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MORPHOLOGY OF THE WORKER DIGESTIVE TUBE OF THE SOIL-FEEDING NASUTE TERMITES (ISOPTERA, TERMITIDAE, NASUTITERMITINAE) FROM THE NEOTROPICAL REGION

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ABSTRACT. The morphology of the parts and the configuration in situ *of the worker digestibe tube of the 8 soilfeeding genera with nasute solidiers from the Neotropical Region are studied. All genera showed a reduced or incomplete gizzard armature, a tubular first proctodeal segment terminating in the left half of the abdomen, an enteric valve armature with trilateral symmetry and often with strong spines, a paunch of two large sections separated by a constriction, and a long colon. In addition, a mixed segment at the mesenteron-proctodeal junction is absent in* Convexitermes, Atlantitermes, Araujotermes, Coatitermes, Subulitermes *and Agnathotermes, and present in Cyranotermes and Angularitermes, the latter having also a gizzard armature stronger than usual in the soilfeeding nasutes. The coiling of the gut and the morphology of some gut parts provide a good means for the identification of undissected workers of all genera.*

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I. INTRODUCTION

The morphology of the parts and the coiling patterns of the worker digestive tube have played an important role in termite systematics and is a valuable assistant in ecological interpretations (Grassé & Noirot, 1954; Noirot & Kovoor, 1958; Kovoor, 1969; Noirot & Noirot-Timothée, 1969; Sands, 1972; Mathews, 1977; Johnson, 1979). This paper is the fourth one of a series on the taxonomy of the 8 genera of soil-feeding nasutes from the Neotropical Region (Fontes, 1979; 1982: 1985), a group which was previously known virtually only from the original descriptions of the taxa. The gut anatomy provided a large collection of characteristics, indispensable for the definition of most of these genera.

II. TERMINOLOGY

The parts of the worker digestive tube are recognized as in Noirot & Noirot-Timothée (1969 : 53, 54, 58, 60), with the nomenclature of Kovoor (1969 : 218, 224) for the enteric valve armature. Subdivisions of the paunch and colon are recognized and named separately in this paper : the anterior part of the paunch and the posterior part of the paunch, both separated by a constriction; the proximal colon and the distal colon, in most cases presenting no clear limit but being located at distinct places in the undistended gut. The parts of the digestive tube are (figs. 4-6, 66, 68, 76) : FOREGUT or STOMODEUM : oesophagus (O); crop (CP); gizzard (G), with internal cuticular armature (fig. 1; 1st, folds of first order; 2nd, folds of second order; 3rd, folds of third order; p, pulvillus); stomodeal valve (SV). MIDGUT or MESENTERON (M). Mesenteron-proctodeal junction : mixed segment (figs. 46-47); Malpighian tubules (T). HINDGUT or PROCTODEUM: first proctodeal segment (P1); second proctodeal segment or enteric valve (p2), with internal cuticular armature (fig. 61; 1st, swellings of first order; 2nd, swellings of second order); third proctodeal segment or paunch (P3), with anterior part (P3a) and posterior part (P3p); colon (C), with proximal colon (Cp) and distal colon (Cd); rectum (R).

The position of the gut parts relative to adjacent sternites or tergites, visible through the body wall of an undissected worker, is explained in figure 3 (based on Sands, 1972, fig. 6).

III. MATERIAL AND METHODS

The specimens studied in this paper are listed in Fontes (1985). Concerning the 6 genera with dimorphic worker caste (Fontes, *l.c*), only the more frequent worker type was studied; the gut, as visible through the body wall of undissected specimens, seems to be identical in both worker types.

Specimens were dissected under ethanol 80% with steel pincers whose points have been sharpened with a commercial abrasive oilstone, thus acting like small knives.

Rupture of the abdomem and dissection of the gut components followed basically the method described by Sands (1972 : 10). A small Petri dish half filled with clean white sand was used for immobilizing the undistended gut for drawing. A Petri dish with a cork plate at the bottom was used for immobilizing the major gut parts for drawing, with the aid of small entomological pins.

Black areas among the parts of the coiled gut mean absence of gut parts (see figs. 78-81).

IV. MORPHOLOGY OF THE PARTS OF THE WORKER DIGESTIVE TUBE
(Table 1)

IV.1. *Foregut or stomodeum*

The oesophagus is a narrow tube, roughly circular in transverse section, and which can be turned leftwards to join the crop, especially in Agnathotermes (fig. 100).

The crop is globose and voluminous. It is the largest in *Agnathotermes* (figs. 29, 98-101), extending through all or almost all the abdominal width, and is the less developed in *Angularitermes* (figs. 32, 102-109).

The proportion between the gizzard and the crop is the highest in *Angularitermes* (fig. 32) and the lowest in *Agnathotermes* (fig. 29). The gizzard internal armature is incomplete and very weakly sclerotised in *Agnathotermes*, having only 6 longitudinal folds of cuticle alternating with 6 less developed longitudinal folds; these two types of folds may correspond to the folds of first order and folds of second order of the complete gizzard, respectively. The other 7 genera have a more sclerotised armature, with well developed folds of first, second and third orders; the folds of fourth order were not studied, as they require histological section of the gizzard to be recognized. The gizzard armature has the highest degree of sclerotisation in *Angularitermes*. The gizzard armature is less sclerotised in *Atlantitermes*, than in *Angularitermes*, less sclerotised in *Subulitermes*, *Convexitermes*, *Araujotermes* and *Cyranotermes* than in *Atlantitermes*, and a little less sclerotised in *Coatitermes* than in the former genera. Very small spines (fig. 1) are scattered over the anterior part of the folds of first, second and third orders in *Angularitermes*, and absent in the remainder genera. The posterior pulvillus of the folds of first order extends over more than half the length of the fold in *Angularitermes* (fig. 1) and *Cyranotermes*, and over about half the length of the fold in *Atlantitermes*, *Convexitermes*, *Coatitermes*, *Araujotermes* and *Subulitermes*. The undissected gizzard of *Angularitermes* was examined in transverse view (fig.2), showing a peculiar appearence of the pulvillus of the folds of first order, with a three-lobed posterior margin. The length (in millimetres) of the folds of first order including the pulvillus, measured in one slide mounted gizzard for each genus, is 0.22 in *Angularitermes*, 0.19 in *Cyranotermes*, 0.16 in *Atlantitermes*, 0.14 in *Convexitermes*, 0.12 in *Subulitermes*, 0.11 in *Araujotermes*, 0.10 in *Coatitermes*, and 0.08 in *Agnathotermes*. These figures correspond to 1 / 17 of the abdominal length in *Angularitermes*, 1/18 in *Atlantitermes* and *Subulitermes*, 1/19 in *Convexitermes* 1/20 in *Coatitermes*, 1/21 in *Araujotermes*, 1/22 in *Cyranotermes*, and 1/25 in *Agnathotermes*.

