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Taxonomy of *Glyptotermes* (Blattodea: Kalotermitidae) in Taiwan

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ABSTRACT: *Glyptotermes* Froggatt, 1897 (Blattodea: Kalotermitidae) is represented by two recorded species in Taiwan, namely *G. fuscus* Oshima, 1912, and *G. satsumensis* (Matsumura, 1907). However, there has been a lack of comprehensively survey taxonomic reviews on *Glyptotermes* in Taiwan for nearly a century. In order to address this gap and update the taxonomy of *Glyptotermes* species in Taiwan, we examined 281 colony specimens collected from Taiwan Island and its offshore islands. Morphological and molecular analyses based on 16S rDNA and COI were conducted, resulting in three distinct species: *G. fuscus*, *G. satsumensis*, and a new species named *Glyptotermes albofemoralis* sp. nov. The winged imago and soldier castes of the three species are described. A male winged imago of *G. fuscus* collected from the type locality is designated as the neotype.

KEY WORDS: *Glyptotermes albofemoralis*, *Glyptotermes fuscus, Glyptotermes satsumensis,* new species, neotype, termite.

INTRODUCTION

Glyptotermes Froggatt, 1897 is the largest genus within Kalotermitidae, comprising 129 extant species and 5 fossil species (Krishna *et al*., 2013; Amina and Rajmohana, 2016; Scheffrahn, 2021; Bouju *et al*., 2022). It represents approximately 28% of the total species diversity within Kalotermitidae. The diagnostic features of *Glyptotermes* include a sclerotized media (M) of the forewing, which runs parallel and in close proximity to the sclerotized radial sector (Rs), as well as short, thick mandibles in the soldier caste (Krishna, 1961). These termites are commonly found in damp forests, where they nest in decaying trees or dead wood. Some species, such as *Glyptotermes brevicaudatus* (Haviland), have been reported as structural pests (Rust and Su, 2012).

In Taiwan, two *Glyptotermes* species have been documented: namely *G. fuscus* Oshima, 1912, and *G. satsumensis* (Matsumura, 1907). The pioneering work of Oshima (1912) ushered in the initial report of these two species within Taiwan. Nevertheless, the absence of subsequent taxonomic reviews or comprehensive surveys delving into the distribution of *Glyptotermes* across the mainland of Taiwan and its neighboring islets persists as a notable gap in the academic discourse.

Identifying Kalotermitidae species can be challenging due to their high interspecific morphological similarity and considerable intraspecies morphological variation. In recent years, molecular approaches have emerged as effective tools for addressing taxonomic issues, as demonstrated by research on *Neotermes* and *Incisitermes* species in Japan (Ide *et al*., 2016; Yashiro *et al*., 2019; Wu *et al*., 2024). Mitochondrial 16S ribosomal DNA (16S rDNA) and cytochrome oxidase subunit I (COI) have been recognized as efficient molecular characters in termite studies (Kambhampati *et al*., 1996; Scheffrahn and Carrijo, 2020). Additionally, the analysis of pairwise genetic distances of 16S rDNA and COI sequences can be valuable in estimating the range of species boundaries. By comparing the genetic differences between individuals within and between species, researchers can gain insights into the level of genetic variation within a species and the degree of divergence between different species.

In the present study, we undertook a comprehensive examination of *Glyptotermes* species in Taiwan, employing both morphological characters and molecular evidence. We provided re-descriptions of all *Glyptotermes* species, along with 16S rDNA and COI sequences for each species. Furthermore, we present identification keys for the winged imago and soldier castes.

MATERIALS AND METHODS

Termite sample collection sites and collection methods

In the present study, a total of 281 collection sites were utilized to gather *Glyptotermes* species samples from Taiwan Island and its adjacent offshore isles, comprising Green Island and Lanyu (Fig. 1A). The samples consisted of soldiers, workers, and some winged imagos, all of which were acquired through hatchets, hand saws, and free hands capture. Additionally, winged imago samples were obtained through flight-intercepted traps and sweep nets. All collected samples were preserved in 95% ethanol and deposited in the National Chung Hsing University Termite Collection (NCHU), Taichung, Taiwan.

DNA extraction, amplification, and sequencing

A total of 37 samples were used for DNA extraction (see Fig. 1A for details). Genomic DNA was extracted

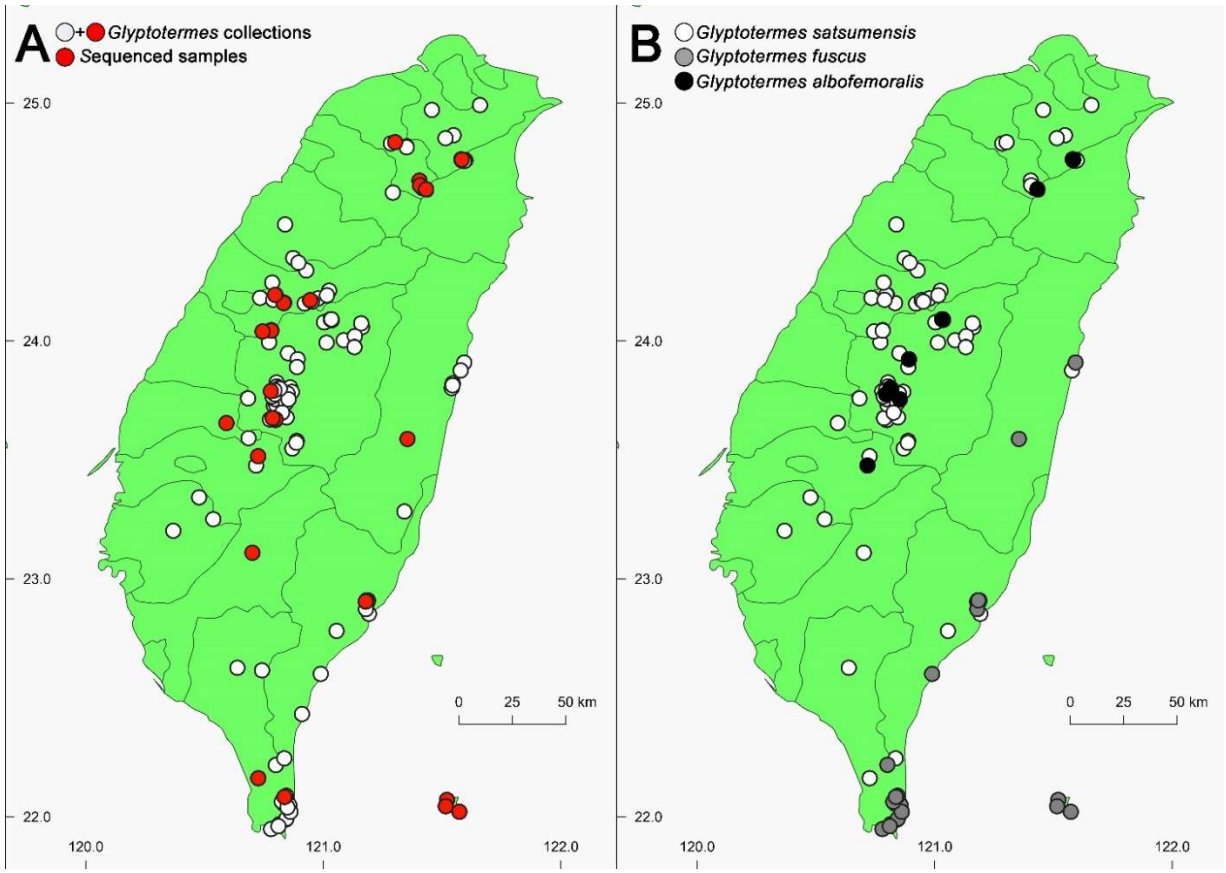

Fig. 1. Distribution of ***Glyptotermes*** termites in Taiwan. **A.** The 281 collection sites of ***Glyptotermes*** species across Taiwan, and 37 samples for sequencing. **B.** The 205 collection sites of ***G. fuscus***, ***G. satsumensis***, and ***G. albofemoralis*** sp. nov.

