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Eight new species, a new record, and redescription of the genus *Discoxenus* Wasmann, 1904: The first record of termitophilous rove beetles in Cambodia (Coleoptera: Staphylinidae: Aleocharinae)

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Abstract

As the first record of the Cambodian termitophilous rove beetles, eight new species of the genus *Discoxenus* Wasmann, 1904 (Aleocharini: Compactopediina) are described, along with a redescription of the genus. *Discoxenus katayamai* Kanao & Maruyama, 2010, which was originally known from Thailand, is newly recorded from Cambodia and redescribed. *Discoxenus* species are morphologically divided into two species groups, namely the *latiabdominalis* and the *assmuthi*. The *latiabdominalis* species group includes *D. latiabdominalis* **n. sp.** and *D. cambodiensis* **n. sp.**, and both species are associated with *Odontotermes maesodensis* Ahmad, 1965. The *assmuthi* species group comprises 11 species: *D. assmuthi* Wasmann, 1904, *D. lepisma* Wasmann, 1904, *D. indicus* Kistner, 1982, *D. malaysiensis* Kistner, 1982, *D. phourini* **n. sp.**, *D. kohkongensis* **n. sp.**, *D. hirsutus* **n. sp.**, *D. minutus* **n. sp.**, *D. lucidus* **n. sp.**, *D. kakizoei* **n. sp.**, and *D. katayamai*. The members in the *assmuthi* species group are associated with *Odontotermes* or *Hypotermes* termites. One of the unique morphological features of the *assmuthi* species group is the strongly developed distal crest of the male aedeagal median lobe while that observed in the *latiabdominalis* species group is not produced, which is general character state in the tribe Aleocharini. The character state of distal crest and several other morphological features such as mouthparts are considered to support the monophyly of respective species groups in *Discoxenus*.

Key words: host specificity, *Hypotermes*, Macrotermitinae, *Odontotermes*, species group, termitophily

Introduction

The subfamily Aleocharinae (Coleoptera: Staphylinidae) includes various termitophilous species. Several aleocharine tribes and subtribes are exclusively composed of termitophilous species (Seevers 1957; Kistner 1969), and one of the termitophilous taxa is the subtribe Compactopediina Kistner, 1970 of the tribe Aleocharini. The Compactopediina comprises of five genera and 12 species of termitophiles from the Indo-Malayan region (Wasmann 1904, 1916; Kistner 1970, 1982; Kanao *et al*. 2010, 2011). The genus *Discoxenus* Wasmann, 1904 includes eight species that are distributed throughout India, Myanmar and Malaysia (Wasmann 1904, 1916; Kistner 1982; Kanao *et al*. 2010). All currently described *Discoxenus* species are associated with *Odontotermes* termites (Termitidae: Macrotermitinae).

Termitophilous rove beetles, together with termites, exhibit high species diversity in tropical regions, although many countries within these regions remain poorly studied. In 2012 and 2014, we conducted field surveys in one of these uninvestigated countries, Cambodia. During the surveys, nine species of *Discoxenus* were collected from nests of *Odontotermes maesodensis* Ahmad, 1965, *O. proformosanus* Ahmad, 1965, *Hypotermes makhamensis* Ahmad, 1965, and *H.* cf. *xenotermitis* (Wasmann, 1896). Detailed morphological observations revealed that eight of these species had not been described; the other species, *D. katayamai* Kanao & Maruyama, 2010, which was

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only known from Thailand, represents a new record for Cambodia. Based on their morphological features, the *Discoxenus* species were divided into two species groups.

The aim of this study is to describe the eight new species found in Cambodia and to redescribe the genus *Discoxenus*. In addition, *D. katayamai* is also redescribed in order to compare it with the new Cambodian species. Their classification into two species groups and host specificities are also discussed.

Material and methods

Field surveys in Siem Reap Province, Cambodia were conducted in four different periods: June and August 2012 by MM, December 2012 by TK, and August 2014 by MM and Mr. S. Kakizoe of Kyushu University. Koh Kong Province was also surveyed in December 2012 by TK.

This study generally follows the technical terminology and procedures described in Sawada (1972) and Maruyama (2006). To prepare a permanent mount, specimens were first cleared in KOH and then washed with distilled water. The specimens were subsequently dehydrated in EtOH and embedded into Euparal mounting medium. Dissections were made within Euparal on a slide or a halved glass cover slip glued onto a halved paper glue board (see Maruyama 2004 for details). Photographs were taken using a Canon 70D camera, equipped with a MP-E65 high magnification lens and an EX-24 twin flash. Pictures were later stacked using the auto-montage software Combine ZM. In line drawings, the antennae and the right side of the pronota, tergites, and sternites were drawn without setae and pores. The number of macrosetae described on the elytra as "on disc" refers to all macrosetae except for those on the lateral margin (the presence of four macrosetae on the lateral margin is a generic feature of *Discoxenus*). Macrochaetotaxy refers to the number of all macrosetae on posterior margin of each abdominal tergite. In spermatheca, basal part indicates a portion with spermathecal duct, and apical part is a portion with spermathecal gland. These two spermathecal portions are divided by weakly sclerotized boundary (Fig. 37). Scale lengths in all pictures are in millimetres (mm).

Host termite species were identified by Dr. Yoko Takematsu of Yamaguchi University (*O. maesodensis*, *O. proformosanus*, *H. makhamensis*), but only termite of colony no. MMCB-T-2012-1-002 was identified as *H.* cf. *xenotermitis* by authors based on the key and original descriptions in Ahmad (1965). Head of *H.* cf. *xenotermitis* is much smaller than that of *H. makhamensis* and *H. xenotermitis*.

Type specimens are deposited in the Kyushu University Museum, Fukuoka Prefecture, Japan.

Taxonomy

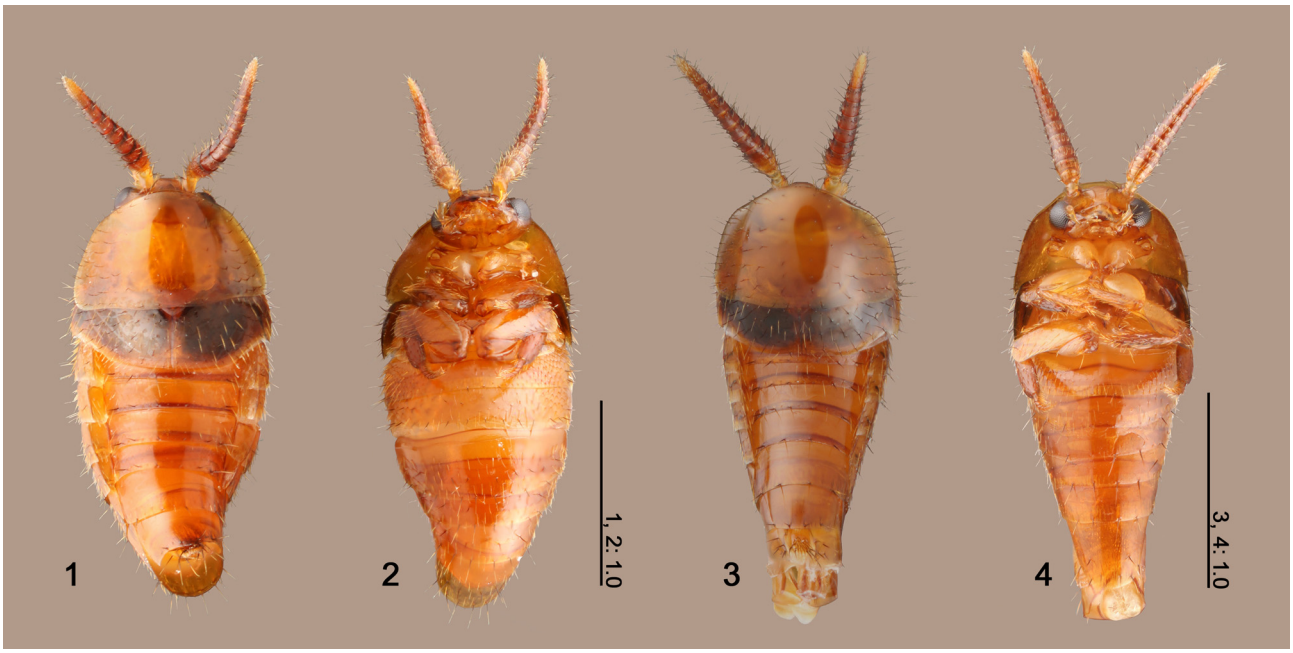
Genus *Discoxenus* Wasmann

Type species: *D. assmuthi* Wasmann, 1904.
Discoxenus Wasmann, 1904: 655; Seevers 1957: 264; Kistner, 1982: 165.

Diagnosis. This genus is distinguished from other genera in Compactopediina by a combination of following characters (states): body shape limuloid with abdomen gradually narrowed posteriorly, head completely covered by pronotum, antennae fusiform, antennal segment II small, petioles completely covered with antennal segments III–X, maxillary basistipes fused with palpifer partly or completely, tarsal formula 4-4-5.

Redescription. Body glossy, overall orange brown, antennae and elytra slightly darker (Figs. 1–18, 165, 166). Head capsule (Figs. 19, 38, 54, 73, 89, 105, 121, 137, 149) transverse, widest at eyes, sparsely covered with minute pores, completely covered by pronotum in dorsal view, several setae present at postgenae and anterior margin of clypeus; antennal shelf well developed, formed by anteriorly produced epicranium and clypeus, covered with several setae and pores; occipital suture absent. Eyes well developed. Gula short, strongly dilated posteriorly, fused to submentum. Antennae (Figs. 20, 39, 55, 74, 90, 106, 122, 138, 150) with 11 segments, fusiform except for segments I and II, widest at segment IV or V; apical margin of each segment fimbriated; segment I long, almost as long as segment XI, with 2 macrosetae; segment II short, narrower than other segments; pedicles invisible externally between segments III–X. Labrum (Figs. 21, 40, 56, 75, 91, 107, 123, 139, 151, left side) transverse, sparsely covered with pseudopores, with anterior margin concave at middle, 2–4 pairs of large primary setae

present on anterior half, a pair of setaceous sensillae and minute sensillae present at middle of anterior margin (probably homologous to *a*- and *b*-sensillae of Sawada [1972]). Epipharynx (Figs. 21, 40, 56, 75, 91, 107, 123, 139, 151, right side) medially covered with few pores. Mandibles (Figs. 22, 23, 41, 42, 57, 58, 76, 77, 92, 93, 108, 109, 124, 125, 140, 141, 152, 153) asymmetric. Right mandibles with a small tooth. Maxilla (Figs. 24, 59) with medial sclerite of stipes (basistipes) somewhat fused with outer sclerite of stipes (palpifer), 2 long setae present at base of basistipes; palpus with 5 segments, segments II and III sparsely covered with setae and pores; lacinia with 10 thick setae apically; galea with 4–5 thick and long setae apically. Mentum (Figs. 25, 43, 60, 78, 94, 110, 126, 142, 154) distinct from submentum, with anterior margin submembranous, difficult to discriminate from membrane connected to labium, with lateral margin rounded, 2 pairs of long setae and a pair of short setae present at anterolateral corners. Prementum (Figs. 26, 61) with a pair of distal setae at anterior margin, a pair of setal pores present on posteromedial area; palpus with 4 segments; segment I with 2–3 setae; segment II with 5 setae on anterior half, aboral one seta longer than other setae.



FIGURES 1–4. Habitus. 1–2. *Discoxenus latiabdominalis* **n. sp.**: 1. Dorsal view, 2. Ventral view. 3–4. *D. cambodiensis* **n. sp.**: 3. Dorsal view, 4. Ventral view.

Pronotum (Figs. 27, 44, 62, 79, 95, 111, 127, 143, 155) semicircular, dorsally convex, sparsely covered with minute pores. Elytron (Figs. 28, 45, 63, 80, 96, 112, 128, 144, 156) with posterior margin subtransparent, 4 long macrosetae present at outer lateral margin. Prosternum short, carinate at middle. Wings fully developed. Mesoventrite (Figs. 29, 64) medially covered with short setae, approximately half as long as metaventrite; mesoventral intercoxal process narrow, acutely developed posteriorly, fused with metaventral process. Metaventrite (Figs. 29, 64) sparsely covered with yellow setae and pores except for mesocoxal cavities, 2 pairs of macrosetae present at middle except for *D. cambodiensis* without macrosetae. Mesocoxal cavity completely margined. Legs short and flat, sparsely covered with setae. Fore coxa with a macroseta around apex; tibia with inner margin densely covered with setae, with 2–5 thick setae and 2 spurs at apex. Mid trochanter with a macroseta at middle; femur with 1–2 macrosetae at base and apex; tibia with apical half of inner margin densely covered with setae, 2–3 macrosetae present at outer margin, with 2–5 thick setae and 2 spurs at apex. Hind coxa with 1–2 macrosetae around inner margin; trochanter with a macrosetae at middle; femur with 1–2 macrosetae at base and apex; tibia with 2–3 macrosetae at outer margin, 2–6 thick setae and 2–3 spurs present at apex; tarsal segment I densely covered with yellow setae on inner margin. Tarsal formula 4-4-5.

Abdomen (Figs. 1–18) narrowed posteriorly. Sternites sparsely covered with yellow setae and macrosetae. Tergite IX (Figs. 33, 49, 68, 84, 100, 116, 132, 147, 160) fully subdivided by tergite X, with 5 pairs of macrosetae on posterior half. Tergite X with 3 pairs of macrosetae around posterior margin. Macrochaetotaxy varied in species.

Male. Median lobe of aedeagus (Figs. 34, 35, 50, 51, 69, 70, 85, 86, 101, 102, 117, 118, 133, 134, 161, 162)

with basal capsule longer or as well as apical lobe; distal crest distinct, strongly developed in the *assmuthi* species group; copulatory piece long, longer or as long as apical lobe. Paramere (Figs. 36, 52, 71, 87, 103, 119, 135, 163) with paramerite covered with several pores at middle; condylite narrow, distinct from paramerite, covered with pores basally; velar sac sclerite (inner surface of paramerite) with 3–6 setae; apical lobe approximately on third as long as paramerite, sparsely covered with pores, several minute setae present.

