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Tucupitermes, the largest Apicotermitinae (Isoptera, Termitidae) from the Amazon Rainforest

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Abstract

Soldierless termites of the Apicotermitinae remain one of the least studied groups in termite taxonomy, particularly within the Amazon Rainforest, a biodiversity hotspot. This study introduces *Tucupitermes ubixaba* Almeida-Azevedo, Acioli & Azevedo **gen. et sp. nov**., the largest Apicotermitinae in the Amazon Rainforest and a new monotypic genus distinguished by unique morphological traits, including an elongated stomodeal valve, Malpighian ampullae developed, a long mesenteric tongue, and small bilobed seating. These features were documented through detailed analyses of the external and internal morphology of the worker caste. The discovery of this genus not only fills a critical gap in the taxonomy of Apicotermitinae but also provides new insights into the diversity and ecological adaptations of soldierless termites in the Amazon.

Key words: Soldierless termites, Digestive tube morphology, Enteric valve, Soil-feeding termites

Introduction

The Neotropical Apicotermitinae, a group of soldierless termites, are among the most abundant termites in South America, comprising up to 50% of termite records in certain assemblages (Ackerman *et al*. 2009; Bourguignon *et al*. 2016). These termites feed on soil organic matter or leaf litter (Donovan 2002; Acioli and Constantino 2015), playing a vital role in the decomposition and recycling of plant material (Jouquet *et al*. 2011; Bourguignon *et al*. 2016). Although, the Apicotermitinae lacks a soldier caste responsible for colony defense, workers of this group have evolved several defensive strategies, including behavioral defenses, like aggressiveness, and physiological mechanisms, such as excreting sticky substances onto predators (Bourguignon *et al*. 2016).

The identification of Apicotermitinae primarily relies on workers and often requires detailed examination of gut morphology, such as the enteric valve, a critical feature for distinguishing genera and species (Bourguignon *et al*.

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2016; Carrijo *et al*. 2023). However, dissecting the digestive tube and enteric valve can be particularly challenging due to the small size of the workers, requiring significant practice to visualize these structures.

In the Amazon Rainforest, a total of 15 Apicotermitinae genera have been recorded, five of which were described in the past five years, revealing the unknown diversity of this group (Almeida-Azevedo *et al*. 2023; Carrijo *et al*. 2023). Among the amazonian Apicotermitinae, the genus *Aparatermes* Fontes, 1986 is the most similar to the new genus described here. *Aparatermes* is characterized by medium sized workers, long and tortuous first proctodeal segment, the presence of a trilobed seating and spines on the enteric valve (Fontes, 1986; Pinzón Florian *et al*. 2019). *Aparatermes abbreviatus* (Silvestri 1901), the type species of the genus, *A. cingulatus* (Burmeister, 1839), and *A. silvestrii* (Emerson, 1925), were all first described as *Anoplotermes* (Fontes, 1998). *Aparatermes silvestrii* (Emerson, 1925), was included in the genus *Ruptitermes* Mathews, 1977 and later synonymized with *Aparatermes cingulatus* (Šobotník *et al*. 2010). However, studies indicate that *A. silvestrii* and *A. cingulatus* can be differentiated by their alates and their distinct geographic distributions (Acioli and Constantino, 2015). The most recently described species in the genus is *Aparatermes thornatus* Pinzón Florian & Scheffrahn, 2019, characterized mainly by its dark orange to reddish-brown coloration and small size compared to other species. Given the taxonomic uncertainties involving some species of the genus, a review of the "silvestrii group" is underway and will be published separately.

Following the effort to address the taxonomic gap for the Apicotermitinae, this study describes a new genus of this subfamily to the Amazon rainforest.

Methods

The examined material was collected in the state of Pará, located in the northern region of Brazil, from a developed forest, with over 20 years old, characterized by yellow latosol with a clay texture at a depth of 10 to 15 cm. Initially, the soil was dug using a hoe, and specimens were subsequently collected from the soil with the aid of an entomological tweezer and stored in vials containing 80% alcohol.

Both external and internal characters from the worker caste were described. The terminology of mandibles follows Fontes (1987), while the digestive tube description follows Noirot (2001). The following morphometric characters were measured for workers (numbers in parentheses correspond to the character measurement codes established by Roonwal (1970)): LH, length of the cephalic capsule until the apical end of the clypeus (8); WH, maximum width of head (17); LT, length of hind tibiae (85); WP, median pronotum width (68).

