SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

Gut Structure of Two Species of the Neotropical Genus *Tauritermes* Krishna (Isoptera: Kalotermitidae)

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Estructura del Tubo Digestivo de Dos Especies del Género Neotropical *Tauritermes* Krishna (Isoptera: Kalotermitidae)

RESÚMEN - En este trabajo se analizó la anatomía del tubo digestivo de dos especies del género neotropical *Tauritermes* Krishna. Se presentan descripciones detalladas del enrollamiento del tubo digestivo y de la armadura cuticular de la molleja y del primer y segundo segmento proctodeal de pseudoergates. Aunque las principales características observadas en *Tauritermes* se incluyen en el patrón previamente conocido para la familia, fueron establecidas varias diferencias entre este género y otros de Kalotermitidae, principalmente con respecto a la longitud del mesenterón, la estructura y ornamentación cuticular del primer y segundo segmento proctodeal, la unión del tercer y cuarto segmento proctodeal y la armadura de la válvula rectal. Los caracteres del intestino, actualmente usados en sistemática y filogenia de termites, permiten diferenciar a *Tauritermes* de otros géneros de Kalotermitidae.

PALABRAS CLAVE: Termite, anatomía intestinal, pseudoergate, morfología

ABSTRACT - Gut morphology of two species of the neotropical genus *Tauritermes* Krishna was analyzed. Detailed description of the coiling gut and the cuticular armature of the gizzard and first and second proctodeal segments of pseudergates are given. The characteristics of *Tauritermes* gut followed the pattern previously known for the family, but some differences among this genus and other Kalotermitidae genera were: the length of the midgut, the structure and cuticular ornamentation of the first and second proctodeal segments, the junction of the third and fourth proctodeal segments and the armature of the rectal valve. *Tauritermes* was differentiated from other Kalotermitidae genera by means of the gut characters, currently used in termite systematics and phylogeny.

KEY WORDS: Termite, intestinal anatomy, pseudergate, morphology

The characteristics of the worker and pseudergate digestive tube are more and more often used in systematics and phylogeny of Isoptera, mainly at the genus level. Many previous studies have confirmed the systematic value of the coiling pattern and morphology of the worker digestive tube in "higher termites" (family Termitidae) (Grassé & Noirot 1954, Noirot & Kovoor 1958, Sands 1972, Johnson 1979, Fontes 1992, Constantino 1998). According to Noirot (1995), although the intestinal anatomy of the so-called "lower termites" (where the family Kalotermitidae is included) is much more uniform than in Termitidae, significant variations appear among families and genera referred to the structure and ornamentations of the different organs of pseudergates.

The gut characters of pseudergates from six Kalotermitidae genera (Noirot 1995) allowed to summarize a pattern for this family as follows: reduced muscle sheath at the end of the crop, midgut ring of medium length, complete absence of midgut coeca, eight Malpighian tubules, cushions of the first proctodeal segment spanning the whole length of this segment, coecum-like paunch, paunch-colon loop twisted to completely untwisted and regression of the armature of the rectal valve.

The neotropical genus *Tauritermes* Krishna has been recorded only in the southern portion of South America (Brazil and Argentina). Two of its three species are cited from Argentina: *T. taurocephalus* (Silvestri) and *T. triceromegas* (Silvestri) (Torales *et al*. 1997, Constantino 1998, Torales 1998).

In this paper, the gut of pseudergates from two species of the genus *Tauritermes* is described, including the coiling pattern, as well as the characteristics of the gizzard and the first and second proctodeal segments. These data contribute to enlarge the knowledge about the intestinal anatomy of this family, since *Rugitermes* is the only genus of neotropical Kalotermitidae whose intestinal anatomy has been previously studied (Gonçalvez 1979, 1980; Oliveira *et al*. 1987).