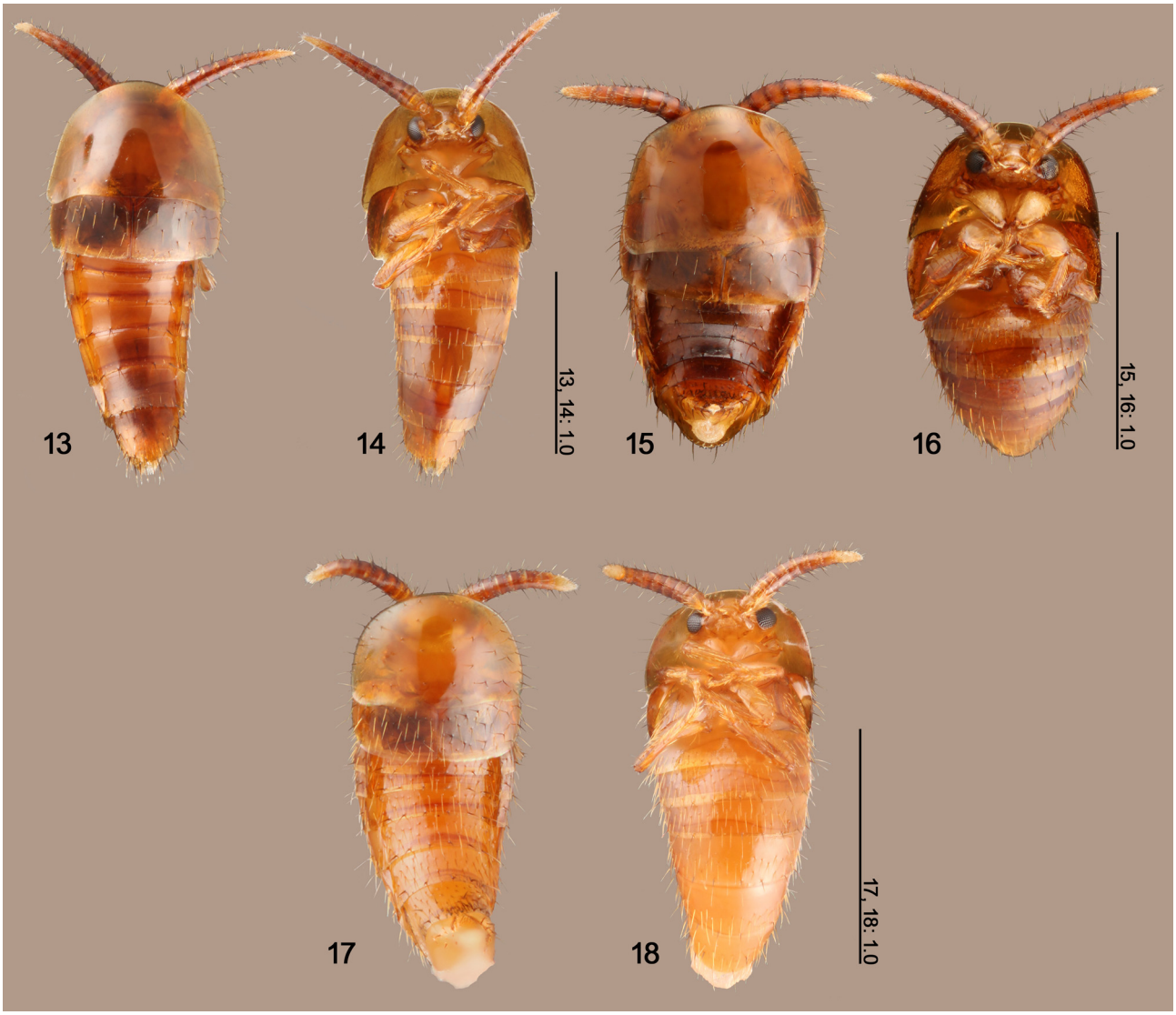
Comments. Morphological characters of small body parts such as mouthparts are important features in Aleocharinae systematics (Sawada 1972). In this paper, we describe such characters observed in all the Cambodian species under study.

FIGURES 5–12. Habitus. 5–6. *Discoxenus phourini* **n. sp.**: 5. Dorsal view, 6. Ventral view. 7–8. *D. kohkongensis* **n. sp.**: 7. Dorsal view, 8. Ventral view. 9–10. *D. hirsutus* **n. sp.**: 9. Dorsal view, 10. Ventral view. 11–12. *D. minutus* **n. sp.**: 11. Dorsal view, 12. Ventral view.

Key to the Southeast Asian species of *Discoxenus*

1. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6 2
- Macrochaetotaxy of abdominal tergites III–VIII variable 7
2. Antennal segment XI approximately 1.4 times longer than wide (Fig. 150); elytra sparsely covered with relatively long setae (Fig. 156). . . . . *D. katayamai*

- Antennal segment IX more than 2 times longer than wide (Figs. 55, 74, 90, 106, 122, 138); elytra covered with no or few short setae except for anterolateral outer corner 3
3. Abdominal sternites IV–VII with 2 rows of macrosetae 4
- Abdominal sternites IV–VII with 1 row of macrosetae at posterior margin. 5
4. Abdominal sternites IV–VII with 1 pair of macrosetae subapically . . . . . *D. phourini* **n. sp.**
- Abdominal sternites IV–VII with more than 5 pairs of macrosetae (10–11 macrosetae) subapically . . . . . *D. hirsutus* **n. sp.**
5. Spermatheca with apical part longer than basal part (Fig. 148) . . . . . *D. kakizoei* **n. sp.**
- Spermatheca with apical part shorter than basal part (Figs. 88, 120) 6
6. Median lobe of male aedeagus with distal crest moderately pointed at apex (Fig. 86); paramere with paramerite narrow (Fig. 87) . . . . . *D. kohkongensis* **n. sp.**
- Median lobe of male aedeagus with distal crest rounded apically (Fig. 118); paramere with paramerite broad (Fig. 119) . . . . . *D. minutus* **n. sp.**
7. Body long, length more than 2.3 mm 8
- Body short, around 2 mm or less. 9
8. Pronotum sparsely covered with macrosetae (Fig. 27); macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 4; median lobe of male aedeagus with basal capsule with distal crest weakly developed (Fig. 35). . . . . *D. latiabdominalis* **n. sp.**
- Pronotum with macrosetae only at lateral margin (Fig. 127); macrochaetotaxy of abdominal tergites III–VIII = 4, 4, 4, 4, 4, 6; median lobe of male aedeagus with distal crest strongly developed (Fig. 134) . . . . . *D. lucidus* **n. sp.**
9. Macrochaetotaxy of abdominal tergites III–V = 6, 6, 6 . . . . . *D. cambodiensis* **n. sp.**
- Macrochaetotaxy of abdominal tergites III–V = 8, 8, 8 10
10. Macrochaetotaxy of abdominal tergites VI–V = 8, 8 . . . . . *D. krishnai* Kistner
- Macrochaetotaxy of abdominal tergites VI–V = 6, 6 . . . . . *D. malaysiensis* Kistner



FIGURES 13–18. Habitus. 13–14. *Discoxenus lucidus* **n. sp.**: 13. Dorsal view, 14. Ventral view. 15–16. *D. kakizoei* **n. sp.**: 15. Dorsal view, 16. Ventral view. 17–18. *D. katayamai*: 17. Dorsal view, 18. Ventral view.

Classification of species groups

We propose a classification of the *Discoxenus* species into two species groups: the *latiabdominalis* and the *assmuthi*. The included species and the detail morphological definition of each species group are described below. Unfortunately, we are not able to determine the affiliations for *D. acuticornis* Wasmann, 1916, *D. crassicornis* Wasmann, 1916, and *D. krishnai* Kistner, 1982 due to the insufficient morphological information and materials.

The *latiabdominalis* species group

Diagnosis. The *latiabdominalis* species group is defined by the following character states: 1) mandible (Figs. 22, 23, 41, 42) covered with more than 60 pores, 2) maxillary basistipes partially fused with palpifer (Fig. 24), 3) sternite VIII (Figs. 31, 32, 47, 48) densely covered with minute pores anteriorly, 4) tergite X (Figs. 33, 49) with posterior third covered with a batch of setae, 5) median lobe of male aedeagus (Figs. 34, 35, 50, 51) with basal capsule large, and 6) basal capsule with distal crest weakly developed.

Comment. The *latiabdominalis* species group includes *D. latiabdominalis* **n. sp.** and *D. cambodiensis* **n. sp.**

Discoxenus latiabdominalis n. sp.

(Figs. 1, 2, 19–37)

Type materials. Holotype: ♂, 1 km S of Angkor Wat, Siem Reap, Cambodia, 18 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-001).

Paratypes: Cambodia: 2♂♂, 3♀♀, same data as holotype (1♂, completely dissected). 1♂, 3♀♀, 1 km S of Ankor Wat, Charles De Gaulle, Siem Reap, 22 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0022) (1♂, completely dissected, 1♀, abdominal segments VIII–X dissected off). 1♂, 2 km SE of Neak Pean, Siem Reap, 18 VIII 2014, Kakizoe S. & Maruyama M. leg. (Colony no. SK001).

Diagnosis. This species is distinguished from all other species by the macrochaetotaxy of abdominal tergites III–VIII (6, 6, 6, 6, 6, 4). This species is most similar to *D. cambodiensis*, but is easily distinguishable from it by a wider body (Figs. 1, 2), hairy abdominal sternites III–IV, paramere with wider paramerite which is more than 5 times wider than condylite (Fig. 36), and spermatheca with short basal part which is as long as apical part (Fig. 37).

Description. Head (Fig. 19) wider than long, with anterior margin of clypeus rounded. Antenna (Figs. 1, 2, 20) with segment II as long as segment IV, with 3 macrosetae; segment III trapezoidal, shorter than other segments; segment IV wider than long, dilated distally; segment V wider than other segments, slightly wider than long; segments VI–X successively narrowed distally; segment VI subquadrate; segments VII–X longer than wide; segment XI longer than other segments, widest at middle. Labrum (Fig. 21, left side) with anterior margin slightly concave; median projection of apodeme triangular, moderately pointed; 5 lateral setae present in ventral view (Fig. 21, right side). Mandibles (Figs. 22, 23) covered with approximately 70 pores. Left mandible (Fig. 22) with adoral margin moderately convex at middle. Right mandible (Fig. 23) with a small and rounded tooth. Maxillary (Fig. 24) palpal segment III approximately 2.2 times longer than wide. Mentum (Fig. 25) short, approximately three times wider than long, covered with more than 60 pores. Labium (Fig. 26) with prementum covered with approximately 40 pores.

Pronotum (Fig. 27) sparsely covered with approximately 90 macrosetae. Elytron (Fig. 28) transverse, sparsely covered with yellow setae, 21–23 macrosetae present on disc. Metaventrite (Fig. 29) 1.3 times longer than mesoventrite.

Tergites (Fig. 1) covered with pores, few setae present on lateral area and posterior margin except for tergites VI–VIII covered with much fewer setae. Tergite VIII (Fig. 30) with posterior margin moderately pointed, 2 pairs of macrosetae present at posterior margin. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 4. Sternites (Fig. 2) sparsely covered with setae, denser on sternites III and IV. Sternites III–VIII densely covered with minute pores anteriorly. Sternites III–VII with 6–12 macrosetae at posterior margin; sternites IV–VI with a row of 4–10 macrosetae at middle.

Male. Sternite VIII (Fig. 31) with 5 pairs of macrosetae on posterior half. Median lobe of aedeagus (Figs. 34,

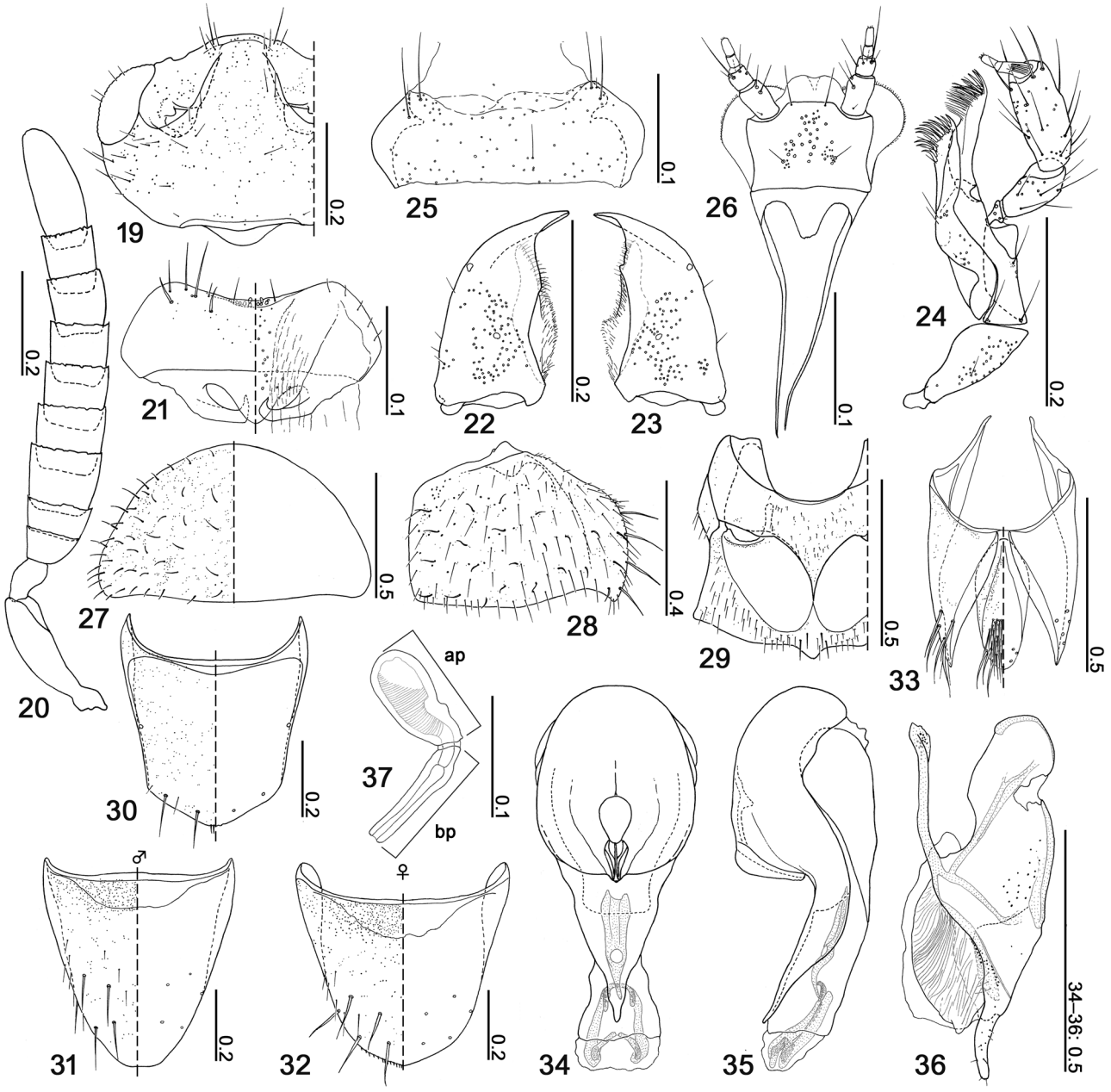
35) with basal capsule longer than apical lobe. Paramere (Fig. 36) with paramerite broad, more than 5 times wider than condylite; velar sac sclerite with 3 setae; apical lobe with 5–6 minute setae.

