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Gut anatomy of the worker caste of Neotropical genera *Cylindrotermes* Holmgren and *Hoplotermes* Light (Infraorder Isoptera, Termitidae)

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ABSTRACT

Studies over the last six decades have shown that the gut anatomy of the termite worker caste provides a valuable set of taxonomic characters. However, the gut anatomy of most American termitine taxa is still little known. This study investigated the anatomy of the worker gut of the Neotropical termitine genera *Cylindrotermes* Holmgren and *Hoplotermes* Light. We provide descriptions and illustrations of the gut *in situ* and the cuticular ornamentation of the gizzard, enteric valve, and first proctodeal segment for both genera.

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Introduction

With 63 genera and 643 living species worldwide (Constantino, 2019), the Termitinae is a heterogeneous group of termites, without diagnostic characters supporting it as a clade among Termitidae subfamilies (Bourguignon et al., 2017). The subfamily is represented in the Neotropical region by 20 genera, occurring from the southern United States (*Gnathamitermes* Light, 1932; *Hoplotermes* Light, 1933) to southern Argentina (*Onkotermes* Constantino, 2002). Three of these genera are cosmopolitan (*Amitermes* Silvestri, 1901, *Microcerotermes* Silvestri, 1901, and *Termes* Linnaeus, 1758).

The South and Central American genus *Cylindrotermes* Holmgren, 1906 was proposed based on specimens collected in Bolivia, during the Nordenskiöld expedition (1904–1905). One century later, Rocha and Canello (2007) revised the genus and described three new species, based on the external morphology of the soldier and worker castes from Brazilian samples, and redescribed four of the five previously described species (except the type species *Cylindrotermes nordenskiöldi* Holmgren, 1906). Noirot (2001, Fig. 12d) illustrated an unidentified species of *Cylindrotermes*, with brief comments on internal structures. With a total of eight nominal species now recognized within *Cylindrotermes*, the geographical distribution of the genus ranges

from the rainforest of southern Central America (Costa Rica) to the savannas (Cerrado) of South America. *Cylindrotermes* species form small colonies, frequently found inside dry dead wood (small trunks and dry sticks on the ground). There are reports of damage to roots and stems of sugarcane caused by members of the genus (Miranda et al., 2004).

Hoplotermes is an uncommon monotypic termite genus, with *Hoplotermes amplus* Light, 1933 as the type-species, described from the external morphology of the soldier and worker castes of specimens from western Mexico; the imago caste remains unknown. The gut anatomy of *Hoplotermes* has never been described. The genus has been recorded in Costa Rica, Guatemala and Nicaragua (Krishna et al., 2013). Colonies of this species are found in wood, under rocks, or cow dung; they build earthen chambers and passageways in, on and near attacked wood (Light, 1933).

Characters of the worker caste digestive tube have come to be widely recognized as key resources for taxonomy over the last six decades (Noirot and Kovoov, 1958; Sands, 1992, 1998; Noirot, 2001), and their description has been mandatory for taxonomic studies in the last two decades. Although many genera are reasonably well represented in museums, the internal morphology of many species is still unknown. To help to fill these lacunae, we provide detailed descriptions and illustrations of the worker gut of seven species of *Cylindrotermes* and *H. amplus*, including the gut coiling *in situ* and the cuticular ornamentation of the gizzard, enteric valve, and first proctodeal segment.

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Fig. 1. *Cylindrotermes brevipilosus*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).

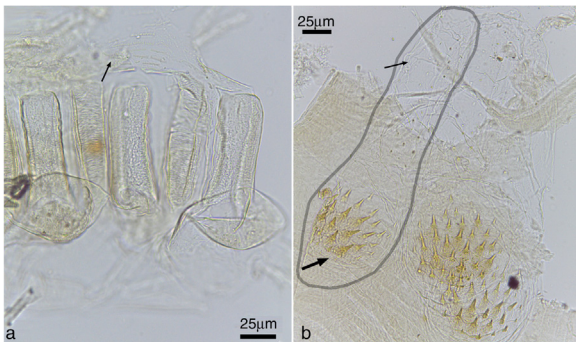


Fig. 2. *Cylindrotermes caata*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).