Material and Methods

Five series of ten late-instars pseudergates from different colonies were fixed in Dubosq -Brazil fixative and placed into labeled vials. Before dissection under a stereomicroscope (40x), the total body length and length of the abdomen were measured on each individual. The gut was observed and drawn *in situ*, after the remotion of the body wall and fat tissue. Each segment of the gut was then isolated and the gizzard, first proctodeal segment and enteric valve were mounted on glass slides, to be described and drawn. The segments, organs and structures of the digestive system were measured in 30 individuals (six from each sample) with an ocular micrometer. The drawings were made with the aid of a camera lucida.

In order to determinate the relative size of the gizzard by reference to the size of the termite, the C/H index was calculated, where C is the length of the columns and H the head width of the termite (Noirot 1995).

The measurements of the digestive organs in this study were included because they allow to establish proportions and comparisons among them. Despite the fact that most of the measured organs have muscular walls and show variations among individuals, those differences do not affect the diagnostic value of the observed characteristics (Fontes 1987).

The portions and structures of the digestive tube are named as in Fontes (1987) and Noirot (1995).

The examined material belongs to the collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura (FACENAC), Universidad Nacional del Nordeste, Corrientes, Argentina.

Material Examined.

- *Tauritermes taurocephalus* (Silvestri). ARGENTINA: Province of Chaco, Capitan Solari, 26/v/1990. Laffont and Torales coll. (FACENAC). Colony on a living tree of *Caesalpinia paraguariensis* (D.Parodi) Burk.
- *Tauritermes taurocephalus* (Silvestri). ARGENTINA: Province of Formosa, Presidente Irigoyen Department, 3/ix/1991. Laffont, Arbino & Torales coll. (FACENAC). Colony on a dead branch of Leguminosae.
- *Tauritermes taurocephalus* (Silvestri). ARGENTINA: Province of Corrientes, Corrientes city, 14/vi/2000. Laffont coll. (FACENAC). Colony on a dead branch of *Fraxinus americana* L.
- *Tauritermes* sp. ARGENTINA: Province of Corrientes, Corrientes city, 23/xii/1986. Laffont & Arbino coll. (FACENAC). Colony on a dead branch of *Tipuana tipu* (Benth) O.Kuntze.
- *Tauritermes* sp. ARGENTINA: Province of Corrientes, Corrientes city, 26/xii/1986. Laffont & Arbino coll. (FACENAC). Colony on a branch of *Tipuana tipu* (Benth) O.Kuntze.

Comparisons between both species were carried out by means of the t test of mean differences ($P < 0.05$).

