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REVIEW

Overview of the Morphology of Neotropical Termite Workers: History and Practice

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Abstract

This contribution deals with the worker caste of the Neotropical termite fauna. It is a compilation of present knowledge about the morphology of pseudergates and workers, including the literature discussing the origin and evolution of this caste, the terminology used in the different taxonomic groups, and the techniques used to study these individuals, especially examination of the gut, mandibles, legs, and nota. In order to assist in identifying workers, it includes a key for the families that occur in the Neotropical Region and a characterization of workers of all families, especially the subfamilies of Termitidae, with descriptions and illustrations of diagnostic morphological features of genera. We point out advances and gaps in knowledge, as well as directions for future research.

Introduction

Adapted to a strict diet of cellulose and lignocellulose compounds, termites are eusocial hemimetabolous insects that live in organized colonies, with castes that can be recognized morphologically and functionally. Although the group contains only a moderate number of species for insects (approximately 3000 species worldwide and 650 Neotropical species), and they are most commonly known as pests (structural, agricultural, and forest), termites have critical roles in tropical and subtropical ecosystems, and are hence termed ecosystem engineers ("soil ecosystem engineers," Jones *et al*., 1994). Most of these roles (e.g., damage and engineering) are largely linked to the worker caste, and these attributes led Noirot (1982) to consider workers as the main caste responsible for the evolutionary success of termites.

Nine families are presently recognized: Mastotermitidae, Hodotermitidae, Archotermopsidae, Stylotermitidae, Kaloter-mitidae, Stolotermitidae, Rhinotermitidae, Serritermitidae and Termitidae; the last five occur in the Neotropical Region (Krishna *et al*., 2013). Today, the Termitidae includes about 75% of termite species worldwide, and according to Krishna *et al.* (2013) is classified in eight subfamilies: Sphaerotermitinae, Macrotermitinae, Foraminitermitinae, Cubitermitinae, Apico-termitinae, Syntermitinae, Nasutitermitinae, and Termitinae. These last four occur in the Neotropical Region and are treated here.

Very generally, termite colonies contain soldier, worker, and reproductive castes, which perform the functions implicit in these terms. However, workers and reproductives cannot be defined simply, without entering into their complex diffe-rentiation of castes and development. It is incorrect to say that soldiers and workers are always sterile as opposed to reproductives, since there are records of soldiers with relatively developed gonads (Imms, 1919) or acting as true reproductives (Thorne *et al*., 2003). As far as workers are concerned, the

possibilities are many, complex and widely debated (e.g., Roisin & Korb, 2011). Thus, the termitology jargon includes several terms that merit more-detailed explanation (see Thorne, 1996; Korb & Harfelder, 2008). Here we will treat the terms relating to juveniles, and subsequently those for workers.

As the soldier caste shows distinct characters, termites have traditionally been identified based on this caste. However, there are practical reasons for attempting to use the worker caste for identification. These include the identification of specimens in samples that lack soldiers (such samples are commonly left unidentified in collections); triage of miscellanea provided from field work; and to better understand the relationships among taxa, i.e., to understand the evolution of the group, since worker characters provide substantial taxonomic information (Donovan *et al.*, 2000; Inward *et al.*, 2007; Rocha *et al.*, 2017).

A fine history of termitology was provided by Krishna *et al.* (2013), who highlighted the role of Niels F. Holmgren as the most important researcher to study the morphology of termites. Holmgren (1909) described the gut *in situ* of imagoes, soldiers, and workers of the same species in several genera representing different groups. Holmgren's work was essential for a classification system of the group, and laid the foundation for all who came after him.

Some early authors investigated the digestive tract of termites, although they were concerned with studying the intestinal symbionts, initially called parasites (e.g., Lespès, 1856, Leidy, 1881, and Grassi & Sandias, 1893). Cleveland (1924), in his seminal work on the relationship between protozoan symbionts and their hosts, provided a detailed history of the studies that dealt with these symbionts, emphasizing that initially, the authors studied either the termites or the protozoa, but few attempted to understand the relationship between them. He cited Buscalione and Comes (1910) and Imms (1920), who referred to a symbiotic relationship between the intestinal protozoa and their hosts, but without a solid experimental basis. Through hundreds of laboratory experiments, Cleveland himself definitively proved that a true symbiotic relationship exists between some of the intestinal protozoa and the termites, and even demonstrated that some other intestinal protozoa were not symbionts but merely commensals. He also stated that no member of Termitidae contains protozoan symbionts, which was evidenced by many later studies. Today there is a vast literature on the intestinal symbionts of Termitidae, which include bacteria and fungi (König & Varma, 2010; Ohkuma & Brune, 2011; Brune & Dietrich, 2015, among others).

Pierre Paul Grassé and Charles Noirot studied many African species, also investigating the digestive tract of workers. In 1955, they proposed a new subfamily, Apicotermitinae (Termitidae), based mainly on the gut anatomy of the workers. They provided detailed comparisons between the new subfamily and the very concept of Termitinae at that time, for both soldiers and workers.

Even after this study, few taxonomic descriptions at that time included such characteristics (Noirot, 1966; Deligne & Pasteels, 1969). Noirot and Kovoor (1958) contributed significantly to knowledge of the comparative anatomy of the gut of African Termitinae, from the perspective of understanding the evolution of these characters. Jacqueline Kovoor (1969) continued these studies of comparative anatomy, including photographs of the enteric valve for the first time. She studied the Nasutitermitinae, which at that time included the genera which are today in Syntermitinae, that is, she also studied Neotropical species. This study was definitive for all researchers who continued to work with termites in the Neotropical Region.

Noirot and Noirot-Thimothée (1969) composed the chapter on the termite digestive system in the first volume of a two-volume work, the fundamental *Biology of Termites* (Krishna & Weesner, 1969, 1970), to this day an obligatory reference for termitologists and a "Bible" for the Isoptera until the publication of the treatise "Termitologia" by Grassé (1982, 1984, 1986). Sands (1972), in his study on soldierless termites of Africa, proposed a new classification of the Termitidae, broadening the definitions of Apicotermitinae (to include *Anoplotermes*) and Termitinae (to include Amitermitinae). For this purpose, he studied in detail the general external morphology, morphology of the mandibles, and the anatomy of the gut of workers. Johnson (1979) perceived that the greatest problem in termite population ecology was to identify workers, which were often collected from soil as mixtures of species. He developed the convention, still in use today, for illustrating the *in situ* gut morphology of Termitidae workers (e.g., Figs 1–4). While Johnson's (1979) studies involved African taxa, Mathews (1977), in his study on the termites of the Mato Grosso region of Brazil, recorded some characters of the gut of certain species (enteric valve and/or uncoiled gut of new genera of Apicotermitinae).

From the 1980s onward, termitologists began to describe workers more completely, especially with descriptions of the gut (Miller, 1984; Fontes, 1985; Constantino, 1991b, 1995; Roisin *et al.*, 1996, among others). Now in the 21st century, virtually all descriptions of new Termitidae taxa and revisions include a study of the gut and mandibles of the workers (e.g., Cancello & Myles, 2000; Cancello & Noirot, 2003; Bourguignon *et al.*, 2008, 2010; Carrijo *et al.*, 2011; Cuezzo & Nickle, 2011; Constantino & Carvalho, 2012; Rocha *et al.*, 2012; Cuezzo *et al.*, 2017; Hellemans *et al.*, 2017).

Noirot (1995, 2001) compiled all the studies on the species of all families of Isoptera, with illustrations and descriptions, including important discussions about the evolutionary significance of the differences among the various parts of the gut, especially in the Termitidae (Noirot, 2001). These two studies are a fundamental basis for this area of research. Even though it deals with African fauna, one cannot fail to mention the book by Sands (1998) on the workers of African termites, with its 1568 drawings and 18 photographic plates.
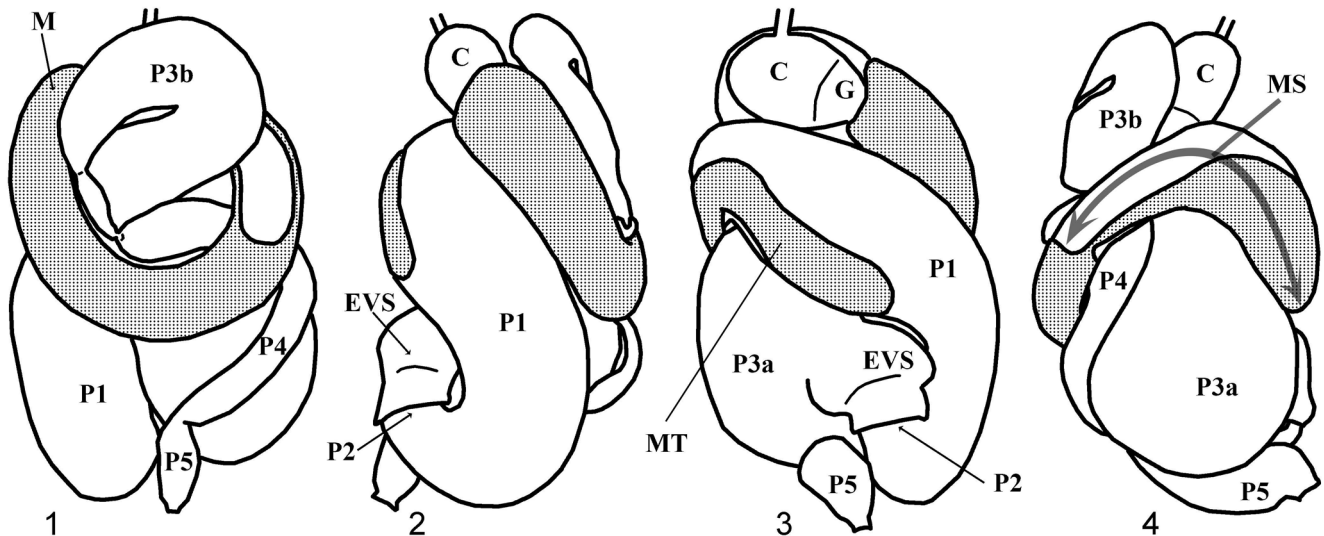
Figs 1–4. Worker gut of *Cornitermes cumulans* in 1- dorsal; 2- left; 3- ventral and 4- right views [foregut with crop (C), gizzard (G); midgut: mesenteron (M); mixed segment (MS), mesenteric tongue (MT) and hindgut with ileum (P1), enteric valve (P2), enteric-valve seating (EVS), paunch (P3a and P3b), colon (P4) and rectum (P5)], (figures not to scale).

The descriptions of the external morphology and of the mandibles are exemplary, and those of the gut are definitive. For a better understanding of the worker caste, it is also important to mention studies of the mandibles, such as those of Ahmad (1950), who proposed a phylogeny of the Isoptera (today completely outdated) based only on the imago-worker mandibles; and Deligne (1966, 1999), who dealt in detail with the functional morphology of the mandibles and their modifications during development.

The origin and evolution of the worker caste have been a subject of discussion, and several studies have investigated this fundamental aspect of termite colonies in the different taxonomic groups (Noirot & Pasteels, 1987; Korb, 2007, 2008; Inward *et al*., 2007; Legendre *et al*., 2008; Roisin & Korb, 2011; Bourguignon *et al*., 2017). In recent years, remarkable insights have been gained on the termite worker caste, with important implications, for example, for the genetic, hormonal and ecological influences on caste differentiation, developmental pathways, and polyethism, and the microbial symbionts in the gut and their co-evolution with termite hosts. This knowledge reinforces the importance of the role of the worker caste and the successful evolution of the group (Bignell *et al*., 2011).

This review summarizes recent progress in morphological characterization of workers of the Neotropical termite fauna, covering all families and subfamilies that occur in this region and their importance in taxonomy and phylogeny. Much advancement is needed, but we indicate several further steps that may accelerate taxonomic decisions and help in other areas such as structural, agricultural, and forest "pest species". We hope that with the present study and those to come, knowledge and identification of workers will become more and more common in the day-to-day routine of the termitologist.

Material and Methods

Descriptive terminology

We use the terminology of Weesner (1969) for the external morphology of the true worker; Noirot (1995, 2001) to refer to the different parts of the gut (Fig 1–4) [foregut with crop (C), gizzard (G); midgut (M); and hindgut with: ileum (P1), enteric valve (P2), enteric-valve seating (EVS), paunch (P3), colon (P4), and rectum (P5)]; and Emerson (1933, 1960) to describe details of the worker mandibles (Fig 5–12). We follow Krishna *et al*. (2013) for the taxonomic classification.

Since termites are hemimetabolous insects, all juveniles should be called nymphs, but the term "larva" has become classic for the first-instar juveniles, with no wing bud or soldier features; and the term "nymph" is used for juveniles with wing buds of different sizes, that is, which are in the imaginal lineage (Roisin & Korb, 2011). The soldier before the last molt is called "white soldier" and already exhibits some of the distinct features of the soldier of the species. The so-called "white-gutted soldier (WGS)" (Scheffrahn *et al*., 2017) in contrast, is fully developed and has functional mandibles

Most simply, one can define the different types of workers as follows (adapted from Korb & Hartfelder, 2008):

1) *Pseudergate sensu stricto*: in all families except Termitidae, the "larvae" are totipotent with respect to development, and can become soldiers or reproductives, or can undergo "stationary molts", without developing wing buds or characteristics of soldiers. They can even undergo regressive molts, when the nymph with a wing bud molts to an instar without a wing bud. Grassé and Noirot (1947) coined the term "pseudergate" for a juvenile that undergoes a regressive molt. However, this raises practical problems, because it is necessary to follow the development of a nymph with wing buds to discover whether it goes through a regressive molt and loses them.

2) *Pseudergate sensu lato*: In this broader definition, any "larva" or nymph that could potentially undergo stationary, regressive or progressive molts is called a "pseudergate".

In both the above definitions, the individuals are little sclerotized and whitish, and may be functional workers. Other terms exist, such as "false worker" and "helper", with different definitions, including in relation to the work that they perform in the colony (see discussions by Noirot & Pasteels, 1987). Here, "pseudergate" is used in the broader sense.

3) *True workers*: These are individuals that differentiate early and irreversibly from the imaginal line of development, and are less flexible than "pseudergates", i.e., they are not totipotent and cannot undergo regressive or stationary molts. Morphologically they lack wing buds and have rudimentary sexual organs. These individuals are responsible for practically all the tasks of the colony except reproduction, including defense. True workers are present in Mastotermitidae, Hodotermitidae, in some Rhinotermitidae, and in all Termitidae. Here, the term "worker" is used.

Digital images and drawings

The line drawings were made with a camera lucida, and the photographs were taken with a digital camera coupled to a stereomicroscope, at different focal points, and merged with software. The enteric valve and crop of workers were mounted on a slide with glycerin and photographed under an optical microscope.

Techniques

For details of methods to study the mandibles and gut of workers, some suggested references include those by Sands (1972, p. 10; 1998, p. 15–17), Fontes (1987b, p. 505) and Constantino (1999, p. 392).

Readers should note that in older workers the mandibles often appear worn, with the tips of the teeth not pointed, tapered but blunt; and the edges of the marginal teeth may appear to be interrupted or serrated due to wear.

Another factor is the degree of filling of the gut, which may alter the relative position of the parts from that in published illustrations and photographs. To prevent large differences between descriptions, it is useful to inspect several individuals before selecting one for illustration. Normally, the relative position does not change so much that it prevents the recognition of the patterns illustrated in more recent studies.