Material and methods

Material examined

We studied specimens deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. We dissected and illustrated the worker gut coiling, gizzard, and enteric valve of *Hoplotermes amplus* (MZUSP-15464, Guatemala, Jutiapa); *Cylindrotermes brevipilosus* Snyder, 1926 (MZUSP-24534: Brazil, Mato Grosso do Sul State, Costa Rica municipality); *Cylindrotermes*

caata Rocha and Canello, 2007 (MZUSP-11266, Brazil, São Paulo State, Luiz Antônio municipality, paratype); *Cylindrotermes capixaba* Rocha and Canello, 2007 (MZUSP-1796, Brazil, Espírito Santo State, Cariacica municipality, paratype); *Cylindrotermes flangiatus* Mathews, 1977 (MZUSP-21322, Brazil, Rondônia State, Porto Velho municipality); *Cylindrotermes macrogathus* Snyder, 1929 (MZUSP-4368, Panama, Barro Colorado Island); *Cylindrotermes parvignathus* Emerson, 1949 (MZUSP-8447, Brazil, Pará State, Benevides municipality); and *Cylindrotermes sapiranga* Rocha and Canello, 2007 (MZUSP-11503, Brazil, Bahia State, Sapiranga Ecological Reserve, paratype).

Illustrations and figures

We adopted the terminology of Noiroit (2001) for the gut coiling, gizzard, and enteric valve cuticular ornaments, and of Rocha and Constantini (2015) for the first proctodeal cuticular ornaments.

Line drawings characterizing the gut *in situ* and the first proctodeal segment were prepared with a drawing tube coupled to a stereomicroscope. The gizzard, enteric valve, and first proctodeal segment were mounted in glycerin on a slide and photographed with an optical microscope. Particularly, the enteric valve of *Cylindrotermes* has a small section and a tightly attached musculature, which is challenging to mount satisfactorily, especially since the number of good-quality specimens for dissection was limited.

Results

After detailed examination, we observed different gut-coiling patterns *in situ* and a particular cuticular ornamentation for each genera, *Cylindrotermes* and *Hoplotermes*, as follows.

Cylindrotermes

Worker digestive tube (Figs. 1–8): Crop slightly asymmetrical, not voluminous, covered with finely pectinate scales (Figs. 1a, 2a, 3a, 4a, 5a, 6a and 7a, arrows). Gizzard with a complete armature arranged in a columnar belt with 24 folds (six first-order, six second-order, and 12 third-order) and a pulvillar belt with 12 folds (six first-order, six second-order); Length ratio between belts about one; pulvilli of first order conspicuous, with tiny pectinate scales, and pulvilli of second order very reduced (Figs. 1a, 2a, 3a, 4a, 5a, 6a and 7a). Stomodeal valve inserted apically in the tubular mesenteron. Mesenteric tongue external