Results

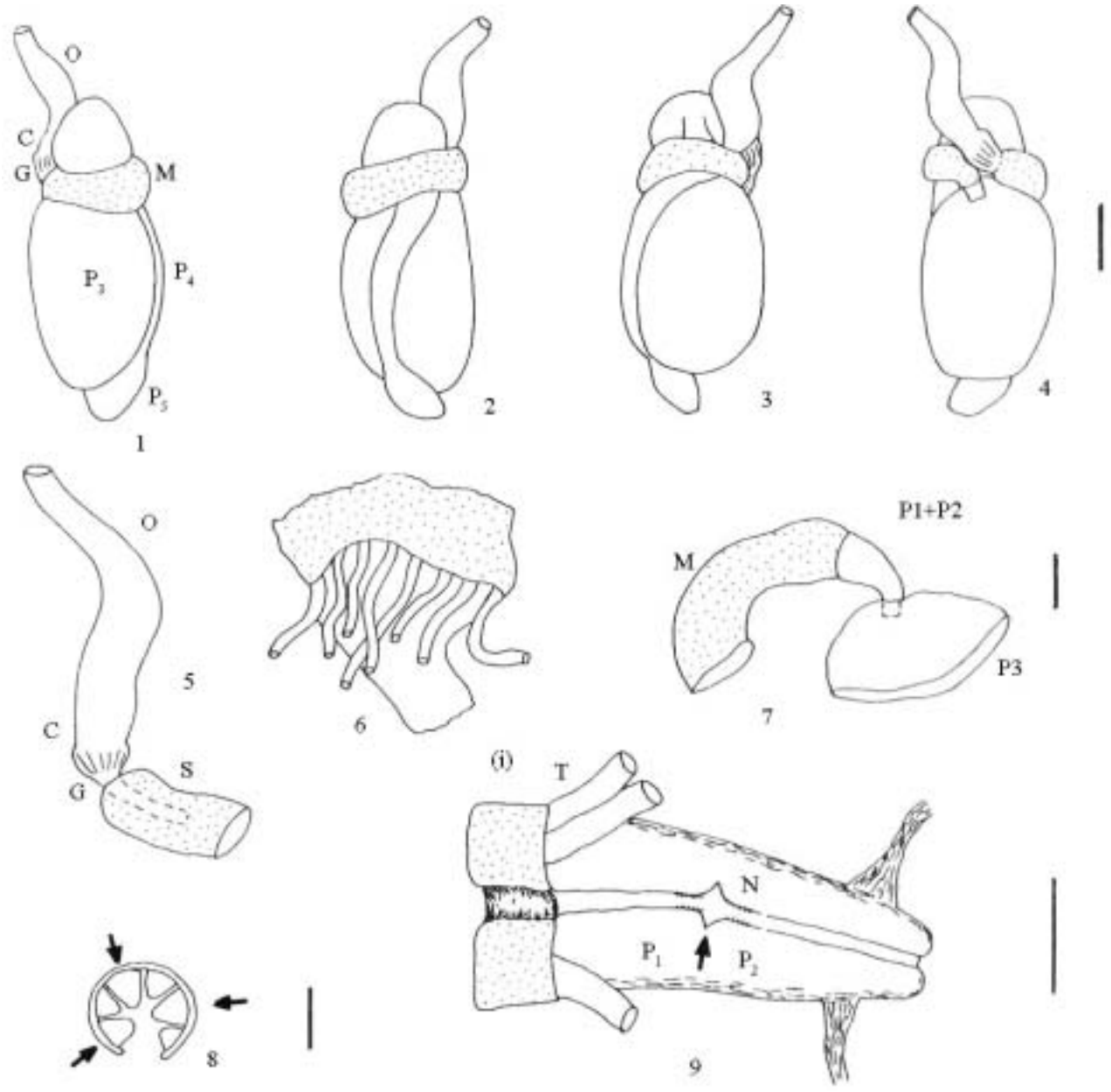
The total length of the digestive tube exceeded, in both species analyzed, the double of the total body length, and it was more than three times as long as the abdomen (mean values) (Table 1). The proctodeum was the most developed portion of the gut, being about 61% of its total length in both species (Table 1), with the third proctodeal segment or paunch (P3) voluminous and dilated, and the colon as the longest organ of the digestive system. The considered measurements (Table 1) did not differ significantly between both species (t test of mean differences, $P < 0.05$)

Coiling of the Gut (Figs.1-4)**.** The oesophagus (O) is located mediodorsally in the thorax; the crop (C) and the gizzard (G) are deflected to the left in the abdomen and situated at the level of the 2nd-3rd abdominal segments. The midgut (M) is cylindrical, describing a medium-length arch with anterior concavity, reaching the 4th abdominal segment. The mesentero-

Table 1. Body and gut measurements (mm) of pseudergates of *T. taurocephalus* (n = 30) and *Tauritermes* sp. (n = 20).