Female. Sternite VIII (Fig. 32) with 5 pairs of macrosetae, several minute setae present at posterior margin. Spermatheca (Fig. 37) with apical part 2 times wider than and as long as basal part.

Measurement. Body length = average 2.70 mm (2.56–2.84 mm, N = 7), pronotal length = average 0.65 mm (0.63–0.68 mm, N = 7), pronotal width = average 1.09 mm (1.04–1.17 mm, N = 7), elytral length = average 0.53 mm (0.49–0.56 mm, N = 7), elytral width = average 0.64 mm (0.63–0.71 mm, N = 7).

Etymology. The specific epithet is a combination of the Latin adjective *latus* meaning "broad" and the Latin adjective *abdominalis*, in reference to the diagnostic wide abdomen of the species.

Host species. *Odontotermes maesodensis* Ahmad, 1965.



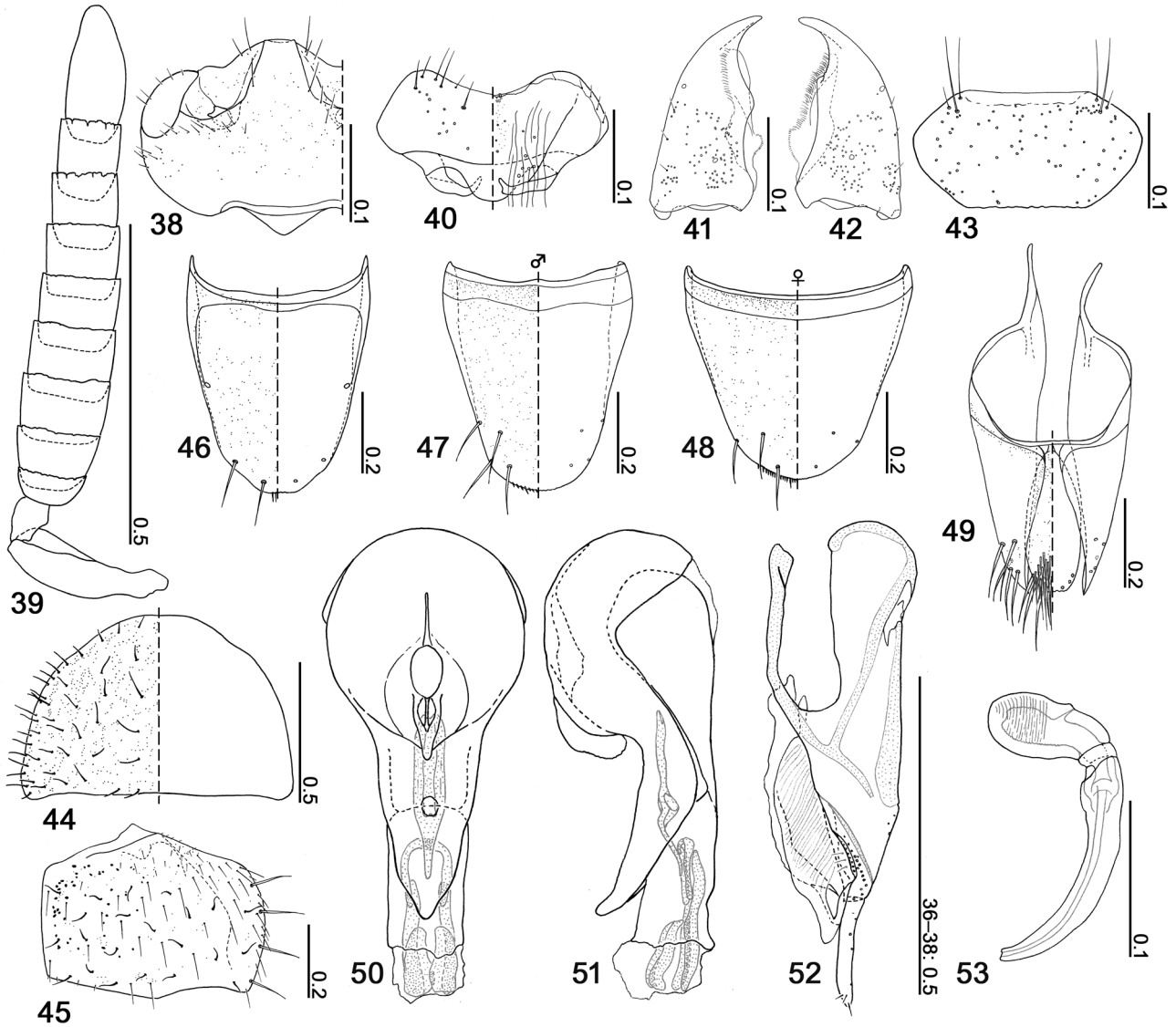
FIGURES 19–37. *Discoxenus latiabdominalis* **n. sp.**: 19. Head, 20. Antenna, 21. Labrum (left side = dorsal view, right side = ventral view), 22. Mandible, left, 23. Mandible, right, 24. Maxilla, 25. Mentum, 26. Labium, 27. Pronotum, 28. Elytron, right, 29. Meso- and metaventrites, 30. Tergite VIII, 31. Sternite VIII, male, 32. Sternite VIII, female, 33. Tergites IX and X, 34. Median lobe of aedeagus, ventral view, 35. Median lobe of aedeagus, lateral view, 36. Paramere, 37. Spermatheca (ap: apical part, bp: basal part).

***Discoxenus cambodiensis* n. sp.**
(Figs. 3, 4, 38–53)

Type materials. Holotype: ♂, 1 km S of Angkor Wat, Siem Reap, Cambodia, 18 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-001).

Paratypes: Cambodia: 11♂♂, 5♀♀, same data as holotype (1♂, 1♀, completely dissected). 11♂♂, 13♀♀, 1 km SW of Angkor Wat, Siem Reap, 20 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0011). 1♀, 1 km W of Banteay Prei, Siem Reap, 21 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0019). 1♂, 1♀, same date and locality data as the former specimens (Colony no. MMCB-T-2012-2-0020). 3♂♂, 7♀♀, 1 km S of Ankor Wat, Charles De Gaulle, Siem Reap, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0022). 2♂♂, 8♀♀, 1.6 km SW of Angkor Wat, Siem Reap, 21 VIII 2014, Kakizoe S. leg. (Colony no. SK010).

Diagnosis. This species is easily distinguished from all other species by the macrochaetotaxy of tergites III–VIII (6, 6, 6, 4, 4, 4). This species is most similar to *D. latiabdominalis*, but is distinguishable from it by a more slender body (Figs. 3, 4), abdominal sternites V–VII without setae except for posterior margin, paramere with narrower paramerite which is approximately 4 times wider than condylite (Fig. 52), and spermatheca with longer basal part which is approximately 2 times longer than apical part (Fig. 53).



FIGURES 38–53. *Discoxenus cambodiensis* **n. sp.**: 38. Head, 39. Antenna, 40. Labrum (left side = dorsal view, right side = ventral view), 41. Mandible, left, 42. Mandible, right, 43. Mentum, 44. Pronotum, 45. Elytron, right, 46. Tergite VIII, 47. Sternite VIII, male, 48. Sternite VIII, female, 49. Tergites IX and X, 50. Median lobe of aedeagus, ventral view, 51. Median lobe of aedeagus, lateral view, 52. Paramere, 53. Spermatheca.

Description. Head (Fig. 38) approximately 1.5 times wider than long, with anterior margin of clypeus rounded. Antenna (Figs. 3, 4, 39) with segment I longer than other segments; segment II as long as segment IV, with 3 macrosetae; segment III bowl shaped, shorter than other segments; segment IV wider than long, dilated distally; segment V wider than other segments, wider than long; segments VI–X successively narrowed distally; segments VI–VII wider than long; segment VIII subquadrate; segments IX–X longer than wide; segment XI approximately 2.3 times longer than wide, widest at middle. Labrum (Fig. 40, left side) with anterior margin concave; median projection of apodeme rounded; 5–6 lateral setae present in ventral view (Fig. 40, right side). Mandibles (Figs. 41, 42) covered with more than 80 pores. Left mandible (Fig. 41) moderately produced adorally at middle. Right mandible (Fig. 42) with a small and rounded tooth. Maxillary palpal segment III approximately 2.3 times longer than wide. Mentum (Fig. 43) 2 times wider than long, covered with more than 70 pores. Labium with prementum covered with 15–20 pores.

Pronotum (Fig. 44) sparsely covered with more than 80 macrosetae. Elytron (Fig. 45) transverse, sparsely covered with yellow setae, 21–23 macrosetae present on disc. Metaventrite 1.3 times longer than mesoventrite, without macrosetae.

Tergites III–VIII (Fig. 3) glabrous, almost without setae except for each posterior margin. Tergite VIII (Fig. 46) with posterior margin moderately rounded, 2 pairs of macrosetae present at posterior margin, with 4 short setae at middle of posterior margin. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 4, 4, 4. Sternites III–IV (Fig. 4) partially covered with setae. Sternites V–VIII almost nude. Sternites III–VIII densely covered with minute pores anteriorly. Sternites III–VI with a row of 4–8 macrosetae at posterior margin.

Male. Sternite VIII (Fig. 47) with 4 pairs of macrosetae on posterior half, minute setae present at posterior margin. Median lobe of aedeagus (Figs. 50, 51) with basal capsule longer than apical lobe. Paramere (Fig. 52) with paramerite approximately 4 times wider than condylite; velar sac sclerite with 3 setae; apical lobe with 3 minute setae at apex.

Female. Sternite VIII (Fig. 48) with 3 pairs of macrosetae, several minute setae present at posterior margin. Spermatheca (Fig. 53) with basal part more than 2 times longer than apical part.

Measurement. Body length = average 1.91 mm (2.11–1.75 mm, N = 10), pronotal length = average 0.66 mm (0.65–0.68 mm, N = 10), pronotal width = average 0.96 mm (0.92–1.00 mm, N = 10), elytral length = average 0.46 mm (0.43–0.51 mm, N = 10), elytral width = average 0.63 mm (0.61–0.66 mm, N = 10).

Etymology. The specific Latinized epithet is derived from Cambodia where its type locality was found.

Host species. *Odontotermes maesodensis* Ahmad, 1965.

The *assmuthi* species group

Diagnosis. The *assmuthi* group is defined by the following character states: 1) mandible (Figs. 57, 58, 76, 77, 92, 93, 108, 109, 124, 125, 140, 141, 152, 153) covered with 15–40 pores, 2) maxillary basistipes (Fig. 59) almost fused with palpifer, 3) sternite VIII (Figs. 66, 67, 82, 83, 98, 99, 114, 115, 130, 131, 146, 158, 159) sparsely covered with minute pores anteriorly, 4) tergite X (Figs. 68, 84, 100, 116, 132, 147, 160) with posterior half covered with a batch of setae, 5) median lobe of male aedeagus with basal capsule small (Figs, 69, 85, 101, 117, 133, 161), and 6) basal capsule of male aedeagal median lobe with distal crest strongly developed (Figs. 70, 86, 102, 118, 134, 162).