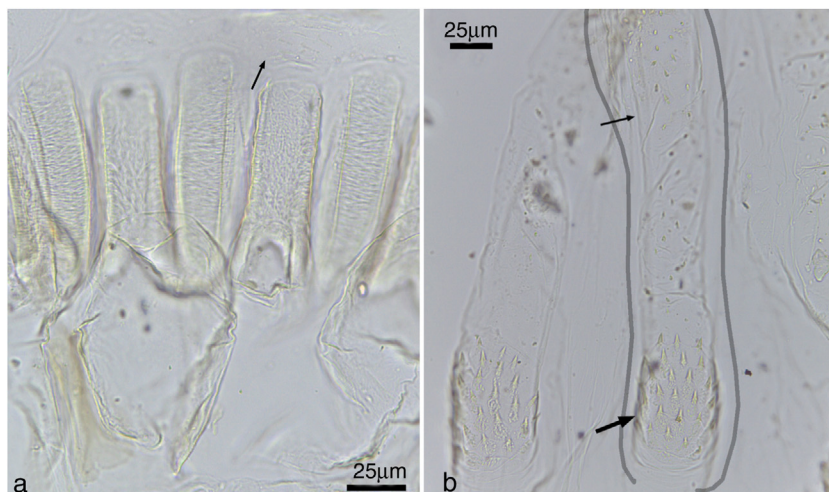


Fig. 3. *Cylindrotermes capixaba*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).



Fig. 4. *Cylindrotermes flangiatus*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).

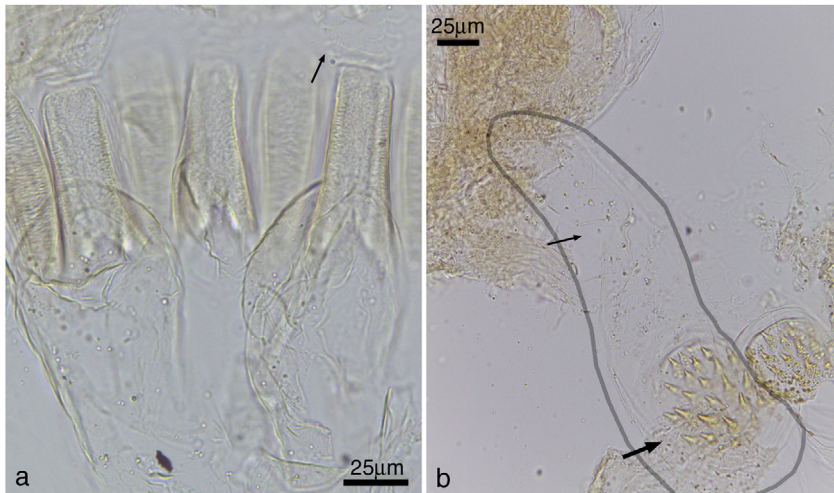


Fig. 5. *Cylindrotermes macrognathus*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).

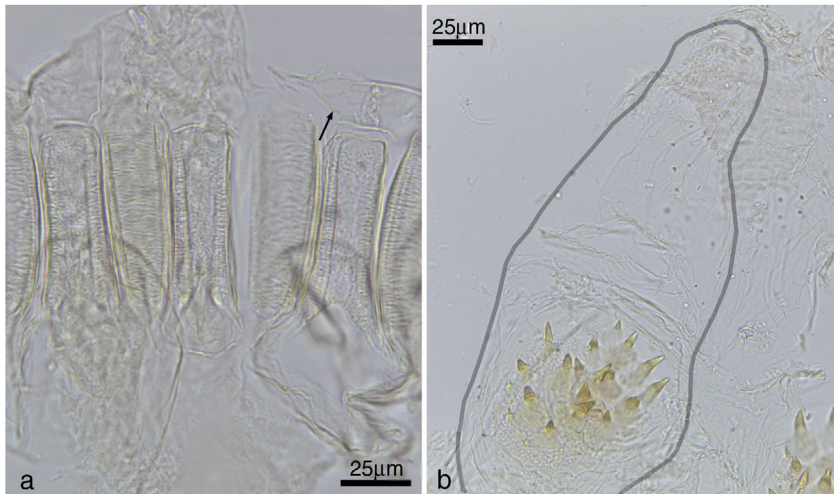


Fig. 6. *Cylindrotermes parvignathus*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).

