

Redescription of the Monotypic Neotropical Genus *Crepititermes* Emerson (Termitidae: Termitinae)

MM ROCHA, C CUEZZO

Museu de Zoologia da Univ de São Paulo, São Paulo, SP, Brasil

Keywords

Neotropics, new records, taxonomy, termites, worker gut

Correspondence

MM Rocha, Museu de Zoologia da Univ de São Paulo, Cx. Postal 42.494, 04218-970 São Paulo, SP, Brasil; mrocha@usp.br

Edited by Roberto A Zucchi – ESALQ/USP

Received 4 February 2015 and accepted 28 May 2015

Published online: 5 August 2015

© Sociedade Entomológica do Brasil 2015

Abstract

Based on a reexamination of specimens of *Crepititermes* Emerson deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (MZUSP), we characterize the morphology and coiling in situ of the digestive tube of workers of *Crepititermes verruculosus* Emerson for the first time. We provide additional notes on the imago and soldier and present digital images and illustrations for all castes. We also update the currently known geographical distribution of *C. verruculosus*, adding some biological remarks.

Introduction

Emerson (1925) described *Crepititermes* as a Neotropical termitine subgenus of *Mirotermes* Holmgren and diagnosed the small species *Mirotermes (Crepititermes) verruculosus*, based on external morphological characters of the imago and soldier castes from six colonies collected at Kartabo, Guyana, but he provided no remarks on field notes or biology. Snyder (1949) recognized the generic status of *Crepititermes*, and Mathews (1977) improved the generic diagnoses of the alate and soldier castes, establishing *Crepititermes verruculosus* Emerson as the type species by monotypy, recording *C. verruculosus* inside the nests of *Cornitermes bequaerti* Emerson, *Cornitermes snyderi* Emerson, and *Silvestritermes euamignathus* (Silvestri) in the “Serra do Roncador,” Mato Grosso, Brasil. Thereafter, the known geographical range of *C. verruculosus* was expanded by several recent records (Davies 2002, Bourguignon *et al* 2011, Palin *et al* 2011, Canello *et al* 2014).

Based on a reexamination of specimens of *Crepititermes* deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (MZUSP), we describe the gut morphology and coiling in situ of the workers for the first time. We provide additional notes on the imago and soldier and present digital images and illustrations for all castes. We also

update the currently known geographical distribution of the species, based on records from different collections of Isoptera, adding some biological notes.

Material and Methods

Biological material

All the specimens examined are housed in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (MZUSP). The list of material examined is sorted by country (uppercase), state or province (italics), and locality. Collection data are listed as date, name of the collector, and lot number (in parentheses); an asterisk after the lot number indicates samples with imagoes. We also examined imagoes, soldiers, and workers of the following Neotropical termitine type species, which are part of the *Termes* group (Krishna *et al* 2013) for comparison: *Cavitermes tuberosus* (Emerson), MZUSP-12224; *Cornicapritermes mucronatus* Emerson, MZUSP-8815; *Dihoplotermes inusitatus* Araujo, MZUSP-16448; *Divinotermes tuberculatus* Carrijo & Canello, MZUSP-12683; *Genuotermes spinifer* Emerson, MZUSP-8383; *Inquilitermes fur* (Silvestri), MZUSP-2062; *Neocapritermes*

opacus (Hagen), MZUSP-3126, 7891; *Planicapritermes planiceps* (Emerson), MZUSP-7413; *Termes fatalis* Linnaeus, MZUSP-3790. The alates of the type species of *Orthognathotermes* Holmgren and *Dentispicotermes* Emerson, both genera that are also assigned to the *Termes* group, have not yet been described; instead, we used *Dentispicotermes brevicarinatus* (Emerson), MZUSP-8815 and *Orthognathotermes insignis*, MZUSP-3272.

Descriptive terminology and morphometric characters

We use the terminology of Fontes (1987) to describe worker mandibles and that of Noirot (2001) for the different parts of the digestive tube of workers. We took measurements with a micrometric reticle in the eyepiece of a Leica M125 stereomicroscope of the following morphometric characters (Roonwal 1970): for imagoes, LH, length of head capsule (9); WH, width of head capsule without eyes (18); DE, diameter of eye (48); LO, length of ocellus (55); WO, width of ocellus (56); EOD, eye-ocellus distance (57); LP, length of pronotum (65); WP, width of pronotum (68); and LT, length of hind tibia (85); for soldiers, LH, length of head capsule (9); WH, width of head capsule (18); HH, height of head excluding postmentum (21); WP, width of pronotum (68); LT, length of hind tibia (85).

Drawings and digital images

We drew the coiled gut in situ of the workers of *C. verruculosus* with a camera lucida, took the photographs of the imago and soldier castes with a digital camera coupled to a stereomicroscope at different focal points, and merged the sequences of images with the software Leica Application Suite V3.lnk®. The foregut and the enteric valve of the worker caste were mounted on a slide with glycerin and photographed under an optical microscope. We mapped the distribution with the records of the specimens examined in the MZUSP and included records of specimens housed at the Museu Paraense Emílio Goeldi, Belém, Pará, Brasil (MPEG); Departamento de Zoologia, Universidade de Brasília, DF, Brasil (UnB); Laboratório de Termitologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brasil (UFPB); and University of Florida Termite collection, Fort Lauderdale Research and Education Center, Davie, Florida, USA (UF).