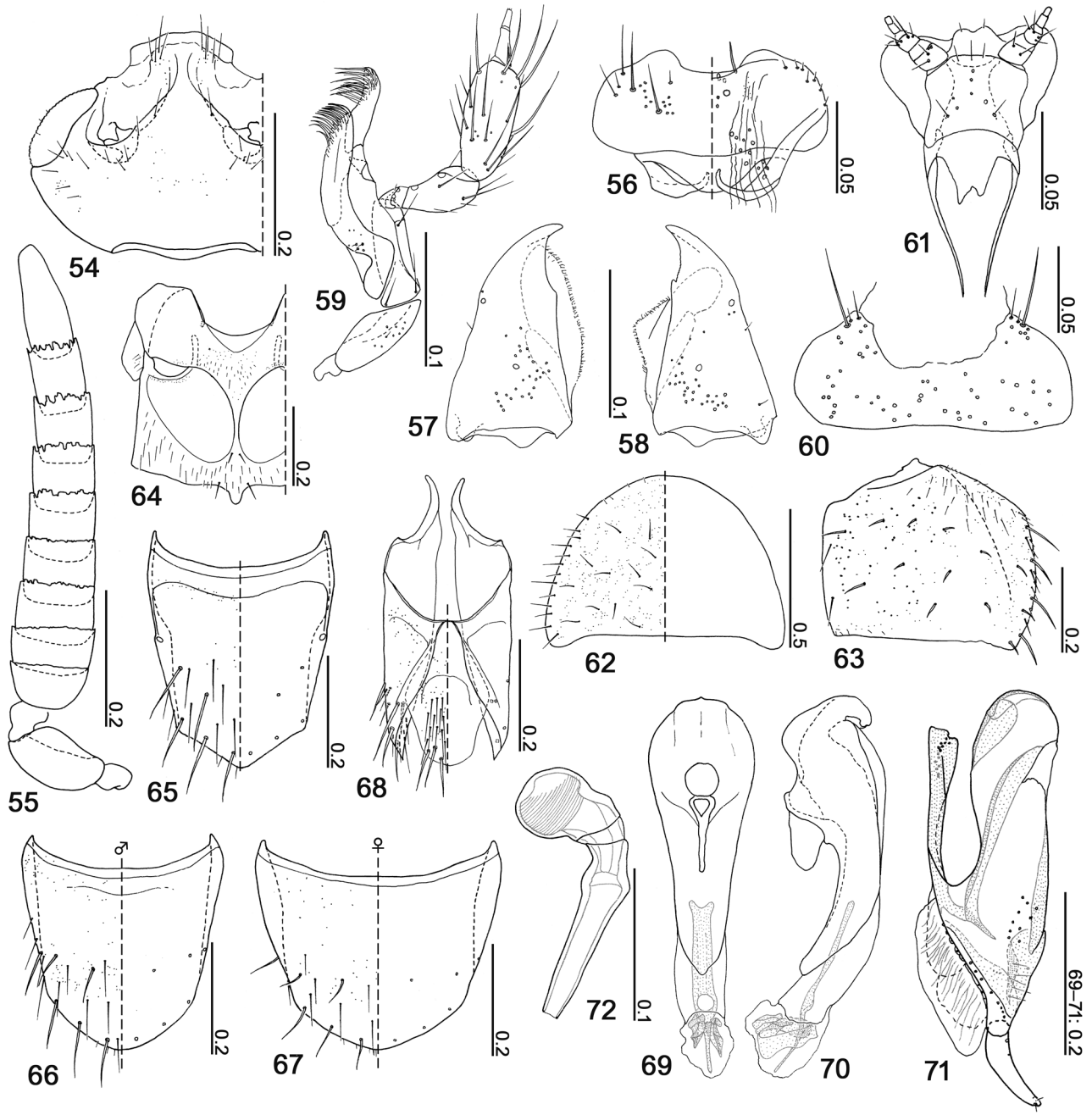
Comments. The *assmuthi* species group includes 11 species: *D. assmuthi* Wasmann, 1904, *D. lepisma* Wasmann, 1904, *D. indicus* Kistner, 1982, and *D. malaysiensis* Kistner, 1982, *D. phourini* **n. sp.**, *D. kohkongensis* **n. sp.**, *D. hirsutus* **n. sp.**, *D. minutus* **n. sp.**, *D. lucidus* **n. sp.**, *D. kakizoei* **n. sp.**, and *D. katayamai.*

The affiliation of the four previously known species, *D. assmuthi*, *D. lepisma*, *D. indicus*, and *D. malaysiensis*, are determined based on the character states of their mouthparts and/or male aedeagus (Kistner 1982), and expected to share other character states typical of the species group.

Discoxenus phourini n. sp.

(Figs. 5, 6, 54–72)

Type materials. Holotype: ♂, Koh Kong, Cambodia, 7 XII 2012, Kanao T. leg. (Colony no. KT428).



FIGURES 54–72. *Discoxenus phourini* **n. sp.**: 54. Head, 55. Antenna, 56. Labrum (left side = dorsal view, right side = ventral view), 57. Mandible, left, 58. Mandible, right, 59. Maxilla, 60. Mentum, 61. Labium, 62. Pronotum, 63. Elytron, right, 64. Meso- and metaventrites, 65. Tergite VIII, 66. Sternite VIII, male, 67. Sternite VIII, female, 68. Tergites IX and X, 69. Median lobe of aedeagus, ventral view, 70. Median lobe of aedeagus, lateral view, 71. Paramere, 72. Spermatheca.

Paratypes: 4♂♂, 7♀♀, same data as holotype (1♂, completely dissected, 1♀, abdominal segments VIII–X dissected off).

Diagnosis. This species is easily distinguished from other *Discoxenus* species by a combination of the following two character states: macrochaetotaxy of tergite III–VIII (6, 6, 6, 6, 6, 6), and sternites IV–VII with two macrosetae at middle of each subapical area. This species is most similar to *D. hirsutus*, but is distinguishable from it by the elytra with 12–13 macrosetae on disc (Fig. 63), and spermatheca with the longer basal part which is 2 times longer than basal part (Fig. 72).

Description. Head (Fig. 54) more than 1.5 times wider than long, with anterior margin of clypeus produced anteriorly. Antenna (Figs. 5, 6, 55) with segment I longer than other segments; segment II as long as segment III,

with 2 macrosetae; segment III bowl shaped; segment IV transverse, wider than other segments; segments V–XI successively narrowed distally; segments V–VI wider than long; segment VI subquadrate; segments VII–X longer than wide; segment XI approximately 2.4 times longer than wide, narrowed apically. Labrum (Fig. 56, left side) with anterior margin deeply concave; median projection of apodeme rounded; 6–7 lateral setae present in ventral view (Fig. 56, right side). Mandibles (Figs. 57, 58) covered with approximately 30 pores. Left mandible (Fig. 57) with adoral margin moderately pointed around middle. Right mandible (Fig. 58) with a tooth moderately pointed. Maxillary (Fig. 59) palpal segment III approximately 2.3 times longer than wide. Mentum (Fig. 60) approximately 2.4 times wider than long, covered with around 50 pores. Labium with prementum covered with 6–7 pores.

Pronotum (Fig. 62) sparsely covered with approximately 50 macrosetae, several minute setae present around anterior margin. Elytron (Fig. 63) transverse, sparsely covered with setae at anterolateral outer corner, 12–13 macrosetae present on disc. Metaventrite (Fig. 64) 1.3 times longer than mesoventrite.

Tergites III–V (Fig. 5) covered with few setae laterally. Tergites VI–VIII with 4–6 setae on posterior half. Tergite VIII (Fig. 65) with posterior margin moderately pointed, 3 pairs of macrosetae present at posterior margin, 2 pairs of macrosetae present around middle. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6. Sternite III (Fig. 6) densely covered with setae. Sternites IV–VIII with posterior half covered with several setae. Sternites III–VII with a row of 6–10 macrosetae at posterior margin. Sternites IV–VII with a pair of macrosetae at middle of subapical area.

Male. Sternite VIII (Fig. 66) with posterior half covered with few setae, 3 pairs of macrosetae at posterior margin and middle. Median lobe of aedeagus moderately narrowed to apical lobe in ventral view (Fig. 69); basal capsule ventrally concave at middle in lateral view (Fig. 70); apical lobe half as wide as basal capsule in lateral view (Fig. 70); distal crest produced with rounded apex. Paramere (Fig. 71) with paramerite more than 3 times wider than condylite; velar sac sclerite with 5 setae; apical lobe with 3 minute setae at apex.

Female. Sternite VIII (Fig. 67) with 3 pairs of macrosetae at posterior margin and middle. Spermatheca (Fig. 72) with basal part approximately 2 times longer than apical part.

Measurement. Body length = average 1.85 mm (1.76–1.93 mm, N = 10), pronotal length = average 0.59 mm (0.57–0.62 mm, N = 10), pronotal width = average 0.88 mm (0.83–0.90 mm, N = 10), elytral length = average 0.40 mm (0.38–0.43 mm, N = 10), elytral width = average 0.44 mm (0.42–0.46 mm, N = 10).

Etymology. This specific name is dedicated to Mr. Phourin Chhang of the Forestry Administration of Phnom Penh, Cambodia, for his hearty support during field surveys in Cambodia by TK.

Host species. *Hypotermes makhamensis* Ahmad, 1965.

***Discoxenus kohkongensis* n. sp.**

(Figs. 7, 8, 73–88, 165)

Type materials. Holotype: ♂, Koh Kong, Cambodia, 7 XII 2012, Kanao T. leg. (Colony no. KT428).

Paratypes: 2♂♂, 25♀♀, same data as holotype (1♂, completely dissected, 1♀, head and abdominal segments VIII–X dissected off).

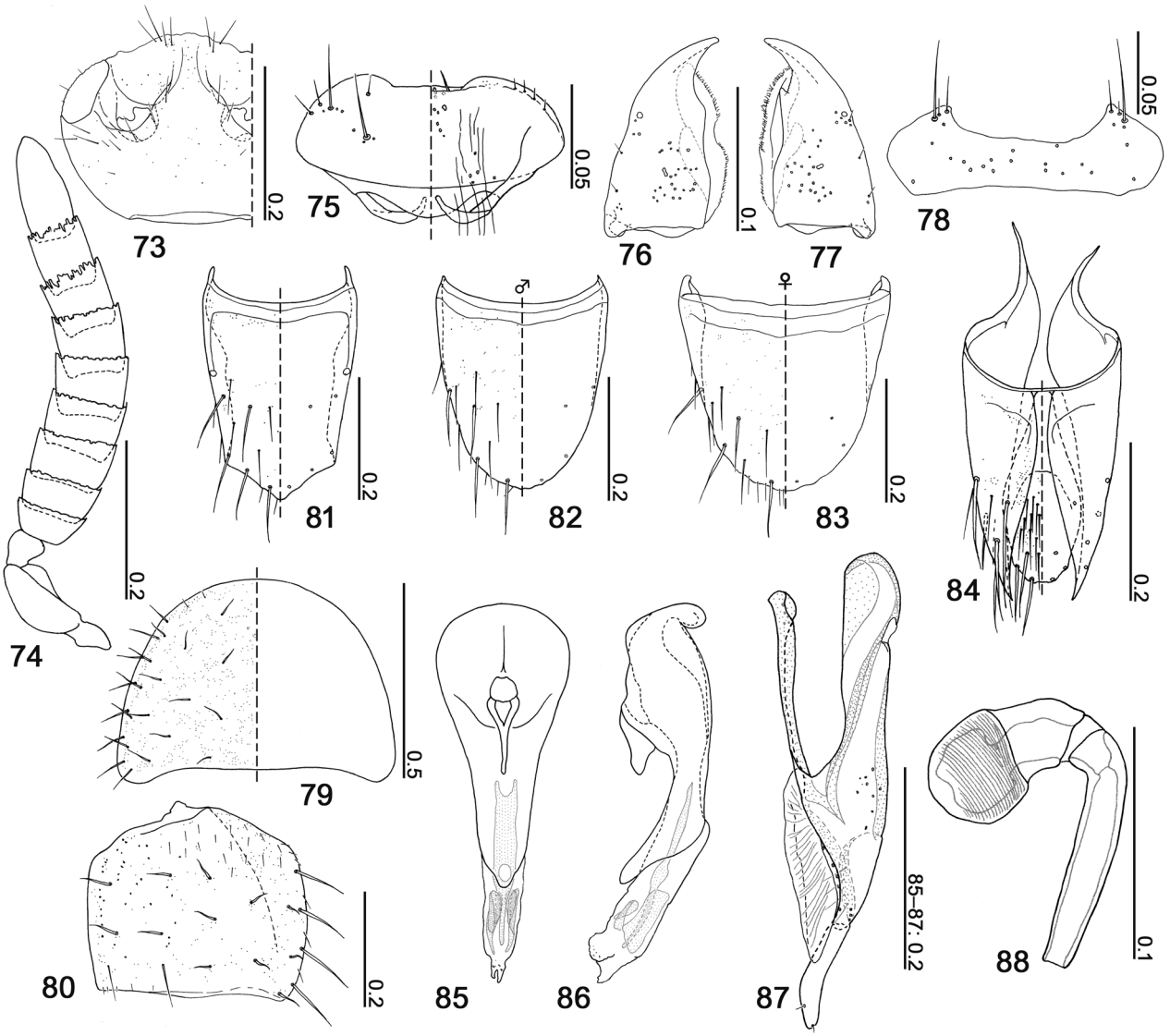
Diagnosis. This species is distinguished from other *Discoxenus* species by a combination of the following four character states: macrochaetotaxy of tergites III–VIII (6, 6, 6, 6, 6, 6), sternites III–VII with macrosetae only at each posterior margin, paramere with paramerite narrow (approximately 3 times as wide as condylite) (Fig. 87), and spermatheca with short basal part (approximately 1.5 times longer than apical part) (Fig. 88). This species is most similar to *D. minutus*, but is distinguishable from it by a male aedeagal median lobe with apically and moderately pointed distal crest (Fig. 86).

Description. Head (Fig. 73) more than 1.3 times wider than long, with anterior margin of clypeus rounded. Antenna (Figs. 7, 8, 74) with segment I longer than other segments; segment II as long as segment IV, with 3 macrosetae; segment III trapezoidal, shorter than other segments; segment IV transverse; segment V wider than other segments; segments VI–XI successively narrowed distally; segments VI–VIII wider than long; segment IX subquadrate; segment X longer than wide; segment XI approximately 2.2 times longer than wide, narrowed apically. Labrum (Fig. 75, left side) with anterior margin concave; median projection of apodeme broadly rounded; 4 lateral setae present in ventral view (Fig. 75, right side). Mandibles (Figs. 76, 77) with 2 scrobal setae, covered with approximately 30 pores. Left mandible (Fig. 76) with adoral margin bisinuate. Right mandible (Fig. 77) with a

distinct tooth. Maxillary palpal segment III approximately 2 times longer than wide. Mentum (Fig. 78) short, approximately 3.2 times wider than long, covered with around 20 pores. Labium with prementum covered with 6–7 pores.