The stomodeal valve is short and strongly dilated backwards in *Agnathotermes* (fig. 29), short and moderately dilated backwards in *Cyranotermes* (fig.36), and moderately long and not especially dilated backwards in *Araujotermes*, *Coatitermes*, *Subulitermes*, *Convexitermes*, *Atlantitermes* and *Angularitermes* (figs. 4, 9, 14, 18, 22, 32).

IV.2. *Midgut or mesenteron*

The mesenteron is an arched tube of uniform diameter without ceca and with the four Malpighian tubules attached at or near its distal end.

IV.3. *Mesenteron-proctodeal junction*

The mesenteron-proctodeal junction is about circular in *Convexitermes* (figs. 18, 79, 83). In *Araujotermes*, *Coatitermes*, *Subulitermes*, *Atlantitermes* and

TABLE 1 – Main characteristics of the worker digestive tube of the soil-feeding genera with nasute soldiers from the Neotropical Region

	Coiled gut	Gizzard armature	Mesenteron-proctodeal junction	Distance between the pairs of Malpighian tubules	Insertion of Malpighian tubules	First proctodeal segment
Convexitermes			circular			
Atlantitermes						
Araujotermes		complete and weakly sclerotised			mesenteric dilation at level of mesenteron--proctodeal junction	
Coatitermes	narrow and long		oblique	short		
Subulitermes						tubular
Agnathotermes		incomplete and weakly sclerotised			mesenteron-proctodeal junction	
				large		
Angularitermes	wide and short	complete and well sclerotised			mesenteron	
			mixed segment			
Cyranotermes	narrow and long	complete and weakly sclerotised		short	mesenteron-proctodeal junction	

TABLE 1 (continuing) – Main characteristics of the worker digestive tube of the soil-feeding genera with nasute soldiers from the Neotropical Region

	Spines of enteric valve armature	Shape of anterior pari of paunch	Paunch at the level of insertion of enteric valve		Posterior part of paunch	Colon
			constriction	lobes		
Convexitermes	small		absent			
				absent		
Atlantitermes	small and large		weak			
		"J"		.....	smaller than anterior part of paunch	
Araujotermes	small		absent	two		
				.....		long and narrow
Coatitermes	small and large		weak			
		.....				
Subulitermes	small	"J" (less pronounced)	absent			
		.....				
Agnathotermes	large	"J"	strong	absent		
.....	.....	.....			.....	.....
Angularitermes		"J" (less pronounced)	weak		larger than anterior part of paunch	short, proximal 2/3 dilated
	small and large	.....			.....	.....
Cyranotermes		"J"	strong		smaller than anterior part of paunch	long, dilated in the middle

Agnathotermes the outer face of the mesenteric arch prolongues a little over the first proctodeal segment, so that the mesenteron-proctodeal junction is weakly oblique (figs. 4, 9, 14, 22, 29, 87).

Angularitermes and *Cyranotermes* have each a distinct pattern of a short (about 1/10 of the mesenteron length) mixed segment whose major component is represented by mesenteric tissue. In *Angularitermes* (figs. 32, 46) the band of proctodeal tissue broadens progressively towards the proctodeum, while in *Cyranotermes* (figs. 36, 47) the proctodeal tissue is a narrow strip with parallel sides which suddenly diverges towards the proctodeal tube.

IV.4 *Malpighian tubules*

The four Malpighian tubules are attached in two pairs at the inner face of the mesenteric arch, near or at the mesenteron-proctodeal junction (figs. 40-47). The tubules form a cluster opposite to the attaching face. In *Angularitermes* this cluster includes the distal third of the mesenteric arch and also the sides of the attachment region, and in the rema inder genera it includes only the proximal part of the first proctodeal segment.

Three patterns of attachment are recognized, acoording to the distance between the pairs of tubules:

1. Pairs attaching distant from the symmetry plane *(Angularitermes* and *Agnathotermes)*

In Agularitermes (fig. 46) the tubules of each pair are attached to the mesenteron a short distance one from the other, a little distant from the mesenteron-proctodeal junction. The tubules are dilated along their proximal course over the mesenteric portion of the mixed segment. The mesenteron-proctodeal junction is weakly concave between the two pairs of tubules and the mesenteron has no swelling at the attaching points.

In *Agnathotermes* (fig. 45) the tubules of each pair are attached to the mesenteron very close to each other, at the level of the mesenteron-proctodeal junction. The tubules are not dilated at their proximal part. The mesenteron-proctodeal junction is very weakly concave between the pairs of tubules and the mesenteron has no swelling at the attaching points.

2. Pairs attaching close to the symmetry plane *(Cyranotermes, Atlantitermes, Coatitermes, Araujotermes* and *Subulitermes)*

The tubules of each pair are attached very close to each other.

In *Cyranotermes* (fig. 47) the tubules are attached to the mesenteron at the level of the mesenteron-proctodeal junction of the proximal end of the mixed segment.Each tubule is dilated into a small ampul at its proximal part and very narrow at the point of insertion. The mesenteron has nos swelling the attaching points.

In *Coatitermes, Atlantitermes, Araujotermes* and *Subulitermes* (figs. 40-43) the tubules are attached at the sides of a small convex mesenteric swelling, very close to the mesenteron-proctodeal junction. The tubules are dilated into a small ampul at their proximal part (less markedly in *Araujotermes)* and narrow at the point of insertion. The mesenteric swelling is more pronounced and extends backwards to the proctodeum in *Coatitermes* and *Atlantitermes* (figs. 40-41), while it is less pronounced and does not extend backwards in *Araujotermes* and *Subulitermes* (figs. 42-43)

3. Pairs attaching adjacent to the symmetry plane *(Convexitermes)*

In *Convexitermes* (fig. 44) the tubules of each pair are fused at their proximal region into a voluminous ampul broadly attached to a weakly developed mesenteric swelling at the level of the mesenteron-proctodeal junction.