from the muscle tissue of the thorax and leg using the standard protocols recommended by the QuickExtract DNA extraction kit from Epicentre Biotechnologies (Madison, WI). Out of the 37 samples, 36 *Glyptotermes* samples were utilized for the 16S rDNA molecular analysis, while 18 samples were employed for the COI molecular analysis. Mitochondrial genes 16S rDNA were amplified by using 16Sar (5'-CGCCTGTTTAACAAAAACAT-3') and 16Sbr (5'-CCGGTCTGAACTCAGATCACGT-3') (Kerr *et al*. 2005). COI sequences were amplified by using LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3'), HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Hebert, 2003). The polymerase chain reaction (PCR) assays were conducted in 25 μl reagent mixtures, containing 1 μl of termite DNA template, 0.5 μl for each forward and reverse primers, 12.5 μl of master mix (amaR OnePCR™). PCR programming of 16S were following: one precycle at 95 °C for 5 min; 35 cycles of 95 °C for 1min, 55 °C for 1min, 72 °C for 2 min; last cycle at 72 °C for 10 min. PCR programming of COI were following: one precycle at 94 °C for 1min; 5 cycles of 94 °C for 1 min, 45 °C for 1.5 min, 72 °C for 1.5 min; 35 cycles of 94 °C for 1 min, 50 °C for 1.5 min, 72 °C for 1 min; and then final extension at 72 °C for 5 min. The 16S rDNA and COI sequcnce from the neotype of *G. fuscus* were extracted using the Gentra Purgene Tissue kit (Gentra Systems, Minneapolis, MN). The extracted DNA was fragmented using Covaris S220 (Covaris Inc., Wobrun, MA). DNA fragments within the size range of 300 and 600 bp were selected, purified and high-throughput sequenced with the Illumina NovaSeq platfrom. All DNA sequence are accessible in GenBank, the accession numbers for the 16S rDNA sequences are LC774784–LC774819, while the COI sequences have accession numbers LC775020–LC775038.

Phylogenetic analyses

All obtained DNA sequences were meticulously edited and verified using BioEdit (Hall, 1999). The sequences were then aligned using the Muscle Alignment option in Mega7.0 (Kumar *et al*., 2016). To serve as an outgroup, *Hodotermopsis sjostedti* Holmgren was used with the following accession numbers: LC774820 for 16S rDNA and LC775039 for COI, and sequences of *G. satsumensis* collected from Yakushima Island, Japan were analyzed (accession number: KP026257, Bourguignon *et al*. 2014). Phylogenetic inference of the 16S rRNA and COI sequences was carried out using the Neighbor-Joining method. The model selected for the

analysis was the maximum composite likelihood model, which accounted for substitutions involving both transitions and transversions. Each node was assessed by performing 1,000 bootstrap replications.

Morphological characters measurement and photography

In this study, a total of 47 winged imagos retrieved from 23 collection sites and 50 soldiers obtained from 28 collection sites were used for character measurement and photography. Character measurements and observations were conducted using a Leica M205 C stereomicroscope, Leica MC170 HD digital camera, and Leica Application Suite (version 4.4.0, Wetzlar, Germany). The morphological character measurements are following Roonwal (1969). For the winged imago caste, seven quantitative characters were measured and compared, including head length without mandible (Roonwal, 1969: fig. 3, line GG'), maximum head width (Roonwal: fig. 6, line SS'), head height (Roonwal: fig. 4, line VV'), compound eye diameter (Roonwal: fig. 11, line BB'), number of antenna articles, pronotum length (Roonwal: fig. 13, line SS'), and pronotum width (Roonwal: fig. 13, line UU'). For the soldier caste, eleven quantitative characters were measured and compared, including head length without mandibles (Roonwal: fig. 4, line JJ'), maximum head width (Roonwal: fig. 6, line RR'), head height (Roonwal: fig. 4, line VV'), number of antenna articles, postmentum maximum width (Roonwal: fig. 12, line QQ'), postmentum minimum width (Roonwal: fig. 12, line RR'), left mandible length (Roonwal: fig. 9, line NN'), labrum length (Roonwal: fig. 8, line FF'), labrum width (Roonwal: fig. 8, line EE'), pronotum length (Roonwal: fig. 13, line SS'), and pronotum width (Roonwal: fig. 13, line UU'). The count of antenna articles is included only if the antenna is complete. Statistical analysis was performed on the morphological characters using analysis of variance (ANOVA) with Tukey's honestly significant difference (HSD) test at a significance level of $\alpha = 0.05$. The specimens were photographed from ethanol-preserved samples. To evaluate the color of the samples, the Munsell color system (Munsell, 1967) was used in combination with the microscope. The photographs were taken using a Canon EOS 760D camera with an MP-E 65mm f/2.8 1-5X micro lens (Canon Inc., Tokyo, Japan) and were combined using Helicon Focus 7.6.4 Pro software (Helicon Soft Ltd., 2000). Subsequently, the figures were contrast-enhanced, scale bars were added using Adobe Photoshop CS6 (Adobe Inc., Mountain View, CA), and the backgrounds were converted to gray or white.

RESULTS

The scrutiny of morphological characters and the neighbor-joining trees inferred from 16S rDNA (Fig. 2A) and COI sequences (Fig. 2B) has yielded the congruent results. Our findings corroborate the existence of three discernible *Glyptotermes* species in Taiwan, encompassing the two previously recorded species, *G. fuscus* and *G. satsumensi*s. Additionally, a new species was discovered and named *G. albofemoralis* sp. nov.

The aligned sequence results for the mitochondrial 16S rRNA, including gaps, have a length of 384 base pairs (bp). The actual sequence lengths for *G. fuscus*, *G. satsumensis*, and *G. albofemoralis* sp. nov. are 328 bp, 328 bp, and 329 bp, respectively. The base compositions for T (Thymine), C (Cytosine), A (Adenine), and G (Guanine) in the 16S rDNA sequences range from 43.5% to 43.9%, 9.5% to 10.6%, 26.5% to 26.9%, and 19.5% to 21.3%, respectively. The genetic divergence of 16S rDNA sequences intraspecies ranges from 0% to 0.9%, while the divergence interspecies ranges from 13.9% to 17.2%. Additionally, the aligned partial sequences for COI are 500 bp in length. The base compositions for T, C, A, and G in the COI sequences vary from 31.2% to 31.6%, 17.2% to 18.2%, 26% to 27.6%, and 23% to 25.4%, respectively. The genetic divergence of COI sequences intraspecies varies from 0% to 0.8%, while the divergence interspecies ranges from 17.8% to 20.1%.

The distribution map of *Glyptotermes* species in Taiwan is presented in Figure 1B and Supplementary Table 1. The study has revealed a new record of *G. fuscus* in Lanyu Island. *G. fuscus* is primarily found in the coastal areas of southern and eastern Taiwan, with altitudes ranging from sea level up to 700 m. On the other hand, *G. satsumensis* and *G. albofemoralis* sp. nov. are distributed in the mountainous regions of Taiwan. The altitude distribution of *G. satsumensis* ranges from 50 m to 1700 m, while *G. albofemoralis* sp. nov. is typically found at altitudes between 400 m and 1100 m. Regarding the dispersal flight behavior, *G. fuscus* and *G. albofemoralis* sp. nov. are known to occur in the afternoon, while *G. satsumensis* is more active during the night.

In an effort to locate the type specimens and confirm the identities of *G. fuscus*, whose type locality is in Taiwan, a thorough examination of all historical collections in Taiwan was conducted. These collections included the Taiwan Agricultural Research Institute in Wufeng (TARI), the Forestry Research Institute (TFRI), the Industry Research Institute (TIRI), the Tropical Medicine Research Institute, and the Insect Museum of National Taiwan University in Taipei (NTU). These institutes were known to have housed termite syntypes during the Japanese rule. Unfortunately, despite the extensive search, none of the syntypes were found, leading to the assumption that they have been lost. In the absence of the original type specimens, a male winged imago collected from type locality (Pingtung, Taiwan) was designated as the neotype in this article.

Table 1. Measurements of winged imagos of ***Glyptotermes fuscus***, ***G. satsumensis***, and ***G. albofemoralis*** sp. nov.

Measurement, mm	***G. fuscus*** [a]		***G. satsumensis*** [b]		***G. albofemoralis* sp. nov.**[c]	
	Range	Mean ± SD	Range	Mean ±SD	Range	Mean ±SD
Head length without mandibles	0.80 – 1.02	0.92 ± 0.06 A	1.17 – 1.57	1.40 ± 0.09 B	1.10 – 1.27	1.20 ±0.08 C
Maximum width of head	0.80 – 0.92	0.86 ± 0.05 A	1.23 – 1.49	1.35 ± 0.06 B	1.03 – 1.17	1.10 ±0.06 C
Maximum height of head	0.54 – 0.66	0.60 ± 0.03 A	0.82 – 1.13	0.95 ± 0.06 B	0.76 – 0.85	0.81 ±0.04 C
Compound eye diameter	0.20 – 0.25	0.22 ± 0.01 A	0.35 – 0.48	0.42 ± 0.04 B	0.23 – 0.29	0.26 ±0.03 A
Pronotum length	0.50 – 0.59	0.55 ± 0.03 A	0.71 – 0.94	0.84 ± 0.05 B	0.74 – 0.85	0.80 ±0.05 B
Pronotum width	0.71 – 0.86	0.80 ± 0.03 A	1.22 – 1.49	1.35 ± 0.07 B	1.00 – 1.18	1.11 ±0.07 C

[a] *G. fuscus*, n = 18, from 7 colonies; [b] *G. satsumensis*, n = 25, from 13 colonies, [c] *G. albofemoralis* sp. nov., n = 4, from 3 colonies.

