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Two new *Incisitermes* (Isoptera: Kalotermitidae) species from the Caribbean Basin, genetic relationships with other regional *Incisitermes*, and synonymy of *Incisitermes tabogae* with *I. schwarzi*

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Abstract

Two new species of *Incisitermes* are described from the soldier and imago caste: *Incisitermes lisae* **sp. nov.** (Yucatan Region) and *Incisitermes mariae* **sp. nov.** (Venezuela and Trinidad and Tobago). *Incisitermes tabogae* (Snyder, 1924) is reduced to a junior synonymy of *Incisitermes schwarzi* (Banks, 1920), known from Florida, the West Indies, and the Caribbean basin mainland. The phylogenetic relationships of these three species are compared with other *Incisitermes* of the region.

Key words: Neotropics, taxonomy, drywood termites

Introduction

The termite genus *Incisitermes* Krishna, 1961 consists of 29 species (Constantino 2020) following the synonymy of *I. nigritus* (Snyder, 1946) into *I. platycephalus* (Light, 1933) by Scheffrahn (2020). *Incisitermes* is primarily a New World group (Scheffrahn 2019a), with eight species found in Australia, India, Pacific Oceana, the Philippines, and Taiwan (Emerson 1969, Krishna *et al.* 2013, Watson and Abbey 1993). Although all *Incisitermes* species nest in relatively dry wood such as dead branches and fence posts, *Incisitermes minor* (Hagen, 1858) endemic to the southeastern Nearctic, is by far the greatest structural pest owing to its low moisture requirement (Cabrera & Scheffrahn 2001).

Herein, is described *Incisitermes lisae* **sp. nov.** from the Yucatan region and *I. mariae* **sp. nov.** from Trinidad and Venezuela. We further place *I. tabogae* **syn. nov.** into *I. schwarzi* which is the most-wide ranging *Incisitermes* in the New World.

Materials and methods

Specimens reported in this study were collected by splitting infested wood with hatchets and aspirating the termites into vials containing 85% ethanol (Scheffrahn *et al.* 2018) and curated in the University of Florida Termite Collection (UFTC) in Davie, Florida (Scheffrahn 2019b). Laboratory microphotographs (Figs 1–8) were taken with a Leica M205C stereomicroscope controlled by Leica Application Suite ver. 3.0 montage software. Specimens were submerged in hand sanitizer (70% ethanol) inside a plastic Petri dish. The distribution map (Fig. 9) was produced using ArcGIS Pro Intelligence 3.0 software (Redlands, Calif.). Field photographs of live specimens (Figs 3, 5, 8) were taken with a Nikon Coolpix S7c digital camera. Terminology follows that of Krishna (1961).

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Molecular analysis

Ethanol (85%)-preserved specimens were allowed to dry on filter paper, and DNA was extracted using a salting-out procedure with in-house reagents (Sambrook & Russell 2001). Extracted DNA was resuspended in 50 µl of Tris: EDTA and stored at -20ºC. Polymerase chain reaction (PCR) of a 428 bp region of the mtDNA 16S rRNA gene was conducted using the primers LR-J-13007 forward: 5'-TTACGCTGTTATCCCTAA-3' (Kambhampati & Smith 1995) and LR-N-13398 reverse: 5'-CGCCTGTTTATCAAAAACAT-3' (Simon *et al.* 1994).

The PCR reactions were conducted with 1 µl of the extracted DNA (Szalanski *et al.* 2000), having a profile consisting of 35 cycles of 94ºC for 45 s, 46ºC for 45 s and 72ºC for 60 s. Amplified DNA from PCR was purified and concentrated with PES 30k filter centrifugal filter devices (VWR, Radnor, PA) according to the manufacturer's instructions. Samples were sent to Eurofins Geonomics (Louisville, KY) for direct sequencing in both directions. Consensus sequences were constructed using Geneious Prime software (Biomatters, Auckland, New Zealand). GenBank accession numbers are OR644510-OR644540 for unique sequences found in this study. DNA sequences were aligned using Geneious Prime with a 65% similarity cost matrix. The following 16S rRNA sequences of *Incisitermes* from GenBank were added to the analysis: *I. snyderi* (HM542459, HM542461, HM542463); *I. minor* (AB036685, HM542449, EF543146, HM542450); *I. schwarzi* (MH182488, MH182496, MH182491, MH182490, MH182489, MH182492, MH182485, MH193383, MH182486, MH182487, MH182484, MH182497, MH182495, MH182493); and *I. tabogae* (EU253745). Four additional mitochondrial 16S sequences from *Cryptocercus punctulatus* (AB425862), *Calcaritermes temnocephalus* (EU253743), *Glyptotermes nakajimai* (AB036689), and *Kalotermes flavicollis* (AY486437) were added as outgroup taxon sequences.

