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A bilateral gynandromorph of *Tenodera sinensis* Saussure, 1871 (Mantodea: Mantidae) from Japan

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Abstract

This is a first description of a complete bilateral gynandromorph in Mantodea, as well as the first description of a complete gynandromorph of *Tenodera sinensis* Saussure. This specimen, collected from Kasai-Rinkai Park in Tokyo, Japan, exhibits predominantly male characteristics on the left side of its body and female characteristics on the right side. The left lateral has some features of male, and the notable differences between right and left lateral were found on the antennae, the ocelli, the compound eyes, the forewings and abdominal sternites VII to IX.

Key words: chinese mantis, Dictyoptera, gynandromorphism, morphology, sexual mosaic, Tenoderinae

Introduction

Typically, an arthropod individual differentiates into either a male or a female. However, with very low frequencies, individuals with both male and female morphological characters have been recurrently observed in natural and laboratory populations of arthropods (Narita *et al*. 2010; Fusco & Minelli 2023). These are termed gynandromorph (i.e., sexual mosaic) or intersexual, and their presence has been noted especially in many orders of insects (Narita *et al*. 2010).

In the order Mantodea, there are few reported cases of individuals with sexual phenotypic combinations. Roy (2003), Lombardo & Umbriaco (2011), and Agudelo (2014) reported cases of intersexuality caused by nematomorph parasites. Bèthoux (2010) presented a particular case of 'feminization' resulting from alterations in the developmental module organization of *Creobroter gemmatus* (Stoll, 1813) (Hymenopodidae), treating it as an instance of mixed gynandromorphism. To date, there have been no observations of a complete bilaterally divided gynandromorph in Mantodea.

The mantis *Tenodera sinensis* Saussure, 1871, is distributed in Asia and Oceania, and has been introduced to North America (Laurent 1898; Ehrmann & Borer 2015; Patel & Singh 2016). It is also probably the most widespread and abundant mantid species in East Asia and North America, as well as being extensively studied in terms of morphology, ecology and ethology for a long time (e.g., Fox 1939; Hurd 1999; Yager & Svenson 2008; Pickard *et al*. 2021). In Japan, excluding the region of Okinawa Prefecture, *T. sinensis* is one of the most common species in Mantodea, and is therefore frequently collected in surveys of entomofauna (e.g., Nagashima 1988; Toshima & Yakuo 1993; Oshima *et al*. 2022, 2023). However, before this study, no gynandromorphous of *T. sinensis* has been reported.

In this paper, we present the first report of a complete gynandromorph individual in *T. sinensis*, where intersexual characters are developed in all the main body segments (head, thorax, abdomen) detailing the morphological characteristics of bilateral gynandromorphism in Mantodea.

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Materials and methods

A gynandromorph of *T. sinensis* was collected by K. Toshima from around the edge of forest in Kasai-Rinkai Park (35°38'32.3"N, 139°51'47.2"E), Tokyo, Japan, on October 30, 2023. Ten normal males and ten normal females, collected in Tokyo or Kanagawa Prefecture, Japan, and deposited at the Research Institute of Evolutionary Biology and the Laboratory of Entomology, Tokyo University of Agriculture, Kanagawa Pref., Japan, were used for comparison. Those specimens were examined under a stereoscopic microscope (Stemi 305; Carl Zeiss AG, Oberkochen, Germany), and photographs were taken using a digital camera (EOS500D Mark IV; Canon, Tokyo, Japan) and digital microscope system (VHX-X1; Keyence, Osaka, Japan). Measurements of body length, pronotum, and profemur were taken directly using a ruler, while other body parts were measured using the digital microscope system's measurement function. Observations and photographs were based on both fresh and dried conditions. The male genitalia was extracted by dissecting the abdomen of the sample with forceps and was boiled in 10% KOH for a while, then processed in water and 99% ethanol. Subsequently, it was mounted in Canada balsam on permanent preparation. The specimen of gynandromorph has been deposited in The Research Institute of Evolutionary Biology.

