RESEARCH PAPER

Termitotrox icarus sp. nov. (Coleoptera: Scarabaeidae): a new termitophilous beetle from Myanmar with observations of carrying behavior by host termites

Showtaro KAKIZOE[1,*)], Wei-Ren LIANG[1,2)], Khin Mar MYINT[3)] & Munetoshi MARUYAMA[1)]

[1)] The Kyushu University Museum, Hakozaki 6-10-1, Higashi-ku, Fukuoka, 812-8581 Japan
[2)] Department of Entomology, National Chung Hsing University, 145 Xingda Rd., Taichung, 40227 Taiwan
[3)] Forest Research Institute, Forest Department, Ministry of Natural Resources and Environmental Conservation, Yezin, Nay Pyi Taw, Myanmar
[*)] corresponding author: e-mail: showtarok@gmail.com

Abstract. A new species of scarab beetle, *Termitotrox icarus* sp. nov., is described from central Myanmar, being the third representative of the genus *Termitotrox* Reichensperger, 1915 from the Indo-Chinese Subregion of the Oriental Region. The majority of the type series was collected from the walls of fungus garden chambers built in the nests of the termite *Odontotermes proformosanus* Ahmad, 1965. *Termitotrox icarus* sp. nov. can be easily distinguished from the known *Termitotrox* as it possesses wing-shaped trichomes on the elytra, the more elongate habitus shape in dorsal view, the basomedian section of pronotum not protruding backwards, a pair of distinct costae on the pronotal basomedian section strongly developed, a median costa on anterior pronotal margin strongly developed, the elytral striae narrower than interstriae, the lack of trichomes at the base of elytral sutural stria, and a mid-range body length of 1.5–1.9 mm. The 'carrying behavior' by the host termites is reported for the first time for *Termitotrox* and a strategy for the dispersal of flightless termitophilous scarabs is hypothesized.

Key words. Coleoptera, Aphodiinae, Termitotrogini, Blattodea, Termitidae, Macrotermitinae, new species, egg gigantism, phoresy, termite association, Indo-Chinese Subregion, Oriental Region

Introduction

Members of the genus *Termitotrox* Reichensperger, 1915 are blind, flightless, termitophilous scarabs associated with the fungus-growing termite genera *Protermes* Holmgren, 1910, *Macrotermes* Holmgren, 1913, *Odontotermes* Holmgren, 1912, and *Hypotermes* Holmgren, 1917 (Blattodea: Termitidae: Macrotermitinae). The genus has previously been reported in the Afrotropical Region (eight species) and the Oriental Region (four species, of which two occur in the Indo-Chinese Subregion) (KRIKKEN 2008, MARUYAMA 2012a, KAKIZOE & MARUYAMA 2015). The authors recently collected an unknown species of *Termitotrox* in Myanmar from the fungus garden chambers of *Odontotermes* termites. This new species is here described, being the third representative of *Termitotrox* in the Indo-Chinese Subregion.

Behavioral observations on *Termitotrox* beetles are limited and known only for *T. cupido* Maruyama, 2012 (MARUYAMA 2012a). In two species of Corythoderini (the other termitophilous scarab tribe associated with fungus-growing termites), beetles are reported to have been carried by worker termites in the same manner that the termites carry their own nymphs (KISTNER 1982, MARUYAMA 2012b), i.e., the worker termite grasped a handgrip-like structure of the beetle, formed by the median lobe of the pronotal base (medially projected backwards) and a median projection of the elytral base (projected upwards and forwards). Though *Termitotrox* species do not possess an elytral median projection (except *T. venus* Kakizoe & Maruyama, 2015), they do possess a well-developed, handgrip-shaped pronotal median lobe. MARUYAMA (2012a), therefore, hypothesized that *Termitotrox* beetles are likewise carried by worker

termites. In the present study, we confirm the prediction of MARUYAMA (2012a) by providing the first recorded evidence of *Termitotrox* "carrying behavior" by host termites. We also discuss a hypothetical dispersal strategy potentially used by flightless termitophilous scarabs that incorporates host termites.