The specimens' dissection followed Almeida-Azevedo *et al*. (2023). A total of 10 individuals were dissected, all following the same pattern of internal characteristics. To examine the gut, sclerites and sternites were removed from preserved specimens using a teasing needle. The enteric valve was removed and placed in a drop of PVA mounting medium to remove the musculature. Later, the enteric valve was fixed on a glass slide and was photographed with a Leica DFC295 camera attached to a CTR5000 microscope. The external morphology was photographed with a Leica DFC295 camera attached to a M205 stereo microscope. The images were edited using Inkscape 1.4 version software and measurements were made with an ocular micrometer.

Results

Tucupitermes Almeida-Azevedo, Acioli & Azevedo gen. nov.

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(Figs 1A–E, 2A–K)

Type species: *Tucupitermes ubixaba* Almeida-Azevedo, Acioli & Azevedo **sp. nov. (Figs 1A–E, 2A–K)**

Etymology: From the Tupi-Guarani "*Tiku'pir*", which means "yellow juice extracted from the root of the wild cassava when peeled, grated and squeezed", in reference to the color of the worker.

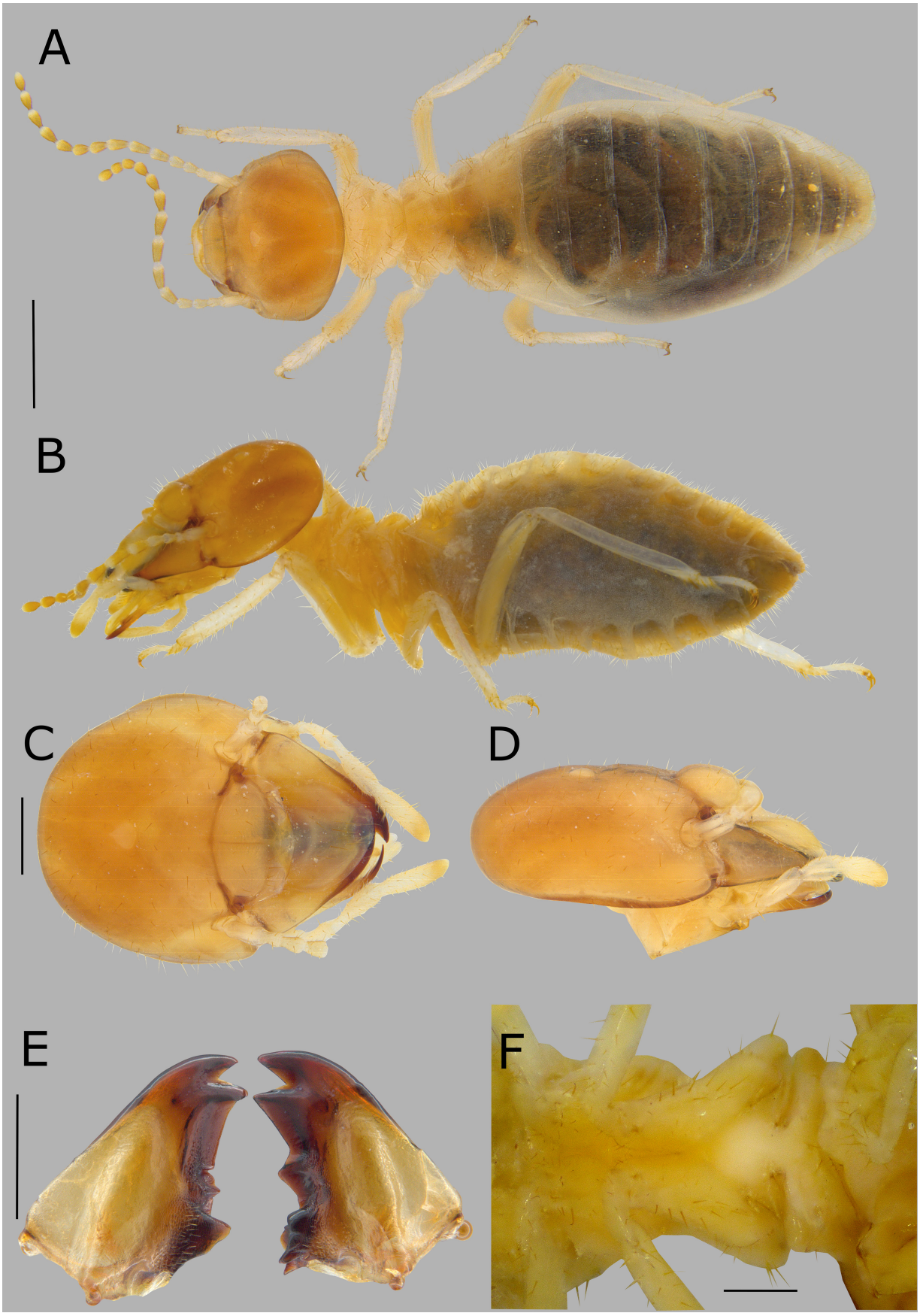

FIGURE 1. *Tucupitermes* **gen.nov**, non-type specimen**.** A. Habitus, dorsal view; B. Habitus, lateral view; C. Head, dorsal view; D. Head, lateral view; E. Mandibles, dorsal view; F. Procoxae. Scale bar: A–B = 1 mm, C–F = 0.5 mm.

Description

Imago. Unknown.

Genus Diagnosis. Left mandible with a cutting-edge length twice as long as the distance between the apical tooth and M1+2 (Fig. 1E). Stomodeal valve long, twice as long as the length of the crop. Malpighian ampullae developed and visible in right lateral and ventral views (Fig. 2B, C, F). Mesenteric tongue is long and slightly globular, reaching midline of abdomen (Fig. 2F). Connection between P1 and P3 not visible in any view in situ, with small bilobed seating (Fig. 2H, I).

Genus Description