The terminology for wing structures follows Battiston *et al*. (2010), and that for male genital structures primarily follows Klass (1997) and Schwarz & Roy (2019), supplemented by Jensen *et al*. (2009), and that for the other body structures follows Brannoch *et al*. (2017). The measurements were defined as follows:

(1) Body length: distance between the anterior apex of the pronotum and the apex of the wing;

(2) Head height: distance between the apex of the vertex and the apex of the labrum;

(3) Head width: distance between the outermost points of both compound eyes in frontal view;

(4) Ocellus height: vertical distance between the outermost points of the ocellus in frontal view;

(5) Ocellus width: horizontal distance between the outermost points of the ocellus in frontal view;

(6) Compound-eye height: vertical distance between the outermost points of the compound eye in frontal view;

(7) Compound-eye width: horizontal distance between the outermost points of the compound eye in frontal view;

(8) Antenna width: distance between the outermost points of the flagellum;

(9) Pronotum length: distance between the two ends of the pronotum along the midline;

(10) Pronotum width: distance between the outermost point of each pronotal side;

(11) Profemur length: distance from the base to the apex of the profemur in lateral view;

(12) Profemur width: distance between the outermost points just before the subbasal spine of the anteroventral-femoral spines in lateral view.

Results

The measurements of body parts of gynandromorph (Figs. 1, 2) and normal specimens (Fig. 3) are summarized in Table 1. This gynandromorph specimen was missing several body parts while alive: several apical segments of both antennae, the tarsus of the left foreleg and the left middle leg, the tarsi of the hind legs, the apical part of the left forewing, and several segments of the right cercus. No parasitism by Nematomorpha was observed.

FIGURE 1. *Tenodera sinensis* Saussure, 1871, gynandromorph (with male genitalia removed), dorsal view. Scale bar: 10 mm.

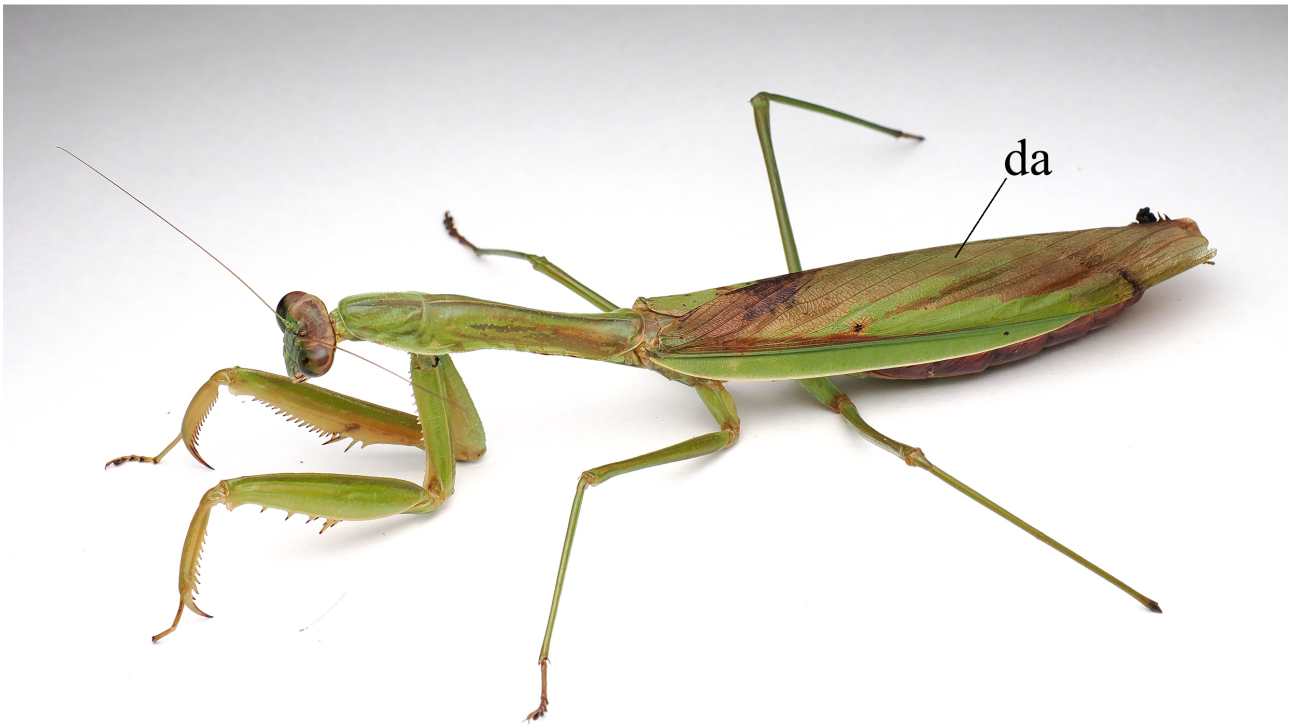

FIGURE 2. *Tenodera sinensis*, gynandromorph, in live. Label: da = discoidal area.