Materials and methods

Field survey. The field survey was conducted in Nay Pyi Taw, Myanmar by S. Kakizoe, W.-R. Liang, and K. M. Miynt in July-August 2019, during which time we inspected the fungus gardens of the termite subfamily Macrotermitinae. We recorded the location of the find of each individual within the fungus garden chamber, i.e., whether "on the chamber wall" or "inside the fungus garden". For behavioral observations, several beetles were placed, along with host termites (soldiers, major workers, and minor workers), into small plastic Petri dishes (5 cm in diameter) lined with slightly moistened filter paper and observed for several hours.
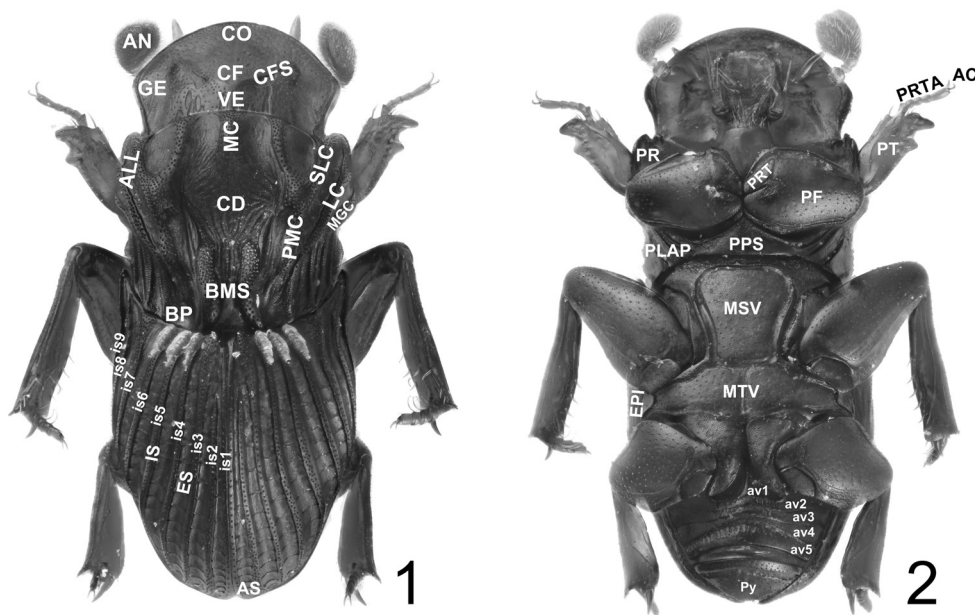
Specimen preparation. Most specimens were killed in a tube (35 ml) using tissue paper soaked with drops of ethyl acetate. They were then dried and mounted for morphological observation, with the exception of the dissected mouthparts and genitalia, which were mounted in Euparal on a small glass plate (10 × 5 mm) and subsequently glued onto paper card (6 × 5 mm) before being pinned under the specimen (MARUYAMA 2004). Some specimens were killed by absolute ethanol for future molecular phylogenetic studies by S. Kakizoe and M. Maruyama.

Image acquisition. Photographs of dried specimens were taken using either an Olympus OM-D E-M1 Mark II camera with a Mitutoyo M Plan Apo 10× objective lens

and a Raynox DCR-150 tube lens or a Sony α7R II camera with a Mitutoyo M Plan Apo 10× objective lens and a Raynox DCR-150 tube lens. Photographs of genitalia and mouthparts were taken using either an Olympus BX43 microscope equipped with an Olympus E-5 camera via a Micronet NY-1S adapter or a Nikon Eclipse 50i microscope equipped with a Sony α7R II camera via a C-TEPF2.5 DSC Port. Photos of dried specimens, genitalia, and mouthparts were stacked using Zerene Stacker software by the PMax method (ver. 1.04, Zerene Systems LLC.). Images were edited using Adobe Photoshop CS6 (ver. 13.0.6 x64, Adobe Systems Inc.).

Statistical analysis. Whereas many termitophiles associated with fungus-growing termites are found from inside the fungus gardens themselves, *Termitotrox* beetles were not found inside the gardens (MARUYAMA 2012a; KAKIZOE & MARUYAMA 2015). Therefore, to determine the distribution of this species within the nests, we statistically analyzed the differences in the number of individuals collected "on the chamber wall" and "inside the fungus garden" using R software (ver. 3.3.2, R CORE TEAM 2016). First, a Shapiro-Wilk normality test was conducted to examine the normality of the data. As normality was rejected, a Wilcoxon signed rank test was performed to examine whether the means between the two locations were equal.

Micro-CT scans. In preparation for micro-CT scans, beetles were killed within a few minutes by a few drops of ethyl acetate and then placed into Bouin's solution for 24 h. After fixation, the beetles were dehydrated in a graded series of ethanol (from 80% to 100%). Before micro-CT scans, the beetles were stained by 1% iodine ethanol (1% iodine metal (I_2) dissolved in 100% ethanol)

Figs 1–2. Terminology used in species description. **Head:** CFS – clypeofrontal suture, CO – clypeal outline, CF – clypeofrons, GE – gena, AN – antenna, VE – vertex. **Pronotum:** ALL – anterolateral lobe, MC – median costa, SLC – sublateral costa, CD – central depression, PMC – paramedian costa, LC – lateral costa, MGC – marginal costa, BMS – basomedian section, BP – base of pronotum. **Elytra:** IS – interstria, ES – elytral stria, is1–is9 – interstriae 1 to 9, AS – apicosutural area, EPI – epipleuron. **Ventral structures of thorax:** PR – propectus, PLAP – posterolateral areas of propectus, PPS – postprosternal surface, MSV – mesoventrite, MTV – metaventrite. **Abdomen:** av1–av5 – abdominal ventrite 1 to 5, Py – pygidium. **Legs:** PF – profemur, PRT – protrochanter, PT – protibia, PRTA – protarsus, AC – anterior claw.

for 24 h and then washed in 100% ethanol several times. Subsequently, the beetles were mounted in pipette tips with 100% ethanol following the method of Metscher (2009). Micro-CT observations were conducted using a Bruker SkyScan 1172 microtomograph (Bruker microCT, Kontich, Belgium). The setting parameters were as follows: voltage = 56 KV; current = 100 μA; voxel size = 2.97 μm; image rotation step = 0.7°; and 180° of rotation scan. The NRecon (Bruker microCT's Skyscan software) was used for reconstructions, following the methods of Alba-Tercedor (2014). Volume rendered images were obtained with FEI's Avizo software (Thermo Fisher Scientific, Waltham, MA, USA).