Taxonomic treatment

Genus *Crepititermes* Emerson

Mirotermes (*Crepititermes*) Emerson 1925: 433; *Crepititermes*, Snyder 1949:177; *Crepititermes*, Mathews 1977: 133; *Crepititermes*, Krishna et al 2013: 2086 (catalog).

Type species. Mirotermes (*Crepititermes*) *verruculosus* Emerson 1925 by monotypy.

Type locality. Guyana: Kartabo.

Distribution (Fig 1). Neotropical region (Bolivia, Brasil, Ecuador, French Guiana, Guyana, Paraguay, Peru, and Trinidad and Tobago).

Diagnosis. The imago is distinguished from other Neotropical Termitinae genera by the following combination of characters: head capsule surface concave in profile, fontanelle area not depressed; postclypeus rather flat in profile; right mandible with the third marginal tooth very reduced to absent (not visible); left mandible with the second marginal tooth absent (not visible); eyes medium-sized and smaller ocelli; pronotum slightly wider than long; posterior margin of the mesonotum and metanotum slightly emarginate, and posterior corners close to each other; pronotum partially overlapping the base of the fore wing pair. The soldier is distinguished by the subrectangular head capsule with a flat forehead, without projection in dorsal view, and symmetrical snapping mandibles. The worker has a unique enteric valve ornamentation; the distal paunch with a conspicuous pear-shaped diverticulum displaced laterally to the right, and the very short mesenteric tongue and short and tubular ileum; the same mandibular pattern as the imago but broader molar areas. For the soldiers and workers examined, we observed that their bodies rupture through a weak area between the metanotum and the first abdominal tergite, resulting in protrusion of at least part of the paunch and the pear-shaped diverticulum.

Remarks. Emerson (1925), Snyder (1949) and Mathews (1977) included *Crepititermes* as part of the non-monophyletic subfamily Termitinae. Following Krishna et al (2013), we compared *Crepititermes* with other Neotropical genera of the *Termes* group. *Crepititermes* has not appeared as a terminal taxon in any phylogenetic scheme.

Crepititermes verruculosus Emerson (Figs 1–19)

Crepititermes verruculosus Emerson 1925: 433, Fig 84a-d; Davies 2002:241 (checklist, feeding group); Costa et al 2009:449 (nesting); Ackerman et al 2007:271 (checklist, nesting); Constantino & Schmidt 2010:201 (checklist); Bourguignon et al 2011:264, 265 (checklist, feeding group); Palin et al 2011:3, supporting information (checklist, feeding group); Krishna et al 2013: 2087 (catalog); Kutalová et al 2013:340, 342, Fig 3C (imagoes frontal gland); Canello et al 2014:6, supporting information (checklist, feeding group).