*Key to the families found in the Neotropical Region, based on the worker or pseudergate (**Stolotermitidae, Kalotermitidae, Rhinotermitidae, Serritermitidae, Termitidae**)*

1a. Pronotum as wide or nearly as wide as head capsule (Fig 13)…2
1b. Pronotum substantially narrower than head capsule (Fig 14)…3

2a. Left mandible with four marginal teeth; right mandible with two marginal teeth and a subsidiary tooth (Fig 5)… **Stolotermitidae** (*Porotermes*)
2b. Left mandible with two marginal teeth (M1+2 and M3); right mandible without subsidiary tooth (Fig 6)… **Kalotermitidae**

3a. Pronotum flat or with very small anterior lobe (Fig 15, 16)… 4
3b. Pronotum saddle-shaped, with clearly defined anterior lobe (Fig 17)… 6

4a. Left and right mandibles with large apical tooth; left mandible with one (*Serritermes*) or two marginal teeth (*Glossotermes*); right mandible without subsidiary tooth (Fig 9)… **Serritermitidae**
4b. Left mandible with three marginal teeth; right mandible with one subsidiary tooth (Fig 8)… 5

5a. Pronotum with very small anterior lobe, less than half as long as posterior lobe (Fig 16), enteric-valve cushions as in figures 18, 19… **Rhinotermitidae** (*Heterotermes*, *Coptotermes,* and *Reticulitermes*)
5b. Pronotum flat, anterior lobe absent (Fig 15), enteric-valve cushions as in Fig 20… **Rhinotermitidae: Prorhinotermitinae** (*Prorhinotermes*)

6a. Left mandible with three marginal teeth; right mandible with one subsidiary tooth (Fig 7), enteric-valve cushions as in figure 21… **Rhinotermitidae: Rhinotermitinae** (*Acorhinotermes*, *Dolichorhinotermes*, and *Rhinotermes*)
6b. Mandibles variable, but left mandible never with three unfused marginal teeth (Fig 10–12)… 7

7a. Left mandible with conspicuous incision between fused first plus second (M1+2) and third marginal teeth (M3) (Fig 10, thick arrow); mesenteric tongue, if present, located on concave face of mesenteric arch, first proctodeal segment long and tubular, forming loop between rectum and paunch in ventral view... **Termitidae: Apicotermitinae**
7b. Left mandible variable, but without incision between M1+2 and M3 (Fig 11, 12); mesenteric tongue, if present, located on convex face of mesenteric arch, first proctodeal segment not forming loop between rectum and paunch in ventral view (*Cylindrotermes* workers have a ventral loop, but the other characters differ from Apicotermitinae)... **Termitidae: Nasutitermitinae, Syntermitinae, and Termitinae**

Families found in the Neotropical Region: characterization of the worker or pseudergate

Stolotermitidae

Engel *et al.* (2009) assigned a *status novo* to this monophyletic family, with Porotermitinae (one extant genus, *Porotermes*, and one fossil genus, *Chilgatermes*) and Stolotermitinae (one extant genus, *Stolotermes*), previously recognized in Termopsidae (Grassé school) or Hodotermitidae (Emerson school).
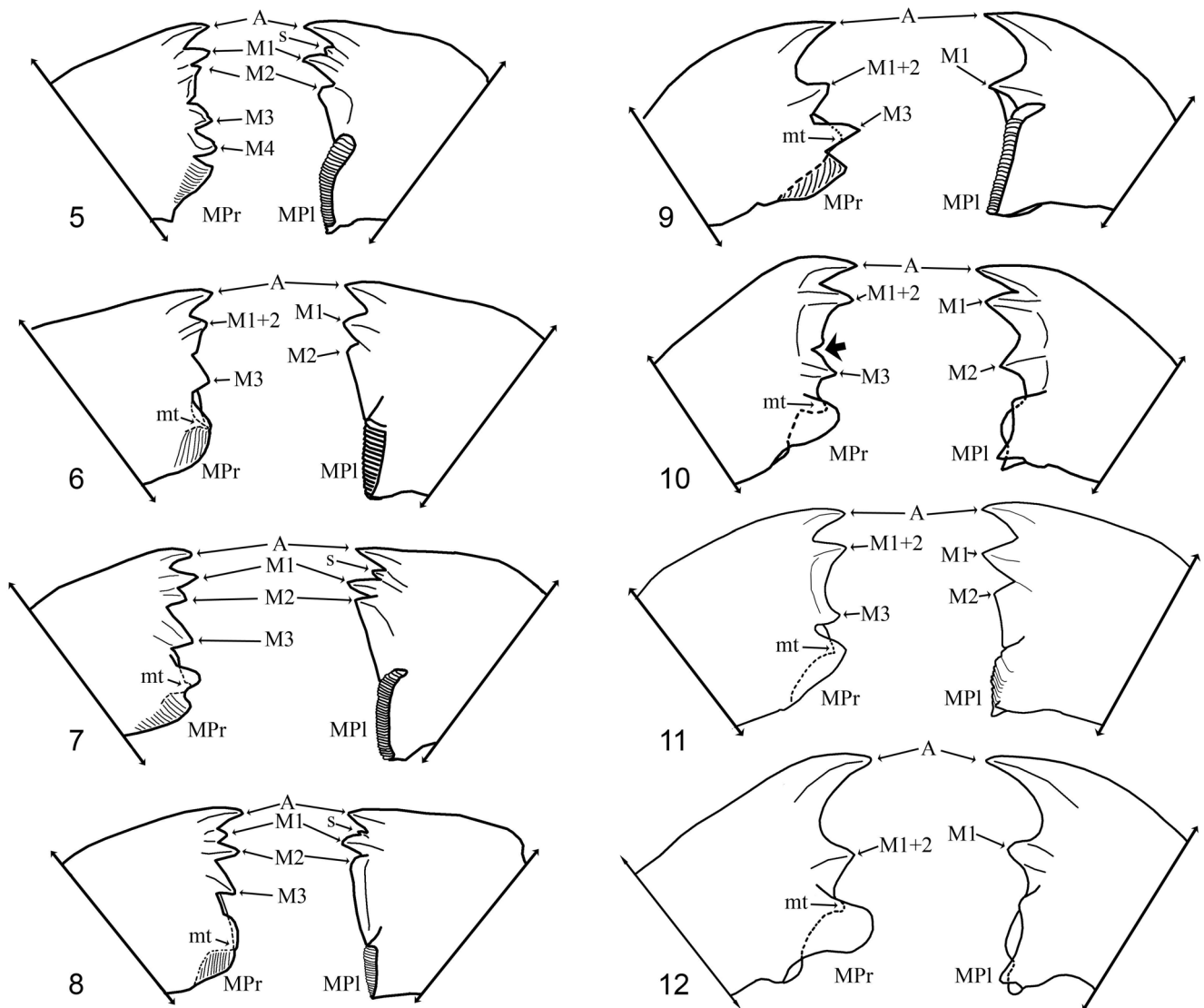
Figs 5–12. Worker mandibles in dorsal view: 5- *Porotermes quadricollis*; 6- *Rugitermes rugosus*; 7- *Rhinotermes marginalis*; 8- *Coptotermes gestroi*.; 9- *Glossotermes oculatus*; 10- *Anoplotermes pacificus*, 11- *Microcerotermes* sp., 12- *Crepititermes verruculosus*, [apical tooth (A), subsidiary tooth (s), marginal tooth 1, 2, 1+2, 3, 4 (respectively M1, M2, M1+2, M3, M4), molar tooth (mt), molar prominence (MPr) and molar plate (MPl)], (figures not to scale).

Porotermes has three extant damp-wood species: *P. adamsoni*, native to coastal and adjacent highland areas from southern Queensland to South Australia, and considered an invasive termite in New Zealand (Pearson *et al.*, 2010); *P. planiceps,* from the western Cape region of South Africa (Coaton & Sheasby, 1976); and *Porotermes quadricollis*, in southern Chile and Argentina (Camousseight & Vera, 2005; Torales *et al.*, 2005). Villan (1972) redescribed *Porotermes,* with new diagnoses and a key to the three species, for imagoes, soldiers, and pseudergates.

Characteristics of the pseudergates of *Porotermes* are: compound eyes more or less developed, depending on the stage of development of the individual; ocelli absent; pronotum half-moon-shaped; tarsi with three tarsomeres on each leg, with a triangular arrangement on the posterior leg; cerci with five articles, styli are present in males and females.

For identification of the pseudergates, in addition to the mandibular pattern, Noirot (1995) described the gut coiling *in situ* and gave details of its anatomy in *P. adamsoni* and *Stolotermes africanus*. Krishna *et al.* (2013) described the gut of Porotermitinae in detail and compared some characters with other families.

Compared to non-wood-nesters, the pseudergates of both Kalotermitidae and Stolotermitidae show proportionally short legs, with an enlarged coxa; and their behavior is different, as they live inside wood, crawling in very slow movements.

Kalotermitidae

Kalotermitidae is represented worldwide by 22 genera and 459 extant species. The Neotropical Region has the largest number of genera (12), although the Oriental Region has the most species diversity. The so-called dry-wood termites,

e.g., certain species of *Cryptotermes*, and *Incisitermes*, can cause enormous damage in urban areas. Constantino (2002) mentioned three species of this family that were introduced from other regions and became urban pests: *Cryptotermes brevis*, *C. dudleyi*, and *C. havilandi*, and noted that there are several yet-undescribed species of *Cryptotermes* in South America. In Brazil, *C. brevis* is a major pest in many cities (Constantino, 2002). We may expect that some species, originally restricted to the natural environment and coming into contact with cities expanding into pristine forests, may become urban pests. An example is *Glyptotermes canellae*, an Atlantic Forest species reported from inside wooden furniture in Santos, state of São Paulo (E.M.C. personal observation).

True workers are absent, and pseudergates contribute to the tasks within the colony. In general, given the uniformity of their external morphology, only the mandibles are usually used for identification, even though they show a similar pattern, as seen in the illustrations by Krishna (1961). No specific diagnoses were provided for pseudergates until Scheffrahn (2011) described the pseudergates of *Calcaritermes,* illustrating their mesonotal "rasp" and/or the concave posterior margin of the pronotum. The mesonotal rasp is the first external character used to provide a diagnostic, generic identification of an immature kalotermitid.

Dr. R. H. Scheffrahn (University of Florida) has been actively studying the taxonomy of Kalotermitidae in the Neotropics, mainly in the Caribbean Basin, alone (Scheffrahn, 1994, 2011, 2014a) or with collaborators (Scheffrahn & Su, 1994; Scheffrahn *et al.*, 1998a, 1999, 2000, 2001, 2009, 2015, among others).

Gonçalves (1979) studied the gut of *Rugitermes niger*, and Noirot (1995) provided some insights on *Kalotermes*, *Neotermes*, *Cryptotermes*, *Glyptotermes,* and *Pterotermes*. More recently, Godoy (2004) treated the Neotropical genus *Tauritermes*. The midgut length, ornamentation, and shape of the P1 and P2, and the ornamentation of the rectal valve seem to be useful for separating taxa, although more studies are needed.

Serritermitidae

Serritermitidae is the only termite family with exclusively extant Neotropical representatives (records from Brazil, Guyana, and French Guiana). The taxon was originally proposed by Holmgren (1910) as a subfamily in the Mesotermitidae (*nomen nudum*, related to Rhinotermitidae) and raised to family rank by Emerson (1965). The family presently contains three species in two genera, *Glossotermes* and *Serritermes,* according to Cancello and DeSouza (2005).

The mandibles of the imago and the pseudergate are unique (Ahmad, 1950; Cancello & DeSouza, 2005), with long acuminate apical teeth, a reduced number of marginal teeth (left mandible with one marginal tooth in *Serritermes,* and two in *Glossotermes*), and the molar regions with well-developed ridges (Fig 9). The gut shares similarities with members of the family Rhinotermitidae, except in the reduction of the stomodeal valve and the simplification of the structures present on P1 and P2 (Noirot, 1995; Cancello & DeSouza, 2005). The clear differences between the worker mandibles in the two genera, *Glossotermes* and *Serritermes*, are easily seen and are enough to separate them.

Figs 13–14. Pseudergates in dorsal view: 13- *Prorhinotermes simplex*; 14- *Rugitermes* sp.

Rhinotermitidae

Rhinotermitidae is the most widely distributed termite family in the world, occurring from tropical to temperate regions. Some species of this family, popularly known as subterranean termites, are especially important because of their potential as pests, and can cause enormous damage (Constantino, 2002; Vargo & Husseneder, 2009).

Rhinotermitidae was initially described as a subfamily of Mesotermitidae (*nomen nudum,* Holmgren, 1910), and was later raised to family rank. The relationship between the genera of Rhinotermitidae and the other termite families, especially Termitidae, Serritermitidae, and Stylotermitidae, has been widely debated. The present consensus is that Rhinotermitidae is not a natural group (Lo *et al*., 2004; Inward *et al*., 2007; Legendre *et al*., 2008, 2013; Bourguignon *et al*., 2014). The family is composed of the genera *Prorhinotermes* (three species in the Neotropical Region), *Termitogeton,* and *Psammotermes* (outside the Neotropical Region)*,* of uncertain position, although each was classified in a different subfamily by Krishna *et al*. (2013); and two relatively consistent groups: the Rhinotermitinae, composed of *Parrhinotermes, Schedorhinotermes,* and *Macrorhinotermes* (outside the Neotropical Region); plus *Acorhinotermes, Rhinotermes,* and *Dolichorhinotermes* (Neotropical); and the group composed of *Coptotermes, Heterotermes,* and *Reticulitermes* (Bourguignon & Roisin, 2011; Bourguignon *et al*., 2014). This last group was traditionally divided into two subfamilies, Coptotermitinae (*Coptotermes*) and Heterotermitinae (*Heterotermes* and *Reticulitermes*); however, in all recent phylogenies using molecular data the genus *Coptotermes* supports the subfamily Heterotermitinae as paraphyletic (e.g., Lo *et al*., 2004; Inward *et al.,* 2007; Legendre *et al*., 2008; Bourguignon *et al*., 2014). Thus, we use here "*Heterotermes* group" for the three genera *Coptotermes*, *Heterotermes*, and *Reticulitermes*. The *Heterotermes* group is probably a sister-group of the Termitidae and will likely be raised to family rank (Lo *et al*., 2004; Legendre *et al*., 2013; Bourguignon *et al*., 2014).

Workers of Rhinotermitidae can be easily recognized by the three marginal teeth on the left mandible, and a subsidiary tooth on the right mandible (Fig 7–8). The gizzard is shorter and considerably more separated from the esophagus than in the other, non-Termitidae families. The transition from P1 to P2 is well marked. P1 is short and narrowed distally. The transition from P1 to P2 has six cushions of two orders (I and II). In P1, the cushions have small homogeneous spines, with cushions I nearly rectangular, and II triangular and narrowed distally. Cushions I are well developed and ornamented in P2; Noirot (1995) described them as a "sharp-pointed escutcheons", with the distal tip protruding at the opening of the P2 in P3. Cushions II are reduced in P2.

The ornamentation of the "escutcheons" is somewhat characteristic of the genera and/or groups of genera. In *Prorhinotermes*, the "escutcheons" are elongated and arranged in a proximal cluster with 3–4 rows of one-, two-, or three-pointed scales (Fig 20). In the Rhinotermitinae, the proximal cluster has scales with larger spines in the center of the "escutcheons", but not as large as the spines in the *Heterotermes* group (Figs 18, 19). Both Rhinotermitinae (Fig 21) and the *Heterotermes* group also have two distal clusters of fine setae, and Rhinotermitinae has a central cluster of spines that are less sclerotized than the proximal cluster, but more so than the corresponding setae of the distal clusters (Noirot, 1995).

Among the groups with Neotropical representatives, the external morphology of the workers is quite varied. In workers of Rhinotermitinae, the second marginal tooth of the mandible is smaller than the first marginal tooth (Krishna *et al.*, 2013); the pronotum is saddle-shaped; the wall of the abdomen may be transparent or slightly opaque; and the head is large in relation to the body size (Fig 17). In workers of the *Heterotermes* group, the first marginal tooth of the left mandible is smaller than (*Coptotermes* and *Heterotermes*) or equal to (*Reticulitermes*) the apical, second and third marginal teeth (Krishna *et al.*, 2013); the pronotum is not saddle-shaped as in Termitidae, with at most a small elevation on the anterior margin (i.e., a very small anterior lobe); the head is relatively smaller in relation to the body; and the abdomen is always whitish and opaque (Fig 16).

Termitidae

This family has the highest diversity of extant genera (261) and species (2097), with 81 genera and 428 species in the Neotropical Region. They occur in a wide diversity of habitats, mainly in tropical and subtropical regions worldwide.

Figs 15–17. 15- *Prorhinotermes simplex,* pseudergate in profile*;* 16- *Coptotermes gestroi*, pseudergate in profile and 17- *Dolichorhinotermes latilabrum*, worker in profile.

Species of Termitidae exploit the most varied types of lignocellulosic substrates as food. Most of the genera of Nasutitermitinae can be considered xylophagous (e.g., *Cortaritermes*, *Caribitermes*, *Nasutitermes*); others are humivores (e.g., *Cyranotermes, Subulitermes*); some feed on leaf litter (e.g., *Velocitermes*); or have specialized diets, such as some species of *Constrictotermes* that have peculiar feeding habits such as scraping lichens and tree bark. The diets of Syntermitinae encompass the entire humification gradient (Rocha *et al*., 2017), so that among its species it is possible to find all the morphotypes associated with their respective food resources. Among the Termitinae, again, the species cover almost the entire humification gradient; some are strict xylophages (e.g., *Cylindrotermes*) and others are humivores (e.g., *Cavitermes*) or are intermediate. Most members of Apicotermitinae are restricted to a humus-rich diet, and others, such as several species of *Ruptitermes*, eat grasses.

A worker caste can be recognized in the Termitidae, with a line of development, morphology, and distinct functions within the colony. Importantly, the mandibles of Termitidae are not the only components needed for rapid identification, as in the other families, but must be considered together with the characters of the gut and external morphology for an accurate determination.

The morphological characters that allow identification of workers have been treated in several studies over time. For example, the numbers of antennomeres and tibial spurs, in addition to the mandibles, were reported in detail by Weesner (1969), Grassé (1982), and Krishna *et al*. (2013). Characters of the internal morphology such as the gut coiling *in situ*, the mixed segment, the shape of the mesenteric tongue, and the insertion and arrangement of the Malpighian tubules (usually numbering four), and the enteric valve are derived mainly from the studies by Grassé and Noirot (1954), Noirot and Kovoor (1958), Kovoor (1969), Sands (1972, 1998), and Noirot (2001).

Apicotermitinae

A total of 50 genera and 217 species are recognized worldwide, with 14 genera and 52 species in the Neotropical Region. Advancement of taxonomic knowledge of Apicotermitinae in the world, and particularly in the Neotropical Region, presents a difficult challenge. Partly this is due to the absence of soldiers in most of the genera, and researchers have concentrated, consequently, on the identification and delimitation of the taxa based on the characters of the gut, which necessarily requires more time and training. Another consideration is the high rates of abundance and diversity of Apicotermitinae in the various ecosystem types, especially in humid forests, emphasizing their ecological importance (Cancello, 1994; Eggleton *et al*., 1996; Kambhampati & Eggleton, 2000; Davies *et al*., 2003; Ackerman *et al*., 2009; Bourguignon *et al*., 2011; Palin *et al*., 2011; Cancello *et al.,* 2014).

The group is presently under study in different laboratories, which have a growing interest in improving taxonomic knowledge of the group and advancing studies in other areas (phylogeny, biogeography, phylogeography, ecology, and behavior).

For 104 years, the genus *Anoplotermes* united all the Neotropical species of termites without soldiers, until the descriptions of *Grigiotermes* and *Ruptitermes* by Mathews (1977) and of *Aparatermes* and *Tetimatermes* by Fontes (1986). These five genera remain the references for non-taxonomist termitologists who use the most widely disseminated keys for the group.

