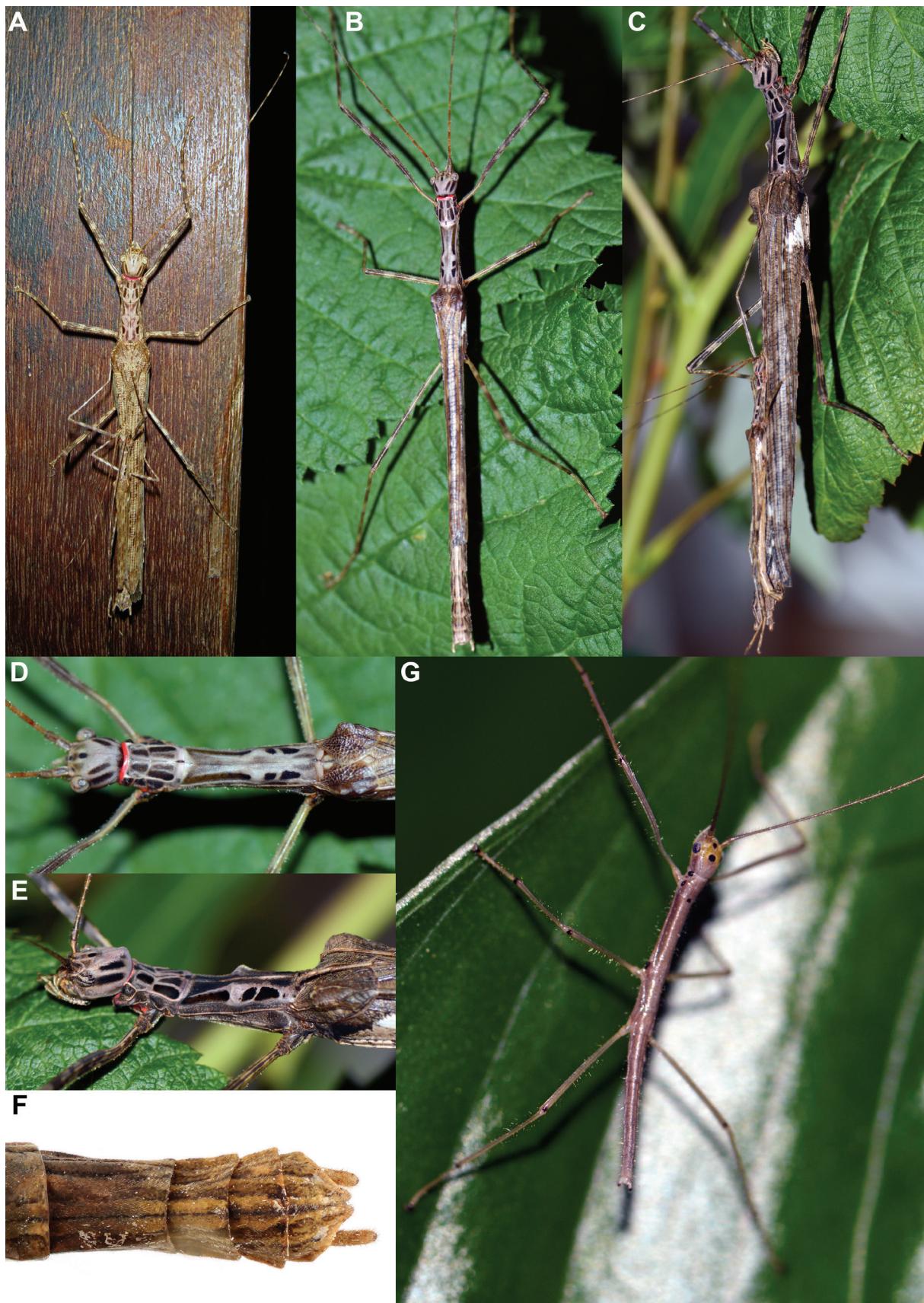


Fig. 28. *Trachythorax maculicollis* (Westwood, 1848) from Cambodia. A, mating pair, Kampot, 12.III.2009. © R. Overtoom. B–G, Kampong Speu prov, Phnom Aural, ex breeding T. Bollens. B, ♂, dorsal view. C, mating pair, lateral view. D, ♂, head and thorax, dorsal view. E, ♀, head and thorax, dorsolateral view. F, ♀ terminalia, dorsal view. G, newly hatched nymph. B–E, G. © T. Bollens. F. © J. Constant.

NOTES. The species was originally described from Silhet, Assam. Today Silhet is known as Sylhet and lies in Bangladesh, close to the Assam border. The species seems to be extremely widespread over Southeast Asia making it one of the most widespread species of stick insect in this region and even on a global point of view. There seems to be some geographical variation to a certain degree, but always with the combination of characters presented in the diagnosis above. The markings on head and thorax can sometimes be less distinct but are always present.