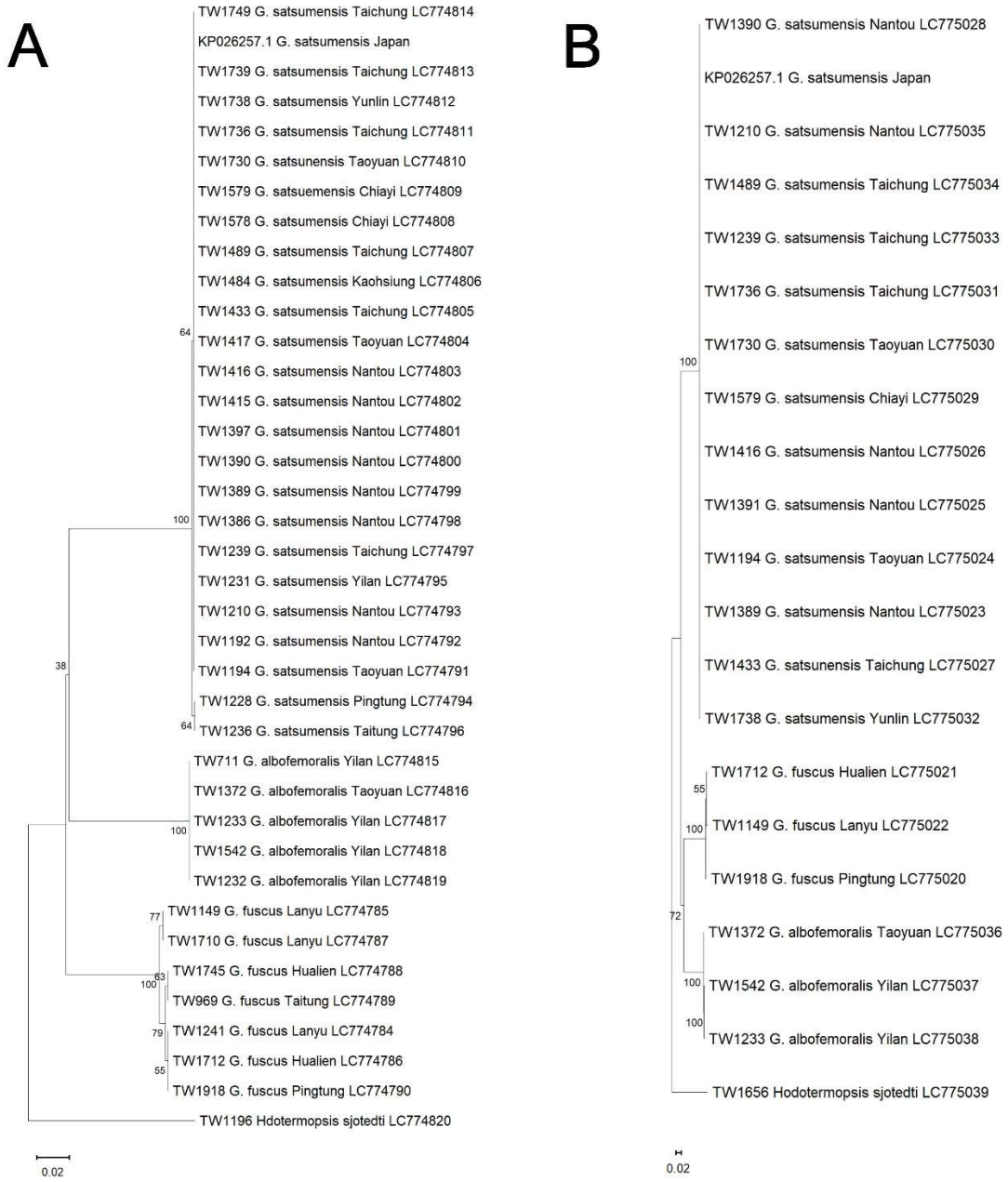

Fig. 2. Neighbor-joining tree of ***Glyptotermes*** species in Taiwan base on mitochondrial gene sequences. **A.** Neighbor-joining tree of ***Glyptotermes*** based on 16S rDNA sequence of 36 samples, a concatenated alignment of 328-329 bp in the final dataset. **B.** Neighbor-joining tree of ***Glyptotermes*** based on COI sequence of 19 Taiwanese samples, and one Japanese sample, a concatenated alignment of 500 bp in the final dataset.

Table 2. Measurements of soldiers of ***Glyptotermes fuscus***, ***G. satsumensis***, and ***G. albofemoralis*** sp. nov.

Measurement, mm	*G. fuscus* [a]		*G. satsumensis* [b]		*G. albofemoralis* sp. nov.[c]	
	Range	Mean ± SD	Range	Mean ±SD	Range	Mean ±SD
Head length without mandibles	1.31 – 1.64	1.49 ± 0.09 A	2.02 – 3.77	2.93 ± 0.44 B	2.04 – 2.62	2.38 ± 0.19 C
Maximum width of head	0.88 – 1.05	0.97 ± 0.04 A	1.30 – 2.02	1.66 ± 0.19 B	1.27 – 1 50	1.37 ± 0.08 C
Maximum height of head	0.79 – 0.98	0.87 ± 0.05 A	1.12 – 1.86	1.52 ± 0.19 B	1.13 – 1.37	1.23 ± 0.08 C
Maximum width of postmentum	0.35 – 0.47	0.39 ± 0.03 A	0.41 – 0.74	0.57 ± 0.08 B	0.45 – 0.56	0.52 ± 0.04 B
Minimum width of postmentum	0.18 – 0.28	0.23 ± 0.02 A	0.18 – 0.33	0.24 ± 0.04 A	0.20 – 0.26	0.23 ± 0.02 A
Left mandible length	0.69 – 0.80	0.75 ± 0.03 A	1.07 – 1.80	1.45 ± 0.18 B	0.99 – 1.15	1.07 ± 0.05 C
Labrum length	0.11 – 0.25	0.19 ± 0.04 A	0.13 – 0.36	0.22 ± 0.06 A	0.21 – 0.29	0.25 ± 0.03 A
Labrum width	0.20 – 0.26	0.23 ± 0.01 A	0.34 – 0.56	0.46 ± 0.06 B	0.31 – 0.44	0.39 ± 0.05 C
Pronotum length	0.45 – 0.68	0.58 ± 0.05 A	0.58 – 1.04	0.82 ± 0.15 B	0.69 – 0.87	0.79 ± 0.06 B
Pronotum width	0.80 – 1.06	0.96 ± 0.06 A	1.07 – 1.95	1.52 ± 0.23 B	1.15 – 1.50	1.34 ± 0.12 B

[a] *G. fuscus*, n = 23, from 15 colonies; [b] *G. satsumensis*, n = 21, from 10 colonies; [c] *G. albofemoralis* sp. nov., n = 6, from 3 colonies.

TAXONOMIC TREATMENT

Glyptotermes fuscus Oshima, 1912

Glyptotermes fuscus Oshima, 1912: 67–68, pl. 1: fig. 15. Syntypes: winged imagos, soldiers, TFRI, TARI, TIRI or Tropical Medicine Research Institute, lost! Type locality: Pingtung (Taiwan).

Calotermes (*Glyptotermes*) *hozawae* Holmgren, 1912: 118–119. Syntype: soldier, Taiwan, Zoötomiska Institute, Hogskolas, Stockholm, Sweden (ZIHS). Synonymized by Hozawa, 1912.

***Neotype*:** Wing imago, TW1918, Nanrenshan, Pingtung Co. (22°4.9′N, 120°50.1′E), 20-V-2022, leg. H.-F. Li, with 16S rDNA, COI sequences, deposited in NMNS (008746-00004). Additional male and female alate, soldier, and worker castes collected with neotype are deposited in NMNS and NCHU.

