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Expanded range of *Nasutitermes callimorphus* Mathews, 1977 (Isoptera: Termitidae: Nasutitermitinae), comparison with *N. corniger* (Motschulsky, 1855) and *N. ephratae* (Holmgren, 1910), and synonymy of *N. dasyopsis* Thorne, 1989 into *N. nigriceps* (Haldeman, 1854)

RUDOLF H. SCHEFFRAHN[1,*], YVES ROISIN[2], ALLEN L. SZALANSKI[3], JAMES W. AUSTIN[4] & EDOUARD DUQUESNE[2]
[1]*Fort Lauderdale Research and Education Center, University of Florida, Institute of Food and Agricultural Sciences, 3205 College Avenue, Davie, Florida, 33314, USA*
rhsc@ufl.edu; *https://orcid.org/0000-0002-6191-5963*
[2]*Behavioral and Evolutionary Ecology, CP 160/12, Université Libre de Bruxelles, Av. F.D. Roosevelt 50, B - 1050 Brussels, Belgium*
Yves.Roisin@ulb.be; *https://orcid.org/0000-0001-6635-3552*
Edouard.Duquesne@ulb.be; *https://orcid.org/0000-0003-2105-9434*
[3]*Department of Entomology and Plant Pathology, 217 Plant Science Bldg., University of Arkansas, Fayetteville, AR 72701, USA*
aszalan@uark.edu; *https://orcid.org/0000-0002-5346-2036*
[4]*BASF Corporation, 26 Davis Drive, P.O. Box 13528, Research Triangle Park, NC 27709, USA*
james.austin@basf.com; *https://orcid.org/0000-0002-0780-4576*
[*]*Corresponding author*

Abstract

The imago of *N. callimorphus* is described for the first time. *Nasutitermes callimorphus* occurs from Mexico to Paraguay. *Nasutitermes callimorphus* is smaller in all measurements but generally resembles its widely distributed sympatric congeners, *N. corniger* (Motschulsky, 1855) and *N. ephratae* (Holmgren, 1910). Molecular phylogenetic analysis of a portion of the mitochondrial 16S rRNA gene and the COII mtDNA marker revealed that *N. callimorphus* forms a distinct clade using both maximum parsimony and maximum likelihood analysis. Unlike *N. corniger* and *N. ephratae*, *N. callimorphus* does not build epigeal or arboreal carton nests. We further regard *N. dasyopsis* Thorne, 1989 as a junior synonym of *N. nigriceps* (Haldeman, 1854).

Key words: taxonomy, molecular genetics, Neotropics, *Nasutitermes corniger, N. dasyopsis*, *N. ephratae, N. nigriceps*

Introduction

Nasutitermes callimorphus Mathews, 1977 was described from two collections of soldiers and workers near Xavantina, Mato Grosso, Brazil (Mathews 1977). Mill (1983) recorded the second encounter of *N. callimorphus* from Roraima State followed by four more Brazilian localities in Pará and Amazonas states (Constantino & Cancello 1993). As recently as 2023, *N. callimorphus* was reported in Acre State, Brazil (Ferreira *et al.* 2023). Outside of Brazil, *N. callimorphus* has been recorded from Ecuador (Mertl *et al.* 2012), French Guiana (Roy *et al.* 2014) and Colombia (Casalla Daza & Korb 2019).

During a stay in Panama in 1991, Y.R. collected soldiers and workers of a *Nasutitermes* sp. from foraging galleries in leaf litter and on a standing tree. These foragers closely resembled those of *N. corniger* (Motschulsky, 1855), however, the former were proportionally smaller. About the same time, J.P.E.C. Darlington (unpubl. obs.) collected this species in Trinidad. She noted an absence of an arboreal nest structure but a striking similarity to small *N. corniger* foragers. In 1996, the first physogastric queen of the same *Nasutitermes* sp. was collected in Tobago, and in 1999 for the first time, many winged imagos were taken on the island of Guadeloupe also in the absence of arboreal or epigeal carton nests. Several samples of the same species, then labeled *Nasutitermes* sp.1, were collected in Panama again during the IBISCA project (Roisin *et al.* 2006). Other samples more recently collected in French

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Guiana and Guadeloupe by the Brussels team also corresponded to this species, mentioned as *Nasutitermes* sp.G in Bourguignon *et al.* (2011).

Recently, R.H.S. reviewed the description of the soldier of *N. callimorphus* (Mathews 1977) and realized that the Panamanian and Trinidadian *Nasutitermes* noted above matched the *N. callimorphus* soldier description. Reexamination of the material in the University of Florida Termite Collection (UFTC) yielded numerous additional samples of *N. callimorphus* from the Neotropics. Although the soldiers are superficially similar, comparison of the *N. callimorphus* imagos with those of *N. corniger* and *N. ephratae*, show that the former is distinctly different from the latter two. We herein redescribe *Nasutitermes callimorphus* based on imago and soldier morphology and DNA sequence data. We compare all three of these widely distributed Neotropical *Nasutitermes* species. We also compare the description of *N. dasyopsis* Thorne, 1989 with soldiers and sequence data with *N. nigriceps* (Haldeman, 1854) and reduce the former to synonymy.

Materials and Methods

Specimens reported in this study were collected by aspirating the termites into vials containing 85% ethanol and curated in the UFTC in Davie, Florida (Scheffrahn 2019) and in the Free University of Brussels termite collection (FUBTC) curated by Y.R. Laboratory. Microphotographs 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 worker enteric valve armatures were prepared for photography by removing the entire worker 2nd proctodeal segment (P2) section in ethanol. Food particles were expelled from the P2 by gentle pressure manipulation. The P2 sections were submerged in a droplet of PVA medium (CMCP-9 Low viscosity mountant, Polysciences Inc.) which eased muscle detachment and removal. The remaining P2 cuticle was longitudinally cut, splayed open, and mounted on a microscope slide. The exposed EVAs were photographed with a Kern ODC832 camera mounted on a Kern OBN135 microscope. The distribution maps (Fig. 13) were produced using ArcGIS Pro Intelligence 3.0 software (Redlands, Calif.). The field photographs were taken with a Nikon Coolpix S7c digital camera.

For the 16S marker, DNA was extracted per Szalanski *et al.* (2004) from workers of two colony samples of *Nasutitermes callimorphus,* one *N. nigriceps,* one *N. rippertii* (Rambur, 1842), and one *N. gaigei* Emerson, 1925 collected from the greater Caribbean Basin. Polymerase chain reaction was applied using the primers LR-J-13007 (5'-TTACGCTGTTATCCCTAA-3') (Kambhampati and Smith 1995) and LR-N-13398 (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. For the COII marker, DNA was extracted from soldiers' heads of *N. callimorphus* found in French Guiana and Guadeloupe using NucleoSpin®Tissue (Macherey-Nagel). DNA amplification was done using the kit BigDye V3.1 (Applied Biosystems™) with two primers ModAtLeu (CAG ATA AGT GCA TTG GAT TT, Miura *et al.*, 2000) and B-tLys (GTT TAA GAG ACC AGT ACT TG, Simon *et al.*, 1994). The amplification was performed on an Eppendorf Mastercycler x50S thermocycler. Once purified, the sequencing was performed on a capillary sequencer (DNA Analyser 3730, Applied Biosystems™). Sequences were then all corrected and aligned using CodonCode Aligner (CodonCode Corporation).Consensus sequences were constructed using Geneious Prime software (Biomatters, Auckland, New Zealand). GenBank accession numbers are PP816771 to PP816781 for the 16S sequences unique to this study, and PP865430 to PP865437 for the COII sequences. DNA sequences were aligned using Geneious Prime with a 65% similarity cost matrix. For the 16S phylogenetic analysis, additional *Nasutitermes* sequences were obtained from Scheffrahn *et al.* (2005), and from GenBank (Fig. 11). Two additional mitochondrial 16S sequences from *Mastotermes darwiniensis* Froggatt (AY380302) and *Zootermopsis angusticollis* (Hagen) (U50778) were added as outgroup taxa sequences. For the COII phylogenetic analysis, additional *Nasutitermes* sequences were obtained from GenBank (Fig. 12). Four additional mitochondrial COII sequences from *Mastotermes darwiniensis* (FJ806882), *Zootermopsis angusticollis* (M83968), *Grigiotermes hageni* (Snyder & Emerson) (KT215794), and *Termes hispaniolae* (Banks) (FJ806886) were added as outgroup taxa sequences.

For both genetic markers, 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 Figs. 11 and 12, which were edited using iTOL v5 (Letunic & Bork 2021).

To determine the potential distribution of *N. callimorphus*, a species distribution model was performed using Biomod2 version 4.2–4 package (Thuiller *et al.*, 2009) in the software R version 4.1.2 (R Core Team, 2021). The occurrences used are the same as shown in Supplementary Table 1. The detailed method for the pseudo-absences making, the bioclimatic variables choice and the modeling is the same as used in Duquesne and Fournier (2024). Here, four variables were chosen: the best three bioclimatic variables (bio5, bio7, bio16) from Worldclim (Fick and Hijmans, 2017) and an elevation layer (median-aggregated, Amatulli *et al.*, 2018). The ensemble model had an excellent evaluation of 0.971 for TSS and 0.879 for ROC and the resulting ensemble projection can be seen in Fig. 14.

TABLE 1. MEASUREMENTS OF *NASUTITERMES CALLIMORPHUS* IMAGO.

Measurement, mm (n = 9 males and 8 females*)	**Range**	**Mean ± S.D.**
Head length with labrum	1.24–1.36	1.30 ± 0.038
Head length to postclypeus	0.78–0.88	0.83 ± 0.032
Head width, maximum at eyes	1.08–1.13	1.11 ± 0.016
Head height without postmentum	0.47–0.56	0.52 ± 0.024
Eye diameter, maximum	0.33–0.34	0.33 ± 0.0040
Eye to head base, minimum	0.07–0.11	0.09 ± 0.011
Ocellus diameter, maximum	0.11–0.12	0.11 ± 0.0046
Eye sclerite to ocellus, minimum	0.07–0.10	0.09 ± 0.011
Pronotum length, maximum	0.44–0.52	0.49 ± 0.030
Pronotum width, maximum	0.74–0.85	0.80 ± 0.037
Total length with wings	9.31–10.77	9.97 ± 0.55
Total length without wings	4.66–6.52	5.59 ± 0.46
Fore wing length from suture	7.58–9.04	8.29 ± 0.46
Fore wing width, maximum	2.27–2.60	2.45 ± 0.095
Hind tibia length	1.24–1.31	1.29 ± 0.022

*From five localities from Guadeloupe, Trinidad, and Tobago.

