ARTHROPOD SYSTEMATICS
& PHYLOGENY

73 (2): 333–348
20.8.2015

SENCKENBERG

A single endemic and three exotic species of the termite genus *Coptotermes* (Isoptera, Rhinotermitidae) in the New World

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Accepted 06.vii.2015.

Editor in charge: Julia Goldberg.

Abstract

The termite genus *Coptotermes* is both large and widespread but, as a whole, lacks robust diagnostic characters for morphological species identification. This has resulted in many taxonomic synonymies leading to the current pool of extant species a few of which are among the world's most destructive pests of wood. The New World diversity of *Coptotermes* is far less complicated, but has not been the subject of critical study. Using a large collection representative of endemic *Coptotermes* from the region, we compared their external morphology and their 16S genetic marker sequences to identify the three described American species: *C. crassus*, *C. niger*, and *C. testaceus*. We found no consistent differences among populations from Mexico to Bolivia, and therefore, we reassign the former two species as junior synonyms of *C. testaceus*. We also compared alates and soldiers of the three non-native species of *Coptotermes*: *C. formosanus*, *C. gestroi*, and *C. sjostedti* (soldiers only) to *C. testaceus* and provide diagnostic characters to identify all four current New World species. An updated distribution map is provided.

Key words

Coptotermes crassus, *Coptotermes formosanus*, *Coptotermes gestroi*, *Coptotermes niger*, *Coptotermes sjostedti*, *Coptermes testaceus*, synonymy.

1. Introduction

The termite genus *Coptotermes* Wasmann currently consists of 67 extant species (Krishna et al. 2013) distributed in Asia, Australia, Africa, and the New World. Because this genus is specious, widespread, pestiferous, and lacks robust diagnostic interspecific morphology, *Coptotermes* has undergone more synonymies than any other termite genus (Krishna et al. 2013). Intraspecific character variability (Emerson 1971) and increased body mass with colony age (Grace et al. 1995) compound the difficulty of sorting species morphologically.

As a result of drastic and provincial proliferation of the Chinese termite fauna (Eggleton 1999), 40 *Coptotermes* species were described from China between 1985 and 1996 (Wang & Grace 1999; Krishna et al.

Table 1. *Coptotermes testaceus* samples used for 16S molecular analysis and measurements. — ***Key***: (*) denotes specimens from near type locality of *C. niger*; (**) denotes specimens from near type locality of *C. crassus*; (***) denotes specimens from near type locality of *C. testaceus*.

Species	UF code	Country	Lat.	Long.	Sample	GenBank
C. testaceus	BZ 5	Belize	17.42	−88.44	DNA	KM588274
C. testaceus	BZ 127	Belize	16.229	−89.094	DNA	KM588268
C. testaceus	BZ 267	Belize	16.879	−88.348	DNA	KM588293
C. testaceus	BO 234	Bolivia	−17.056	−64.76	DNA	KM588280
C. testaceus	BO 463	Bolivia	−14.424	−64.861	DNA	KM588281
C. testaceus	SA 271	Costa Rica	8.78	−82.95	DNA	KM588285
C. testaceus	EC 86	Ecuador	−1.383	−79.425	DNA	KM588269
C. testaceus	EC 86a	Ecuador	−1.383	−79.425	DNA	KM588269
C. testaceus	EC 93	Ecuador	−0.91	−79.5	DNA	KM588279
C. testaceus	EC 159	Ecuador	−2.193	−79.958	DNA	KM588289
C. testaceus	FG 151	French Guiana	5.038	−52.956	DNA	KM588277
C. testaceus	GR 61	Grenada	12.117	−61.733	DNA	KM588278
C. testaceus	GUA 658	Guatemala	15.686	−88.645	DNA	KM588292
*C. testaceus***	CTA 59	Honduras	15.0	−86	DNA	KM588271
*C. testaceus***	CTA 71	Honduras	15.5	−88.05	DNA	KM588267
C. testaceus	MX 8	Mexico	16.478	−95.157	DNA	KM588276
*C. testaceus**	PN 161	Panama	8.669	−80.592	DNA	KM588266
*C. testaceus**	PN 453	Panama	9.577	−79.409	DNA	KM588284
*C. testaceus**	PN 961	Panama	8.22	−81.861	DNA	KM588286
*C. testaceus**	PN 1091	Panama	8.344	−82.281	DNA	KM588287
*C. testaceus**	PN 1173	Panama	8.827	−82.697	DNA	KM588290
*C. testaceus**	PN 1386	Panama	9.32	−78.999	DNA	KM588275
C. testaceus	SA 255	Peru	−3.442	−72.85	DNA	KM588288
C. testaceus	TT 11	Trinidad/Tobago	10.597	−61.208	DNA	KM588282
C. testaceus	TT 603	Trinidad/Tobago	11.285	−60.601	DNA	KM588291
C. testaceus	TT 766	Trinidad/Tobago	10.596	−61.207	DNA	KM588272
C. testaceus	TT 1705	Trinidad/Tobago	10.159	−61.005	DNA	KM588273
C. testaceus	SA 205	Venezuela	3.173	−65.675	DNA	KM588283
C. testaceus	SA 204	Venezuela	3.173	−65.675	DNA	KM588270
*C. testaceus****	FG 493	French Guiana	5.063	−53.058	Measure	—
*C. testaceus***	HN 61	Honduras	15.755	−87.455	Measure	—
*C. testaceus***	HN 375	Honduras	14.358	−87.149	Measure	—
*C. testaceus**	PN 299	Panama	9.122	−79.716	Measure	—
*C. testaceus**	PN 290	Panama	8.614	−80.113	Measure	—
C. testaceus	TT 1720	Trinidad/Tobago	10.214	−61.631	Measure	—

2013) of which 18 were reverted into synonymy (Huang et al. 2000; Li et al. 2011). Twenty-two species of *Coptotermes* are currently recognized in China of the 44 total species in the Oriental Region. Since 1968, a single new species has been described outside of China in New Guinea (Bourguignon & Roisin 2010). Three *Coptotermes* species are known from Africa (Harris 1966) and recent 16S marker evidence indicates a new species from Tanzania and Mozambique (JWA, pers. comm.). Six *Coptotermes* species are recorded from Australia; however, their identities are still not fully resolved (Lo et al. 2006). The five Papuan species are well defined morphologically (Bourguignon & Roisin 2010). The field of molecular genetics is emerging as primary evidence for identifying cryptic species and synonymies in the morphologically challenging rhinotermitid genera of *Reticulitermes* (Austin et al. 2005), *Heterotermes* (Szalanski et al. 2004), and *Coptotermes* (Scheffrahn et al. 2004; Yeap et al. 2009).

The history of *Coptotermes* in the New World is relatively uncomplicated. Only three endemic species of *Coptotermes* have been described, all from tropical America: *C. crassus* Snyder, *C. niger* Snyder, and *C. testaceus* (Linnaeus). The two exotic species from Asia, *C. formosanus* Shiraki and *C. gestroi* (Wasmann), have become invasive pests in the subtropical Nearctic region and the Neotropics, respectively (Constantino 2002; Scheffrahn & Su 2005). A third enigmatic non-native species from Africa, *C. sjostedti* (Holmgren), is established on the West Indian island of Guadeloupe (Scheffrahn et al. 2004).

Coptotermes crassus, *C. niger*, and *C. testaceus* have traditionally been identified based on geographical location with *C. crassus* spanning Mexico to Panama, *C. niger* from Guatemala to Colombia, and *C. testaceus* from Panama through South America (Becker 1953; Constantino 1998). Scheffrahn et al. (2005) began to doubt the validity of *C. crassus* and *C. niger* based on regional morphological comparisons and elected to list the senior moniker, *C. testaceus*, as the species they found in Nicaragua. Over the last 25 years, we have conducted many deliberate termite diversity surveys throughout

