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Systematics of rove beetles (Coleoptera: Staphylinidae: Aleocharinae) associated with Hodotermopsis sjostedti (Isoptera: Termopsidae)

Taisuke KANAO¹, Munetoshi MARUYAMA² and Ryûtarô IWATA³
¹Entomological Laboratory, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, Fukuoka, Japan, ²The Kyushu University Museum, Fukuoka, Japan and ³Department of Forest Science and Resources, College of Bioresource Sciences, Nihon University, Fujisawa, Japan

Abstract
Members of the termitophilous subtribe Termitozyrina (Aleocharinae: Lomechusini) associated with Hodotermopsis sjostedti are taxonomically treated. The genera Hodotermophilus Naomi & Terayama and Termophidoholus Naomi & Hirono, and each type species (monotypic) are redescribed. Termophidoholus formosanus, originally described from Taiwan, and its host termite H. sjostedti are newly recorded from Laos. Yakuus iwatai Kanao & Maruyama gen. & sp. nov. and H. gloriosus were collected sympatrically in the same nests in Yaku-shima, Japan. All of the above species, belonging to the three genera, share the presence of a batch of spurs at the tibial apex of fore and mid legs. Habitus photographs and illustrations of diagnostic features are provided for these species, and their phylogenetic relationships are discussed based on morphological similarities and the extant distribution of the host termite species.

Key words: host specificity, limuloid shape, Lomechusini, sympatry, termitophily, Termitozyrina, Yakuus iwatai gen. & sp. nov.

INTRODUCTION
Rove beetles (Coleoptera: Staphylinidae) are the most biologically and morphologically diverse insect guests of termite colonies (Kistner 1982), and such termite symbionts are called termitophiles. Most termitophilous rove beetle species belong to the subfamily Aleocharinae. Currently, 17 tribes include termitophilous species, and termitophily is considered to have evolved multiple times independently in the subfamily. Generally, these termitophilous species have species-specific relationships with their host termites (Kistner 1969).

Additionally, termitophiles exhibit convergent ecomorphs that are classified as physogastric and limuloid body forms. Physogastric species have large swollen abdomens, which contribute to beetles resembling the habitus of host termites. Therefore, physogastry is considered to have a mimetic function and taxa to be relatively highly integrated into termite societies (e.g. Kistner 1982; 2001). On the other hand, limuloid species are teardrop-shaped and the dorsum often has explanate lateral margins, which are able to conceal its appendages under the body. Given appendage concealment and the often extremely compact nature of appendages have contributed to the hypothesis that limuloid body forms are adaptive for a defensive life history strategy in termite nests (Kistner 1969).

The Termitozyrina Seevers, 1957 (Lomechusini) is a small termitophilous subtribe. Sixteen species across 11 genera are known from the Neotropical and Oriental regions (Bernhauer 1912; Silvestri 1945; Borgmeier 1950; Seevers 1957; Kistner 1970a,b; 1971; Naomi & Terayama 1986; Naomi & Hirono 1996). Morphology of the Termitozyrina spans both physogastric and limuloid body shapes. This morphological convergence clouds phylogenetic relationships and almost nothing is known about evolutionary relationships within the subtribe. In addition, previous taxonomic descriptions
of the subtribe (Seevers 1957), and lineages within, are no longer sufficient for adequate taxonomic study.

In light of need for an updated taxonomic treatment, we redescribe two genera and species in the Termitozyrina, Hodoterophilus gloriosus Naomi & Terayama and Termophidoholus formosanus Naomi & Hirono, and additionally, describe a new genus and species from Japan. All taxa treated here are associated with Hodoteropsis sjostedti Holmgren, 1911 (Isoptera: Termopsidae). We also discuss the phylogenetic relationships between these species based on observed morphological characters.

MATERIALS AND METHODS

Field surveys were conducted in the island of Yaku-shima, Japan in 2000 and 2002 by Dr Masaru Hojo and M. Maruyama, and again in 2010 by M. Maruyama and 2012 by T. Kanao. Dr Hiroshi Sugaya made a study trip in Taiwan in 2002. R. Iwata conducted fieldwork in Laos in 2002. Specimens were initially preserved in 2.0-mL vials of 80% ethanol.

The technical terminologies and procedures used for this study generally follow those described in Sawada (1972) and Maruyama (2006). When a permanent mount was made, KOH-cleared specimens or parts were washed in water, and then dehydrated by successively transferring specimens/parts to higher ethanol (EtOH) concentrations until finally reaching 100% EtOH. Dehydrated specimens/parts were then embedded in Euparal mounting medium, and when appropriate, dissections were made within Euparal on a glass mounting substrate prior to medium solidification. Full body dissections were made and preserved on glass microscope slides. Dissected body parts were preserved and mounted on halved glass cover slips, subsequently glued onto a halved paper glue board, and mounted under the respective specimen (see Maruyama 2004 for details).

In the descriptions, macrochaetotaxy formulas depict raw numbers of setae and not the numbers of setal pairs. The right half of figures of pronota, tergites and sternites depict only macrosetae.