Terminology (Figs 1 and 2). The terminology used for the species description follows that of Krikken (2008) and Kakizoe & Maruyama (2015). All measurements in this study are given as the minimum length–maximum length range in mm (mean ± SD, n = number of individuals).

Examined specimens are deposited in the following collections:

CMN   Canadian Museum of Nature, Ottawa, Canada (A. Smith);
FRINM   Forest Research Institute, Nay Pyi Taw, Myanmar (Khin Mar Myint);
KUM   Munetoshi Maruyama collection, deposited at the Kyushu University Museum, Fukuoka, Japan;
MNHN   Muséum national d'Histoire naturelle, Paris, France (Olivier Montreuil);
NCHU   Termite collection, Department of Entomology, National Chung Hsing University, Taiwan (Hou-Feng Li);
NHMUK   Natural History Museum, London, United Kingdom (Maxwell V. L. Barclay);
NMPC   National Museum, Prague, Czech Republic (Jiří Hájek);
NSMT   National Museum of Nature and Sciences, Tsukuba, Japan (Shûhei Nomura);
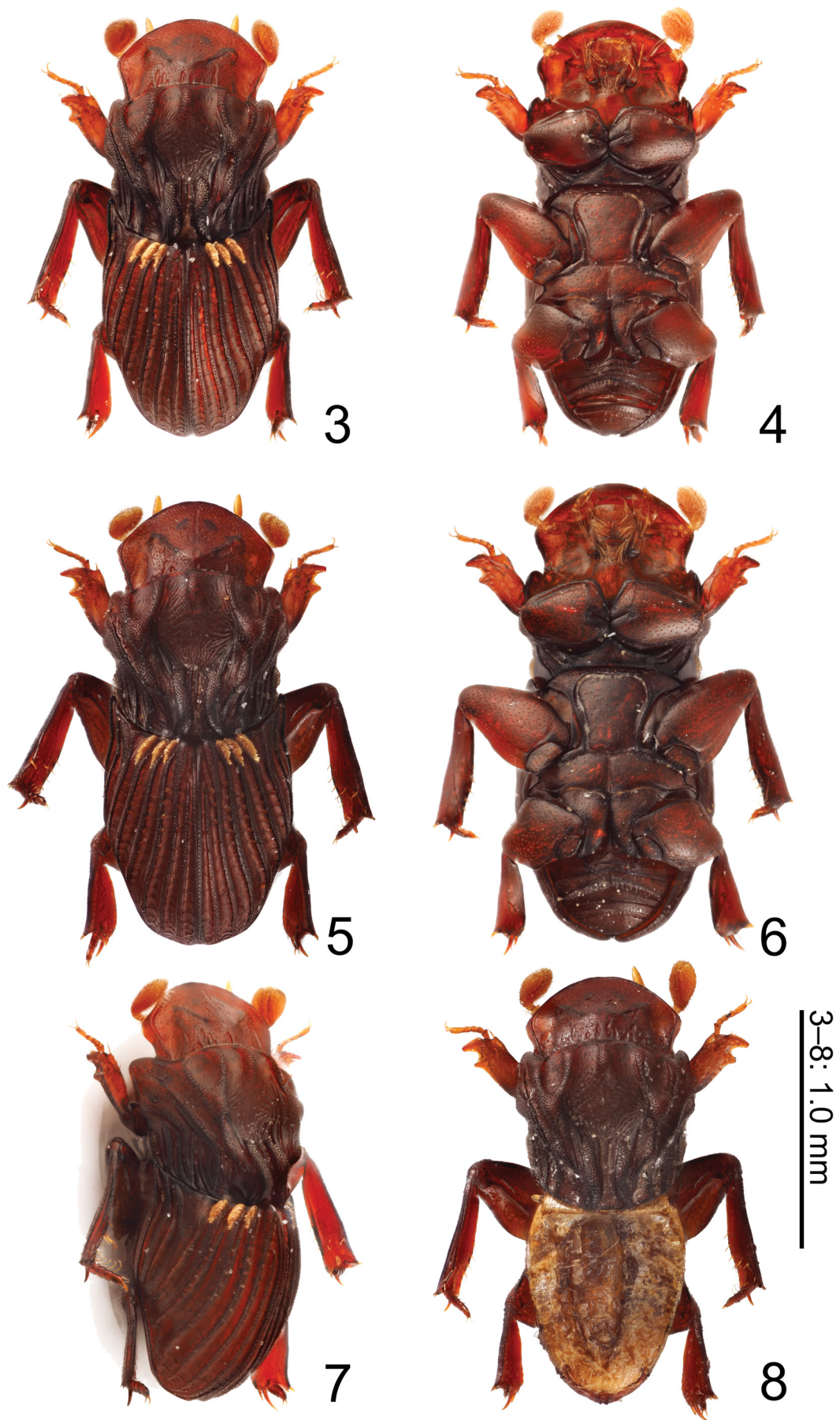SKC   Showtaro Kakizoe private collection, Fukuoka, Japan.