Nasutitermes callimorphus **Mathews, 1977**

"*N. indistinctus*" [nomen nudum] page 161, fig. 110 (Mathews 1977) should read *Nasutitermes callimorphus* (Constantino and Cancello 1999).

IMAGO (Fig. 1A, B; Table 1). Head capsule dark sepia brown with light brown postclypeus, genae, and paler spotting at all setal insertions; fontanelle slit whitish. Only faint posterior remnants of epicranial suture visible. Compound eyes black, ocelli glossy tan. Numerous pale setae of different lengths on head capsule, pronotum, and postclypeus; few on labrum. Pronotum pale sepia brown, distinctly paler than head capsule and with pale T-shaped mark; pronotum more distinctly and more densely pimpled setal insertions than on head capsule. In lateral view, vertex and anterior occiput slightly bulging; eyes subcircular and medium sized. In dorsal view, head capsule trapezoidal; ocelli small; eyes and ocelli separated by distance about maximum diameter of ocelli. Head capsule, pronotum, and wing scales densely pilose with long setae. Antennae with 15 articles; relative length formula 2=3<4=5. In dorsal view, pronotum narrow, subtriangular; anterior margin rectate and with minute median indentation; pronotum sides distinctly convergent; anterior margin of pronotum barely elevated, elevation posteriorly delimited with short dark line on each side of T-shape mark. Pronotum posterior margin half width of anterior margin and slightly emarginate or concave. Mandible morphology typical for *Nasutitermes* (Ahmad 1950).

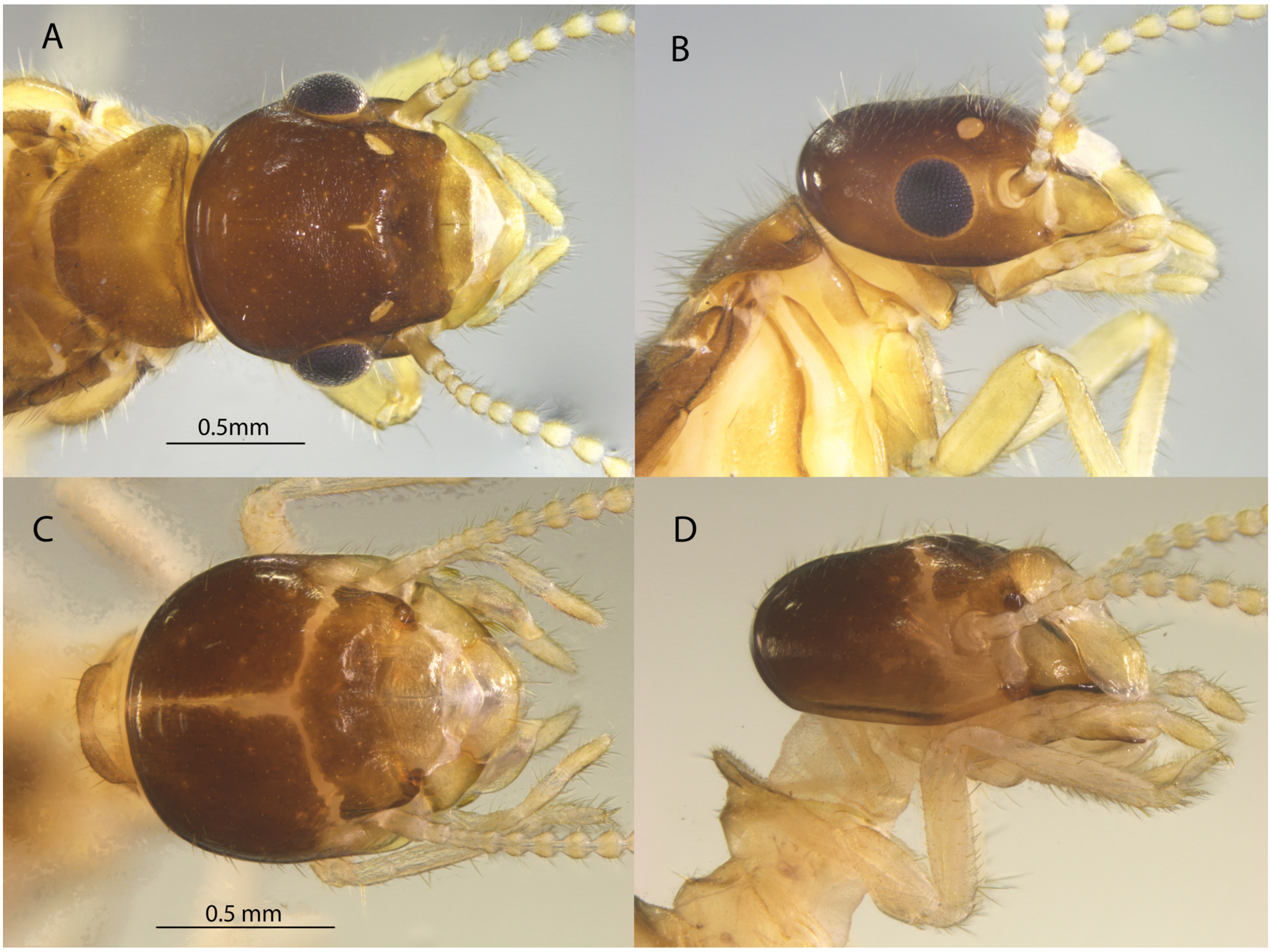

FIGURE 1. *Nasutitermes callimorphus* from Guadeloupe (GU499). Imago head (dorsal A, lateral B) and major worker head (dorsal C, lateral D).

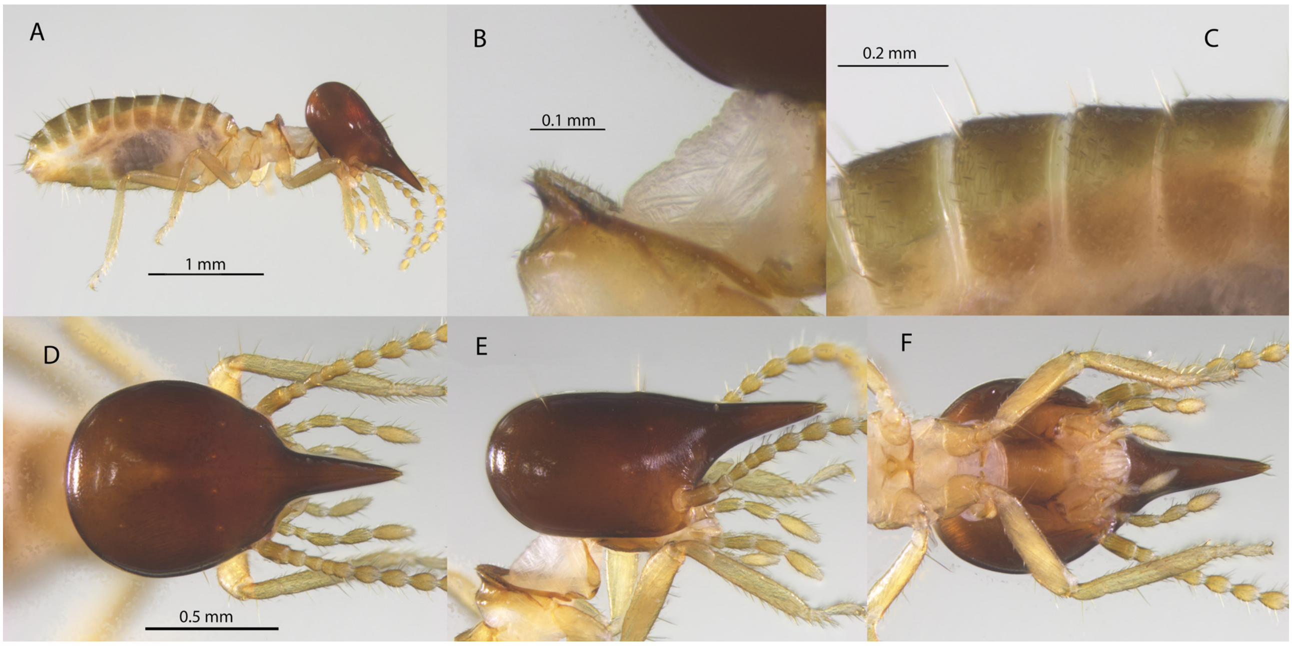

FIGURE 2. *Nasutitermes callimorphus* soldier from Peru (PU361). Habitus (A); lateral view of pronotum (B); tergites (C); and dorsal, lateral, and ventral views of head capsule (D, E, and F, respectively).

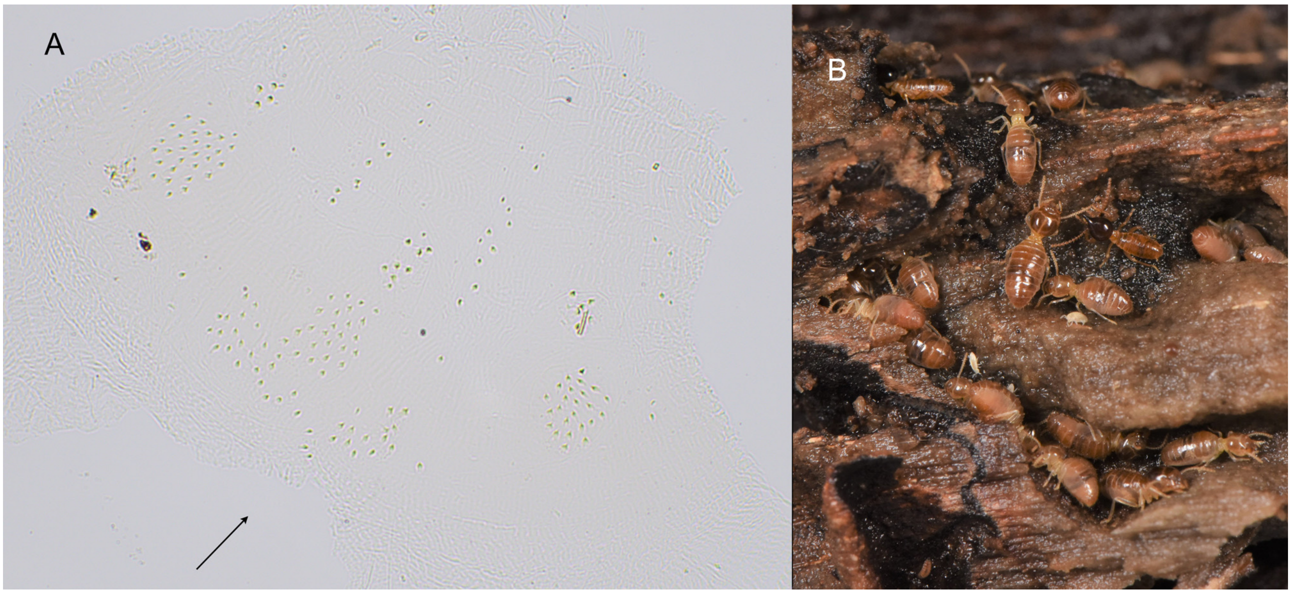

FIGURE 3. *Nasutitermes callimorphus* worker enteric valve armature (arrow: direction of food flow; A) and field habitus of foragers (B).