The head shape shows a certain degree of variation. In most cases, like in the type-series, it bears a conical elevation posteriorly, with the cone directed upwards. However, this elevation can be less distinct or even absent; in the latter case, the back of the head only being convex. Morphometrics of the wings of specimens from different localities also show small but stable differences (Bresseel & Constant, personal observations).

MAOSHENG (2016) and SEOW-CHOEN (2017) recently reported the species from Singapore based on the same record. BROCK (1999) doubted its presence in Peninsular Malaysia. The recorded specimen is peculiar for having the markings on head and pronotum as well as the profemora green instead of black and the lateral markings on the mesonotum black. A picture on iNaturalist from Kelantan, Malaysia shows the same “aberrant” colouration and more research is needed to confirm whether these records truly represent *T. maculicollis*.

The synonym *T. atrosignatus* (Brunner von Wattenwyl, 1893), synonymised by SEOW-CHOEN (2017), shows no clear morphological differences, and has the exact same markings on the head, pro- and mesonotum. The synonymy of *T. conspersa* (Redtenbacher, 1908), synonymised by BROCK, 1998, warrants further research. The species was described from the Nicobar Islands, but without additional material at hand it is hard to confirm if this species is actually *T. maculicollis*. Therefore, it is here retained as a synonym. *Trachythorax illaesa* (Redtenbacher, 1908) stat. rev. comb. nov., synonymised by BROCK & DELFOSSE (2005) differs from *T. maculicollis* by the markings on the head, pro- and mesonotum. It is therefore here reinstated as a valid species (see comment under *T. illaesa*).

DISTRIBUTION. (Fig. 29). The species is widespread in Southeast Asia, with historical records from India, Bangladesh, Myanmar, Thailand, China, Vietnam, Singapore, Sumatra and Java.

New records show that this species is widespread in Vietnam, from Sa Pa (“Chapa”), Lao Cai Province in the north to the Con Son Archipelago in the South. The species is recorded from Cambodia for the first time.

***Trachythorax planiceps* Redtenbacher, 1908**
(Fig. 30)

Trachythorax planiceps REDTENBACHER, 1908: 508 [described].

Trachythorax planiceps – BROCK, 1998: 50 [type material]. — OTTE & BROCK, 2005: 336 [catalogued].

MATERIAL EXAMINED. TYPE MATERIAL. (examined from photographs – Fig. 30) INDIA: HT ♀: coll. Br. v. W., Sikkim, Staudinger, 22.868 (NHMW).

COMMENTS. See comment under *T. sparaxes* (Westwood, 1859).