Pronotum (Fig. 79) sparsely covered with approximately 46 macrosetae, few minute setae present around anterior margin. Elytron (Fig. 80) transverse, sparsely covered with pores, several setae present at anterolateral outer corner, 12 macrosetae present on disc. Metaventrite approximately 1.5 times as long as mesoventrite.

Tergites III–IV (Fig. 7) covered with few setae laterally. Tergites V–VIII with posterior half covered with several setae. Tergite VIII (Fig. 81) with posterior margin pointed, 3 pairs of macrosetae present at posterior margin, 2 pairs of macrosetae present around middle. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6. Sternite III (Fig. 8) sparsely covered with setae. Sternites IV–VIII with a row of yellow setae at middle. Sternites III–VII with 6–10 macrosetae at posterior margin.



FIGURES 73–88. *Discoxenus kohkongensis* **n. sp.**: 73. Head, 74. Antenna, 75. Labrum (left side = dorsal view, right side = ventral view), 76. Mandible, left, 77. Mandible, right, 78. Mentum, 79. Pronotum, 80. Elytron, right, 81. Tergite VIII, 82. Sternite VIII, male, 83. Sternite VIII, female. 84, Tergites IX and X. 85, Median lobe of aedeagus, ventral view, 86. Median lobe of aedeagus, lateral view, 87. Paramere. 88. Spermatheca.

Male. Sternite VIII (Fig. 82) with posterior half covered with few setae, 2 pairs of macrosetae present at posterior margin and middle. Median lobe of aedeagus narrowed toward apical lobe in ventral view (Fig. 85); basal capsule slightly concave at middle, with distal crest moderately pointed apically in lateral view (Fig. 86); apical lobe less than half as wide as basal capsule in lateral view (Fig. 86). Paramere (Fig. 87) with paramerite narrow,

approximately 3 times as wide as condylite; velar sac sclerite with 4–5 setae; apical lobe with 2 minute setae at apex.

Female. Sternite VIII (Fig. 83) with 2 pairs of macrosetae at posterior margin and middle. Spermatheca (Fig. 88) with basal part approximately 1.5 times longer than apical part.

Measurement. Body length = average 1.40 mm (1.38–1.50 mm, N = 10), pronotal length = average 0.47 mm (0.41–0.51 mm, N = 10), pronotal width = average 0.70 mm (0.67–0.73 mm, N = 10), elytral length = average 0.32 mm (0.28–0.36 mm, N = 10), elytral width = average 0.36 mm (0.33–0.41 mm, N = 10).

Etymology. The specific Lathinized epithet is derived from its type locality of Koh Kong Province.

Host species. *Hypotermes makhamensis* Ahmad, 1965.

***Discoxenus hirsutus* n. sp.**
(Figs. 9, 10, 89–104)

Type materials. Holotype: ♂, 500 m S of Ankor Wat, Siem Reap, Cambodia, 5 VI 2012, Maruyama M. (Colony no. MMCB-T-2012-1-002).

Paratypes: Cambodia: 4♂♂, 16♀♀, same as holotype (1♂, completely dissected, 1♂, abdominal segments VIII–X dissected off). 6♂♂, North Wall of Preah Khan, Siem Reap, 19 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-005) (1♂, completely dissected). 1♀, 1 km W of Banteay Prei, Siem Reap, 21 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0017) (abdominal segments VIII–X dissected off). 2♂♂, 1♀, Ankor Thom, Siem Reap, 12 XII 2012, Kanao T. leg. (Colony no. KT433) (1♂, completely dissected). 1♂, 2♀♀, 0.76 km NE of Preah Kham, Siem Reap, 18 VIII 2014, Kakizoe S. & Maruyama M. leg. (Colony no. SK002). 1♀, same locality data to SK002, 19 VIII 2014, Kakizoe S. leg. (Colony no. SK007).

Diagnosis. This species is easily distinguished from other *Discoxenus* species by a combination of the following two character states: the macrochaetotaxy of tergites III–VIII (6, 6, 6, 6, 6, 6), and sternites VI–VII with two transverse rows of 6–14 macrosetae at middle and posterior margin. This species is most similar to *D. phourini*, but is distinguishable from it by the elytra with 10 macrosetae on disc (Fig. 96), and spermatheca with shorter basal part which is less than 2 times longer than apical part (Fig. 104).

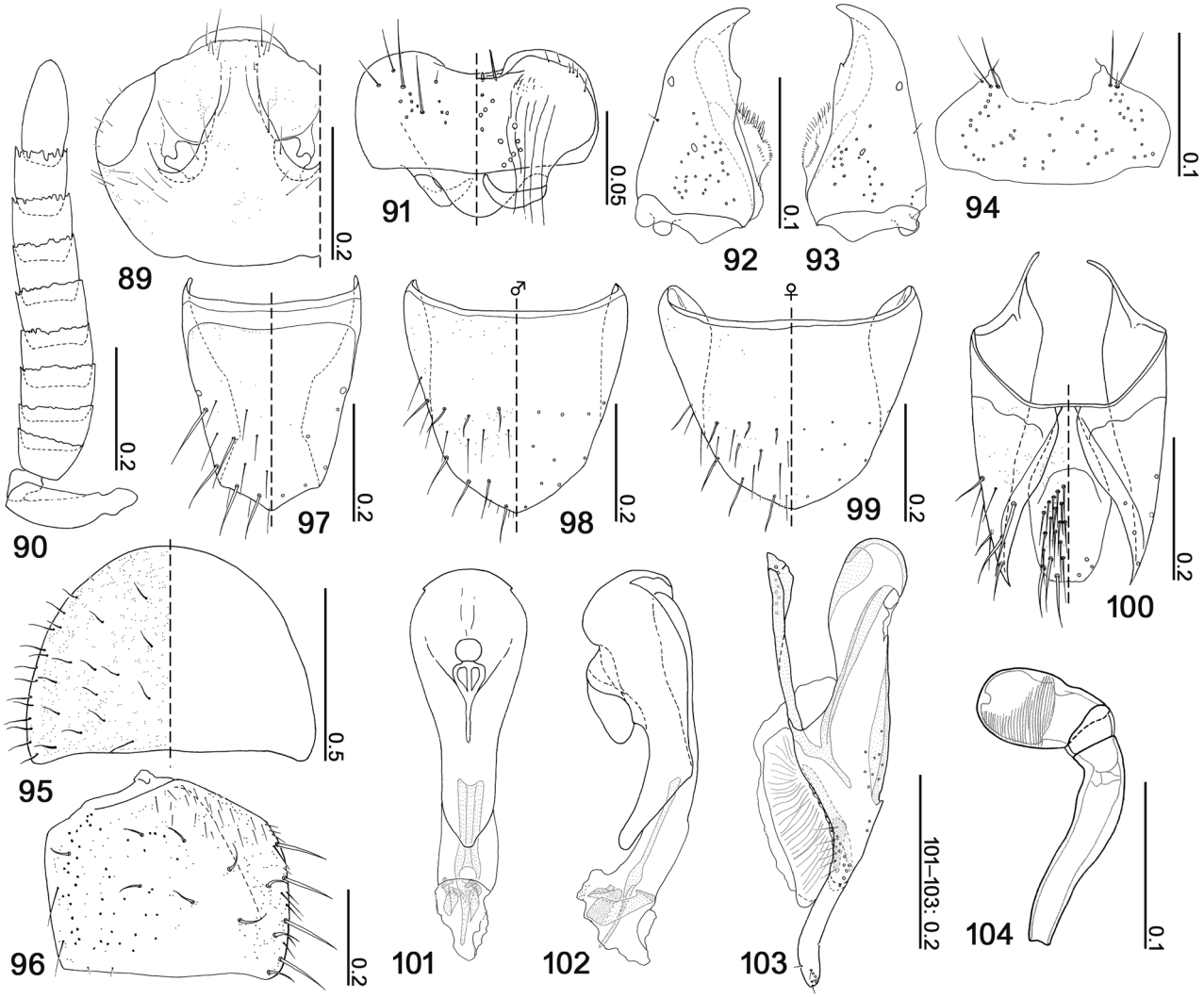
Description. Head (Fig. 89) approximately 1.3 times wider than long. Antenna (Figs. 9, 10, 90) with segment I longer than other segments; segment II as long as segment III with 2 macrosetae; segment III dilated apically; segment IV transverse; segment V wider than other segments; segments VI–XI successively narrowed distally; segments VI–VII wider than long; segment VIII subquadrate; segments IX–X longer than wide; segment XI approximately 2 times longer than wide, widest around middle. Labrum (Fig. 91, left side) with anterior margin deeply concave at middle; median projection of apodeme produced posteriorly, with apex rounded; 5–6 lateral setae present in ventral view (Fig. 91, right side). Mandibles (Figs. 92, 93) covered with 20–30 pores. Left mandible (Fig. 92) with adoral margin moderately pointed around middle. Right mandible (Fig. 93) with a small tooth. Maxillary palpal segment III approximately 2 times longer than wide. Mentum (Fig. 94) approximately 2 times wider than long, covered with around 50 pores. Labium with prementum covered with 12–14 pores.

Pronotum (Fig. 95) sparsely covered with approximately 46 macrosetae, 6 minute setae present around anterior margin. Elytron (Fig. 96) transverse, sparsely covered with several setae at anterolateral outer corner, 10 macrosetae present on disc. Metaventrite approximately 1.5 times as long as mesoventrite.

Tergites III–VI (Fig. 9) almost without yellow setae. Tergite VII with a row of yellow setae subapically. Tergite VIII (Fig. 97) with posterior margin pointed, 3 pairs of macrosetae present at posterior margin, 2 pairs of macrosetae present around middle. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6. Sternite III (Fig. 10) with posterior half densely covered with setae. Sternites IV–VIII with a row of 4–6 yellow setae at middle. Sternites III–VII with 6–10 macrosetae at posterior margin, a row of 10–16 macrosetae present at middle.

Male. Sternite VIII (Fig. 98) with 4 pairs of macrosetae around posterior margin and middle, respectively. Median lobe of aedeagus moderately narrowed towards apical lobe in ventral view (Fig. 101); basal capsule with distal crest rounded apically (Fig. 102); apical lobe less than half as wide as basal capsule in lateral view (Fig. 102). Paramere (Fig. 103) with paramerite more than 3 times wider than condylite; velar sac sclerite with 5–6 setae; apical lobe with 2–4 minute setae at apex.

Female. Sternite VIII (Fig. 99) with 3 pairs of macrosetae at posterior margin, 11–12 macrosetae present around middle. Spermatheca (Fig. 104) with basal part less than 2 times longer than apical part.



FIGURES 89–104. *Discoxenus hirsutus* **n. sp.**: 89. Head, 90. Antenna, 91. Labrum (left side = dorsal view, right side = ventral view), 92. Mandible, left, 93. Mandible, right, 94. Mentum, 95. Pronotum, 96. Elytron, right, 97. Tergite VIII, 98. Sternite VIII, male, 99. Sternite VIII, female, 100. Tergites IX and X. 101. Median lobe of aedeagus, ventral view, 102. Median lobe of aedeagus, lateral view, 103. Paramere, 104. Spermatheca.

Measurement. Body length = average 1.68 mm (1.55–1.70 mm, N = 10), pronotal length = average 0.60 mm (0.58–0.63 mm, N = 10), pronotal width = average 0.84 mm (0.80–0.87 mm, N = 10), elytral length = average 0.43 mm (0.41–0.44 mm, N = 10), elytral width = average 0.47 mm (0.46–0.51 mm, N = 10).

Etymology. The specific epithet *hirsutus* is a Latin adjective meaning "hairy," in reference to the diagnostic number of macrosetae on the abdominal sternites.

Host species. *Hypotermes makhamensis* Ahmad, 1965 and *H.* cf. *xenotermitis* (Wasmann, 1896).

Comments. A total of ten specimens of *D. hirsutus* were found in three colonies of *H. makhamensis* (colony no. MMCB-T-2012-2-005, MMCB-T-2012-2-017, and KT433) while 21 specimens were found in one nest of *H.* cf. *xenotermitis* (MMCB-T-2012-1-002). All these beetles were directly collected from the fungus gardens of the two termite species, and never attacked by their hosts. It is unlikely that the one of these host species may be accidental.

There were no morphological differences between the specimens collected from nests of *H. makhamensis* and *H.* cf. *xenotermitinis*.

***Discoxenus minutus* n. sp.**
(Figs. 11, 12, 105–120)

Type materials. Holotype: ♀, 500 m S of Ankor Wat, Siem Reap, Cambodia, 5 VI 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-1-002).

Paratypes: Cambodia: 2♂♂, 3♀♀, same data as holotype (2♂♂, completely dissected). 2♀♀, 1 km S of Angkor Wat, Siem Reap, 18 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-003) (1♀, abdominal segments dissected off). 1♀, North Wall of Preah Khan, Siem Reap, 19 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-005). 1♂, 1♀, Siem Reap, Ankor Thom, Bayon, 20 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-009). 1♂, 1♀, 1 km W of Banteay Prei, Siem Reap, 21 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0017) (1♂, completely dissected). 1♂, 1♀, 0.76 km NE of Preah Kham, Siem Reap, 18 VIII 2014, Kakizoe S. & Maruyama M. leg. (Colony no. SK002). 2♂♂, same locality data to SK002, 19 VIII 2014, Kakizoe S. leg. (Colony no. SK007).

Diagnosis. This species is distinguished from other *Discoxenus* species by a combination of the following four character states: macrochaetotaxy of tergites III–VIII (6, 6, 6, 6, 6, 6), sternites III–VII with macrosetae only at each posterior margin, paramere with paramerite more than 3 times wider than condylite (Fig. 119), and spermatheca with basal part more than 1.5 times longer than apical part (Fig. 120). This species is most similar to *D. kohkongensis*, but is distinguishable from it by a male aedeagal median lobe with apically rounded crest (Fig. 118).