TAXONOMY

Subtribe Termitozyrina Seevers

Hodoterophilus Naomi & Terayama
(Figs 1–27)
Hodoterophilus Naomi & Terayama, 1986: 504.
Type species: Hodoterophilus gloriosus Naomi & Terayama, 1986.
than lacinia, dilated apically, apex sparsely covered with minute setae, median sclerotized area densely setulate adorally; palpus with 4 segments; segment I trapezoidal; segment II dilated apically; segment III more than three times longer than wide, widest at middle, sparsely covered with long setae; segment IV narrowed apically, with apical margin approximately one-fourth as wide as base; stipes triangular, with a seta at basal aboral corner; palpifer with a seta at middle of adoral margin. Mentum (Fig. 9) trapezoidal, approximately six times wider than long, sparsely covered with pseudopores and 8–9 small setae, with a pair of long setae at anterior and lateral margin, respectively; anterolateral corners slightly produced; anterior margin submembranous, difficult to discriminate from membrane connected to labium; posterior margin straight. Labial palpus (Fig. 10) with 3 segments; segment I with 2 setae at aboral anterolateral corner and a seta at dorsal anterolateral corner, a pore present at middle; segment II half as long as segment I, with a seta and two pores at middle, a pore present at aboral postero-lateral corner; segment III as long as segment I, three pores present around apex; ligula bifid at apical half, a pair of minute setae at apex; prementum almost as wide as long, disc with a pair of setal pores and 2 pairs of real pores at middle, pseudopores present medially and laterally, basal pores present; apodemes almost two thirds as long as prementum, posteriorly curved internally.

Pronotum (Fig. 11) semicircular, anterior margin arcuate, posterior margin straight with anterolateral corners slightly bluntly produced posteriorly, dorsally moderately convex. Prosternum reduced in length. Elytra (Fig. 12) subquadrate, wider than long, with lateral margin deflexed. Hind wing rudimentary. Mesoventrite (Fig. 13) short, less than half as long as metaventrite; mesoventral process carinate, developed posteriorly; mesocoxal cavity deep, narrowly separated and marginal bead complete. Legs (Figs 14,16,18) overall short, sparsely covered with setae; tibiae with several spurs around apical margin (Figs 14–17); tarsi with tarsomeres slender and parallel-sided; tarsal formula 4–5–5. Fore leg (Fig. 14) with coxa subequal in length to femur; trochanter subtriangular; femur narrowed apically; tibia thin, as long as femur; tarsomeres I–III subequal in length, tarsomere IV longest. Mid leg (Fig. 16) with coxa oval; trochanter subtriangular; femur narrowed apically; tibia thin; tarsomere I longer than other segment except for tarsomere V. Hind leg (Fig. 18) with coxa subtriangular; trochanter subtriangular; femur slightly narrowed apically; tibia thin, widest at middle; tarsus long, as long as tibia; tarsomere I longer than other segments except for tarsomere V, tarsomere V more than twice as long as IV.
Figures 11–23 *Hodotermophilus gloriosus*. 11 Pronotum; 12 elytron, right; 13 meso- and metaventrite, anatomical right side; 14 foreleg; 15 foretibia with spurs; 16 mid leg; 17 mid tibia with spurs; 18 mid leg; 19 tergite VIII; 20 male sternite VIII; 21 female sternite VIII; 22 male tergites IX–X; 23 female tergite IX–X.

Figures 24–27 *Hodotermophilus gloriosus*. 24 Median lobe of male aedeagus, aparameral view; 25 median lobe of male aedeagus, lateral view; 26 right paramere, lateral view; 27 spermatheca.
Abdomen (Figs 1,2) narrowed posteriorly. Segment I represented only by tergite I fused to metanotum. Segment II represented only by tergite II. Segments III–VII with 1 tergite, 1 sternite and 2 pairs of paratergites. Tergite VIII (Fig. 19) subquadrate, slightly narrowed posteriorly, with posterior margin medially produced. Sternite VIII (Figs 20,21) with posterior margin rounded. Tergite IX (Figs 22,23) fully subdivided dorsally by tergite X. Tergite X (Figs 22,23) with posterior margin emarginated. Median lobe of male aedeagus (Figs 24,25) successively narrowed apically in aparameral view (Fig. 24), with apical lobe longer than basal capsule; apical part of suspensoria fused with apical process of copulatory piece. Paramere (Fig. 26) with condylite velum acutely apically produced; apical lobe almost fused with paramerite; weakly sclerotized copulatory piece. Paramere (Fig. 26) with condylite velum acutely apically produced; apical lobe almost fused with paramerite; weakly sclerotized copulatory piece. Paramere (Fig. 26) with condylite velum acutely apically produced; apical lobe almost fused with paramerite; weakly sclerotized copulatory piece. Paramere (Fig. 26) with condylite velum acutely apically produced; apical lobe almost fused with paramerite; weakly sclerotized copulatory piece. Paramere (Fig. 26) with condylite velum acutely apically produced; apical lobe almost fused with paramerite; weakly sclerotized copulatory piece.

**Diagnosis.** This species is diagnosable based on the generic diagnosis above.

**Redescription.** Body (Figs 1,2) average length 3.33 mm (3.00–3.64 mm, n = 3), females larger than males, almost uniformly orange brown, shiny and subtransparent.

Dorsal surface of head (Fig. 3, left side) sparsely covered with pores, 2 pairs of long setae present at anterior margin of clypeus, several setae present behind eyes. Ventral surface of head (Fig. 3, right side) with postgena sparsely covered with setae laterally; hypostoma sparsely covered with pores; submentum with 4 pairs of long setae at anterior margin; gula with 2 pairs of setae at middle. Eyes with uniform cover of inter-ommatidial setae. Antennae (Fig. 4) sparsely covered with setae; segments I–III covered with fewer setae than other segments; segment I with two long macrosetae at anterior margin of dorsal surface; segments II–X with 4–6 macrosetae at apical margins; segment XI with several macrosetae near middle and apex. Dorsal surface of labrum (Fig. 5, left side) covered with 6 pairs of setae at anterior half, a pair of conspicuously longer setae at anterolateral corner, a pair of setae at anterior margin, and 2 pairs of shorter setae at lateral margin. Epipharynx (Fig. 5, right side) covered with 2 pairs of short lateral setulae. Mandible (Figs 6,7) dorsally with 5 scrobal setae along aboral margin. Maxillary (Fig. 8) lacinia with posterior half ventrally covered with several setae; maxillary palpal segment I with a long seta at middle, segment II sparsely covered with setae and a strong seta at apical margin, one large pore and two pores present at middle of inner margin and anterior margin, respectively, segment III sparsely covered with setae and 2 stronger setae at apical margin adorally.