***Description*: Winged imago** (Fig. 3A–D, 4A, 5A; Table 1) Head capsule dark reddish brown (7.5R 2/6, Fig. 3A). Head subcircular, length longer than width, length without mandibles with 0.92 ± 0.06 mm (mean ±SD), maximum width with 0.86 ± 0.05 mm, heigh 0.6 ± 0.03 mm. Eye oval (Fig. 3B), with diameter 0.22 ± 0.01 mm. Ocelli circular. Antennae with 10–11 articles (10.9 ± 0.3, n = 9). 1st article longer than 2nd article, last article longest, oblong. Labrum linguiform, anterior margin with 10–12 long setae, tip of labrum overlapping the tip of mandibles. Postclypeus whitish, trapezoid, posterior margin broader than anterior margin. Left mandible with one apical tooth, and two distinct marginal teeth; 1st + 2nd marginal tooth slightly shorter than apical tooth (Fig. 3C); anterior margin of 3rd marginal tooth wider than posterior margin of 1st + 2nd marginal tooth. Right mandible with one apical tooth, two distinct marginal teeth and one molar tooth; 1st marginal tooth slightly shorter than apical tooth; 2nd marginal tooth two times wider than 1st marginal tooth; 2nd marginal tooth slightly notched at tip; posterior margin of 2nd marginal tooth longer than molar tooth.

Pronotum dark reddish brown (7.5R 2/6), broader than length, with length 0.55 ± 0.03 mm, and width 0.8 ± 0.03 mm; anterior margin slightly concave, with 25–30 short setae; sides slightly arcuate, with about 10 long setae each side; posterior margin almost straight, with 10–15 short setae (Fig. 3D). Wing brown (Fig. 4A), membranous, cover with pimples scales (prominent scales). Radius of forewing run into costa at anterior one-sixth of costa; radial sector and media without branches, close and parallel to each other; cubitus unsclerotized, with 10–13 branches. Hindwing shorter than forewing, redial sector and media meet before anterior one-fourth, split at anterior one-fourth, parallel till apex. Cubitus unsclerotized, with 10–14 branches. Leg with coxa, trochanter and femur reddish brown (10R 4/4), tibia and tarsus whitish (Fig. 5A). Tibia spur formula 3:3:3, tarsi 4-jointed. Abdomen oblong.

Soldier (Fig. 6A–D, 6M; Table 2) Head capsule dark muted orange (2.5YR 5/10, Fig. 6A). Head rectangular, length longer than broad, sides parallel, anterior margin slightly protuberance, middle of frons concave, length without mandibles with 1.49 ± 0.09 mm, maximum width with 0.97 ± 0.04 mm, hight 0.87 ± 0.05 mm. Eye spot small, oval (Fig. 6B). Antennae with 9–11 articles (10.4 ± 0.59, n = 17), 1st article longest, 2nd article shorter than other articles; last article oblong, longer than 2nd–8th articles, shorter than 1st article. Postmentum longer than width (Fig. 6C); maximum width at anterior one-third, width 0.39 ± 0.03 mm; minimum width at about posterior one-third, width 0.23 ± 0.02 mm. Labrum linguiform, length longer than width, anterior margin with 7–10 setae, with length 0.19 ± 0.04 mm, width 0.23 ± 0.01 mm. Left mandible with one apical tooth, and three distinct marginal teeth (Fig. 25), length with 0.75 ± 0.03 mm; 1st marginal tooth as long as 2nd marginal tooth; 3rd marginal tooth slightly longer than 1st and 2nd marginal tooth. Right mandible with one apical tooth, and two distinct marginal teeth; 1st marginal tooth longer than 2nd marginal tooth.

Pronotum reddish yellow (5YR 7/8), rectangular, broader than length, length 0.58 ± 0.05 mm, width 0.96 ± 0.06 mm; anterior margin concave, lateral margin converging posteriorly, posterior margin with weak median notched; lateral margin with 2–4 setae each side, pronotum fringed with 30–35 short setae (Fig. 6M). Leg whitish. Tibia spur formula 3:3:3, tarsi 4-jointed. Abdomen oblong.

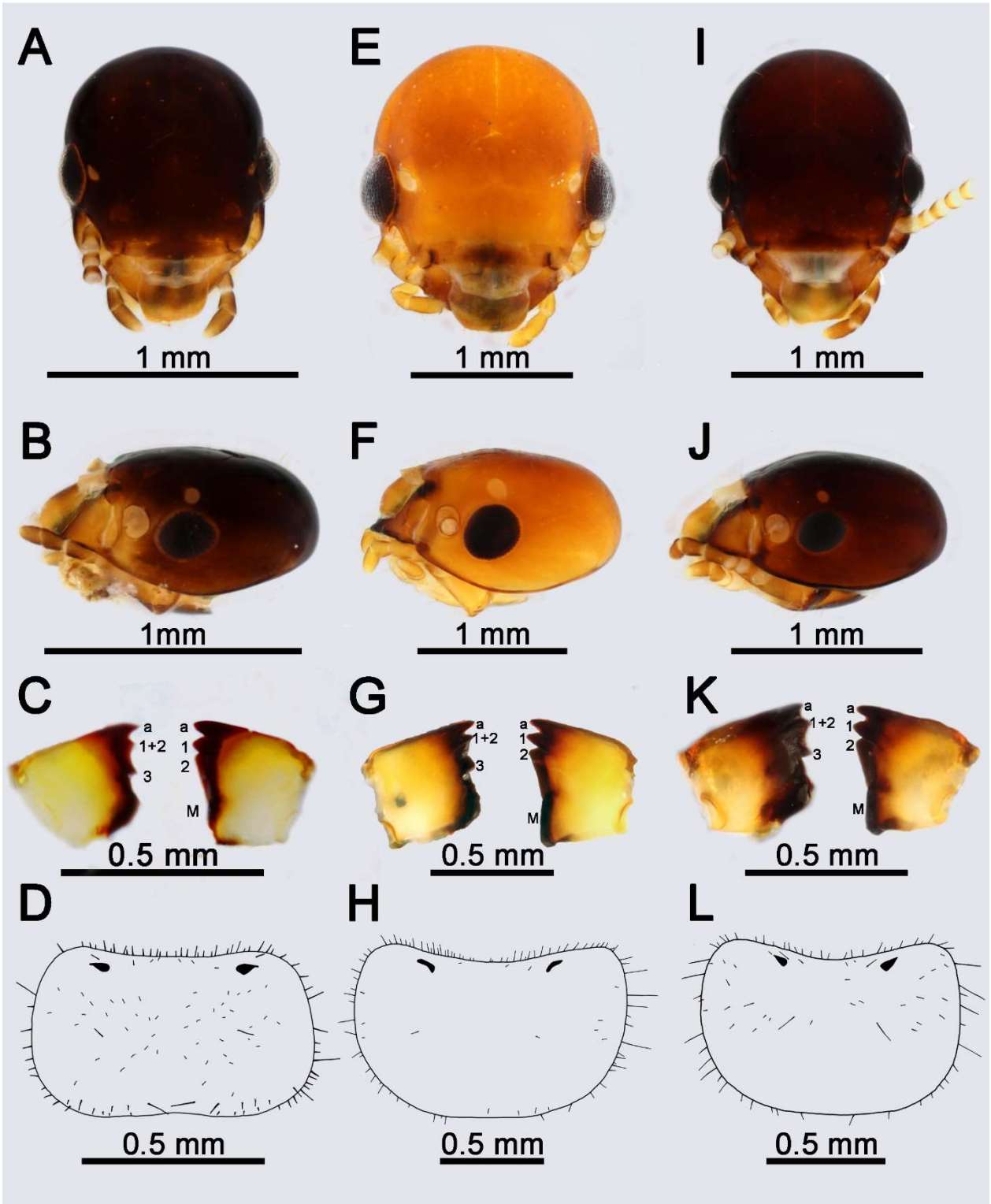

Fig. 3. Winged imago caste of ***Glyptotermes*** species in Taiwan. **A.** Head of ***G. fuscus*** in dorsal view. **B.** Head of ***G. fuscus*** in lateral view. **C.** Mandibles of ***G. fuscus***. **D.** Pronotum of ***G. fuscus***. E: Head of ***G. satsumensis*** in dorsal view. **F.** Head of ***G. satsumensis*** in lateral view. **G.** Mandibles of ***G. satsumensis***. **H.** Pronotum of ***G. satsumensis***. **I.** Head of ***G. albofemoralis*** sp. nov. in dorsal view. **J.** Head of ***G. albofemoralis*** sp. nov. in lateral view. **K.** Mandibles of ***G. albofemoralis*** sp. nov. **L.** Pronotum of ***G. albofemoralis*** sp. nov. a: Apical tooth. 1: 1st marginal tooth. 2: 2nd marginal tooth. 3: 3rd marginal tooth. M: Molar tooth.