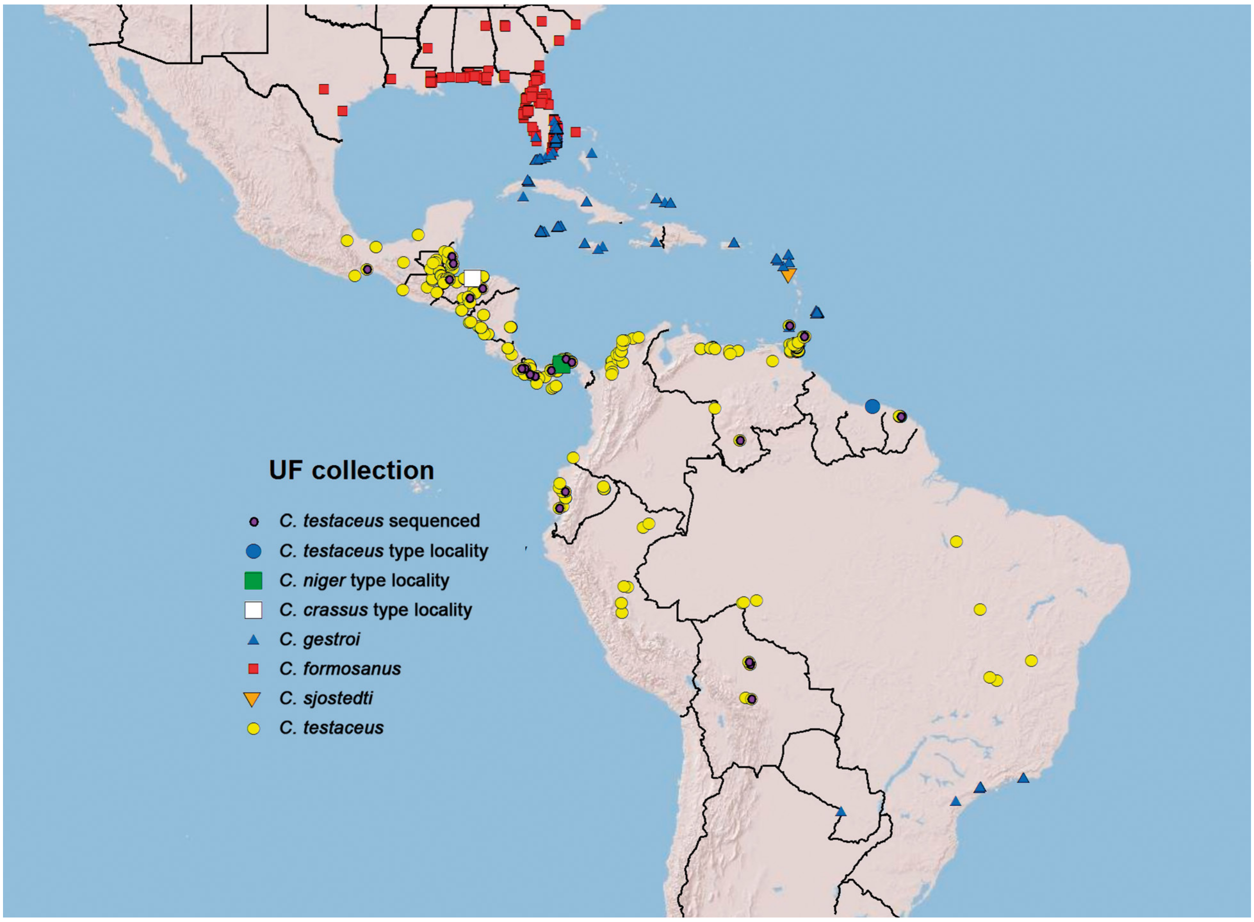

Fig. 1. New World *Coptotermes* localities from the University of Florida (UF) collection and type localities from literature. An intercepted shipment and extirpated population of *C. formosanus* in San Francisco and La Mesa, Calif., respectively, are excluded. All other UF *Coptotermes* samples were collected from land-based populations.

tropical America yielding over 34,000 colony samples of which *Coptotermes* compose about 5% of the total. We herein use morphology and molecular genetic sequences derived from the surveyed material to reduce, by synonymy, the endemic New World *Coptotermes* fauna to a single species, *C. testaceus*.

2. Materials and methods

2.1. Morphology

The distribution map (Fig. 1) was created using ArcGIS desktop ver. 10.1 (ESRI, Redlands, CA) from data exclusive to the University of Florida termite collection, Fort Lauderdale Research and Education Center, Davie, Florida. The photographs of the soldiers and alates were taken using a Leica M205C stereomicroscope attached to a Leica DFC 425 camera and then the image sequences were combined with Helicon Focus 6 software. The anterior wings were mounted on slides with PVA Mounting Medium (BioQuip #6371A) and the images were taken with a Leica DM5500B compound microscope attached to a Leica DFC 425 camera. Measurements were taken with a micrometric reticule on the eyepiece of an Olympus SZX9 stereomicroscope.

We microscopically examined and identified 1,977 samples of the New World-collected *Coptotermes*. Of these, we measured specimens selected from colony samples collected at or near the type localities (Table 1): *C. crassus* (Honduras), *C. niger* (Panama) and *C. testaceus* (French Guiana and Trinidad and Tobago). The following morphometric characters were measured, indicating, in parenthesis, the numbered measurement as defined by Roonwal (1970): soldiers (Table 2) – LH, length of head capsule (9); HH, height of head without postmentum (21); WH, maximum width of head (19); LM, maximum length of left mandible (37); HF, height of fontanelle; WF, width of fontanelle; LP, length of pronotum (65); WP, width of pronotum (68) and LT, length of hind tibia (85). Alates (Table 3) – LW, length of anterior wing with scale (73); WW, maximum width of anterior wing; LS, length of anterior wing scale (76); LP, length of pronotum (65); WP, width of pronotum (68); WH, width of head without eyes (18); LH, length of head capsule (9); DE, diameter of eye (48); DO, maximum diameter of ocellus (55) and LT, length of hind tibia (85). Types for *C. crassus* (described from soldiers only) and

C. niger, held in the Smithsonian collection (USNM), are currently unavailable because the termite holdings have been inactivated due to budget constraints (D.G. Furth, pers. comm.).

2.2. Molecular genetics

85%-ethanol-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 the DNA core sequencing facility at The University of Arkansas Medical, Little Rock for direct sequencing in both directions. Consensus sequences were constructed using Geneious v6.1.6 (Biomatters, Auckland, New Zealand). GenBank accession numbers are KM588266 to KM588293 for unique sequences found in this study. DNA sequences were aligned using Geneious v6.1.6 and adjusted manually. Twenty nine (29) samples of *C. testaceus* were sequenced for the 16S rRNA gene and used in the analysis (Table 1), as well as four samples of *C. acinaciformis* (KT215875, KT215889, KT215878, KT21589), one of *C. curvignathus* (KT215900), five of *C. formosanus* (KT215873, KT215882, KT215886, KT215871, KT215888), 14 of *C. gestroi* (KT215880, KT215896, KT215885, KT215877, KT215890, KT21 5895, KT215883, KT215897, KT215870, KT215872, KT215894, KT215874, KT215879, KT222676), two of *C. heimi* (KT215892, KT215887), one of *C. intermedius* (KT215898), two of *C. michaelseni* (KT215876, KT215893) and three of *C. sjostedti* (KT215899, KT215881, KT215884). The following 16S rRNA sequences of *Coptotermes* from GenBank were also added to the analysis: *C. acinaciformis* (AY302701, AY302702, AY558912, AY558913, AY957654, AY957655), *C. curvignathus* (AY558909, AY683210), *C. formosanus* (U17778, AY558911, AY168225, AY302703, AY302704, AY302706, AY302707, AY302708, D89831), *C. gestroi* (AY302711, AY302712, AY302713, AY558906, AY302709, AY558905, AY558907), *C. heimi* (AY558908), *C. intermedius* (AY558904), *C. lacteus* (AY303548, AY302710, JX144934, NC018125), *C. michaelseni* (AY558914), *C. sjostedti* (AY558903, AY558902), and *C. testaceus* (AY558899, AY558900, AY558901). Two additional mitochondrial 16S sequences from *Heterotermes cardini* and *H. convexinotatus* (GenBank: AY380275, AY380281) were added as outgroup taxon sequences.

The distance matrix option of PAUP* 4.0b10 (Swofford 2001) was used to calculate genetic distances according to the Kimura 2-parameter model of sequence evolution (Kimura 1980). DNA sequences were aligned using Geneious v6.1.6 (Biomatters Ltd., Auckland, New Zealand). Maximum parsimony analysis on the alignments was performed with PAUP* 4.0b10 (Swofford 2001). Gaps were treated as missing characters for all analysis. The reliability of trees was tested by applying a bootstrap test (Felsenstein 1985). Parsimony bootstrap analysis included 1,000 resamplings using the Branch and Bound algorithm of PAUP*.