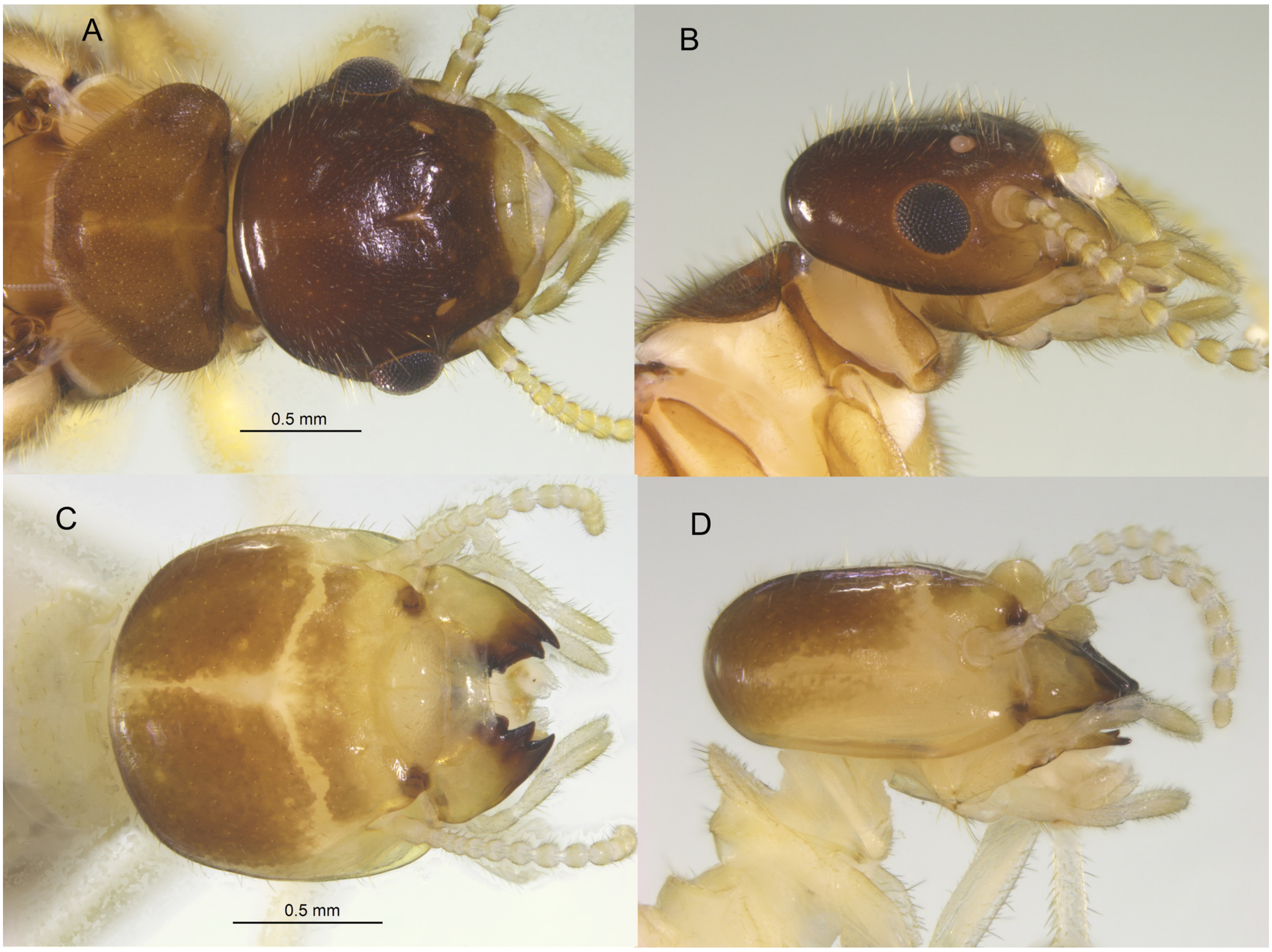

FIGURE 4. *Nasutitermes corniger* from Grenada (GR223). Imago head (dorsal A, lateral B) and major worker head (dorsal C, lateral D).

Comparisons

The *N. callimorphus* imago superficially resembles those of *N. corniger* (Figs. 4A, B) and *N. ephratae* (Figs. 7A, B). Imagos of both have very similar coloration, but *N. callimorphus* is distinctly smaller in most measurements, e.g., maximum head width at eyes (1.08–1.13, 1.34–1.57, and 1.31–1.40 mm; maximum pronotum width (0.74–0.85, 1.05–1.36, and 0.97–1.11 mm), and total length with wings (9.31–10.77 mm vs. 12.10–15.83 mm) and fore wing length to suture (7.58–9.04, 9.44–12.77, and 12.2–12.8 mm) for *N. callimorphus*, *N. corniger*, and *N. ephratae*, respectively (Scheffrahn *et al.* 2005, Mathews 1977). The dorsal outline of the *N. callimorphus* pronotum is subtriangular (Fig. 1A), while in *N. corniger* it is more trapezoidal (Fig. 4A), and in N. *ephratae* the lateral and posterior margins are nearly evenly rounded (Fig. 7A). In dorsal view, the compound eyes of *N. ephratae* bulge upward and forward while in *N. callimorphus* and *N. corniger* the eyes project more laterally. The compound eyes of *N. callimorphus* are nearly round (Fig. 1B), while in *N. corniger* (Fig. 4B) and in *N. ephratae* (Fig. 7B) they are elliptical. Both the compound eyes and ocelli of *N. ephratae* are proportionally larger than the other two species. The head capsule and pronotum pilosity of the *N. callimorphus* imago is less dense and that of *N. corniger* or *N. ephratae*.

SOLDIER (Fig. 2A–F, Table 2). The description of *N. callimorphus* soldier by Mathews (1977) is adequate.

TABLE 2. MEASUREMENTS OF *NASUTITERMES CALLIMORPHUS* SOLDIER.

Measurement in mm (n = 18*)	Range	Mean ± S.D.
Head length with nasus	1.19–1.3	1.29 ± 0.050
Head length without nasus	0.75–0.85	0.82 ± 0.031
Head width, maximum	0.72–0.79	0.76 ± 0.022
Nasus width at base	0.20–0.25	0.22 ± 0.018
Nasus width at middle	**0.10–0.13**	**0.11 ± 0.010**
Nasus length	0.43–0.51	0.48 ± 0.022
Head height, without postmentum	0.49–0.57	0.53 ± 0.027
Pronotum, maximum width	0.37–0.39	0.38 ± 0.0096
Pronotum, maximum length	0.11–0.15	0.13 ± 0.0092
Hind tibia length	0.82–0.92	0.87 ± 0.025
Total length	3.18–3.77	3.47 ± 0.17

*From eleven localities.

Comparisons

The *N. callimorphus* soldier (Fig. 2) superficially resembles that of the *N. corniger* (Fig. 5) and the *N. ephratae* soldier (Fig. 8). The *N. callimorphus* soldier is distinctly smaller in most measurements, e.g., head length with nasus (1.19–1.36, *1.28–1.39*, 1.37–1.77, and 1.29–1.56 mm); maximum head width (0.72–0.79, *0.77–0.83*, 0.82–1.31, and 0.68–97 mm); and maximum pronotum width (0.37–0.39, *0.37–0.42*, 0.44–0.65, and 0.37–0.49 mm); for *N. callimorphus* herein, *N. callimorphus* (Mathews 1977 *in italics*), *N. corniger* (Scheffrahn *et al.* 2005), and *N. ephratae* (Mathews 1977), respectively.

The anterior pronotal lobe of the *N. callimorphus* soldier has only very short anterior marginal setae (Fig. 2B), while the anterior pronotal lobes of *N. corniger* (Fig. 5B) and *N. ephratae* (Fig. 8B) soldiers also bear much longer setae. The antennal relatively length formula of *N. callimorphus* is 2=3>4<5, while in *N. corniger* and in *N. ephratae* the formulae are 2<3>4<5. Both *N. callimorphus* (Fig. 2C) and *N. corniger* (Fig. 5C) soldiers have fine short setae on the tergite interiors of while in *N. ephratae*, setae are pronouncedly more minute (Fig. 8C).

The vertex of *N. callimorphus* in lateral view (Fig. 2E) is nearly straight while in *N. corniger* (Fig. 5E) and in *N. ephratae* (Fig. 8E) they have a median concavity.

WORKER (Figs. 1C, D). Dimorphic; major workers more common. Head capsule dark brown with broad whitish cranial sutures, with scattered medium setae. Pronotum with light brown margins, lighter interior; a row of very small setae along anterior lobe, a few long setae on both lobes. Gut configuration very similar to *N. corniger* (Fontes 1998). Enteric valve armature composed of a single basal grouping of ca. 36 scattered spines, three median quadrate patches of ca. 20–25 spines, and three anterior elongate groupings of 4–10 spines; a few additional spines scattered randomly. Major workers (mean ± S.D.) maximum head width 0.96 ± 0.032 mm; maximum pronotum width 0.48 ± 0.031 mm. Minor workers (mean ± S.D.) maximum head width 0.78 ± 0.026 mm; maximum pronotum width 0.40 ± 0.023 mm.