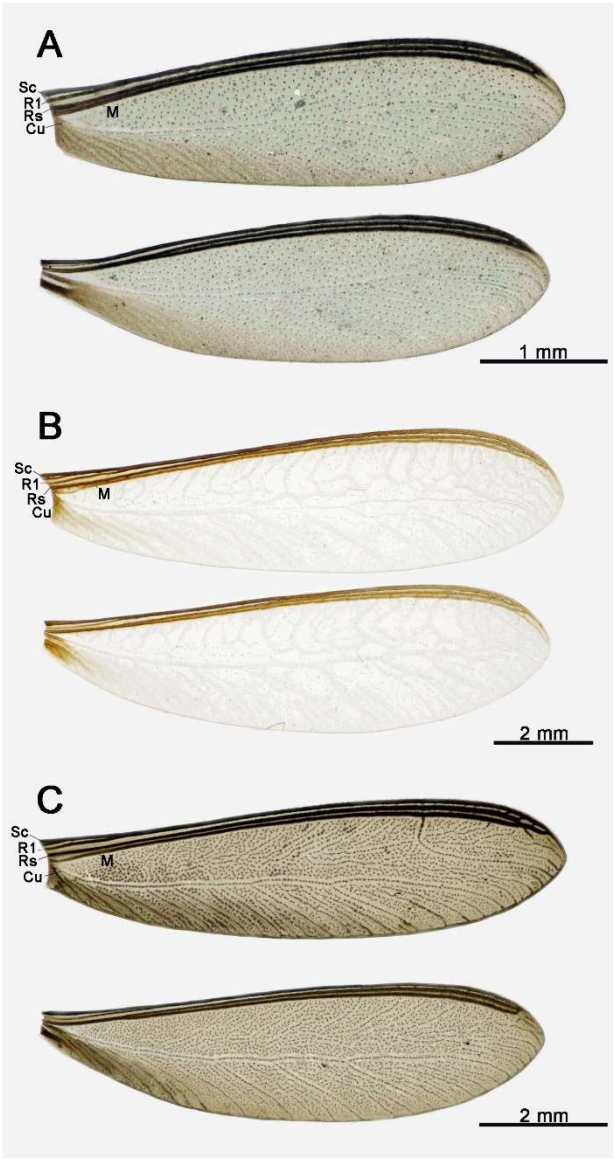

Fig. 4. Wings of winged imago of ***Glyptotermes*** species in Taiwan. **A.** Wings of ***G. fuscus***. **B.** Wings of ***G. satsumensis***. **C.** Wings of ***G. albofemoralis*** sp. nov.. In each pair of wings, the upper one is the forewing, and the lower one is the hindwing. Sc: Subcosta. R1: radius. Rs: Redial sector. M: Media. Cu: Cubitus.

***Distribution*:** China (Tsai and Chen, 1964), Japan (Nawa, 1912), Taiwan (Oshima, 1912).

***Material examined*: TAIWAN.** TW708, Pingtung, 15-VI-2006, leg. H.-F. Li, 1 soldier; TW709, Pingtung, 15-VI-2006, leg. H.-F. Li, 1 winged imago; TW855, Pingtung, 23-VI-2009, leg. C.-C. Chang, W.-M. Chung, Y.-C. Lan, H.-F. Li, and S.-H. Tzeng, 1 soldier; TW863, Pingtung, 24-VI-2009, leg. C.-C. Chang, W.-M. Chung, Y.-C. Lan, H.-F. Li, and S.-H. Tzeng, 3 soldiers; TW874, Pingtung, 25-VI-2009, leg. C.-C. Chang, W.-M. Chung, Y.-C. Lan, H.-F. Li, J.-F. Tsai, and S.-H. Tzeng, 1 soldier; TW875, Pingtung, 25-VI-2009, leg. C.-C. Chang, W.-M. Chung, Y.-C. Lan, H.-F. Li, and S.-H. Tzeng, 2 soldiers; TW983, Taitung, 23-V-2010, leg. N. Kanzaki, Y.-C. Lan, and S.-H. Tzeng, 1soldier, 3 winged imagos; TW969, Taitung, 21-V-2010, leg. Y.-C. Lan, H.-F. Li, and S.-H. Tzeng, 16S; TW1007, Pingtung, 20-X-2008, leg. H.-F. Li, 1 soldier; TW1030, Pingtung, 27-VI-2009, leg. N. Kanzaki, Y.-C. Lan, H.-F. Li, J.-F. Tsai, and S.-H. Tzeng, 1 soldier; TW1033, Pingtung, 27-VI-2009, leg. N. Kanzaki, Y.-C. Lan, H.-F. Li, J.-F. Tsai, and S.-H. Tzeng, 2 soldiers, 1 winged imago; TW1149, Lanyu, 25-I-2014, leg. C.-I Chiu, F.- S. Huang, B.- C. Lai, and W.- R. Liang, 16S, COI, 1 soldier; TW1241, Lanyu, 3-IV-2014, leg. Y.-J. Jiang, 16S, 1 soldier; TW1710, Lanyu, 5-IV-2020, leg. R.-H. Liu, 16S, 3 soldiers, 5 winged imagos; TW1712, Hualien, 2-XI-2019, leg. G.-Y. Chen, 16S, COI, 1 soldier, 2 winged imagos; TW1745, Hualien, 2-XI-2019, leg. G.-Y. Chen, 16S; TW1917, Pingtung, 20-V-2022, leg. H.-F. Li, 1 soldier, 3 winged imagos; TW1918, Pingtung, 20-V-2022, leg. H.-F. Li, 16S, COI.

Glyptotermes satsumensis (Matsumura, 1907)

Termes satsumensis Matsumura, 1907: 53, fig. 43. Syntypes: winged imagos, Systematic Entomology, Faculty of Agriculture, Hokkaido University. ***Type***: Kagoshima (Japan).
Calotermes (*Glyptotermes*) *satsumaensis* Holmgren, 1912: 116–117. Syntypes: winged imago, soldier, Kagoshima Prefecture (Satsuma), Japan, ZIHS. Synonymized by Oshima (1913).
Glyptotermes longicephalus Oshima, 1912: 64–66, fig. 4, pl. 1: fig. 2, pl. 2: figs. 6, 26. ***Syntypes***: winged imagos, soldier, Taiwan, depository unknown. Synonymized by Oshima (1913).

***Description*: Winged imago** (Fig. 3E–H, 4B; Table 1) Head capsule middle washed orange (5YR 7/12, Fig. 3E). Head subcircular, longer than width, length without mandible 1.4 ± 0.09 mm, width with 1.35 ± 0.06 mm, hight 0.95 ± 0.06 mm. Eye oval, with diameter 0.42 ± 0.04 mm. Ocelli subcircular (Fig. 3F). Antennae with 12–16 articles (14.5 ± 1.2, n = 10), 1st article longest, 3rd or 4th article shortest; last article oblong. Labrum reddish yellow (5YR 6/8), linguiform, tip of labrum overlapping middle or tip of mandibles. Postclypeus transparent, long rectangle, wider than length. Left mandible with one apical tooth, and two distinct marginal teeth (Fig. 3G); 1st + 2nd marginal tooth shorter than apical tooth; 1st + 2nd marginal tooth slightly longer than 3rd marginal tooth. Right mandible with one apical tooth, two distinct marginal teeth, and one molar tooth; apical tooth as long as 1st marginal tooth; 2nd marginal tooth shorter than 1st marginal tooth; posterior margin of 2nd marginal tooth slightly wider than molar tooth.

Pronotum reddish yellow (7.5YR 8/10), subrectangular, wider than length, with length 0.84 ± 0.07 mm, and width 1.35 ± 0.07 mm; anterior margin with slightly concave; lateral margin slightly arcuate, with 15–20 setae each side; posterior margin straight (Fig. 3H). Wing transparent, membranous (Fig. 4B). Radius of forewing meet subcosta at anterior one-seventh; radial sector without branch, close to costa; media parallel to radial sector, without branch; cubitus unsclerotized, with 10–12 branches. Hindwing shorter than forewing; radius run into costa at anterior one-seventh; redial sector without branches; redial sector and media meet before anterior one-fifth, split at anterior one-fifth, parallel till apex; cubitus unsclerotized, with 10–12 branches. Leg with coxa, trochanter and femur whitish yellow (2.5Y 8.5/6), tibia and tarsus whitish. Tibia spur formula 3:3:3, tarsi 4-jointed. Abdomen oblong.