Description. Head (Fig. 105) approximately 1.3 times wider than long. Antenna (Figs. 11, 12, 106) with segment I longer than other segments; segment II as long as segment III, with 3 macrosetae; segment III trapezoidal; segment IV transverse; segment V wider than other segments; segments VI–XI successively narrowed distally; segments VI–VII wider than long; segment VIII subquadrate; segments IX–X longer than wide; segment XI approximately 2.5 times longer than wide, widest at middle. Labrum (Fig. 107, left side) with anterior margin slightly concave at middle; median projection of apodeme short, with apex broadly rounded; 5 lateral setae present in ventral view (Fig. 107, right side). Mandibles (Figs. 108, 109) covered with approximately 30 pores. Left mandible (Fig. 108) with adoral margin moderately pointed at apical third. Right mandible (Fig. 109) with a distinct tooth. Maxillary palpal segment III approximately two times longer than wide. Mentum (Fig. 110) approximately 2.3 times wider than long, covered with around 40 pores. Labium with prementum covered with 12–14 pores.

Pronotum (Fig. 111) sparsely covered with approximately 44 macrosetae, 6 minute setae present around anterior margin. Elytron (Fig. 112) transverse, sparsely covered with several setae at anterolateral outer corner, 12 macrosetae present on disc. Metaventrite approximately 1.3 times as long as mesoventrite.

Tergites III–IV (Fig. 11) almost without seta. Tergites V–VII with a row of setae anteapically. Tergite VIII (Fig. 113) with posterior margin pointed, 3 pairs of macrosetae present at posterior margin, with 2 pairs of macrosetae around middle. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6. Sternite III (Fig. 12) with posterior half densely covered with setae. Sternites IV–VIII with a row of yellow setae at middle. Sternites III–VII with 6–10 macrosetae at posterior margin.

Male. Sternite VIII (Fig. 114) with 3 pairs of macrosetae at posterior margin, 2 pairs of macrosetae present at middle. Median lobe of aedeagus moderately narrowed toward apical lobe in ventral view (Fig. 117); basal capsule with distal crest rounded apically in lateral view (Fig. 118); apical lobe less than half as wide as basal capsule in lateral view (Fig. 118). Paramere (Fig. 119) with paramerite more than 3 times wider than condylite; velar sac sclerite with 5–6 setae; apical lobe with 4 minute setae at apex.

Female. Sternite VIII (Fig. 115) with 2 pairs of macrosetae at posterior margin and middle, respectively. Spermatheca (Fig. 120) with basal part approximately 1.8 times longer than apical part.

Measurement. Body length = average 1.62 mm (1.53–1.73 mm, N = 10), pronotal length = average 0.54 mm (0.51–0.56 mm, N = 10), pronotal width = average 0.73 mm (0.68–0.77 mm, N = 10), elytral length = average 0.38 mm (0.36–0.39 mm, N = 10), elytral width = average 0.41 mm (0.39–0.43 mm, N = 10).

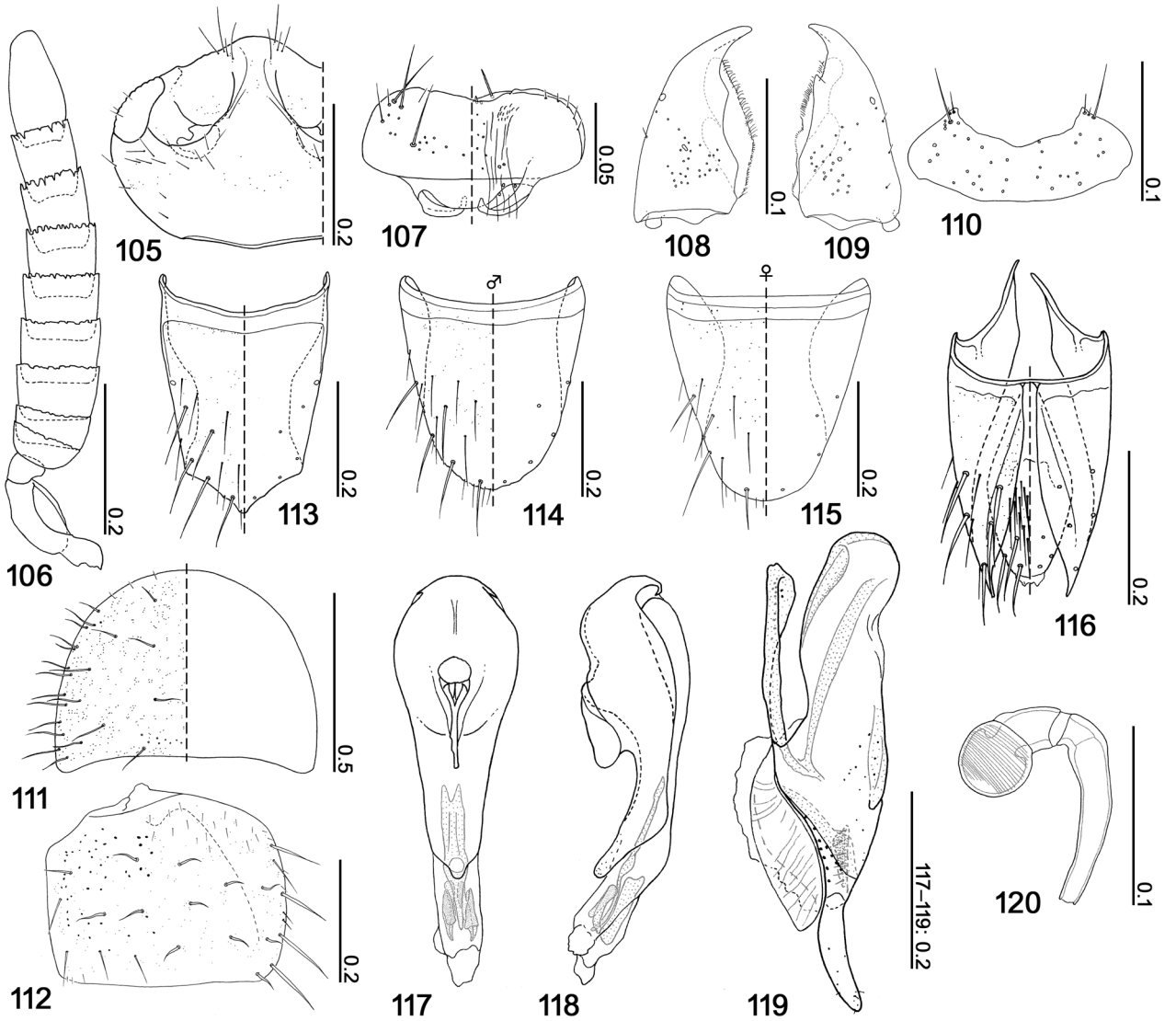
Etymology. The specific epithet *minutus* is a Latin adjective meaning "small," in reference to the small body size of this species.

Host species. *Hypotermes makhamensis* Ahmad, 1965 and *H.* cf. *xenotermitis* (Wasmann, 1896).

Comments. Total of 13 specimens of *D. minutus* were collected and morphologically observed in the present

study. Six beetle specimens were collected from only one colony (Colony no. MMCB-T-2012-1-002) of *H.* cf. *xenotermitis*. The other seven beetle specimens were found in four different nests of *H. makhamensis*. All specimens of *D. minutus* were directly collected from the fungus gardens of their host termites, and it is unlikely that the beetles may have accidentally intruded in the nest of one of these host species.

There are small morphological differences between the specimens collected from the nests of *H. makhamensis* and *H.* cf. *xenotermitinis*. The specimens collected from *H. makhamensis* nests have slightly narrower elytra and broader paramerites of paramere than those of the specimens collected from *H.* cf. *xenotermitinis* nests. However, given the present data, we consider these differences to be insufficient for a species-level distinction. Examination of further material and DNA analysis will provide more data for species delimitation.



FIGURES 105–120. *Discoxenus minutus* **n. sp.**: 105. Head, 106. Antenna, 107. Labrum (left side = dorsal view, right side = ventral view), 108. Mandible, left, 109. Mandible, right, 110. Mentum, 111. Pronotum, 112. Elytron, right, 113. Tergite VIII, 114. Sternite VIII, male, 115. Sternite VIII, female, 116. Tergites IX and X, 117. Median lobe of aedeagus, ventral view, 118. Median lobe of aedeagus, lateral view, 119. Paramere, 120. Spermatheca.

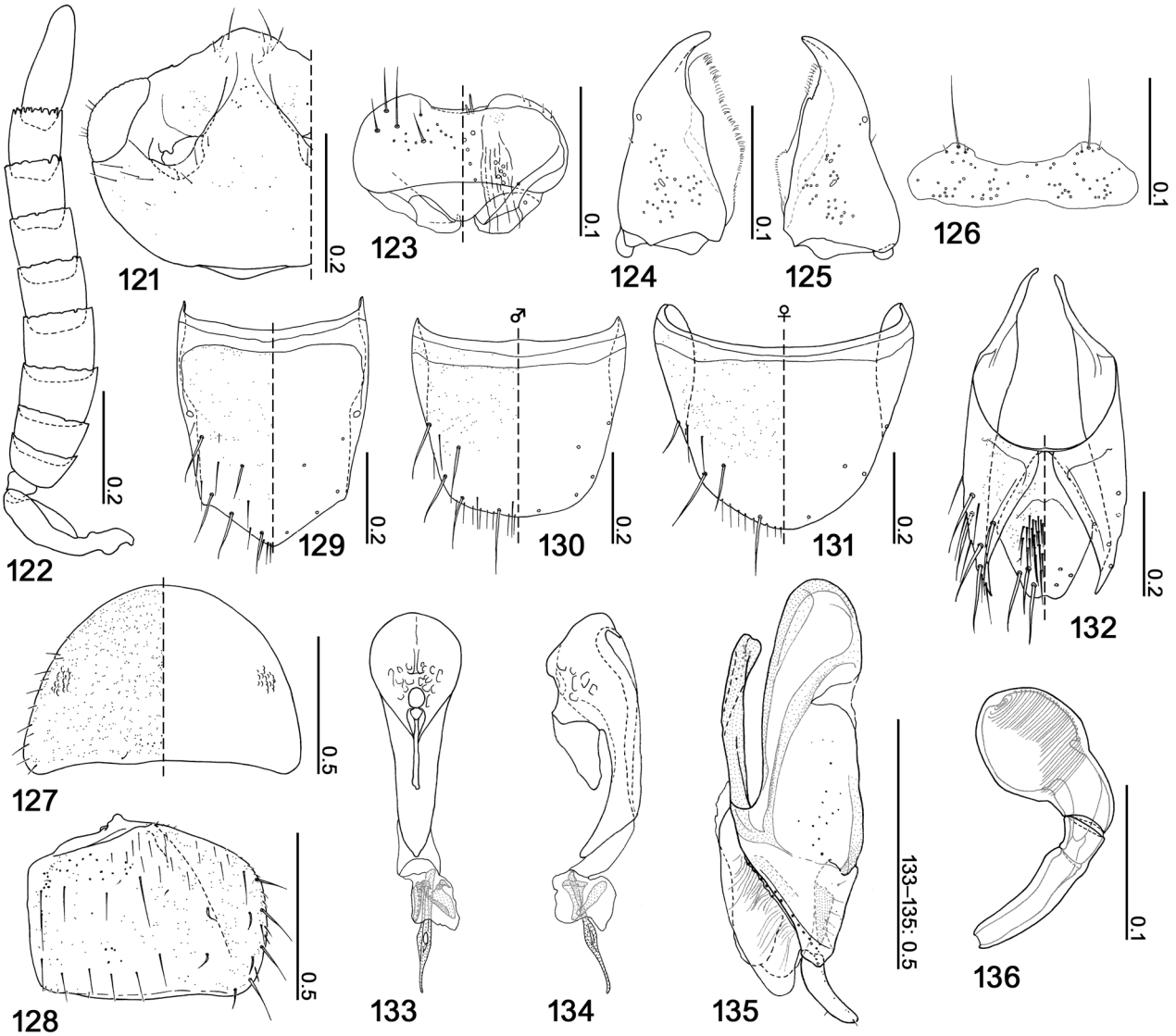
***Discoxenus lucidus* n. sp.**
(Figs. 13, 14, 121–136, 166)

Type materials. Holotype: ♂, Koh Kong, Cambodia, 7 XII 2012, Kanao T. leg. (Colony no. KT428).

Paratypes: Cambodia: 1♂, 49♀♀, same data as holotype (1♂, 1♀, abdominal segments VIII–X dissected off).

1♀, Ankor Thom, Siem Reap, 17 XII 2012, Kanao T. leg. (Colony no. KT439). 1♀, 5 sex ?, 500 m S of Ankor Wat, Siem Reap, 5 VI 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-1-002). 2♂♂, 1♀, 1 km S of Angkor Wat, Siem Reap, 18 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-003). 1♂, 4♀♀, North Wall of Preah Khan, Siem Reap, 19 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-005). 1♂, 1 km W of Banteay Prei, Siem Reap, 21 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0017) (completely dissected).

Diagnosis. This species is distinct, and is easily distinguishable from other *Discoxenus* species by a combination of the following two character states: a pronotum without macrosetae on disc (Fig. 127), and macrochaetotaxy of abdominal tergites (4, 4, 4, 4, 4, 6).



FIGURES 121–136. *Discoxenus lucidus* **n. sp.**: 121. Head, 122. Antenna, 123. Labrum (left side = dorsal view, right side = ventral view), 124. Mandible, left, 125. Mandible, right, 126. Mentum, 127. Pronotum, 128. Elytron, right, 129. Tergite VIII, 130. Sternite VIII, male, 131. Sternite VIII, female, 132. Tergites IX and X, 133. Median lobe of aedeagus, ventral view, 134. Median lobe of aedeagus, lateral view, 135. Paramere, 136. Spermatheca.