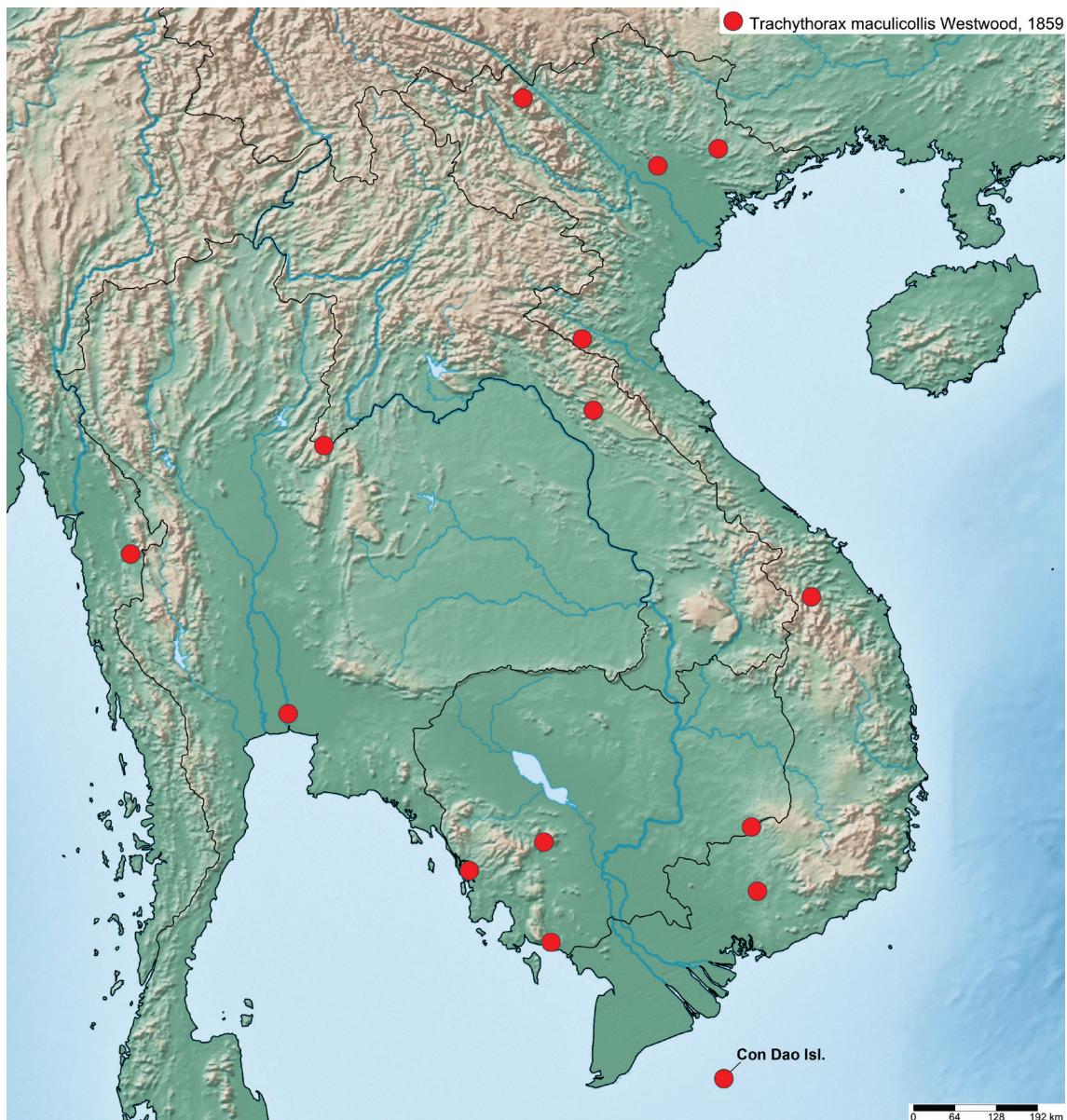


Fig. 29. *Trachythorax maculicollis* (Westwood, 1848) distribution map with data from specimens in RBINS.



Fig. 30. *Trachythorax planiceps* Redtenbacher, 1908. © NHMW. A, HT ♀, head and thorax, dorsal view. B, HT labels.

Trachythorax sexpunctatus (Shiraki, 1911)

Necroscia sexpunctata SHIRAKI, 1911: 304, plate 12: 4 [described and figured].

Trachythorax sexpunctatus — MATSUMURA & HIRAYAMA, 1931: 819 [transferred to *Trachythorax*, figured]. — SHIRAKI, 1935: 78, plate 9: 4–6 [female, described and figured]. — CAI, 1989: 322 [differentiation]. — HUANG, 2002: 108 [as “*sixpunctatus*”; figured, distribution, egg, host plant]. — OTTE & BROCK, 2005: 336 [catalogued]. — HENNEMANN *et al.*, 2008: 41 [catalogued]. — CHEN & HE, 2008: 179; fig. 144 [in China, illustrated]. — GAO & LIANG, 2021: 1 [in key to Chinese species].

TYPE MATERIAL (examined from photographs on PSF – BROCK *et al.*, 2021). TAIWAN: HT ♂: Formosa, Koshun, Nitobe, 746 (NTU).

COMMENTS. *Trachythorax sexpunctatus* (Shiraki, 1911) was originally described based on a unique male holotype by SHIRAKI (1911) and placed in the genus *Necroscia* Audinet-Serville, 1838. MATSUMURA & HIRAYAMA (1931) transferred the species to *Trachythorax* Redtenbacher, 1908 and SHIRAKI (1935) subsequently described the female. The species is closely related to *T. chinensis* (Redtenbacher, 1908) and *T. longialatus* Cai, 1989 but can be differentiated by the shorter wings that do not reach the apex of the abdomen, the longer anal segment and smooth subgenital plate (CAI, 1989). HUANG (2002) provided a figure of the eggs and a distribution map. The species seems to be spread along the southeastern coast of Taiwan and is considered to be endemic on the island.

Trachythorax sparaxes (Westwood, 1859)

(Fig. 31)

Necroscia sparaxes WESTWOOD, 1859: 153, plate 9: 6; 20:4 [described and figured].

Necroscia sparaxes — KIRBY, 1904: 377 [catalogued].

Trachythorax sparaxes — REDTENBACHER, 1908: 508 [transferred to *Trachythorax*, key]. — BEDFORD, 1978: 126 [oviposition]. — CARLBERG, 1986: 643 [reproduction adaptation]. — CARLBERG, 1987: 47 [ovarian structure]. — OTTE & BROCK, 2005: 337 [catalogued]. — MANDAL & YADAV, 2010: 16 [catalogued]. — BROCK *et al.*, 2015: 196 [catalogued].

MATERIAL EXAMINED. TYPE MATERIAL (examined from photographs on PSF – BROCK *et al.*, 2021).

SRI LANKA: 2 ST (1♂, 1♀): 1♂: Ceylon, (R. Templeton) [BMNH(E) #844861] (NHMUK); 1♀: Ceylon, ‘var. of Templeton’s Ceylon species’ (R. Templeton) [BMNH(E) #844862] (NHMUK).