Worker. (Fig. 1A–F). Head capsule dark yellow with darker longitudinal muscles converging towards vertex (Fig. 1A). Worker with a whitish, convex fontanelle, resembling a drop (Fig. 1C, D). Head capsule with few bristles of varying sizes distributed throughout the head, except in the posterior region. Postclypeus small, slightly inflated and with few bristles of the same size as bristles of head capsule (Fig. 1D). Labrum convex, longer than the postclypeus+clypeus, with bristles thicker than the bristles of head capsule (Fig. 1C, D). Antenna with 13 antennomeres, with antennomere I < II, III < than remaining. Mandibles robust; Left mandible with apical tooth shorter than M1+2 (Fig. 1E); distance between apical tooth and M1+2 is proportionally closer compared to other structures of mandible; cutting-edge length twice as long as the distance between the apical tooth and M1+2 (Fig. 1E); incision between M1+2 and M3 clear and very distant from M1+2; tooth M3 acute, with short distance between M3 and molar prominence; molar prominence conical, with groove-like texture and scales at its base (Fig. 1E). Right mandible with apical tooth slightly smaller than M1; right mandible with the first marginal tooth significantly enlarged compared to the other teeth (Fig. 1E); posterior margin of tooth M1 wider than the molar prominence (Fig. 1E); margin between teeth M1 and M2 forming angle of 130º (Fig. 1E); M2 conical; molar plate concave, without grooves, groove-like texture and scales at its base. Yellowish thorax, pronotum wider than half width of head, with many bristles on edges (Fig. 1A, B); meso- and metanotonum with several bristles on lateral and posterior margins (Fig. 1A, B). Tibiae lighter than femora (Fig. 1A); tibiae and femora with many irregular spines on anterior surface (Fig. 1B); procoxae with a distinct longitudinal row of spine-like bristles on anterior surface (Fig. 1B, F). Abdomen translucent, tergites and sternites covered with many bristles of different sizes (Fig. 1B). Measurement (mm) of 20 workers in table 1.

TABLE 1. Comparative measurements (range and mean in mm) of workers of *Tucupitermes ubixaba* **sp. nov.** with workers of *Aparatermes thornatus* (Pinzón Florian *et al*. 2019), *Aparatermes abbreviatus* (Fontes 1986), *Aparatermes silvestrii* (personal observations Acioli 2007) e *Aparatermes cingulatus* (Šobotník *et al*. 2010).