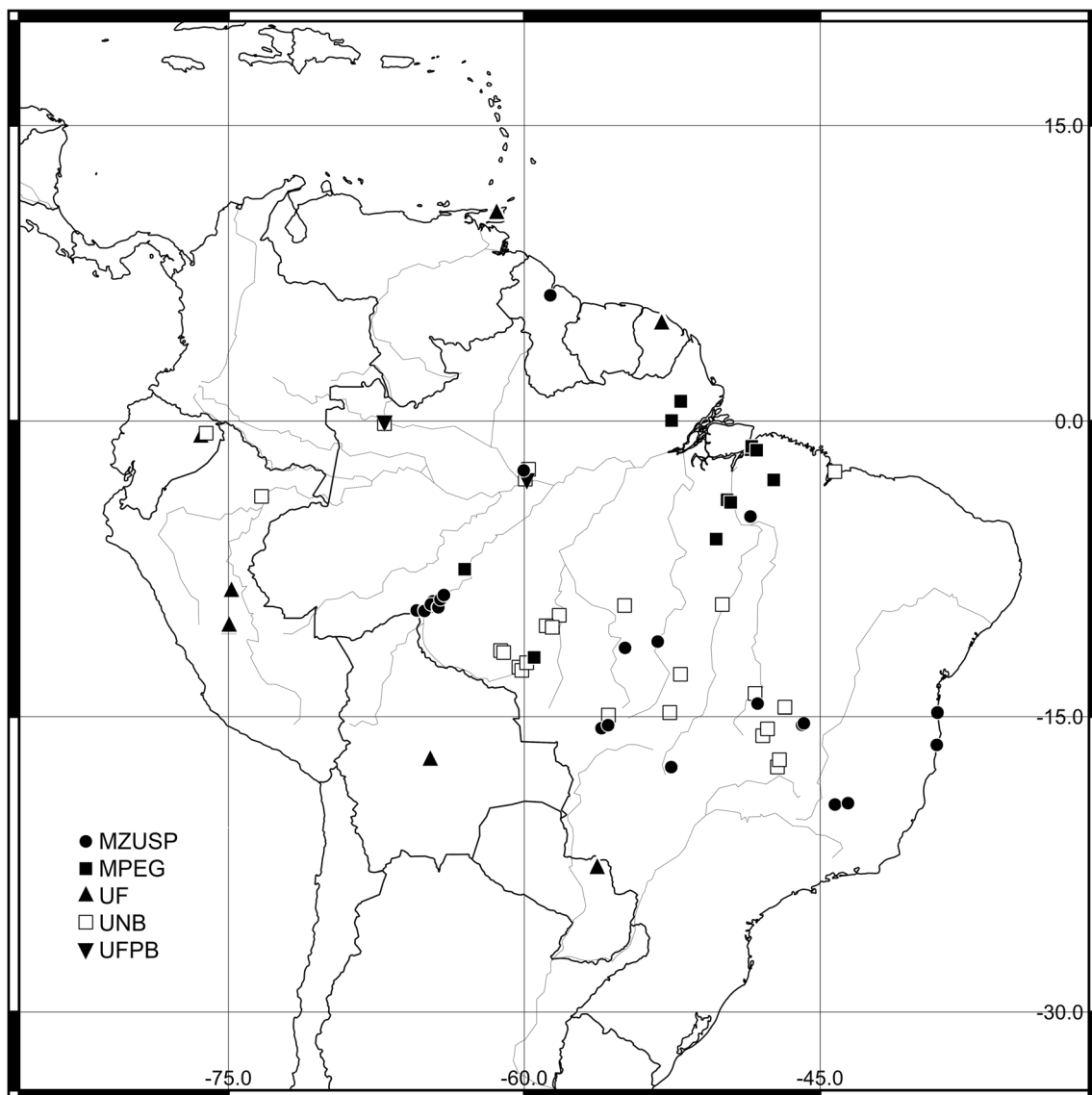


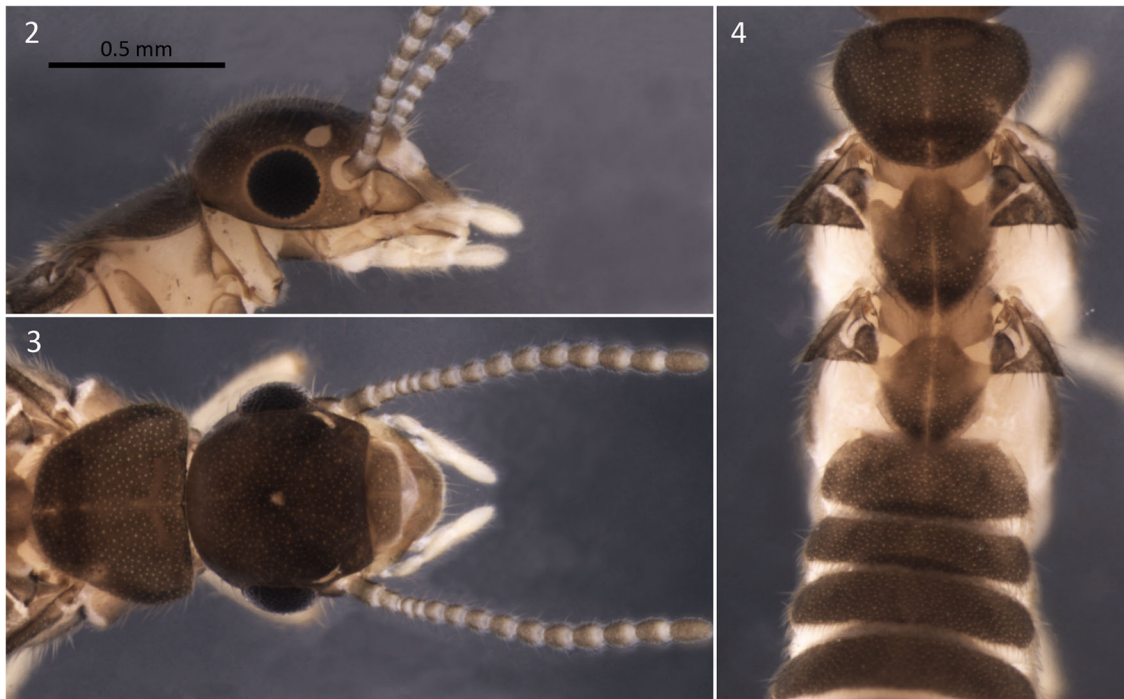
Fig 1 Current known distribution of *Crepititermes verruculosus*.

Description of worker and additional notes on imago and soldier castes

Imago (Figs 2–4). Vide Emerson (1925:434), Mathews (1977:134) and Roonwal & Verma (1980:462). Range of measurements (mm) of six females (two each from MZUSP 3521, 21231, and 21216) and three males (one from MZUSP 3521 and two from 21216): LH, 0.50–0.53; WH, 0.48–0.50; DE, 0.17–0.20; WO, 0.06–0.09; EOD, 0.03–0.05; LP, 0.44–0.47; WP, 0.53–0.59; LT, 0.59–0.66. No apparent dimorphism in characters or size between female and male. Among all the specimens studied, those from Rondônia, Brasil, are darker colored, with larger eyes and ocelli (Figs 2–4) than those from Guyana.

Comparisons. *Crepititermes tuberosus* (see Emerson 1925: Figs 88a, b, p 443) resembles *C. verruculosus* in having an

arched postclypeus; the head capsule slightly concave in profile; a different thoracic nota shape; tibial spurs; but differs in having the same mandibular dentition and molar area pattern (left M3 very reduced but not obsolete), the fontanelle tiny and barely depressed, and number of antennal articles as *C. verruculosus*. *Dihoplotermes inusitatus* (see Krishna 1968: Fig 38, 311) has different mandibular dentition and molar area, as well as pronotum shape, but shares with *C. verruculosus* a slightly arched postclypeus, size of the eyes and ocelli, and the tiny rounded fontanelle. *Divinotermes tuberculatus* (see Carrijo & Canello 2011: Figs 1C, D, p 540) differs from *C. verruculosus* in the arched postclypeus; head capsule slightly concave in profile; different thoracic nota shape; tibial spurs; but has the same mandibular dentition and molar area pattern (left M3 very reduced but not obsolete); fontanelle tiny but not depressed; and number of antennal articles. *Dentispicotermes brevicarinatus*



Figs 2–4 *Crepititermes verruculosus*, female: 2 head capsule and pronotum in profile, 3 head capsule in dorsal view, and 4 thoracic nota in dorsal view.