ADDITIONAL MATERIAL. INDIA: 1♀: South India, Madras State, Coimbatore, 1400 ft a.s.l., I.1960, coll P.S. Nathan, F3224.266 (MMUE); 1♀: S. India, Madras st., Coimbatore, XI.1966, P.S. Nathan, F3224.142 (MMUE); 1♂, 1♀: Karnataka, Kolar distr., Chick Ballapur, leg H. Mühlle, 27-28.VIII.1998, FH 0270 – 2 and 3 (FH) (examined from photographs provided by F. Hennemann); 1♂: Umgebung, Trivandrum, Whest-Ghats, Leg Rautenstrauch, FH 0270 – 1 (FH) (examined from photographs provided by F. Hennemann).

NOTE. BROCK *et al.* (2015) also mentioned 2 additional syntypes (1♂, 1♀) in OUMNH, but WESTWOOD (1859) only cited the material from NHMUK.

PHOTOGRAPHIC RECORD. INDIA: maiting pair (Fig. 31): Tamil Nadu, Dindigul, Thadiyankudisai, 10° 17'51.70"N 77° 42'38.40"E, 21.VII.2018, at light trap, H. Sankararaman.



Fig. 31. *Trachythorax sparaxes* (Westwood, 1859), South India, Tamil Nadu, 2018. © H. Sankaraman. A, mating pair, dorsal view. B, mating pair, dorsolateral view. C, ♀, head and thorax, dorsal view.

COMMENTS. *Trachythorax sparaxes* (Westwood, 1859) was described from Sri Lanka based on both sexes by WESTWOOD (1859) who originally placed the species in *Necroscia* Audinet-Serville, 1838. REDTENBACHER (1908) transferred the species to *Trachythorax* and described *T. planiceps* Redtenbacher, 1908 from Assam in the same publication. He differentiated *T. planiceps* from *T. sparaxes* by the saffron-coloured anterior and posterior margins of the pronotum and the smooth mesonotum. However, examination of pictures of the type-series of *T. sparaxes*, shows a smooth mesonotum in this species as well. The saffron-coloured anterior and posterior margins in *T. planiceps* are in fact pink in living specimens and specimens of *T. sparaxes* photographed from South India and Sri Lanka also show the same colouration. MANDAL & YADAV (2010) recorded the species from Bihar and Sikkim states in Northeast India. The species is here recorded from Madras state, South India for the first time.

No clear diagnostic differences could be observed between *T. planiceps* and *T. sparaxes*. Despite the long distance between the two type localities, additional data from iNaturalist (iNATURALIST, 2021) could allow to fill the gap between south India and North-east India. The possible synonymy between the two species needs to be confirmed or refuted by the examination of more material from different localities.

***Trachythorax unicolor* Redtenbacher, 1908**

Trachythorax unicolor REDTENBACHER, 1908: 507 [described].

Trachythorax unicolor – OTTE & BROCK, 2005: 337 [catalogued].

MATERIAL EXAMINED. TYPE MATERIAL (examined from photographs on PSF – BROCK *et al.*, 2021). INDONESIA: ST ♂, ♀: Tjibodas, Java, 1400 m, Schröter., 29 (ETHZ).

COMMENTS. This species is only known from the type specimens and was collected by Schröter during his voyage around the world (1898–99). He stayed in West-Java from end December 1898 to January 1899 where he collected in mangrove forest and at Buitenzorg, Tjibodas on December 29, 1898 (VAN STEENIS & VAN STEENIS, 1950). Most probably the label with only the number 29, refers to the collecting date.

The Tjibodas Forest Reserve, with the twin volcanoes Mt Gede and Mt Pangerango, was founded during the Dutch colonial period. The former Tjibodas reserve ranged in altitude from 1400–2900m and the area is currently included in the Mount Gede Pangrango National Park. The Tjibodas “Bergtuin” was located at the foot at an altitude of 1400 m and is currently named the Cibodas Botanical Garden (CBG) (MEIJER, 1959; HIDAYAT & WINARNI, 2017).

The type-specimens are in poor condition. They were probably preserved in alcohol prior to mounting, and this may have altered their colouration. The species needs a re-description, preferably based on recent material. More material including eggs and pictures of living individuals are needed for comparison and for an accurate differentiation from other species. The species morphologically resembles *T. gohi* ant *T. albomaculatus* sp. nov.

Discussion

EGG MORPHOLOGY AND PARASITISM

FATOUROS *et al.* (2020) showed that insect orders including species with a herbivorous life style and exposed oviposition sites on plants appear to be at higher risk of being targeted by egg parasitoids. They showed that hosts developed numerous intriguing ways to counteradapt to ooparasitism and several characteristics are considered to have evolved from egg parasitism pressure such as reduced incubation time, small egg size, production of ootheca, application of egg coatings or thick chorions preventing egg penetration. Egg parasitism in stick insect was

reported on several occasions (HEATHER, 1965; KIMSEY *et al.*, 2013; BAKER, 2015). Hymenoptera: Chrysidae in the subfamilies Amiseginae and Loboscelidiinae, which are a group of primitive cuckoo wasps, are known to be obligatory parasitoids of stick insect eggs. For both subfamilies, only few hosts are known (KROMBEIN, 1983), but they represent at least five subfamilies in three families of stick insects (Phasmatidae: Phasmatinae, Tropidoderinae; Pseudophasmatidae: Pseudophasmatinae and Prisopodinae; Diapheromeridae: Diapheromerinae). Female wasps pierce the egg capsule with their mandibles for oviposition and the fully developed wasp hatches by bursting the operculum (KROMBEIN, 1983).