In the last eight years, nine genera and 21 species have been described, a product of the revisions of part of *Anoplotermes* (*Longustitermes*; Bourguignon *et al*., 2010), *Grigiotermes* (*Amplucrutermes*, *Humutermes*, *Hydrecotermes*, *Patawatermes* and *Rubeotermes*; Bourguignon *et al*., 2016)

50μm
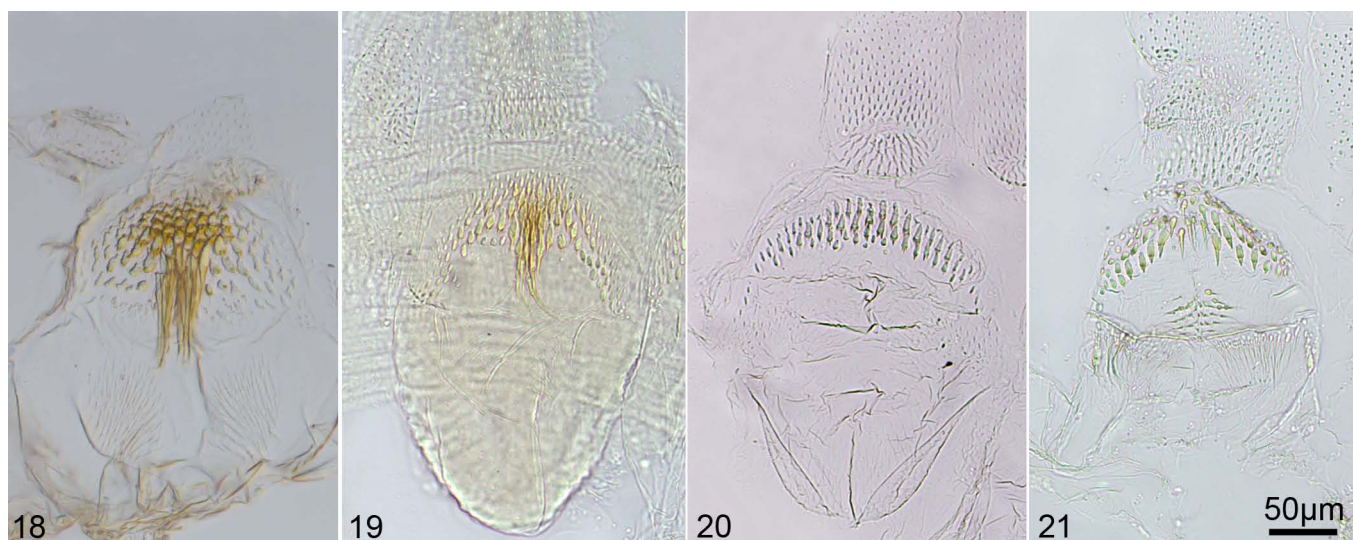
Figs 18–21. Enteric valve armature of: 18- *Heterotermes tenuis*; 19- *Coptotermes testaceus*; 20- *Prorhinotermes oceanicus* and 21- *Rhinotermes marginalis*.

Figs 22–23. Ventral view of the gut: 22- *Compositermes bani* and 23- *Anoplotermes pacificus*. The arrows indicate the mesenteron limit (22) and the inflated portion of the mesenteric tongue (23, highlighted).

and of *Ruptitermes* (Acioli & Constantino, 2015), in addition to the descriptions of *Compositermes* (Scheffrahn, 2013; Carrijo *et al*., 2015), *Disjunctitermes* (Scheffrahn *et al*., 2017), and *Echinotermes* (Castro *et al.* 2018).

The available keys for workers of Apicotermitinae are those of Fontes (1985, 1992), based mainly on characters of the gut coiling; Constantino (1999, 2002), who concentrated on characters of the external morphology; and Bourguignon *et al*. (2016), who used the ornamentation of the enteric valve. This last is the most up-to-date key at present, although it does not include *Disjunctitermes* or *Echinotermes*. These keys can serve as a point of departure for identification, but as discussed above, the great diversity among the Apicotermitinae remains understudied. Attempts to group new taxa within these known genera have been very common in surveys of the termitofauna, which are consequently inadequate and counterproductive, rendering unreliable those ecological analyses that include the Apicotermitinae.

The Neotropical genera present the following set of characters: the absence of the soldier caste; the presence of an incision between the M1+2 and the M3 on the left mandible (Fig 10, arrow); the P1 long, forming a loop that in ventral view surrounds the P3 (Figs 22, 23); and the presence, in most genera, of an enteric-valve seating (EVS, not exclusive to Apicotermitinae) (Noirot, 2001; Fig 24, arrow). The EVS is the distinct proximal region of the P3, shaped as a tubular ring or trilobate, and separated from the main portion of the P3 by a constriction. The P2, with variable organization and ornamentation, is invaginated in the EVS.

Fig 24. *Ruptitermes maraca*, right view of the gut (arrow: trilobate enteric-valve seating- EVS).

Certain recurring features aid in the delimitation of morphospecies and establishment of identity for Apicotermitinae; many of these are derived from the studies of Sands (1972, 1998) and Noirot (2001). The foreleg shows several characters that deserve attention. The foretibia may show a gradient of intumescences, from heavily inflated (*Amplucrutermes inflatus*, fig 2B of Bourguignon *et al.*, 2016) to slender (*Ruptitermes arboreus*, fig 4B of Acioli & Constantino, 2015), and a modified spoon-like tibia, possibly used for excavation (*Tetimatermes oliveirae*, Fig 25). The presence of thick bristles on the foretibia and forefemur, arranged in rows or not, and of thick bristles on the forecoxa has also been observed in certain described species (*Rubeotermes jheringi*, Fig 26, *Ruptitermes* spp., Acioli & Constantino, 2015) and species awaiting description (e.g., Apicotermitinae sp., Fig 27).

In studying the gut coiling, for most groups there is no need for dissection is not needed, since the gut can be examined through the transparent body. In this examination it is important to evaluate certain features that are briefly discussed here.
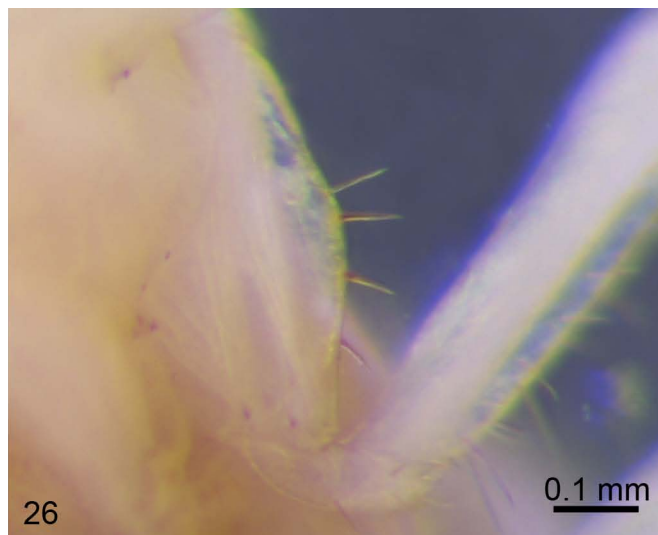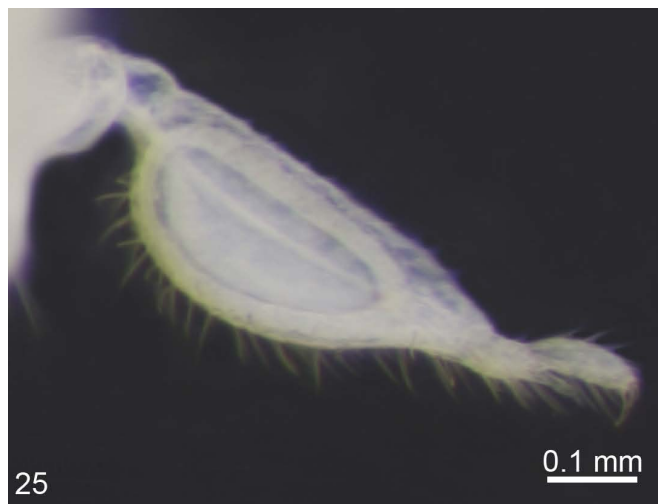
Figs 25–26. Worker legs of Apicotermitinae: 25- *Tetimatermes oliveirae*, spoon-like tibia; 26- *Rubeotermes jheringi*, thick bristles on forecoxae.

The mixed segment is an informative region for the study of Apicotermitinae. Noirot (2001) defined the absence (Fig 22) or presence of the mixed segment (Fig 23); or even vestigial mixed segments, in which there is no proper mesenteric tongue, but an oblique portion of the midgut. The joining of the P1 (through the P2) with the P3 may be visible in dorsal view, right lateral view (and in this case can be seen both dorsally and ventrally), or in ventral view. The shapes of EVS often vary. Both the gizzard and the insertion of the Malpighian tubules in the Neotropical Apicotermitinae have been little studied.
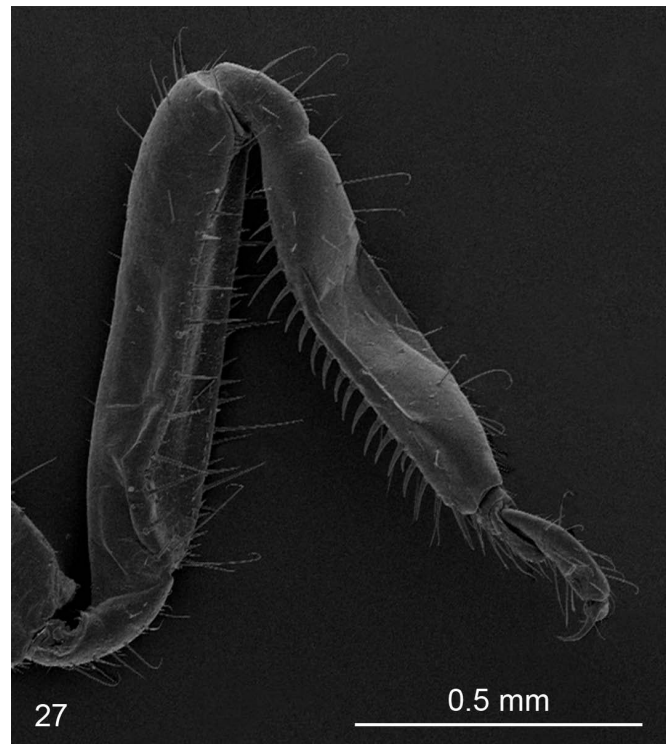
Fig 27. Worker leg of Apicotermitinae sp., one of two rows of tick bristles on tibia.

Among the important characteristics is the enteric valve or P2, which, differently from the mixed segment, requires dissection. Analysis of the P2 under a microscope offers the possibility of studying the arrangement and ornamentation of the scales that form the cushions. As observed for the species of *Anoplotermes* (including those recently revised by Bourguignon, 2010), the external morphology of the worker is very homogeneous, and it is impossible to distinguish them without examining the P2. The enteric valve is also very important for identification of the species of *Patawatermes*, although *P. turricula* and *P. nigripunctatus* are more easily distinguished through their morphometry and pilosity.

Examination of the enteric valve alone, however, is sometimes not enough to distinguish some Apicotermitinae, such as species of *Hydrecotermes* (see Bourguignon *et al.*, 2016, fig. 4A, B; and a new species currently being described by JPC, Fig 28). The same can be said of some species within the same genus, such as *Ruptitermes* (figs 24F and K, 25A and E of Acioli & Constantino, 2015) and *Aparatermes* (Figs 29
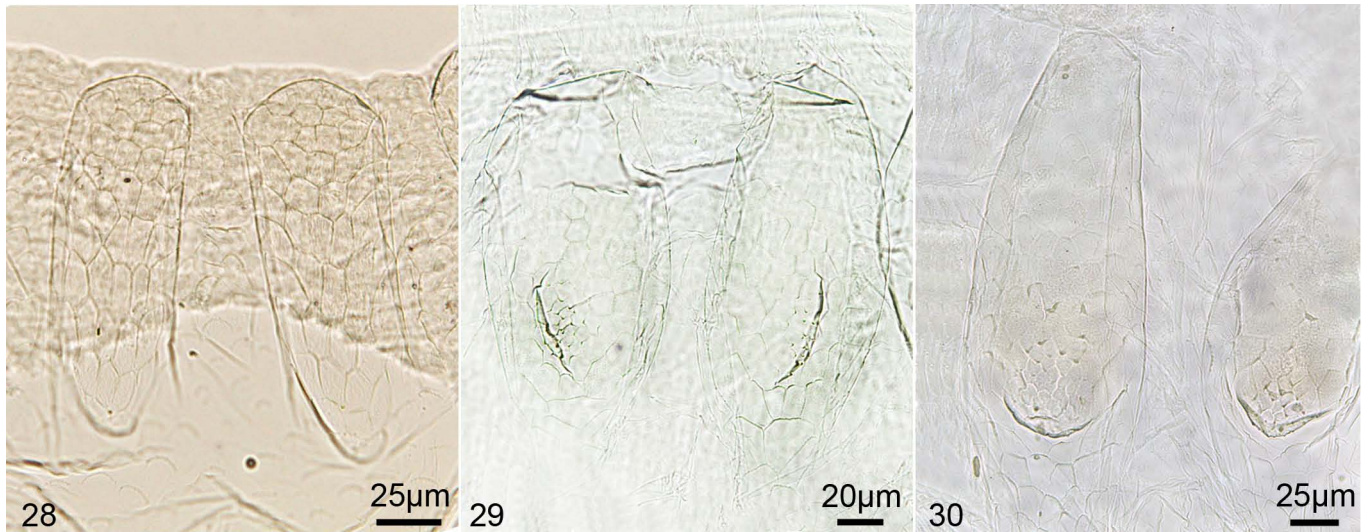
Figs 28–30. Enteric valves of Apicotermitinae: 28- *Hydrecotermes* sp.; 29- *Aparatermes abbreviatus*; 30- *Aparatermes cingulatus*.

and 30); or even between species of different genera, such as *Ruptitermes franciscoi* (fig. 24 J–K of Acioli & Constantino, 2015) and *Aparatermes cingulatus* (Fig 30), or *Ruptitermes bandeirai* (Fig 31) and *Tetimatermes oliveirae* (Fig 32), where the scale distribution and/or spine ornamentation is very similar. Also, it is crucial to consider the existence of intraspecific variations, such as those observed in *Anoplotermes janus* (compare fig. 2E of Bourguignon *et al.*, 2010 and Fig 33) and *Anoplotermes pacificus* (Figs 34, 35, JPC and TFC, personal observation).

Nasutitermitinae

Nasutitermitinae constitutes a well-established monophyletic group, but the evolutionary relationships among its genera remain unknown (Bourguignon *et al.*, 2017; Inward *et al.*, 2007). The subfamily includes 81 genera and more than 600 species worldwide; of these, 172 species and 31 genera are Neotropical (Table 1).
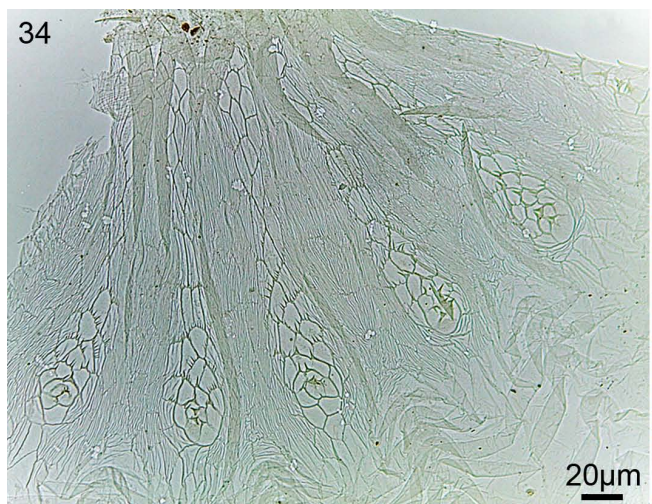
Nasute soldiers have vestigial, non-functional mandibles, and practice a chemical defense; components of the frontal gland open in a narrow-tipped frontal tube, termed the nasus, non-homologous with that of the Syntermitinae subfamily (see above). The workers vary little in their external morphology, but some characters can easily associate workers of the same genus in a mixed sample without the need to dissect the mandibles or the gut. *Angularitermes, Caetetermes, Coendutermes, Constrictotermes, Tenuirostritermes,* and *Velocitermes* have comparatively longer tibiae; *Agnathotermes* has relatively short tibiae and characteristic tarsi (Fig 36); open-forager genera such as *Constrictotermes, Velocitermes, Tenuirostritermes,* and some species of *Nasutitermes* often have black or dark-brown, well-sclerotized tergites, while in the remaining genera the tergites are usually translucent, allowing examination of the gut coiling in species with few or no fat bodies.