FIGURE 3. *Tenodera sinensis*, dorsal view. A, male; B, female. Scale bar: 10 mm.

TABLE 1. Measurements (mm) and aspect ratio (times) of body parts of *Tenodera sinensis*.

	Gynandromorph	Males (N=10)	Females (N=10)
Body length	88.5	79.0–88.5	83.5–90.5
Head height	7.72	5.15–5.93	7.83–8.20
Head width	9.54	7.55–8.80	9.60–9.90
Aspect ratio of head	0.81	0.67–0.68	0.81–0.83
Left-lateral-ocellus height	0.56	0.36–0.43	0.31–0.38
Left-lateral-ocellus width	0.40	0.32–0.40	0.32–0.35
Right-lateral-ocellus height	0.40	0.36–0.37	0.31–0.36
Right-lateral-ocellus width	0.36	0.30–0.32	0.31–0.35
Median-ocellus height	0.41	0.42–0.47	0.33–0.34
Median-ocellus width	0.63	0.58–0.69	0.47–0.61
Left-compound-eye height	3.98	2.98–3.51	4.10–4.23
Left-compound-eye width	3.28	2.53–3.06	3.15–3.25
Right-compound-eye height	4.45	3.00–3.50	4.12–4.30
Right-compound-eye width	3.05	2.53–3.00	3.18–3.20
Left-antenna width	0.20	0.20–0.22	0.14–0.15
Right-antenna width	0.14	0.20–0.22	0.14–0.15
Pronotum length	30.5	24.0–26.0	27.5–30.5
Pronotum width	8.5	6.0–7.5	7.5–9.0
Aspect ratio of pronotum	3.6	3.9–4.2	3.3–3.6
Left-profemur length	23.0	15.8–19.5	21.5–23.5
Left-profemur width	4.0	2.5–3.2	4.0–4.3
Right-profemur length	23.0	15.7–19.5	21.5–23.5
Right-profemur width	4.0	2.5–3.2	4.0–4.3
Aspect ratio of left-profemur	5.8	6.0–6.3	5.4–5.5
Aspect ratio of right-profemur	5.8	6.0–6.3	5.4–5.5

Head. (Fig. 4)

The left-lateral ocellus is 1.1 times larger in height and 1.4 times larger in width than the right-lateral ocellus. The left-compound eye is 0.9 times smaller in height and 1.1 times larger in width than the right-compound eye. The left antenna is 1.4 times thicker than the right antenna.

FIGURE 4. Head of *Tenodera sinensis*, frontal view. A, gynandromorph; B, male; C, female.

Thorax. (Figs. 1, 2, 5)

The pronotum is green in color, and 3.6 times as long as its maximum width, exhibiting a slight leftward curvature in its anterior half, with serrate lateral margins, except for the basal third on the left side. The colors of the forewings are asymmetrical: the discoidal area on the left forewing is primarily brown with areas of green; in contrast, the right forewing is entirely green.