**Proronotum (Fig. 11)** sparsely covered with minute pores, with 6–7 pairs of macrosetae at lateral margin, 4 macrosetae at anterior margin, 4 macrosetae at posterior margin, and 8 macrosetae and few pores at middle (pronotal length = 0.84–0.94 mm, average length 0.89 mm; pronotal width = 1.40–1.48 mm, average width 1.44 mm, n = 5). Elytra (Fig. 12) sparsely covered with pores, with anterolateral margin covered with setae, 6 macrosetae at lateral margin, 4 macrosetae posterior margin, 2 macrosetae at inner margin, and 6 macrosetae on disc (elytral length = 0.72–0.80 mm, average length 0.75 mm; elytral width = 0.66–0.84 mm, average width 0.73 mm, n = 5). Mesoventrite (Fig. 13) sparsely covered with minute setae at middle and lateral areas. Metaventrite (Fig. 13) with posterior one third sparsely covered with setae. Fore leg (Fig. 14) uniformly covered with setae; coxa with two macrosetae near apicolateral margin, basal third glabrous; tibia with 2 long and 12 short spurs around apical margin (Fig. 15).
Mid leg (Fig. 16) uniformly covered with setae except for coxa; coxa with several setae at femoral cavity, a long seta and few setae present at middle of inner margin; trochanter with a macroseta at anterior middle; femur with a macroseta at base of inner margin and anterolateral margin, each; tibia with 2 long and 11 short spurs around apical margin (Fig. 17), 2 macrosetae present at lateral margin. Hind leg (Fig. 18) uniformly covered with setae except for coxa; coxa without seta at basal half, 4–5 long setae present along femoral cavity margin; trochanter with a macroseta at middle of inner margin; femur with a macroseta at apical outer margin, and 5 long setae at apical margin; tibia with 3 macrosetae at outer margin, a long and 3 short spurs present at apical margin.

Tergites, sternites and paratergites III–VIII (Figs 1, 2) sparsely covered with setae, anterior one-third sparsely covered with pores, each outer paratergite with a macroseta. Macrochaetotaxy of abdominal tergites III–VII = 8–8–8–8–6. Tergite VIII (Fig. 19) with anterior one third sparsely covered with pores, 2 pairs of macrosetae present around middle, 4 pairs of macrosetae present at posterior margin. Tergite X (Figs 22, 23) with anterior one third sparsely covered with pores, several setae present near middle of disc, and 5 pairs of macrosetae posteriorly.

Male: Sternite VIII (Fig. 20) with 3 pairs of macrosetae on disc, 2 pair of macrosetae at lateral margin, and 3 pairs of macrosetae at posterior margin. Tergite IX (Fig. 22) with anterior one third sparsely covered with pores, 5 pairs of macrosetae around middle, and 2 pairs of macrosetae apically. Median lobe of aedeagus (Figs 24, 25) with suspensoria broad and large, as long as basal capsule. Paramere (Fig. 26) with apical lobe with pores at base; paramerite covered with pores at apical area; condylite sparsely covered with pores.

Female: Sternite VIII (Fig. 21) covered with 2 pairs of macrosetae on disc, 2 pair of macrosetae at lateral margin, and 3 pairs of macrosetae at posterior margin. Tergite IX (Fig. 23) with 4 pairs of macrosetae around middle, and 2 pairs of macrosetae at apex. Tergite X (Fig. 23) apex more deeply emarginated than in male. Spermatheca (Fig. 27) with thick cuticle overall.

Distribution. Only known from Yaku-shima, Kagoshima-ken, Japan.

Yakuus Kanao & Maruyama gen. nov.
(Figs 28–52)
Type species: Yakuus iwatai sp. nov.

Diagnosis. This monotypic genus is distinguished from other termityzine genera by its transverse pronotum (Fig. 38), meso-metaventral processes separated (Fig. 40), and lacinia covered with a lot of strong setae adorally (Fig. 35).

Description. Overall shape (Figs 28, 29) limuloid.