For the phylogenetic analysis conducted with Bayesian inference (BI), the substitution model (HKY+G) was selected through the Akaike Information Criterion (AIC) with the jModelTest v.2.1.3 (Darriba et al. 2012). The XML input file was generated with BEAUti 1.7.4, and the BI was performed with BEAST 1.7.4 (Drummond et al. 2012). The Yule speciation process and a random starting tree were used as tree priors. Final Markov chain Monte Carlo (MCMC) searches were conducted for 100,000,000 generations. Convergence and stationarity were assessed with Tracer 1.5 (Rambaut & Drummond 2007) and the first 10,000 generations were discarded as burn-in with TreeAnnotator 1.7.4 and visualized using FigTree 1.3.1.

To test the molecular species, the Species Delimitation Plugin (SDP; Masters et al. 2011) was used with a Neighbor-Joining tree built in the Geneious software. The SDP evaluates the phylogenetic exclusivity of putative species by testing the probability that this exclusivity or monophyly has occurred by chance in a coalescent process, and assesses the probability with which a putative species can be diagnosed successfully on a phylogenetic tree by comparing intra- and interspecific genetic distances (Masters et al. 2011). SDP was used to calculate the average pairwise tree distance between (Inter Dist) and among (Intra Dist) members of putative species; the ratio of Intra to Inter Dist; the mean probability of making a correct identification of an unknown specimen; the mean distance between the most recent common ancestor of a species and its members; and Rosenberg's PAB (Rosenberg 2007), a test for taxonomic distinctiveness based on the null hypothesis that monophyly is a chance outcome of random branching.

3. Results

3.1. Morphology

The identifications and collection localities of the 1,977 *Coptotermes* samples examined are summarized in Fig. 1. Of these, 831 samples were identified as *C. testaceus*. As often noted for workers (Campora & Grace 2004; Grace et al. 1995), *Coptotermes* posit considerable variability

Table 2. Measurements of New World *Coptotermes* soldiers. — ***Abbreviations***: LH, length of head capsule; HH, height of head without postmentum; WH, maximum width of head; LM, maximum length of left mandible; HF, height of fontanelle; WF, width of fontanelle; LP, length of pronotum; WP, width of pronotum; and LT, length of hind tibia.

Measure (in mm) of:	***C. testaceus*** (type locality)	***C. testaceus*** (Mathews 1977)	***C. niger*** (type locality)	***C. niger*** (type)	***C. crassus*** (type locality)	***C. crassus*** (Light 1933)
LH	1.38–1.50	1.29–1.52	1.35–1.45	1.20–1.30	1.39–1.45	1.40–1.50
HH	0.73–0.90	0.65–0.94	0.75–0.85		0.78–0.83	
WH	1.13–1.30	1.13–1.33	1.08–1.13	1.15–1.20	1.10–1.18	1.10–1.35
LM	0.85–0.95	0.97–1.10	0.88–0.93	0.80–0.85	0.86–0.93	0.90–0.95
HF	0.15–0.15		0.13–0.16		0.14–0.18	
WF	0.18–0.23		0.18–0.20		0.16–0.19	
LP	0.48–0.55	0.46–0.54	0.43–0.50	0.40–0.40	0.50–0.50	0.31–0.41
WP	0.83–0.95	0.82–1.05	0.83–0.90	0.70–0.75	0.85–0.90	0.81–0.95
LT	1.03–1.05	1.09–1.26	1.03–1.13	0.80–0.90	1.00–1.10	1.00–1.01

Table 3. Measurements of New World *Coptotermes* alates. — ***Abbreviations***: LW, length of anterior wing with scale; WW, maximum width of anterior wing; LS, length of anterior wing scale; LP, length of pronotum; WP, width of pronotum; WH, width of head without eyes; LH, length of head capsule; DE, diameter of eye; DO, maximum diameter of ocellus; and LT, length of hind tibia. (*) = with eyes.

Measure (in mm) of:	***C. testaceus*** (type locality)	***C. testaceus*** (Mathews 1977)	***C. niger*** (type locality)	***C. niger*** (type)	***C. crassus*** (type locality)	***C. crassus*** (Light 1933)
LW	11.90–12.10	12.00–12.50	12.20–13.60	10.50–11.50	12.90–13.50	12.75
WW	3.25–3.65		3.49–3.97	3.00–3.25	3.33–3.65	3.50
LS	1.13–1.20		1.13–1.28	1.00–1.00	1.13–1.23	
LP	0.93–1.00	0.99–1.05	0.95–1.00	0.90–0.90	0.88–0.99	0.88
WP	1.43–1.43	1.47–1.56	1.43–1.50	1.30–1.40	1.38–1.43	1.46
WH	1.35–1.38	1.40–1.46*	1.36–1.43	1.30–1.40	1.33–1.38	1.50*
LH	1.10–1.18		1.15–1.20	1.60–1.65	1.10–1.20	1.20
DE	0.38–0.40	0.36–0.40	0.38–0.40	0.30–0.31	0.38–0.40	0.36
DO	0.13–0.15	0.12–0.14	0.13–0.15		0.14–0.15	0.12
LT	1.38–1.48	1.30–1.39	1.43–1.48	1.30–1.30	1.40–1.48	1.35

among soldier and imago characters as pointed out by Mathews (1977) who separated his specimens into two "morphs". This may be owed to the kind of clinal, developmental, and nutritional variability observed in species which often leads to erroneous classifications and error. For example, latitude has been demonstrated to have significant influence on *Reticulitermes grassei* in Europe, even influencing genetic colony structure (Vargo et al. 2013). The measurements of alates and soldiers from the type localities and from the literature (Tables 2, 3) reflect this range of intraspecific measurements to support our hypothesis that there is single endemic *Coptotermes* species in the New World, *C. testaceus*. It should be noted that measurements of the type series of *C. niger* (Snyder 1922; Tables 2, 3) fall within the smaller range of our measurements.

3.2. Molecular genetics

Molecular phylogeny (Fig. 2) elucidates a single endemic and monophyletic New World branch (Posterior Probability = 95%). Two clades diverge inside this group, but with low branch support (PP = 40% and 22%). The two colonies sampled near the type locality of *C. crassus* (from Honduras) were nested in different clades, one with samples from Panama, Belize, and Guatemala and the other with samples from Belize, Trinidad and Tobago, and Ecuador. Of samples collected near the type locality of *C. niger* (Panama), most were nested in the same clade, but with low branch support (PP = 39%). One was nested with samples from Honduras, Belize, and Guatemala, and the last one was nested in a well supported branch (PP = 100%) with colonies from Costa Rica, Belize, Ecuador, and Mexico. Aside from this, one other clade, composed of samples from Venezuela, Bolivia, and Peru, had good branch support (PP = 98%). These two well-supported branches were morphologically reexamined for characters that could be used to diagnose these putative species, however, all the samples were within the range of morphometric variation of *C. testaceus*. Thus, our decision to synonymize *C. crassus* and *C. niger* into *C. testaceus* using the Principle of Priority (ICZN 1999) is based on both morphological grounds and molecular evidence.

The Neighbor-Joining tree (Fig. S1 in El. Suppl.) was congruent with the Bayesian tree (Fig. 2), grouping all species determined a priori. The SDP result corroborates a single endemic Neotropical species (Table 4). The probability of making a correct identification of an unknown specimen of *C. testaceus* is relatively high: both P IDs (strict and liberal) are very similar to the other species. Also, Rosenberg's P (Table 4) is highly significant for