The general time reversible (GTR) model (Rodríguez *et al.* 1990) was determined as the best-fit model of evolution by jModeltest (Darriba *et al.* 2012) and implementing the Akaike information criterion (AIC) (Posada & Buckley 2004). A maximum likelihood (ML) analysis with 1000 bootstrap replicates was performed using PhyML (Guidon *et al.* 2010) as implemented in Geneious Prime, with all parameters optimized and the GTR model. Clades with bootstrap values (BV) ≥ 70% were considered significant and strongly supported (Hillis & Bull 1993). Bayesian analyses were performed using MrBayes v 3.2.6 (Huelsenbeck & Ronquist 2001) under the above model using Geneious Prime. Clades with BPP ≥ 95% were considered significant and strongly supported (Alfaro *et al.* 2003; Larget & Simon 1999). GenBank accession numbers for all taxa included in the analyses are shown after taxa names in Fig. 10, which was edited using iTOL v5 (Letunic & Bork 2021).

Results

Taxonomy

Incisitermes lisae Scheffrahn sp. nov.

Holotype. Small soldier from UFTC MX120.

Type locality. MEXICO. Yucatan: Hwy 295 km 15; 20.82460, -88.19358.

Paratypes. BELIZE: 5km S. Hopkins (costal mangroves); 16.81441, -88.26035; 10m asl; 1-Dec-2006; J Chase, J Mangold, J Nixon, R Scheffrahn coll.; UFTC BZ149; 2 small, 2 large soldiers, 3 alates. GUATEMALA: Saljalal; 16.66433, -89.67839; 234m asl; 31-May-2006; J Chase coll.; UFTC GUA335; 5 large soldiers. Road to Flores; 16.74441, -90.12638; 185m asl; 30-May-2006; B Bahder, T Nishimura coll.; UFTC GUA869, several large and small soldiers. MEXICO: Yucatan, Hwy 295 km 15; 20.82460 -88.19358; 21m asl; 7-Dec-1997; J Chase, R Mangold coll.; UFTC MX120, 3 small soldiers, one marked as holotype. Yucatan, Chichen Itza; 20.69, -88.59; 23m asl; 20-Jan-2001; J Chase, R Mangold coll.; UFTC MX234, 1 small soldier. Quintana Roo, Laguna Bacalar; 18.76662 -88.33867; 12m asl; 21-Jan-2001; J Chase, R Mangold coll.; UFTC MX245, 1 small, 2 large soldiers. Yucatan, 83 km E. Merida; 20.77625, -88.88070; 22m asl; 16-Jan-2003; J Chase, R Mangold coll; UFTC MX350, 1 small soldier. Yucatan, past Kinchil in mangroves; 20.89066, -90.01006; 5m asl; 18-Jan-2003; J Chase, R Mangold coll.; UFTC MX402, 5 small and 5 large soldiers, 4 alates. Same data: UFTC MX405, 6 small, 6 large soldiers. Yucatan, Hwy 261 along coast 16.5 km E. Progreso; 21.31277 -89.51048; 3m asl; 19-Jan-2003; J Chase, R Mangold coll.; UFTC MX428, 1 small soldier, several alates. Yucatan, Road to Yalsihon; 21.39084, -88.59289; 9m asl; 19-Jan-2003; J Chase, R Mangold coll.; UFTC MX449, 3 small, 1 large soldier, and 3 alates.

Material examined. Forty-three colonies mapped in Fig. 9 (collection data in Scheffrahn 2019).

Description

Large soldier (Fig. 1, Table 1). In dorsal view, vertex and labrum ferruginous orange. Frons anteriorly dark chestnut brown, posteriorly chestnut brown. Third antennal article darkest, sepia brown; first and second articles paler brownish, all distal articles pale brown. Mandibles pale chestnut brown at base, remainder black. Epicranial suture very faint. Eye spot whitish. Head capsule ferruginous orange; postmentum with darker anterior portion slightly darker compared to orange-yellow genae. Thoracic nota, abdominal dorsum, sternum, and legs pale yellow-whitish; tibiae and tarsi pale brownish, except for distinctly pigmented tibial spurs and claws. Pronotum with faint orange tinge.

FIGURE 1. Large soldier head of *Incisitermes lisae* **sp. nov**.

TABLE 1. Measurements of *Incisitermes lisae* **sp. nov.** large soldier.