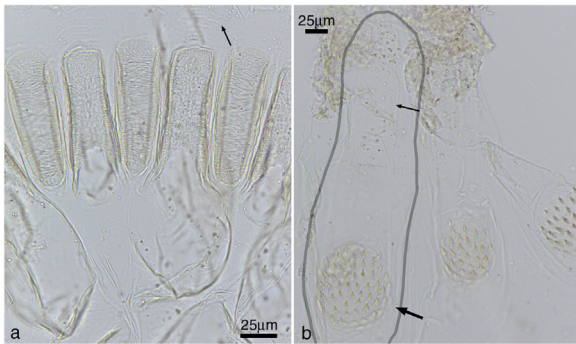


Fig. 7. *Cylindrotermes sapiranga*: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve, with one of the cushions outlined (large arrow: proximal pad, small arrow: distal portion).

to the mesenteric arch, tapering broadly, and connected at the mesenteron only by a filiform mesenteric tissue (Fig. 8a, arrow). Two pairs of Malpighian tubules attached at the mesenteron-proctodeum junction, with distinct insertions on opposite sides of the segment (Fig. 8e, arrow). First proctodeal segment (P1) tubular and elongated, forming a marked loop below the rectum (P5) (Fig. 8a–d), distally attached to the paunch (P3) at the dorsal/right side of the abdomen (Fig. 8b, arrow) and deeply inserted at the P3, surrounded by a thick band of muscle. P1 without cuticular ornamentation. Enteric-valve armature (P2) weakly sclerotized, composed by three nearly equal cushions, each cushion with two distinct spine-covered areas, the pad closest to P1, with robust spines (Figs. 1b, 2b, 3b, 4b, 5b, 6b, and 7b, large arrows); and an elongated portion, covered with small scattered spines, closest to

P3, very faintly defined (Figs. 1b, 2b, 3b, 4b, 5b, 6b, and 7b, small arrows).

P3 well developed and elongated, but little protruded through the mesenteric arch. Isthmus short (Fig. 8a). Fourth proctodeal segment (P4) dilated throughout (tubular but with larger diameter than in P1). All examined specimens of the different species follow the same gut pattern, including the gut coiling *in situ*, and the P2 cuticular ornamentation shows distinctive variations in the density and degree of sclerotization of the spines on the proximal ring (Figs. 1b, 2b, 3b, 4b, 5b, 6b, and 7b).

Comparisons among termitine genera: The gut pattern *in situ* and particularly the P1 and P4, and the cuticular ornamentation of the enteric valve in *Cylindrotermes* are distinct among the Neotropical termitine genera. Even though, we were unable to obtain reliably identified specimens for *Cylindrotermes nordenskioldi*, to be considered herein, we expect a similar pattern. *Cylindrotermes* shares with the Ethiopian genus *Cephalotermes* Silvestri, 1912 and the soldierless Oriental genus *Protohamitermes* Holmgren, 1912, the tubular P1 forming a ventral loop. In *Cephalotermes* the P1 forms a shorter loop than in *Cylindrotermes*, the mesenteric tongue lacks a filiform connection, and the enteric valve has six unequal cushions (Noirot, 2001, Figure 12 D, E; Sands, 1998, Figs. 669–681), *Protohamitermes* worker mandibles (Ahmad, 1976, Fig. 8A) differ considerably from those of *Cylindrotermes* and *Cephalotermes*, and the enteric valve has six cushions (Ahmad, 1976, Fig. 10A). Another possibly related genera is *Orientotermes* Ahmad, 1976, a soldierless Oriental termite (Bourguignon et al., 2017), but since little information on the worker gut anatomy is available, it is not possible to make a complete comparison. The mandibles clearly differ from those of *Cylindrotermes* (Ahmad, 1976, Fig. 8B) and the enteric valve has six cushions (Ahmad, 1976, Fig. 11A).