IV.5. *Hindgut or proctodeum*

The first proctodeal segment is tubular and moderately long (a little shorter to a little longer than the mesenteric arch) in all genera studies. It is a little broadened near the mesenteric junction.

The enteric valve is a short muscular segment partially invaginated into the paunch, with a variable development of an internal cuticular armature near or at the level of invagination. The valve is cylinder-shaped, with about constant width throughout its whole length, in *Atlantitermes, Cyranotermes,* and *Subulitermes* (figs. 48-50), and is conical in the remainder genera (figs. 51-56). The valve invaginated the most deeply into the paunch in *Subulitermes* (fig.50), most of the inner armature being also invaginated. In the remainder genera the armature is not invaginated; the valve is deeply invaginated in *Convexitermes* (fig.51), a little less invaginated in *Angularitermes* (fig.52), and weakly invaginated in *Atlantitermes, Cyranotermes, Agnathotermes, Coatitermes* and *Araujotermes* (figs. 48, 49, 53-56).

The enteric valve armature of the studied genera consists of three longitudinal major swellings (swellings of first order) alternating with three longitudinal minor swellings (swellings of second order), both types being gradually more developed towards their apex, where they partially obstruct the intestinal lumen. The swellings are provided with a variety of spines and sclerotisations. Three types of enteric valve armature can be defined, according to the development of the spines (the degree of sclerotisation has been tentatively shown in the figures) :

1. Enteric valve armature with small spines *(Convexitermes, Araujotermes* and *Subulitermes)*

The enteric valve armature seems to be unsclerotised and has scattered small spines which are similarly developed in both first and second order swellings. The spines occur in higher number and larger extension in *Convexitermes* (fig.57), and are restricted to a few distally placed unities in *Subulitermes* (fig. 59). In *Araujotermes* (fig. 58), the number and distribution of the spines is intermediate between *Convexitermes* and *Subulitermes.*

2. Enteric valve armature with small and large spines *(Coatitermes, Atlantitermes, Angularitermes* and *Cyranotermes)*

The distal spines are large, sclerotised and closely placed. They are stronger and more numerous in the swellings of first order. The number and disposition of the distal spines are different in the various genera, being evident a tendency towards linear arrangement as the spines become more numerous. In *Coatitermes* (fig. 60) there are 8-10 distal spines in the swellings of first order and 5-7 distal spines in the swellings of second order; the spines are less developed than in the other genera and are randomly distributed. In *Atlantitermes* (fig. 61) there are 9-12 distal spines in the swellings of first order and 5-6 distal spines in the swellings of second order; the spines of the swellings of first order are a little larger and are arranged in an approximately straight row. In *Angularitermes* (fig.62) there are 6-9 distal spines in the swellings of firts order and 3-5 distal spines in the swellings of second order; the spines of the swellings of first order arelarger and are arranged in a straight row, and the spines of the swellings of second order seem also to be arranged in a row. *Cyranotermes* (fig 63) has about 30 distal spines in the swellings of first order and up to 20 distal spines in the swellings of second order; they are formidably arranged in a bowed line, and the middle spines are larger than the lateral ones.

The proximal spines are small, scattered, and similarly developed in the swellings of first and second orders (although less numerous in the latter). *Coatitermes* (fig. 60) has the lowest number, and *Cyranotermes* (fig. 63) the highest

number, of proximal spines; in *Cyranotermes* the proximal spines are also larger and more densely placed than in the other genera.

3. Enteric valve armature with large spines *(Agnathotermes)*

In Agnathotermes (figs. 64-65) the spines are large, numerous, closely placed and sclerotised. The are more numerous in the swellings of first order. The distal spines are a little longer than the proximal ones. A few small spines can exist mainly is the swellings of second order.

The paunch is composed of two parts : a dilated and mo e or less J-shaped anterior part, and a more tubular posterior part separated from the anterior part by a constriction.

The anterior part of the paunch is less voluminous than the posterior part in *Angularitermes* (fig. 33), a little more voluminous than the posterior part in *Cyranotermes* (fig. 37-38), and considerably more voluminous than the posterior part in the remainder genera. The J-shape is less marked in *Angularitermes* (figs. 33, 35) and *Subulitermes* (fig. 15), and evident in the remainder genera (figs. 5, 10, 19, 23, 30. 37). The region of attachment of the enteric valve is separated by a marked ringed constriction in *Agnathotermes* and *Cyranotermes* (figs. 30-31, 37), by a shallow and incomplete constriction in *Coatitermes, Atlantitermes* and *Angularitermes* (figs. 10,23, 33, 35), and is not separated by constriction in *Araujotermes, Subulitermes* and *Convexitermes* (fig. 5,15, 19). The region of attachment of the enteric valve is distinctly bilobed in *Araujotermes* (fig.5), and not lobed in the remainder genera. In *Atlantitermes,* the anterior part of the paunch has a typical transversal fold in the middle, alloowing considerable volumetric expansion (figs. 23, 25-28, 92, 96); this fold, however, has been found only in *A. guarinim,* being apparently absent in the other species of the genus.

The posterior part of the paunch is very voluminous in *Angularitermes* (figs. 33-34) and *Cyranotermes* (fig. 38), and proportionally less voluminous in the remainder genera. It is more tubular and proportionally more elongated in *Coatitermes* (figs. 10-13,74). The posterior part of the paunch narrows progressively and drains into the colon. The limit between the paunch and the colon is well defined in *Angularitermes* (figs. 33, 102), less defined in *Agnathotermes* (figs. 30,98), *Atlantitermes* (figs. 24, 90), *Cyranotermes* (figs. 38, 110), *Coatitermes* (figs. 11, 74) and *Subulitermes* (figs. 15, 86), and virtually imperceptible in *Convexitermes* (figs. 20, 78) and *Araujotermes* figs. 6, 66).

The colon is a narrow and long tube in *Araujotermes, Coatitermes, Subulitermes, Convexitermes, Atlantitermes* and *Agnathotermes* (figs. 6, 11, 15, 20, 24, 30), a long tube with a dilation in the middle of its course in *Cyranotermes* (fig. 38), and a shorter tube, which is more voluminous in its proximal 2/3, in *Angularitermes* (fig. 33). The part preceding the rectum is narrow.