The mandibles of the workers have been used for identification for more than a century. *Diversitermes, Ngauratermes, Muelleritermes, Parvitermes*, *Obtusitermes,*
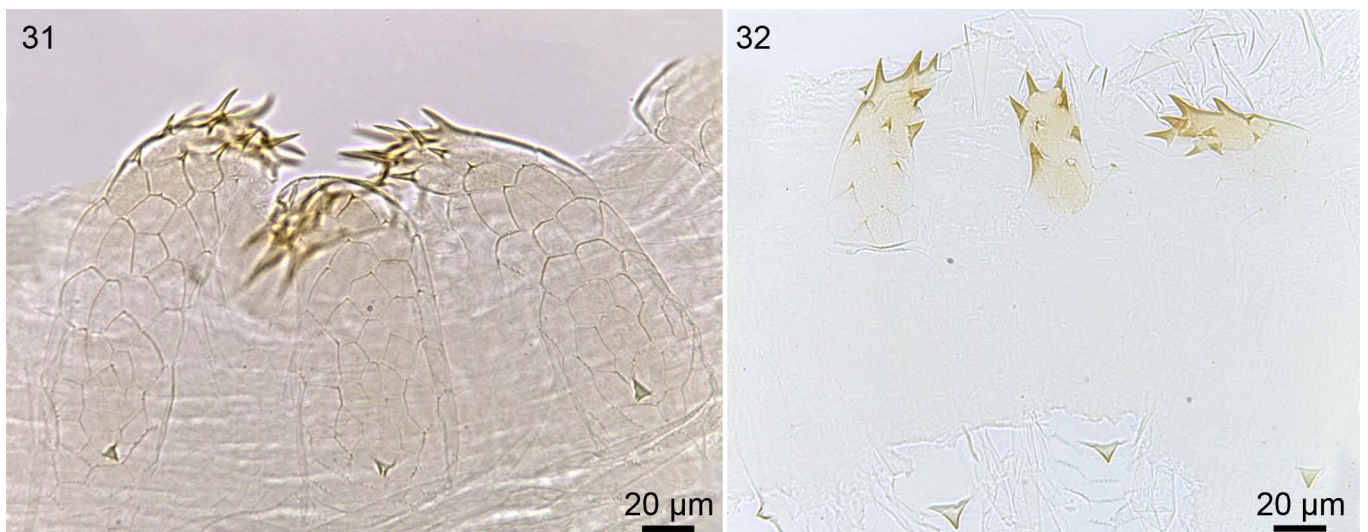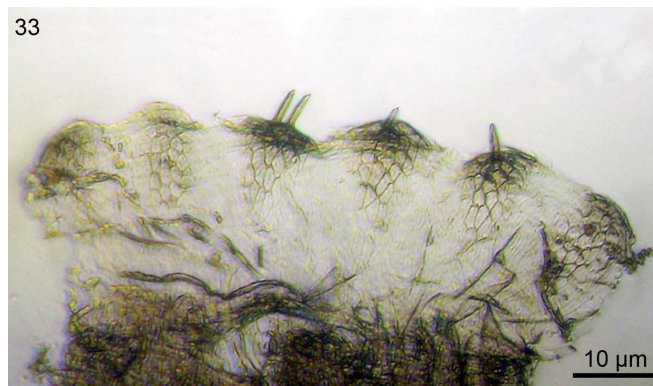

Figs 31–32. Enteric valves of Apicotermitinae: 31- *Ruptitermes bandeirai*; 32- *Tetimatermes oliveirae*.

Velocitermes, and *Tenuirostritermes* have a striated and slightly concave molar plate, well-developed marginal dentition, and a small apical tooth; the left mandible has a sharp edge, a left-mandible index of less than 1.0, and the margin between M1 + 2 and M3 concave (Figs 37, 38). *Caetetermes,* *Coendutermes, Rotunditermes,* and *Sandsitermes* have a similar mandibular pattern, although the molar ridges are more apparent (Fig 39). In *Caribitermes, Constrictotermes, Cortaritermes,* and *Nasutitermes* the marginal dentition is similar, but the molar plate is flat, with conspicuous ridges. In *Agnathotermes*, *Araujotermes*, *Atlantitermes*, *Coatitermes*, *Convexitermes*, *Paraconvexitermes*, and *Subulitermes* the mandibles have a well-developed apical tooth and a comparatively less-prominent marginal dentition, with a wide, concave, less-striated molar plate. In *Anhangatermes,* *Angularitermes,* *Cyranotermes,* *Sinqasapatermes,* and *Tiunatermes* the marginal dentition is incomplete (M3 of the left mandible and M2 of the right mandible are reduced or absent) and the molar plate is concave and without ridges or with a few shallow ridges (Fig 40).
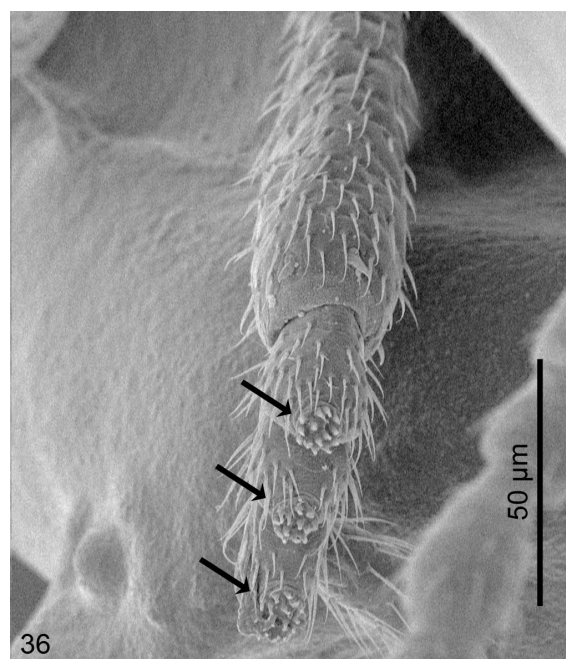

Fig 33. Enteric valve of *Anoplotermes janus.*

In contrast to Apicotermitinae, Syntermitinae, and Termitinae, in Nasutitermitinae it is possible to recognize more than one type of worker by a mandibular dimorphism (Fontes, 1981, 1987a). The gap between M3 and the molar plate on the left mandible can be narrow or broad (Figs 37, 38). This character has been recorded for all Neotropical genera of Nasutitermitinae except *Angularitermes*, *Cyranotermes*, *Sinqasapatermes*, and *Tiunatermes*. Considering that this mandibular dimorphism appears not to be associated with sex, it is probably related to the instar of the worker (a narrow gap in the first instar and a broad gap in the second instar), a hypothesis that is presently under investigation.

The characters of the gut are certainly the most important for accurate identification of the workers. The crop of *Constrictotermes* is strongly dilated and, when full, occupies almost half of the anterior region of the abdomen. The ornamentation of the gizzard is well developed, with both columns and pulvilli; the exception is *Agnathotermes*,

Figs 34–35. Enteric valves of Apicotermitinae: 34- *Anoplotermes pacificus, from* Ilha do Cardoso, SP; 35- *Anoplotermes pacificus,* from Santa Teresa, ES.

Fig 36. Tarsi of *Agnathotermes* sp. (arrows: specialized regions).

which has the columns completely reduced, leaving only the first- and second-order pulvilli. In turn, the first- and second-order columns can bear some characteristic structures: *Angularitermes* and *Coendutermes* have spines (Fig 41); and *Anhangatermes* and *Tiunatermes* have a single, well-developed projection on the anterior margin (Fig 42).

The midgut forms an arch around the P3 and shows no diagnostic characteristics. The Malpighian tubules are generally difficult to observe, especially in old material. They are inserted on the margin between the midgut and P1, generally internal to the midgut arch, but in *Angularitermes* and many species of *Velocitermes* they are inserted directly on the midgut. In *Anhangatermes, Araujotermes,* some species of *Atlantitermes, Coatitermes, Ereymatermes, Diversitermes, Paraconvexitermes,* and *Subulitermes* the Malpighian tubules are inserted in pairs on a nodule that is more or less developed from the mesenteric tissue, and are dilated only proximally. In genera such as *Caribitermes, Cortaritermes, Rotunditermes, Nasutitermes,* and *Triangularitermes* the Malpighian tubules appear to be dilated along the length of the mixed segment, with varying patterns of insertion.

The P1 of *Agnathotermes*, *Angularitermes*, *Anhangatermes, Araujotermes*, *Atlantitermes*, *Caetetermes*, *Coatitermes, Convexitermes, Cyranotermes, Constrictotermes, Ereymatermes, Paraconvexitermes, Singasapatermes, Subulitermes,* and *Tiunatermes* is short compared to the length of the midgut, and generally terminates on the left side of the abdomen. *Sandsitermes* and *Cortaritermes* have the P1 terminating in a semicircular loop in the dorsal or right lateral region of the abdomen, respectively; in *Caribitermes,*

*Obtusitermes,* and *Parvitermes sensu stricto* (excluding *P. bacchanalis*) the P1 forms a long loop with parallel sides ventral or transverse to the P3 (Fig 43). In *Antillitermes* the P1 forms three loops on the sides of the abdomen before the insertion in the P3, on the left side. *Parvitermes bacchanalis* is the only species of Nasutitermitinae in which the P1 follows a counterclockwise direction and terminates beneath the mixed segment, in the dorsal region (Fig 44).

The P2 varies widely in its location, and can be found on the dorsal, left or right side of the abdomen. The ornamentation of the enteric valve is widely variable among the genera, as it is among the species, and because of this it deserves special attention in the identification. Generally, the enteric valves of soil-feeding Nasutitermitinae are more variable and complex than those of wood-feeding species. The extent of its variation must be described case by case, which is outside the scope of this contribution, although we mention some references in Table 1. In *Diversitermes,* Oliveira & Constantino (2016) suggested that an identification of the species based on the soldiers should be confirmed through analysis of the enteric valve of the workers.

The P3 is generally globose or ellipsoid, with little taxonomic importance. In many groups there is a torsion in the direction of the P2, giving the appearance of an inverted "J" in ventral view. In some genera the enteric-valve seating (EVS) is quite differentiated. This is the case for *Agnathotermes*, *Araujotermes*, *Atlantitermes*, *Caetetermes*, *Coatitermes*, *Coendutermes*, *Cyranotermes*, *Diversitermes* (Figs 45, 46), *Ereymatermes, Muelleritermes*, *Rotunditermes*, *Sandsitermes*, *Singasapatermes,* and *Tiunatermes*.
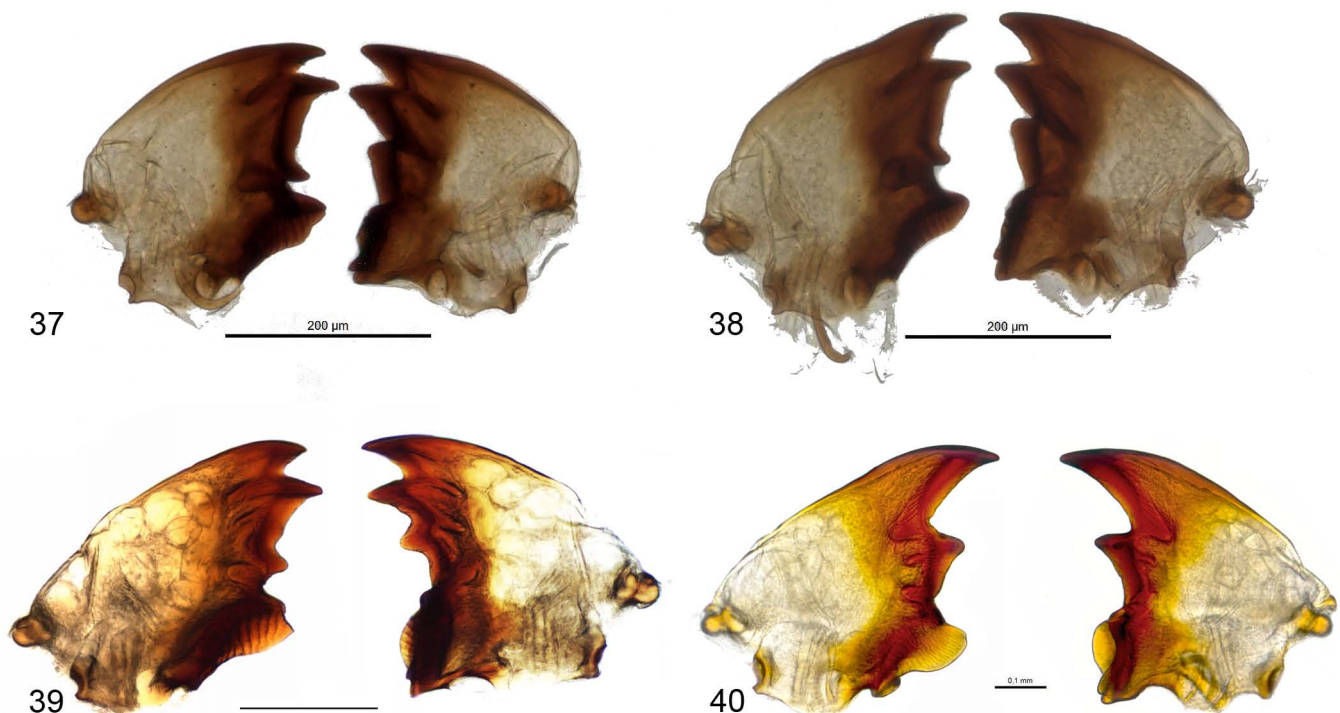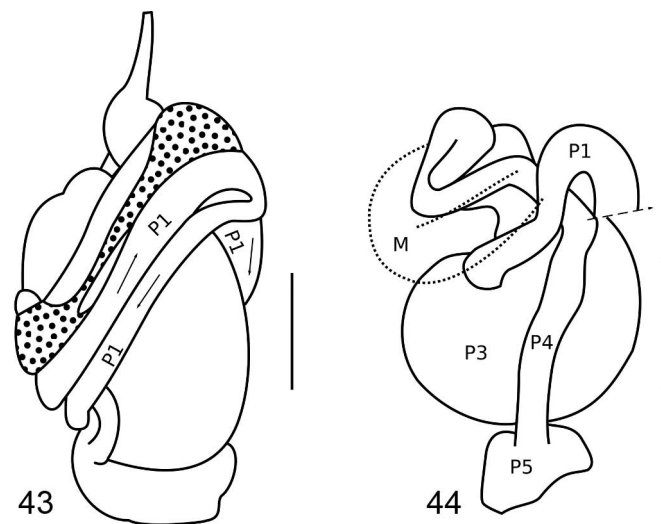

Figs 37–40. Worker mandibles in dorsal view: 37- *Diversitermes diversimiles*, narrow gap; 38- *Diversitermes diversimiles*, broad gap; 39- *Caetetermes taquarussu*, broad gap; 40- *Tiunatermes mariuzani*.
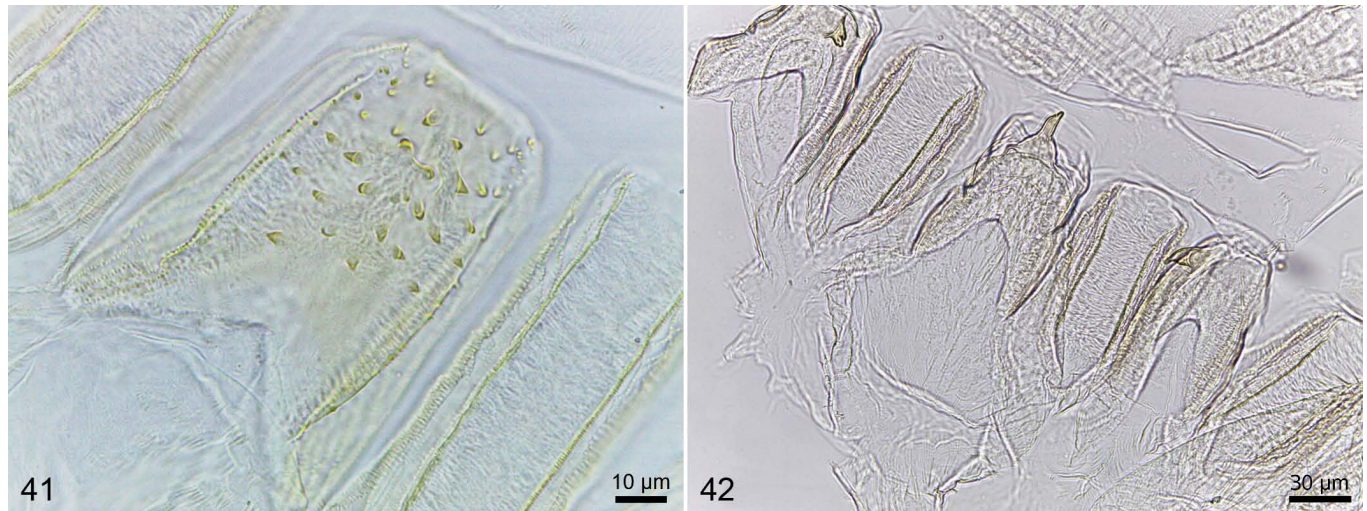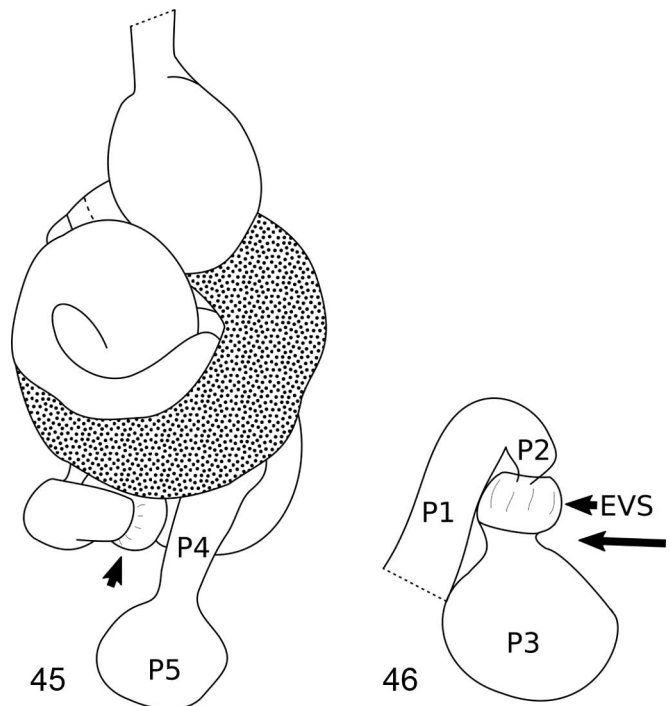
Figs 41–42. Gizzard columns: 41- *Coendutermes tucum* and 42- *Tiunatermes mariuzani*, showing spines.