Measurement in mm (n = 5 from 3 colonies[1])	Range	Mean ± S.D.
Head length to tip of mandibles	2.73–3.12	2.89 ± 0.18
Head length to postclypeus	1.94–2.37	2.13 ± 0.19
Head width, maximum	1.11–1.18	1.14 ± 0.027
Antennal carinae, outside span	1.05–1.13	1.08 ± 0.031
Head height, excluding postmentum	0.72–0.83	0.77 ± 0.054
Labrum, maximum width	0.31–0.36	0.34 ± 0.025
Left mandible length, tip to ventral condyle	0.98–1.10	1.04 ± 0.043
Postmentum, length in middle	1.46–1.68	1.59 ± 0.12
Postmentum, maximum width	0.46–0.49	0.47 ± 0.012
Postmentum, minimum width	0.16–0.23	0.20 ± 0.026

...*Continued on the next page*

TABLE 1. (Continued)

Measurement in mm (n = 5 from 3 colonies[1])	Range	Mean ± S.D.
Pronotum, maximum width	1.13–1.26	1.19 ± 0.066
Pronotum, maximum length	0.95–1.10	1.02 ± 0.060
Hind femur length	0.74–0.83	0.79 ± 0.039
Hind femur width	0.51–0.60	0.56 ± 0.039
Hind tibia length	0.85–0.93	0.90 ± 0.035
Total length	7.10–7.81	7.47 ± 0.33

[1]GUA869 (2), MX402 (1), MX405 (2).

In dorsal view head capsule elongate, with sides subparallel; eye spots slightly protuberant. Posterior corners of head evenly rounded and posterior margin subrectate. Mandibles stout with slight basal humps. Dentition as in Fig. 1; apical hook distinct. Frons with dense very faint granulation including frontal carinae and antennal socket carinae. Frontal ridge moderately distinct. Labrum medium-sized, linguiform, and with long terminal setae. Antennae with 10–12 articles, usually 11; relatively length formula 2<3>4=5. Third antennal article stoutly clavate, equal in length to articles four and five combined. About six medium-length setae on vertex. Frons with about ten short or very short setae. Anterior margin of pronotum distinct, noticeably incised at 150º, sides slightly convergent and posterior margin faintly emarginate.

In lateral and oblique view, head capsule strongly dorsoventrally flattened and planar. Frons slopes very indistinctly from vertex at 30º. Eye spots large, ovoid. Mandibles moderately curved upward. Hind femora strongly swollen.

Small soldier (Fig. 2, Table 2). Coloration similar to large soldier but slightly paler. Consequently, frons anterior ferruginous; its posterior and vertex ferruginous orange. Mandibular base pale chestnut brown, distally very dark chestnut brown. Frontal granulation finer than large soldier. Epicranial suture absent. Eye spots not protuberant. Mandibles slightly less stout. Head capsule about 2/3 length of large soldier but proportionally wider than large soldier with sides distinctly divergent compared to subparallel in large soldier. Frons and antennal carinae less pigmented and sclerotized than large soldier. Hind femora moderately swollen. All other characters comparable to large morph.

TABLE 2. Measurements of *Incisitermes lisae* **sp. nov.** small soldier.

Measurement in mm (n = 9 from 7 colonies[1])	Range Mean ± S.D.	Holotype	
Head length to tip of mandibles	2.17–2.37	2.28 ± 0.059	2.25
Head length to postclypeus	1.46–1.70	1.58 ± 0.072	1.58
Head width, maximum	1.03–1.23	1.00 ± 0.034	1.01
Antennal carinae, outside span	0.88–1.00	0.94 ± 0.038	0.96
Head height, excluding postmentum	0.65–0.72	0.69 ± 0.024	0.69
Labrum, maximum width	0.29–0.31	0.30 ± 0.008	0.29
Left mandible length, tip to ventral condyle	0.92–1.00	0.97 ± 0.032	1.00
Postmentum, length in middle	1.00–1.08	1.04 ± 0.027	1.05
Postmentum, maximum width	0.38–0.43	0.41 ± 0.018	0.43
Postmentum, minimum width	0.16–0.23	0.19 ± 0.021	0.21
Pronotum, maximum width	0.90–1.05	0.99 ± 0.049	1.01
Pronotum, maximum length	0.62–0.80	0.71 ± 0.061	0.72
Hind femur length	0.60–0.75	0.65 ± 0.045	0.65
Hind femur width	0.29–0.39	0.33 ± 0.029	0.33
Hind tibia length	0.69–0.74	0.71 ± 0.018	0.70
Total length	5.40–6.25	5.79 ± 0.29	5.40

[1]GUA869 (3), GUA335 (1), GU707 (1), MX120 (1), MX234 (1), MX225 (1), MX350 (1).

FIGURE 2. Small soldier head of *Incisitermes lisae* **sp. nov.**

Comparisons. The *I. lisae* soldiers are closest to those of *I. platycephalus* (Light, 1933) as both are similar in size and the head capsules of both are dorsoventrally flattened. The third antennal articles of *lisae* **sp. nov.** are shorter and the dentition of both mandibles is more pronounced than those of *I. platycephalus*. Unlike the eye spot in the large soldier of *I. lisae* **sp. nov.**, the eye spot in the large soldier of *I. platycephalus* is not protuberant.