Several methods for possible protection against egg parasites have been documented. The eggs of many stick insects resemble plant seeds and bear a capitulum mimicking a seed elaiosome (fleshy structures attached to the seeds of many plant species, rich in lipids and proteins, that attract ants, which take the seed to their nest and feed the elaiosome to their larvae). The capitulum attracts the ants and promotes the transportation of the stick insect eggs to the ant nest. Capitula are found only in phasmids which drop their eggs freely onto litter and not in the taxa which bury their eggs or attach them to the vegetation (HUGHES, 1992). YAMADA *et al.* (2021) recently recorded this form of myrmecochory for the first time from the Oriental Region. Whether being deposited in ant nests, protects the phasmid eggs from parasites and promotes survival, still needs to be further studied (O'HANLON, 2020).

In some cases, as shown in the genus *Korinnis* Günther, 1932, phasmids can produce an ootheca. A dense layer coating the surface of the ootheca likely provides protection as does the tight egg arrangement which largely decreases the capsule surface accessible to parasitoids. Parasitism and host plant specificity (the latter selecting for methods allowing nymphs a direct access to the right food plant) most probably triggered the rapid evolution of this unique oviposition strategy among stick insects (GOLDBERG *et al.*, 2015).

Egg morphology and egg deposition in Trachythorax

The egg clutches of *Trachythorax* spp. are deposited in three rows of eggs and form, after the drying process, an almost single structure that, thanks to the several morphological adaptations of the egg capsule and operculum, considerably decreases the accessible capsule surface and effectively forms a physical protective barrier (Fig. 32 A, C, E, G).

The egg morphology of the different *Trachythorax* species is diverse and exhibits structures not present in other Phasmatodea. The eggs in most species of the genus are characterised by the different morphological adaptations radiating from the opercular collar, produced by a splitting away of the surface of the capsule. Care must be taken not to confuse it with structures on the opercular rim that come away with the operculum during hatching. Freshly laid eggs have all extensions of the opercular collar folded against the capsule (Figs 6 A–C, 26 A–B). Shortly after laying, during the “drying” process, the capsule surface cracks open and the extensions are lifted from the capsule surface and overlap with adjacent eggs laterally. The egg of *Trachythorax sexpunctatus* (Shiraki, 1911) was figured by HUANG (2002) and CHEN & HE (2008) and has the opercular collar somewhat elongate but lacks lateral extensions. However, it shares with other *Trachythorax* species, the ovoid egg shape and laterally compressed posterior portion of the capsule. The eggs of *T. maculicollis* and *T. yunnanensis* (Figs 19, 32 A–B) have a fairly simple structure with frills radiating from the opercular collar and a small triangular to semi-circular extension on the ventral margin of the operculum, here named opercular flap (*of*). The eggs of *T. illaesae* are more complex and have the opercular collar with