Head (Fig. 30) transverse, widest behind eyes, occipital suture present, epicranium produced dorsally over antennal fossae and obscuring complete view of segment. Antennae (Fig. 31) with 11 segments; antennal segment pedicles externally visible; segments I and XI longer, approximately twice as long as other segments; segment I elongate, widest at middle; segments II and III trapezoidal, longer than wide, apical margins twice longer than base; segment IV subquadrate, slightly wider than long, shorter than other segments; segments V and VI slightly longer than wide; segments VII–X trapezoidal, longer than wide; segment XI narrowed apically, approximately as long as segments IX + X combined. Labrum (Fig. 32) transverse, anterior margin concave at middle, with several pores at mesal area; epipharynx (Fig. 32, right side) sparsely irregularly covered with pores, median part and lateral part relatively smooth, mesolateral part with membraneous sculpture. Mandibles (Figs 33, 34) asymmetrical, with anterior one-fifth adorally moderately curved, basal half covered with pores, a large pore present at middle of disc, and 2–2 pairs of macrosetae adorally.
of aboral margin, prosthecae present. Left mandible (Fig. 33) with moderately developed tooth at middle of aboral margin. Right mandible (Fig. 34) with small acute tooth at apical one fourth of aboral margin. Maxillary (Fig. 35) lacinia furnished with 4 short strong setae at apical adoral margin, approximately 20 strong setae present at marginally dilated area, with posterior half uniformly covered with setae; galea as long as lacinia, sparsely covered with minute setae at apex, with median sclerotized area densely setulate adorally; palpus with 4 segments; segment I trapezoidal; segment II dilated apically, three times longer than wide; segment III more than three times longer than wide, approximately 1.5 times longer than segment II, widest at middle, sparsely covered with long setae; segment IV narrowed apically, apical margin approximately one fourth as wide as base; stipes triangular, with a seta at each basal corner; palpifer with a seta apically. Mentum (Fig. 36) trapezoidal, more than four times wider than wide, approximately 1.5 times longer than segment II, widest at middle, sparsely covered with long setae; posterior margin moderately posteriorly convex. Labial (Fig. 37) palp with 3 segments; segment I with 4 setae at anterior margin, a pair of pores present at inner anterolateral corner; segment II one-half as long as segment I, with 2 setae at middle, a pore present adorally at apicolateral corner; segment III as long as segment I, approximately half as wide as segment II, 2 pores present around apex; ligula divided apically, with a minute seta at apex; prementum transverse, twice wider than long, with disc covered with a pair of setal pores and 2 pairs of real pores at middle, basal pores present; apodemes almost twice as long as prementum.

Pronotum (Fig. 38) transverse, widest at base, with anterior and posterior margin almost straight, slightly produced posteriorly at posterolateral corners. Prosternum reduced in length. Elytra (Fig. 39) subquadrate, longer than wide with outer margin longer than inner margin. Hind wings vestigial. Mesoventrite (Fig. 40) short, less than half as long as metaventrite; mesoventral process developed to middle of mesocoxal cavity; mesocoxal cavity deep with completed marginal bead. Legs (Figs 41–43) slender; tibiae with several spurs around apical margin; tarsomeres slender and parallel-sided; tarsal formula 4–5–5. Fore leg (Fig. 41) with coxa slightly longer than femur, narrowed apically; trochanter small; femur slightly narrowed apically; tibia thin, as long as femur; tarsomeres I–III subequal in length; tarsomere IV as long as tarsomeres I + II. Mid leg (Fig. 42) with oval coxa; trochanter subtriangular; femur with apical one third narrowed; tibia thin,
slightly widened at middle; tarsomere I as long as tarsomeres II + III combined; tarsomeres II–IV subequal in length; tarsomere V longer than other segments. Hind leg (Fig. 43) with subtriangular coxa; trochanter subtriangular, one-half as long as femur; femur slightly narrowed apically; tibia thin, widest at middle; tarsi long but shorter than tibia; tarsomere I longer than other segments; tarsomeres II–IV subequal in length; tarsomere V approximately as long as tarsomeres II + III combined.
Abdomen (Figs 28,29) narrowed posteriorly. Segment I represented only by tergite I fused to metastomast. Segment II represented only by tergite II. Segments III–VII with 1 tergite, 1 sternite, and 2 pairs of paratergites, each. Tergite VIII (Fig. 44) longer than wide, slightly narrowed posteriorly, with posterior margin moderately medially convex. Sternite VIII with posterior margin rounded in males (Fig. 45), straight in females (Fig. 46). Tergite IX (Figs 47,48) fully subdivided dorsally by tergite X; tergite X (Figs 47,48) with posterior margin emarginate. Median lobe of male aedeagus (Figs 49,50) with basal capsule as long as apical lobe; suspensoria fused with apical process of copulatory piece. Paramere (Fig. 51) with condylyte almost fused with paramerite; condylyte velum weakly sclerotized, extended apically; apical lobe elongate, clearly divided from paramerite, with a long seta at base and 2 short setae at apex. Spermatheca (Fig. 52) with basal part longer than apical part, inner wall of apical part wrinkled, spermathecal gland present at boundary between apical and basal part.

Etymology. The generic name is derived from the type locality, Yaku-shima. The gender is masculine.

Yakuus iwatai Kanao & Maruyama sp. nov.


All specimens are deposited in the Kyushu University Museum (KUM).

Diagnosis. This species is diagnosable based on the generic diagnosis above.

Description. Body (Figs 28,29) average length 3.64 mm (3.15–4.10 mm, n = 5), female larger than male, uniformly orange brown, shiny and subtransparent.

Dorsal surface of head (Fig. 30, left side) sparsely covered with setae and pores, 2 pairs of long setae present at anterior margin of clypeus, with 2 pairs of short thick setae along lateral margin of produced epicranium, a pair of setae present at middle of inner margin of eyes. Ventral surface of head (Fig. 30, right side) with postgena sparsely covered with setae laterally; hypostoma sparsely covered with pores; submentum sparsely covered with pores, a pair of long setae present at posterolateral margin; gula sparsely covered with pores. Eyes sparsely covered with inter-ommatidial setae. Antennae (Fig. 31) sparsely covered with setae; segment I partially covered with fewer setae than other segments, and several pores at base; segment II with apical half covered with fewer setae; segments II–X with 4–6 macrosetae at apical margin; segment XI moderately pointed at apex, with several macrosetae around middle and apex. Dorsal surface of labrum (Fig. 32, left side) covered with 6 pairs of setae at anterior half, 3 pairs at anterolateral corner longer. Epipharynx (Fig. 32, right side) covered with 2 pairs of short lateral setulae. Mandible (Figs 33,34) dorsally with 7–8 scrobal setae along aboral margin. Maxillary (Fig. 35) lacinia with posterior half dorsally covered with several setae; maxillary palpal segment I with a long seta at middle, segment II sparsely covered with setae, one large pore present at inner basal margin, segment III sparsely covered with setae and 3 stronger setae anterolaterally.