Species	Head length	Head width	Hind tibia length	Pronotum width	Number of specimens
Tucupitermes ubixaba **sp. nov.**	1.98–2.12 (2.05)	1.90–1.93 (1.90)	1.46–1.75 (1.64)	0.96–1.21 (1.03)	20
Aparatermes thornatus (Pinzón Florian *et al*. 2019)	0.63–0.93 (0.80)	0.82–1.11 (0.92)	0.53–0.84 (0.68)	-	19
Aparatermes abbreviatus (Fontes 1986)	1.00–1.20 -	1.05–1.27 -	0.85–0.98 -	-	10
Aparatermes Silvestrii (personal observations Acioli 2007)	0.91–1.22 (1.03)	1.06–1.53 (1.26)	0. –1.03 (0.89)	-	42
Aparatermes cingulatus (Šobotník *et al*. 2010)	-	(1.38)	-	-	10

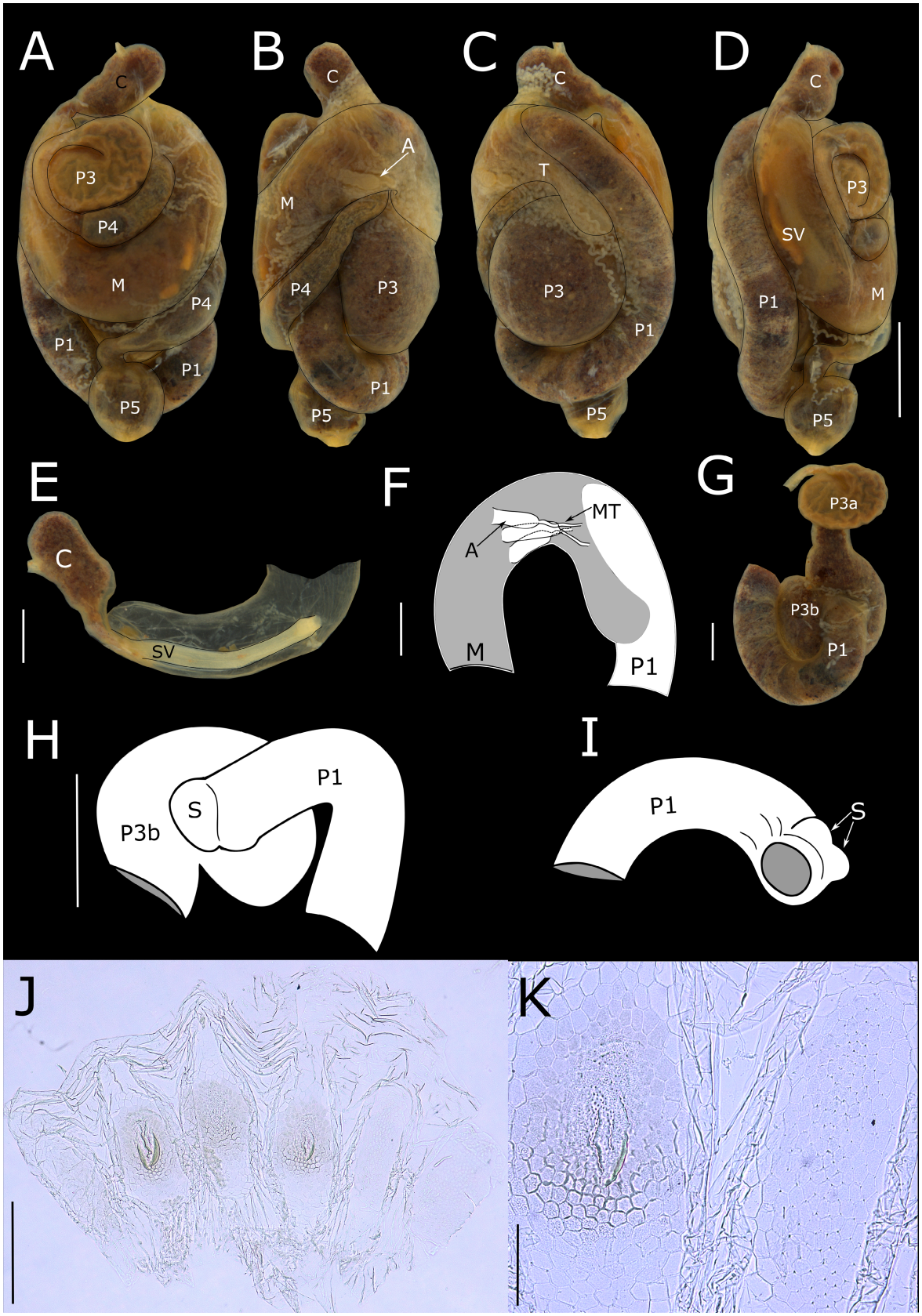

FIGURE 2. Digestive tube of *Tucupitermes* **gen.nov.**, non-type specimen. A–D. Digestive tube; A. Dorsal view; B. Right lateral view; C. Ventral view; D. Left lateral view; E. Stomodeal valve; F. Ampullae and Malpighian tubules; G. Connection P1–P3; H–I. Connection P1–P3 with bilobed seating. C = crop, M = mesenteron, P1 = first proctodeal segment, P3, P3a, P3b = paunch, P4 = colon, P5 = rectum; T = tougue; MT = Malpighian tubule; SV = Stomodeal valve; A = Malpighian ampullae. S = Seating. J–K. Enteric valve. Scale bar: A–D = 1 mm, E = 0.5 mm, F–G = 1 mm, H = 200 µm, J = 50 µm.

Digestive tube. (Fig. 2A–K). Crop small and located immediately after thorax, directed towards right side of body in dorsal view, narrowing toward gizzard (Fig. 2A). Gizzard vestigial, visible in dorsal and left lateral views, without armour, and with six first-order pulvilli; surface of pulvilli scaly with alternating scales, with posterior part with tiny spines; space between puvilli is smooth; stomodeal valve very long, twice as long as length of crop, and visible through mesenteron (Fig. 2A, E); mesenteron uniform, with diameter larger than P1; mesenteron with four well-developed, elongated Malpighian ampullae, with at least two ampullae visible in right lateral and ventral views (Fig. 2B, C, F); four independent Malpighian tubules, one in each ampulla (Fig. 2F). Mesenteric tongue long and slightly globular, almost reaching midline of body (Fig. 2C, F). P1 long, starting on the right side of body in ventral view and connecting to P3 on right side, covered by P4 in dorsal view (Fig. 2A–C). Small bilobed seating (Fig. 2H, I); P2 not visible externally; asymmetric enteric valve, with three lobes with small, poorly defined scales, each scale with minute spine at apex; three lobes with large, defined scales converging toward median