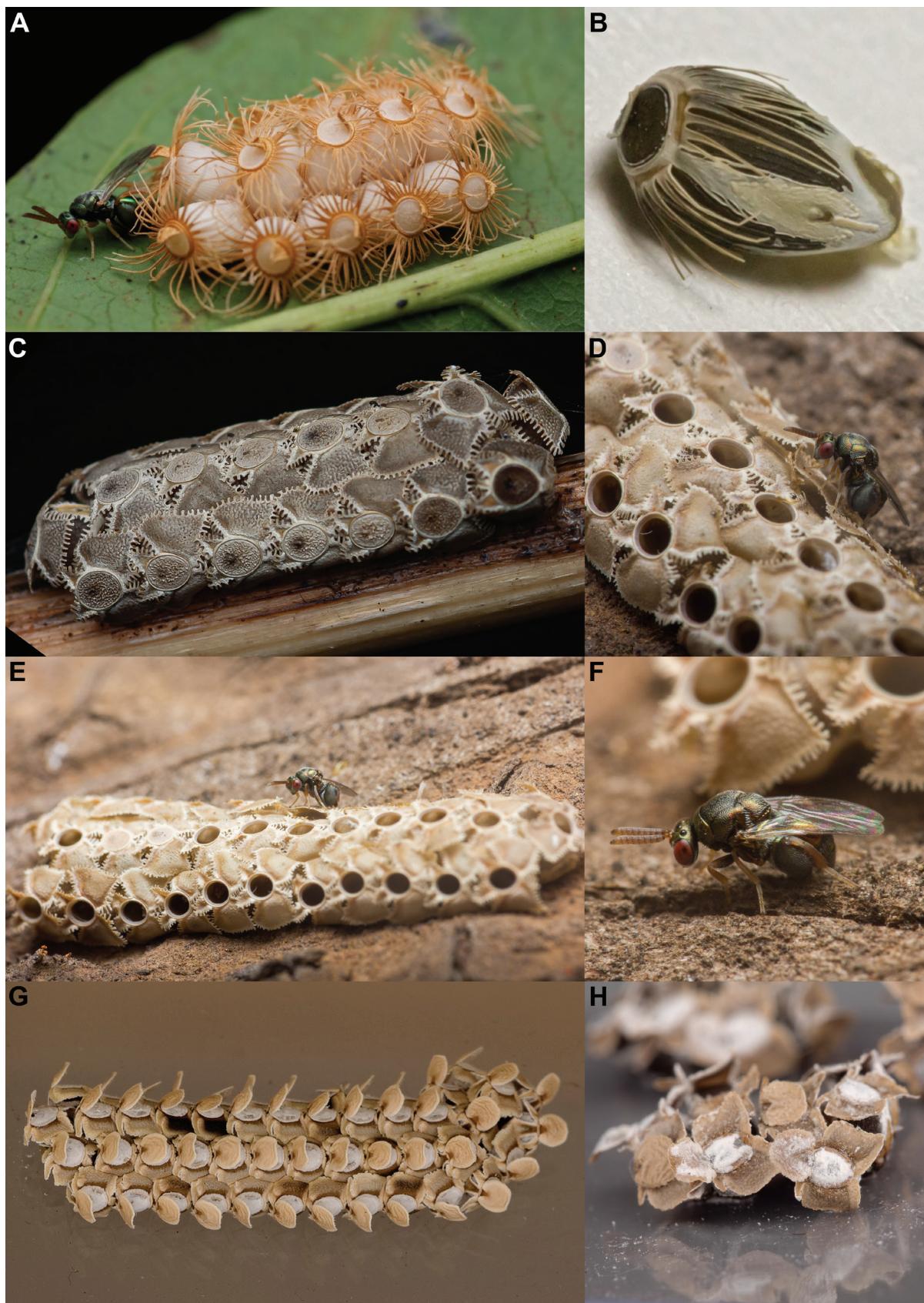


Fig. 32. *Trachythorax* spp. Egg forms and parasites A–B, *Trachythorax maculicollis* (Westwood, 1848). A, egg clutch with parasitoid wasp, Ankor Wat, Cambodia, 24.XI.2013. © P. Bertner. B, Con Dao Island, Vietnam, 2012. © B. Kneubühler. C–F, *Trachythorax illaes* (Redtenbacher, 1908) stat. rev. comb. nov. C, Agumbe, Karnataka state, X.2020. © V. Gowda. D–F, hatched eggs with parasitoid wasp, Nagla trail, Mumbai, Maharashtra state, 2018. © Prajwal Ullal. G–H, *Trachythorax albomaculatus* sp. nov. © B. Kneubühler.

two large, trapezoidal flaps laterally and two small, triangular flaps lateroventrally. These flaps are armed with distinct teeth on their margins and the operculum is simple, with a distinct tubercle ventromedially (Fig. 32 C). The eggs of *T. albomaculatus* sp. nov. (Fig. 32 G–H) resemble those of *T. illaes*a and have two large lateral flaps (*lf*) and two slender, elongate lateroventral flaps (*lvf*); the opercular flap (*of*) is a large round extension protruding from the ventral margin, acting as a false lid when the egg is deposited and popping open when the egg dries, leaving a silk-like substance covering the true operculum (*op*). The eggs of the other species remain unknown.

Records of egg parasitism in *Trachythorax*

CHEN & HE (2008) reported the first case of egg parasitism in the genus *Trachythorax* and figured a parasitoid wasp emerging from a *T. sexpunctatus* egg (CHEN & HE, 2008, pl. 8, fig. 1). Two photographic records are here provided of a small chalcidoid wasp (Hymenoptera: Chalcidoidea) on egg clutches of *T. illaes*a in India, Karnataka and *T. maculicollis* in Cambodia, Angkor Wat (Fig. 32 A, D–F) and it is assumed that these are parasites threatening the eggs of *Trachythorax* species. Only one previous record of this Hymenoptera superfamily parasitizing stick insects in the New World genus *Prisopus* Peletier de Saint Fargeau & Audinet-Serville, 1828, is available (GATES, 2008).