Pronotum (Fig. 38) sparsely covered with minute macrosetae, densely covered with minute pores, 10–11 pairs of minute macrosetae at anterior and lateral margin, and 2 pairs of macrosetae at posterior margin (pronotal length = 0.76–0.88 mm, average length 0.83 mm; pronotal width = 1.08–1.26 mm, average width 1.18 mm, n = 5). Elytra (Fig. 39) sparsely covered with pores, several setae present between anterolateral and posterolateral corners, 6 minute macrosetae at lateral margin, 3 macrosetae at inner margin, 7 macrosetae on disc, and with 4 macrosetae and several minute setae at posterior margin (elytral length = 0.70–0.82 mm, average length 0.73 mm; elytral width = 0.56–0.64 mm, average width 0.60 mm, n = 5). Mesoventrite (Fig. 40) sparsely covered with setae and pores at middle and lateral areas. Metaventrite (Fig. 40) sparsely covered with setae. Fore leg (Fig. 41) uniformly covered with setae; coxa with a macroseta at middle of outer margin, and 3–4 long setae at apicalmargin; trochanter with several pores at middle; femur with a long seta at inner basal corner; tibia with anterior half of inner margin densely covered with setae, 2 long and 11 short spurs present around apical margin. Mid leg (Fig. 42) with coxa covered with minute setae at basal outer margin, 2 long setae present around apical inner margin; trochanter with a seta at middle, and several pores on basal half; femur sparsely covered with setae
except for basal area, a macroseta at middle of inner margin, and longer setae at inner apicolateral margin; tibia sparsely covered with setae, with apical half of inner margin densely covered with setae, 3 macrosetae at outer margin, and 3 long and 8 short spurs around apical margin; tarsi sparsely covered with setae. Hind leg (Fig. 43) uniformly covered with setae except for coxa; coxa covered with minute setae at femur receiver, several long setae present along femoral cavity margin; trochanter with a short macroseta at middle; femur with 6 short macrosetae at outer lateral margin; tibia with 4 short macrosetae at outer lateral margin, 4 pores at base, and 2 spurs at apical margin.

Tergites, sternites and paratergites III–VIII (Figs 28, 29) sparsely covered with setae, each outer paratergite with 2 macroseta. Macrochaetotaxy of abdominal tergites III–VII = 8–8–8–8–6. Tergite VIII (Fig. 44) with 3 pairs of macrosetae medially, and 4 pairs of macrosetae at posterior margin. Tergite X (Figs 47,48) with posterior half densely covered with setae medially, 5 pairs of long macrosetae present at posterior margin.

Male: Sternite VIII with posterior three fourth covered with setae, 3 pairs of macrosetae on disc, 2 pairs of macrosetae at lateral margin, and 3 pairs of macrosetae and 20–21 setae present at posterior margin. Tergite IX (Fig. 47) with anterior one third sparsely covered with pores, 9 pairs of macrosetae present posteriorly. Median lobe of aedeagus (Figs 49,50) with apical lobe shorter than basal capsule. Paramere (Fig. 51) with apical lobe sparsely covered with pores; paramerite covered with pores apically; condylite sparsely covered with pores.

Female: Sternite VIII (Fig. 46) with anterior margin sparsely covered with pores, 2 pairs of macrosetae on disc, 3 pairs of macrosetae at lateral margin, 2 pairs of macrosetae at posterior margin, and 20–21 setae at posterior margin which are shorter than in male. Tergite IX (Fig. 48) with basal half sparsely covered with pores, 8 pairs of macrosetae present posteriorly. Tergite X (Fig. 48) with posterior margin more deeply emarginate than in male. Spermatheca (Fig. 52) with apical part covered with thick cuticle.

**Distribution.** Only known from Yaku-shima, Kagoshima-ken, Japan.

*Host termite. Hodotermopsis sjostedti.*

*Ecology. Yakuus iwatai* was collected together with *H. gloriosus* from nests of *H. sjostedti* in fallen trees (Fig. 78). Like *H. gloriosus, Y. iwatai* chased after the host termites, and sometimes crawled under termites during laboratory observation. *Yakuus iwatai* moved faster than *H. gloriosus*. Host termites ignored the beetles regardless of frequent contact.

**Etymology.** The specific name is dedicated to R. Iwata, the person who first noticed the species.

**Termophidoholus Naomi & Hirono** (Figs 53–52)


*Diagnosis.* This monotypic genus is most similar to *Hodotermophilus* but easily distinguishable by its approximately 1-mm smaller body size, the shorter antennae and the body overall sparsely covered with setae (Figs 53,54). This genus is also distinguished from other genera of Termityrzyina by its robust and compact antennae (Fig. 56) and the short apical lobe of paramere (Fig. 75).

*Redescription.* Overall shape (Figs 53,54) limuloid and dorsoventrally flattened. Head completely covered by pronotum in dorsal view (Fig. 53).

Head (Fig. 55) oval, wider than long, widest at eyes, occipital suture present, with epicranium produced dorsally over antennal fossae and obscuring complete view of segment I. Antennal fossae deep; lateral margin of clypeus extended anteriorly and obscuring visibility of basal third of segment I. Eyes produced anterolaterally. Antennae (Fig. 56) with 11 segments; pedicles invisible externally; segments II–XI successively widening distally; segment I subquadrangular, longer than wide, slightly dilated apically; segment II transverse, longer than wide, widest at middle; segment III trapezoidal with apical margin twice as wide as basal margin; segment IV trapezoidal, slightly wider than long; segments V–X transverse; segment XI narrowed apically, longer than other segments. Labrum (Fig. 57) transverse, with anterior margin of membranous area slightly produced.