Soldier (Fig. 6E–H, 6N; Table 2) Head capsule dark washed orange (2.5YR 6/14, Fig. 6E). Head subrectangular, longer than width, middle of frons slightly concave, length

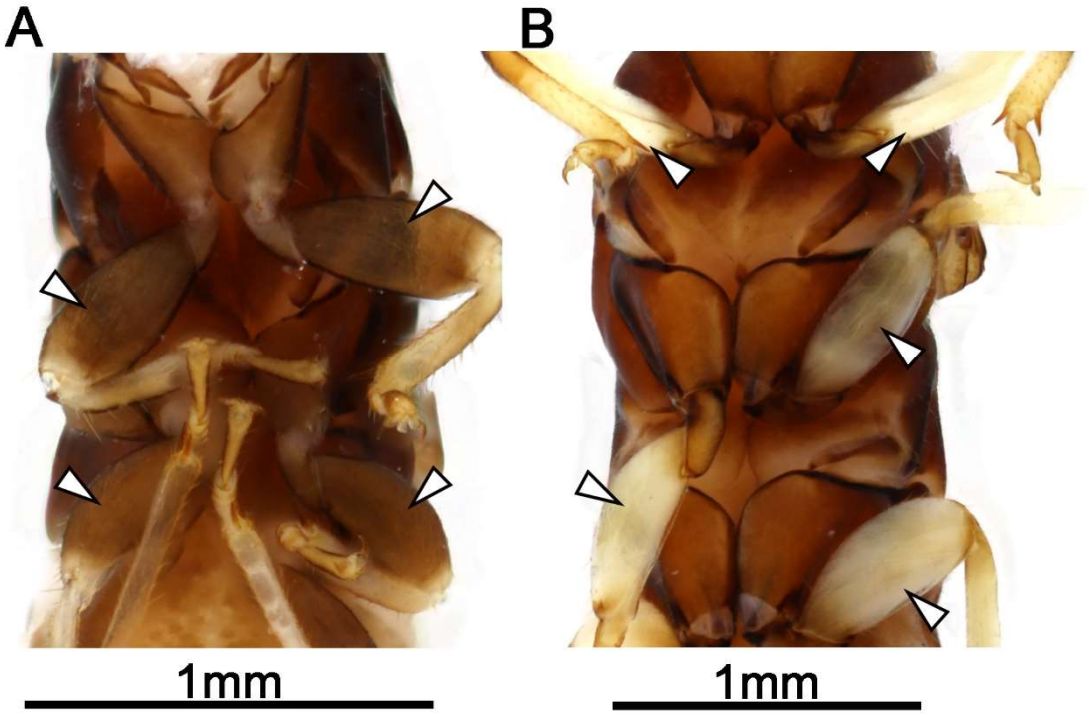

Fig. 5. Thorax of winged imago of ***G. fuscus*** and ***G. albofemoralis*** sp. nov. in ventral view. **A.** ***G. fuscus***. **B.** ***G. albofemoralis*** sp. nov. White triangle: Femur.

without mandible with 2.93 ± 0.44 mm, maximum width 1.66 ± 0.19 mm, heigh with 1.52 ± 0.19 mm. Eye spot whitish, small, oval (Fig. 6F). Antennae with 11–14 articles (12.43 ± 0.9, n = 7), 1st article longer than other articles, 3rd or 4th article shortest, last article oblong. Postmentum club-shaped (Fig. 6G), broadest at anterior one-fourth, width 0.54 ± 0.06 mm, middle part with sides parallel, minmum width with 0.24 ± 0.03 mm. Labrum linguiform, width longer than length, with length 0.22 ± 0.06 mm, width 0.46 ± 0.06 mm, anterior margin with about 10 setae. Mandibles short; slightly humped at base. Left mandible with one apical tooth, and three distinct marginal teeth (Fig. 6H), with length 1.45 ± 0.18 mm; 1st marginal tooth as long as 2nd marginal tooth; 3rd marginal shortest. Right mandible with one apical tooth, and two marginal teeth; 1st marginal tooth as large as 2nd marginal tooth.

Pronotum middle washed orange (7.5YR 7/12), reniform, broader than length, with length 0.82 ± 0.15 mm, and width 1.52 ± 0.23 mm; anterior margin slightly concave, with 20–30 short setae; lateral margin converging posteriorly, with 5–10 setae at anterior of lateral margin each side; posterior margin with weak media notched (Fig. 6N). Leg whitish, tibia spur formula 3:3:3, tarsi 4-jointed. Abdomen oblong.

***Distribution*:** China (Tsai and Chen, 1964), Japan (Matsumura, 1907), Taiwan (Oshima, 1912).

***Material examined*: TAIWAN.** TW961, Taitung, 20-V-2010, leg. Y.-C. Lan, H.-F. Li, and S.-H. Tzeng, 2 soldiers, 2 winged imagos; TW990, Taitung, 21-V-2012, leg. Y.-C. Lan, H.-F. Li, and S.-H. Tzeng, 1 winged imago; TW995, Hualien, 6-X-2010, leg. N. Kanzaki, H.-F. Li, and Y.-C. Lan, 3 soldiers; TW1192, Nantou, 23-III-2014, leg. W.-R. Liang, 16S; TW1194, Taoyuan, 1-IV-2014, leg. H.- F. Li, C.- I Chiu, and W.- R. Liang, 16S, COI; TW1206, Nantou, 16-VI-2014, leg. C.-Y. Quo, 1 winged imago; TW1207, Nantou, 16-VI-2014, leg. C.-Y. Quo, 1 Winged imago; TW1210, Nantou, 16-VI-2014, leg. C.-Y. Quo, 16S, COI, 5 winged imagos; TW1228, Pingtung, 26-V-2014, leg. Y.-T. Chung, 16S; TW1231, Yilan, 21-VIII-2014, leg. W.-R. Liang, 16S; TW1236, Taitung, 1-IX-2014, leg. W.-R. Liang, 16S, 1 soldier; TW1239, Taichung, 5-XII-2014, leg. W.-R. Liang, 16S, COI, 3 soldiers; TW1251, Miaoli, 27-V-2015, leg. W.-R. Liang, 3 winged imagos; TW1256, Nantou, 5-VI-201, leg. W.-R. Liang, 3 winged imagos; TW1386, Nantou, 17-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, 16S; TW1389, Nantou, 19-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, 16S, COI, 3 soldiers; TW1390, Nantou, 19-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, 16S, COI; TW1391, Nantou, 19-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, COI, 2 soldiers; TW1397, Nantou, 19-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, 16S; TW1415, Nantou, 20-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, 16S, 1 winged imago; TW1416, Nantou, 20-VIII-2015, leg. C.- I Chiu, I.- I. Tsai, Y.-Y Lai, and H.-K. Wang, 16S, COI; TW1417, Taoyuan, 17-X-2016, leg. W.-R. Liang, 16S; TW1433, Taichung, 27-II-2017, leg. G.-H. Chen, 16S, COI, 2 soldiers; TW1480, Tainan, 14-V-2017, leg. Y.-J. Jiang, 1 winged imago; TW1484, Kaohsiung, 29-V-2017, leg. W.-J. Wang, 16S, 3 winged imagos; TW1489, Taichung, 25-VII-2017, leg. H.-F. Li, C.-I Chiu, W.-R. Liang, 16S, COI; TW1578, Chiayi, 9-I-2019, leg. H.-F. Li, 16S, 1 soldier; TW1579, Chiayi, 9-I-2019, leg. H.-F. Li, 16S, COI, 3 soldiers; TW1585, Nantou, 8-III–5-V-2019, leg. H.-F. Li, C.-I Chiu, W.-R. Liang, S.-Y. Huang, Y.-N. Chiu, Y.-Y. Lai, and C.-C. Wu, 1 winged imago; TW1588, Nantou, 28-III–5-V-2019, leg. W.-R. Liang, and F.-S. Ho, 2 winged imagos; TW1730, Taoyuan, 14-VII-2019, leg. K.-W. Jhan, 16S, COI, 1 soldier; TW1736, Taichung, 27-VI- 2020, leg. W.-R. Liang, 16S, COI; TW1738, Yunlin, 21-VI-2020, leg. W.-J. Lin, and C.-I Chiu, 16S, COI; TW1739, Taichung, 14-IV-2018, leg. K.-Y. Liu, 16S; TW1749, Taichung, 16-II-2019, leg. W.-R. Liang, 16S, 1 winged imago.

Glyptotermes albofemoralis C.-C. Wu, J.-F. Tsai, H.-F. Li, ***sp. nov.*** **白足樹白蟻**

urn:lsid:zoobank.org:pub:**D30B7F94-ED3C-4B1A-A342-DCF6CFC839B3**

***Type material*: Holotype:** TW1542, Fushan Botanical Garden, Yilan Co. (24°45.7'N, 120°34.9'E), 13-VIII-2018, leg. H.-F. Li, G.-H. Chen, C.-I Chiu, W.-R. Liang, and C.-C. Wu, male alate, with 16S rDNA and COI sequences, deposited in NMNS (No. 008746-00005). **Paratypes**: TW 1542, Fushan Botanical Garden, Yilan Co. (24°45.7'N, 120°34.9'E), 13-VIII-2018, leg. H.-F. Li, G.-H. Chen, C.-I Chiu, W.-R. Liang, and C.-C. Wu, with male, female alate, soldier and worker castes, deposited in NMNS (No. 008746-00006) and NCHU.