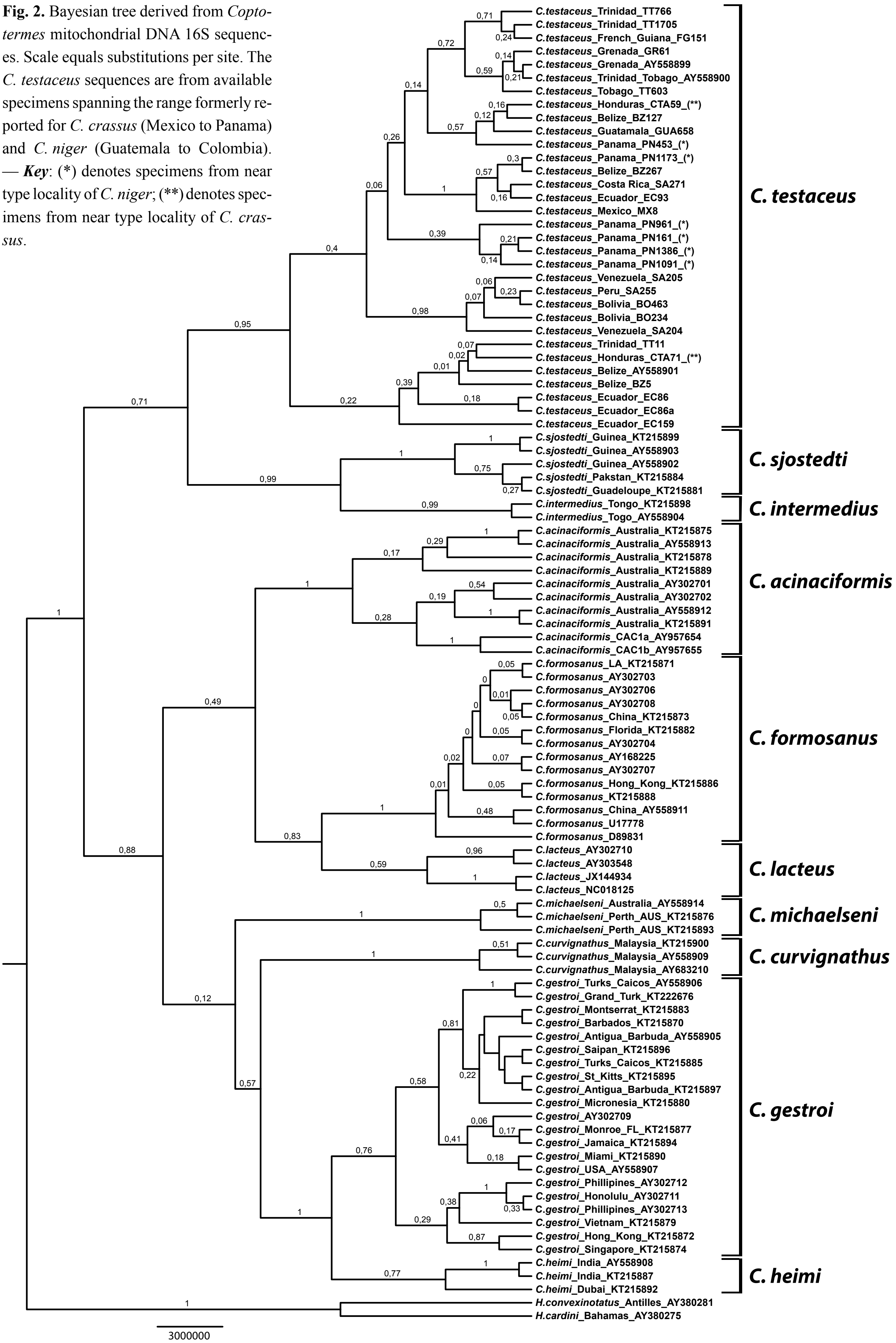

Fig. 2. Bayesian tree derived from *Coptotermes* mitochondrial DNA 16S sequences. Scale equals substitutions per site. The *C. testaceus* sequences are from available specimens spanning the range formerly reported for *C. crassus* (Mexico to Panama) and *C. niger* (Guatemala to Colombia). — ***Key***: (*) denotes specimens from near type locality of *C. niger*; (**) denotes specimens from near type locality of *C. crassus*.

Table 4. Species Delimitation Plugin results for *Coptotermes* Neighbor-Joining tree. Average pairwise tree distance between (Inter Dist) and among (Intra Dist) members of putative species; Intra to Inter Dist ratio; mean probability of making a correct identification of an unknown specimen (P ID strict and liberal); mean distance between the most recent common ancestor (Av-MRCA); and Rosenberg's P.

Species	Intra Dist	Inter Dist	Intra/Inter	P ID(Strict)	P ID(Liberal)	Av-MRCA	Rosenberg
C. testaceus	0.014	0.022	0.64	0.80 (0.74, 0.85)	0.95 (0.92, 0.98)	0.0082	3.40E-09
C. intermedius	3.39E-05	0.018	1.89E-03	0.59 (0.44, 0.74)	0.98 (0.83, 1.0)	1.70E-05	0.02
C. sjostedti	0.005	0.018	0.27	0.75 (0.62, 0.88)	0.94 (0.84, 1.0)	0.0034	0.02
C. curvignathus	0.002	0.027	0.07	0.75 (0.57, 0.92)	0.97 (0.83, 1.0)	9.19E-04	2.60E-05
C. gestroi	0.006	0.022	0.27	0.91 (0.85, 0.96)	0.97 (0.94, 1.00)	0.0066	4.20E-05
C. heimi	0.008	0.022	0.35	0.56 (0.38, 0.74)	0.81 (0.67, 0.96)	0.0053	4.20E-05
C. michaelseni	0.002	0.042	0.04	0.76 (0.59, 0.94)	0.98 (0.84, 1.0)	9.80E-04	3.10E-04
C. acinaciformis	0.025	0.042	0.6	0.77 (0.70, 0.83)	0.93 (0.89, 0.98)	0.019	3.10E-04
C. formosanus	0.002	0.024	0.08	0.96 (0.89, 1.0)	0.99 (0.95, 1.0)	0.0015	3.80E-05
C. lacteus	0.01	0.024	0.4	0.60 (0.45, 0.74)	0.86 (0.75, 0.97)	0.0072	3.80E-05

Fig. 3. Live habitus of *Coptotermes testaceus* castes nesting in a tree stump in Trinidad.

C. testaceus, meaning that the probability of reciprocal monophyly under a random coalescent model is high. Although the genetic diversity within *C. testaceus* was relatively high compared to the other species (Intra Dist, Table 4), this was an expected consequence of the huge endemic distribution of this species.

3.3. Taxonomy

***Coptotermes testaceus* (Linnaeus)**

Imagos: Figs. 3–5, Table 3; Soldiers: Figs. 6–10, Table 2

Coptotermes crassus Snyder, 1922: 21. syn. nov.
Coptotermes niger Snyder, 1922: 19. syn. nov.
Previous nomenclatural history in Krishna et al. 2013.

Description. Mathews' (1977) description is adequate with the following additions: ***Imagos***: Fore wing: proximal one-fifth of wing membrane without setae; setae in remainder of membrane numerous; pilosity of costal margin and radial sector robust. Membrane contains thousands of dark tubercules which blanket most of the wing membrane and contribute to its pigmentation. Costal margin and radial sector, basal branch of cubitus, and all subordinate veins dark brown relative to membrane when backlit. ***Soldiers***: Three pairs of setae, best seen in lateral view, surrounding the fontanelle; a seventh seta often adjoining fontanelle. Head, in dorsal view, converging before mid-length (Mathews 1977, second morph).

Material examined. All material examined in this study is housed in the University of Florida termite collection, Fort Lauderdale Research and Education Center, Davie, Florida. Measured material listed in Table 1.

Diagnosis. Imagos of *C. testaceus*, *C. gestroi*, and *C. formosanus*, can be easily identified by wing and body coloration. *Coptotermes testaceus* is the darkest of the three