**Figures 53,54 Habitus of Termophidoholus formosanus. 53, dorsal view; 54 ventral view.**
Epipharynx (Fig. 57, right side) sparsely covered with pores, median part smooth, and mesolateral part with membranous sculpture. Mandibles (Figs 58, 59) asymmetrical, apex acute, with anterior one fourth curved adorally, dorsally sparsely covered with pores, scrobal pore present, a large pore present at middle of dorsal surface, prosthecae present. Left mandible (Fig. 58) with adoral margin deeply concave at middle. Right mandible (Fig. 59) with a tooth. Maxillary (Fig. 60) lacinia ventral surface sparsely covered with setae, and several strong marginal setae directed adorally; apical 2 of 7 apicomarginal setae short; 7 setae at marginally dilated area short, two of them thicker; galea slightly longer than lacinia, dilated apically, apex sparsely covered with minute setae, median sclerotized area densely setulate adorally; palp with 4 segments; segment I small, trapezoidal; segment II dilated apically; segment III longer and wider than segment II; segment IV narrowed apically; stipes triangular, with a seta at each basal corner; palpifer with a seta apically. Mentum (Fig. 61) trapezoidal, with apical half sparsely covered with pseudopores, a pair of setae at anterior margin, a pair of long setae and short setae at mesal area, and a pair of setae and pores at basal margin; anterior margin obscure, slightly fused with membrane area proceeding submentum; posterior margin moderately arcuate posteriorly. Labial (Fig. 62) palp with 3 segments; segment I rectangular, longer than other segments, with a seta at middle of outer lateral margin, and 4 setae around apical margin; segment II rectangular, shorter than other segments, with 2 pairs of setae present at middle; segment III more than four times longer than wide; ligula bisected apically with a pair of setae at middle; prementum wider than long, distal setae present, disc with a pair of setal pores and 2 pairs of real pores, basal pores present; apodemes longer than prementum.

Pronotum (Fig. 63) semicircular, with posterolateral corner slightly produced, posterior margin straight. Elytra (Fig. 64) subquadrate, with posterolateral corner produced. Hind wings stumped. Mesoventrite (Fig. 65) short, less than half as long as metaventrite; mesoventral process developed posteriorly connecting metaventral process; mesocoxal cavity extremely deep with completed marginal bead. Legs (Figs 66, 67) sparsely covered with setae; tibiae with several spurs around apical margin; tarsomeres slender and parallel-sided; tarsal formula 4–5–5. Fore leg (Fig. 66) with coxa longer than other segments; trochanter subtriangular; femur narrowed apically; tibia slender, parallel-sided, as long as femur; tarsomeres I–III subequal in length, tarsomere IV longer than combined length of tarsomeres I–III. Mid leg (Fig. 67) with coxa oval; trochanter
subtriangular; femur narrowed apically; tibia slender, parallel-sided; tarsomere I long, as long as tarsomeres II + III combined; tarsomeres II–IV all equal in length; tarsomere V longer than other segment. Hind leg (Fig. 68) with coxa transverse; trochanter subtriangular; femur slightly narrowed apically; tibia slender, slightly wider at middle; tarsomere I longer than other segments; tarsomeres II–IV equal in length; tarsomere V slightly shorter than tarsomere I.

Abdomen (Figs 53, 54) narrowed posteriorly, sparsely covered with setae. Segment I represented only by tergite I fused to metanotum. Segment II represented only by tergite II. Segments III–VII with 1 tergite, 1 sternite, and 2 pairs of paratergites, each. Tergite VIII

Figures 63–72 Termophidobolus formosanus. 63 Pronotum; 64 elytron, right; 65 meso- and metaventrite, anatomical right side; 66 foreleg; 67 mid leg; 68 hindleg; 69 tergite VIII; 70 male sternite VIII; 71 female sternite VIII; 72 tergites IX–X.

Figures 73–76 Termophidobolus formosanus. 73 Median lobe of male aedeagus, aparameral view; 74 median lobe of male aedeagus, lateral view; 75 right paramere, lateral view; 76 spermatheca.
long setae at anterolateral corner, a pair of long setae present at middle anteriorly, a pair of long setae present at lateral margin. Ventral surface of head (Fig. 55, right side) with several setae behind eyes; hypostoma sparsely covered with pores; submentum sparsely covered with pores, 2 pairs of setae present at anterolateral corner. Eyes with uniform cover of inter-ommatidial setae. Antennae (Fig. 56) sparsely covered with setae; segments I–IV covered with fewer setae than other segments; segment I with a long macroseta at outer apicolateral corner; segment II with a long seta at middle of inner lateral margin; segments III–X with 4–6 macrosetae at apical margin; segments XI with several macrosetae at middle and apex. Dorsal surface of labrum (Fig. 57, left side) with a pair of long setae and 3 pairs of setae at mesal area, a pair of setae at anterolateral corner, 2 pairs of setae at lateral margin, and a pair of short setae at middle of anterior margin. Epipharynx (Fig. 58, right side) with a pair of lateral setulae. Mandible (Figs 59) dorsally with 5 scrobal setae along aboral margin. Maxillary (Fig. 60) lacinia with 2–3 setae at base of adoral margin, and a seta and 3 pores at middle of aboral half; maxillary palpal segment II with 4–5 setae at aboral margin, and 1–2 setae at adoral margin; segment III sparsely covered with setae, a stronger seta present at aboral apicolateral corner. Pronotum (Fig. 63) densely covered with setae and pores, with anterior and lateral margin covered with several minute setae (pronotal length = 0.56–0.68 mm, average length 0.62 mm; pronotal width = 1.08–1.20 mm, average width 1.13 mm, n = 10). Elytra (Fig. 64) uniformly covered with setae and pores, and 7–8 short macrosetae at lateral margin (elytral length = 0.56–0.68 mm, average length 0.62 mm; elytral width = 0.54–0.64 mm, average width 0.58 mm, n = 10). Mesoventrite (Fig. 65) with several setae at middle and lateral area. Metaventrite (Fig. 65) sparsely covered with setae. Foreleg (Fig. 66) with coxa apical two third sparsely covered with setae; trochanter with 4–5 setae at apical half, several pores present at middle; femur uniformly covered with setae; tibia sparsely covered with setae thickened apically, and a long and 12 short spurs around apical margin; tarsus sparsely covered with setae. Mid leg (Fig. 67) with coxa sparsely covered with setae at lateral area, a long macroseta present at inner apicolateral part; trochanter with 2–3 setae, several pores present at middle; femur sparsely covered with setae; tibia sparsely covered with thick setae, 2 long and 8 short spurs present around apical margin; tarsi sparsely covered with setae. Hind leg (Fig. 68) uniformly covered with setae; coxa without seta at middle, with several setae at base of marginal bead longer than other setae; tibia with 5 spurs around apical margin.