Results

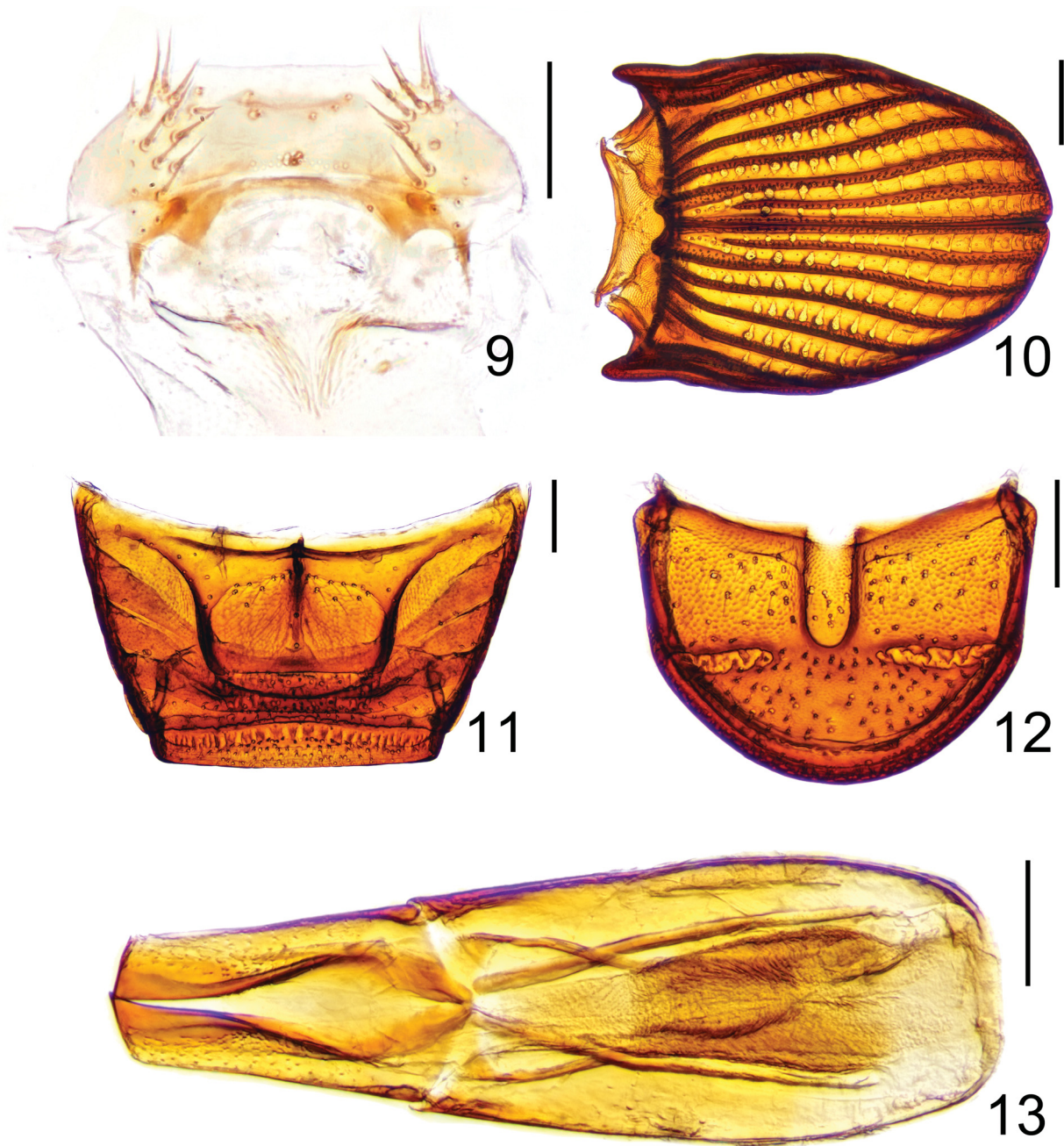## *Termitotrox icarus* sp. nov.
(Figs 3–13, 17, 21, 22)

Type material. Holotype: ♂ (deposited in NSMT collection), Myanmar, Nay Pyi Taw, Zeya Thiri Township, (alt. 120 m), 19.77°N, 96.31°E, 28–29 VII 2019, S. Kakizoe, W.-R. Liang, and K. M. Myint leg. (from the nests of *Odontotermes proformosanus*). Paratypes: 20 ♂♂ 20 ♀♀, and 1256 unsexed specimens: **MYANMAR: Nay Pyi Taw:** same data as holotype; 13 unsexed specimens: same data as holotype but 27.vii.2019 and collected from different termite colony of same termite species than the 28–29.vii.2019 series. Paratypes will be distributed to CMN, FRINM, KUM, MNHN, NCHU, NHMUK, NMPC, NSMT, and SKC.

Diagnosis. This species is similar to *T. cupido* and *T. venus* in having wing-shaped trichomes on the elytral base, but it is easily distinguished from these species because of the following combination of characters: a) the more elongate habitus shape in dorsal view, b) the basomedian section of pronotum not protruding backwards, c) a pair of distinct costae on the pronotal basomedian section are strongly developed, d) a median costa on anterior pronotal margin is strongly developed, e) the elytral striae narrower than interstriae, e) the lack of trichomes at the base of elytral sutural stria, and f) a size intermediate between the two aforementioned species (1.5–1.9 mm) vs. 1.2 mm in *T. cupido* and 2.4 mm in *T. venus*.