Particularly in *Araujotermes* and *Sinqasapatermes* the EVS is trilobate. *Tenuirostritermes* has a diverticulum in the P3. The distal region of the P3 passes through the mesenteric arch and can be spiral, quite variable in size, or only protrude and connect to the P4 without forming a "dorsal torsion" as in *Constrictotermes*, *Caribitermes*, *Cortaritermes*, *Obtusitermes*, *Parvitermes sensu stricto,* and *Nasutitermes*. In these genera, the isthmus is not apparent in the right dorsal region, which separates the P3 from the P4. In *Constrictotermes* the distal region of the P3 is completely covered by the crop.

The P4 is generally tubular and forms an arch that passes beneath the midgut to the P5. In *Angularitermes*, *Cyranotermes*, *Ereymatermes,* and *Sinqasapatermes* the P4 is dilated in this passage beneath the midgut. In *Antillitermes* the P4 is entirely displaced to the ventral region. The P5 is fusiform or globose and has no taxonomic significance.

Figs 45–46. Worker gut *in situ* of *Diversitermes diversimiles*: 45- dorsal view; 46- detail of P3, in posterior view (EVS, short arrow, constriction, long arrow, figures not to scale).

Syntermitinae

The subfamily Syntermitinae is endemic to the Neotropical Region, and presently includes 18 genera and 103 species (Constantino, 2018). The soldiers have the frontal tube of various sizes, and functional mandibles for defense, which has given them the informal designation of "mandibulate nasutes". The earliest classifications considered the group to be part of the subfamily Nasutitermitinae (Holmgren, 1912; Hare, 1937), which also included the "true nasutes" (whose soldiers have vestigial mandibles). However, phylogenetic studies showed that the frontal tube arose independently in the two groups during the evolution of termites (Inward *et al*., 2007;
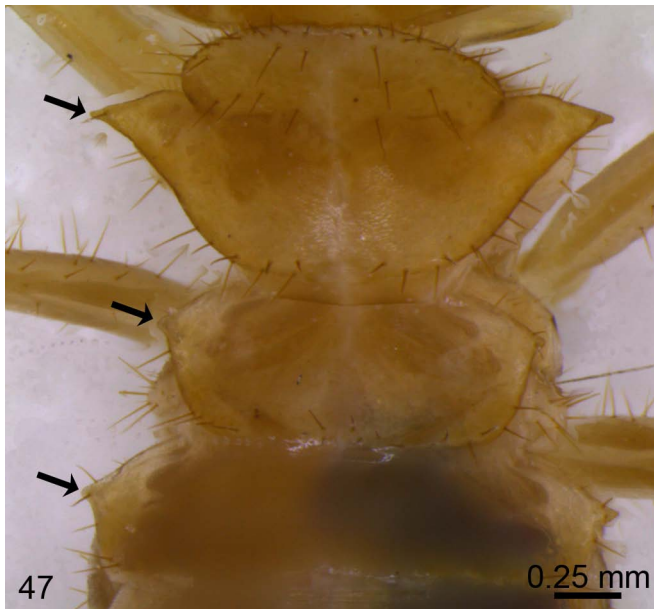

Figs 43–44. Worker gut *in situ*: 43- *Caribitermes discolor*, right view; 44- *Parvitermes bacchanalis*, dorsal view (the mesenteron position is indicated by the dotted lines, figures not to scale).

Fig 47. Thoracic nota of *Syntermes spinosus* worker (arrows: lateral projections).

Bourguignon *et al*., 2017). Even though the "mandibulate nasutes" and the "true nasutes" were recognized very early in the development of termitology, the subfamily Syntermitinae was only formally described by Engel and Krishna (2004), and a more-detailed diagnosis was provided by Constantino and Carvalho (2011).

Among the studies on the gut anatomy of species of Syntermitinae, the pioneer was that of Kovoor (1969), who compared some species of "mandibulate nasutes" and "true nasutes". However, Kovoor (1969) did not question the unity of Nasutitermitinae, and interpreted the differences between the groups in accordance with the proposal of Ahmad (1950), who suggested that the "true nasutes" were derived from the "mandibulate nasutes".
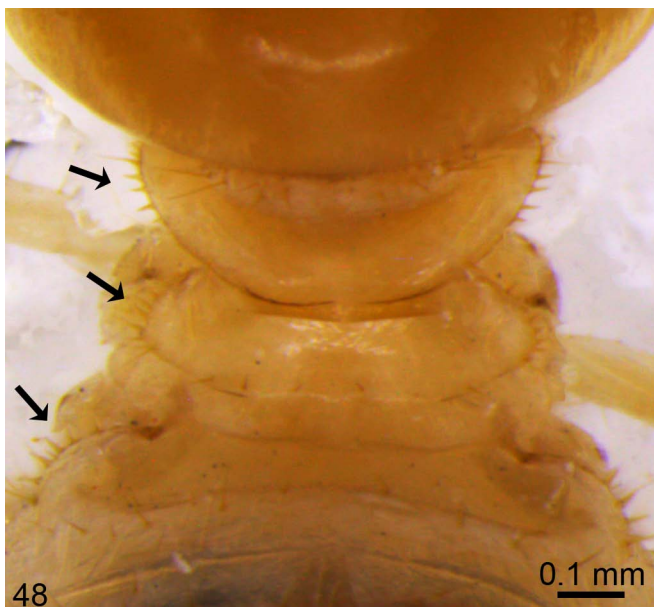
Fig 48. Thoracic nota of *Armitermes armiger* worker (arrows: serrated margins).

At present, among Neotropical termites the gut anatomy of the Syntermitinae is best known, with consistent and updated descriptions for most of the species and genera (Table 1). There are also studies of comparative anatomy, such as that of Rocha and Constantini (2015), who described patterns of internal ornamentation of the P1 of 36 species of Syntermitinae, including representatives of all the genera. The most recent treatment is the phylogenetic scheme proposed by Rocha *et al*. (2017), where the authors proposed homologies among gut structures of a representative portion of the Syntermitinae.

When collecting in the field, most samples of Syntermitinae include the soldier caste, mainly when it was collected inside the nests. On the other hand, the nests of Syntermitinae serve as shelter for a large number of other species of Isoptera, of both Syntermitinae as well as other subfamilies, and it is common for samples to contain a mixture of soldiers and workers of many species. Therefore, to correctly screen the material and associate both workers and soldiers with their respective species, knowledge of the worker anatomy is essential.
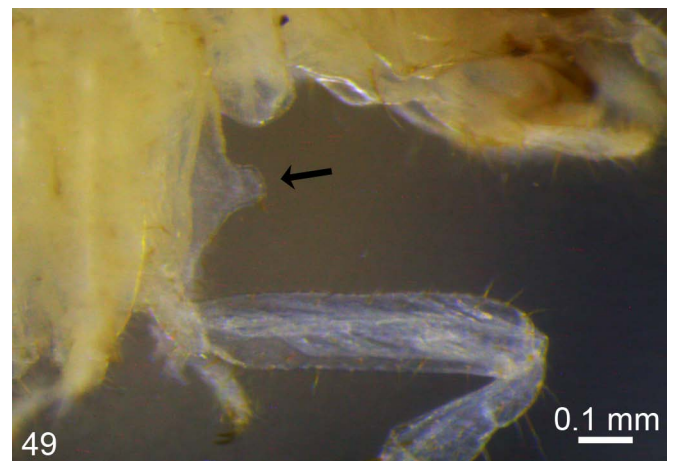
Fig 49. Forecoxa of *Embiratermes neotenicus* worker (arrow: lateral projection).

Some characteristics of the external morphology that help in the identification of workers of Syntermitinae are the shape and the margins of the thoracic nota and the structures on the legs. Nota with lateral projections (Fig 47) occur exclusively in the workers of *Syntermes* (except in *S. nanus* and *S. molestus*), and the margins with serrate structures (Fig 48) are exclusive to the workers of *Labiotermes* (present only on the meta- and mesonotum), *Macuxitermes,* and *Armitermes* (present on all three nota); in *Uncitermes* and *Mapinguaritermes* they are polymorphic (they may or may not be present in different individuals). With respect to the leg structures, workers of *Embiratermes festivellus*, *E. chagresi*, *E. neotenicus*, *E. latidens*, and *E. transandinus* (= *Embiratermes sensu stricto*) and those of *Rhynchotermes* (see Scheffrahn, 2010; Constantini & Cancello, 2016) have a characteristic projection on the forecoxa (Fig 49). Workers

of *Cornitermes* have a row of short thick setae on the inner margin of the foretibia (Fig 50), which characterizes the genus (but which also can be found in some species of *Neocapritermes,* Termitinae).

**Fig 50.** Foretibia of *Cornitermes cumulans* worker.

Certain species or groups of species of Syntermitinae show marked synapomorphic characteristics of the internal anatomy. The gizzard and crop generally follow the basic plan for the Termitidae (as described by Noirot, 2001), but *Ibitermes curupira*, *Embiratermes robustus*, and the species of *Mapinguaritermes* show a very characteristic ornamentation of spines at the base of the first-order pulvilli (Fig 51).


Fig 51. *Mapinguaritermes* sp., ornamentation of spines at the base of the first-order pulvillus of the gizzard.

The insertion of the stomodeal valve varies depending on the species and genus; in the majority the position is apical and above the midgut, but in the species of *Procornitermes* it is displaced and continues into the mesenteric arch (Fig 52).

The members of Syntermitinae have a well-developed mesenteric tongue that is quite varied in shape and may have filiform parts, rounded forms, and a smaller, secondary tongue (Figs 53–55). However, in general the midgut does not possess diagnostic characteristics, except for the species of *Silvestriterme*s belonging to the "*lanei* group" (*S. duende*, *S. gnomus*, *S. lanei*, and *S. minutus*), which have a nodule of mesenteric tissue that surrounds the base of the Malpighian tubules [the Termitinae genera of the *Termes-Cavitermes* group (see below) also have a nodule of mesenteric tissue in a similar position, but it is separated from the Malpighian tubules].
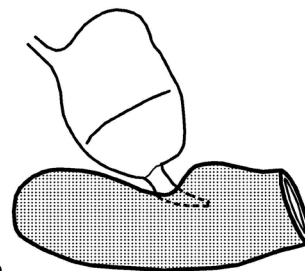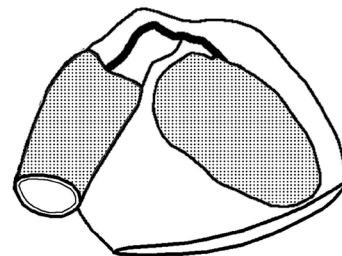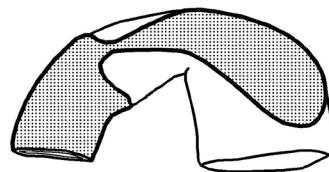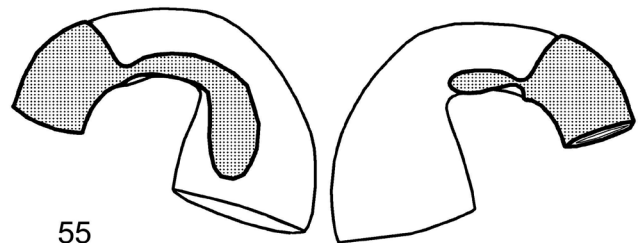

Figs 52–55. Details of gut structures in Syntermitinae species. 52- stomodeal valve insertion in *Procornitermes striatus*; 53- mesenteric filiform connection of *Armitermes armiger*; 54- proximal constricted mesenteric tongue of *Procornitermes araujoi*; 55- detail of external (left) and internal (right) mesenteric tongues of *Cornitermes cumulans* (figures not to scale).

Except for *Cyrilliotermes* species and *Procornitermes araujoi*, all other Syntermitinae have the four Malpighian tubules, with the insertion in two distinct pairs or with the four bases very close together; some species have well-developed ampules (*Procornitermes araujoi* with four tubules and *P. triacifer* with two ampules, each with two tubules), but as with the tongue, these structures by themselves have no diagnostic value.

The P1 is dilated, ranging from fusiform to globose depending on the species, and the enteric valve (P2) is always located on the left side of the body. These characteristics are not exclusive to the species of this subfamily: some genera of Termitinae also have the first proctodeal segment inflated, although these can be differentiated from the Syntermitinae by certain combinations of characteristics. The internal ornamentation patterns of the P1 are generally quite characteristic for each species but dissection of this region of the gut is not easy, making them impractical as a diagnostic feature for identification (Rocha & Constantini, 2015).

Although the P2 is always on the left side of the body, the direction in relation to the antero-posterior axis varies greatly among the genera. The connection may be simple and wide (Fig 56) or by means of a constricted portion, forming a loop (Fig 57). The position along the abdomen is a diagnostic feature of some genera: in *Cyrilliotermes* and *Embiratermes sensu stricto* (species that form a homogeneous group (Rocha *et al*., 2012): *E. festivellus, E. chagresi, E. neotenicus, E. latidens*, and *E. transandinus)*, the P2 is located near the midlength of the abdomen (Figs 56, 58), while in the other genera it is located much farther distally (Fig 59). The ornamentation of the P2 varies widely among the species, with different patterns and combinations of symmetry, shape,

number of cushions, and types of ornamentation, and is quite useful to confirm identifications (see Table 1 for references).

The P3 is relatively unimportant as a diagnostic character, although in some species it shows marked features, such as the EVS just after the P2 (tubular or globose), or a partial diverticulum (*Armitermes armiger* and *A. bidentatus*). The distal portion of the P3 is generally strongly protracted dorsally, forming a characteristic "U" in most species. The connection between the P3 and P4 can show a distinct isthmus, depending on the genus. The isthmus is inserted apically on the P4 in most of the Syntermitinae, but subapically (Fig 59, arrow) in a very peculiar group of taxa (*Acangaobitermes, Noirotitermes, Ibitermes tellustris, Embiratermes parvirostris, E. ignotus, E. brevinasus*, and *E. silvestrii*), which is composed of the smallest species of the subfamily; otherwise the P4 and P5 are not known to be informative.
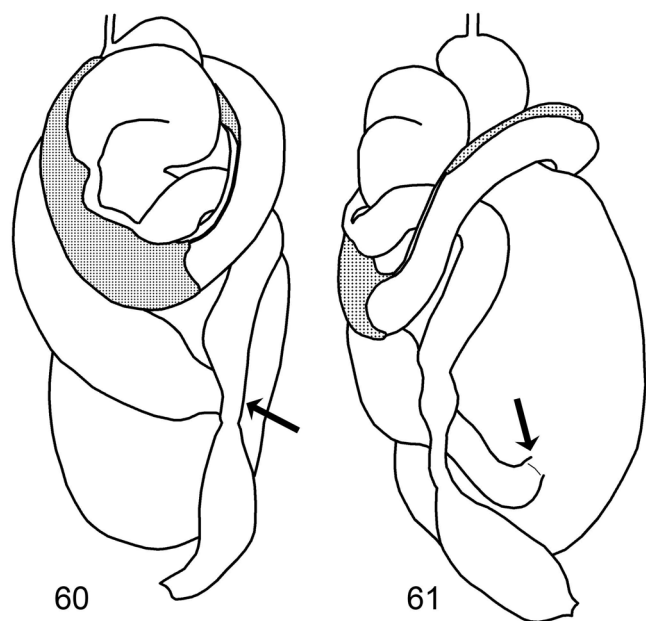
Termitinae

Termitinae is presently composed of 107 species in 20 genera in the Neotropical Region, and 662 species in 65 genera worldwide (Constantino, 2018).