The rectum is a dilated ampul, somewhat elongated in most cases. It is capable of strong dilation, so that its volume and shape vary greatly according to the amount of faeces there contained.

V. COILING OF THE WORKER DIGESTIVE TUBE

The prothorax and mesothorax delimit a narrow and straight tubular chamber traversed by the oesophagus. The metathoracic cavity increases markedly backwards, both in height (the metanotum is vertical or almost vertical) and in width, thus being the foremost part of the large, mostly abdominal chamber that acommodates the coiled intestine. The coiled gut forms a broad and short mass in *Angularitermes* (figs. 102-109), and a narrower and longer mass in the other genera (figs. 66-101, 110-113).

The oesophagus joins the crop near the sagital plane or in the left half of the body, at the level of the last thoracic and first abdominal segments. The crop, except in *Angularitermes,* is voluminous and occupies the middle of the segments, being visible in all views (figs. 66-101, 110-113; in the dorsal view the crop is partially hidden by the posterior part of the paunch); it is the foremost part of the digestive tube following the oesophagus. In *Angularitermes* (figs. 102-109) the crop is completely dislocated to the left half of the body, being comparatively smaller than in the other genera and not visible in dorsal and right views. The gizzard follows the crop in the left side of the abdomen.

The mesenteron leads from the gizzard at first backwards on the left side in a loop round the posterior part of the paunch, describing an arch with anterior concavity, and then passes forwards and downwards on the right side to join the first proctodeal segment. The mesenteron-proctodeal junction is placed ventro-lateraly in *Angularitermes* (figs. 103-104) and laterally in the remainder genera.

The proctodeum is voluminous, filling most of the abdomen. The first proctodeal segment leads from the mesenteron and, except in *Angularitermes,* extends firstly forwards and downwards, then continuing obliquely backwards in the ventral face towards the left half of the abdomen, not passing to the dorsum. In *Angularitermes* (figs. 102-109), the first proctodeal segment extends directly backwards in the ventral face towards the left half of the abdomen, then turning dorsally to end in the dorsum. The enteric valve is located at the left half of the abdomen, positioned ventrally to ventro-laterally in *Convexitermes, Cyranotermes, Coatitermes* and *Subulitermes,* ventro-laterally to laterally in *Araujotermes* and *Atlantitermes,* laterally to dorso-laterally in *Agnathotermes,* and dorsally in *Angularitermes.* It is placed between the fourth and fifth abdominal segments in *Convexitermes,* in the fifth abdominal segment in *Cyranotermes,* between the fifth and sixth abdominal segments in *Coatitermes,* in the sixth abdominal segment in *Agnathotermes, Atlantitermes, Araujotermes* and *Subulitermes,* and in the seventh abdominal segment in *Angularitermes;* the position of the valve along the longitudinal body axis roughly corresponds to the length of the first proctodeal segment. The enteric valve is oriented roughly downwards in *Angularitermes* (fig.109), and roughly backwards in the remainder genera. The paunch is the most voluminous part of the digestive tube. The anterior part of the paunch forms the central long axis of the gut. It is well visible in ventral view, while in dorsal view, it is visible behind the mesenteric arch and is partially hidden by the colon; in *Angularitermes* the anterior part of the paunch can be completely obscured in dorsal view, according to the filling of the various parts of the intestine (fig. 102). The posterior part of the paunch lies dorsally inside the mesenteric concavity and is well developed in all genera. The posterior part of the paunch passes firstly to the right, then looping to the left side of the abdomen, describing an arch whose concavity roughly faces backwards. In ventral view, the posterior part of the paunch is well visible in *Angularitermes* (figs. 104,108), is completely obscured by the voluminous crop in *Agnathotermes* (fig. 100), and is visible, although less than in *Angularitermes,* in the remainder genera. The proximal colon lies inside the mesenteric arch, between the mesenteron and the posterior part of the paunch. The proximal colon, always bordering the inner face of the mesenteric arch, extends to the right and, at the right half of the abdomen, bends downwards and loops beneath the mesenteron, from where it continues as the distal colon. The distal colon runs over the anterior part of the paunch and passes to the rectum. The distal colon emerges from beneath the mesenteron, behind the mesenteron-proctodeal junction in *Araujotermes* and *Subulitermes* (figs. 67, 71, 87) and about at the level of the mesenteron-proctodeal junction in the remainder genera (see right views). In ventral view, the distal colon is completely visible in *Angularitermes* (figs. 104, 108), is medially obscured by the anterior part of the paunch in *Coatitermes,*

Atlantitermes, Agnathotermes and *Cyranotermes* (figs. 76, 92, 96, 100, 112), and is almost completely obscured in *Convexitermes* and *Subulitermes* (figs. 80, 84, 88); in *Araujotermes,* the commonly dilated anterior part of the paunch allows visualization of the distal colon only posteriorly, joining the rectum (fig. 68). In *Cyranotermes,* the dilated part of the colon is visible in right and ventral views (figs. 111-112), emerging between the mesenteron-proctodeal junction and the paunch. The rectum lies posteriorly, behind the paunch.

VI. VARIATIONS IN THE VOLUME, SHAPE AND COILING OF THE PARTS OF THE WORKER DIGESTIVE TUBE

The examination of several workers of each studied species of soil-feeding termites showed variation in the volume and shape of some gut parts, sometimes modifying a little the aspect of the coiled gut. The most interesting specimens, of the genera *Convexiterme, Araujotermes, Atlantitermes* and *Angularitermes,* were figured, as similar variations were not previously reported in the literature.

In *Cyranotermes* the crop and the colon dilation are often larger than in figures 110-113. The crop of *Coatitermes* and *Subulitermes* (figs.76, 88) is commonly as large as the crop of *Convexitermes* (fig. 80). In *Subulitermes,* the posterior part of the pauch can be less voluminous than in figure 86. In *Convexitermes* (figs. 82-25), a less replete first proctodeal segment looks differently than usual (fig 80), and the more voluminous crop dislocated to the left the posterior part of the paunch. In *Araujotermes* (figs. 70-73) the crop is shaped differently than usual (figs. 66-69), and the less voluminous anterior part of the paunch allows the visualization of most of the distal colon in ventral view. In *Atlantitermes* (figs. 94-97) the crop and the first proctodeal segment are shaped differently than usual (figs. 90-93), the voluminous colon is more visible in ventral and side views, and the voluminous posterior part of the paunch is placed more dorsally and hiddens most of the mesenteron. The transverse fold of the anterior part of the paunch of *A. guarinim* varies according to the repletion of the paunch (figs. 92, 96). In *Angularitermes* (figs. 106-109) the full crop is much more voluminous at rear, narrowing abruptly towards the gizzard, the slender mesenteron is more obscured by the first proctodeal segment and the posterior part of the paunch, and the enteric valve is more visible in dorsal and left side views.