Description. Head (Fig. 121) approximately 1.3 times wider than long. Antenna (Figs. 13, 14, 122) with segment I longer than other segments; segment II shorter than other segments, with 2 macrosetae; segment III trapezoidal; segment IV transverse; segment V wider than other segments; segments VI–XI successively narrowed distally; segment VI subquadrate; segments VII–X longer than wide; segment XI narrow, approximately 3 times longer than wide. Labrum (Fig. 123, left side) with anterior margin deeply concave at middle; median projection of apodeme triangular, with apex rounded; 4–5 lateral setae present in ventral view (Fig. 123, right side). Mandibles (Figs. 124, 125) covered with 20–30 pores. Left mandible (Fig. 124) with adoral margin moderately pointed around

middle. Right mandible (Fig. 125) with a small tooth. Maxillary palpal segment III approximately 2.7 times longer than wide. Mentum (Fig. 126) short, approximately 3.7 times wider than long, covered with around 60 pores. Labium with prementum covered with approximately 20 pores.

Pronotum (Fig. 127) covered with approximately 22 short macrosetae laterally. Elytron (Fig. 128) transverse, sparsely covered with yellow setae, 5 macrosetae present laterally. Metaventrite approximately 1.8 times longer than mesoventrite.

Tergites III–VII (Fig. 13) with 1–2 setae at each lateral margin. Tergite VIII (Fig. 129) with posterior margin pointed, 3 pairs of macrosetae present at posterior margin, with 2 pairs of macrosetae around middle. Macrochaetotaxy of abdominal tergites III–VIII = 4, 4, 4, 4, 4, 6. Sternite III (Fig. 14) with posterior half densely covered with setae. Sternites IV–VI with posterior half sparsely covered with setae. Sternite VII with a row of yellow setae at middle. Sternites III–VII with 6–10 macrosetae at posterior margin.

Male. Sternite VIII (Fig. 130) with 3 pairs of macrosetae at posterior margin, 2 pairs of macrosetae present mediolaterally. Median lobe of aedeagus moderately narrowed apically in ventral view (Fig. 133); basal capsule with distal crest triangular, strongly produced apically in lateral view (Fig. 134); apical lobe less than half as wide as basal capsule in lateral view (Fig. 134). Paramere (Fig. 135) with paramerite broad, approximately 4 times wider than condylite; velar sac sclerite with 5–6 setae; apical lobe with 2 minute setae at apex.

Female. Sternite VIII (Fig. 131) with 2 pairs of macrosetae at posterior margin and middle. Spermatheca (Fig. 136) with basal part as long as apical part.

Measurement. Body length = average 2.67 mm (2.30–2.94 mm, N = 10), pronotal length = average 0.70 mm (0.63–0.75 mm, N = 10), pronotal width = average 0.93 mm (0.87–1.02 mm, N = 10), elytral length = average 0.52 mm (0.48–0.54 mm, N = 10), elytral width = average 0.58 mm (0.54–0.61 mm, N = 10).

Etymology. The specific epithet is derived from the Latin adjective *lucidus* meaning "lucid," in reference to the diagnostic glossy and smooth body of this species.

Host species. *Hypotermes makhamensis* Ahmad, 1965 and *H.* cf. *xenotermitis* (Wasmann, 1896).

Comments. Six of 65 *D. lucidus* specimens used in this study were collected form a nest of *H.* cf. *xenotermitis* (Colony no. MMCB-T-2012-1-002) while the other 59 specimens were collected from five colonies of *H. makhamensis*. It is unlikely that the one of these host species may be accidental.

There were no morphological differences between the specimens collected from nests of *H. makhamensis* and *H.* cf. *xenotermitinis*.

***Discoxenus kakizoei* n. sp.**
(Figs. 15, 16, 137–148)

Type materials. Holotype: ♀, Bayon, Ankor Thom, Siem Reap, Cambodia, 20 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-009) (abdominal segments VIII–X dissected off).

Paratypes: 1♀, North Wall of Preah Khan, Siem Reap, Cambodia, 19 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-005) (completely dissected). 2♀♀, 0.76 km NE of Preah Kham, Siem Reap, 19 VIII 2014, Kakizoe S. leg. (Colony no. SK007).

Diagnosis. This species is distinct, and is distinguishable from other *Discoxenus* species by a combination of the following three character states: right mandible with a distinct and blunt tooth (Fig. 141), macrochaetotaxy of abdominal tergites III–VIII (6, 6, 6, 6, 6, 6), and spermatheca with the basal part being shorter than the apical part (Fig. 148).

Description. Head (Fig. 137) approximately 1.4 times wider than long. Antenna (Figs. 15, 16, 138) with segment I rectangular; segment II as long as segment III, with 4 macrosetae; segment III short, trapezoidal; segment IV transverse, wider than other segments; segments V–XI successively narrowed distally; segments V–VI wider than long; segment VII subquadrate; segments VIII–X longer than wide; segment XI approximately 2.6 times longer than wide. Labrum (Fig. 139, left side) with anterior margin deeply concave at middle; median projection of apodeme with posterior margin truncate; 3 lateral setae present in ventral view (Fig. 139, right side). Mandibles (Figs. 140, 141), covered with 30–40 pores. Left mandible (Fig. 140) with adoral margin moderately convex at apical third. Right mandible (Fig. 141) with a tooth broadly convex at middle of adoral margin, rounded apically. Maxillary palpal segment III approximately 2.3 times longer than wide. Mentum (Fig. 142) approximately

3 times wider than long, covered with around 50 pores. Labium with prementum covered with approximately 16 pores.

Pronotum (Fig. 143) covered with approximately 44 macrosetae, 6 minute setae present around anterior margin. Elytron (Fig. 144) transverse, sparsely covered with several setae at anterolateral outer corner, 12 macrosetae present on disc. Metaventrite approximately 1.7 times as long as mesoventrite.

Tergites III–VI (Fig. 15) with 1–2 setae laterally. Tergite VII with a row of 5–6 setae subapically. Tergite VIII (Fig. 145) with posterior margin pointed, 3 pairs of macrosetae present at posterior margin, with 2 pairs of macrosetae around middle. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6. Sternite III (Fig. 16) with posterior half densely covered with setae. Sternites IV–V with posterior half sparsely covered with setae. Sternites VI–VII with a row of yellow setae at middle. Sternites III–VII with 6–10 macrosetae at posterior margin.

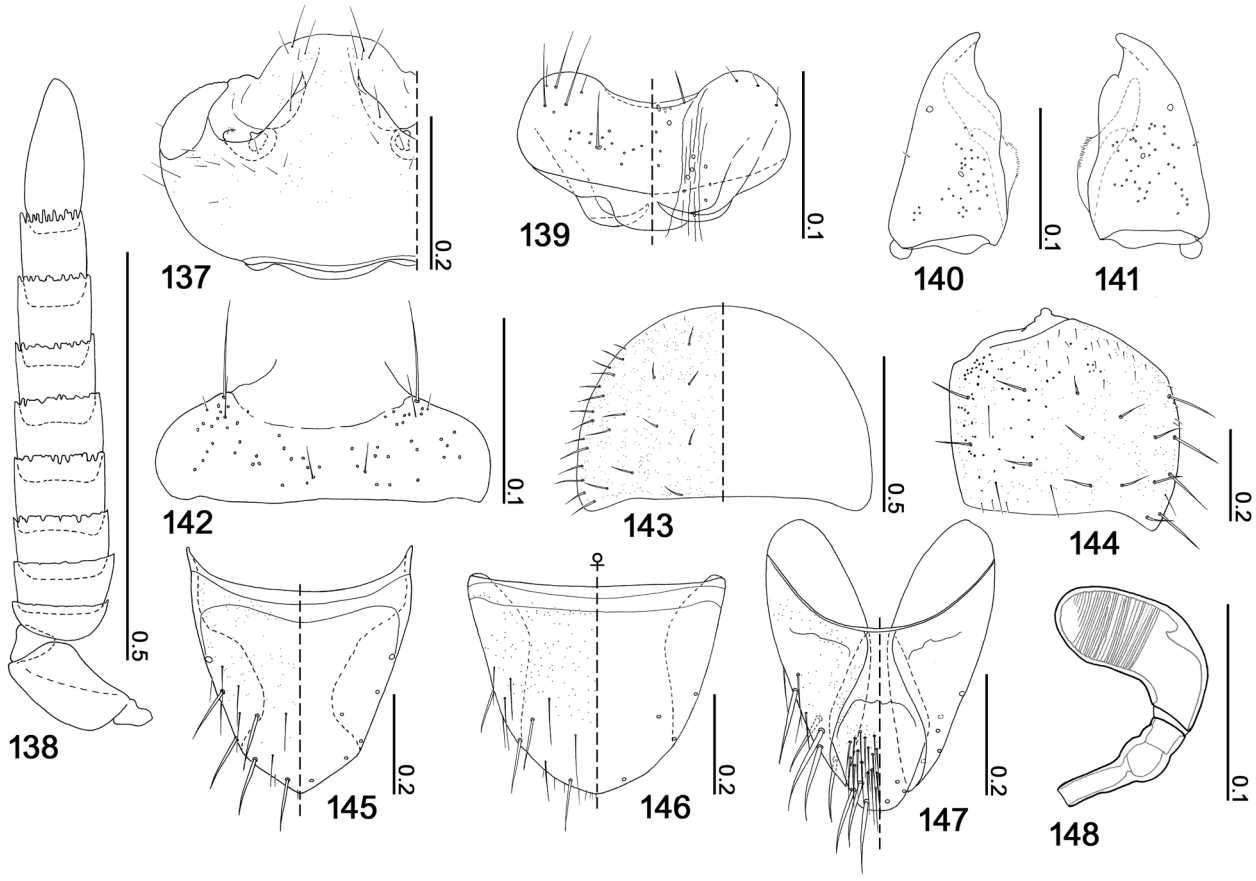
Male. Unknown.

Female. Sternite VIII (Fig. 146) with 2 pairs of macrosetae at posterior margin and middle. Spermatheca (Fig. 148) with apical part longer than basal part.

Measurement. Body length = average 1.82 mm (N = 1), pronotal length = average 0.60 mm (0.58–0.62 mm, N = 2), pronotal width = average 0.85 mm (0.83–0.86 mm, N = 2), elytral length = average 0.44 mm (0.43–0.45 mm, N = 2), elytral width = average 0.50 mm (0.49–0.51 mm, N = 2.

Etymology. The specific epithet is named after Mr. Shotaro Kakizoe of Kyushu University, who collected and kindly provided the specimens of this rare species.

Host species. *Hypotermes makhamensis* Ahmad, 1965.



FIGURES 137–148. *Discoxenus kakizoei* **n. sp.**: 137. Head, 138. Antenna, 139. Labrum (left side = dorsal view, right side = ventral view), 140. Mandible, left, 141. Mandible, right, 142. Mentum, 143. Pronotum, 144. Elytron, right, 145. Tergite VIII, 146. Sternite VIII, 147. Tergites IX and X, 148. Spermatheca.

***Discoxenus katayamai* Kanao & Maruyama, 2010**
(Figs. 17, 18, 149–164)

Discoxenus katayamai Kanao & Maruyama, 2010: 79.

Additional materials. Cambodia: 8 sex?, 500 m S of Ankor Wat, Siem Reap, 5 VI 2012, Maruyama M. (Colony no. MMCB-T-2012-1-001). 2♀♀, 1 km S of Angkor Wat, Siem Reap, 18 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-002). 3♂♂, 2♀♀, North Wall of Preah Khan, Siem Reap, 19 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-006) (1♂, completely dissected, 1♀, abdominal segments dissected off). 2♂♂, 6♀♀, Bayon, Ankor Thom, Siem Reap, 20 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-008) (1♂, 1♀, abdominal segments dissected off). 1♀, 1 km W of Banteay Prei, Siem Reap, 21 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0016). 1♂, 9♀♀, 1 km S of Ankor Wat, Charles De Gaulle, Siem Reap, 22 VIII 2012, Maruyama M. leg. (Colony no. MMCB-T-2012-2-0023) (1♀, completely dissected). 3♂♂, 1♀, 2 km SE of Neak Pean, Siem Reap, 18 VIII 2014, Kakizoe S. & Maruyama M. leg. (Colony no. SK001). 2♂♂, 2♀♀, 0.76 km NE of Preah Kham, Siem Reap, 18 VIII 2014, Kakizoe S. & Maruyama M. leg. (Colony no. SK003). 1♀, 0.65 km N of Preah Kham, Siem Reap, 19 VIII 2014, Kakizoe S. leg. (Colony no. SK004). 3♀♀, 0.76 km NE of Preah Kham, Siem Reap, 19 VIII 2014, Kakizoe S. leg. (Colony no. SK008). 7♂♂, 17♀♀, 0.77 km E of Angkor Wat, Siem Reap, 24 VIII 2014, Kakizoe S. & Maruyama M. leg. (Colony no. SK015). 2♂♂, 2♀♀, same locality data to SK002, 25 VIII 2014, Kakizoe S. leg. (Colony no. SK019). 1♀, 1.8 km W of Neak Pean, Siem Reap, 26 VIII 2014, Kakizoe S. leg. (Colony no. S022).

Diagnosis. This species is distinct, and is easily distinguishable from other *Discoxenus* species by a combination of the following character states: antennal segment XI thick and approximately 1.4 times longer than wide (Fig. 150), elytra and abdominal tergites sparsely covered with yellow setae (Fig. 17).

Redescription. Head (Fig. 149) approximately 1.6 times wider than long. Antenna (Figs. 17, 18, 150) with segment I longer than other segments; segment II as long as segment III, with 3 macrosetae; segment III bowl shaped; segment IV transverse; segments V–VII wider than other segments; segments VIII–X gradually narrowed distally; segment VIII slightly wider than long; segments IX–X subquadrate; segment XI approximately 1.4 times longer than wide, widest around middle. Labrum (Fig. 151, left side) with anterior margin slightly concave at middle; median projection of apodeme short, with apex rounded; 4–5 lateral setae present in ventral view (Fig. 151, right side). Mandibles (Figs. 152, 153) covered with 15–20 pores. Left mandible (Fig. 152) with adoral margin moderately pointed around middle. Right mandible (Fig. 153) with a distinct tooth. Maxillary palpal segment III approximately 2 times longer than wide. Mentum (Fig. 154) approximately 2.8 times wider than long, covered with around 40 pores. Labium with prementum covered with approximately 6 pores.