(see Emerson 1950: Fig 3, p 7) has different mandibles with the posterior margin of the apical teeth not concave, the left M3 and right M2 well visible, and the molar tooth visible as well between the molar plate and left M3; head capsule surface not

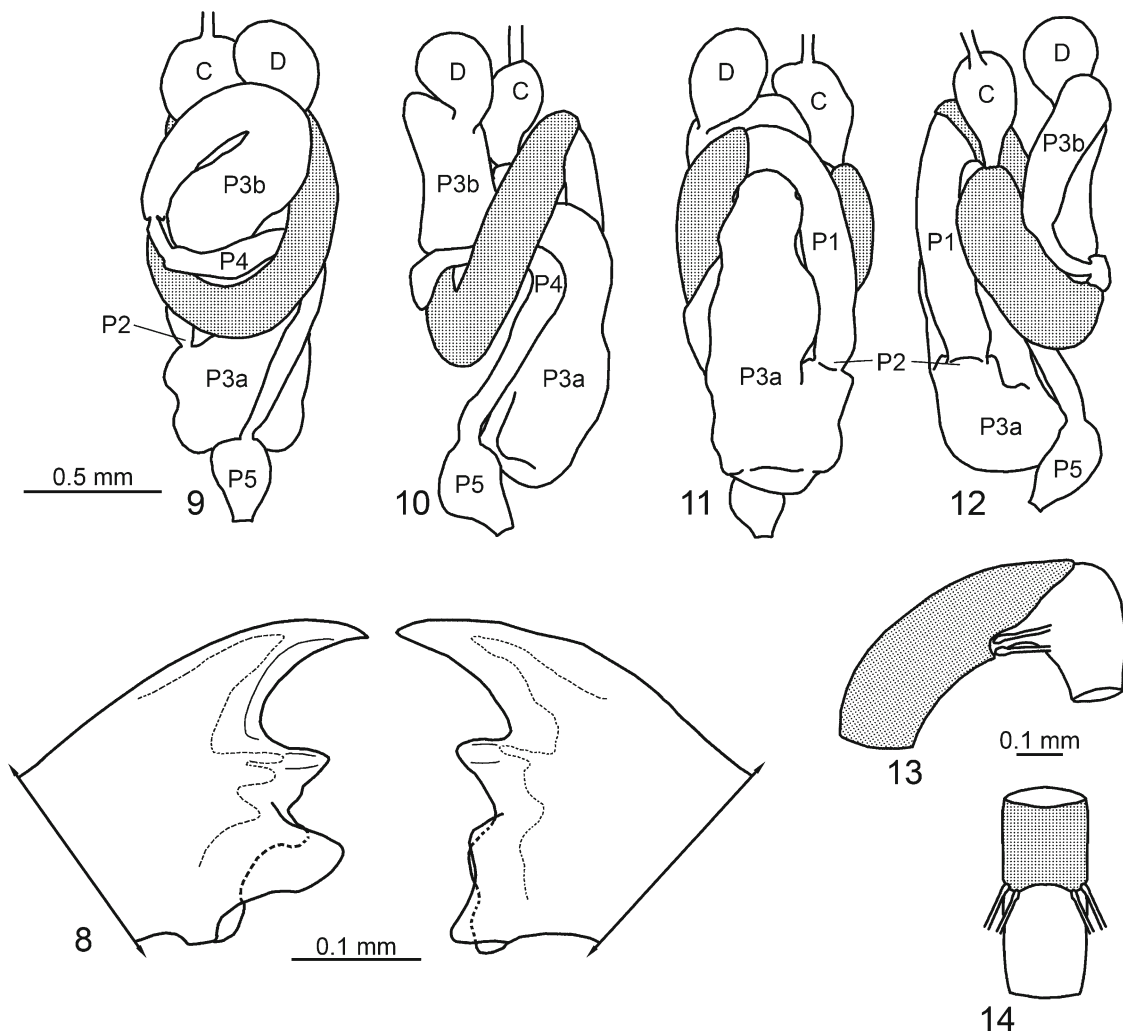
concave in profile; fontanelle conspicuous in dorsal view, depressed in profile; postclypeus arched; number of antennal articles; thoracic nota shape; and tibial spurs. *Genuotermes spinifer* (see Rocha 2013: Figs 3–5, p 110) has different mandibles with



Figs 5–7 *Crepititermes verruculosus*, soldier: 5 dorsal, 6 profile, and 7 ventral view, showing molar plate and prominence in detail.