**Hodotermopsis guest of Termitozyrina**

**Termophidoholus formosanus**

**Naomi & Hirono**

*Termophidoholus formosanus* Naomi & Hirono, 1996: 86. Type locality: Hewangshan, Nantou Hsien, Taiwan. **Materials examined.** 6♂♂♂♂, 1♀♀, 13 unsexed, Taiwan, Nantou-hsien, Tehuashe (1300 m a.s.l.), 10.iv.2002, Dr H.Sugaya leg. (♂♂♂♂, ♀♀♀, completely disarticulated; 2♂♂♀♀, all abdominal segments dissected off). 22♂♂♂♂, 1♀♀, 34 unsexed, Laos, Houa Phan, Ph. Pan (1800 m a.s.l.), (43 km SE of Xam Neua), 4.iii.2003, R.Iwata leg. (2♂♂♂♂, 1♀♀, completely disarticulated; ♂♂♂♂, abdominal segments VII–X dissected off; ♀♀♀, abdominal segments VIII–X dissected off).

All specimens are deposited in the Kyushu University Museum (KUM).

**Diagnosis.** This species is diagnosable based on the generic diagnosis above.

**Redescription.** Body (Figs 53,54) average length 1.89 mm (1.74–2.10 mm, n = 10), female larger than male, uniformly orange brown, sparsely covered with setae.

Dorsal surface of head (Fig. 55, left side) with posterior half sparsely covered with setae; clypeus with a pair of

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**Figures 77,78** Beetles photographed in situ. 77 *Hodoter-mophilus gloriosus*; 78 *Yakuus iwatai* gen. & sp. nov.
Tergites, sternites and paratergites III–VIII (Figs 53, 54) sparsely covered with setae, with anterior one third sparsely covered with pores, each outer paratergite with a macroseta. Macrochaetotaxy of abdominal tergites III–VII = 6–6–6–6–6–0. Tergite VIII (Fig. 69) with anterior one fifth sparsely covered with pores, 2 pairs of macrosetae at lateral margin, and a pair of macrosetae at posterolateral corner. Tergite VIII (Figs 70,71) with anterior one third sparsely covered with pores. Tergite IX (Fig. 72) with several pores at anterior one third, 12 pairs of setae and 5 pairs of macrosetae present in posterior half. Tergite X (Fig. 73) densely covered with setae at mesal area, and 4 pairs of macrosetae at posterolateral margin.

Male: Sternite VIII (Fig. 70) with 2 pairs of macrosetae on disc, 2 pairs of macrosetae at lateral margin, and 3 pairs of macrosetae at posterior margin. Median lobe of aedeagus (Figs 73,74) with suspensoria half as long as apical lobe. Paramere (Fig. 75) with paramerite laterally covered with pores.

Female: Sternite VIII (Fig. 71) with 2 pairs of macrosetae on disc, 2 pairs of macrosetae at lateral margin, and 2 pairs of macrosetae at posterior margin. Spermatheca (Fig. 76) with thick cuticle overall.

Distribution. Taiwan and Laos. New record from Laos.

Host termite. Hodotermopsis sjostedti. New record from Laos.

Ecology. Host termites were observed to ignore the beetles upon contact, similar to H. gloriosus and Y. iwatai.

Remarks. There are several morphological differences between the specimens of Taiwan and Laos. For instance, distal setae of labium of Taiwanese specimens are shorter than those of Laotian specimens. In addition, the Taiwanese specimens’ mentum is slightly wider than that of Laotians'. However, other morphological characters including genitalia are quite congruent with each other. Therefore, these two populations are thought to be conspecific.

Key to species (genera) of Termitozyrina associated with Hodotermopsis sjostedti

1. Body small, around 2.0 mm; pronotum and elytra covered with minute setae .................................................................

   Termophidoholus formosanus

   − Body more than 3.0 mm; pronotum and elytra shiny and subtransparent, without minute seta but with macrosetae. .................................................................2

2. Pronotum semicircular; antennae as long as pronotum; metaventral process developed .................................................. Hodotermophilus gloriosus

   − Pronotum transverse; antennae longer than pronotum; metaventral process not developed .................................................. Yakuus iwatai gen. & sp. nov.