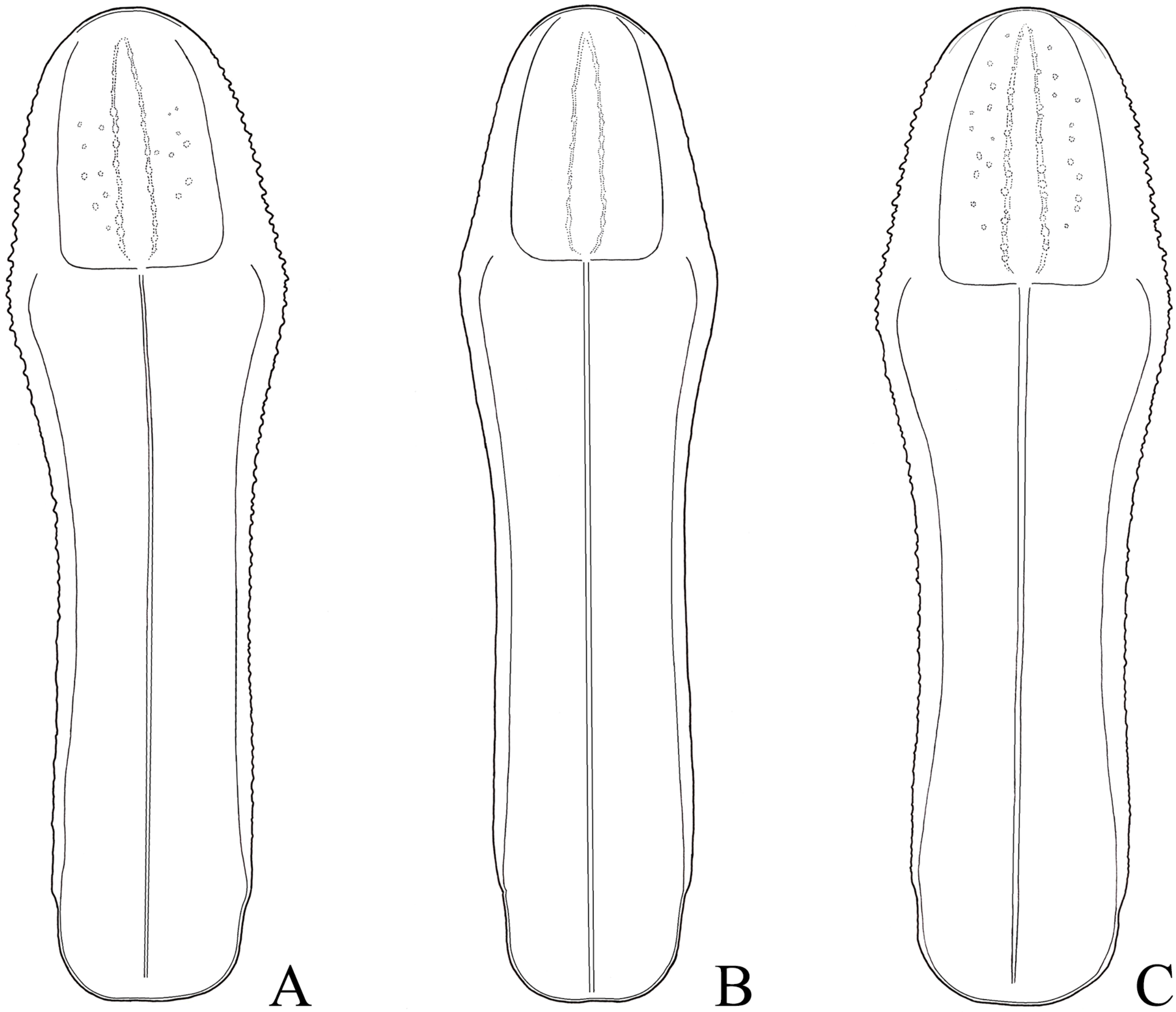

FIGURE 5. Pronotum of *Tenodera sinensis*, dorsal view. A, gynandromorph; B, male; C, female.

Abdomen. (Figs. 6, 7)

The abdominal tergites and sternites are brown in color. The right side of sternite VII extends posteriorly. The posterior margin of sternite VIII is equipped with a pair of immature gonapophyses. The right side of sternite IX is irregular in shape, lacking a stylus. In the male genitalia, the anterior lobe of phalloid apophysis (= acutolobus) is rounded, lacking acute angles. The posterior lobe of phalloid apophysis (= pseudophallus) is broader at its posterior end than at the bend, and the structure of its anterior margin is irregular and not smooth. The lateral secondary distal process (= hypophallus) is partially irregular at the anterior and posterior margins. The right phallomere is absent.