Imago (Fig. 3, Table 3). In dorsal view, general color sepia brown, including sclerotized veins of fore wing; membrane pale brown without prismatic iridescence. Frons and vertex sepia brown except for tiny pale dots of setae seatings. Pronotum and abdominal tergites sepia brown. Thoracic nota with distinct median line. Antennae, labrum and legs pale brown. Abdominal sternites pale brown. Tibiae lightly paler than femora. Head shortly oval; cranial sutures absent. Eyes very small for genus, moderately protruding, slightly elongate and rectate along antennal fossae. Ocelli small, oval, touching eyes. Antennae with 1316 articles, usually 14–15. Formulae mostly 2<3>4=5, also variable because elongation of 3rd article indistinct. Pronotum with medium and long setae along lateral margins. Pronotal anterior margin evenly shallowly concave, posterior margin faintly emarginate, sides slightly convex. Crossbar mark and midline of pronotum distinct. Fore wing radius reaching costal margin about 1/3 of wing length from suture; radial sector with 5–7 branches. Arolia small.

Comparisons. Among dark *Incistermes* imagos, *I. lisae* **sp. nov.** is closest to *I. platycephalus* although the former has a slightly lighter pigment. *Incisitermes playcephalus* lacks light spots at seating of setae on vertex. Both are similar in size.

Etymology. Species name "lisae" is given for the younger daughter of RHS, Lisa.

Comments. *Incisitermes lisae* **sp. nov.** has only been collected from dead wood mostly in lowland forests of the Yucatan (3–23 m asl). In Guatemala, *I. lisae* **sp. nov.** was collected at elevations up to 272 m asl. A few alates were observed in flight on a sunny morning of December 1, 2006, in a mangrove habitat in Belize.

FIGURE 3. Dorsal view of the imago head (left) and habitus (right) of *Incisitermes lisae* **sp. nov.**

TABLE 3. Measurements of *Incisitermes lisae* **sp. nov.** alate.

Measurement in mm (n = 9, 6 males, 3 females from 4 colonies[1])	Range	Mean ± S.D.
Head length with labrum	1.01–1.12	1.09 ± 0.055
Head length to postclypeus	0.77–0.90	0.84 ± 0.044
Head width, maximum at eyes	0.83–0.93	0.88 ± 0.034
Eye diameter with sclerite, maximum	0.22–0.26	0.25 ± 0.016
Eye to head base, minimum from sclerite	0.11–0.13	0.12 ± 0.006
Ocellus diameter, maximum	0.08–0.11	0.09 ± 0.007
Pronotum, maximum width	0.75–0.90	0.83 ± 0.043
Pronotum, maximum length	0.57–0.69	0.63 ± 0.033
Total length with wings	7.10–8.52	7.90 ± 0.48
Total length without wings	4.69–5.82	5.33 ± 0.49
Fore wing length from suture	4.83–5.54	5.29 ± 0.21
Fore wing, maximum width	1.32–1.38	1.36 ± 0.026

[1]BZ149 (1♂), MX402 (1♂, 1♀), MX428 (1♂, 2♀), MX449 (3♂).

Incisitermes mariae Scheffrahn sp. nov.

Holotype. Soldier from UFTC TT1169.

Type locality. TRINIDAD AND TOBAGO: Creek trail NW of Pax Guest House; 10.7, -61.4.

Paratypes. TRINIDAD AND TOBAGO: Creek trail NW of Pax Guest House; 10.7, -61.4; 320m asl; 25-May-2003; J Chase, J Křeček J Mangold, B Maharajh, R Scheffrahn, J Warner coll.; UFTC TT1169, 4 soldiers (1 marked holotype), 1 alate. VENEZUELA: Falcon, Carizalito; 11.14170, -69.74407; 1156m asl; 28-May-2008; P Ban, J Chase, J Křeček J Mangold, B Maharajh, T Myles, T. Nishimura, R Scheffrahn coll.; UFTC VZ870, 1 soldier. Same data: UFTC VZ881, 2 alates. Same data: UFTC VZ882, 1 soldier. Same data: UFTC VZ882, 1 soldier. Lara, Churaguara; 10.67215, -69.24857; 341m asl: 28-May-2008; same collectors as VZ882; UFTC VZ984, 1 soldier.

Description

Soldier (Figs 4–5, Table 4). Apparently monomorphic, very small. In dorsal view, head capsule grading from pale ferruginous anterior to pale yellow posterior. Two proximal antennal articles yellow-orange, third antennal article slightly darker, concolorous with mandible bases. Pronotum pale yellow. Mandible base dark castaneous, distally almost black. Epicranial suture a faint line. Eye spots whitish, borders poorly defined. Postmentum pale ferruginous, genae yellowish. Head capsule glossy, without superficial sculpturing.

FIGURE 4. Soldier head of *Incisitermes mariae* **sp. nov.**

TABLE 4. Measurements of *Incisitermes marie* **sp. nov.** soldier.