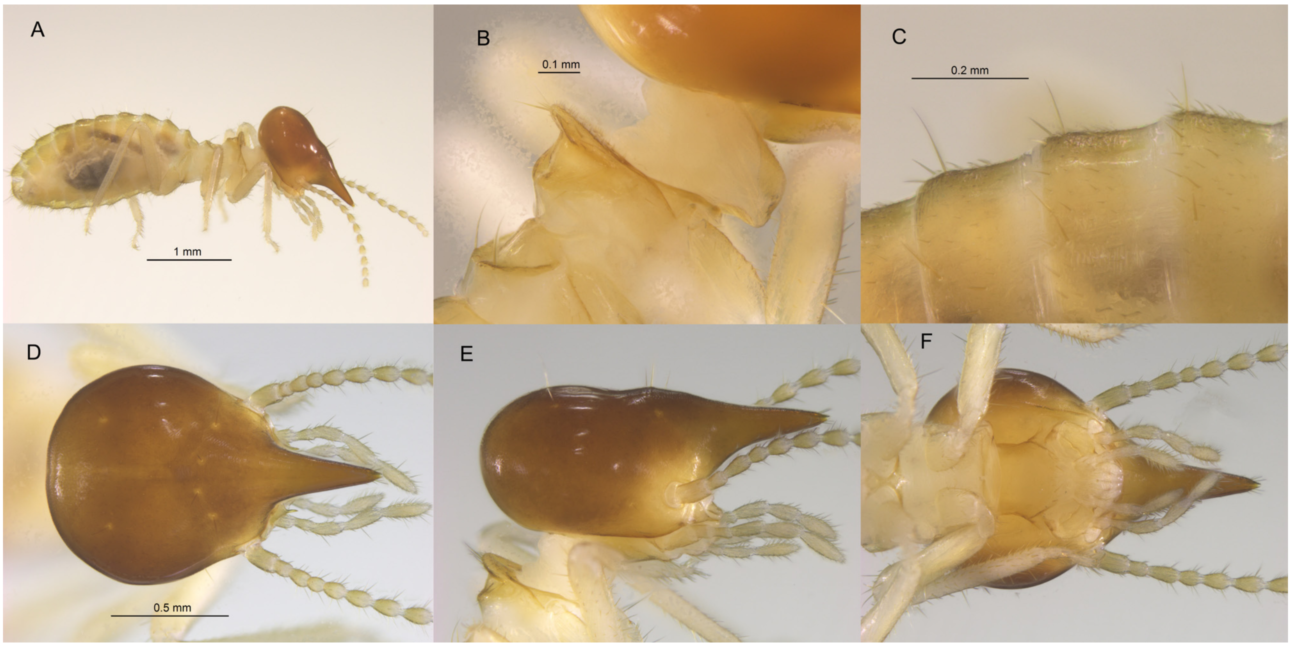

FIGURE 5. *Nasutitermes corniger* soldier from Grenada (GR223). Habitus (A); lateral view of pronotum (B); tergites (C); and dorsal, lateral, and ventral views of head capsule (D, E, and F, respectively).

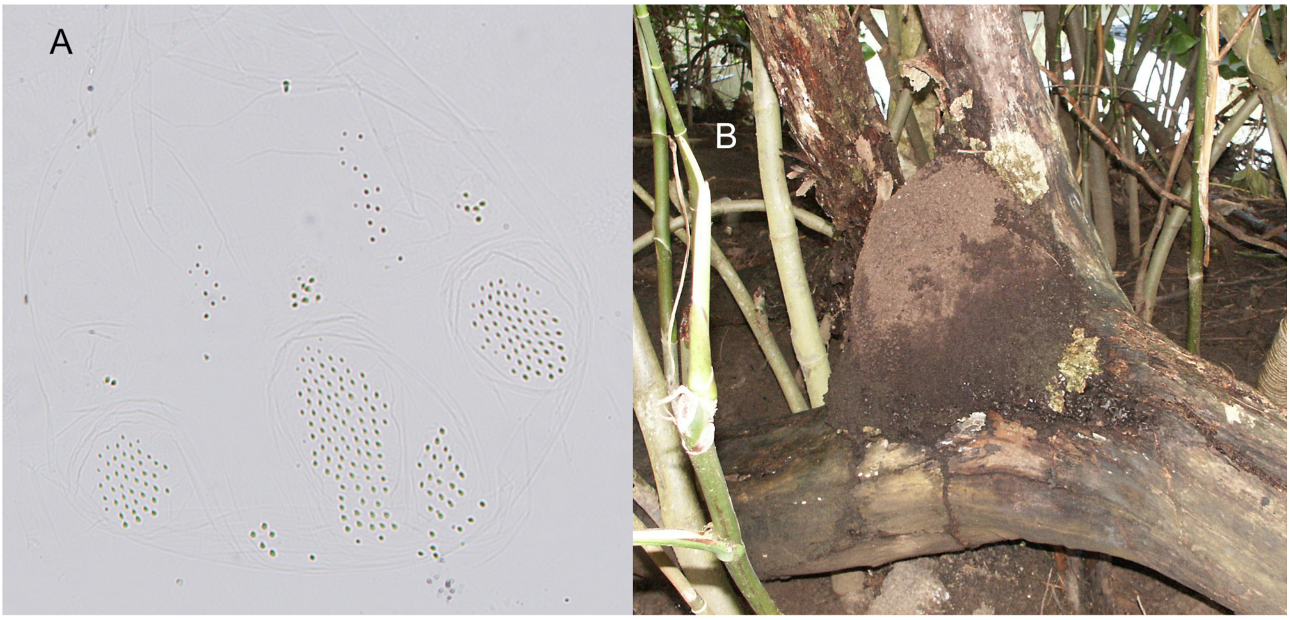

FIGURE 6. *Nasutitermes corniger* worker enteric valve armature (A) and nest (B).

Comparisons

The *N. callimorphus* worker superficially resembles those of *N. corniger* (Figs. 4C, D) and *N. ephratae* (Figs 7C, D) but the head capsule and pronotum is darker especially in the genal region. In lateral view, the postclypeus of *N. callimorphus* rises as a gentle ca. 120° peak, while in the other two species, the postclypeus in bulbous and inflated. In lateral view, the pronotum of *N. callimorphus* has a couple of long and many minute setae on the anterior lobe while in the other species, there are more long setae and the minute setae are longer. The EVA spines of *N.*

callimorphus workers (Fig. 3A) are smaller and more delicate that either *N. corniger* (Fig. 6A) or *N. ephratae* (Fig. 9A). The *N. callimorphus* workers are distinctly smaller in all measurements.

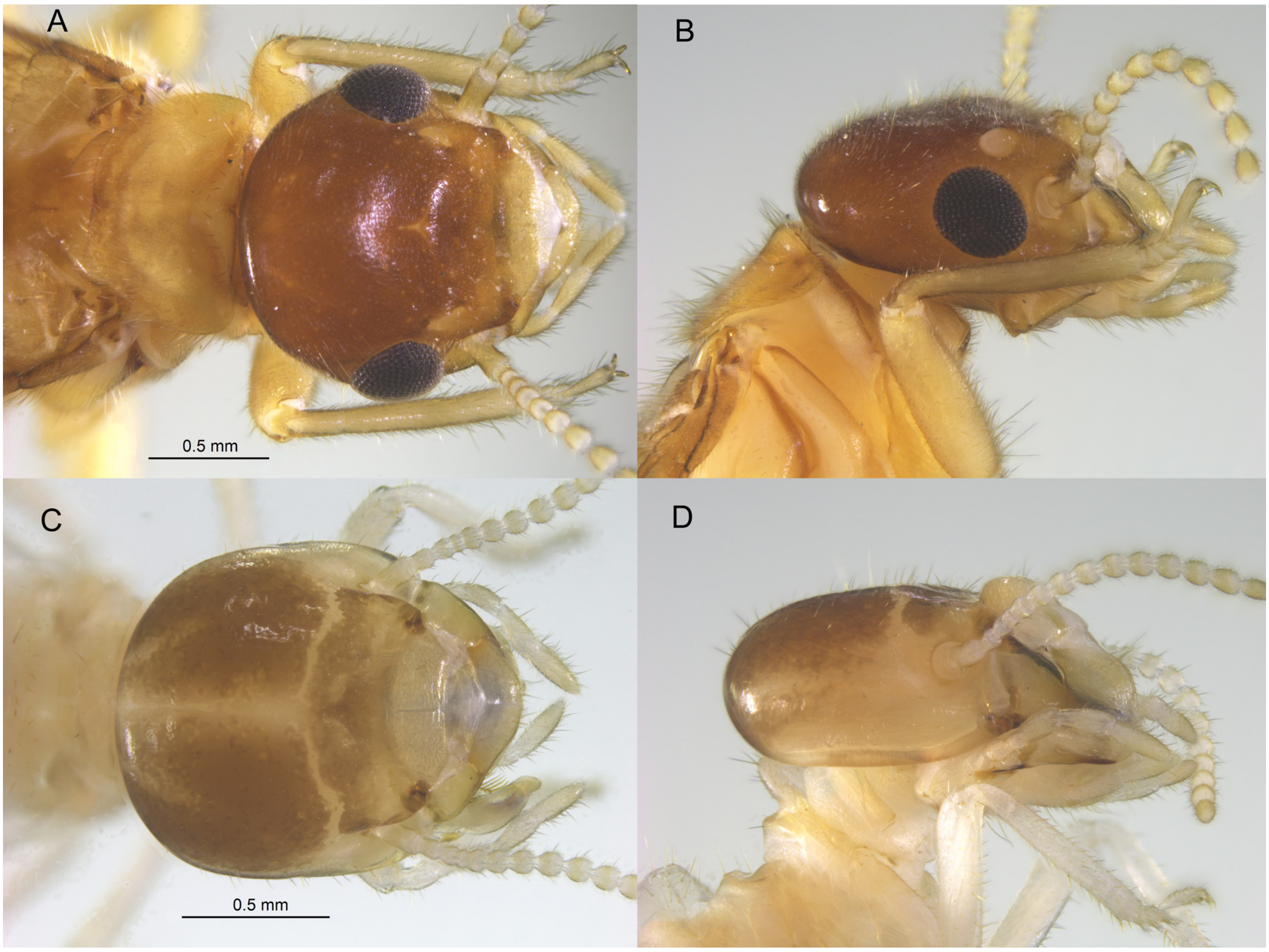

FIGURE 7. *Nasutitermes ephratae* from Guadeloupe (GU873). Imago head (dorsal A, lateral B) and major worker head (dorsal C, lateral D).