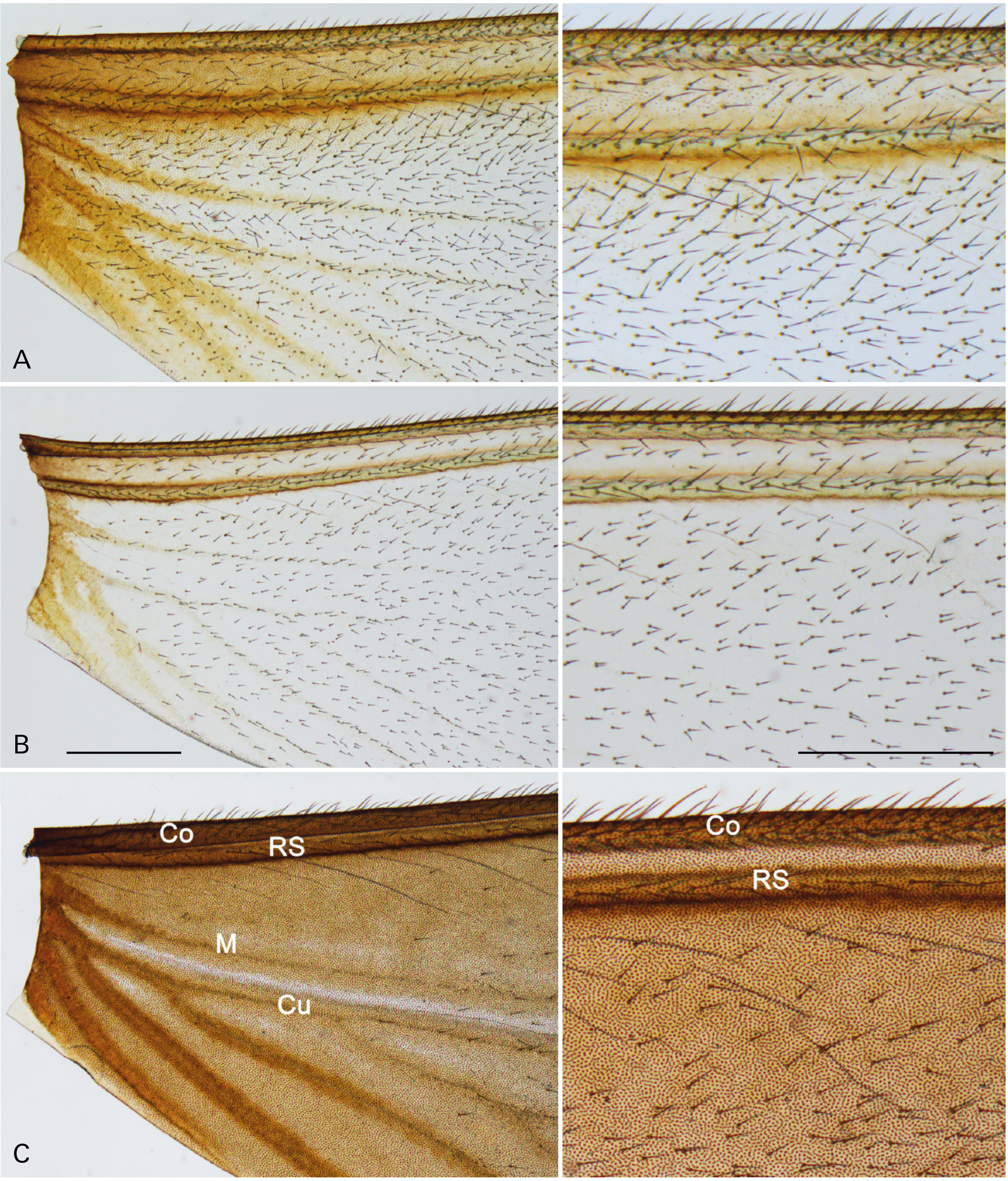

Fig. 4. Proximal and median sections of *Coptotermes* right forewings. **A**: *C. formosanus*; **B**: *C. gestroi*; **C**: *C. testaceus*. — ***Abbreviations***: Co = costal margin, RS = radial sector, M = median vein, Cu = cubitus vein. All images in each column use the same scale bar (= 500 µm).

with shiny-black wings in live specimens (Fig. 3) and dark-brown wings in those preserved in ethanol (Fig. 4). The wing membrane and basal veins of *C. testaceus* are very darkly pigmented, while in *C. formosanus* and *C. gestroi*, they are, respectively, lighter. The costal margin (C), radial sector (RS), and basal veins of *C. formosanus* have a brownish halo; almost absent in *C. gestroi* (Fig. 4). *Coptotermes testaceus* has the darkest dorsal body coloration followed by *C. gestroi*, and finally *C. formosanus* (Fig. 5). Among these three species, only *C. gestroi* has a clearly discernible "antennal spot" (Su & Scheffrahn 1998). Harris (1966) reports the body coloration of *C. sjostedti* to be red-brown, which would place this species intermediate between *C. formosanus* and *C. gestroi*. As in all *Coptotermes* imagos, the bodies are covered with medium short to long setae which are densely spaced.

Fig. 5. Lateral and dorsal views of head and nota of *Coptotermes*. **A**: *C. formosanus*; **B**: *C. gestroi*; **C**: *C. testaceus*. All images in each column use the same scale bar (= 1 mm).

The wing pilosity is also diagnostic for the three species. The wing of *Coptotermes testaceus* is almost glabrous at the basal fourth; with sparse setae near the RS and a denser coverage on the middle of the RS and along the cubitus (Cu) vein in the second third; the distal third is homogeneously pilose. The wing pilosity of *C. formosanus* and *C. gestroi* are nearly homogeneous along the entire surface, but *C. formosanus* has longer and thicker setae than *C. gestroi*. Harris (1966) reported that the wings of *C. sjostedti* are brown, with the membrane densely covered with short bristles with a fore wing length of 12 – 13 mm (Garamba, Congo) and 10 mm (southern Nigeria).

Soldiers of the three common species can be separated by setal patterns around the fontanelle. Compared with *Coptotermes formosanus* (two pairs) and *C. gestroi* (one pair), soldiers of *C. testaceus* normally have three pairs of setae bordering the fontanelle. *Coptotermes sjostedti* has only one pair, like *C. gestroi*, but the former is considerably smaller than all the other species of the genus in the New World and has a more oval head capsule shape. In lateral view, the vertex of *C. formosanus* forms a weak even curve before ending in an abrupt slope at the fontanelle, while in *C. gestroi*, the vertex has a sloping curvature before reaching the fontanelle (Fig. 6). The head capsule of *C. testaceus* has the greatest pilosity followed in order by *C. formosanus*, *C. gestroi*, and *C. sjostedti*. In dorsal view, the maximum head width of *C. testaceus* occurs proximal the midpoint of the head capsule while in the other species the maximum head width is near or slightly distal to the midpoint.

4. Discussion

The imago of *Coptotermes testaceus* was described from "America" by Linnaeus (1758) as *Hemerobius testaceus* and was doubtless part of Daniel Rolander's 1755 insect collection from Suriname (Dobreff 2010). This was one of three termite species to be described by Linnaeus from Rolander's Suriname material (Krishna et al. 2013). The soldier was later described by Hagen (1858a) as *Termes Marabitanas* (sic) from Brazil. Hagen (1858b) reported this species from Brazil, Chile (?), French Guiana, Guyana, Suriname, and Venezuela. Snyder (1922) described *C. niger* from soldiers and imagos collected in Panama. His remarks on alate coloration noted that the head, pronotum, and dorsal surface of the abdomen were "very dark castaneous-brown to black"; and the wings were "dark gray-brown". Snyder (1925) expanded the range of *C. niger* to include Colombia, Costa Rica, and Guatemala. Emerson's (1925) redescription of the *C. marabitanas* (= *testaceus*) imago noted that coloration of the head and pronotum was "brownish black" and wings,