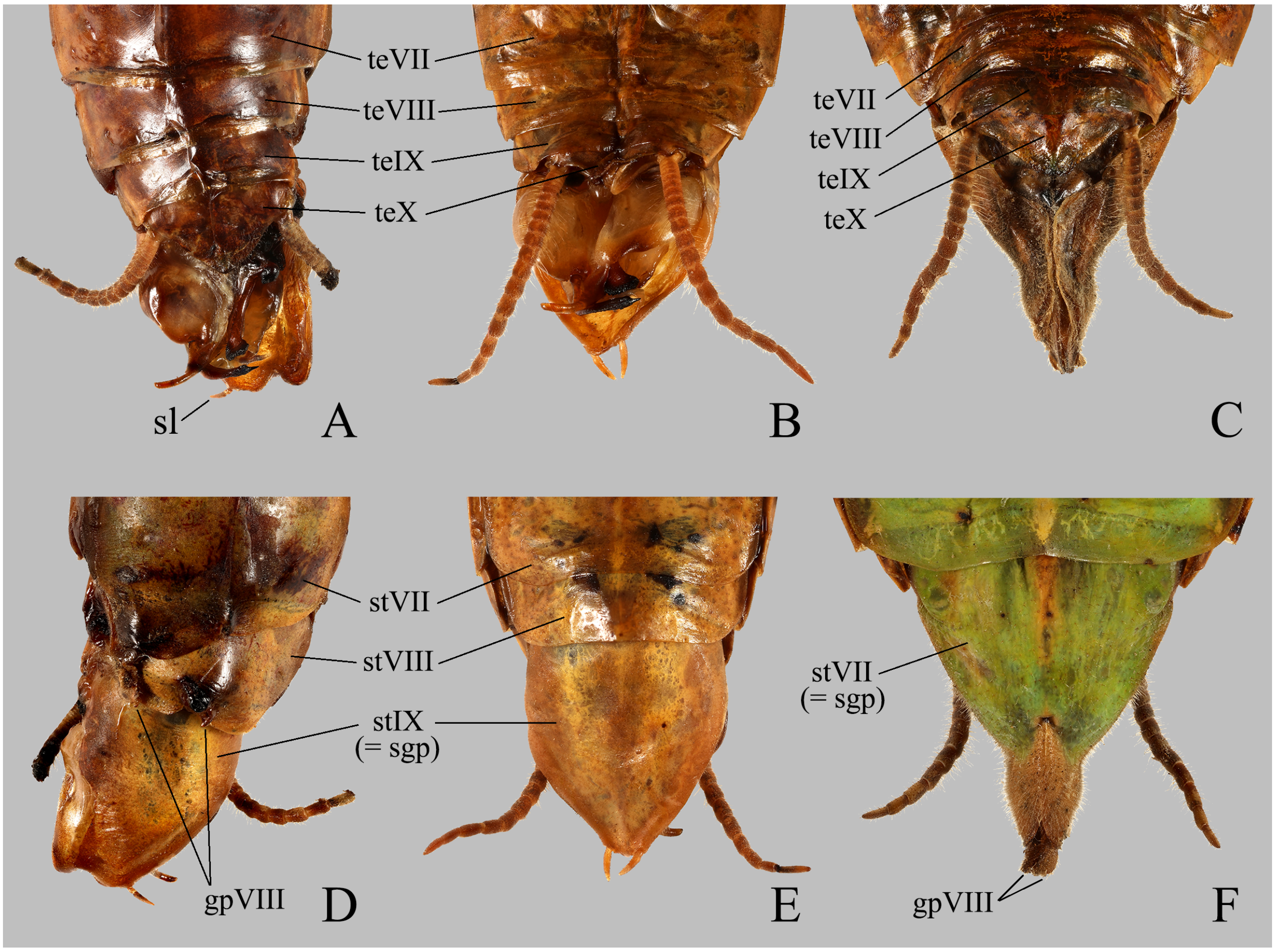

FIGURE 6. Abdomen and genitalia of *Tenodera sinensis*. A, D, gynandromorph; B, E, male; C, F, female; A–C, abdominal tergites VII to X and genitalia, dorsal view; D–F, abdominal sternites VII to IX and genitalia, ventral view. Labels: gpVIII = gonapophyses VIII; sgp = subgenital plate; sl = stylus; stVII = sternite VII; stVIII = sternite VIII; stIX = sternite IX; teVII = tergum VII; teVIII = tergite VIII; teIX = tergite IX; teX = tergite X.

Discussion

The emergence period of adult *T. sinensis* in Japan generally spans from August to November. The gynandromorph individual reported in this study was collected in late October, during the latter part of the emergence period, suggesting that it is probably an old individual. It is common for wild individuals during the late emergence period to exhibit damage, including but not limited to missing antennae or legs; thus, the observed damage to various body parts of this gynandromorph is considered incidental.