Measurement in mm (n = 6 from 4 colonies[1])	Range	Mean ± S.D.	Holotype
Head length to tip of mandibles	1.90–2.07	1.98 ± 0.064	1.98
Head length to postclypeus	1.26–1.36	1.33 ± 0.037	1.31
Head width, maximum	0.75–0.85	0.79 ± 0.034	0.75
Antennal carinae, outside span	0.72–0.82	0.76 ± 0.034	0.72
Head height, excluding postmentum	0.53–0.65	0.59 ± 0.043	0.57
Labrum, maximum width	0.26–0.29	0.28 ± 0.013	0.29
Left mandible length, tip to ventral condyle	0.87–0.98	0.91 ± 0.052	0.90
Postmentum, length in middle	0.83–0.92	0.87 ± 0.029	0.85
Postmentum, maximum width	0.35–0.39	0.37 ± 0.015	0.36
Postmentum, minimum width	0.15–0.18	0.16 ± 0.013	0.16
Pronotum, maximum width	0.78–0.87	0.82 ± 0.032	0.80
Pronotum, maximum length	0.52–0.60	0.57 ± 0.029	0.59
Hind femur length	0.56–0.64	0.59 ± 0.030	0.57
Hind femur width	0.20–0.25	0.23 ± 0.019	0.23
Hind tibia length	0.57–0.62	0.60 ± 0.017	0.59
Total length	4.04–5.23	4.60 ± 0.44	4.77

[1]TT1169 (3), VZ870 (1), VZ882 (1), VZ 984(1).

In dorsal view, head capsule narrowly elongate with parallel sides or very slightly convergent posteriorly; posterior margin faintly concave. Mandibles slender, long, with very faint basal humps and 60º apical curvature. A few setae on vertex and frons only. Labrum distinct, subtrapezoidal. Antennae with 9–10 articles, usually 10, their relatively length formula 2<3 4=5. Third antennal article with conspicuously long stem and widely clavate distally;

equal in length to next three articles. Pronotum anterior margin evenly and shallowly concave, not incised; sides slightly convex and posterior margin subrectate.

In lateral and oblique view, head capsule moderately dorsoventrally flattened. Frons sloping about 20º from vertex. Rim of frons forming very faint biconvexity. Eyespots widely oval. Left mandible moderately curved upward compared to right.

Comparisons. The *I. mariae* **sp. nov.** soldier is the smallest known congener in all measured parameters. *Incisitermes mariae* **sp. nov.** is closest to *I. rhyzophorae* Hernandez, 1994, but *I. mariae* **sp. nov.** differs in having a thinner stem of the third antennal article. The anterior margin of the *I. rhyzophorae* pronotum is very deeply incised while in *I. mariae* **sp. nov.** the anterior pronotal margin is shallowly concave.

Imago (Fig. 5, Table 5). In dorsal view, general color dark sepia brown, concolorous with sclerotized veins of fore wing; membrane pale brown without prismatic iridescence. Frons and vertex dark sepia brown except for tiny pale basal socket of setae. Pronotum and abdominal tergites dark sepia brown. Thoracic nota with rather indistinct median line. First four antennal articles very pale brown, distal articles dark sepia brown. Labrum pale brown. Legs, including femora dark sepia brown, tibiae and tarsi contrastingly paler. Abdominal sternites pale brown, terminally grading to dark sepia brown. Head elongate and rather subquadrate; cranial sutures absent. Eyes very small, moderately noticeably protruding, slightly subtriangular. Ocelli small, shortly oval, very narrowly adjacent to eyes. Antennae with 13–15 articles (only 2 specimens). Formulae 2<3>4=5; elongation of 3rd article slight. Anterior margin of pronotum very shallowly incised, posterior margin similarly emarginated, sides subparallel. Crossbar mark and midline of pronotum indistinct. Fore wing radius reaching costal margin about 1/5 of wing length from suture; radial sector with 7–8 branches; first branch of radial sector precedes intersection of radius at costal margin. Arolia very small.