COMPARISON WITH RELATED TAXA

GOLDBERG *et al.* (2015) found *Trachythorax* not to be closely related to Korinninae in their molecular phylogeny and concluded that the “egg forms” observed in *Trachythorax* could not precede the ootheca formation observed in *Korinnis* Günther, 1932 in the track of the evolutionary process. However, other and more recent phylogenetic studies have placed *Trachythorax* in a lineage comprising *Korinnis*, *Sipyloidea* Brunner von Wattenwyl, 1893, *Asceles* Redtenbacher, 1908, *Diesbachia* Redtenbacher, 1908 and allies (BRADLER *et al.*, 2014; ROBERTSON *et al.*, 2018). These species exhibit a diverse range of oviposition strategies and the authors state it is unclear what selective pressures may have promoted this diversification (ROBERTSON *et al.*, 2018). O’HANLON *et al.* (2020) suggest that the functional benefits of the varied oviposition strategies involving specific placement may include access to host plants and protection from predators and parasites. Several species from this lineage use adhesion for egg deposition and glue their eggs to the substrate (like *Trachythorax*). In the majority of cases, the adhesion is on the ventral surface of the capsule and the operculum is displaced towards or onto the dorsal surface (e.g. *Calvisia* Stål, 1875, *Sipyloidea* and *Tagesoidea* Redtenbacher, 1908). However, eggs of *Trachythorax* and of the ootheca producing *Korinnis* sp. are glued by their posterior pole, the operculum remaining anterior (SELLICK, 1997; GOLDBERG *et al.*, 2015). Eggs of *Korinnis* sp. (Fig. 33 A–B), like those of *Trachythorax*, have a specialised structure radiating from the opercular collar (*oc*), which is present as a broad band completely encircling the capsule and overlapping with adjacent eggs. There is little information on the act of egg laying in *Korinnis*, but the specialised structure of the opercular collar might be folded against the egg capsule during oviposition and unfold the same way as in *Trachythorax* when dehydration takes place. Other characters relating *Trachythorax* and *Korinnis* are the small-sized males, the elongate wings and capability of sustained flight, the shortened tegmina and arboreal lifestyle (Bresseel & Constant, personal observation).

The eggs of the supposedly closely related genera such as *Asceles*, *Loxopsis* Westwood, 1859 and of some species within *Marmessoidea* Brunner von Wattenwyl, 1893 e.g. *M. alata alata* Ho, 2018 (Fig. 33 C–H) are also attached by their posterior pole, sometimes by a collared,