In Mantodea, males typically have longer and thicker antennae than females (Carle *et al*. 2014), a characteristic that is also distinctly evident in *T. sinensis* (Ando 2021) (Fig. 3A, B). In the gynandromorph studied, both antennae lacked several apical segments (Figs. 1, 2), precluding a comparison of their lengths. However, the left antenna was thicker than the right, exhibiting characteristics of males (Fig. 4A). It is plausible that, originally, the morphology of the antennae varied between the left and right, not only in thickness but also in length, with the left antenna being longer than the right. In this gynandromorph, the aspect ratio and the shape of the lateral margins of the pronotum closely resembled those typical of females (Fig. 5A, C). However, the basal third of the left side of the lateral margin exhibited less developed serrulation, a feature similar to male characteristics (Fig. 5B). Additionally, in *T. sinensis*, the discoidal area on the forewings typically exhibits brown in males, even if the pronotum and legs are green, whereas in females, it displays green when these parts are also green (Ando 2021). In this gynandromorph, the color of the discoidal area of the left forewing exhibited a brown, albeit partially, despite the pronotum being green

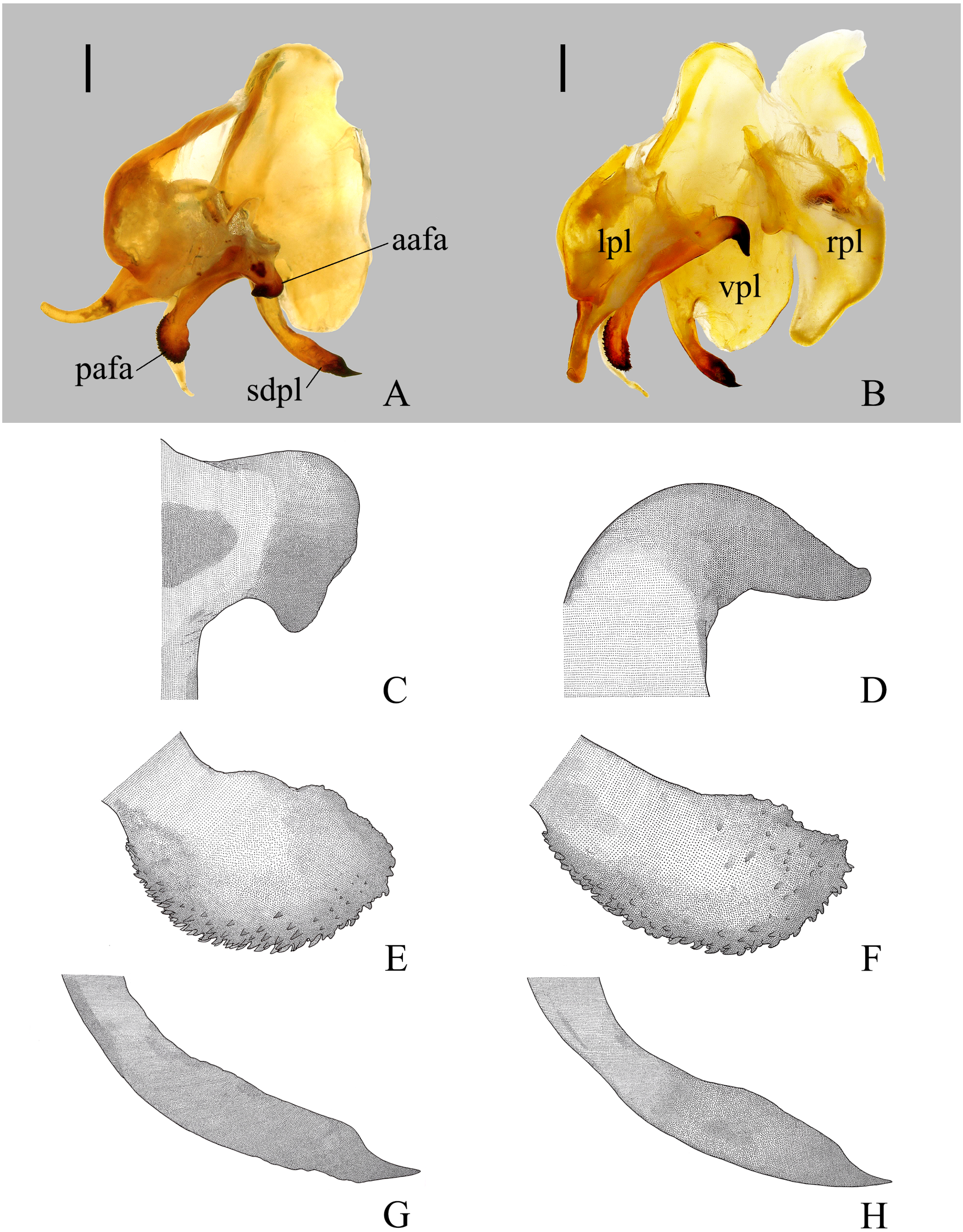

FIGURE 7. Male genitalia of *Tenodera sinensis*, dorsal view. A, C, E, G, gynandromorph; B, D, F, H, normal male; A, B, genital complex; C, D, anterior lobe of phalloid apophysis; E, F, posterior lobe of phalloid apophysis; G, H, lateral secondary distal process. Labels: aafa = anterior lobe of phalloid apophysis; lpl = left phallomere; pafa = posterior lobe of phalloid apophysis; rpl = right phallomere; sdpl = lateral secondary distal process; vpl = ventral phallomere. Scale bars: 1 mm.

(Figs. 1, 2). This is considered to reflect a slight yet discernible characteristic of the male. Abdominal sternites VII to IX in this gynandromorph, predominantly exhibited male morphology on the left side and female morphology on the right side, with both male and female genitalia present in an incomplete form (Fig. 6D).

Considering these observations and the four common patterns of gynandromorphy presented by Fusco & Minelli (2023), the gynandromorph described in this study can be categorized as bilateral, based on the presence of male characteristics on one side of the body and female characteristics on the other. This is markedly different from previously known examples of gynandromorphs in Mantodea. Most