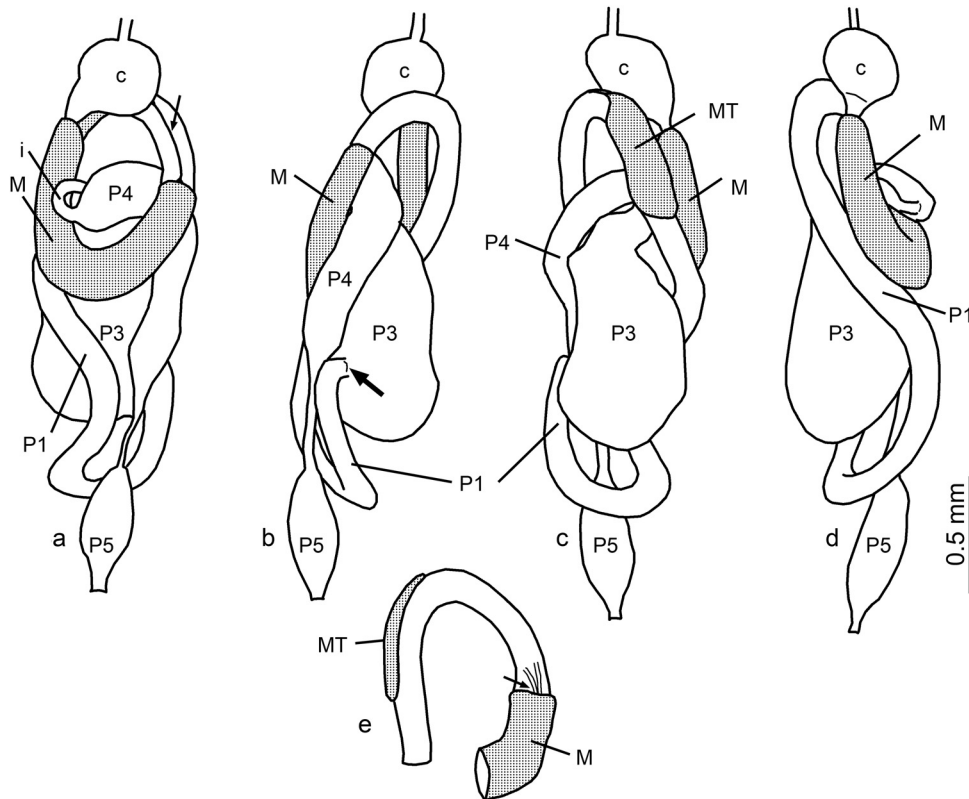


Fig. 8. *Cylindrotermes parvignathus* worker gut *in situ*: (a) dorsal, (b) right (arrow: enteric valve insertion), (c) ventral, and (d) left views, and (e) detail of mixed segment and Malpighian tubules insertion (arrow). Gray indicates mesenteric tissue; c: crop; M: mesenteron; MT: mesenteric tongue; i: isthmus; P1: first proctodeal segment (ileum); P3: third proctodeal segment (paunch); P4: fourth proctodeal segment (colon); P5: fifth proctodeal segment (rectum).

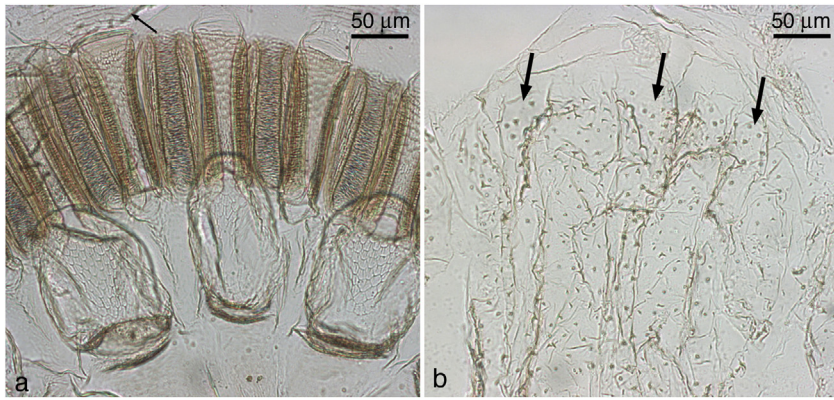


Fig. 9. *Hoplotermes amplus* worker: (a) detail of gizzard armature (small arrow: crop pectinate scales), (b) enteric valve (large arrows: cushions).