Description. *Male* (holotype). General color (Figs 3–8) uniformly reddish-brown, matt, body length 1.75 mm. *Head* (Figs 3–7). Surface generally evenly convex, clypeofrontal suture imbricate apart from a slight callosity in the middle (at high magnification). Lateral margins of head entirely, finely marginate. Clypeal outline evenly rounded over entire length. Clypeofrontal border at suture strongly grooved except for a callosity, straight to genal tip. Clypeofrons reddish brown, glabrous, distinctly, moderately punctate, with few small deep elongate punctures. Vertex with 10 elongate deep punctures (in dorsal view). Genae obtusely angular (in dorsal view); genal surface depressed, distinctly imbricate. Antennae (Fig. 4) yellowish-brown, 9-segmented, including the 3-segmented club. Compound eyes absent. Maxillae small, longer than wide; galeae toothed distally; basistipites and palpifer with long setae on lateral side. Maxillary palpus 4-segmented and well developed; segment I small, bent outwards; segment II about 3 times as long as segment I; segment III small, about 2 times as long as segment I, slightly bent inwards; segment IV large, approximately 1.5 times as long as segment II; numerous digitiform sensillae present on ventrolateral side of proximal half of segment IV. Mandibles asymmetrical, pointed apically, numerous serrate ridges on molar surface. Epipharynx (Fig. 9) with anterior margin almost straight, epitorma almost indistinct, pedia almost glabrous, chaetoparinae and adelochaetae very strong and elongate. *Pronotum* (Figs 3, 5, 7). Prothorax dark brown, as wide as elytra, sides (in dorsal view) almost straight over anterior 2/3. Anterolateral lobes obtusely angular (in dorsal view), edge slightly projecting downward (forming side of anterolateral propectoral cavity). Pronotal sides steeply declivous. Posterolateral sections of pronotum rounded. Base of pronotum evenly rounded, immarginate; basolateral area with few narrow ridges and grooves. Pronotal surface glabrous except for costae. Costae densely punctate, microsetose, intercostal sulci distinctly wrinkled. Central depression deep; surface winkled. Pronotal pattern of longitudinal costae as follows: median costa at anterior margin broad, becoming indistinct around anterior 1/4; basomedian section narrow, surface winkled, strongly concave, with a pair of distinct costae. Central depression posterolaterally delimited by extra grooves along paramedian costae. Paramedian costae narrow, distinct, posteriorly interrupted by deep sulcus. Sublateral costae anteriorly broad, distinct, tapering posteriad to about 1/5 of pronotal length, reaching paramedian costa. Lateral costae anteriorly broad, distinct, extending from anterolateral lobe caudad, tapering to base of pronotum. Marginal costae anteriorly broad, evenly curved, tapering to base of pronotum. *Elytra* (Figs 3, 5, 7, 10). Elytra, elongate, strongly convex dorsally, as high as pronotum, reddish brown, with 9 interstriae and intervening striae, and with short trichomes at base of interstriae 4–6 forming wing-shaped patches. Humeral and apical elytral calli absent; apicosutural angle nearly rectangular, slightly protruding. Epipleuron wide. Elytral striae distinct, deeply impressed, with transverse weak costae forming quadrate cells present from base to apex. Discal interstrial costae generally broadly rounded (in cross-section), surface with

3–8: 1.0 mm

Figs 3–8. Habitus of *Termitotrox icarus* sp. nov. (holotype and paratypes). 3 – holotype male, dorsal view; 4 – paratype male, ventral view; 5 – paratype female, dorsal view; 6 – ditto, ventral view; 7 – holotype male, antero-lateral view; 8 – paratype male, dorsal view (elytra removed). Scale bar = 1.0 mm.

Figs 9–13. Body parts of *Termitotrox icarus* sp. nov. (paratype male). 9 – epipharynx, ventral view; 10 – elytra, dorsal view; 11 – abdomen, ventral view; 12 – pygidium, postero-lateral view; 13 – aedeagus, dorsal view. Scale bars: 0.05 mm (Fig. 9); 0.20 mm (Fig. 10); 0.10 mm (Figs 11–13).

dense, scattered micropunctations, microsetose. Elytral pattern of interstrial costae as follows: interstria 1 (next to suture) narrow, almost rectilinear; interstria 2 tapering in front, stopping at basal 1/5; interstria 3 complete, slightly narrow at middle, weakly protruding in front; interstria 4 complete, narrow; interstriae 5 and 6 complete, strongly developed; interstria 7 complete, basally broad, strongly developed; interstria 8 complete, strongly developed; interstriae 9 and 10 apparently fused together. Apterous (Fig. 8). Scutellum notably small, invisible in dorsal view. ***Prosternum*** (Figs 4, 6). Anterolateral part of propectus deeply excavate. Preprosternal apophysis notably small, invisible in ventral view. Propectus glabrous, dark brown. Posterolateral areas of propectus narrow, with two distinct

grooves in each area. Postprosternal surface reddish brown, glabrous, imbricate flattened. ***Mesoventrite*** (Figs 4, 6). Surface reddish brown, glabrous, imbricate, flattened, moderately micropunctate. Mesoventrite with distinct trapezoidal shaped groove bordering mesocoxae; anterior side distinct, slightly curved; lateral sides notably broad, slightly curved; posterior side between posterior edges of mesocoxae distinct, straight, not completely reaching mesocoxae. ***Metaventrite*** (Figs 4, 6). Metaventrite reddish brown, glabrous, imbricate, flattened, moderately micropunctate, with fine median and perimarginal grooves all around. ***Abdomen*** (Figs 4, 6, 11). Venter with 5 fairly sclerotized abdominal ventrites, all reddish brown, glabrous, imbricate, moderately micropunctate; abdominal ventrites