Pronotum (Fig. 155) covered with approximately 48 macrosetae. Elytron (Fig. 156) transverse, sparsely covered with yellow setae, 14 macrosetae present on disc. Metaventrite approximately 1.6 times longer than mesoventrite.

Tergites (Fig. 17) and sternites (Fig. 18) sparsely covered with yellow setae. Tergite VIII (Fig. 157) with posterior margin rounded, 3 pairs of macrosetae present at posterior margin, with 2 pairs of macrosetae around middle. Macrochaetotaxy of abdominal tergites III–VIII = 6, 6, 6, 6, 6, 6. Sternites III–VII (Fig. 18) with 4–8 macrosetae at posterior margin.

Male. Sternite VIII (Fig. 158) with posterior margin slightly rounded, 3 pairs of macrosetae present at posterior margin, with 2 pairs of macrosetae at middle. Median lobe of aedeagus narrowed apically in ventral view (Fig. 161); basal capsule with distal crest large in lateral view (Fig. 134); apical lobe less than half as wide as basal capsule in lateral view (Fig. 162). Paramere (Fig. 163) with paramerite approximately 3 times wider than condylite; velar sac sclerite with 7–8 setae; apical lobe with 2 minute setae at apex.

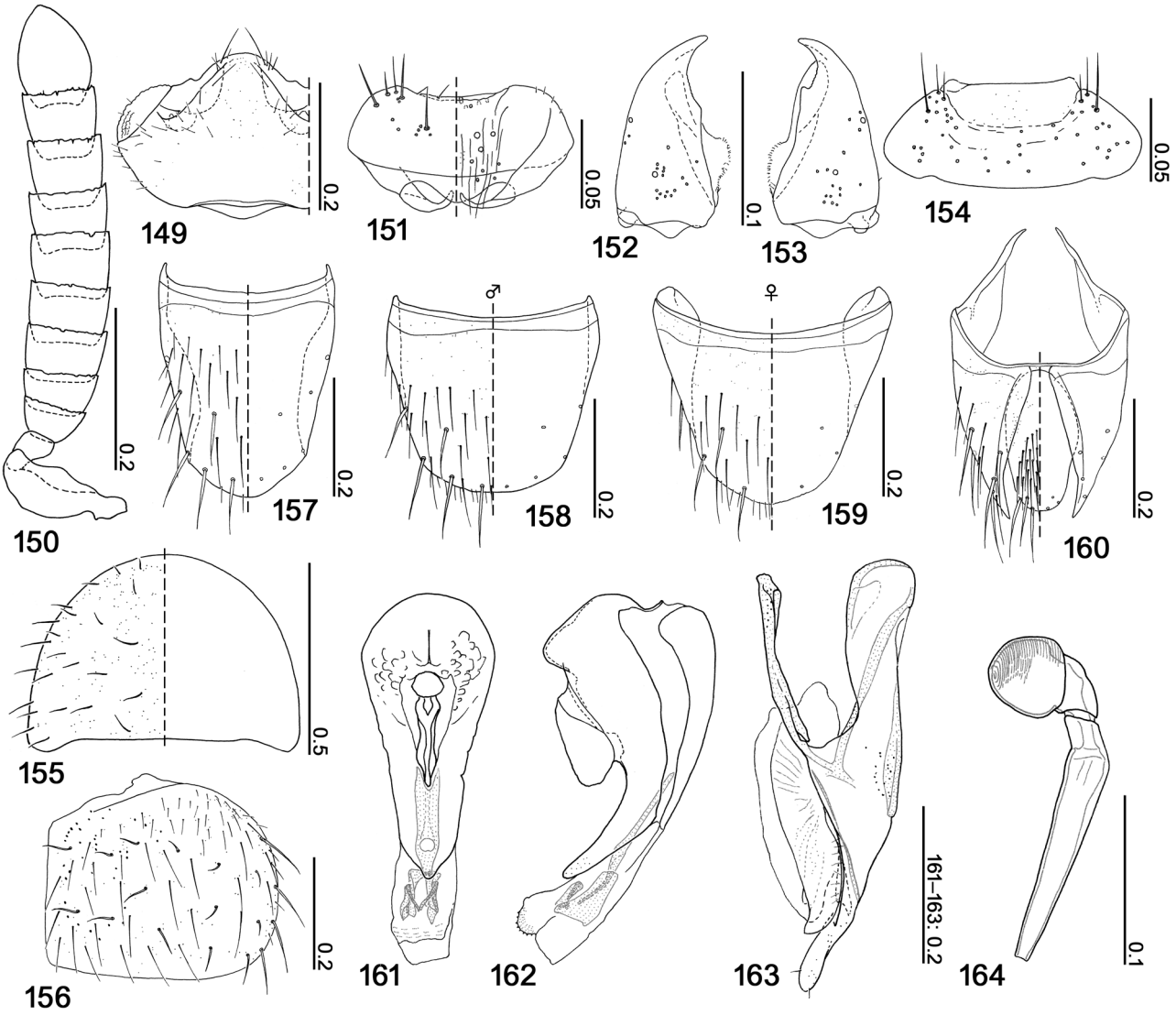
Female. Sternite VIII (Fig. 159) with 2 pairs of macrosetae at posterior margin and middle, respectively. Spermatheca (Fig. 164) with basal part more than 3 times longer than apical part.

Measurement. Body length = average 1.52 mm (1.46–1.58 mm, N = 10), pronotal length = average 0.52 mm (0.49–0.56 mm, N = 10), pronotal width = average 0.74 mm (0.71–0.78 mm, N = 10), elytral length = average 0.38 mm (0.36–0.41 mm, N = 10), elytral width = average 0.41 mm (0.39–0.44 mm, N = 10).

Host species. *Odontotermes proformosanus* Ahmad, 1965.

Comments. This species was originally described from Thailand (Kanao & Maruyama 2010). The close

morphological comparisons revealed that there are only a few morphological differences between the Thai and the Cambodian specimens: the elytra of the Cambodian specimens are slightly wider than that of the Thai specimens; the Cambodian specimens have a slightly broader distal crest of the median lobe. We, therefore, consider these populations as conspecific. In this paper, we have redescribed this species to include additional morphological details.



FIGURES 149–164. *Discoxenus katayamai*: 149. Head, 150. Antenna, 151. Labrum (left side = dorsal view, right side = ventral view), 152. Mandible, left, 153. Mandible, right, 154. Mentum, 155. Pronotum, 156. Elytron, right, 157. Tergite VIII, 158. Sternite VIII, male, 159. Sternite VIII, female, 160. Tergites IX and X, 161. Median lobe of aedeagus, ventral view, 162. Median lobe of aedeagus, lateral view, 163. Paramere, 164. Spermatheca.

Behavioural observations

All *Discoxenus* species described in this paper were found in the fungus gardens of their host termites (Figs. 165, 166), and their behaviours were observed with their host termites for 5–15 minutes in plastic case. During the observation, species-specific behaviours were not recognized. The beetles moved quickly or hid in the hollow fragments of the fungus gardens when nests were broken. Contact between the beetles and their host termites were frequently observed. Termites never attacked the beetles, instead ignored or palpated them. The beetles often raised their abdomens during contact with their hosts, and the termites touched the abdomens of beetles using their antennae. It seems that the termite antennations were made not for a particular part but for overall beetle abdomen. Kistner (1982) has also reported these behaviours.

FIGURES 165–166. Habitus. 165. *Discoxenus kohkongensis* **n. sp.**, 166. *D. lucidus* **n. sp.**

Discussion

Discoxenus species can be classified into two species groups, the *latiabdominalis* and the *assmuthi*. These species groups are clearly defined by several characteristics of their mouthparts and the male aedeagus. Especially, the strongly developed distal crest of the median lobe observed in the *assmuthi* species group may uniquely derived within *Discoxenus*. Species in the *latiabdominalis* group have a short distal crest, and this character states is a general feature of the tribe Aleocharini. The character state of distal crest is considered to support the monophyly of the respective species groups in *Discoxenus*.

An association with *Hypotermes* termites was only observed in a part of the Cambodian species that belong to the *assmuthi* species group. All other *Discoxenus* species distributed throughout Asia are associated with the *Odontotermes* termites (Wasmann 1904, 1916; Kistner 1982; Kanao *et al*. 2010). In the termite subfamily Macrotermitinae, *Odontotermes* and *Hypotermes* are known to have a sister relationships (Ohkuma *et al*. 2004). The *Discoxenus* rove beetles have possibly co-diversified with their host termites.

TABLE 1. The host relationships of the Cambodian *Discoxenus* species.

Species of *Discoxenus*	Host termites
The *latiabdominalis* species group	
D. latiabdominalis	*Odontotermes maesodensis*
D. cambodiensis	*O. maesodensis*
The *assmuthi* species group	
D. katayamai	*O. proformosanus*
D. phourini	*Hypotermes makhamensis*
D. kohkongensis	*H. makhamensis*
D. hirsutut	*H. makhamensis* *H.* cf. *xenotermitis*
D. minutus	*H. makhamensis* *H.* cf. *xenotermitis*
D. lucidus	*H. makhamensis* *H.* cf. *xenotermitis*
D. kakizoei	*H. makhamensis*

Discoxenus hirsutus, *D. minutus*, and *D. lucidus* were collected from the nests of two termite species, *H. makhamensis* and *H.* cf. *xenotermitis* (Table 1). During detailed morphological observations, no evident morphological differences were found between the rove beetle specimens collected from the nests of the two termite species. However, termitophilous rove beetles are often known to have species-specific relationships with their host termites (Kistner 1969). It is possible that *D. hirsutus*, *D. minutus*, and *D. lucidus* include cryptic species. Although the morphological character states and host relationships of *Discoxenus* species may provide insights of

the monophyly of the respective species groups and the phylogenetic relationships across species, data from western Asia are insufficient to draw further conclusions. It is highly possible that further species will be discovered. More comprehensive field surveys and molecular data are necessary to clarify species diversity and phylogenetic relationships within *Discoxenus*.

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References

Ahmad, M. (1965) Termites (Isoptera) of Thailand. *Bulletin of the American Museum of Natural History*, 131 (1), 1–114.

Haviland, G.D. (1898) Observations on termites; with descriptions of new species. *Journal of the Linnean Society (Zoology)*, 26, 358–442.
http://dx.doi.org/10.1111/j.1096-3642.1898.tb00405.x

Kanao, T., Maruyama, M. & Sakchoowong, W. (2010) Two new species of Aleocharinae (Coleoptera, Staphylinidae) found in the fungus gardens of *Odontotermes* termites (Isoptera, Termitidae, Macrotermitinae) in Khao Yai National Park, Thailand. *Zookeys*, 49, 77–86.
http://dx.doi.org/10.3897/zookeys.49.468

Kanao, T., Maruyam, M. & Rosli, H. (2011) A new genus of Compactopediina (Coleoptera: Staphylinidae) associated with *Longipeditermes* (Isoptera: Termitidae) in Peninsular Malaysia with a key to and phylogenetic analysis of all genera of the subtribe. *Insect Systematics & Evolution*, 42, 1–16.
http://dx.doi.org/10.1163/187631211X603605

Kistner, D.H. (1969) The Biology of Termitophiles. *In*: Krishna, K. & Weesner, F.M. (Eds.), *Biology of Termites. Vol. 1*. Academic Press, New York, pp. 525–557.

Kistner, D.H. (1970) New termitophiles associated with *Longipeditermes longipes* (Haviland). II. The genera *Compactopedia*, *Emersonilla*, *Hirsitilla*, and *Limulodilla*. *The New York Entomological Society*, 128, 17–32.

Kistner, D.H. (1982) A revision of the termitophilous genus *Discoxenus* with a study of the relationships of the genus and notes on its behavior (Coleoptera, Staphylinidae). *Sociobiology*, 7 (2), 165–186.

Maruyama, M. (2004) A permanent slide under a specimen. *Elytra*, 32 (2), 276.

Maruyama, M. (2006) Revision of the Palearctic species of the myrmecophilous genus *Pella* (Coleoptera, Staphylinidae, Aleocharinae). *National Science Museum Monographs*, 32, 1–207.

Ohkuma, M., Yuzawa, H., Amornsak, W., Sornnuwat, Y., Takematsu,Y., Yamada, A., Vongkaluang, C., Sarnthoy, O., Kirtibutr, N., Moparatnaraporn, N., Kudo, T. & Inoue, T. (2004) Molocular phylogeny of Asian termites (Isoptera) of the families Termitidae and Rhinotermitidae based on mitochondrial COII sequences. *Molecular phylogenetics and evolution*, 31, 701–710.
http://dx.doi.org/10.1016/j.ympev.2003.09.009

Sawada, K. (1972) Methodological research in the taxonomy of Aleocharinae. *Contribution from the Biological Laboratory Kyoto University*, 24, 31–59.

Seevers, C.H. (1957) A monograph on the termitophilous Staphylinidae (Coleoptera). *Fieldinana: Zoology*, 40, 1–334.

Wasmann, E. (1896) Neue Termitophilen und Termiten aus Indien. *Annali del Museo civico di storia naturale di Genova*, 2, 613–630.

Wasmann, E. (1904) Zur Kenntnis der Gaste der Treiberameisen und ihrer Wirthe am obern Congo nach den Sammlungen und Beobachyungen. *Zoologische Jahrbucher*, 7, 611–682.

Wasmann, E. (1912) Neue Beitrage zur Kenntnis der Termitophilen und Myrmekophilen. *Zeitschrift fur wissenschaftliche Zoologie*, 101, 70–115.

Wasmann, E. (1916) Wissenshaftliche Ergebnisse einer Forschungsreise nach Ostindien, V, Termitophile und Myrmekophile Coleopteren, gesammelt. *Abteilung fur Systematik, Geographie und Biologie der Tiere*, 39, 169–210.