the posterior margin of the apical teeth not concave, left M3 reduced but visible, gap between molar plate and M3 filled by molar tooth, right M2 conspicuous; fontanelle conspicuous and depressed in dorsal view, postclypeus arched; number of antennal articles; thoracic nota shape; and tibial spurs. *Inquilitermes fur* (see Mathews 1977: Fig 81, p 136) has the left mandible with M3 reduced but visible, fontanelle conspicuous in dorsal view, slightly depressed in profile; head capsule surface not concave in profile; postclypeus arched; number of antennal articles; mesonotum and metanotum more emarginate, posterior corners not close together, and tibial spurs; but *I. fur* also has mandibles with the apical tooth very prominent and the posterior margin concave and the right M2 absent and a similar pronotum shape as *C. verruculosus*. *Neocapritermes opacus* (see Krishna 1968: Fig 42, p 315) has different mandibles, with the apical teeth not more prominent than the marginal dentition, the left M3 and right M2 well visible, posterior margin of the right M2 not concave; head capsule surface not concave

in profile; fontanelle conspicuous in dorsal view, slightly depressed in profile; postclypeus arched; number of antennal articles; thoracic nota shape; and tibial spurs. *Orthognathotermes insignis* (see Rocha & Cancellato 2009: Fig 20, p 19) has different mandibles, with the left M3 and right M2 reduced but well visible, left M1 + 2 connected with M3 by a sinuous margin; fontanelle conspicuous in dorsal view, depressed in profile; head capsule surface not concave in profile; postclypeus arched; number of antennal articles; thoracic nota shape; and tibial spurs. *Planicapritermes planiceps* (see Mathews 1977: Fig 82, p 136) has different mandibles, with the apical teeth not more prominent than the marginal dentition, left M3 and right M2 well visible, posterior margin of right M2 not concave, thoracic nota shape, and tibial spurs; however, *P. planiceps* has the same number of antennal articles; head capsule surface concave in profile; postclypeus not arched, as in *C. verruculosus*. *Termes fatalis* has different mandibles, with the apical teeth not as prominent and the posterior margin



Figs 8–14 *Crepititermes verruculosus*, worker: 8 mandibles; coiling gut in 9 dorsal 10 right, 11 ventral, and 12 left view; 13 mixed segment in detail; and 14 Malpighian tubules in detail. C crop, D diverticulum, P1 ileum, P2 enteric valve, P3 paunch, P4 colon, and P5 rectum.



Figs 15–17 *Crepititermes verruculosus*, worker: 15 gizzard in plain view; 16 major cushion of the enteric valve in detail, and 17 cushions in plain view. Arrow shows the food flow (P1–P3).

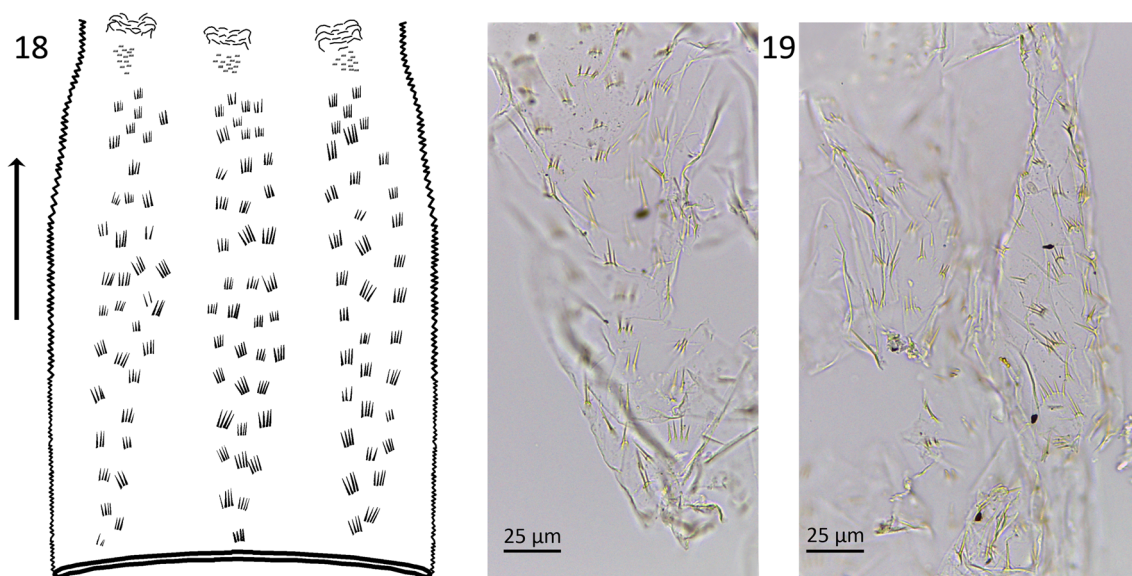
concave, right M2 and left M3 reduced but visible; fontanelle conspicuous, not depressed; larger eyes and ocelli; and postclypeus arched; although *T. fatalis* has the same number of antennal articles; head capsule concave in profile; thoracic nota shape; and tibial spurs as in *C. verruculosus*. *Cornicapritermes mucronatus* has no alate described.

Soldier (Figs 5–7). Vide Emerson (1925:434) and Mathews (1977:134). Head capsule covered with erect hairs and very short hairs, only short hairs on front. Postclypeus with scattered erect bristles and short hairs. Labrum with long decumbent bristles plus few short hairs. Pronotum with anterior lobe slightly emarginate, scattered erect bristles on margins, and very short hairs over surface. Tergites densely covered with erect hairs, IX and X tergites with scattered long

erect bristles on posterior margin. Sternites densely covered with decumbent hairs and some long erect bristles on posterior margin. Anterior face of procoxa with discrete hump and few short hairs over surface. Tibial spurs 3:4:2. Range of measurements (mm) for one soldier from each of MZUSP lots 12222, 22708, 3522, two soldiers from MZUSP 6589, 9481; three soldiers from MZUSP 12601: LH, 0.91–0.94; WH, 0.58–0.63; HH, 0.47–0.53; WP, 0.34–0.38; LT, 0.41–0.47.