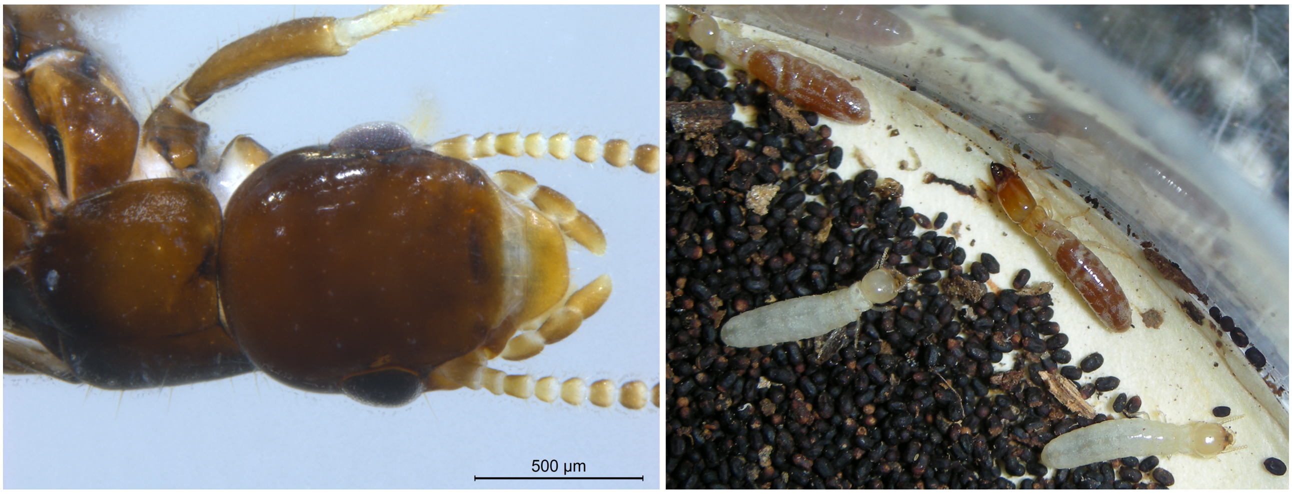

FIGURE 5. Dorsal view of the imago head (left) and habitus (right) of *Incisitermes mariae* **sp. nov.**

TABLE 5. Measurements of *Incisitermes marie* **sp. nov.** alate.

Measurement in mm (n = 2 from one colony[1])	Range	Mean ± S.D.
Head length with labrum	1.01–1.05	1.03 ± 0.023
Head length to postclypeus	0.82–0.83	0.83 ± 0.012
Head width, maximum at eyes	0.82–0.87	0.84 ± 0.035
Eye diameter with sclerite, maximum	0.27–0.28	0.27 ± 0.006
Eye to head base, minimum from sclerite	0.10–0.11	0.11 ± 0.012
Ocellus diameter, maximum	0.07–0.08	0.08 ± 0.003
Pronotum, maximum width	0.75–0.82	0.78 ± 0.046
Pronotum, maximum length	0.57–0.64	0.60 ± 0.046
Total length with wings	8.09–8.24	8.17 ± 0.10
Total length without wings	5.11–5.25	5.18 ± 0.10
Fore wing length from suture	5.40–5.54	5.47 ± 0.10
Fore wing, maximum width	1.25–1.29	1.27 ± 0.023

[1]VZ881 (1♂, 1♀).

Comparisons. The imago of *I. mariae* **sp. nov.** is the smallest of the darkly pigmented *Incisitermes* species and indistinguishable from *I. rhyzophorae* however, the latter is known only from Cuba and The Bahamas.

Etymology. Species name "mariae" is given for the older daughter of RHS, Mary.

Comments. *Incisitermes mariae* **sp. nov.** has been only been collected from dead wood in mountainous forests between 320 m and 1156 m asl. In both Trinidad and Venezuela, mature alates were collected from their galleries in late May, suggesting late spring flights.

Additional taxonomic changes

Incisitermes schwarzi (Banks, 1920), Figs. 6–8

= *tabogae* (Snyder, 1924), **syn. nov.** (4-5), imago from Taboga Island, Panama. Snyder (1926), 8, soldier from Taboga Island, Panama. Nickle and Collins (1992) figs 13.47, 13.48, soldiers.

Material examined. One thousand five hundred seventy-five colonies mapped in Fig. 9 (collection data in Scheffrahn 2019).

FIGURE 6. Large soldier head of *Incisitermes schwarzi*.

FIGURE 7. Small soldier head of *Incisitermes schwarzi*.

FIGURE 8. Dorsal view of the imago head (left) and habitus (right) of *Incisitermes schwarzi* .