***Description*: Winged imago** (Fig. 3I–L, 4C, 5B; Table 1) Head capsule very dusky brown (10R 2/4, Fig. 3I). Head oval, length longer than broad, length without mandible with 1.2 ± 0.08 mm, width 1.1 ± 0.06 mm, height with 0.81 ± 0.04 mm. Eye circular, with diameter 0.26 ± 0.03 mm. Ocelli oval (Fig. 3J). Antennae with 13–14 articles (13.5 ± 0.5, n = 2); 2nd article shortest; 1st article about two times longer than 2nd article, last article oblong. Labrum reddish yellow (7.5YR 8/10), linguiform, tip of labrum overlapping tip of mandibles. Postclypeus pale yellow (7.5Y 9/4), trapezoid, posterior margin broader than anterior margin. Left mandible with one apical tooth, and two distinct marginal teeth (Fig. 3K); 1st + 2nd marginal tooth as long as apical tooth; 3rd marginal tooth shortest; posterior margin of 1st + 2nd marginal tooth slightly wider than anterior margin of 3rd marginal tooth. Right mandible with one apical tooth, two distinct marginal teeth, and one molar tooth; apical tooth as long as 1st marginal tooth, and wider than 1st marginal tooth; 2nd marginal tooth shorter than 1st marginal tooth; posterior margin of 2nd marginal tooth longer than molar tooth.

Pronotum very dusky brown (10R 2/4), as broad as head, with length 0.8 ± 0.05 mm, width 1.11 ± 0.07 mm, fringed with 30–40 setae; anterior margin slightly concave at middle; sides parallel, posterior margin almost straight (Fig. 3L). Wing brown (Fig. 4C), membranous, cover with pimples scales (prominent scales). Radius of forewing run into costa at anterior one-tenth of costa; radial sector and media without branches, close and parallel to each other; cubitus unsclerotized, with about 12–15 branches. Hindwing shorter than forewing, redial sector and media meet before anterior one-fifth, split at anterior one-fifth, parallel till apex. Cubitus unsclerotized, with 12–15 branches. Leg with coxa and trochanter reddish brown (2.5YR 4/6), femur whitish, tibia and tarsus of foreleg yellowish brown (5YR 5/8), tibia and tarsus of midleg and hindleg whitish (Fig. 5B). Tibia spur formula 3:3:3, tarsi 4-jointed. Arolium present. Abdomen oblong.

Soldier (Fig. 6I–L, 6O; Table 2) Head capsule dark muted orange (5YR 6/10, Fig. 6I). Head rectangular, length longer than broad, with length 2.38 ± 0.19 mm, width 1.37 ± 0.08 mm, height1.23 ± 0.08 mm, sides parallel, with 5–8 setae each side, anterior margin slightly prominence, middle of frons concave. Eye spot whitish, oval (Fig. 6J). Antennae with 11–12 articles (11.7 ± 0.47, n = 3). 1st article longest, 1st article about two times longer than 2nd article, 3re or 4th article shortest, last article oblong. Postmentum club-shaped (Fig. 6K), longer than broad; maximum width at the anterior one-fourth, width 0.52 ± 0.04 mm, minimum width at the posterior one-fourth, width 0.23 ± 0.02 mm. Labrum linguiform, wider than length, with length 0.25 ± 0.03 mm, width 0.39 ± 0.05 mm; anterior margin with 9–12 long setae. Left mandible with one apical tooth, three distinct marginal teeth (Fig. 6L), length with 1.07 ± 0.05 mm; 1st marginal tooth as large as 2nd marginal tooth; 3rd marginal tooth smallest. Right mandible with one apical tooth, two distinct marginal teeth; 1st marginal tooth larger than 2nd marginal tooth.

Pronotum light muted orange (7.5YR 8/10), width longer than length, with length 0.79 ± 0.06 mm, width 1.34 ± 0.12 mm, fringed with 25–30 setae; anterior margin concave; lateral margin parallel; posterior margin with media notched (Fig. 6O). Leg whitish, tibia spur formula 3:3:3, tarsi 4-jointed. Abdomen oblong.

***Etymology*:** The species is named based on the characteristic of having a whitish femur. The term "albo" is derived from Latin and means "white." Therefore, the species is named *Glyptotermes albofemoralis* sp. nov., reflecting the presence of white femurs in this species.

***Distribution*:** Taiwan.

***Material examined*: TAIWAN.** TW711, Yilan, 30-V-2007, leg. H.-F. Li, 16S, 2 soldiers; TW1232, Yilan, 21-VIII-2014, leg. W.- R. Liang, 16S; TW1233, Yilan, 21-VIII-2014, leg. W.- R. Liang, 16S, COI, 1 soldier; TW1372, Taoyuan, 8-XI-2015, leg. T. Sie, 16S, COI, 1 winged imago; TW1542, Yilan, 13-VIII-2018, leg. H.-F. Li, G.-H. Chen, C.-I Chiu, W.-R. Liang, and C.-C. Wu, 16S, COI, 3 soldiers; TW1727, Nantou, 30-X-2020, leg. C.W. Xi, 2 winged imagos; TW1748, Nantou, 23-X-2019, leg. Y.-H. Ho, 1 winged imago.

***Note*:** In this study, *G. albofemoralis* sp. nov. was compared with the remaining 51 species occurring in China, Japan, and the Philippines. The comparison was based on eight characters taken from the original descriptions of these species. The characters used for comparison included the color of the head, pronotum, wings, and tibia, as well as the number of antenna articles, maximum width of the head, head length without mandible, and maximum width of the pronotum. Among the species, *G. chinpingensis* Tsai and Chen, 1963, and *G. nakajimai* Morimoto, 1973 were found to be similar to *G. albofemoralis* sp. nov. However, the new species can be distinguished from these two species based on the forewing venation. *G. albofemoralis* sp. nov. has 11–12 cubitus branches, while *G. chinpingensis* has 14 cubitus branches, and *G. nakajimai* has 8–10 cubitus branches. Additionally, when comparing the soldiers of these species, the head length of the *G. albofemoralis* sp. nov. soldier is shorter, and their mandibles are longer than those of *G. nakajimai*.