	T. taurocephalus		*Tauritermes* sp.	
	$\bar{X}$	Sd	$\bar{X}$	Sd
Total body length	4.7	0.48	4.7	0.36
Length of the abdomen	2.8	0.33	2.9	0.29
Oesophagous + Crop(O + C)[1]	1.6	0.15	1.6	0.18
Gizzard (G)	0.1	0.03	0.1	0.03
Midgut (M)	2.4	0.30	2.3	0.27
First proctodeal segment + enteric valve (P1 + P2)[1]	0.4	0.06	0.4	0.04
Paunch (P3)	2.8	0.25	2.9	0.27
Colon (P4)	2.9	0.28	3.0	0.33
Rectum (P5)	0.6	0.12	0.6	0.10
Stomodeum	1.8	0.16	1.8	0.13
Proctodeum	6.6	0.59	6.6	0.55
Total length of the digestive tube	10.9	0.64	10.8	0.71

[1]The external limit between both structures could not be differentiated.



Figures 1-9. Digestive tube of pseudergates of *Tauritermes taurocephalus*. Coiling of the gut: dorsal (1), right (2), ventral (3), left (4). Details of the stomodeal valve (5). Insertion of the Malpighian tubules (6). First proctodeal segment and enteric alve (7). First proctodeal segment showing the transverse section of the longitudinal swellings: I (arrows) and II in alternance (8). Sagittal section of the first proctodeal segment and enteric valve separated by the limiting groove (arrow) (9). O: oesophagous, C: crop, G: gizzard, S: stomodeal valve, M: midgut, P1: first proctodeal segment, P2: enteric valve, P3: paunch, P4: colon, P5: rectum, N: spines, T: Malpighian tubules. Scale - bars: (1)-(4) = 0.5 mm, (5)-(7) = 0.25 mm, (8) = 0.15 mm, (9) = 0.15 mm

proctodeal junction is situated ventro-laterally on the left side of the body. The first proctodeal segment or ileum (P1) and second proctodeal segment or enteric valve (P2), are also placed ventro-laterally to the left, at the level of the 3rd-4th abdominal segments. The P3 is voluminous, filling most of the posterior part of the abdomen, containing symbiotic flagellates. Its posterior portion lies dorsally inside the mesenteric arch, where it loops downwards to the right, joining the fourth proctodeal segment or colon (P4) with an incomplete torsion. The P4 passes underneath the mesenteron and runs dorsally over the anterior portion of P3. A notable constriction, the rectal valve, shows the limit between P4 and the fifth proctodeal segment or rectum (P5), moderately dilated.

Morphology of the Organs.

a) Foregut or Stomodeum. The oesophagous (O) broadens out into the elongated crop (C), without a precise limit. The cuticle of the crop bears pectinated scales. The gizzard (G) is

well developed (C/H index: 1/16). Its internal armature follows the common pattern for termites of 48 longitudinal folds of four different types: I, II, III and IV. The columns (anterior part) of folds I and II with concave lateral borders and prominent teeth. Those teeth are double in size in folds II than in I. Pulvilli (posterior part) of folds I are wider and longer than the columns. Pulvilli of folds II are smaller. The folds III have an ornamentation of transversal irregular striation. The measurements of the gizzard folds (Table 2) did not differ significatively between both species (t test of mean differences, $P < 0.05$). The stomodeal valve (S) is very long and without dilatation at its posterior end (Fig. 5).

b) Midgut or Mesenteron. The cylindrical midgut (M) is a tube of uniform diameter, without anterior coeca or mixed segment. The eight Malpighian tubules (T) are attached at the mesentero-proctodeal junction, surrounding the whole diameter of the gut, with a symmetrical distance among them (Fig. 6).

c) Hindgut or Proctodeum. The first proctodeal segment (P1) is short and not dilated. The structure composed by P1 + P2 (enteric valve), similar to both species, is cone-shaped, with P1 slightly shorter than P2 (Fig. 7). The limiting groove (internal circular furrow that separates both segments) is poorly marked. The internal armature of both segments is composed by six longitudinal swellings of slightly different size in alternance: I and II, extended through the whole length of P1 and P2 (Figs. 8-9). The swellings bear small spines (2-3 µm) directed backwards, more numerous in the posterior region of P1 and the anterior portion of P2. The tip of P2 is partially invaginated in P3 (Fig. 7). The paunch (P3) is voluminous, with the attachment of P2 near to its distal portion, giving to this organ a sac-like appearance. On the cuticle of P3, there are narrow and short scattered spines. The colon (P4) is a long tube, more voluminous at its proximal end, whose cuticle bears hemispherical humps. The armature of the rectal valve is absent. The rectum (P5) is a dilated ampoule, of variable volume according to its content. Internally, six rectal pads and a slightly humped cuticle can be recognized.