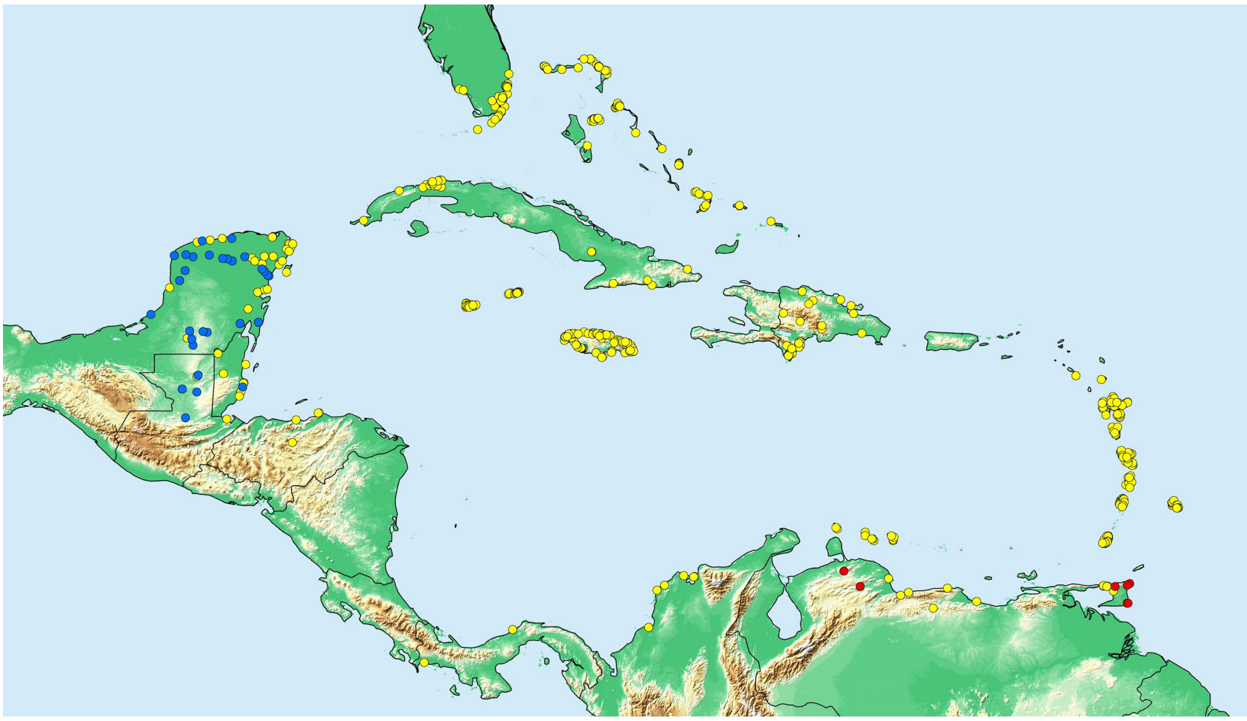

FIGURE 9. Distribution of *Incisitermes lisae* **sp. nov.** (blue dots), *I. mariae* **sp. nov.** (red dots), and *I. schwarzi* (yellow dots).