The first genus described in this subfamily was *Termes* (Linnaeus, 1858), and the most recent was *Palmitermes* (Hellemans *et al*., 2017). Among all the Neotropical genera, only five keys to identify the species have been developed, for *Neocapritermes* (Krishna & Araujo, 1968), *Cavitermes* (Krishna, 2003), *Cylindrotermes* (Rocha & Cancello, 2007), *Orthognathotermes* (Rocha & Cancello, 2009), and *Divinotermes* (Carrijo & Cancello, 2011). All these keys are based on the morphology of the soldiers.
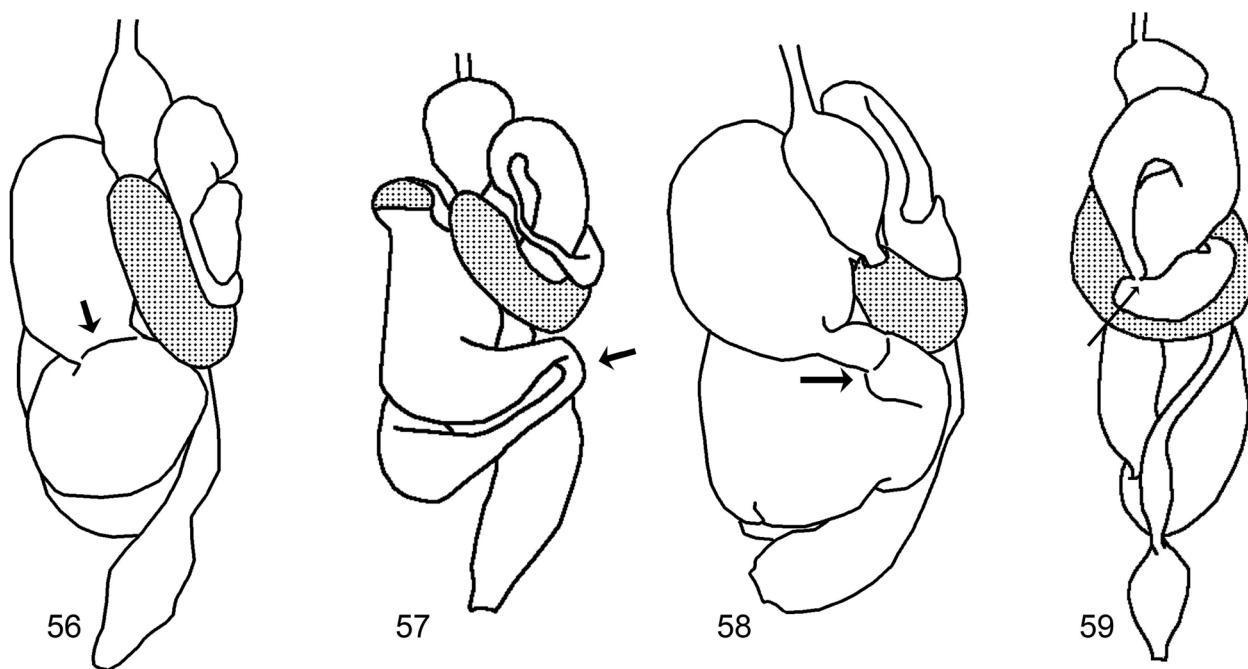
Figs 56–59. Worker gut: 56- left view of *Embiratermes neotenicus* (arrow: P1-P3 wide connection); 57- left view of *Silvestritermes lanei* (arrow: dorsal loop); 58- left view of *Cyrilliotermes* sp. (arrow: P1-P3 connection); 59- dorsal view of *Acangaobitermes krishnai* (arrow: subapical P4 connection, figures not to scale).

Figs 60–61. Worker gut of *Amitermes amifer* 60- dorsal view; 61- right view (arrows: insertion of enteric valve on the right side of P3).

Termitinae has constantly been recovered as a non-monophyletic group (Donovan *et al.*, 2000; Inward *et al.*, 2007; Bourguignon *et al.*, 2014; Bourguignon *et al.*, 2017). This reflects the morphological diversity found in the soldier and worker castes of the taxa that are presently included in this subfamily. In the near future, it is probable that new subfamilies will be designated or re-erected to accommodate some of the genera that are recognized today as members of Termitinae. In view of this likelihood, and the absence of diagnostic characteristics for the subfamily, here we will treat the characteristics that group some of the genera.

Based on the characteristics of the soldiers, the Neotropical Termitinae can be divided into the following groups of genera: the *Amitermes* group, composed of *Amitermes*, *Gnathamitermes*, and *Hoplotermes*; the *Cavitermes-Termes* group, which includes the *Cavitermes* subgroup: *Cavitermes*, *Cornicapritermes*, *Dihoplotermes*, *Divinotermes*, *Palmitermes*, and *Spinitermes*, and the *Termes* subgroup: *Inquilinitermes* and *Termes*; the *Neocapritermes* group, composed of *Neocapritermes*, *Planicapritermes*, and *Crepititermes*; and the *Orthognathotermes* group, which includes *Dentispicotermes* and *Orthognathotermes*. Some genera, such as *Cylindrotermes*, *Genuotermes*, *Microcerotermes*, and *Onkotermes*, are so distinct that they cannot be assigned to a group.

In the *Amitermes* group, the mandibles of the workers are all characteristic of xylophages, i.e., with the apical tooth equal to or smaller than the marginal teeth, and the molar regions with a distinct ridge. In the gut, the stomodeal valve is situated far apically; the mixed segment is very distinct and the mesenteric tongue is long; the P1 is dilated, being fusiform in *Gnathamitermes* and *Amitermes* and broader in *Hoplotermes*; and the P2 inserts on the right side of the body (Figs 60, 61). In *Gnathamitermes* the region of the EVS is differentiated, appearing as a small sac in ventral view. Examples of enteric valves are given in Figs 62 and 63.

The workers of the *Cavitermes-Termes* group have humivorous mandibles, i.e., with a large apical tooth, much larger than the marginal teeth, and with the molar plate concave and without ridges. The principal characteristic of the gut is the displaced and subapical insertion of the stomodeal valve, and the mesenteric nodule internal to the arch, at the junction with the P1, i.e., at the base of the mixed segment. The enteric valve is inserted on the left side of the body. In the *Cavitermes* subgroup, the P1 is always tubular, whereas it is more voluminous in the *Termes* subgroup. The P3 has a fold, which is visible in ventral view, and occurs in all genera except in *Cornicapritermes*, where the enteric valve is inserted ventrally and the P1 is longer, in the shape of an inverted "C". In the *Termes* subgroup, the proximal region of the mesenteric tongue is relatively narrow (see Table 1). Examples of enteric valves are given in Figs 64–66.
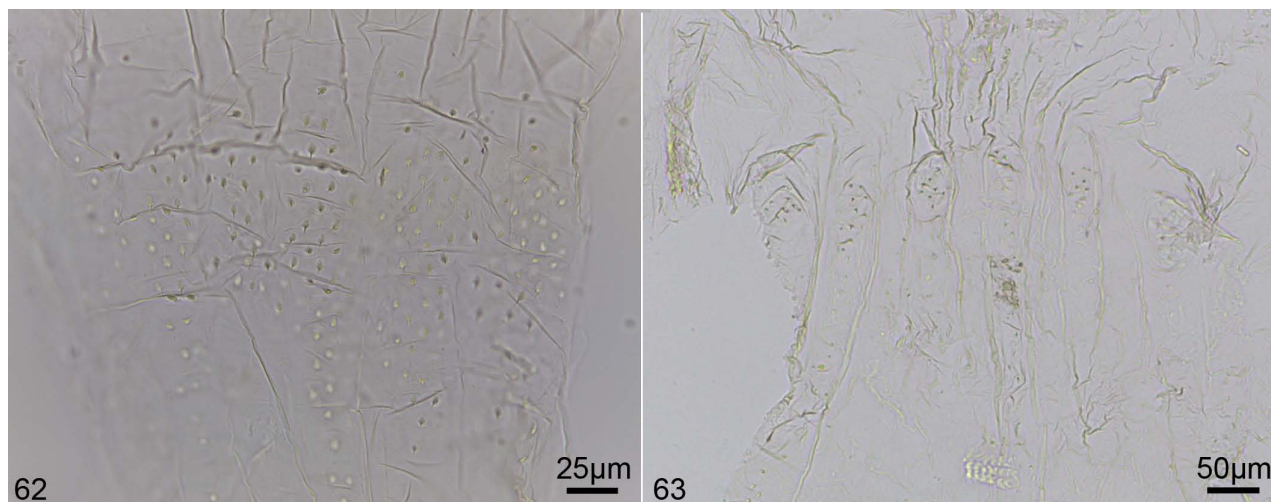

Figs 62–63. Enteric valve armature of: 62- *Amitermes amifer*; 63- *Gnathamitermes perplexus*.
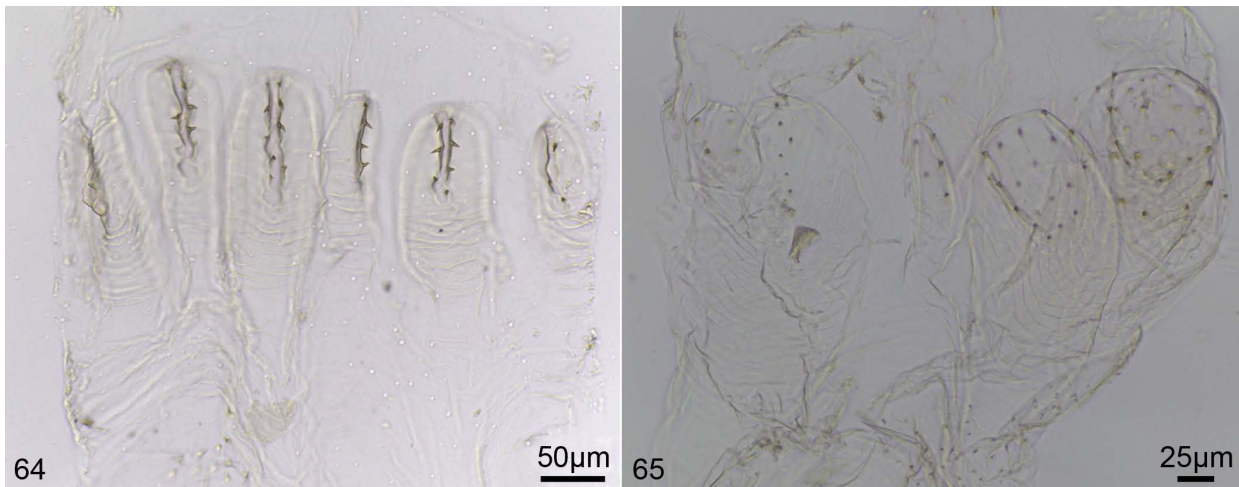
Figs 64–65. Enteric valve armature of: 64- *Cavitermes tuberosus*; 65- *Dihoplotermes inusitatus*.

The workers of the *Neocapritermes* group are heterogeneous in both the mandibles and the gut, but the group was recovered as monophyletic by Bourguignon *et al.* (2017). A possible synapomorphy is the abscission line on the first abdominal tergite (Fig 67, arrow), present in all species of this group (autothysis occurs in other Termitinae, but apparently the abdomen breaks in other regions).
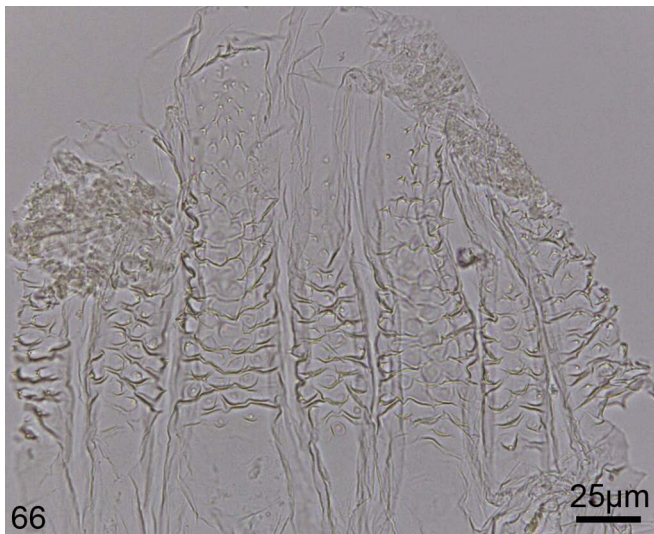
Fig 66. Enteric valve armature of *Termes fatalis*.

Fig 67. *Crepititermes verruculosus* worker (arrow: abscission line on the first abdominal tergite, highlighted).

In workers of *Neocapritermes,* the most obvious character is the pair of protuberances in the distal region of the midgut, which are visible on the right side, and may differ in shape among the species (Fig 68, arrow). An external feature that can be used to identify several species of *Neocapritermes* is a row of bristles on the inner part of the foretibia, as is also found in *Cornitermes* (Syntermitinae). The enteric valve of *Neocapritermes opacus* is shown in Fig 69.

In *Crepititermes* the P1 is very short. The workers of this genus may be confused with some small nasutes such as *Subulitermes* and *Coatitermes*, although generally the midgut has a characteristic appearance, with more-distinct punctations, which differentiates them from the small nasutes whose midgut has a more homogeneous texture. In workers of *Crepititermes* the distal region of the P3 has a diverticulum (Fig 70), which is a good diagnostic character, since this is the only genus in the Neotropical Termitinae with this feature. The enteric valve of *Crepititermes* is also diagnostic (Rocha & Cuezzo, 2015).

Fig 68. *Neocapritermes opacus* worker gut *in situ*, right view (arrow: bilobate protuberance in the distal region of the mesenteric tongue).
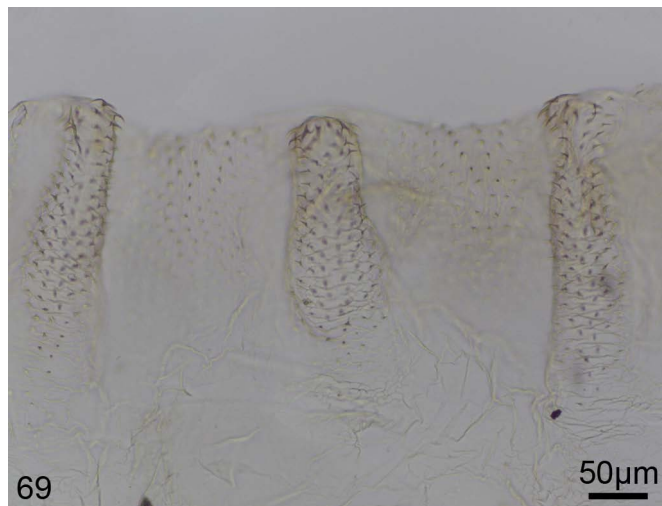
**Fig 69.** Enteric valve armature of *Neocapritermes opacus*.

The workers of *Planicapritermes* have a somewhat flat body, due to their habitat beneath the bark of fallen tree trunks. Refer to the description by Constantino (1998).

The *Orthognathotermes* group unites species whose workers have mandibles with a marked geophagous pattern, the stomodeal valve is inserted apically, and the mixed segment is very distinct. The P1 is characteristic, long and tubular, passing parallel to the mesenteric arch, with the enteric valve inserted on the right side of the body in dorsal position (Fig 71). The P2 in both genera is very characteristic, with digitiform projections directed toward the lumen of the P3 (Figs 72, 73). The workers of this group have a characteristic profile, with the abdomen very globose.

The genus *Cylindrotermes* is easily recognized by the tubular P1, which forms a clockwise loop (in ventral view) that crosses the abdomen distally, ending on the left side in ventral view (i.e., on the individual's right) (Figs 74, 75). The Neotropical Apicotermitinae have a similar loop, but its members are easily recognized by the mandibles, as mentioned above; and when a mesenteric tongue is present,

it is situated in the inner part of the mesenteric arch, whereas in *Cylindrotermes* it is in the outer part. The enteric valve of these species is very difficult to dissect (Fig 76).

The workers of *Microcerotermes* have xylophagous mandibles and construct an arboreal nest, with covered tunnels passing down the trunk to the ground, very similar to several species of *Nasutitermes*. Because of this it is common for only workers to be collected, without the soldiers. Although this is not a diagnostic characteristic, the head of some of the workers has a peculiar coloration, ranging from light yellow to brown. The gut is not very informative; the P1 is slightly dilated, with a distal loop; and the P2 insertion is on the left side of the body. None of these characteristics is striking compared to the other Neotropical genera, and the lack of a revision for the Neotropical Region makes their identification difficult. Specimens of *Microcerotermes* should be carefully compared with the illustrations provided by Sands (1998).
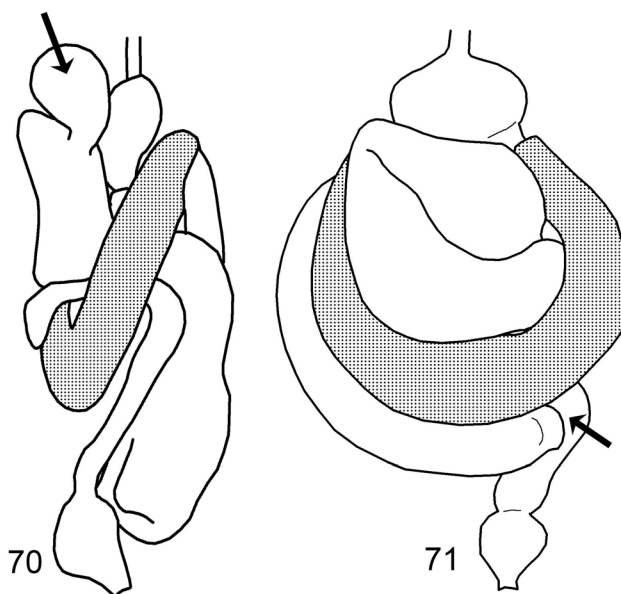
Figs 70–71. Worker gut *in situ*: 70- *Crepititermes verruculosus*, right view (arrow: distal P3 diverticulum); 71- *Orthognathotermes* sp., dorsal view (arrow: P1-P3 connection).
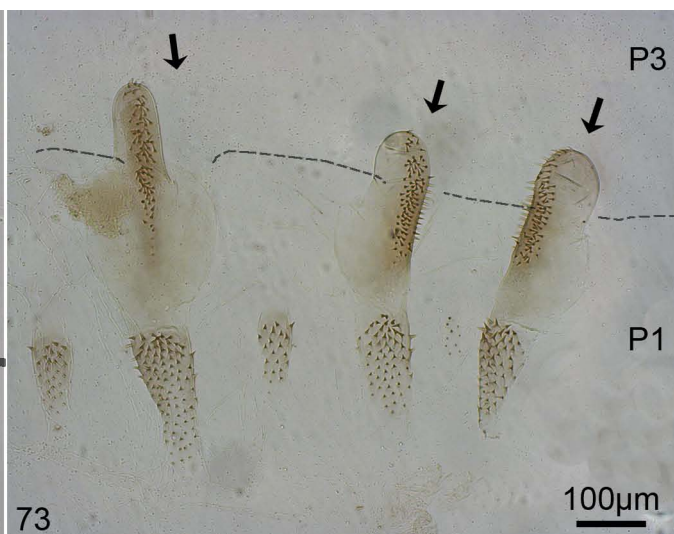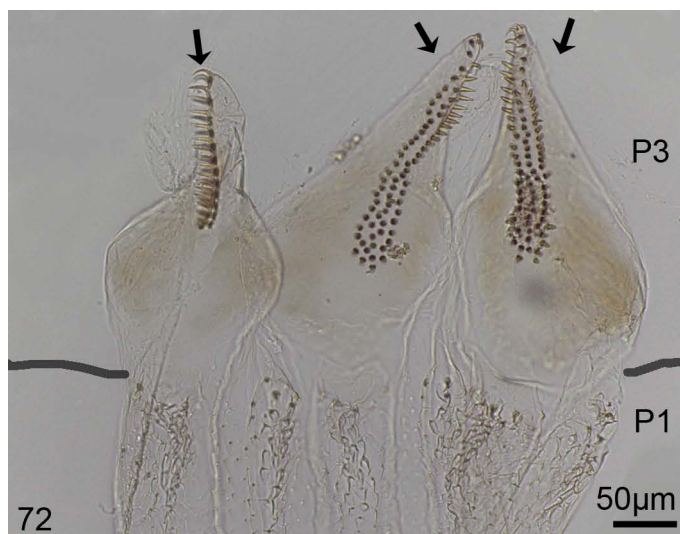
Figs 72–73. Enteric valve armature of: 72- *Dentispicotermes conjunctus;* **73-** *Orthognathotermes* sp. (arrows: digitiform projections into P3 lumen).
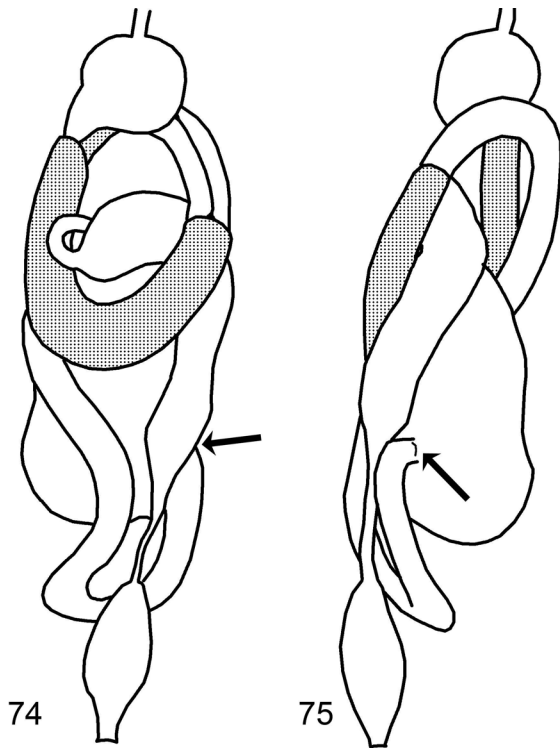
Figs 74–75. Worker gut of *Cylindrotermes parvignathus* in 74-dorsal and 75- right view (arrows: P1-P3 connection).