Discussion

The characteristics of the gut of *Tauritermes* fit in the pattern established by Noirot (1995) for Kalotermitidae, as well as the number of its Malpighian tubules, that also correspond to the tentative number suggested for the family and the value of the C/H index, situated on the upper limit recorded for the family.

It was established that in *Tauritermes*, the proctodeum constitute the longest portion of the digestive tube, as seen in three genera from other families measured in the same way: *Heterotermes* Froggatt of Rhinotermitidae and *Termes* Linné, *Nasutitermes* Dudley and *Syntermes* Holmgren of Termitidae (Godoy & Torales 1993, 1996, 1998; Martegani & Torales 1994).

According to its morphological characteristics, the genus *Tauritermes* was at first established as closer to *Incisitermes* Krishna, *Marginitermes* Krishna, *Proneotermes* Holmgren and *Allotermes* Wasmann (Krishna 1961). Araujo and Fontes (1979) support these conclusions, placing *Tauritermes* near *Allotermes*. Considering the characteristics of the pseudergates gut, the digestive tube of *Tauritermes* seems to be similar to *Glyptotermes* Froggatt, sharing some of the characters that vary from genus to genus, like the configuration of P1-P2, the incomplete torsion of P3-P4 and the absence of the armature of the rectal valve (Noirot 1995).

Some morphological differences related to the gut characteristics can be pointed out in order to distinguish *Tauritermes* from other Kalotermitidae genera. In *Glyptotermes* the P1 + P2 swellings are nearly equal, as opposed to the P2 being larger than P1 in *Tauritermes*. The mesenteron is longer in *Pterotermes* Holmgren and the circular armature of P1 + P2 is more robust than in *Tauritermes*. *Neotermes* Holmgren has a P1 + P2 of cylindrical structure, a greater length of P1 and the P3-P4 junction with a very clear torsion, compared to *Tauritermes*. In *Postelectrotermes* Krishna, a longer and more curved structure of P1 + P2 and the rectal valve armature are the most important differences between this genus and *Tauritermes*. *Kalotermes* Hagen has a shorter mesenteric arch, more prominent humps of the colon and rectal valve with armature of pectinated scales. In the case of *Cryptotermes* Banks, the most important differences with *Tauritermes* are: P1 a little longer than P2, P3-P4 junction twisted and the rectal valve with pectinated scales (Noirot 1995). The gut characteristics previously described contribute to the taxonomic identification of *Tauritermes* pseudergates from samples without soldiers or alates and, could help to elucidate the phylogenetic relationships of this genus.

Table 2. Measurements (mm) of the longitudinal folds of the gizzard in *T. taurocephalus* (n = 30) and *Tauritermes* sp. (n = 30) pseudergates.

	Folds	Columns		Pulvilli		Total length		Width	
		x	sd	x	sd	x	sd	x	sd
T. taurocephalus	I	0.6	0.03	0.8	0.02	1.5	0.12	0.2	0.02
	II	0.5	0.03	0.3	0.02	0.9	0.05	0.2	0.02
	III	-		-		0.5	0.02	0.2	0.01
Tauritermes sp.	I	0.6	0.05	0.8	0.03	1.5	0.10	0.2	0.03
	II	0.6	0.02	0.3	0.02	0.9	0.06	0.2	0.01
	III	-		-		0.5	0.03	0.2	0.02

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