VII. DISCUSSION

The worker digestive tube, visible through the body wall of undissected workers, of the following species was examined for consistency with the descriptions given for the species studied in this paper . *Angularitermes nasutissimus, Atlantitermes ibitiriguara, A. raripilus, A. oculatissimus, A. sp. n* (colony number 8074 of the Museu de Zoologia da Universidade de São Paulo), *Convexitermes manni, C. nigricornis junceus, Araujotermes parvellus, Coatitermes kartaboensis, Subulitermes baileyi* and *S. sp. n.* (colony number 7602 of the Museu de Zoologia). The major differences were, in *Atlantitermes,* the absence of a transversal fold in the anterior part of the paunch, as seen in *A. guarinim* (figs. 92,96), and, in *Subulitermes,* the colon of *S. sp. n.*, which emerges from beneath the mesenteron at the level of the mesenteron-proctodeal junction, and not so posteriorly as in *S. microsoma* (fig. 87).

VII.1 *Morphology of the parts of the worker digestive tube*

The morphology of the worker gut components of the Nasutitermitinae was

studied by Kovoor (1969); this work included all six genera of soil-feeding nasutes from the Ethiopian Region. Mathews (1977) described some gut components of several Neotropical genera, including the enteric valve armature of *Angularitermes* (p. 234-235, fig. 54) and *Cyranotermes* (p. 239, fig. 35); he erroneously reported the absence of a mixed segment in *Cyranotermes*. Johnson (1979) figured the coiled gut of the Ethiopian genera *Eutermellus* and *Mimeutermes*.

Kovoor (1969) separated the genera of Nasutitermitinae into 3 groups, according to the characteristics of the gizzard, mesenteron-proctodeal junction, first proctodeal segment and enteric valve. The soil-feeding nasutes compose her *Postsubulitermes*-group, including the Ethiopian genera *Mimeutermes, Eutermellus, Tarditermes, Afrosubulitermes, Postsubulitermes* and *Verrucositermes*, all having in common a weak or incomplete gizzard armature, absence of mixed segment, tubular and short first proctodeal segment, and enteric valve usually very well armed, showing trilateral symmetry on which bilateral symmetry may sometimes be superposed. According to Kovoor's descriptions, other characteristics of the *Postsubulitermes*-group are: crop voluminous; mesenteron-proctodeal junction usually circular (weakly oblique only in *Postsubulitermes);* Malpighian tubules dilated into a small ampul, or not dilated, near their point of insertion, and forming a cluster at the level of the mesenteron-proctodeal junction and over the proximal region of the first proctodeal segment; paunch composed of a voluminous anterior part and a tubular, voluminous and arched posterior part (in *Tarditermes, Postsubulitermes* and *Mimeutermes,* the posterior part of the paunch is much longer and more coiled, obscuring most of the mesenteron); colon long and tubular, voluminous in *Mimeutermes* and narrow in the remainder genera.

The Neotropical genera *Agnathotermes, Atlantitermes, Araujotermes, Convexitermes, Coatitermes* and *Subulitermes* all have the same general characteristics of the *Postsubulitermes*-group of Kovoor, although the first proctodeal segment is never as short as, and the posterior part of the paunch never as long and coiled as in *Mimeutermes, Postsubulitermes* and *Tarditermes* (Kovoor, 1969: 218, 222, 225, figs. 18-21; Johnson, 1979, figs. 5-6). Indeed, these differences are strong enough to raise the question whether the *Postsubulitermes*–group of Kovoor does not includes two phylogenetically distinct groups of Ethiopian genera, with different patterns of worker digestive tube and worker mandibles. The Neotropical genera *Cyranotermes* and *Angularitermes,* although having most of the general characteristics of the *Postsubulitermes*-group of Kovoor, have a mixed segment very peculiar to each genus.

Considering the characteristics of the worker gut of both the Neotropical and Ethiopian genera of soil-feeding nasutes, four general patterns of gut can be recognized :

1. *Convexitermes, Atlantitermes, Araujotermes, Coatitermes, Subulitermes* and *Agnathotermes,* from the Neotropical Region, and *Eutermellus, Afrosubulitermes* and *Verrucositermes,* from the Ethiopian Region, all have in common the following set of characteristics: weak or incomplete gizzard armature; absence of mixed segment; Malpighian tubules attached to the mesenteron, at the level of the mesenteron-proctodeal junction inside the mesenteric arch, and being dilated into a small ampul, or not dilated, near the insertion point; mesenteron with or without a small lump for the insertion of the Malpighian tubules; first proctodeal segment tubular, a little shorter or a little longer than the mesenteron; enteric valve well armed, with sclerotisations and developed spines , or weakly armed, and with bilateral (only *Eutermellus)* or trilateral symmetry; paunch with a large and more or less J-shaped anterior part, separated from a smaller and tubular posterior part by a constriction inside the mesenteric arch; colon long and tubular. The workers of the genera grouped under this pattern of digestive tube have mandibles with complete

marginal dentition and no reduced teeth (Fontes, 1985), what suggests a close phylogenetic relationship of these genera.

2. *Postsubulitermes, Mimeutermes* and *Tarditermes,* from the Ethiopian Region, are distinguished from pattern 1 by the following set of characteristics; first proctodeal segment very short, much shorter than the mesenteron; enteric valve armature well armed, with bilateral (only *Postsubulitermes)* or trilateral symmetry; posterior part of the paunch tubular, very long and coiled, turning back on itself several times before passing to the colon. The workers of the three genera grouped here have mandibles with incomplete marginal dentition (Fontes, 1985), like the Neotropical genus *Cyranotermes,* with a different gut pattern (gut pattern 4).