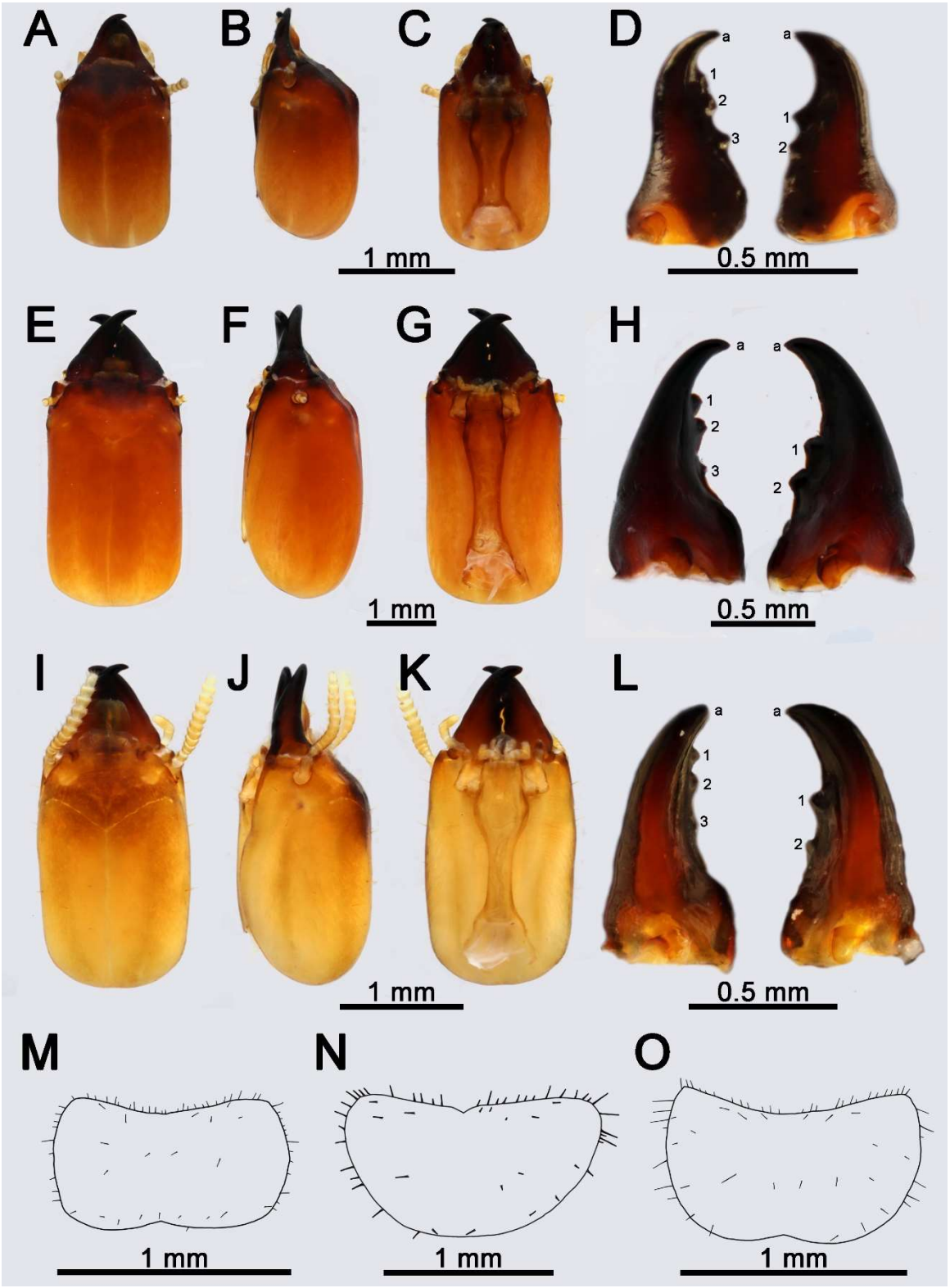

Fig. 6. Soldier caste of ***Glyptotermes*** species in Taiwan. **A.** Head of ***G. fuscus*** in dorsal view. **B.** Head of ***G. fuscus*** in lateral view. **C.** Head of ***G. fuscus*** in ventral view. **D.** Mandibles of ***G. fuscus***. **E.** Head of ***G. satsumensis*** in dorsal view. **F.** Head of ***G. satsumensis*** in lateral view. **G.** Head of ***G. satsumensis*** in ventral view. **H.** Mandibles of ***G. satsumensis***. **I.** Head of ***G. albofemoralis*** sp. nov. in dorsal view. **J.** Head of ***G. albofemoralis*** sp. nov. in lateral view. **K.** Head of ***G. albofemoralis*** sp. nov. in ventral view. **L.** Mandibles of ***G. albofemoralis*** sp. nov. **M.** Pronotum of ***G. fuscus***; **N.** Pronotum of ***G. satsumensis***. **O.** Pronotum of ***G. albofemoralis*** sp. nov. a. Apical tooth. 1. 1st marginal tooth. 2. 2nd marginal tooth. 3. 3rd marginal tooth.

Fig. 7. Winged imagos of ***Glyptotermes*** species in Taiwan. **A.** ***G. fuscus***. **B.** ***G. satsumensis***. **C.** ***G. albofemoralis*** sp. nov.

The winged imago caste of the three *Glyptotermes* species in Taiwan exhibit distinct body size variations. *G. albofemoralis* sp. nov. appears smaller compared to *G. satsumensis* but larger than *G. fuscus* (Fig. 7; Table 1). The count of antenna articles in *G. fuscus* (10–11 articles) is lower than that in *G. satsumensis* (12–16 articles) and *G. albofemoralis* (13–14 articles). *G. satsumensis* stands out easily due to its larger size and yellowish-brown body color. On the other hand, the other two species, *G. fuscus* and *G. albofemoralis* sp. nov., are smaller in size than *G. satsumensis*, and they both have a dark brown body color. To differentiate between *G. albofemoralis* sp. nov. and *G. fuscus*, one can look at the color of their femurs. The femurs of *G. albofemoralis* sp. nov. are white (Fig. 5B), while the femurs of *G. fuscus* are brown (Fig. 5A).

In the soldier caste, the three *Glyptotermes* species can be distinguished by several morphological characters, including the pronotum, postmentum, the front of the head, and the size of the head. Regarding the pronotum, *G. satsumensis* exhibits a curved junction between the

anterior and lateral margins (Fig. 6N), while *G. fuscus* (Fig. 6M) and *G. albofemoralis* sp. nov. (Fig. 6O) have slightly sharp lateral margins. The maximum width of the postmentum in *G. fuscus* is shorter compared to *G. satsumensis* and *G. albofemoralis* sp. nov. (Table 2). The slope of the head forms a weak curve in *G. satsumensis* (Fig. 6F), while in *G. fuscus* (Fig. 6B) and *G. albofemoralis* sp. nov. (Fig. 6J), the slope is more abrupt. The frontal part of *G. fuscus* is darker in color than *G. albofemoralis* sp. nov. Furthermore, the head size in *G. albofemoralis* sp. nov. is larger than in *G. fuscus* but smaller than in *G. satsumensis*. The number of antenna articles in *G. fuscus* (9–11 articles) is fewer than that in *G. satsumensis* (11–14 articles) and *G. albofemoralis* (11–12 articles).

Based on the molecular evidence, the three *Glyptotermes* species in Taiwan show significant differences from each other. The genetic divergence of 16S rDNA and COI between the three *Glyptotermes* species ranges from 0.14 to 0.17 and 0.178 to 0.2, respectively. In comparison to the data from Wu (2021), the genetic divergence of 16S rDNA between *Neotermes* species ranges from 0.06 to 0.09, while for COI, it ranges from 0.136 to 0.16. The genetic divergence of 16S rDNA between the genera *Cryptotermes*, *Glyptotermes*, *Incisitermes*, and *Neotermes* ranges from 0.13 to 0.23, and for COI, it ranges from 0.17 to 0.24. It is apparent from these findings that the three *Glyptotermes* species in Taiwan are likely belong to different genera. However, reaching a conclusive decision is challenging due to the high diversity within the *Glyptotermes* genus. The resolution of this taxonomic issue would necessitate a comprehensive revision of the entire generic complex.

Glyptotermes satsumensis is widely distributed in the mountainous areas of Taiwan, with an altitude range from 50 to 1,700 m. *G. albofemoralis* is also primarily found in the mountainous regions of Taiwan, with altitudes ranging from 650 to 1,100 m. *G. fuscus* is distributed in the coastal areas of southern and eastern Taiwan, as well as Lanyu Island, with altitudes ranging from 0 to 700 m. The dispersal flight season of *G. satsumensis* occurs from April to June, often attracted by light traps. *G. fuscus* has a dispersal flight season from March to June, while *G. albofemoralis* disperses in October to November. Both *G. fuscus* and *G. albofemoralis* exhibit dispersal flights in the midday to afternoon timeframe.

Key to the species of *Glyptotermes* occurring in Taiwan

Winged imago

1. Forewing median vein unsclerotized, running midway between redial sector and cubitus ..... ***Cryptotermes* or *Incisitermes***
- Forewing median vein running close and parallel to redial sector till tip of wing (Fig. 4)..... 2
2. Redial sector with branches ..... ***Neotermes***
- Redial sector without branches (Fig. 4) 3
3. Head capsule and abdomen light orange yellow to dark orange yellow (Fig. 3E) ..... ***Glyptotermes satsumensis*** (Matsumura)
- Head capsule and abdomen darker reddish brown to black (Fig. 3A& I) 4
4. Head width less than 1.1 mm; femur light brown (Fig. 5A) ....***Glyptotermes fuscus*** Oshima
- Head width more than 1.2 mm; femur white (Fig. 5B)..... .....***Glyptotermes albofemoralis*** sp. nov.

Soldier

1. Mandibles longer than half of head capsule …… ……..…. ***Neotermes*** or ***Incisitermes***
- Manidble shorter than half of head capsule ……..... 2
2. Head strongly phragmotic.……. ***Cryptotermes***
- Head not phragmotic or weak phragmotic.…….…..….…....3
3. Anterior-lateral margin of pronotum curved (Fig. 6N) …… ……..…..….***Glyptotermes satsumensis*** (Matsumura)
- Anterior-lateral margin of pronotum slightly sharp (Fig. 6M, 6O) .. 4
4. Head width less than 1.1 mm; anterior part of head as darker as mandible (Fig. 6A) ……..…… ***Glyptotermes fuscus*** Oshima
- Head width more than 1.2 mm; anterior part of head lighter than mandible (Fig. 6I) ……. ***Glyptotermes albofemoralis*** sp. nov.

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