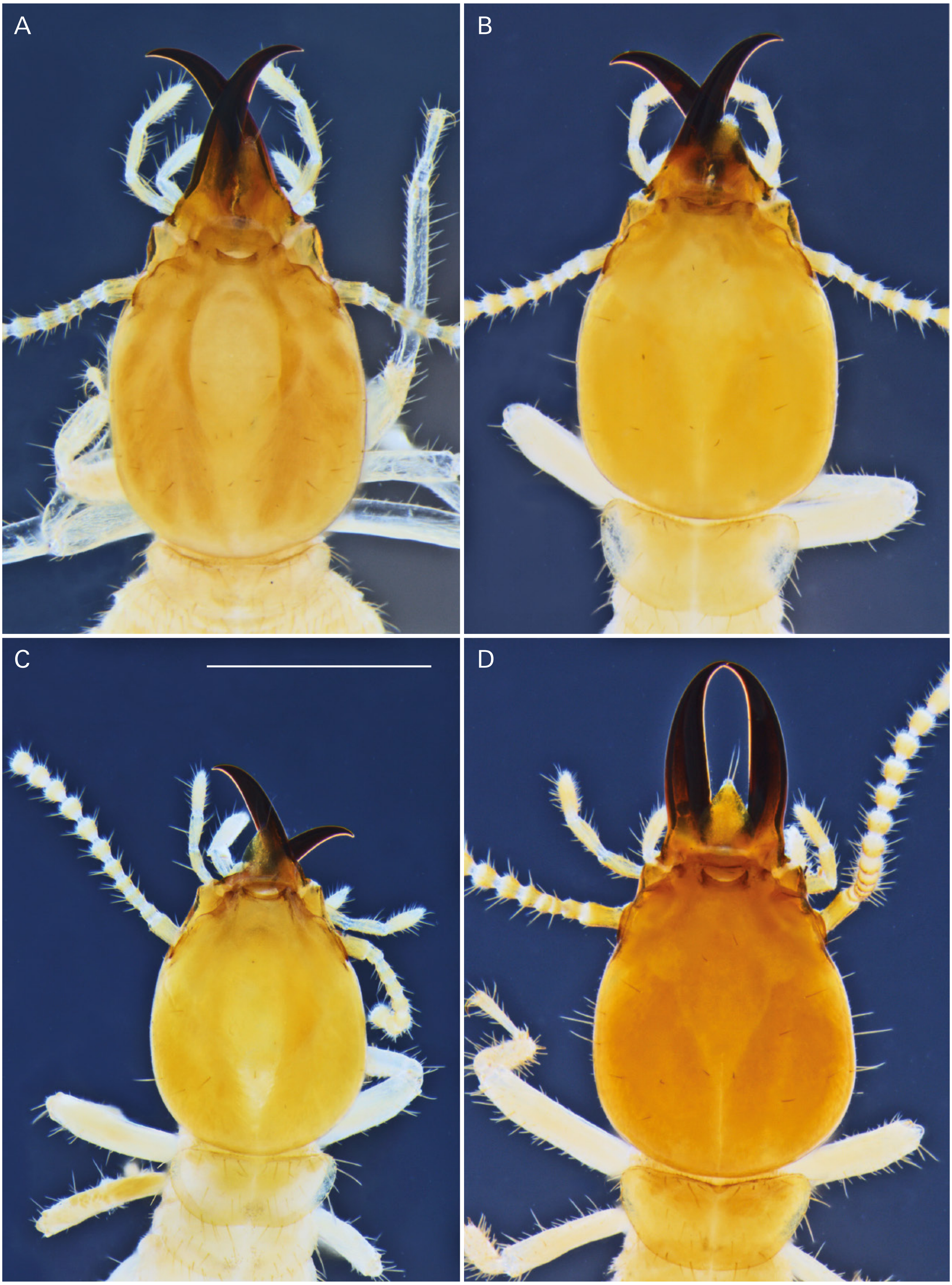

Fig. 6. Dorsal view of soldier head and pronotum of *Coptotermes*. **A**: *C. formosanus*; **B**: *C. gestroi*; **C**: *C. sjostedti*; **D**: *C. testaceus*. Scale bar same for each image (= 1 mm).

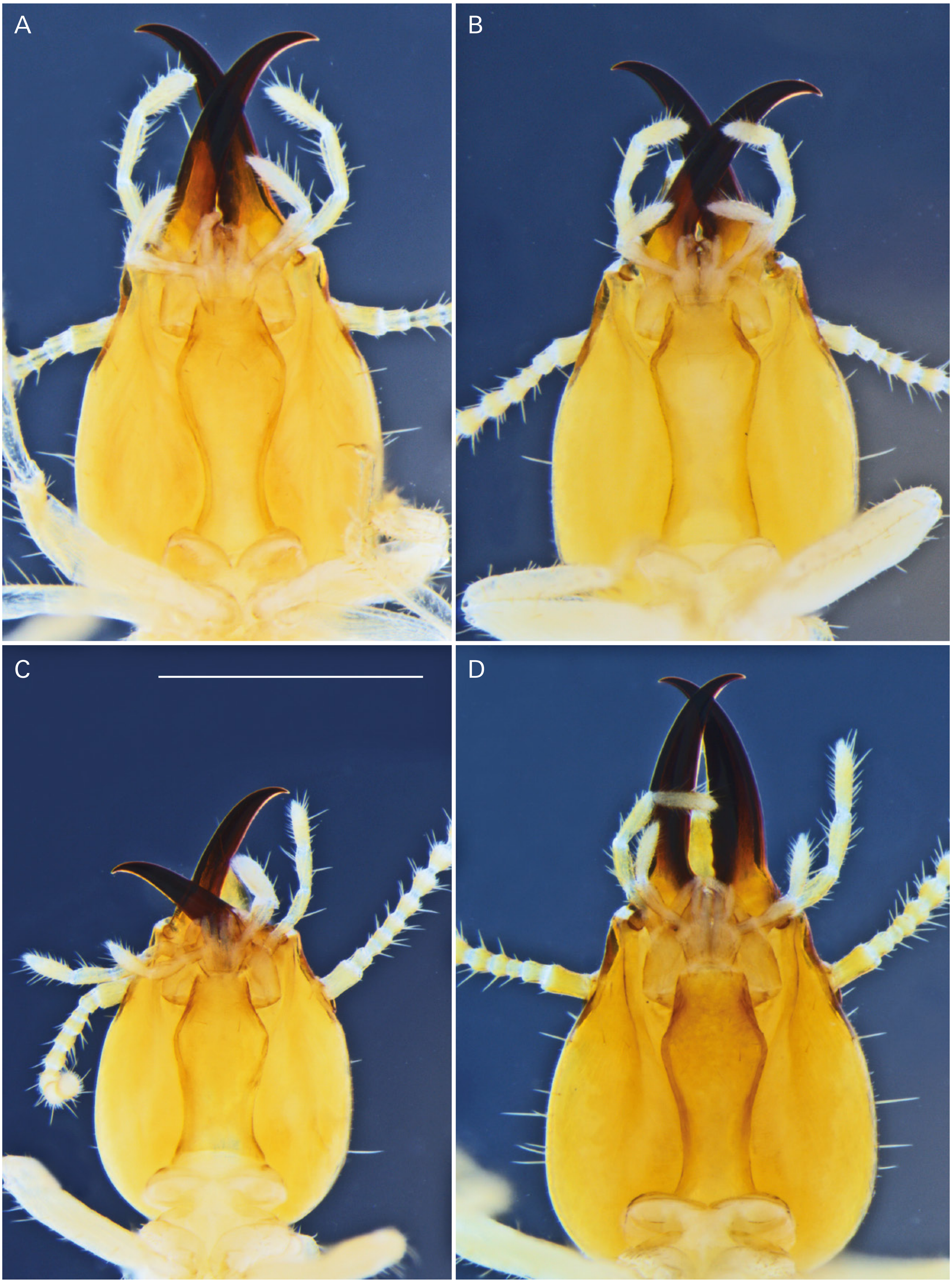

Fig. 7. Ventral view of soldier head of *Coptotermes*. **A**: *C. formosanus*; **B**: *C. gestroi*; **C**: *C. sjostedti*; **D**: *C. testaceus*. Scale bar same for each image (= 1 mm).

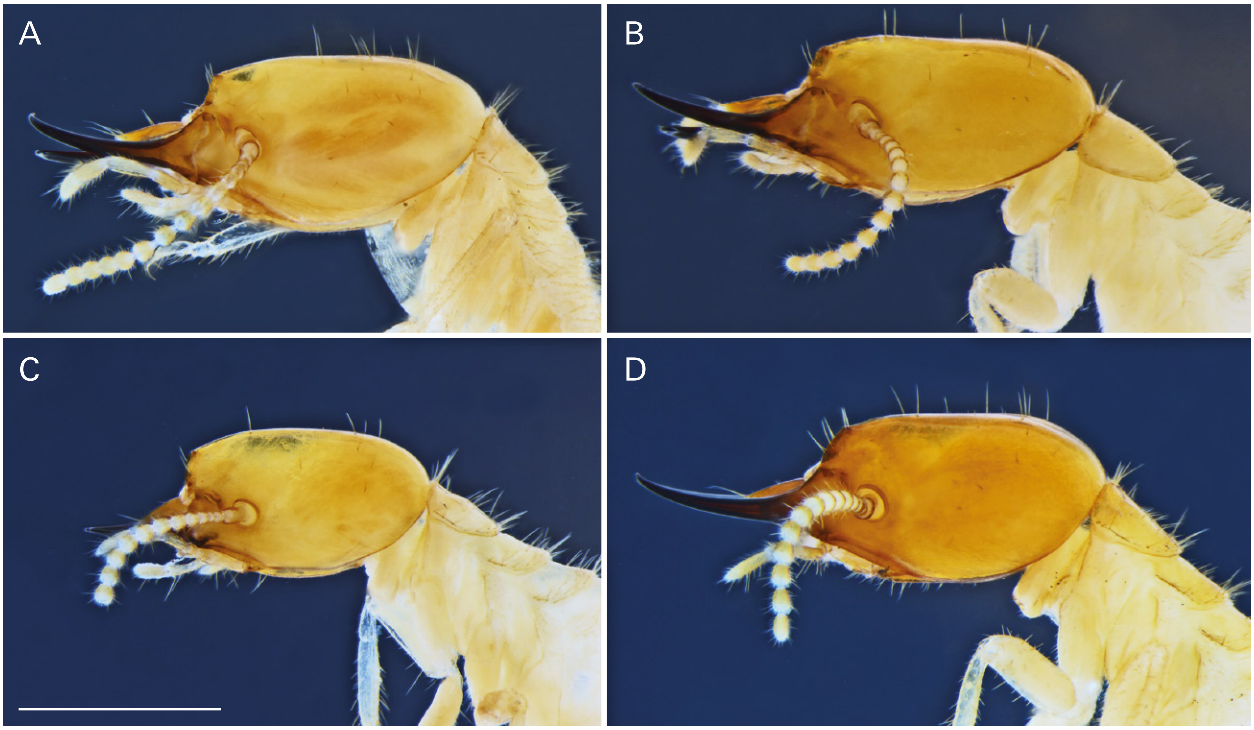

Fig. 8. Lateral view of soldier head and nota of *Coptotermes*. **A**: *C. formosanus*; **B**: *C. gestroi*; **C**: *C. sjostedti*; **D**: *C. testaceus*. Scale bar same for each image (= 1 mm).