3. *Angulariterms,* fron the Neotropical Region, is distinguished from pattern 1 by the following set of characteristics: well armed, stronger sclerotised gizzard; mixed segment present, typical (fig. 46); Malpighian tubules dilated along their promixal course over the mesenteric part of the mixed segment and attached to the mesenteron, a short distance from the mesenteron-proctodeal junction of the promixal end of the mixed segment; enteric valve well armed and with trilateral symmetry; posterior part of the paunch more voluminous than the anterior part; colon long, dilated te the proximal 2/3. *Angularitermes* workers have mandibles with complete marginal dentition and two vestigial teeth (Fontes, 1985). This genus is exceptional among the 14 genera of soil-feeding nasutes from both the Neotropical and Ethiopian Regions by its distinctive patterns of worker gut and worker mandibles.

4. *Cyranotermes,* from the Neotropical Region, is distinguished from pattern 1 by the following set of characteristics : mixed segment present, typical (fig. 47); enteric valve well armed and with trilateral symmetry; colon long, tubular, and with a dilation in the middle of its course. *Cyranotermes* workers have mandibles with incomplete marginal dentition (Fontes, 1985), like the Ethiopian genera *Postsubulitermes, Mimeutermes* and *Tarditermes* (gut pattern 2). The digestive tube of *Cyranotermes,* however, is of a different pattern, so that despite the occasionally similar mandibles *Cyranotermes* is quite distinct from the other 13 genera of soil-feeding nasutes from the Neotropical and Ethiopian Regions.

The four patterns above, although apparently phylogenetically closely related, clearly represent different evolutionary tendencies in the branch of the soil-feeding Nasutitermitinae. Among the characteristics common to all three groups, the one that represents the most remarkable adaptation to the soil-feeding habit is the great development of the proctodeum, which occurs also in the soil-feeding genera with mandibulate soldiers of the Nasutitermitinae. In these genera, however, the proctodeal hypertrophy is due mainly to the development of the first proctodeal segment, which is dilated and can be more voluminous than the paunch; conversely, in the soil-feeding nasutes the first proctodeal segment is always tubular, the paunch being the most voluminous intestinal segment. A development of the proctodeum similar to that of the soil-feeding nasutes of gut pattern 1 is showed by *Caetetermes* (Fontes, 1981, figs. 13, 16-19), a nasute which feed on rotten wood; this convergence is probably due to the habit of feeding on similarly soft materials.

VII.2 *Coiling of the worker digestive tube*

The coiling pattern is determined by the length and shape of the various parts of the gut and in most cases is easily recognized through the body wall of undissected workers. The importance of the gut configuration for termite taxonomy was emphasized by Sands (1972), in his study of the African soldierless Apicotermitinae. Johnson (1979) showed the importance of this character for the recognition of some Termitidae genera, including in his study the Ethiopian soil-feeding genera *Eutermellus* and *Mimeutermes.*

The coiling pattern of the gut of the Neotropical soil-feeding nasutes, except for *Angularitermes*, is strictly similar to that of *Eutermellus* (Johnson, 1979: 34, figs. 7-8): coiled gut forming a narrow and long mass, more than twice as long as broad; crop and gizzard partially obscured by the posterior part of the paunch in dorsal view; mesenteron-proctodeal junction in the right body half; first proctodeal segment with its proximal part extending forwards, then turning at the anterior part of the abdomen and extending obliquely backwards; enteric valve at the left body half and roughly parallel to the long body axis; proximal colon long. The coiling of the gut of *Afrosubulitermes* and *Verrucositermes*, from the Ethiopian Region, should prove to be similar. The pattern presented by *Angularitermes*, as a rule is also similar, differing as follows: coiled gut forming a broad and short mass, less than twice as long as broad; crop and gizzard completely hidden by the posterior part of the paunch, in dorsal view; first proctodeal segment extending directly backwards from its beginning; enteric valve roughly oriented downward.

A varying pattern, with no similar among the Neotropical and Ethiopian soil-feeding nasutes, is presented by the Ethiopian soil-feeding genus *Mimeutermes* (Johnson, 1979: 34, figs. 5-6) and most probably also by *Postsubulitermes* and *Tarditermes*. These three genera have a very short first proctodeal segment which extends directly backwards from about the middle of the ventral view of the abdomen, and a very long tubular posterior part of the paunch, which is coiled on the dorsum and obscures most of the gut in dorsal view.

The gut of the Neotropical genus *Caetetermes* (Fontes, 1981: 137, figs. 16-19), which feed on rotten wood, is coiled in the same general pattern prensented by *Eutermellus* and most of the Neotropical soil-feeding nasutes.

VII.3. *Variations in the volume, shape and coiling of the parts of the worker digestive tube*

The variations described depend basically upon the amount of food taken by the workers in the couse of their normal feeding activities, and the degree of contraction or relaxion of the muscular wall of the gut parts by occasion of their fixation in alcohol. The rectum is especially variable in volume and shape and these seem to be related to the fact that the soil-feeding workers usually defecate whe handled and immersed in alcohol. It is important to note that none of the observed variations modifies the diagnostic value of the characteristics described in the preceding sections; a study of workers with different repletions of the mesenteron and first proctodeal segment revealed no modification in the pattern of insertion of the Malpighian tubules, in *Araujotermes* and *Atlantitermes*.