Figs 14–17. Habitat of *Termitotrox icarus* sp. nov. 14–15 – termite mound of host termite *Odontotermes proformosanus* Ahmad, 1965; 16 – a fungus garden chamber of host termite; 17 – alive specimen of *Termitotrox icarus* sp. nov. walking on the wall of fungus garden chamber.

2 and 3 with series of distinct, short, elongate punctures along base at middle; abdominal ventrite 4 without series of distinct elongate punctures at middle; abdominal ventrite 5 with series of distinct, short, elongate punctures along base over entire length in anterior half. Pygidium reddish brown, glabrous, generally convex, moderately micropunctate; base broadly marginate. Propygidium (Fig. 12) with basal longitudinal groove. *Legs* (Figs 3–7). Procoxae protuberant. Profemora brown, underside glabrous, imbricate, moderately micropunctate; outline broadly elliptical, emarginate distally. Protibiae pale brown, broad, sparsely and shortly setose, microsculpture poorly pronounced; shape strongly complanate with 2 external denticles, no basal serration; apex oblique-sinuate, transverse, with distinct apico-internal spine; internal side strongly dilated from slender base. Protarsi pentamerous, two times longer than width of tibial apex, slender, yellowish brown; segment 1 inserted in fine groove, as long as segments 2–4 combined. Anterior claws normal, symmetrical. Mesocoxae dark brown, widely separated, slightly divergent anteriad. Mesofemora reddish brown, broadly elliptic in outline, distally emarginate, surface moderately micropunctate, glabrous, imbricate. Mesotibiae reddish brown, with several setae, broad, abruptly dilated near base, nearly parallel-sided from apex, edges entire; tibial apex slightly emarginate,

with pair of acuminate apico-internal spurs, external one long, slightly curved, internal one short, straight; upper side of mesotibia with fine longitudinal ridge near outer edge, few weak costae at basal half, underside with two fine sinuate ridges from base to apico-internal section; with long setae around apical half. Metatibiae similar to mesotibia, but shorter and gently dilated apically, with apex shallowly emarginate. Meso- and metatarsi reddish brown, compacted-complanate, segments 1–4 short. Length of outer apical spur of metatibia 1/4 length of metatibia, reaching base of tarsal segment 5. Middle and hind claws normal, symmetrical. *Aedeagus* (Fig. 13) symmetrical, length of aedeagus 0.71 mm (40.5% of body lengh). Phallobase elongate, cylindrical. Parameres short, almost half-length of basal piece. Apophyses of parameres long, almost same length of phallobase. Median lobe weakly sclerotized apically, with long apophyses (temones) almost same length of phallobase; anterior angle acute.

Female. Secondary sexual dimorphism not appreciable.

Measurements (*N* = 18). Body length 1.51–1.88 (1.69±0.100); maximum width of head 0.56–0.68 (0.64±0.030); median dorsal length of pronotum 0.66–0.76 (0.71±0.030), maximum width 0.73–0.85 (0.78±0.032); sutural length of elytra 0.73–0.95 (0.81±0.052), maximum width 0.73–0.85 (0.79±0.036).

Etymology. In Greek mythology, Icarus was the son of Daedalus. He is famous for having approached the sun with wings made of feathers and wax, which melted and gradually became smaller, thus eventually causing his falling into the sea. The name refers to the smaller elytral wing-shaped trichomes compared to the other known species of the genus having wing-shaped trichomes (i.e., *Termitotrox cupido* and *T. venus*). Noun in apposition.

Symbiotic host. *Odontotermes proformosanus* Ahmad, 1965 (identified by Dr. Yoko Takematsu).

Remarks. In some female specimens, we observed a single giant egg (Figs 21 and 22). We randomly chose 20 females and dissected them, 17 of them had one single egg while the others did not bear any egg.

Collecting circumstances. We found more than 1000 *T. icarus* sp. nov. individuals in the fungus garden chambers of *Odontotermes proformosanus*. We found *T. icarus* sp. nov. individuals from two colonies of *Odontotermes proformosanus*. Almost all individuals (>99%) were collected from a single colony. The colonies were located on the edge of a small secondary forest, and the soil was laterite. Collection season (July) was the rainy season. We carefully examined the walls of the fungus garden chambers and the inside of the fungus garden combs, but we did not find *Termitotrox* eggs, larvae, or pupae. We recorded the location from which adult *Termitotrox* beetles were collected in the 44 fungus garden chambers surveyed on July 29, 2019. The analysis yielded no significant difference in the mean number of individuals collected "on the chamber wall" and "inside the fungus garden" (Wilcoxon signed rank test, $V = 446$, $P = 0.1558$, Fig. 20).