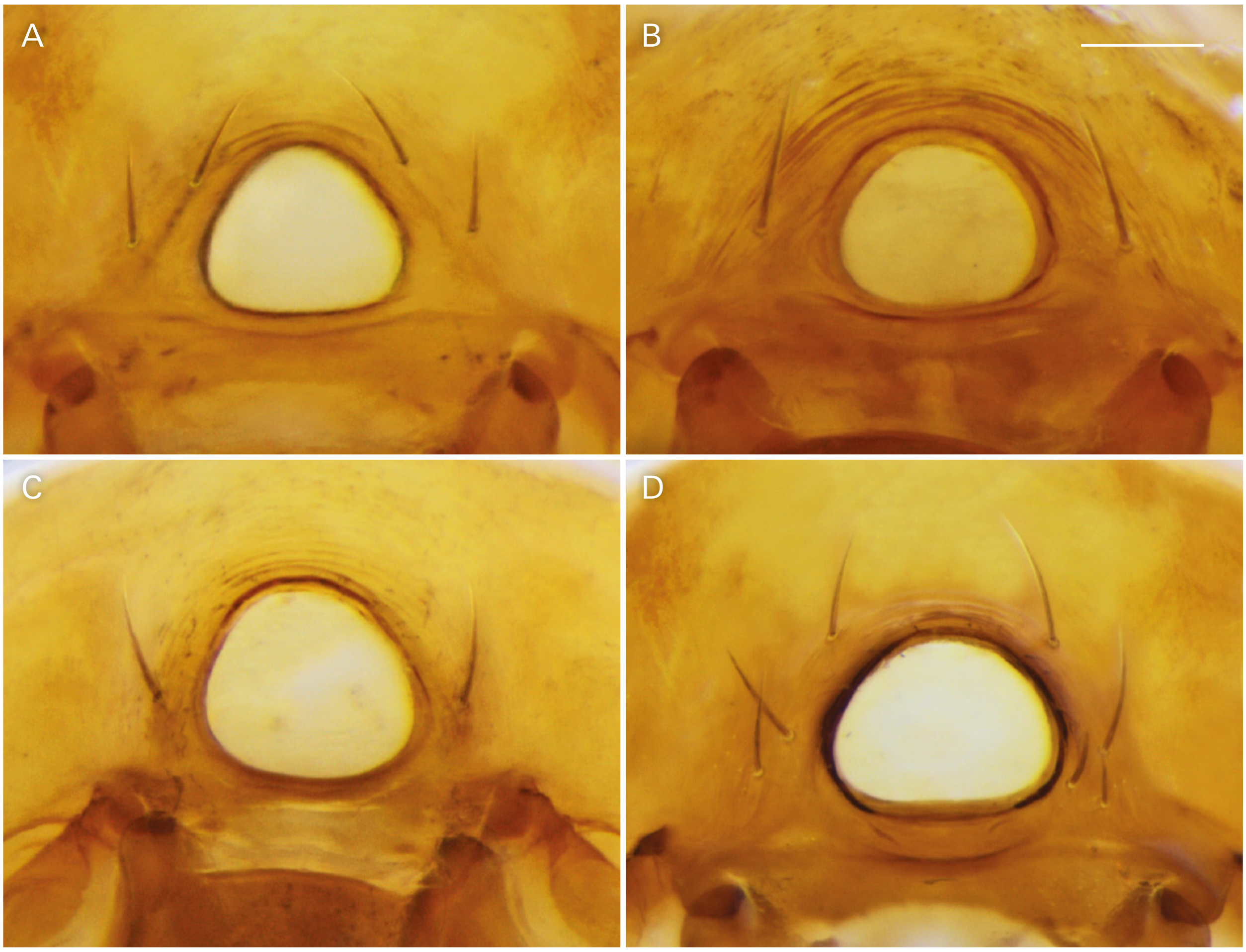

Fig. 9. Anterior view of soldier fontanelle of *Coptotermes*. **A**: *C. formosanus*; **B**: *C. gestroi*; **C**: *C. sjostedti*; **D**: *C. testaceus*. Scale bar same for each image (= 0.1 mm).

Fig. 10. Live habitus of *Coptotermes testaceus* foragers in nest carton in Ecuador.

"dark smokey". Emerson (1925) wrote the following: "*C. marabitanas* is distinguished from *C. niger* Snyder in the ocelli being less than their length from the eye" and "*C. niger* Snyder is difficult to distinguish from this [*marabitanas*] species". We found ocellus position to be a variable intraspecific character. *Coptotermes crassus* was described only from soldiers collected in Honduras (Snyder 1922). The imago was later described from southern Mexico by Light (1933) who noted them to be "extremely dark". Our examination now indicates that the preceding descriptions of *C. niger* and *C. crassus* were provincial accounts of a single very dark species, *C. testaceus*, described by Linnaeus nearly two centuries earlier. *Coptotermes testaceus* appears to be the only *Coptotermes* species worldwide with very dark alates.

Most, if not all *Coptotermes* initiate nests in living trees worldwide (Greaves 1962; Cowie et al. 1989; Osbrink et al. 1999). *Coptotermes testaceus* is the dominant live tree nester in Amazonia (Apolinário & Martius 2004). Infested trees are detected by a patch of feces/soil which covers galleries leading from the surface to the interior nest (Fig. 11). The lack of nest-site competition with other wood-feeding termites to exploit this niche along with the stability of heartwood habitats, may have allowed this species to occupy a very large range (Fig. 1). This includes all neotropical habitats with sufficient moisture to support tree growth, including mangrove and littoral forests. *Coptotermes* are among the strongest and most distant termite fliers (Mullins et al. 2015) compared to the short flights of *Cryptotermes brevis* (Walker) and *Nasutitermes corniger* (Motschulsky) (Guerreiro et al. 2013 and Tonini et al. 2013, respectively).

Live tree nesting may account for the commonality of *C. testaceus* foragers in prefossil inclusions of Colombian copal (Woodruff and Scheffrahn pers. obs.; Lavelle 2012; Penney & Preziosi 2013). Four fossil species are known from Mexican and Dominican amber (Oligocene/Miocene) (Emerson 1971; Krishna & Grimaldi 2009), which suggest a transoceanic arrival of one or more ancestral *Coptotermes* to the New World. The lone Mexican fossil species, *C. sucineus* Emerson, compares favorably with *C. testaceus* (Emerson 1971) regarding overall pilosity, with the exception of a larger, darker forewing in the latter.

As with other *Coptotermes* species (Chouvenc et al. 2015), flights of *C. testaceus* can be massive. During a flight northeast of Tegucigalpa, Honduras (30 May 2007, 1700 hrs), net catches from a moving vehicle were used to estimate that over 4.3 million alates / km^2 were flying at the moment of sampling (Scheffrahn et al. unpublished data). Alates were observed flying that day along 200 km of highway from Salamá during and after intermittent rainfall followed by sunshine. If the totality of flight area was 2,000 km^2 (10-km-wide swath along highway), over 8 billion *C. testaceus* flew in the area on that day. Alates were observed to be strong fliers but shed wings as soon as they alighted on stationary objects.

Unlike invasive *Coptotermes*, *C. testaceus* apparently does not have the qualities for dispersal using anthropogenic assistance (Su 2013). Unlike crepuscular/nocturnal flights of *C. formosanus* and *C. gestroi*, the diurnal dispersal flights of *C. testaceus* (e.g., Honduras flight record above, Emerson 1938) would negate attraction to lights of marine vessels where colonization by the former two

Fig. 11. Soil/fecal patches of *Coptotermes testaceus* on live trees. **A**: A patch 2.5 m above ground in a Panamanian rainforest. **B**: A patch 0.5 m above ground in seasonally flooded savanna in central Bolivia (inset shows galleries leading into tree where patch was removed). Scale bar same for A and B (scale bar = 0.2 m).

species is common (Scheffrahn & Crowe 2011; Hochmair & Scheffrahn 2010). This is evident by the predominant absence of *C. testaceus* in the West Indies where *C. gestroi* has been widely introduced (Fig. 1). The origin of *C. testaceus* on Trinidad and Tobago is undoubtedly due to the Late Pleistocene emergence of the Venezuelan shelf on which both islands sit. The Grenada populations of *C. testaceus*, being the nearest island to Trinidad and Tobago, suggest ancient overwater dispersal, as less than 70 km separated the emergent Venezuelan shelf from the Grenada bank (Google Earth) during the Pleistocene sea level minimum.