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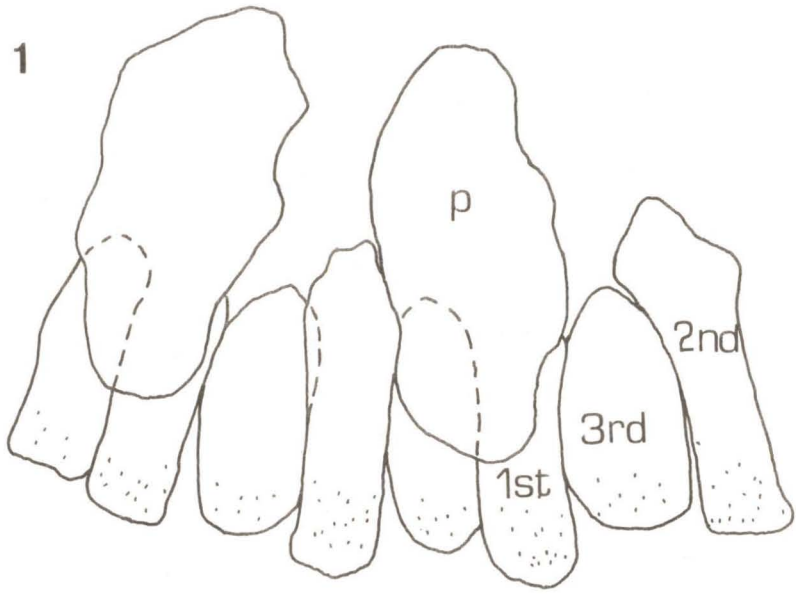
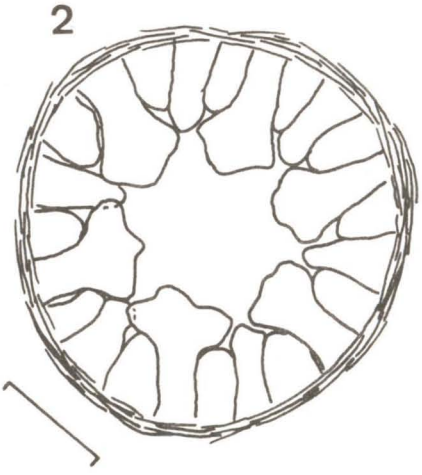
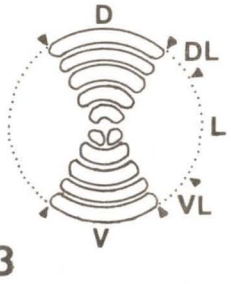
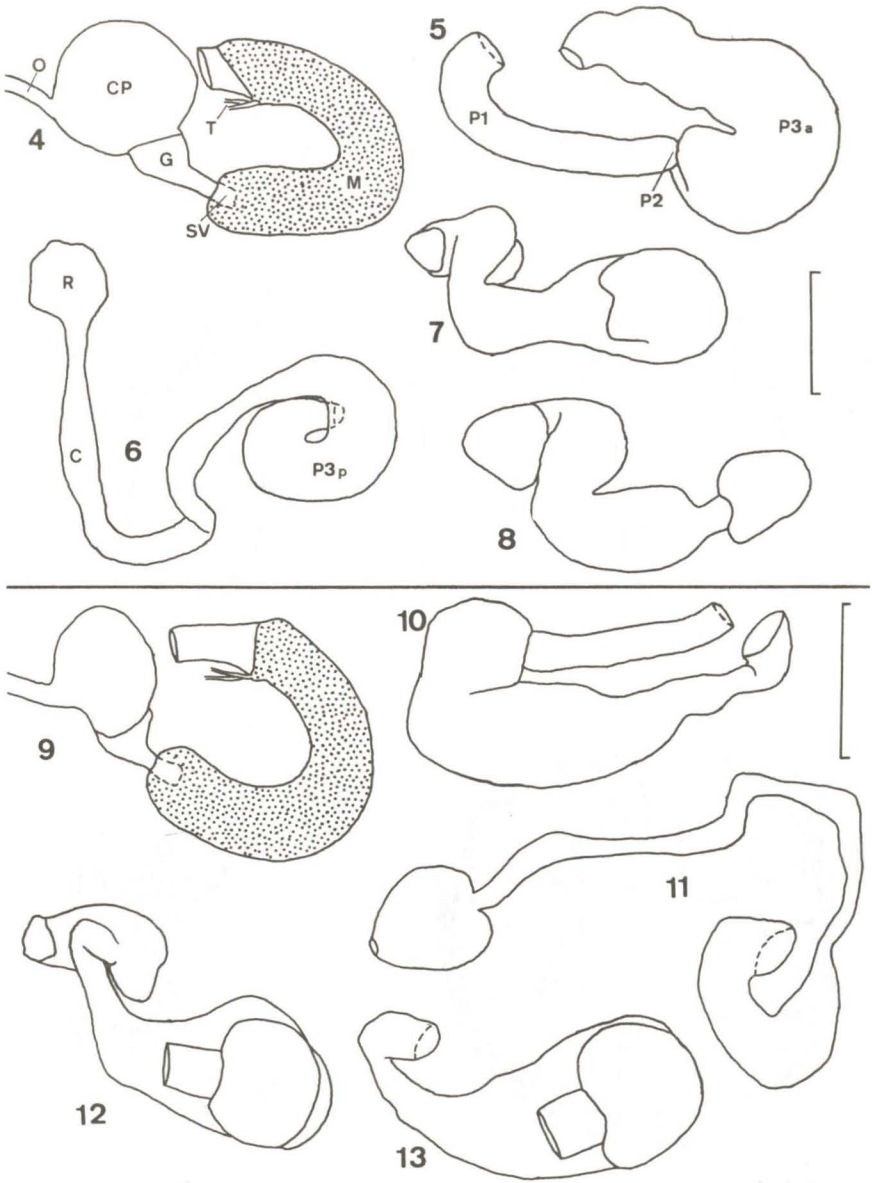