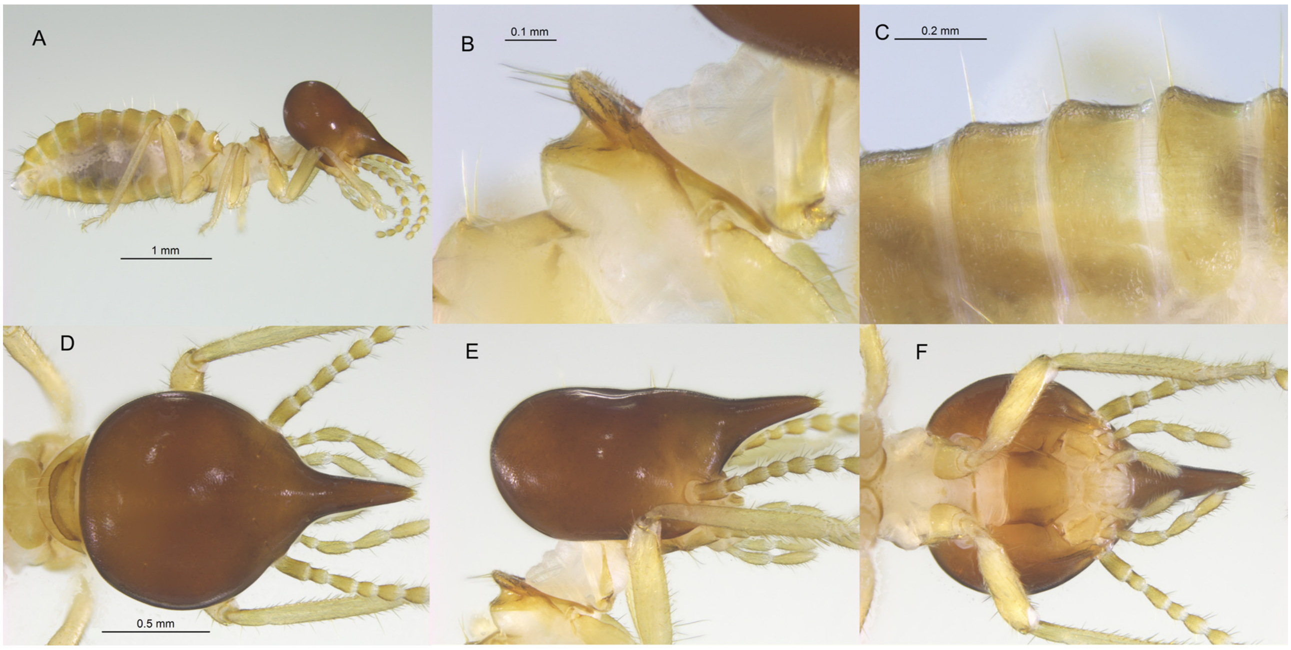

FIGURE 8. *Nasutitermes ephratae* soldier from Bolivia (BO181). Habitus (A); lateral view of pronotum (B); tergites (C); and dorsal, lateral, and ventral views of head capsule (D, E, and F, respectively).

FIGURE 9. *Nasutitermes ephratae* worker enteric valve armature (A) and nest (B).

FIGURE 10. *Nasutitermes nigriceps* soldier from Panama (PN207). Soldier head capsule dorsal, lateral, and ventral views (A, B, and C, respectively).

Distribution and biology

Nasutitermes callimorphus (suppl. Table 1, Fig. 13A) along with *N. corniger* (Fig. 13B, Santos *et al.* 2017) and *N. ephratae* (Fig. 13C, Scheffrahn *et al.* 2005, Santos *et al.* 2022) are among the most broadly distributed termites in the Neotropics. All are wood feeders and can be pestiferous (Constantino 2002). *Nasutitermes callimorphus* is a forest species, while *N. corniger* and *N. ephratae* are found in nearly all habitats. Its preference for the forest is confirmed by the species distribution model which shows a high suitability in most of the neotropical forests (Fig. 14). It lives in small colonies and nests in dead, often thin branches, including those still on living trees, an unusual habit among congeners. Colonies are also located underneath logs on the forest floor (Fig. 3B). Foragers behave much like *N. corniger* and *N. ephratae* with which they are usually sympatric. *Nasutitermes callimorphus* may be monogynous based on a single functional physogastric queen collected. Presence of mature alates in tree branch galleries on Guadeloupe at the end of May and beginning of June suggests that flights commence in the beginning of the rainy season. *Nasutitermes corniger* builds both epigeal and arboreal nests with a friable carton texture (Fig. 6B) while *N. ephratae* builds globous arboreal nests that are covered with a smooth skin (Fig. 9B). *Nasutitermes nigriceps*, a larger species, is found in dryer coastal zones of Central America, northern South America, and parts of the West Indies (Fig. 13D).

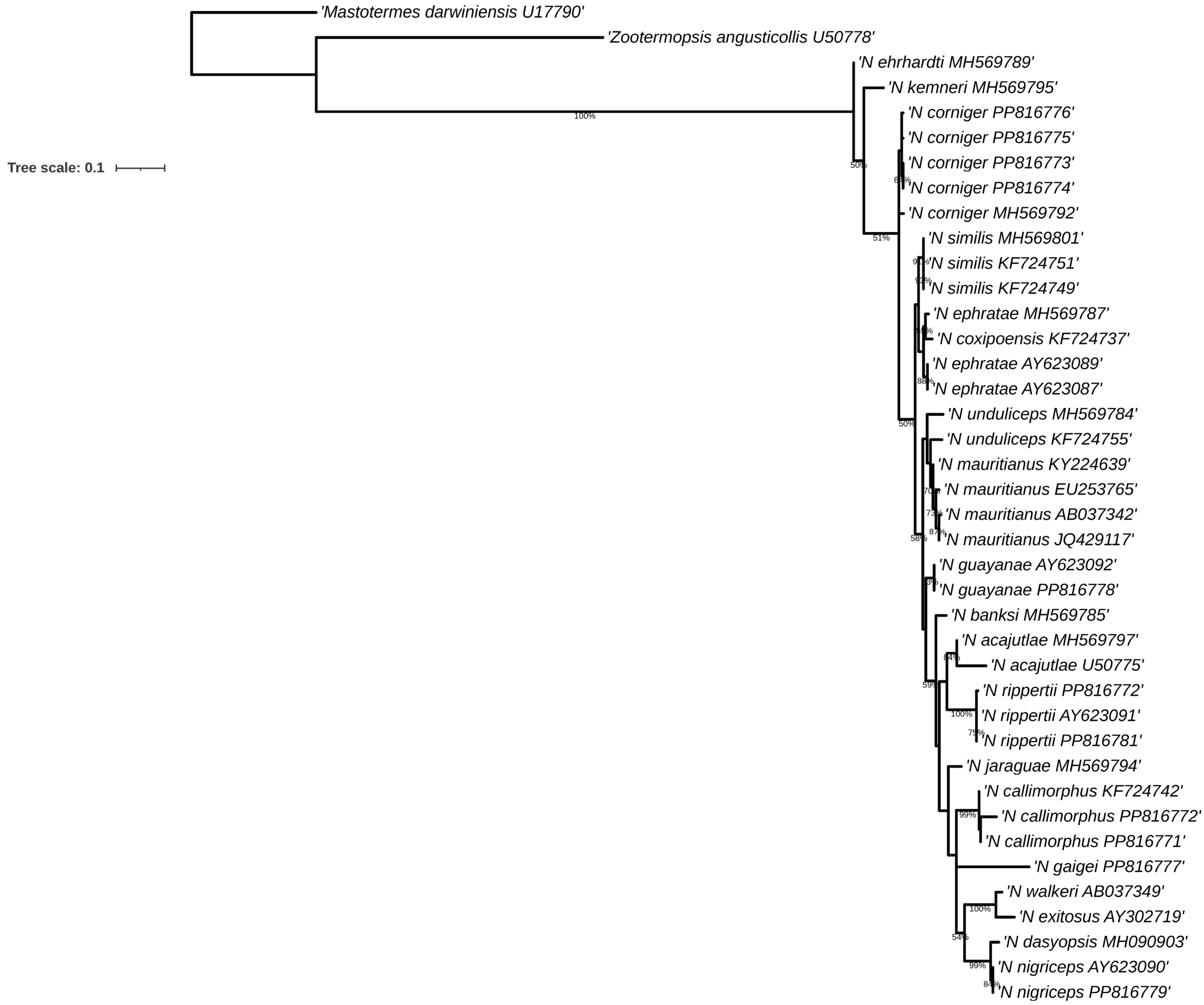

FIGURE 11. Phylogenetic tree (ln L = -2792.71626) of *Nasutitermes* taxa, based on 16S rRNA sequences constructed using the PhyML maximum likelihood method with 1000 bootstrap replications.

Genetic relationships

Based on the maximum parsimony analysis of the 16S rRNA sequences (length = 248, CI = 0.774) *N. callimorphus* formed a distinct clade. With maximum likelihood analysis (Fig. 11), *N. callimorphus* is sister species of *N. intermedius* (whose transfer to *Cortaritermes* was proposed by Cuezzo *et al.* 2015, but not supported by phylogenetic evidence) and within the same clade as *N. corniger*, *N. coxipoensis*, *N. ephratae*, and *N. globiceps* (Fig. 11). With the COII genetic marker, the maximum likelihood analysis revealed that all of the *N. callimorphus* samples formed a distinct clade, that was a sister group to *N. intermedius* (Fig. 12). This clade fell within a group consisting of *N. corniger*, *N. ephratae*, *N. coxipoensis*, and *N. globiceps*. Similarly, Roy *et al.* (2014), using the combined sequences of 16S and COII genes, comes to the same conclusion.

Additional taxonomic note

Nasutitermes nigriceps (Haldeman, 1854)

= *dasyopsis* Thorne, 1989, **syn. nov.** (figs. 1–4), soldier from "Guayabo Grande" which is presumed to be Punta Guayabo Grande, Darién, Panama (Thone & Levings 1985 thank Stephan Garrity for field assistance at site studied by Garrity & Levings 1985), and specimens from "Saboga Island" which lies in eastern Panama. Nickle and Collins (1992) figs 13.86, 13.87, soldier.