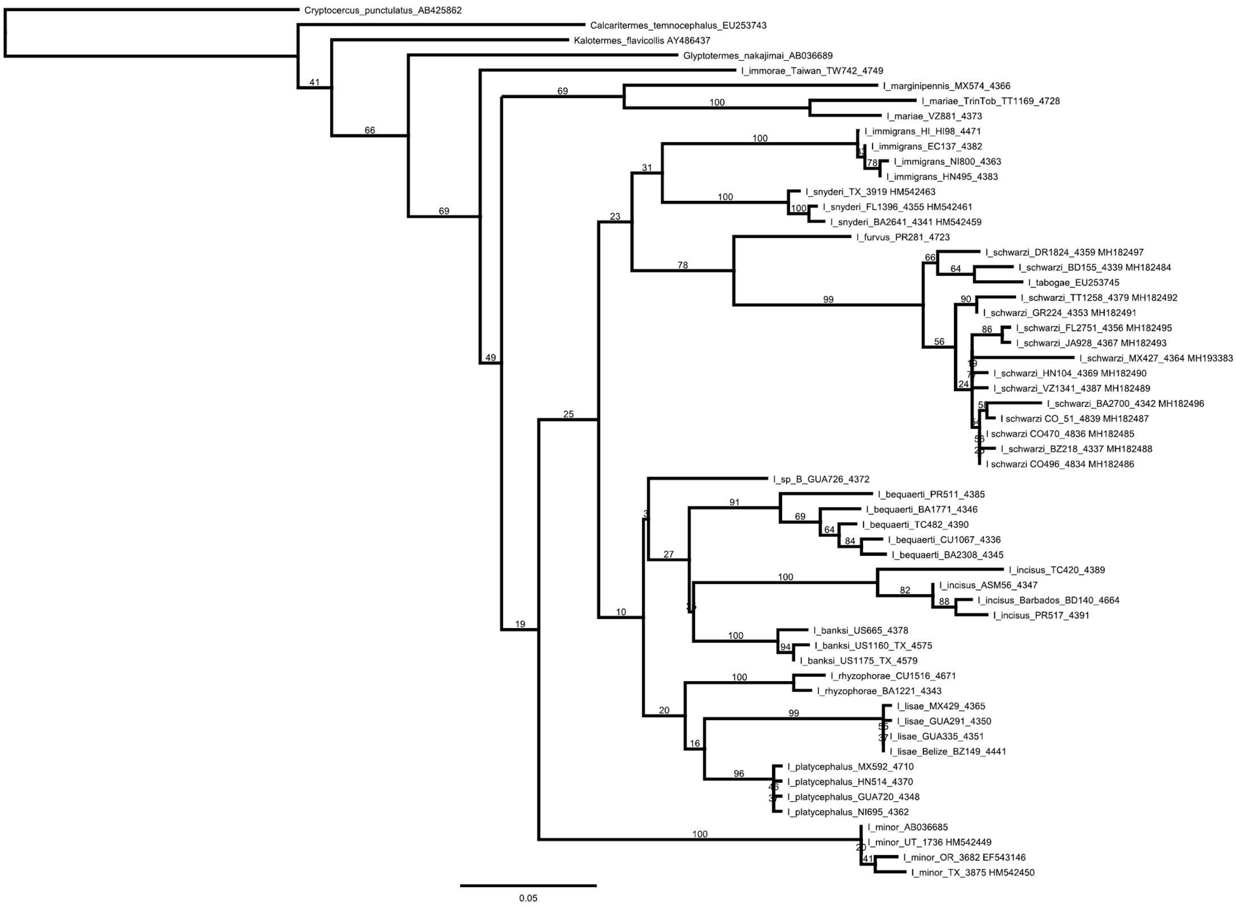

FIGURE 10. Phylogenetic tree (ln = 3840.5) of *Incisitermes* taxa, based on 16S rRNA sequences constructed using the PhyML maximum likelihood method with 1000 bootstrap replications. Bootstrap values ≥ 50% from PhyML analyses are shown. Thickened branches indicate Bayesian posterior probabilities ≥ 95%. The two new species of *Incisitermes* are bolded. GenBank accession numbers are given after taxon names.

Justification of synonymy

Banks (1920) described the alate and two soldier morphs of *Incisitermes schwarzi* from Florida and western Cuba. When Snyder (1924, 1926) described *I. tabogae* from Panama, he apparently did not compare the specimens to *I. schwarzi*, probably under the assumption that they had distant allopatric distributions. Nickle and Collins (1992) illustrated both *I. tabogae* soldier morphs from Panama. Although the descriptions and illustrations of both species were identical, the allopatric separation of *I. tabogae* was perpetuated by Scheffrahn *et al.* 1994 (Cayman Islands, Dominica, Guadeloupe, and Martinque); Scheffrahn *et al.* 2003 (Trinidad and Tobago); and Scheffrahn *et al.* 2005 (Nicaragua). The perpetuation began to unravel when Strassert *et al.* (2012) discovered a new lineage of endosymbiotic *Actinobacteria* attached to *Trichonympha* protists from the hindguts of *Incisitermes*. They found '*Candidatus* Ancillula trichonymphae' on both *I. schwarzi* from Florida and *I. tabogae* from Belize (Becker *et al.* 1972). Boscaro *et al.* (2017) found sister species of *Trichonympha* in *I. tabogae* and *I. schwarzi* inferring that the former species was a junior synonym of the latter. It is now clear that *I. schwarzi* is a dominant and widespread species from southern Florida to the northern coast of South America.

Molecular analysis

Molecular phylogeny (Fig. 10) provided support for several clades. Relative to all of the other *Incisitermes* species studied, *I. minor* formed the most distal taxon. One of the new species described in this paper, *I. mariae* **sp. nov.** formed a distinct clade with *I. marginipennis* (Snyder, 1922). *I. immigrans* (Snyder, 1922) also formed a distinct clade. All of the other *Incisitermes* taxa formed two distinct groups. The first group consisted of *I. schwarzi,* and *I. furvus* Scheffrahn, 1994. The second group consisted of *I. snyderi* (Light, 1933), being the most distal, followed by *I. bequaerti* (Snyder, 1929), *I. banksi* (Snyder, 1920), and *I. incises* (Silvestri, 1901). The newly described species, *I. lisae* **sp. nov.**, formed a clade with *I. platycephalus*, which formed a sister group with *I. rhyzophorae*.

A recent study by Buček *et al.* (2022) on the molecular phylogeny of drywood termites using entire mtDNA genomic sequences of drywood termites, had five *Incisitermes* in it, of which, four were in our study. They found *I. incisus* forming a clade with *I. rhyzophorae*, and *I. snyderi* with *I. schwarzi*. The relationship of *I. schwarzi* relative to *I. snyderi* that we observed has also been observed by Austin *et al.* (2012) and Janowiecki *et al.* (2020) using the same mtDNA 16S genetic marker. Another study by Ide *et al.* (2016) on *Incisitermes* species in Japan used seven of the same species as our study for their mtDNA 16S phylogenetic tree. Results from their phylogenetic analysis were similar to ours, with *I. minor* forming the most distal clade relative to the other taxa. As with our study, they found an *I. tabogae* sample from GenBank (accession number EU253745) to fall in with the *I. schwarzi* clade. This provides further evidence that this *I. tabogae* sample is actually *I. schwarzi*.

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