region of the lobe and forming concavity with cluster of minute spines; region between lobes without scales (Fig. 2J, K); P3 globular, connecting to P4 by isthmus, visible dorsal view (Fig. 2A). Isthmus arched, positioned near left anterolateral margin, visible in dorsal view (Fig. 2A). In dorsal view, P3 wide, with striated appearance just above P4. P4 width twice as small as width of mesenteron in dorsal view (Fig. 2A). Connection P4 and P5 forming loop facing left side of body, visible in dorsal and left lateral views (Fig. 2A, D).

Comparisons

The new genus exhibits external characteristics that are very similar to some species of *Aparatermes* Fontes, 1986, such as the coloration of the head capsule and spines present on the legs (Pinzón Florian *et al*. 2019) (Fig. 1A, B). However, the size of the individuals of the new genus exceeds the size of the *Aparatermes* spp. (Table 1), and the left mandible of *Tucupitermes* **gen. nov.** has a cutting blade length twice as long as the distance between the apical tooth and M1+2, differing from some *Aparatermes* (*A*. *abbreviatus*, *A*. *silvestrii*, *A*. *thornatus* – personal observations) (Fig. 1E and Table 1). In *Aparatermes* the mesenteric tongue is short and non-globular, whereas in *Tucupitermes* **gen. nov.** is long, widened and slightly globular (Fig. 2 C, F). This characteristic is uncommon for medium/large-sized Apicotermitinae, being described for *Patawatermes* Bourguignon & Roisin 2016, and for small-sized termites, such as *Anoplotermes* Müller 1873, *Chasitermes* Scheffrahn & Carrijo 2023, *Disjunctitermes* Scheffrahn 2017 and *Humutermes* Bourguignon & Roisin 2016. Furthermore, the P1–P3 connection in *Tucupitermes* **gen. nov.** is only visible with dissection (Fig. 2G, H), while in *Aparatermes* it can be observed in dorsal view in situ. The P1–P3 connection visible only with dissection is uncommon in the Neotropical Apicotermitinae, only known for *Anoplotermes parvus* (Bourguignon *et al*. 2010). The shape and size of the enteric valve seating, which is bilobed, with very small lobes is also unique in the new genus (Fig. 2I). The absence of scales around the lobes of the enteric valve of *Tucupitermes* **gen. nov.** (Fig. 2J, K) is shared with *Aparatermes*, but also *Ruptitermes* and *Mangolditermes* (Acioli & Constantino 2015; Carrijo *et al*. 2023), so this structure is not determinant to distinguish these genera.