Behavioral observations. In laboratory-based observations, we recorded multiple instances of host termite minor workers carrying *T. icarus* sp. nov. individuals with their mandibles (Figs 18 and 19, and S1). The beetle constantly exposed its antennae and legs and frequently moved its legs. In each instance, the carrying period was about 5 minutes. This behavior was also observed multiple times in the field. However, nutrient exchange (trophallaxis) between the termite and beetle was not observed during either field or laboratory observations.

Distribution. Central Myanmar.

Discussion

Termite association / phoresy of *Termitotrox* beetles. During our behavioral observations, we did not observe any attack from host termites on *T. icarus* sp. nov. individuals. Provided the large number of *T. icarus* sp. nov. individuals found in one termite mound into consideration, it is likely that the lack of aggressive behaviour by termites indicates that this new species falls within the synoekete or symphilic species. We also observed the host termites carrying *Termitotrox* beetles at both the field site and in Petri dishes, suggesting that *T. icarus* sp. nov., like *T. venus*, is a symphilic species. This is a new example of transport symbiosis (i.e., phoresy). *Termitotrox icarus* sp. nov. is small with short legs and flightless, and therefore the dispersal abilities are likely low; however, being carried in the host termite's mouth, makes it possible for *T. icarus* sp. nov. to move rapidly and over long distances.

Despite its poor capacity for migration because of its inability to fly, the genus *Termitotrox* has a wide distribution range from Africa to Asia. An important question, therefore, is how do beetle populations living in a certain termite nest effectively disperse into another nest. Without such dispersal, the beetle population would become extinct once their host termite colony dies. The observed carrying behavior displayed by the host termite allows the beetle to rapidly move within the territory of a termite colony, but it is an unlikely method of dispersal to another termite nest given the antagonistic behavior between termite colonies. Considering the long life of a termite colony (up to 10 years), a dispersal event is unlikely to occur in every generation of the beetles, but probably occurs only when the original host termite colony dies. When this happens, "homeless" beetles probably move to the territory of another termite colony (i.e., the foraging tunnels or wood/litter currently occupied by termites). The beetle's strong and up-bending middle leg is probably an adaptation for movement in the termites' tunnels (similar to the leg adaptations observed in ants of the genus *Melissotarsus* Emery, 1877 living inside tree tunnels (KHALIFE et al. 2018)). Once a "homeless" beetle enters the termites' foraging tunnel, the carrying behavior of the termites would enable the beetle to rapidly enter the fungus garden.

Figs 18–19. Carrying behavior by host termite *Odontotermes proformosanus* Ahmad, 1965 to *Termitotrox icarus* sp. nov. (observed in laboratory).
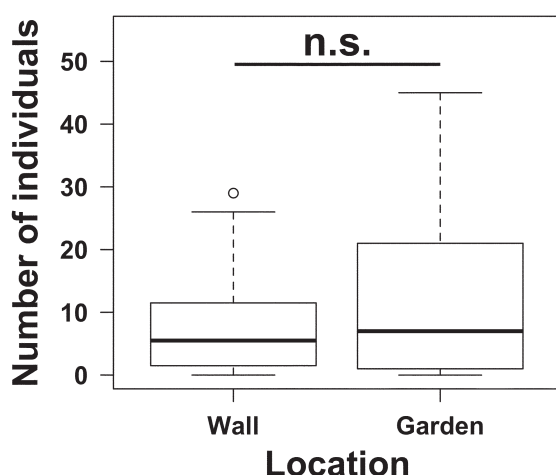
Fig. 20. The number of *Termitotrox icarus* sp. nov. found on the wall of chamber or inside the fungus garden comb. There was no significant difference in the number of individuals between the two locations (Wilcoxon signed rank test, $V = 446$, $P = 0.1558$).

In *Termitotrox icarus* sp. nov., the large central depression of the pronotum corresponds to the size of the minor worker termites' mouthparts (especially the labrum). Therefore, there is likely a positive correlation between the body length of the host termite and the body length of the inquiline. These results support the hypothesis of KAKIZOE & MARUYAMA (2015) that the body length of the host is correlated with the body length of the inquiline.

Carrying behavior by host termites has also been observed in *T. cupido* (Kakizoe, personal observation), as hypothesized by MARUYAMA (2012a), suggesting that such phoresy may be a universal behavior in the genus *Termitotrox*. Similar to other beetles that inhabit subterranean environments, *Termitotrox* species are apterous and eyeless and therefore highly specialized to the dark termite nest environment. However, unlike other subterranean beetles that can be collected by bait trapping in the ground, *Termitotrox* beetles cannot be collected using attraction methods. In addition, some other termitophilous scarabs (e.g., Corythoderini and Stereomerini) are occasionally collected by flight intercept trapping or light trapping (TANGELDER & KRIKKEN 1982, STOREY & HOWDEN 1996); however, as *Termitotrox* beetles are flightless, it is not possible to use either of these collection methods. Consequently, it is extremely difficult to collect even known *Termitotrox* species and, with the exception of the recently described species (*T. cupido* and *T. venus*), to our knowledge, additional specimens of the other known species have not been collected in over 50 years (KRIKKEN 2008, MARUYAMA 2012a, KAKIZOE & MARUYAMA 2015). To solve this problem, researchers should consider the relationship between the host termites and *Termitotrox* species highlighted in the present study, i.e., estimating the body length of host termites, even for *Termitotrox* species whose host is unknown. This method might be useful for re-discovering known species.