5. Acknowledgements

We thank Terminix International, BASF Corporation, and Tom Nishimura for travel support. We thank Amber Tripodi for assisting with the molecular genetics analysis and recognize the São Paulo Research Foundation (FAPESP) for research scholarships 2013/03767-0 and 2013/20247-0 to T.F. Carrijo. All specimens were collected with appropriate permits in the possession of the first author. This paper is dedicated to Jill Halliburton Su (1955–2014).

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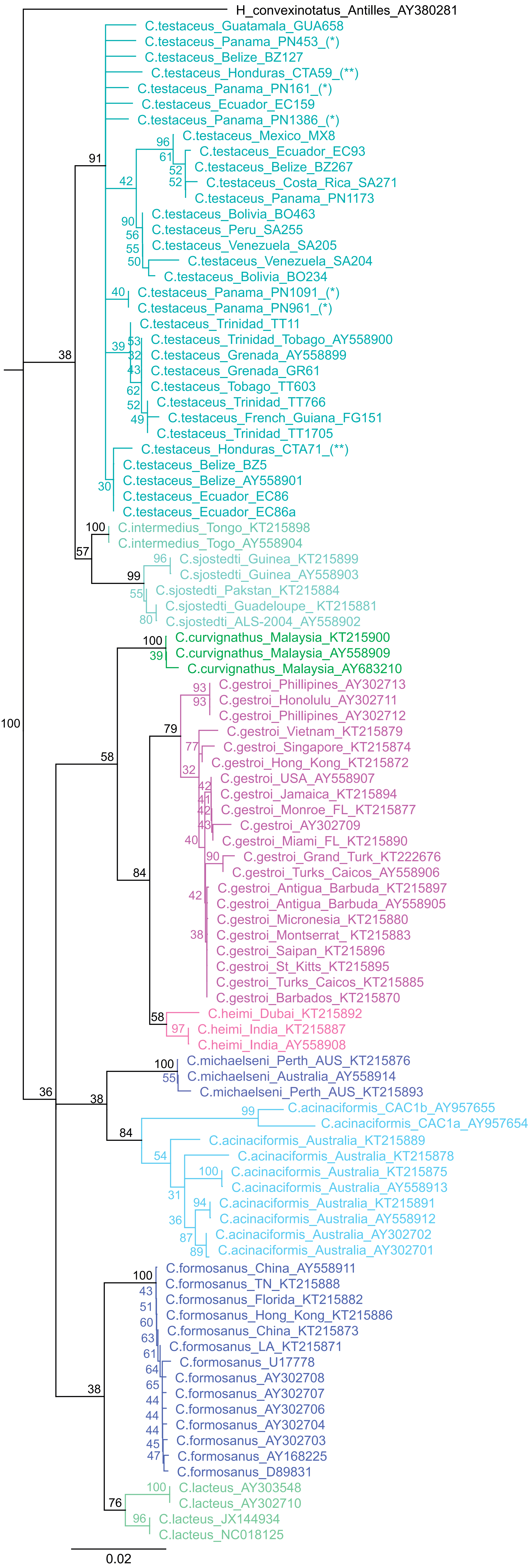
Electronic Supplement File

at http://www.senckenberg.de/arthropod-systematics (“Contents”)

File 1: scheffrahn&al-coptotermes-asp2015-electronicsupplement-1.pdf. – **Fig. S1.** Neighbor-joining species delimitation tree from same *Coptotermes* sequences used to construct Fig. 2. Key: (*) denotes specimens from near type locality of *C. niger*, and (**) denotes specimens from near type locality of *C. crassus*.


H_convexinotatus_Antilles_AY380281
C.testaceus_Guatamala_GUA658
C.testaceus_Panama_PN453_(*)
C.testaceus_Belize_BZ127
C.testaceus_Honduras_CTA59_(**)
C.testaceus_Panama_PN161_(*)
C.testaceus_Ecuador_EC159
C.testaceus_Panama_PN1386_(*)
96
C.testaceus_Mexico_MX8
C.testaceus_Ecuador_EC93
61
91
C.testaceus_Belize_BZ267
52
52
C.testaceus_Costa_Rica_SA271
42
C.testaceus_Panama_PN1173
C.testaceus_Bolivia_BO463
90
C.testaceus_Peru_SA255
56
C.testaceus_Venezuela_SA205
55
C.testaceus_Venezuela_SA204
50
C.testaceus_Bolivia_BO234
40
C.testaceus_Panama_PN1091_(*)
C.testaceus_Panama_PN961_(*)
C.testaceus_Trinidad_TT11
53
C.testaceus_Trinidad_Tobago_AY558900
39
38
32
C.testaceus_Grenada_AY558899
43
C.testaceus_Grenada_GR61
C.testaceus_Tobago_TT603
62
C.testaceus_Trinidad_TT766
52
C.testaceus_French_Guiana_FG151
49
C.testaceus_Trinidad_TT1705
C.testaceus_Honduras_CTA71_(**)
C.testaceus_Belize_BZ5
C.testaceus_Belize_AY558901
30
C.testaceus_Ecuador_EC86
C.testaceus_Ecuador_EC86a
100
C.intermedius_Tongo_KT215898
C.intermedius_Togo_AY558904
57
96
C.sjostedti_Guinea_KT215899
99
C.sjostedti_Guinea_AY558903
C.sjostedti_Pakstan_KT215884
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C.sjostedti_Guadeloupe_ KT215881
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C.sjostedti_ALS-2004_AY558902
100
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C.curvignathus_Malaysia_AY683210
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C.gestroi_Phillipines_AY302713
93
C.gestroi_Honolulu_AY302711
C.gestroi_Phillipines_AY302712
100
79
C.gestroi_Vietnam_KT215879
77
C.gestroi_Singapore_KT215874
58
C.gestroi_Hong_Kong_KT215872
32
C.gestroi_USA_AY558907
42
C.gestroi_Jamaica_KT215894
41
42
C.gestroi_Monroe_FL_KT215877
43
C.gestroi_AY302709
40
C.gestroi_Miami_FL_KT215890
90
C.gestroi_Grand_Turk_KT222676
84
C.gestroi_Turks_Caicos_AY558906
42
C.gestroi_Antigua_Barbuda_KT215897
C.gestroi_Antigua_Barbuda_AY558905
C.gestroi_Micronesia_KT215880
38
C.gestroi_Montserrat_ KT215883
C.gestroi_Saipan_KT215896
C.gestroi_St_Kitts_KT215895
C.gestroi_Turks_Caicos_KT215885
C.gestroi_Barbados_KT215870
58
C.heimi_Dubai_KT215892
97
C.heimi_India_KT215887
C.heimi_India_AY558908
100
C.michaelseni_Perth_AUS_KT215876
55
C.michaelseni_Australia_AY558914
36
38
C.michaelseni_Perth_AUS_KT215893
99
C.acinaciformis_CAC1b_AY957655
C.acinaciformis_CAC1a_AY957654
84
C.acinaciformis_Australia_KT215889
54
C.acinaciformis_Australia_KT215878
100
C.acinaciformis_Australia_KT215875
31
C.acinaciformis_Australia_AY558913
94
C.acinaciformis_Australia_KT215891
36
C.acinaciformis_Australia_AY558912
87
C.acinaciformis_Australia_AY302702
89
C.acinaciformis_Australia_AY302701
100
C.formosanus_China_AY558911
43
C.formosanus_TN_KT215888
51
C.formosanus_Florida_KT215882
60
C.formosanus_Hong_Kong_KT215886
63
C.formosanus_China_KT215873
61
C.formosanus_LA_KT215871
64
C.formosanus_U17778
65
38
C.formosanus_AY302708
44
C.formosanus_AY302707
44
C.formosanus_AY302706
44
C.formosanus_AY302704
45
C.formosanus_AY302703
47
C.formosanus_AY168225
C.formosanus_D89831
100
C.lacteus_AY303548
76
C.lacteus_AY302710
96
C.lacteus_JX144934
C.lacteus_NC018125
0.02

Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2015

Band/Volume: 73

Autor(en)/Author(s): Scheffrahn Rudolf H., diverse

Artikel/Article: A single endemic and three exotic species of the termite genus Coptotermes (Isoptera, Rhinotermitidae) in the New World 333-348