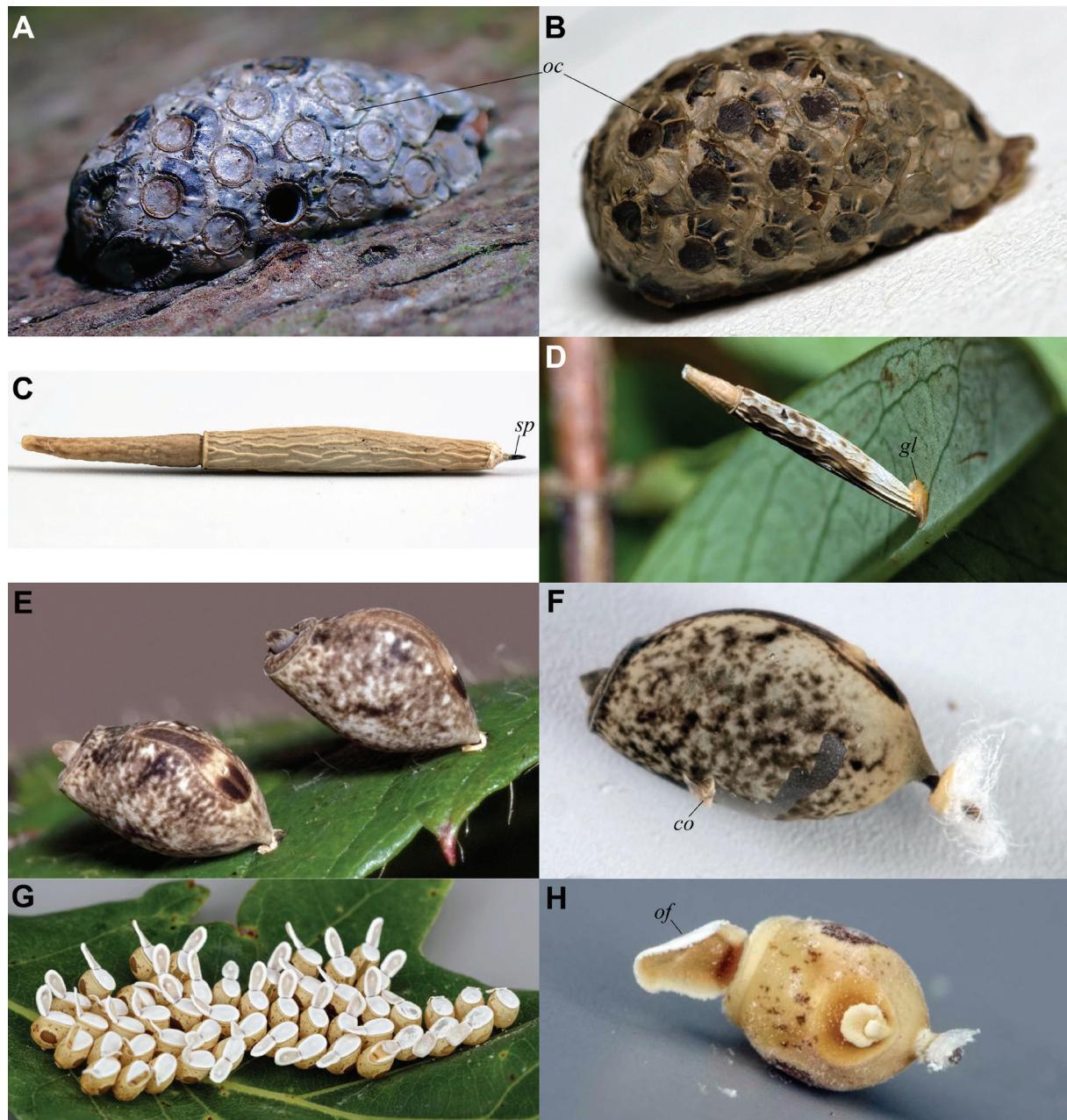


Fig. 33. Necrosciinae egg morphology and egg deposition methods. A–B, *Korinnis* spp. ootheca. A, Malaysia, Penang, 2020. © A. Kang. B, Cat Tien N.P., Vietnam, 2012. C–D, *Asceles* sp., Cat Tien N.P. E–F, *Marmessoidea alata alata* Ho, 2018, Bach Ma N.P., Vietnam (ex breeding). G–H, *Loxopsis* sp. Tawau, Borneo. B–H. © B. Kneubühler; *oc* = opercular collar; *of* = opercular flap; *sp* = spine; *gl* = glue; *co* = coating.

spine-like extension (*sp*) which is used to pierce and fix eggs to leaves (SELLICK, 1997). Eggs of these genera have an outer layer or coating (*co*) on the capsule that can peel off, but it does not radiate from the opercular collar (Fig. 33 F). Several representatives (e.g. *Asceles glaber* Günther, 1938 and *Marmessoidea alata alata*) of this lineage have the egg membrane covered with a thin surface layer and have a non-alveolar capsule, leaving the egg more vulnerable although coating eggs with secretions can protect them against predators, parasitoids, and pathogens (FATOUROS *et al.*, 2020). Sometimes the species showing this behaviour can also produce some eggs without coating (Bresseel & Constant, pers. obs.). Certain species in the genus *Asceles* (Fig. 33 C–D) use a combination of piercing leaves with a posterior spine (*sp*), with adhesion from “glue” (*gl*), which was overlooked by previous authors (SELLICK, 1997; ROBERTSON *et al.*, 2018).

The eggs of an unidentified *Loxopsis* species from Tawau, Borneo (Fig. 33 G–H) have a specialised opercular flap (*of*) on the operculum similar to the one of *T. albomaculatus* sp. nov., acting as a false lid. The opercular flap opens shortly after egg laying, leaving a silk-like material covering the true operculum. The species is being reared in captivity and deposits its eggs in groups underneath leaves of its host plant. The opercular flap opens after drying, but when the egg gets wet to a certain degree, the opercular flap will re-close rapidly, and open again after drying (M. Duytschaever pers. comm., 2021). Whether this is also the case in eggs of *T. albomaculatus* currently remains unknown, but this phenomenon might provide some direction to investigate the function of the opercular flap.

Conclusion

With the description of *T. albomaculatus* sp. nov. and *T. auranticollis* sp. nov., the reinstated valid species status of *T. illaesa* (Redtenbacher, 1908) stat. rev. comb. nov. and the new status of *T. yunnanensis* Gao & Liang, 2021 stat. nov., *Trachythorax* now comprises 15 known species. Some species are sometimes difficult to differentiate morphologically, e.g. *T. gohi* Brock, 1999 and *T. albomaculatus* sp. nov. or *T. yunnanensis* Gao & Liang, 2021 and *T. maculicollis* (Westwood, 1848). Their close resemblance, wide distribution as well as the morphological variability relating to their geographical distribution, makes them a suspect for harbouring cryptic species. Molecular studies on different populations could provide some interesting insight on species delimitation. Therefore, the true number of species is probably greater than currently known.

All currently available information combined allow to hypothesize that the diverse egg morphology in *Trachythorax* spp. and the diverse range of oviposition strategies of closely related taxa may be, at least partially, the evolutionary result of parasitism pressure.

Rearing the parasites and hosts in controlled condition could provide interesting insights on the true identity of the parasite species and could shed light on their behaviour including the oviposition, the larval development and the function of the specialised structures of the stick insect eggs. Species of *Trachythorax*, as well as several closely related taxa (e.g. *Loxopsis*, *Asceles*, *Marmessoidea* and *Syphloidea* sp.) are easy to rear in captivity considering the correct food plant is provided (T. Bollens pers. comm., 2020).

Molecular studies using a larger taxon sampling of the lineage including *Trachythorax* will provide a significantly more robust phylogeny and could provide answers on their higher classification, on the evolution of the different egg laying methods and accompanying egg morphology. It could also provide more information to support a hypothesis on the ancestral oviposition method in the group.

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