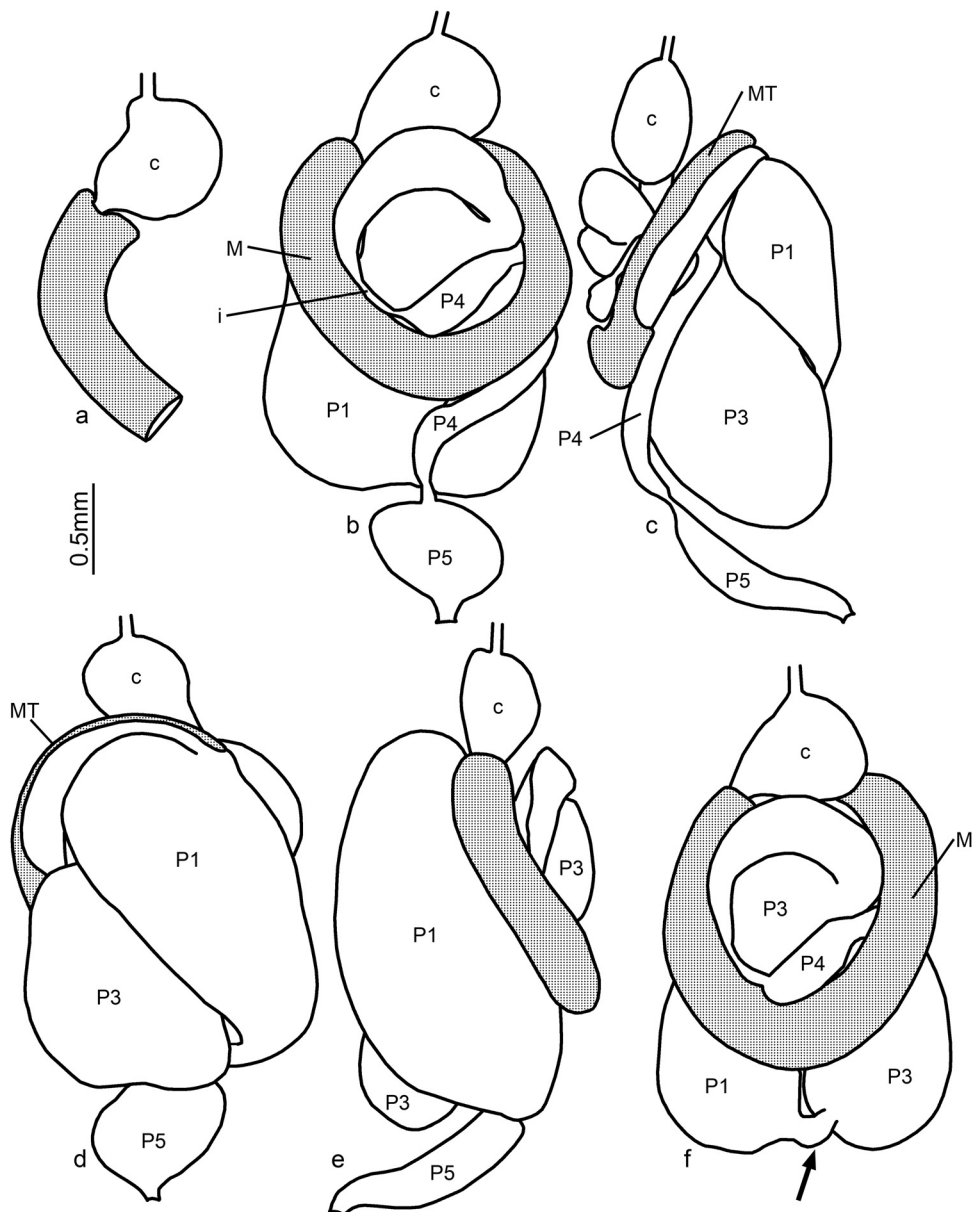


Fig. 10. *Hoplotermes amplus* worker gut *in situ*: (a) detail of stomodeal valve insertion, (b) dorsal, (c) right, (d) ventral and (e) left views; (f) detail of enteric-valve insertion in dorsal view (P4 and P5 removed, arrow: enteric-valve insertion). Gray area indicates mesenteric tissue; c: crop; M: mesenteron; MT: mesenteric tongue; i: isthmus, P1: first proctodeal segment (ileum); P3: third proctodeal segment (paunch); P4: fourth proctodeal segment (colon); P5: fifth proctodeal segment (rectum).

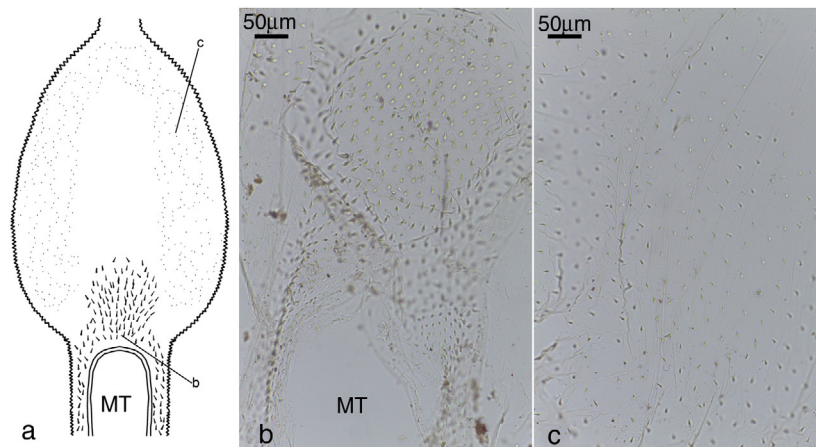


Fig. 11. *Hoplotermes amplus* P1 ornaments: (a) schematic drawing of P1 showing arrangement of spines, with b indicating robust spines in proximal region, and indicating sparse short spines laterally and distally; (b) detail of robust proximal spines; (c) detail of sparse short spines (MT, mesenteric tongue space).

On the other hand, all Neotropical apicotermitine genera and some Oriental genera (e.g., *Euhamitermes* Holmgren, 1912) have a similar looped P1 (Noirot, 2001; Fig. 10H, L). They differ from *Cylindrotermes* in having the left mandible with a conspicuous notch before the third marginal tooth, and the mesenteric tongue, when present, internal to the mesenteric arch.

Hoplotermes