The length of the stomodeal valve in *Tucupitermes* **gen. nov.** is extremely long, and was not previously observed in any other Apicotermitinae. This is also true for the Malpighian ampullae, that have not been reported in any genus of soldierless termites, but it may have gone unnoticed in some species of *Aparatermes* Fontes, 1986 and *Ruptitermes* Mathews, 1977 (Personal observations of *Aparatermes thornatus*, *Aparatermes silvestrii* and *Ruptitermes* spp.). However, these two genera have features distinct from *Tucupitermes* **gen. nov.**, such as the short mesenteric tongue, the trilobed enteric valve seating, and an enteric valve with well-developed spines (Fontes, 1986; Pinzón Florian *et al*. 2019) Acioli and Constantino, 2015).

Tucupitermes ubixaba Almeida-Azevedo, Acioli & Azevedo sp. nov.

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(Figs 1A–F, 2A–K)

Etymology. from the Tupi-Gurani "*ub-i-xaba*", which means "indigenous leader, foreman, enormous, large, immense" in reference to the size of the workers, which are comparatively larger than other Neotropical Apicotermitinae.

Holotype: worker, in 80% alcohol, separated in a microtube. Original label: Brasil, Pará, Santarém, 2º41'13.90"S,

54º55'3.30"W. Manual sampling, 22.05.2015. A. N. S. Acioli col. The holotype was deposited at the Invertebrate Collection of the National Institute of Amazonian Research—INPA (INPA-ISO 000013) (in a bottle separated from the rest of the sample).

Paratypes: 25 workers with the same data as the holotype. From these, 20 paratypes were deposited in the Invertebrate Collection of the National Institute for Amazonian Research—(INPA INPA-ISO 000014) and five deposited at the National Museum of Rio de Janeiro—(MNRJ-ENT9-1349).

Species Diagnosis. As described for the genus.

Species Description. As described for the genus.

Distribution. Brazil, Pará, Santarém. Termites were collected directly from the soil using a hoe. In the yellow soil, termites were very agile, fleeing into underground tunnels. No imago or nesting structures were found. Workers of *Tucupitermes* **gen. nov.** were very abundant, becoming visible at the first excavation. Very large termites that impressed the collector.

Discussion

Tucupitermes **gen. nov.** is the largest Apicotermitinae ever described from the Amazon Rainforest, standing out for having well-developed Malpighian ampullae, a long globose mesenteric tongue and a small bilobed enteric valve seating. This set of characteristics is unusual among the Neotropical genera of Apicotermitinae described.

The stomodeal valve and the Malpighian ampullae are poorly described structures in taxonomic studies of soldierless termites, probably because they are not well developed in most genera. We suggest they should be incorporated into new descriptions for possible comparisons between taxa. The stomodeal valve is located immediately after the gizzard and is involved in particle filtering and peristalsis and antiperistalsis, having a similar function to the gizzard during food passage (Noirot 1995, 2001; Barsotti and Costa-Leonardo 2000; Romero Arias *et al*. 2020). The size of this structure in the new species may be related to the type of food consumed.

The mesenteric tongue and the first proctodeal segment are structures that vary in size and shape. In *Tucupitermes* **gen. nov.**, they are considered long, and this characteristic is rarely observed among the Neotropical genera of Apicotermitinae. For example, in *Mangolditermes* Scheffrahn, Carrijo & Castro 2023, a very long mesenteric tongue and P1 can be observed, and *Hirsutitermes* Scheffrahn, Carrijo & Castro 2023 is diagnosed with a long mesenteric tongue. However, these two genera have a visible enteric valve seat in the left lateral view, distinguishing them from *Tucupitermes* **gen. nov.**

Tucupitermes **gen. nov.** presents a combination of characteristics that link it to several genera within the subfamily Apicotermitinae. The shape of the mandibles is similar to some *Ruptitermes* (Acioli and Constantino, 2015), the long mesenteric tongue resembles that of *Hirsutitermes* and *Mangolditermes* (Carrijo *et al.* 2023), and the elongated P1 is similar to that of *Aparatermes* (Fontes, 1986; Pinzón Florian *et al*. 2019). This set of characteristics makes *Tucupitermes* **gen. nov.** unique and the largest Neotropical Apicotermitinae described, and its phylogenetic position relative to other genera is essential to understand the evolutionary relationships of these characteristics within Apicotermitinae. The description of this new genus further enriches our knowledge about termite diversity in the Amazon.

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