The gut of *Genuotermes* was described in detail by Rocha (2013) and shown to be more closely related to genera of Syntermitinae than to other members of Termitinae (Rocha *et al.*, 2017). The gut morphology is very similar to *Cyrilliotermes* and *Silvestritermes*, but with the peculiarity that the insertion of the isthmus in the P4 is subapical.

Onkotermes was described by Constantino *et al.* (2002), who transferred the species *Amitermes brevicorniger* to the new genus, basing this, among other arguments, on the morphology of the gut, which is highly peculiar in this genus. Members of *Onkotermes* are found in open areas in the southern Neotropics (Pampas and Chaco Seco regions), and it is highly uncommon to find soldiers in collections, which

Fig 76. Enteric valve armature of *Cylindrotermes sapiranga* partially dissected, the musculature is partially removed, one of the three cushionsis highlighted in the figure.

makes identification of the workers particularly important. In the workers, the mandibles are highly developed for xylophagy, the mesenteric arch shows the mixed segment convexly arched, and the P1 is inserted in a well-marked EVS in the P3 (Torales & Fontes, 2008).

Final considerations

The ability to identify termites using only the worker caste is increasingly necessary. For example, various ecological studies use collection methods (using soil monoliths or termite mounds) that indiscriminately sample the diversity of termite species present, often represented only by the workers. This contribution summarizes the recent advances in the taxonomy of Neotropical termite workers. Modern descriptions of taxa treat the worker caste in detail, although many questions remain to be answered. Little is known about the internal anatomy of pseudergates, especially in the Kalotermitidae, and it is possible that other taxonomically useful features exist, that have not yet been explored, including a better study of the mandibles or gizzard (Myles, 1997). Also, there is a need to continue and expand comparative studies of members of Termitidae, particularly for Termitinae and Apicotermitinae. As noted above, the Termitinae is not a natural group, and investigating the internal anatomy of workers based on established characters, or possibly new characters, will help in analyses of the relationships and evolutionary history of the species, and will also help in the rapid identification of pest or ecologically important species. Further studies of the internal morphology of the various parts of the gut may help to test the hypotheses on fixation and movement of intestinal symbionts. Outside of the field of taxonomy and systematics, it is necessary to encourage research on the actual diets, such as analyses of gut contents, of several species of Termitidae, to enable comparison with the fine morphology of the mandibles and the gut.

For all the subfamilies of Termitidae the number of specific studies on feeding behavior is insufficient, and current hypotheses are based more on the morphology of the mandibles and characteristics of the gut anatomy of workers, as well as information on the collection site. To better understand the true food sources of many species of Termitidae, more effort is needed, including studies of gut contents, which can provide clues to the food type.

The present contribution is an attempt to summarize a broad array of characters, so that the process of screening and identifying termites using the worker caste can be decentralized from the hands of experienced taxonomists and made useable by any interested researcher. In the near future, it is hoped that every termitologist, even with little experience, will be able to identify termites regardless of the availability of the soldier or imago caste.

Table 1. List of taxonomic studies that treat the worker caste of Neotropical Termitidae genera.

Apicotermitinae	
Amplucrutermes	Bourguignon *et al*. (2016; *A. inflatus*: figs 2c, 7b, enteric valve; fig. 8b, digestive tube)
Anoplotermes	Bourguignon *et al*. (2010; *A. pacificus*: fig. 2f P2, fig. 6a, digestive tube; *A. banksi*: fig. 2d, enteric valve; *A. janus*: fig. 2e, enteric valve; *A. parvus*: fig. 3bc, enteric valve; fig. 6b, digestive tube); Scheffrahn *et al*. (2006; *A. bahamensis*: fig. 4i, enteric valve; fig. 4l, digestive tube; *A. inopinatus*: fig. 4m, digestive tube). There is no information on the digestive tube of the other *Anoplotermes* species, whose descriptions were based on the external morphology of the imagoes and need revising.
Aparatermes	Fontes (1986; *A. abbreviatus*: figs 23–26, gut coiling; figs 26–29, digestive tube. Fig 25 shows the insertion region of P2 in P3 without an apparent EVS.; Fontes (1998; *A. cingulatus*: new combination; there is no digestive tube information)
Compositermes	Scheffrahn (2013; *C. vindai*: fig. 3, digestive tube; fig. 4, EVS; fig. 5, enteric valve); Carrijo *et al*. (2015; *C. bani* fig. 6, digestive tube; figs 7–8, enteric valve; figs 9–11, EVS/P3 junction. The ventral view in fig. 6 wrongly indicates P4, where P3b should be)
Disjunctitermes	Scheffrahn *et al*. (2017; *D. insularis*: fig. 2, digestive tube; figs 3a–d, enteric valve. Fig 2a wrongly indicates P4, where P3b should be)
Echinotermes	Castro *et al*. (2018; *E. biriba*: fig. 1, head, mandibles, foreleg and digestive tube; fig. 2, enteric valve)
Grigiotermes	Bourguignon *et al*. (2016; *G. hageni*: figs 1a, 7a, enteric valve; fig. 8a, digestive tube)
Humutermes	Bourguignon *et al*. (2016; *H. krishnai*: figs 3e, 7c, enteric valve; fig. 8c, digestive tube; *H. noiroti* figs 3d, 7d, enteric valve)
Hydrecotermes	Bourguignon *et al*. (2016; *H. arienesho*: figs 4a, 7e, enteric valve; fig. 8d, digestive tube; *H. kawaii*: figs 4b, 7f, enteric valve)
Longustitermes	Bourguignon *et al*. (2010; *L. manni*: fig. 4b, enteric valve; fig. 6c, digestive tube)
Patawatermes	Bourguignon *et al*. (2016; *P. turricola*: figs 5a, 7g, enteric valve; *P. nigripunctatus* figs 5b, 7h, enteric valve; fig. 8e, digestive tube)
Rubeotermes	Bourguignon *et al*. (2016; *R. jheringi*: figs 6be, 7i, enteric valve; fig. 8f, digestive tube)
Ruptitermes	Acioli and Constantino (2015; fig. 23, digestive tube and comparative gut coiling for *Ruptitermes* spp.; figs 24–26, enteric valve of all species)
Tetimatermes	Fontes (1986; *T. oliveirae*: figs 7–10, digestive tube)
Nasutitermitinae*	
Agnathotermes	Fontes (1987a; *A. glaber*: figs 29–30, digestive tube; fig. 45, Malpighian tubules; figs 64–65, enteric valve; figs 98–101, gut coiling); Constantino (1990a; *A. crassinasus*: fig. 3, enteric valve)
Angularitermes	Mathews (1977; *A. orestes*: Plate 54, enteric valve); Fontes (1987a; *A. orestes*: fig. 1, gizzard; figs 32–35, digestive tube; fig. 46, Malpighian tubules; fig. 62, enteric valve; figs 102–109, gut coiling); Carrijo *et al*. (2011; *A. coninassus*: figs 4–6, digestive tube *in situ* and Malpighian tubules, fig. 7, gizzard; fig. 8, enteric valve)
Anhangatermes	Constantino (1990b; *A. macarthuri*: figs 9–10, enteric valve; fig. 11, Malpighian tubules; figs 12–15, gut coiling); Oliveira *et al*. (2014; *A. anhanguera*: fig. 2, gizzard; fig. 3a, enteric valve; *A. eurycephalus*: figs 3b, c, enteric valve; *A. juruena:* fig. 3d, enteric valve; *A. pilosus*: fig. 3e, enteric valve); Carrijo *et al*. (2015; *A. macarthuri*, fig. 18, gizzard; fig. 22, enteric valve)
Antillitermes	Roisin *et al*. (1996; *A. subtilis*: fig. 1f, gut coiling, figs 2e–f, enteric valve)
Araujotermes	Fontes (1987a; *A. caissara*: figs 4–8, digestive tube; fig. 42, Malpighian tubules; fig. 58, enteric valve; figs 66–73, gut coiling); Roisin (1995; *A. zeteki*: fig. 16, gut coiling; fig. 20, enteric valve); Constantino (1991b; *A. nanus*: fig. 58, enteric valve)
Atlantitermes	Fontes (1987a; *A. guarinim*: figs 22–28, digestive tube; fig. 41, Malpighian tubules; fig. 61, enteric valve; figs 90–97, gut coiling); Roisin (1995; *A. kirbyi*: fig. 18, gut coiling; fig. 22, enteric valve); Constantino and DeSouza (1997; *A. stercophilus*: figs 7–8, enteric valve); Cancello and Noirot (2003; *A. guarinim*: fig. 8h, Malpighian tubules; figs 8j–n, enteric valve; *A. raripilus*: fig. 8e, P3)
Caetetermes	Fontes (1981; *C. taquarussu*: figs 13, 16–19, gut coiling; fig. 14, Malpighian tubules; fig. 15, gizzard); Cuezzo *et al*. (2015; *C. taquarussu*: figs 13–14, gizzard; fig. 15, enteric valve cushions)
Caribitermes	Roisin *et al*. (1996; *C. discolor*: fig. 1e, gut coiling, fig. 2h, enteric valve)

Table 1. List of taxonomic studies that treat the worker caste of Neotropical Termitidae genera. (Continuation)

Nasutitermitinae*	
Coatitermes	Fontes (1987a; *C. clevelandi*: figs 9–13, digestive tube; fig. 40, Malpighian tubules; fig. 60, enteric valve; figs 74–77, gut coiling); Roisin (1995; *C. clevelandi*: fig. 24, enteric valve)
Coendutermes	Cuezzo (2016; *C. tucum*: fig. 13, gizzard; fig. 14, enteric valve)
Constrictotermes	Křeček *et al.* (1996; *C. guantanamensis*: fig. 4, gut coiling; fig. 5, enteric valve); Constantino and Acioli (2009; *C. cyphergaster*: fig. 6g, enteric valve)
Convexitermes	Fontes (1987a; *Convexitermes* sp.: figs 18–20, digestive tube; fig. 44, Malpighian tubules; fig. 57, enteric valve; figs 78–85, gut coiling); Cancello and Noirot (2003; *C. convexifrons*, fig. 8d, P3; *C. manni*: fig. 8g, Malpighian tubules)
Cortaritermes	Cuezzo *et al.* (2015; *C. intermedius*: figs 13–14, gizzard; fig. 15, enteric valve)
Cyranotermes	Mathews (1977; *C. timuassu*: Plate 55, enteric valve); Fontes (1987a; *C. timuassu*: figs 36–38, digestive tube; fig. 47, Malpighian tubules; fig. 63, enteric valve; figs 110–113, gut coiling); Constantino (1990c; *C. glaber*: fig. 11, enteric valve; *C. caete*: fig. 12, enteric valve); Rocha *et al.* (2012; *C. karipuna*: fig. 5, enteric valve); Carrijo *et al.* (2015; *C. timuassu*: fig. 19, enteric valve)
Diversitermes	Constantino and Acioli (2009; *D. diversimiles*: figs 6c–d, enteric valve); Oliveira and Constantino (2016; *D. castaniceps*: figs 10a–d, digestive tube; 10e, junction P2-P3; figs 10f–g, mixed segment, Malpighian tubules; *D. diversimiles*: figs 10h–k, digestive tube; figs 10l–m, junction P2-P3; figs 10n–o, mixed segment, Malpighian tubules; *D. tiapuan*: figs 10p–s, digestive tube; figs t–u, junction P2-P3, figs 10v–x, mixed segment, Malpighian tubules)
Ereymatermes	Constantino (1991a; *E. rotundiceps*: fig. 13, enteric valve; figs 14–17, digestive tube; fig. 18, Malpighian tubules); Roisin (1995; *E. panamensis*: fig. 19, gut coiling; fig. 23, enteric valve); Cancello and Cuezzo (2007; *E. piquira*: figs 3a–f, digestive tube, gut coiling; fig. 4a, gizzard; fig. 4b, enteric valve)
Muelleritermes	Oliveira *et al.* (2015; *M. fritzi*: fig. 5a–b, gizzard; figs 6a–d, digestive tube; figs 6g–h, mixed segment, Malpighian tubules; figs 7ab, enteric valve)
Nasutitermes	Constantino and Acioli (2009; *N. corniger*: fig. 6a, enteric valve; *N. surinamensis*: fig. 6b, enteric valve); Cuezzo *et al.* (2017; *N. aquilinus*: fig. 24, enteric valve; *N. stricticeps*: fig. 26, enteric valve; *N surinamensis*: fig. 26, enteric valve; *N. rotundatus*: fig. 27, enteric valve; *N. octopilis*: fig. 28, enteric valve; *N. comstockae*: fig. 29, enteric valve; *N. acangussu*: fig. 30, enteric valve; *N. macrocephalus*: fig. 31, enteric valve; *N. similis*: fig. 32, enteric valve; *N. wheeleri*: fig. 34, enteric valve; *N. hubbardi*: fig. 34, enteric valve; *N. banksi*: fig. 35, enteric valve)
Ngauratermes	Constantino and Acioli (2009; *N. arue*: figs 3a–d, digestive tube; figs 3ef, Malpighian tubules; fig. 4a, gizzard; figs 4b–d, enteric valve)
Obtusitermes	Roisin *et al.* (1996; *O. panamae*: fig. 1c, digestive tube; fig. 2h, enteric valve); Cuezzo and Cancello (2009; *O. formosulus*: figs 4a–d, digestive tube; figs 4g–i, mixed segment, Malpighian tubules; fig. 5a, gizzard; fig. 5b, enteric valve)
Paraconvexitermes	Cancello and Noirot (2003; *P. acangapua*: figs 8a–c, gut coiling; fig. 8f, Malpighian tubules; figs 8i–l, enteric valve)
Parvitermes	Roisin *et al.* (1996; *P. aequalis*: fig. 2b, enteric valve; *P. antillarum*: fig. 2c, enteric valve; *P. brooksi*: fig. 1a, gut coiling; fig. 2a, enteric valve; *P. toussainti*: fig. 1b, gut coiling; fig. 2, enteric valve); Scheffrahn and Roisin (1995; *P. pallidiceps*: fig. 15, gut coiling; *P. collinsae*: fig. 17, enteric valve); Scheffrahn *et al.* (1998; *P. dominicanae*: fig. 9, enteric valve); Scheffrahn (2016; *P. brooksi*: figs 1b–c, enteric valve; *P. mexicanus*: figs 2a–b, enteric valve; *P. mesoamericanus*: figs 2c–d, enteric valve; *P. yucatanus*: figs 2e–f, enteric valve)
Rotunditermes	Fontes (1998, *R. bragantinus*: figs 81–84, digestive tube *in situ*)
Sandsitermes	Cuezzo *et al.* (2017; *S. robustus*: figs 15–18, digestive tube; fig. 20, Malpighian tubules, mixed segment; fig. 21, enteric valve; figs 22–23, gizzard)
Sinqasapatermes	Cuezzo and Nickle (2011; *S. sachae*: figs 8–11, digestive tube; fig. 13, Malpighian tubules; fig. 15, enteric-valve seating)
Subulitermes	Fontes (1987a; *S. microsoma*: figs 14–1,7 digestive tube, fig. 43, Malpighian tubules, fig. 59, enteric valve, figs 86–89, digestive tube); Roisin (1995; *S. denisae*: fig. 17, gut coiling; fig. 21, enteric valve)
Tenuirostritermes	Fontes (1998, *T. tenuirostris:* figs 73–76, digestive tube *in situ*)
Tiunatermes	Carrijo *et al.* (2015; *T. mariuzani*: figs 11–12, digestive tube; fig. 13, Malpighian tubules; figs 14–17, gizzard; figs 20–21, enteric valve)
Triangularitermes	Constantino and Acioli (2009; *T. triangulariceps*: fig. 6e, enteric valve)
Velocitermes	Constantino and Acioli (2009; *V. heteropterus*: fig. 6f, enteric valve); Roisin *et al.* (1996; *V. barrocoloradensis*: fig. d, gut coiling; fig. 2i, enteric valve)