Worker digestive tube (Figs. 9–11): Crop slightly asymmetrical, moderate in size, covered with finely pectinate scales (Fig. 9a, arrow). Gizzard with a complete armature arranged in a columnar belt with 24 folds (six first-order, six second-order, and 12 third-order) and a pulvillar belt with 12 folds (six first-order, six second-order); Length ratio between belts about one; pulvilli of first order ornamented with recognizable pectinate scales, pulvilli of second order inconspicuous (Fig. 9a). Stomodaeal valve insertion slightly displaced to the inner region of the mesenteric arch (Fig. 10a). Mesenteron tubular, with a single well-developed mesenteric tongue of length nearly equal to half that of the mesenteric arch, ending just at the beginning of the P1 dilated portion (Fig. 10d). It was not possible to examine the Malpighian tubules, since we had few specimens for dissection. P1 strongly dilated, its size nearly equal to the P3 (Fig. 10c, d and f), and attached to it by a narrow connection at the distal region of the abdomen, below the P5 (Fig. 10f, arrow); cuticular ornamentation of P1 with robust spines located around the border of the mesenteric tongue and just distal to it (Fig. 11a, b), and with sparse short spines laterally and distally (Fig. 11a, c). P2 with a single ring of three elongated cushions (Fig. 9b, arrows), weakly marked, radially arranged, and covered sparsely with small spines. P3 well developed, protruded through the mesenteric arch. Isthmus marked (Fig. 10b), P4 with a short U-turn (Fig. 10c).