Comparisons. No other Neotropical termitine genera have the combined characters of symmetrical snapping mandibles and no frontal projection.

Worker (Figs 8–19). Head capsule rounded, with fontanelle region inconspicuous in dorsal view. Postclypeus arched



Figs 18–19 *Crepititermes verruculosus*, worker: 18 sketch and 19 photograph of the ornamented cuticle of the ileum. Arrow shows the food flow (P1–P3).

and fontanelle region slightly depressed in profile. Antenna with 13 articles. Anterior lobe of pronotum more developed than posterior lobe; anterior margin of pronotum slightly emarginate. Anterior face of procoxa with discrete hump. Tibial spurs 3:4:2. Head capsule covered with abundant erect hairs. Postclypeus with short hairs over surface and erect bristles on anterior margin. Labrum with decumbent bristles larger than those of postclypeus. Thoracic nota and abdomen with similar pilosity to soldier. Body pale yellow overall. **Mandibles** (Fig 8). Apical teeth acute and more prominent than first marginal teeth; posterior margin of apical teeth concave, forming acute angle with anterior margin of first marginal teeth. Left mandible: M1 + 2 tooth conspicuous, its posterior margin slightly sinuous; third marginal tooth absent (not visible); apex of molar tooth beneath molar prominence; molar prominence concave without ridges. Right mandible: first marginal tooth conspicuous; second marginal tooth absent (not visible); molar plate concave, without ridges; and a broad basal notch. **Digestive tube** (Figs 9–19). Coiled gut in situ visible through abdominal wall as in Figs 9–12. Crop slightly more developed than gizzard (Fig 11); crop cuticle armed with pectinate scales. Gizzard with completely sclerotized cuticular armature (hexaradial symmetry); pulvillar belt more developed than columnar belt, pulvillus I more developed than pulvillus II, both with their entire surface smooth, with no apparent ornamentations (Fig 15); columns I and II, also with the entire surface smooth (Fig 15). Mesenteron passing through right side of abdomen to join the ileum (P1), reaching just before medial line in ventral view (Fig 11). Very short mixed segment external to mesenteric arc, with lateral margins converging distally (Fig 13). Malpighian tubules arranged in two closely set pairs

but attached individually at mesenteron-proctodeum junction on inner face of mesenteric arc; tubules slightly dilated at attachment point (Fig 14). P1 tubular, about half as long as abdomen; P1 cuticle with triradial symmetry (Fig 18), three recognizable cushions, each one armed with cluster of several rows of three to five aciculiform spines (Fig 18), distally, cushions unarmed but with crenate appearance. Enteric valve (P2) in ventral view at right side of abdomen (Fig 11); P2 cuticle with triradial symmetry (Fig 17), armed with one asymmetrical ring of major cushions alternating with slightly shorter ones; both cushions with small subtriangular spines on proximal region, followed by crenulated area and ending in cluster of larger subtriangular spines in curved line, bending in the direction of the food-flux distal surface (Figs 16, 17). Paunch (P3) with proximal region very enlarged, displaced to left side of body; distal part of P3 voluminous, protruding through mesenteric arc with a noticeable pear-shaped diverticulum, right-laterally displaced; diverticulum not visible in unopened abdomen; isthmus relatively short and conspicuous. Dorsal torsion well developed. “U-turn” tubular, not dilated. Distal colon tubular, joining the rectum in dorsal view.

Comparisons. No other Neotropical termitine genera has the enteric valve ornamentation, the distal paunch with a conspicuous pear-shaped diverticulum displaced laterally to the right, and coiled gut described for *Crepititermes*, neither the African Termitinae genera (Sands 1998) nor the Australian species of the *Termes-Capritermes* complex (Miller 1991). Nevertheless, the coiled gut in situ resembles that of the nasute genus *Subulitermes* Holmgren.

Material examined. Paratype. GUYANA. Kartabo, 21.vi.1919, A.E. Emerson, one soldier (3522). Other material.