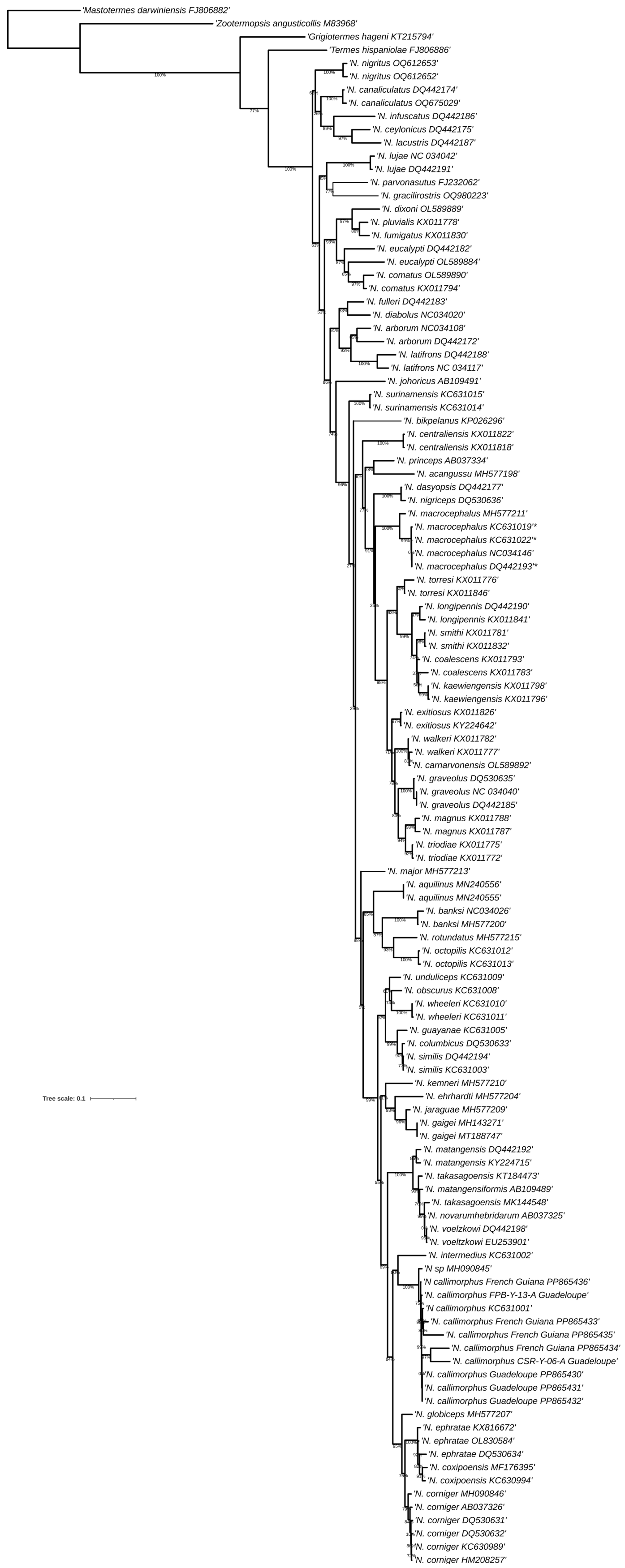

FIGURE 12. Maximum likelihood tree of the COII mtDNA gene subjected to sequencing, -ln L = 9946.57113. Bootstrap values ≥ 50% from PhyML analyses are shown. Thickened branches indicate Bayesian posterior probabilities ≥ 75%. Bootstrap values ≥ 50% from PhyML analyses are shown.

Material examined. Four hundred eighty-nine colony samples from the Caribbean Basin including thirteen from Panama (UFTC collection data in Scheffrahn 2019).

Justification of synonymy

Haldeman (1854) described the soldier of *N. nigriceps* from Mexico. When Thorne (Thorne & Levings 1989) described the *N. dasyopsis* syn. nov. soldier from Panama, she compared it to *N. nigriceps*: "*N. dasyopsis* soldiers are smaller than *N. nigriceps*, with fewer head capsule bristles. The head bristles of *N. dasyopsis* are two distinct lengths, with the long ones in the specific pattern described above". The head capsule photograph in Thorne & Levings (1989) shows pilosity identical to the *N. nigriceps* soldiers (Fig. 10). Light (1933) gives soldier measurements of seven *N. nigriceps* soldiers from Mazatlan and Colima, Mexico having a maximum head length range of 1.47–1.81 mm and a maximum head width range of 0.97–1.18 mm. This compares with the measurements by Thorne & Levings (1989) of 1.42–1.62 mm and 0.90–1.02 mm, respectively. The nest structure of *N. dasyopsis* syn. nov. (Thorne & Levings 1989, figure 10) is identical to that of *N. nigriceps* (Harris 1961, plate V) from Belize ("British Honduras" in the original citation). The presumed Panamanian localities (see above) of *N. dasyopsis* (Fig. 13D) are central to the distribution of *N. nigriceps*. The two *N. nigriceps* 16S sequences were identical to each other and were 98.3% similar to the *N. dasyopsis* **syn. nov.** sequence (Fig. 11).

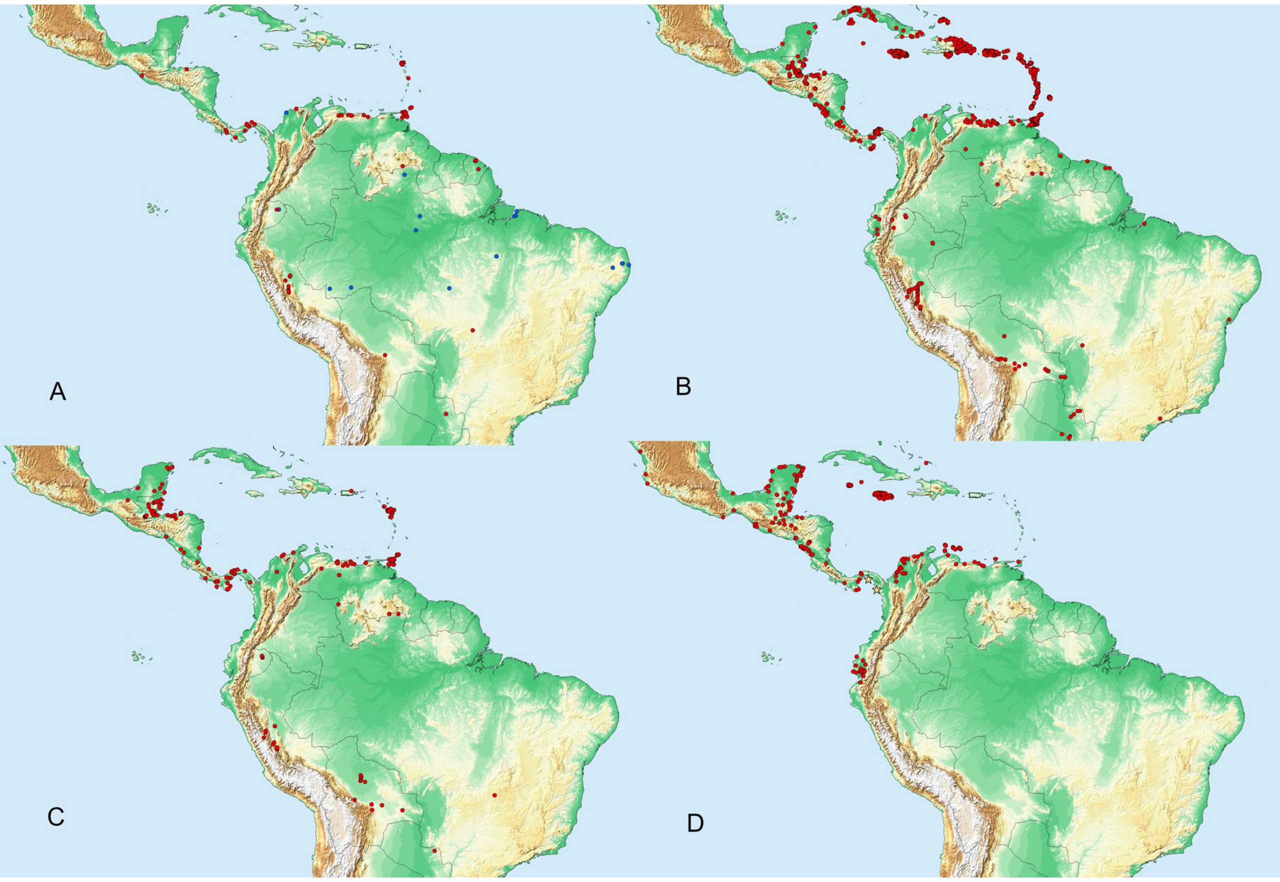

FIGURE 13. Distribution of *Nasutitermes* spp. from the University of Florida Termite Collection (red dots). A, *N. callimorphus* (blue dots from literature); B, *N. corniger*; C, *N. ephratae*; and D, *N. nigriceps* (orange dots *N. daysiopsis* **syn. nov**. presumed localities).

Inward *et al.* (2007) reported that their *N. nigriceps* sample (DQ442193) was from French Guiana but this species does not occur there (Fig. 13D). The Inward *et al.* 2007 sample was very likely a misidentification of *N. macrocephalus* (Silvestri, 1903). Likewise, Roy *et al.* 2014 (KC631019 and KC631021) misidentified *N. macrocephalus* from French Guiana as *N. acajutlae* (Holmgren, 1910). *Nasutitermes macrocephalus* occurs in

French Guiana (Scheffrahn 2019) while *N. acajutlae* is a West Indian species (Scheffrahn 2019). Both locality errors for French Guiana appear to stem from Ensaf & Eggleton (2004).

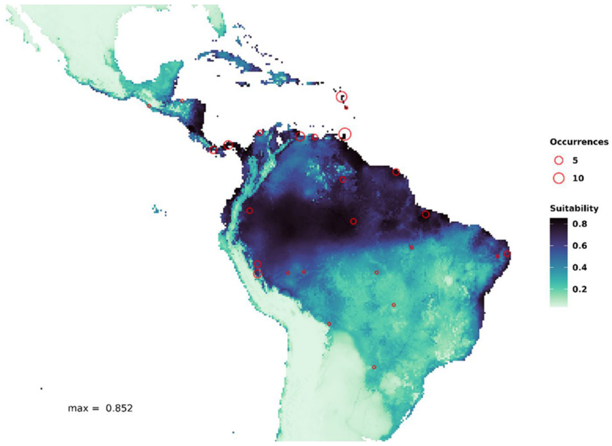

FIGURE 14. Potential current suitability of *N. callimorphus* according to the species distribution modeling.