In the three species with wing-shaped trichomes distributed through the Indo-Chinese Subregion (*T. cupido*, *T. venus*, and *T. icarus* sp. nov.), secretion of chemical signals to manipulate host termites using wing-shaped trichomes may trigger the carrying behavior by the host. To fully understand the symbiotic relationship of these species, additional research is required in order to identify potential chemical signaling agents and their effects on the behavior of host termites. For other species of *Termitotrox* that do not have wing-shaped trichomes, it remains unclear whether a close symbiotic relationship with a host termite, as typified by carrying behavior, exists; thus, further studies are also required in this area.

Unlike *Termitotrox cupido* and *T. venus*, *T. icarus* sp. nov. was collected not only from the walls of the fungus garden chambers but also from inside the fungus gardens. This result highlights the importance of exploring a variety of inner-nest microhabitats in order to search for termitophilous insects.

Egg gigantism. The gigantism of eggs, as revealed by micro-CT scans in females of *T. icarus* sp. nov., has also previously been observed in *T. cupido* (MARUYAMA 2012a). This is likely a result of *K*-selection in the *r/K*-selection theory proposed by MACARTHUR & WILSON (1967). The inside of a termite nest is an extremely stable, localized environment managed by termites and is unlikely to produce an accidental niche space. Therefore, strategies to ensure the rearing of a small number of offspring (i.e., strategies with a low intrinsic growth rate *r* and a high carrying capacity *K*) are considered adaptive. This strategy of having a single giant egg or a few mature eggs, generally connected to an extremely short larval stage, is also known from other termitophilous insects (Coleoptera, Staphylinidae: SEEVERS 1957; LIANG et al. in prep.; Coleoptera, Scarabaeoidea: MARUYAMA 2012a; KAKIZOE in prep.; Diptera, Phoridae: DUPONT & PAPE 2009).

Phylogenetic relationships. Since *Termitotrox icarus* sp. nov. has wing-shaped trichomes on the elytra, it is likely to be closely related to the previously known species from the Indo-Chinese Subregion, *T. venus* and *T. cupido*. As stated by KAKIZOE & MARUYAMA (2015), wing-shaped trichomes are likely to be synapomorphic character states in these three species. On the other hand, two species from India (*Termitotrox minutus* (Arrow, 1920) and *T. permirus* Wasmann, 1918) and eight species from the Afrotropical Region do not have elytral wing-shaped trichomes. It is possible that the presence or absence of wing-shaped trichomes affects the type of relationship with the host termites. However, to confirm this speculation, it will be necessary to observe the field behavior of the species without wing-shaped trichomes.

Biogeography. In the Oriental Region, *Termitotrox* was previously known only from India and Cambodia (KAKIZOE & MARUYAMA 2015). The discovery of the genus *Termitotrox* in Myanmar in the present study suggests that undescribed species could also be found in neighboring areas, such as Thailand, Laos, and Bangladesh.

Also, the genera of termites known to be the host of *Termitotrox* until now, *Odontotermes* and *Macrotermes*, are distributed in the Oriental and Afrotropical Regions, and *Hypotermes* in the Oriental Region (KAMBHAMPATI &

Figs 21–22. Single large egg in a female *Termitotrox icarus* sp. nov. (21 – dorsal view; 22 – lateral view).

EGGLETON 2000). Therefore, additional surveys in areas where these macrotermitine genera are distributed may lead to the discovery of undescribed species of *Termitotrox*.

KRIKKEN (2008) suggested that the distribution of *Termitotrox* is similar to that of Corythoderini, another termitophilous group of scarabs. In contrast to India, where numerous species of Corythoderini are known, only one Corythoderini species, i.e. *Termitopisthes termiticola* (Gestro, 1891), is known from Myanmar (TANGELDER & KRIKKEN 1982). Our discovery of *Termitotrox* in Myanmar therefore complements Krikken's suggestion. MARUYAMA (2012a) postulated that since the fungus-growing termite originated in Africa (AANEN & EGGLETON 2005), *Termitotrox* and Corythoderini also likely originated in Africa and expanded their distribution following their host termites. However, considering the morphological diversity of these taxa in the Oriental Region, including the presence or absence of wing-shaped trichomes in *Termitotrox*, and the large number of genera and species of Corythoderini found in India, they may in fact have originated in the Oriental Region. Comprehensive molecular phylogenetic studies of these two taxa in the Oriental and Afrotropical Regions are needed to address this issue.

Acknowledgments

Supplementary data

Video S1. Carrying behavior by host termite *Odontotermes proformosanus* to *Termitotrox icarus* sp. nov. (observed in laboratory). Available at:
- http://doi.org/10.5281/zenodo.3948312 (Zenodo archive)
- https://www.aemnp.eu/acta-entomologica/60-2/60_2_427.html (web page of AEMNP)
- https://youtu.be/Rw_OC-c5Enc (YouTube)

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