GUYANA. Kartabo, 9.iv.1924, A.E. Emerson (3521*). BRASIL. Amazonas: Manaus, BR 174 Km 45, 15.viii.1990, A.G. Bandeira (9481). *Bahia*: Ilhéus, Mata Esperança, 23.v.2001, Y. Reis (12222); Porto Seguro, ESPAB, 22.i.2003, Y. Reis (12221). Goiás: Mineiros, Mata farm, 25.vii.2011, T.F. Carrijo (22434); Niquelândia, 16.xi.2013, T.F. Carrijo (22707). Mato Grosso: Chapada dos Guimarães, Chapada dos Guimarães National Park, 11.ii.1976, R.L. Araujo (6589, 6749), 1-5.viii.2009, T.F. Carrijo (12601, 12609, 12625); Cláudia, 13.x.2010, Q.C.L. Santos (15928), 25.viii.2011 (15957); Confresa, Parque do Xingu, 2.xi-11.xii.1973, G.R. Kloss (5304); Cuiabá, 7 km NO, 16.ii.1976, R.L. Araujo (6540). Minas Gerais: Chapada Gaúcha, Grande Sertão Veredas National Park, 12.x.2012, M.M. Rocha (16149, 16191), T.F. Carrijo (22785); Jaboticatubas, Serra do Cipó National Park, 7.x.1012, M.M. Rocha (16266), T.F. Carrijo (22783, 22784); Sete Lagoas, 13.ii.1986, D.J. Domingos (8973). Pará: Abel Figueiredo, Juca Marhe farm, 27.xi.2013, T.F. Carrijo (22708). Rondônia: Porto Velho, District of Abunã, Jirau Hydroelectric Reservoir, 17.ix.2010, M.M. Rocha and V.T.C. Mercado (21193, 21194*), 15.v.2010, T.F. Carrijo and M.M. Rocha (21186), 09.iii.2010, T.F. Carrijo and R.G. Santos (12881), 30.vi.2010, T.F. Carrijo and S.P. Rosa (21189*), 27.vi.2011, S.P. Rosa and G.R. Mazão (21220), 11-12.ix.2011, T.F. Carrijo and L.R. Fernandes (21224, 21223), 08.iv.2011, V.T.C. Mercado and R.S. Probst (21214), 05.iv.2012, M.M. Rocha and R.G. Santos (21231*, 21232*), 27.vi.2012, R.G. Santos and K. Kawamishi (21238), 13.ix.2012, T.F. Carrijo and R.G. Santos (21239, 21240, 1241, 21242) District of Fortaleza do Abunã, Jirau Hydroelectric Reservoir, 11.iii.2010, T.F. Carrijo and R.G. Santos (12882, 12883), 28.vi.2010, T.F. Carrijo and S.P. Rosa (21190), 6.iv.2011, V.T.C. Mercado and R.S. Probst (21215, 21216*), 09.ix.2011, T.F. Carrijo and L.R. Fernandes (21225, 21226), District of Jaci Paraná, Santo Antônio Hydroelectric Reservoir, 13-20.ix.2010, T.F. Carrijo and R.G. Santos (21252, 21253, 21254, 21255), 03-13.vi.2011, M.M. Rocha and J. Cabral (21260, 21261), 24.xi.2011, M.M. Rocha and J. Cabral (21262, 21263, 21264), 02-06.vi.2012, M.M. Rocha and J. Cabral (21268, 21269), District of Mutum Paraná, Santo Antônio Hydroelectric Reservoir, 01-05.iii.2010, T.F. Carrijo and R.G. Santos (12885, 12886, 12884*, 12887, 12888, 12889, 12890), 11.ix.2010, M.M. Rocha and V.T.C. Mercado (21196), 11.v.2010, T.F. Carrijo and M.M. Rocha (21187, 21188), 12-16.ix.2010, M.M. Rocha and V.T.C. Mercado (21195, 21197, 21201, 21202, 21198, 21199, 21200), 23-25.vi.2010, T.F. Carrijo and S.P. Rosa (21192, 21191), 05-12.i.2011, M.M. Rocha and L.P. Prado (21203, 21207, 21204, 21205, 21206, 21208, 21210, 21209*, 21211*, 21212, 21213), 14-18.ix.2011, T.F. Carrijo and L.R. Fernandes (21230, 21229, 21227, 21228), S.P. Rosa and G.R. Mazão (21221, 21222), 28-30.iii.2011, V.T.C. Mercado and R.S. Probst (21217, 21218, 21219), 08-10.ix.2012, T.F. Carrijo and R.G. Santos (21247, 21248, 21243, 21244, 21245, 21246), 29-30.iii.2012, M.M. Rocha and R.G. Santos (21233, 21234, 21235, 21236, 21237, 05-08.v.2013, F. Andriolli and P.

Manholer (21251, 21249, 21250), District of Porto Velho, Santo Antônio Hydroelectric Reservoir, 19-22.ix.2010, T.F. Carrijo and R.G. Santos (21256, 21257), 06.iv.2011, R.G. Santos and C.Y. Mandai (21259), 19.i.2011, (21258), 28.xi.2011, M.M. Rocha and J. Cabral (21265, 21266), 09.iii.2012, T.F. Carrijo and J. Cabral (21267).

Other material, not examined. Records from termite collections in Brasil (MPEG, UFPA, UnB) and the United States of America (UF).

Biological notes

Crepititermes verruculosus was found inside nests (occupied or abandoned) of apicotermittines (*Grigiotermes* Mathews, and unidentified species), nasutitermittines (*Nasutitermes* Dudley) and syntermittines (*Cornitermes* Wasmann, *Embiratermes* Fontes, *Labiatermes* Holmgren, *Silvestritermes* Rocha & Canello, *Syntermes* Holmgren) as well as inside fallen logs. Nevertheless, some field notes from voucher specimens in the MZUSP suggest that the species can build a small “nest” among rootlets, but this is not clear if these places are structured nests or only diffuse galleries among the roots. Roper (2013) demonstrated the behavior of *C. verruculosus* in the presence and absence of *Cornitermes cumulans* (Kollar).

For the soldiers and workers examined, we observed that their bodies rupture through a weak area between the metanotum and the first abdominal tergite, resulting in protrusion of at least part of the paunch and the pear-shaped diverticulum. The question of whether chemical substances are released during the suicidal behavior by autothysis remains hypothetical, as well as of whether the pear-shaped diverticulum is involved in defense or simply as a site for microorganism settlement.

Acknowledgments We are grateful to R Constantino (UnB), A Vasconcellos (UFPA), and RH Scheffrahn (UF) for providing records of *C. verruculosus* samples housed in their institutions; CRF Brandão for allowing us to use the optical equipment at the MZUSP for image capture; and EM Canello for helpful suggestions. We received financial support from the São Paulo Research Foundation, Brasil (FAPESP) through grants 2012/00952-9 to MM Rocha and 2013/05610-1 to C Cuezco.