Table 1. List of taxonomic studies that treat the worker caste of Neotropical Termitidae genera. (Continuation)

Syntermitinae	
Acangaobitermes	Rocha *et al.* (2011; *A. krishnai*: fig. 3, worker mandibles; figs 4a–e, worker digestive tube *in situ*; fig. 5, worker molar plate; fig. 6, enteric-valve armature)
Armitermes	Rocha *et al.* (2012; *A. armiger*: figs 21B, worker mandibles, C–G digestive tube *in situ*, figs 22 C, detail of first-order pulvillus of gizzard, D, E. enteric-valve armature; *A. bidentatus*: figs 23 B–F, digestive tube *in situ*; fig. 24, detail of enteric-valve armature; *A. spininotus*: figs 26B, worker mandibles, C–D, digestive tube *in situ*)
Cahuallitermes	Constantino (1994; *Cahuallitermes intermedius*: figs 14–17, digestive tube; figs 19–21, worker mandibles; fig. 22, enteric-valve armature)
Cornitermes	Fontes (1998: *C. cumulans*: figs 29–32, digestive tube *in situ*)
Curvitermes	Fontes (1998; *C. odontognathus*: figs 53–56, digestive tube *in situ*); Carvalho and Constantino (2011; *C. minor:* figs 3 A–H, digestive tube *in situ*; I, crop and gizzard; J, mixed segment and attachment of Malpighian tubules; figs 4, C. odontognathus: A, gizzard armature; C, enteric-valve armature; D, worker mandibles; C. minor: E, enteric-valve armature; F, worker mandibles.); Rocha *et al.* [2012; *C. odontognathus:* fig. 11B, worker mandibles in dorsal view (left mandible) and in frontal view (right mandible)]
Cyrilliotermes	Constantino and Carvalho (2012; figs 10, worker mandibles: A, *C. angulariceps*; B, *C. brevidens*; C, *C. crassinasus*; D, *C. strictinasus*; E, *C. strictinasus*: molar plate; figs 11, A–D; *C. strictinasus:* digestive tube *in situ*; E, mixed segment; F, attachment of Malpighian tubules; figs 12, enteric-valve armature, A–B, *C. angulariceps*; C–D, *C. brevidens*; E–F, *C. crassinasus*; G–H, *C. strictinasus*; fig. 13, *C. angulariceps,* gizzard armature). Fontes (1998; *C. cupim,* digestive tube *in situ,* figs 45–48; jun. syn. of *C. strictinasus*).
Embiratermes	Fontes (1998: *E. festivellus,* figs 41–44, digestive tube *in situ*)
Ibitermes	Fontes (1998: *I. curupira,* figs 37–40, digestive tube *in situ*)
Labiotermes	Constantino *et al.* (2006; figs 13, worker mandibles: A, *L. brevilabius*; B, *L. emersoni*; C, *L. guasu*; D, *L. labralis*; E, *L. laticephalus*; F, *L. leptothrix*; G, *L. longilabius*; H, *L. oreadicus*; I, *L. orthocephalus*; J, *L. pelliceus*; figs 14, digestive tube *in situ*, A, *L. guasu*; B, *L. labralis*; C, *L. laticephalus*; D, *L. leptothrix*; E, *L. oreadicus*, F, *L. orthocephalus*; figs 15, mixed segment of workers, A–B, *L. brevilabius*; C–D, *L. emersoni*; E–F, *L. guasu*; G–H, *L. labralis*; I–J, *L. laticephalus*; K–L, *L. leptothrix*; M–N, *L. longilabius*; O–P, *L. oreadicus*; Q–S, *L. orthocephalus*; T–U, *L. pelliceus*; figs 16: enteric-valve armature, A, *L. brevilabius*; B, *L. emersoni*; C, *L. guasu*; D, *L. labralis*; E, *L. laticephalus*; F, *L. leptothrix*; G, *L. longilabius*; H, *L. oreadicus*; I, *L. orthocephalus*; J, *L. pelliceus*). Fontes (1998*, L. emersoni:* figs 17–20, digestive tube *in situ; L. brevilabius:* figs 21–24, digestive tube *in situ*)
Macuxitermes	Constantino (1997; *M. triceratops*: figs 1–4, digestive tube *in situ*; fig. 5, enteric valve; fig. 6, insertion of Malpighian tubules; fig. 7, enteric-valve armature; Postle & Scheffrahn (2016; *M. colombicus*: fig. 3, digestive tube *in situ*; figs 4A, worker head and thorax; B, worker mandibles; figs 5A, P2 and connection with P3; B, enteric-valve ridges; C, aciculiform spines near junction of P1 and mixed segment; fig. 7, P1 showing position and arrangement of spines)
Mapinguaritermes	Rocha *et al.* (2012; *M. peruanus*: figs 12B, 13B, mesenteric tongue; *M. grandidens*: figs 41C–G, digestive tube *in situ*; fig. 42B, detail of first-order pulvillus of gizzard; C, enteric valve)
Noirotitermes	Cancello & Myles (2000; *N. noiroti*: figs 9–10, worker mandibles; fig. 11, digestive tube, uncoiled; fig. 12, digestive tube *in situ*; fig. 13, enteric-valve armature, fig. 14, insertion of Malpighian tubules)
Paracurvitermes	Constantino & Carvalho (2011; *P. manni*: figs 2A, B, head; C, mandibles; D, crop and gizzard; E, mixed segment; F, insertion of Malpighian tubules; G–J, digestive tube *in situ*; E, enteric-valve armature; F, gizzard armature)
Procornitermes	Cancello & Rocha (2013; figs 1–3, digestive tube *in situ*: 1. *P. striatus*, 2. *P. araujoi*; 3. *P. triacifer*; figs 4–6, (a) Insertion of stomodeal valve; (b) detail of Malpighian-tubule attachment and mesenteric tongue on inner face of gut coil: 4. *P. striatus*; 5. *P. araujoi*; 6. *P. triacifer*; fig. 7, P1, proximal portion and mesenteric tongues: (a) *P. lespesii,* (b) *P. araujoi*). Fontes (1998; *P. lespesii,* digestive tube *in situ,* figs 26–28)
Rhynchotermes	Constantini and Cancello (2016; *R. perarmatus*: fig. 8 A–C, worker habitus; *R. piauy*: fig. 8 D worker mandibles; *R. nasutissimus*: fig. 9 A and B, Gizzard; C, enteric valve, fig. 10 A–D, digestive tube *in situ*). Scheffrahn (2010; *R. bulbinasus*: fig. 5 habitus of workers, fig. 6 enteric valve). Fontes (1998; *R. nasutissimus,* digestive tube *in situ,* figs 33–36)
Silvestritermes	Rocha *et al.* (2012; *S. euamignathus*: fig. 12 A, D, fig. 13 C, mesenteric tongue, fig. 27 C, worker mandibles, F–I, digestive tube *in situ,* fig. 28B, enteric valve; *S. almirsateri*: fig. 32. C–F, digestive tube *in situ; S. duende:* fig. 33A, worker mandibles, *C–G,* digestive tube *in situ; S. lanei:* fig. 36A, worker mandibles, C–F, digestive tube *in situ; S. minutus:* fig. A, worker mandibles)

Table 1. List of taxonomic studies that treat the worker caste of Neotropical Termitidae genera. (Continuation)

Syntermitinae	
Syntermes	Constantino (1995; figs 18–19, worker mandibles: 18. *S. grandis*; 19. *S. spinosus*; 20. *S. brevimalatus*; 21. *S. longiceps*; 22. *S. nanus; S. wheeleri:* figs 28–31, digestive tube *in situ;* figs 32–33, mixed segment; fig. 34. insertion of Malpighian tubules*; S. tanygnathus:* fig. 35, mixed segment; *S. barbatus:* fig. 36–37, mixed segment; fig. 38*,* insertion of Malpighian tubules; *S. dirus:* figs 39–40*,* mixed segment; *S. longiceps:* figs 41–44, digestive tube *in situ;* 45–46, mixed segment; fig. 47, insertion of Malpighian tubules; *S. molestus:* fig. 48–51, digestive tube *in situ*, 52–53, mixed segment). Fontes (1998: *S. dirus:* figs 13–16, digestive tube *in situ)*
Uncitermes	Rocha *et al.* (2012; *U. teevani:* fig. 12 C, fig. 13 D, mesenteric tongue*;* fig. 17, enteric-valve armature; fig. 39 D–G, digestive tube *in situ*). Carrijo *et al.* (2016; *U. almerie*: fig. 3, head capsule; fig. 4 A, gizzard; 4 B, enteric valve armature).
Termitinae	
Amitermes	Holmgren (1909; *A. amifer*, fig. 19, head; fig. 60, digestive tube *in situ*); Hare (1937; *A. foreli*, pl. 13, fig. 51a, mandibles); Ahmad (1950; *A. amifer*, fig. 13, mandibles); Mélo and Fontes (2003; *A. nordestinus*, fig. 7, mandibles)
Cavitermes	Hare (1937; *C. tuberosus*, pl. 12, fig. 46a, mandibles); Ahmad (1950; *C. tuberosus*, fig. 16, mandibles); Mathews (1977; *C. parvicavus*, fig. 62, mandibles; pl. 24, enteric valve); Noirot (2001; *Cavitermes* sp., fig. 7G, enteric valve); Hellemans *et al.* (2017; *C. tuberosus*, fig. 7A, enteric valve)
Cornicapritermes	Ahmad (1950; *C. mucronatus*, fig. 17, mandibles); Krishna (1968; *C. mucronatus*, fig. 37, mandibles)
Crepititermes	Ahmad (1950; *C. verruculosus*, fig. 16, mandibles); Rocha and Cuezzo (2015; *C. verruculosus*; fig. 8, mandibles; figs 9–12, digestive tube *in situ;* figs 13, mixed segment; fig. 14, insertion of Malpighian tubules; fig. 15, gizzard; figs 16–17, enteric valve; figs 18–19, ornamented cuticle of ileum)
Cylindrotermes	Hare (1937; *C. macrognathus*, pl. 13, fig. 52a, mandibles); Ahmad (1950; *C. nordenskioldi*, fig. 13, mandibles); Noirot (2001; *Cylindrotermes* sp., fig. 12D, digestive tube *in situ*); Rocha and Cancello (2007; *Cylindrotermes* sp., fig. 1, mandibles)
Dentispicotermes	Ahmad (1950; *D. brevicarinatus*, fig. 16, mandibles); Mathews (1977; *D. pantanalis*, fig. 65, mandibles; pl. 27, enteric valve); Bandeira and Cancello (1992; *D. cupiporanga*, fig. 11, mandibles)
Dihoplotermes	Krishna (1968; *D. inusitatus,* fig. 39, mandibles); Mathews (1977; *D. inusitatus*, fig. 69, mandibles)
Divinotermes	Mathews (1977; *D. allognathus*, fig. 60, mandibles; Pl. 23, enteric valve); Carrijo and Cancello (2011, *D. tuberculatus*, fig. 8A and 8C, pronotum; *D. allognathus*, fig. 9A, mandibles; fig. 9B, galea and lacinia; figs 10A–D, digestive tube *in situ;* fig. 10E, insertion of Malpighian tubules; fig. 11A, gizzard; fig. 11B, enteric valve)
Genuotermes	Mathews (1977; *G. spinifer*, pl. 26, enteric valve); Rocha (2013; *G. spinifer*, figs 14–19, digestive tube *in situ;* fig. 18, insertion of Malpighian tubules*;* fig. 19, mandibles*;* figs 20–21, gizzard*;* figs 22–23, enteric valve)
Gnathamitermes	Ahmad (1950; *G. perplexus*, fig. 13, mandibles); Noirot (2001, *G. perplexus*, fig. 6J, mixed segment and insertion of Malpighian tubules)
Hoplotermes	Ahmad (1950; *H. amplus*, fig. 12, mandibles);
Inquilinitermes	Scheffrahn (2014b; *I. johnchapmani*, fig. 5, enteric valve; fig. 6, worker in lateral view; fig. 7, mandibles; fig. 8; digestive tube *in situ)*
Microcerotermes	Holmgren (1909; *M. strunckii*, fig. 22, head; fig. 61, digestive tube *in situ*); Ahmad (1950; *M. strunckii*, fig. 12, mandibles); Sands (1998; *M. strunckii,* figs 640–642, mandible of largest worker; figs 643–645, mandibles of smallest worker; figs 652–653, digestive tube in situ; fig. 662, digestive tube, dissected and uncoiled; fig, 667, mixed segment and insertion of Malpighian tubules); Hare (1937; *M. arboreus*, pl. 13, fig. 55a, mandibles)
Neocapritermes	Holmgren (1909; *N. opacus*, fig. 18, head); Krishna and Araujo (1968; *N. opacus*, fig. 1, mandibles); Krishna (1968; *N. opacus*, fig. 43, mandibles); Hare (1937; *N. angusticeps*, pl. 12, fig. 49a, mandibles); Ahmad (1950; *N. angusticeps*, fig. 14, mandibles); Constantino (1991c; *N. pumilis*, fig. 2, mandibles; *N. unicornis*, fig. 4, mandibles); Constantino (1998; *N. opacus*, figs 14–17, digestive tube *in situ;* fig. 18, mixed segment and insertion of Malpighian tubules); Constantino (1999; *N. villosus*, fig. 10, mandibles); Constantino (2002; *N. opacus*, fig. 214, right view of gut, showing the two lobes on mixed segment)
Onkotermes	Constantino *et al.* (2002; *O. brevicorniger*, figs 5–6, head; figs 7–9, large worker mandibles; figs 10–12, small worker mandibles; figs 16–19, digestive tube *in situ;* fig. 20, mixed segment; fig. 21, insertion of mesenteric valve in P3)
Orthognathotermes	Hare (1937; *O. wheeleri*, pl. 12, fig. 47a, mandibles); Ahmad (1950; *O. wheeleri*, fig. 16, mandibles); Mathews (1977; *O. aduncus*, pl. 26, enteric valve); Constantino (1991b; *O. humilis*, fig. 29, enteric valve; fig. 30, mandibles); Rocha and Cancello (2009; *O. insignis*, figs 24A–D, digestive tube *in situ;* fig. 26, mandibles; fig. 26, enteric valve; fig. 28A, gizzard; fig. 28B, mixed segment; *O. humilis,* fig. 27, enteric valve)

Table 1. List of taxonomic studies that treat the worker caste of Neotropical Termitidae genera. (Continuation)

Termitinae	
Palmitermes	Hellemans *et al.* (2017; *P. impostor*, fig. 4, mandibles; fig. 5, digestive tube *in situ;* fig. 6A–B, gizzard; fig. 6C–D, enteric valve)
Planicapritermes	Ahmad (1950; *P. planiceps*, fig. 14, mandibles); Constantino (1998; *P. longilabrum*, figs 4–7, digestive tube *in situ; P. planiceps*, figs 8–11, digestive tube *in situ;* fig. 12, mixed segment; fig. 13, position of enteric valve insertion in P3)
Spinitermes	Ahmad (1950; *S. nigrostomus*, fig. 15, mandibles); Mathews (1977; *S. nigrostomus*, pl. 21, enteric valve; *S. trispinosus*, pl. 22, enteric valve); Constantino (1991b; *S. longiceps*, fig. 22, mandibles; fig. 24, enteric valve); Constantino (1999; *S. longiceps*, fig. 9, mandibles); Noirot (2001; *Spinitermes* sp., fig. 12C, paunch); Carrijo and Cancello (2011; *S. robustus*, fig. 8B, pronotum)
Termes	Hare (1937; *T. panamaensis*, pl. 12, fig. 48a, mandibles); Ahmad (1950; *T. fatalis*, fig. 16, mandibles); Mathews (1977; *Termes* sp., pl. 28, enteric valve); Miller (1991) (*T. fatalis* only); Bandeira and Cancello (1992; *T. ayri*, fig. 16, mandibles); Godoy and Torales (1993; *T. riograndensis*, figs 1–4, digestive tube *in situ;* fig. 5, stomodeal valve; fig. 6, mixed segment and insertion of Malpighian tubules; fig. 7, position of enteric valve; fig. 12, gizzard; fig. 13, enteric valve; fig. 15, uncoiled digestive tube; *T. nigritus*, figs 8–11, digestive tube *in situ;* fig. 14, enteric valve); Godoy and Torales (1999; *T. riograndensis*, figs 3 and 6, digestive tube *in situ;* fig. 9, mixed segment); Hellemans *et al.* (2017; *T. fatalis*, fig. 7B, enteric valve)

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