documented cases have been attributed to parasitism by Nematomorpha; prior reports highlight specific morphological alterations: Roy (2003) reported a reduction in the male genitalia of *Prohierodula ornatipennis* (Bolivar, 1893) (Mantidae) and *P. picta* (Gerstaecker, 1883); Lombardo & Umbriaco (2011) reported reductions in the size of ocelli and male genitalia, along with feminization of hindwing coloration, of *Parastagmatoptera flavoguttata* (Serville, 1839) (Mantidae); Agudelo (2014) reported a *Photina vitrea* (Burmeister, 1838) (Photinaidae) individual exhibiting the typical female general habitus of the genus *Photina* Burmeister, 1838, while retaining fully developed external male genitalia. Additionally, Bèthoux (2010) reported a *C. gemmatus* showing typical male wing shape and venation, yet possessing certain female wing coloration characteristics, though the underlying causes remain unknown. The gynandromorph of *T. sinensis* in this study was not parasitized by Nematomorpha and exhibits male and female characteristics on the left and right sides of the head, thorax, and abdomen, respectively, representing a highly unusual case that is inconsistent with any previously known cases.

Species of *Tenodera* are morphologically similar to each other. The characteristics of the male genitalia, particularly the features of the anterior lobe of phalloid apophysis (= acutolobus) (Fig. 7C, D), posterior lobe of phalloid apophysis (= pseudophallus) (Fig. 7E, F), and lateral secondary distal process (= hypophallus) (Fig. 7G, H), are pivotal for differentiating *T. sinensis* from other morphologically similar species (Jensen *et al*. 2009). However, in this gynandromorph, the anterior lobe of phalloid apophysis (Fig. 7C) exhibits deformations diverging from its typical morphology of *T. sinensis*, and the posterior lobe of phalloid apophysis (Fig. 7E) assumes an irregular shape. In Japan, *T. sinensis* can be identified not only by the characteristics of the male genitalia but also by the color of the prosternum between coxal cavities and the pattern of the hindwings (Okada 2001; Nakamine 2016). However, should gynandromorphs of *T. sinensis*, exhibiting characteristics similar to those described in this study, be found in regions where their distribution overlaps with closely related species identifiable solely by male genitalia, species identification based on external morphology may prove challenging. In such cases, genetic analysis is considered necessary.

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