Discussion

Nasutitermes Dudley, 1890, is one of the few pantropical Termitidae genera. There are currently 66 *Nasutitermes* species recognized from the Neotropics (Constantino 2020) of which 33 species described by Holmgren (1906, 1910) are still considered valid, whereas 25 of Holmgren's (1910) new taxa have been synonymized with other *Nasutitermes* species, among which 13 are considered synonyms of *N. corniger* alone (Scheffrahn *et al.* 2005; Krishna *et al.* 2013; Constantino 2020). Unfortunately, the descriptions by Holmgren (1906, 1910) are typically very brief, line drawings are not detailed (especially the setal patterns of the soldier head capsule), and measurements are few. Consequently, most decisions to synonymize or not Holmgren's names are based on poor evidence and are subject to caution: only a few cases, such as that of *N. costalis* (Scheffrahn *et al.* 2005), have been the subject of a detailed critical assessment.

The situation of the group of species including *N. corniger* and *N. ephratae* is especially complex. Although alates of these two species are clearly distinct, soldiers are very difficult to distinguish. Both species are widespread throughout South and Central America, including the Antilles, a broad distribution accounting for substantial morphological variability. Hybridization is possible, at least in the laboratory (Hartke & Rosengaus 2011). Even mitochondrial DNA data are far from diagnostic: some haplotypes (16S and COII), distributed from southern Mexico to northern Brazil, are identical or nearly so between the two species (haplogroup Hg4 of *N. ephratae* and related sequences in Santos *et al.* 2022; compare with GenBank data and 16S sequences from Santos *et al.* 2017). For all these reasons, it is understandable that *N. callimorphus*, being very similar to small *N. corniger* and *N. ephratae* specimens, has long gone unnoticed or treated as doubtfully different from them until Mathews (1977) described it as new. Considering the broad distribution of this species, there is still some risk that it could have been named prior to Mathews (1977) and neglected or mistakenly synonymized with *N. corniger* or *N. ephratae*. However, since it is impossible to ascertain the identity of all *corniger*-like taxa described by Holmgren (1906, 1910) and other authors without a detailed study—including sequencing—of type material, the recognition and characterization of *N. callimorphus* as one of the most widely distributed species in South and Central America should constitute a useful step in the clarification of the confuse taxonomy of *Nasutitermes* in the Neotropics.

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SUPPLEMENTARY TABLE 1. Author and literature localities of *Nasutitermes callimorphus* (Fig 13A).

Code	Number	Collector	Country	Latitude	Longitude	Location	Date or Reference
BO	49	UF group	Bolivia	-17.4989	-63.6524	Flora & Fauna Hotel	25-May-13
BO	51	UF group	Bolivia	-17.4989	-63.6524	Flora & Fauna Hotel	25-May-13
BO	52	UF group	Bolivia	-17.4989	-63.6524	Flora & Fauna Hotel	25-May-13
BO	53	UF group	Bolivia	-17.4989	-63.6524	Flora & Fauna Hotel	25-May-13
CO	575	UF group	Colombia	11.1256	-74.1197	Above Minca	5-Jun-09
CO	576	UF group	Colombia	11.1256	-74.1197	Above Minca	5-Jun-09
CO	577	UF group	Colombia	11.1256	-74.1197	Above Minca	5-Jun-09
CO	583	UF group	Colombia	11.1256	-74.1197	Above Minca	5-Jun-09
EC	604	UF group	Ecuador	-0.6718	-76.3979	Yasuni station area, all trails	29-May-11
EC	689	UF group	Ecuador	-0.6718	-76.3979	Yasuni station area, all trails	29-May-11
EC	1212	UF group	Ecuador	-0.6718	-76.3979	Yasuni station area, all trails	1-Jun-11
EC	1375	UF group	Ecuador	-0.6718	-76.3979	Yasuni station area, all trails	2-Jun-11
FG	507	Krecek	French Guiana	5.0634	-53.0578	Sinnamary River	15-Feb-08
GU	96	UF group	Guadeloupe	16.1817	-61.6847	Parc National Hwy D23	23-May-99
GU	499	UF group	Guadeloupe	16.2834	-61.73	Rain Forest, Sainte-Rose	27-May-99
GU	511	UF group	Guadeloupe	16.356	-61.7297	beach E Pointe Allegre	27-May-99
GU	512	UF group	Guadeloupe	16.356	-61.7297	beach E Pointe Allegre	27-May-99
GU	513	UF group	Guadeloupe	16.356	-61.7297	beach E Pointe Allegre	27-May-99
GU	514	UF group	Guadeloupe	16.356	-61.7297	beach E Pointe Allegre	27-May-99
GU	807	Ch.Bordereau	Guadeloupe	16.2	-61.6333	Petit-Bourg, Prise d'Eau	25-Jan-05
GU	944	T. Ramage, T. Jourdan & M. Coulis	Guadeloupe	16.4308	-61.4876	Espérance	19-Feb-23
HN	17	UF group	Honduras	15.6669	-87.0011	Hwy 13 E La Ceiba	27-May-07
MA	273	Thibault	Martinique	14.6356	-60.9011	Rocher Leclerc	28-Oct-19
MX	582	R.Setter	Mexico	14.9	-92.28	Tapachula Cacao plantation	10-Jun-06
PA	222	UF group	Paraguay	-23.9456	-56.4962	E. Neuva Germania	28-May-12
PN	26	UF group	Panama	8.6144	-80.1129	El Valle, Hotel Campestre	28-May-05
PN	27	UF group	Panama	8.6144	-80.1129	El Valle, Hotel Campestre	28-May-05

......continued on the next page

SUPPLEMENTARY TABLE 1. (Continued)

Code	Number	Collector	Country	Latitude	Longitude	Location	Date or Reference
PN	28	UF group	Panama	8.6144	-80.1129	El Valle, Hotel Campestre	28-May-05
PN	29	UF group	Panama	8.6144	-80.1129	El Valle, Hotel Campestre	28-May-05
PN	224	UF group	Panama	8.6144	-80.1129	El Valle, Hotel Campestre	29-May-05
PN	253	UF group	Panama	8.6131	-80.1448	El Valle trail west of town	31-May-05
PN	288	UF group	Panama	8.6141	-80.1129	El Valle Campestre trail	31-May-05
PN	289	UF group	Panama	8.6141	-80.1129	El Valle Campestre trail	31-May-05
PN	384	UF group	Panama	9.0917	-79.6155	Forest Reserve Aquas Buenas	1-Jun-05
PN	385	UF group	Panama	9.0917	-79.6155	Forest Reserve Aquas Buenas	1-Jun-05
PN	449	UF group	Panama	9.5751	-79.3492	5 km W Palenque	2-Jun-05
PN	627	UF group	Panama	9.359	-79.9516	Fort Sherman swamp	3-Jun-05
PN	787	UF group	Panama	8.6162	-80.1103	Campestre Nematode transects	31-May-05
PN	793	UF group	Panama	8.6162	-80.1103	Campestre Nematode transects	31-May-05
PN	795	UF group	Panama	8.6162	-80.1103	Campestre Nematode transects	31-May-05
PN	1034	UF group	Panama	8.6662	-82.426	Caldera road S Boquette	31-May-10
PN	1035	UF group	Panama	8.6662	-82.426	Caldera road S Boquette	31-May-10
PN	1036	UF group	Panama	8.6662	-82.426	Caldera road S Boquette	31-May-10
PN	1037	UF group	Panama	8.6662	-82.426	Caldera road S Boquette	31-May-10
PN	1038	UF group	Panama	8.6662	-82.426	Caldera road S Boquette	31-May-10
PN	1051	UF group	Panama	8.6467	-82.3934	SE Boquette	31-May-10
PN	1115	UF group	Panama	8.3438	-82.281	SE Chiriqui coast	31-May-10
PN	1299	UF group	Panama	7.8013	-81.2582	Rd to S. Catalina	3-Jun-10
PN	1417	UF group	Panama	9.3261	-78.9992	Kuna Rd stop 4	5-Jun-10
PN	1418	UF group	Panama	9.3261	-78.9992	Kuna Rd stop 4	5-Jun-10
PN	1419	UF group	Panama	9.3261	-78.9992	Kuna Rd stop 4	5-Jun-10
PN	1420	UF group	Panama	9.3261	-78.9992	Kuna Rd stop 4	5-Jun-10
PN	1421	UF group	Panama	9.3261	-78.9992	Kuna Rd stop 4	5-Jun-10
PU	216	UF group	Peru	-10.3545	-74.9862	8 km S Pte. Bermudez	26-May-14
PU	218	UF group	Peru	-10.3545	-74.9862	8 km S Pte. Bermudez	26-May-14

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SUPPLEMENTARY TABLE 1. (Continued)

Code	Number	Collector	Country	Latitude	Longitude	Location	Date or Reference
PU	219	UF group	Peru	-10.3545	-74.9862	8 km S Pte. Bermudez	26-May-14
PU	242	UF group	Peru	-9.6377	-75.0164	29 km S Puerto Inca	27-May-14
PU	318	UF group	Peru	-10.0492	-75.0286	21 km S Constitucion	27-May-14
PU	320	UF group	Peru	-10.0492	-75.0286	21 km S Constitucion	27-May-14
PU	361	UF group	Peru	-10.1072	-75.0195	28 km S Constitucion old growth	27-May-14
PU	362	UF group	Peru	-10.1072	-75.0195	28 km S Constitucion old growth	27-May-14
PU	364	UF group	Peru	-10.1072	-75.0195	28 km S Constitucion old growth	27-May-14
PU	398	UF group	Peru	-10.1552	-75.0091	33 km S Constitucion	27-May-14
PU	399	UF group	Peru	-10.1552	-75.0091	33 km S Constitucion	27-May-14
PU	639	UF group	Peru	-8.3701	-74.8437	34 km W Pucallpa, farmland	29-May-14
PU	640	UF group	Peru	-8.3701	-74.8437	34 km W Pucallpa, farmland	29-May-14
PU	641	UF group	Peru	-8.3701	-74.8437	34 km W Pucallpa, farmland	29-May-14
PU	644	UF group	Peru	-8.3701	-74.8437	34 km W Pucallpa, farmland	29-May-14
PU	674	UF group	Peru	-8.4887	-74.8585	6 km W Campoverde	29-May-14
PU	790	UF group	Peru	-8.9568	-75.4053	76 km NE Tingo Maria, disturbed	30-May-14
PU	793	UF group	Peru	-8.9568	-75.4053	76 km NE Tingo Maria, disturbed	30-May-14
PU	1014	UF group	Peru	-8.3701	-74.8437	34 km W Pucallpa, farmland	29-May-14
SA	297	UF group	Venezuela	4.4514	-61.6006	El Pauji, Gallery Forest	1-May-04
SA	307	UF group	Venezuela	4.4514	-61.6006	El Pauji, Gallery Forest	1-May-04
SA	312	UF group	Venezuela	4.4514	-61.6006	El Pauji, Gallery Forest	1-May-04
SA	316	UF group	Venezuela	4.4514	-61.6006	El Pauji, Gallery Forest	1-May-04
SA	329	UF group	Venezuela	4.4514	-61.6006	El Pauji, Gallery Forest	24-Apr-04
TT	140.2	UF group	Trinidad/ Tobago	10.6653	-61.4025	Mt. St. Benedict foothills	27-May-96