DISCUSSION

Systematic status of subtribe Termitozyrina

The subtribe Termitozyrina was established by Seevers (1957) to include four genera and seven species of Neotropical termitophiles. He referred to the probable natural grouping of the subtribe within the tribe “Myrmedoniini” (now Lomechusini). However, he gave no definition of the subtribe due to paucity of knowledge on the Lomechusini at that time (Seevers 1957). Subsequently, five physogastric species across two genera and three limuloid species across three genera were added to the subtribe from the Oriental region (Kistner 1970a,b; Naomi & Terayama 1986; Naomi & Hirono 1996). However these authors also did not mention a definition of the subtribe. Therefore, systematic state of the Termitozyrina has been highly ambiguous, and no monophyletic relationship has been documented.

The morphological states of the three species across three genera described in this paper, especially the mouthparts and male aedeagus, are quite different from the Oriental physogastric species, namely, those of genera Longipedoxenus Kistner, 1970a and Longipedisymbia Kistner, 1970a associated with Longipeditermes longipes (Haviland, 1898) (Kistner 1970a,b; T. Kanao, pers. obs., 2013). For example, the maxillary galea of the limuloid species is slightly longer than, or almost as long as, the lacinia (Figs 8,35,60) but that of the physogastric species is much longer than lacinia. In addition, the limuloid species share an exposed compressor plate of median lobe of the male aedeagus (Figs 25,50,74) but the physogastric species do not. These states of the physogastric species are typical for some members of the tribe Lomechusini. The morphological differences indicated above suggest distant relationships between the physogastric and limuloid groups. In fact, the morphological features in the limuloid species are not applicable even to the current definition of the Lomechusini but are applicable to the tribe Athetini Casey, 1910 (Seevers 1978; Newton et al. 2000) or another termitophilous tribe, Termitopaediini Seevers, 1957 (Kistner 1968; 2001). Therefore, it is possible that Hodotermophilus, Termophidoholus and Yakuus are not members of Termitozyrina. The other Oriental limuloid genera of Termitozyrina, Limulodilla Kistner, 1970b and Havilandoxenus Kistner, 1971, also do not share the above characters seen in physogastric species. However, the insufficient original descriptions prevent us from referring to further morphological information of these two genera.

Although systematic affiliations of these genera are problematic, recent phylogenetic analysis based on molecular data revealed some unexpected relationships...
in Lomechusini (Elven et al. 2012). Moreover, the morphology of the mouth parts and the male aedeagus in the Termitopaeidini are quite variable and its monophyly is highly doubtful even though most species have relatively short lacinia and galea, and the developed condylite velum of the paramere as for the Japanese genera. In order to clarify the classification of Termitozyrina, and the systematic placement of Hodotermophilus, Termophidobolus and Yakuus, more comprehensive studies including molecular analysis will be needed.

Tentative phylogenetic relationships and speciation of three genera

Monophyly of the three species described in this paper may be supported by the following character states: (i) anterior margin of mentum submembranous (Figs 9, 36,61); (ii) fore and mid tibiae with a batch of spurs (Figs 14–17,41–43,66,67); (iii) suspensoria of median lobe of male aedeagus fused with apical process of copulatory piece (Figs 24,25,49,50,73,74); and (iv) condylite velum apically produced (Figs 26,51,75). Although the relationships among the Japanese species are unknown, these states are currently thought to be apomorphic within higher Aleocharinae (Ashe 1994, 2005), and in conjunction are considered preliminary evidence to support their monophyly. Furthermore, the condylite of paramere almost fused with the paramerite (Figs 26,51,75) also characterizes these three genera; even though this character state is plesiomorphic in Aleocharinae, we hypothesize this character to have experienced a reversal among the three termitozyrine genera discussed here.

In addition to the hypothesized synapomorphies discussed above, the following morphological similarities between Hodotermophilus and Yakuus suggest a close relationship between the two genera: the shiny and subtransparent body (Figs 1,2,28,29), short mentum (Figs 9,36), distribution of the pores on prementum (Figs 10,37), large copulatory piece of median lobe of male aedeagus (Figs 24,25,49,50) and the long apical lobe of paramere (Figs 26,51). Termophidobolus is, on the other hand, covered with minute setae overall (Figs 53,54) and has a relatively long mentum (Fig. 61), a smaller copulatory piece of median lobe of male aedeagus (Figs 73,74) and an extremely short apical lobe of paramere (Fig. 75). These characters do not directly associate with termitophily and demonstrate a smaller chance for convergence, and possibly allude to a close relationship between Hodotermophilus and Yakuus. Therefore, the tentative relationship between these three genera is (Termophidobolus, (Hodotermophilus, Yakuus)).

The previous biogeographical studies of the host termite, H. sjostedti, may support this relationship. Currently, the host termite H. sjostedti is known to be distributed in the southern part of mainland China, Taiwan, Vietnam and the southern islands of Japan (Matsumoto et al. 1990; Beljaeva 2004). Here we add northern Laos as a new distribution locality of H. sjostedti. The ancestor of H. sjostedti is considered to have extended its distribution to Japan from mainland China in the Pliocene (Morimoto 1975) or Pleistocene (Wang et al. 1992; Maekawa et al. 1998). Therefore, considering the strong host specificity of termophilous species, it is hypothesized that Japanese termophilous species, H. gloriosus and Y. iwatai, are derivative. The limited morphological differences of the genitalia between these genera also indicate recent speciation. Interestingly, it is possible that these two species, H. gloriosus and Y. iwatai, have acquired different niches in the sympatric environment of the Hodotermopsis nest because their mouthpart morphologies, such as the length of mentum, the tooth on the right mandible and the number of strong setae on maxillary lacinia, are quite different. Also, these two species can be collected from the same colonies of host termites at the same time. Field surveys in China and phylogenetic and behavioral studies will elucidate the speciation of these species.

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