References

- Ackerman IL, Teixeira WG, Riha SJ, Lehmann J, Fernandes ECM (2007) The impact of mound-building termites on surface soil properties in a secondary forest of Central Amazonia. *Appl Soil Ecol* 37(3):267–276. doi:10.1016/j.apsoil.2007.08.005
- Bourguignon T, Šobotník J, Lepoint G, Martin JM, Hardy OJ, Dejean A, Roisin Y (2011) Feeding ecology and phylogenetic structure of a complex Neotropical termite assemblage, revealed by nitrogen stable isotope ratios. *Ecol Entomol* 36(2):261–269. doi:10.1111/j.1365-2311.2011.01265.x

- Canello EM, Silva RR, Vasconcellos A, Reis YT, Oliveira LM (2014) Latitudinal variation in termite species richness and abundance along the Brazilian Atlantic Forest hotspot. *Biotropica* 46(4):441–450. doi:10.1111/btp.12120
- Carrijo TF, Canello EM (2011) *Divinotermes* (Isoptera, Termitidae, Termitinae), a new genus from South America. *Sociobiology* 58:537–556
- Constantino R, Schmidt K (2010) Cupins (Insecta: Isoptera). In: Diniz IR, Marinho-Filho J, Machado RB, Cavalcanti RB (eds) Cerrado: conhecimento científico quantitativo como subsídio para ações de conservação. Thesaurus, Brazil, pp 187–202
- Costa DA, Carvalho RA, Lima Filho GF, Brandão D (2009) Inquilines and invertebrate fauna associated with termite nests of *Cornitermes cumulans* (Isoptera, Termitidae) in the Emas National Park, Mineiros, Goiás, Brazil. *Sociobiology* 53:443–453
- Davies RG (2002) Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation. *Oecologia* 133:233–242. doi:10.1007/s00442-002-1011-8
- Emerson AE (1925) The termites from Kartabo, Bartica District, Guyana. *Zoologica* 6(4):291–459
- Emerson AE (1950) Five new genera of termites from South America and Madagascar (Isoptera, Rhinotermitidae, Termitidae). *Am Mus Novit* 1444:1–15
- Fontes LR (1987) Morphology of the alate and worker mandibles of the soil-feeding nasute termites (Isoptera, Termitidae, Nasutitermitinae) from the Neotropical region. *Rev Bras Zool* 3(8):503–531. doi:10.1590/S0101-81751986000400003
- Krishna K (1968) Phylogeny and generic reclassification of the termites of the *Capritermes* complex (Isoptera, Termitidae, Termitinae). *Bull Am Mus Nat Hist* 138(5):265–323
- Krishna K, Grimaldi DA, Krishna V, Engel MS (2013) Treatise on the Isoptera of the world: 6. Termitidae (Part Three), Incertae Sedis, Taxa excluded from Isoptera. *Bull Am Mus Nat Hist* 377(6):1993–2432. doi:10.1206/377.6
- Kutalová K, Bourguignon T, Sillam-Dussès D, Hanus R, Roisin Y, Šobotník J (2013) Armed reproductives: evolution of the frontal gland in imagoes of Termitidae. *Arthropod Struct Dev* 42:339–348. doi:10.1016/j.asd.2013.04.001
- Mathews AGA (1977) Studies on termites from the Mato Grosso State, Brazil. *Academia Brasileira de Ciências*, Rio de Janeiro, p 267
- Miller LR (1991) A revision of the *Termes-Capritermes* branch of the Termitinae in Australia (Isoptera: Termitidae). *Invertebr Taxon* 4(6):1147–1282. doi:10.1071/IT9901147
- Noirot C (2001) The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. II. Higher termites (Termitidae). *Ann Soc Entomol Fr* 37(4):431–471
- Palin OF, Eggleton P, Malhi Y, Girardin CAJ, Rozas-Dávila A, Parr CL (2011) Termite diversity along an Amazon-Andes elevation gradient, Peru. *Biotropica* 43(1):100–107. doi:10.1111/j.1744-7429.2010.00650.x
- Rocha MM (2013) Redescription of the enigmatic genus *Genuotermes* Emerson (Isoptera, Termitidae, Termitinae). *ZooKeys* 340:107–117. doi:10.3897/zookeys.340.6131
- Rocha MM, Canello EM (2009) Revision of the Neotropical termite genus *Orthognathotermes* Holmgren (Isoptera: Termitidae: Termitinae). *Zootaxa* 2280:1–26
- Roonwal ML (1970) Measurement of termites (Isoptera) for taxonomic purposes. *J Zool Soc India* 21(1):9–66
- Roonwal ML, Verma SC (1980) Evolution and systematic significance of wing micro-sculpturing in termites (Isoptera). IX. Subfamily Termitinae of Family Termitidae. *Proc Indian Natl Sci Acad B* 46(4):455–469
- Ropero MCG (2013) Coabitação e interação entre formigas e cupins em ninhos de *Cornitermes cumulans* em áreas de Cerrado e pastagem no Brasil Central. PhD Thesis, Universidade de Brasília, Brasília, Brasil, p 99. http://repositorio.unb.br/bitstream/10482/13580/1/2013_Mar%20C3%ADaCristinaGallegoRopero.pdf Accessed 30 Jan 2015
- Sands WA (1998) The identification of worker castes of termite genera from soils of Africa and the Middle East. CAB International, Wallingford, p 512
- Snyder TE (1949) Catalog of the termites (Isoptera) of the World. *Smithson Misc Collect* 112:1–490