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SUPPLEMENTARY TABLE 1. (Continued)

Code	Number	Collector	Country	Latitude	Longitude	Location	Date or Reference
TT	147	UF group	Trinidad/ Tobago	10.6653	-61.4025	Mt. St. Benedict foothills	27-May-96
TT	150	UF group	Trinidad/ Tobago	10.6653	-61.4025	Mt. St. Benedict foothills	27-May-96
TT	152.3	UF group	Trinidad/ Tobago	10.6653	-61.4025	Mt. St. Benedict foothills	27-May-96
TT	169.3	UF group	Trinidad/ Tobago	10.2462	-61.5008	Mangrove SW San Fernando	27-May-96
TT	227	UF group	Trinidad/ Tobago	10.1083	-61.6472	Erin Savanna trail end	27-May-96
TT	301	UF group	Trinidad/ Tobago	10.7387	-61.6187	Maqueripe Bay	28-May-96
TT	364.2	UF group	Trinidad/ Tobago	10.7905	-61.318	Blanchisseuse	28-May-96
TT	444	UF group	Trinidad/ Tobago	10.308	-61.0837	Mayaro Road E Ecclesville	29-May-96
TT	446	UF group	Trinidad/ Tobago	10.308	-61.0837	Mayaro Road E Ecclesville	29-May-96
TT	532	UF group	Trinidad/ Tobago	10.6653	-61.4025	Mt. St. Benedict foothills, pine trail	30-May-96
TT	586	UF group	Trinidad/ Tobago	11.267	-60.5858	Roxborough Rd., NNW Roxborough	31-May-96
TT	594	UF group	Trinidad/ Tobago	11.2817	-60.5898	Roxborough Rd., N Roxborough	31-May-96
TT	595.1	UF group	Trinidad/ Tobago	11.2817	-60.5898	Roxborough Rd., N Roxborough	31-May-96
TT	654	UF group	Trinidad/ Tobago	11.208	-60.7053	Belmont	31-May-96
TT	702	UF group	Trinidad/ Tobago	11.3	-60.5417	Charlotteville Rd., nr Tyrrel's Bay	1-Jun-96
TT	1215	UF group	Trinidad/ Tobago	10.6679	-61.3997	Creek trail NW PAX	25-May-03
TT	1410	UF group	Trinidad/ Tobago	10.7133	-61.304	S. end Arima Hwy	26-May-03
TT	1415	UF group	Trinidad/ Tobago	10.7133	-61.304	S. end Arima Hwy	26-May-03
TT	1908	UF group	Trinidad/ Tobago	10.1835	-61.057	Rio Claro Rd. #1	30-May-03
TT	2128	UF group	Trinidad/ Tobago	10.5937	-61.2035	Aripo Savannah	31-May-03
VZ	111.1	UF group	Venezuela	10.1891	-65.6721	SW El Coco	24-Sep-07
VZ	118	UF group	Venezuela	10.1891	-65.6721	SW El Coco	24-Sep-07
VZ	167	UF group	Venezuela	10.3738	-66.1374	Mamporal	24-Sep-07
VZ	399	UF group	Venezuela	10.3378	-67.6553	Henri Pittier Guamito trails	29-Sep-07
VZ	404	UF group	Venezuela	10.3378	-67.6553	Henri Pittier Guamito trails	29-Sep-07
VZ	494	UF group	Venezuela	10.335	-67.5764	Henri Pittier Natl. Park 3	25-May-08

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SUPPLEMENTARY TABLE 1. (Continued)

Code	Number	Collector	Country	Latitude	Longitude	Location	Date or Reference
VZ	534	UF group	Venezuela	10.3942	-67.7504	Henri Pittier Natl. Park 4	25-May-08
VZ	1199	UF group	Venezuela	10.3377	-69.1344	Licua	30-May-08
VZ	1200	UF group	Venezuela	10.3377	-69.1344	Licua	30-May-08
VZ	1226	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1227	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1228	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1229	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1230	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1231	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1232	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1233	UF group	Venezuela	10.417	-68.8768	Copper mine above Acoa	30-May-08
VZ	1286.3	UF group	Venezuela	10.3643	-68.7498	P.N. Yurubi	30-May-08
VZ	1302	UF group	Venezuela	10.3643	-68.7498	P.N. Yurubi	30-May-08
VZ	1318	UF group	Venezuela	10.3643	-68.7498	P.N. Yurubi	30-May-08
VZ	1369	UF group	Venezuela	10.4025	-68.0004	P.N. San Sabastian	31-May-08
VZ	1372	UF group	Venezuela	10.4025	-68.0004	P.N. San Sabastian	31-May-08
VZ	1373	UF group	Venezuela	10.4025	-68.0004	P.N. San Sabastian	31-May-08
VZ	1377	UF group	Venezuela	10.4025	-68.0004	P.N. San Sabastian	31-May-08
ULBTC	PANT101	Y.Roisin	Panama	9.2	-79.79	Pipeline Road, Río Agua Salud	17-May-91
ULBTC	IBISCA05730	Y.Roisin, M.Leponce	Panama	9.2793	-79.9762	San Lorenzo P.A.	17-May-04
ULBTC	IBISCA05518	Y.Roisin, M.Leponce	Panama	9.2793	-79.9762	San Lorenzo P.A.	22-May-04
ULBTC	CPB-X-19-A	E.Duquesne, D.Fournier	Guadeloupe	16.189	-61.5996	Petit-Bourg	1-May-23
ULBTC	FPB-Y-13-A	E.Duquesne, D.Fournier	Guadeloupe	16.198	-61.671	Rivière Bras David, Petit-Bourg	4-Apr-23
ULBTC	CSR-X-01-B	E.Duquesne, D.Fournier	Guadeloupe	16.3275	-61.6915	Sainte-Rose	2-May-23
ULBTC	CSR-Y-06-A	E.Duquesne, D.Fournier	Guadeloupe	16.3284	-61.6904	Sainte-Rose	5-May-23
ULBTC	FSR-X-10-A	E.Duquesne, D.Fournier	Guadeloupe	16.3086	-61.7299	Sofaïa, Sainte-Rose	5-Jun-23
ULBTC	FBM-X-19-A	E.Duquesne, Y.Roisin	Guadeloupe	16.2231	-61.6843	Forêt Guyonneau, Lamentin	25-May-23
ULBTC	Nour2-23e	T.Bourguignon, Y.Roisin	French Guiana	4.092	-52.677	Nouragues Inselberg Station	28-Mar-06

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SUPPLEMENTARY TABLE 1. (Continued)

Code	Number	Collector	Country	Latitude	Longitude	Location	Date or Reference
ULBTC	L-10-13-A	C.Legrand, Y.Roisin	French Guiana	5.101	-52.9656	Petit Saut road	Feb. 2019
ULBTC	L-10-21-B	C.Legrand, Y.Roisin	French Guiana	5.1092	-52.9658	Petit Saut road	31-Jan-08
ULBTC	L-30-13-A	C.Legrand, Y.Roisin	French Guiana	5.11	-52.9658	Petit Saut road	Feb. 2019
ULBTC	L-100-22-F	C.Legrand, Y.Roisin	French Guiana	5.1095	-52.9667	Petit Saut road	2-Feb-19
ULBTC	PA-30-07-H	C.Legrand, Y.Roisin	French Guiana	5.1104	-52.9657	Petit Saut road	Feb. 2019
ULBTC	PA-30-16-A	C.Legrand, Y.Roisin	French Guiana	5.1098	-52.9658	Petit Saut road	Feb. 2019
lit			Brazil	-7.466	-36.866	Fazenda Almas Private Reserve	Araújo *et al.* 2015
lit			Brazil	-6.966	-35.7	Mata do Pau Ferro	Araújo *et al.* 2015
lit			Brazil	-1.438	-48.473	Pará Belém	Bandeira 1989
lit			Brazil	-9.8682	-56.0835	Alta Floresta Mato Grosso	Cipriani *et al.* 2019
lit			Brazil	-3.079	-60.013	Amazonas, Manaus	Constantino & Cancello 1993
lit			Brazil	-1.365	-48.241	Pará, Benevides	Constantino & Cancello 1993
lit			Brazil	-6.14	-50.53	Pará, Serra dos Carajás	Constantino & Cancello 1993
lit			Brazil	-0.856	-48.139	Pará, Vigia	Constantino & Cancello 1993
lit			Brazil	-7.145	-34.9771	Paraíba, Santa Rita	Couto *et al.* 2019
lit			Brazil	-1.4277	-59.5445	Amazonas, Presidente Figueiredo	Dambros *et al.* 2012
lit			Brazil	-6.962	-35.754	Paraíba, Mata do Pau Ferro	Eloi *et al.* 2020
lit.			Brazil	-14.676	-53.354	Xavantina, Matto Grosso	Mathews 1977
lit			Brazil	3.45	-61.35	Maracá, Roraima	Mill 1983
lit			Brazil	-9.9208	-70.1625	Acre, Chandless State Park	Ferreira *et al.* 2023
lit			Brazil	-9.7636	-67.644	Acre, Humaitá Forest Reserve	Ferreira *et al.* 2023
lit			Colombia	10.6807	-75.2627	Ceibal; Santa Catalina, Bolívar	Casalla Daza & Korb 2019
lit			Ecuador	-0.645	-76.1499	Tiputini Biodiversity Station	Mertl *et al.* 2012
lit	NOU25		French Guiana	4.088	-52.68	Nouragues	Roy *et al.* 2014