Comparisons among recognized termitine genera: *Hoplotermes*, some species of *Amitermes* (Sands, 1998, Figs. 609–628), *Genuotermes* Emerson, 1950, and most syntermitine genera (see Rocha et al., 2017) have a strongly inflated globose or fusiform P1 and similar cuticular ornamentation of the P2, with spines organized in distinct patterns (Rocha et al., 2017; Engel et al., 2009). *Hoplotermes* and some syntermitine genera have a similar distribution of spines in the P1 cuticular ornamentation (Rocha and Constantini, 2015), with the most robust spines concentrated in the proximal portion. No other American termitine genera have this combination of morphological features.

Discussion

Noirot and Kovoov (1958) proposed two groups within Termitinae, defined by the anatomy of the gut: the Thoracotermes and the Termes, based only on African taxa. Later, Noirot (2001), with a large number of specimens from different regions, distinguished five groups: the pantropical Termes group, the Oriental Pericapritermes group, the pantropical Amitermes group, the Ethiopian Cubitermes group [the Thoracotermes group of Noirot and Kovoov (1958)], and the African Foraminitermes group (hypothetical new subfamily). Engel et al. (2009) formally raised the last two groups to subfamily rank, the Cubitermitinae and Foraminitermitinae. These subfamilies were supported as natural clades in studies by Inward et al. (2007) and Bourguignon et al. (2017). Rocha et al. (2019) recognized in the American region, the Amitermes group, comprising the genera *Amitermes*, *Gnathamitermes*, and *Hoplotermes*; the Cavitermes–Termes group, with the Cavitermes subgroup, comprising *Cavitermes* Emerson, 1925, *Cornicapritermes* Emerson, 1950, *Dihoplotermes* Araujo, 1961, *Divinotermes* Carrizo and Cancellato, 2011, *Palmitermes* Hellems and Roisin, 2017, and *Spinitermes* Wasmann, 1897, and the Termes subgroup, comprising *Inquilinitermes* Mathews, 1977, and *Termes*; the Neocapritermes group, comprising *Neocapritermes* Holmgren, 1912, *Planicapritermes* Emerson, 1949 (in Snyder, 1949), and *Crepititermes* Emerson, 1925; and the Orthognathotermes group, comprising *Dentispicotermes* Emerson, 1949 (in Snyder, 1949) and *Orthognathotermes* Holmgren, 1910; while separating *Cylindrotermes*, *Genuotermes*, *Microcerotermes*, and *Onkotermes* as truly distinct genera.

The present study examined in detail the internal morphology of the worker caste of *Cylindrotermes* and *Hoplotermes*, complementing their original descriptions. Based on this new information, we consider that *Cylindrotermes* cannot be assigned to the Amitermes group (*sensu* Noirot, 2001). Evidence from the gut morphology supports *Cylindrotermes* as a relative of the Ethiopian genus *Cephalotermes*, a hypothesis previously advanced by Inward et al. (2007) and Bourguignon et al. (2017), in their phylogenetic reconstructions.

Hoplotermes has not yet been included in any evolutionary scheme, but based on our morphological observations, it may be related to the *Amitermes*–*Drepanotermes* lineage. To overcome this limitation and to reach firm conclusions about the kinship of *Hoplotermes*, we strongly recommended that this termitine genus be included in future phylogenetic analyses. Author contributions

M.M.R. conceived the research and edited the figures; M.M.R. and C.C. collected and analyzed data and wrote the paper.

Conflicts of interest

The authors declare no conflicts of interest.

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