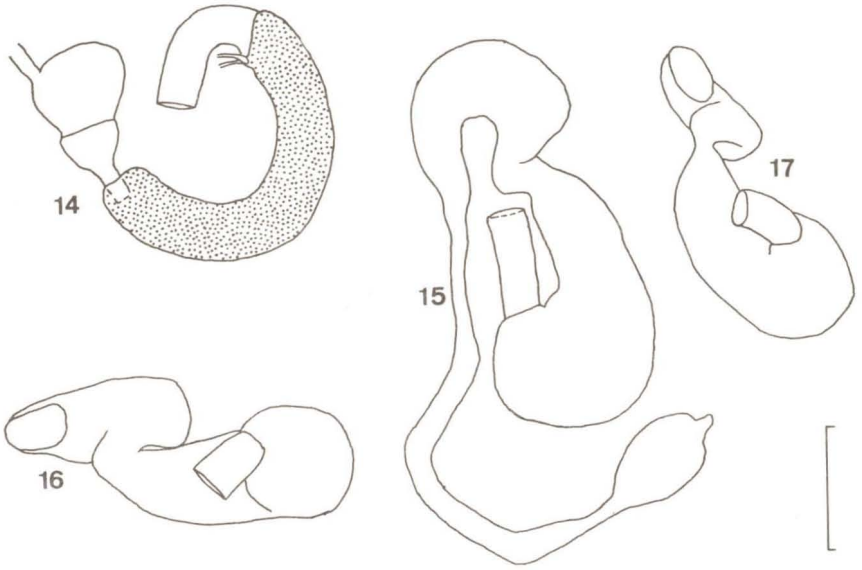


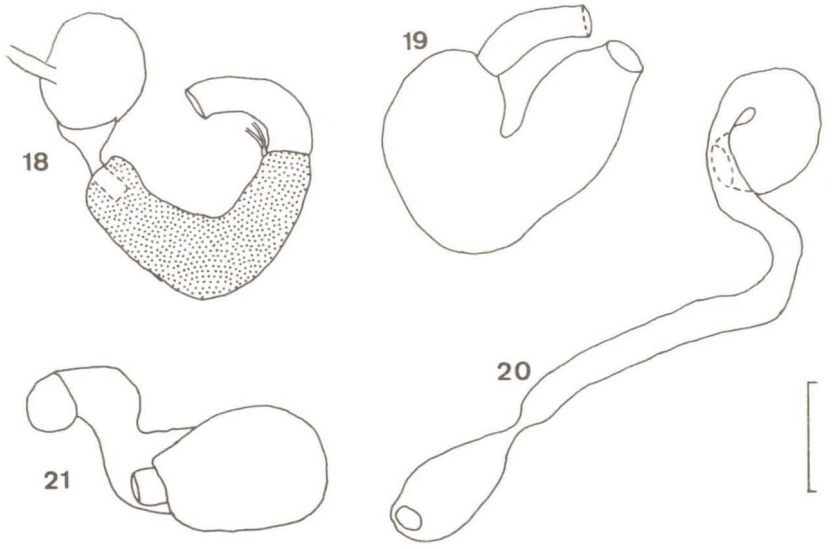


Gizzard of *Angularitermes orestes* : 1, internal cuticular armature (part) of slidemounted gizzard; 2, transverse view of unmounted gizzard. Position of the gut parts relative to adjacent sternites and tergites (based on Sands, 1972, fig. 6): 3. 1st, 2nd, 3rd, folds of firts, second and third orders, respectively; p. pulvillus; D, dorsal; DL, dorso-lateral; L, lateral; VL, ventro-lateral; V, ventral Scales 0.10 mm.

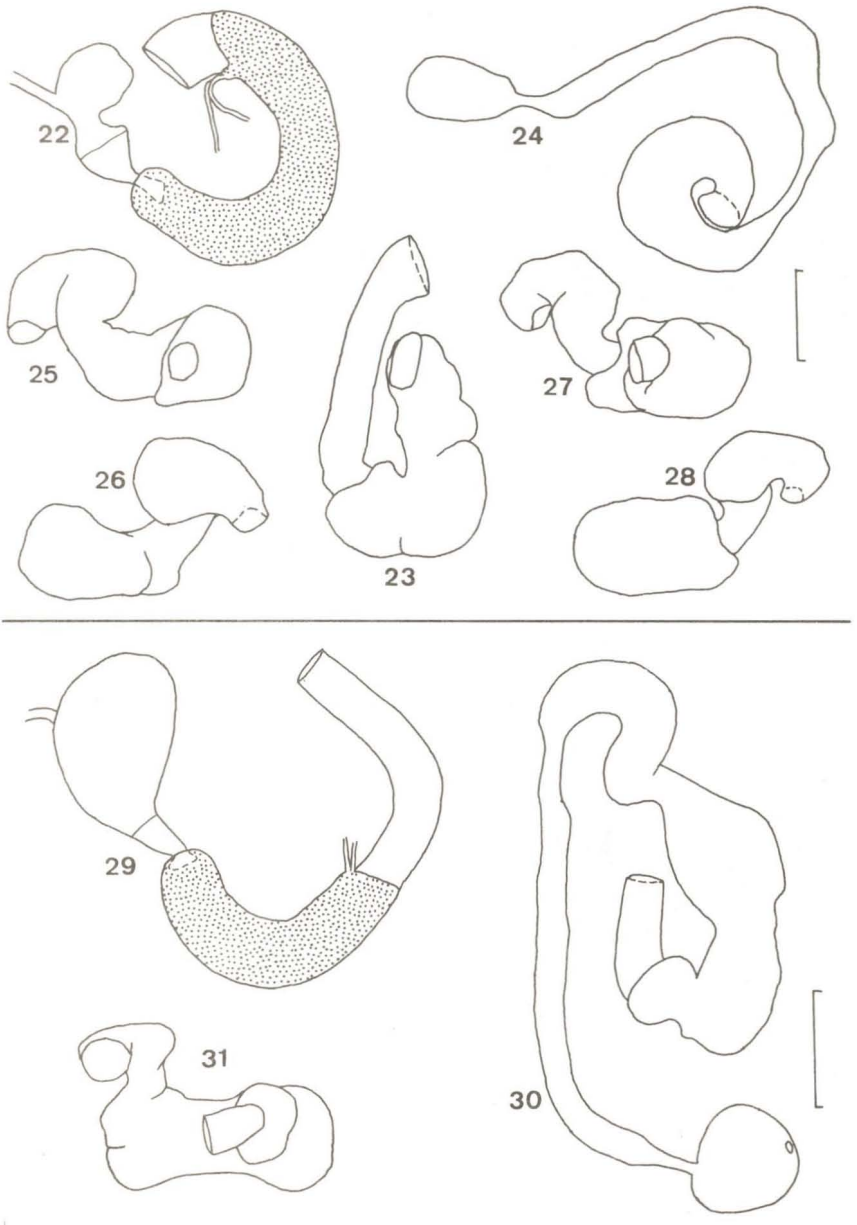


Parts of worker digestive tube. *Araujotermes caissara* : 4-6, dorsal view; 7-8, lateral view of paunch. *Coatitermes clevelandi* : 9-11, dorsal view; 12-13, lateral view of paunch. Cd, distal colon; Cp, proximal colon; CP, crop; G, gizzard; M, mesenteron; O, oesophagus; P1, first proctodeal segment; P2, enteric valve; P3a, anterior part of paunch; P3p, posterior of paunch; R, rectum; SV, stomodeal valve; T, Malpighian tubules. Scales 0.50 mm.

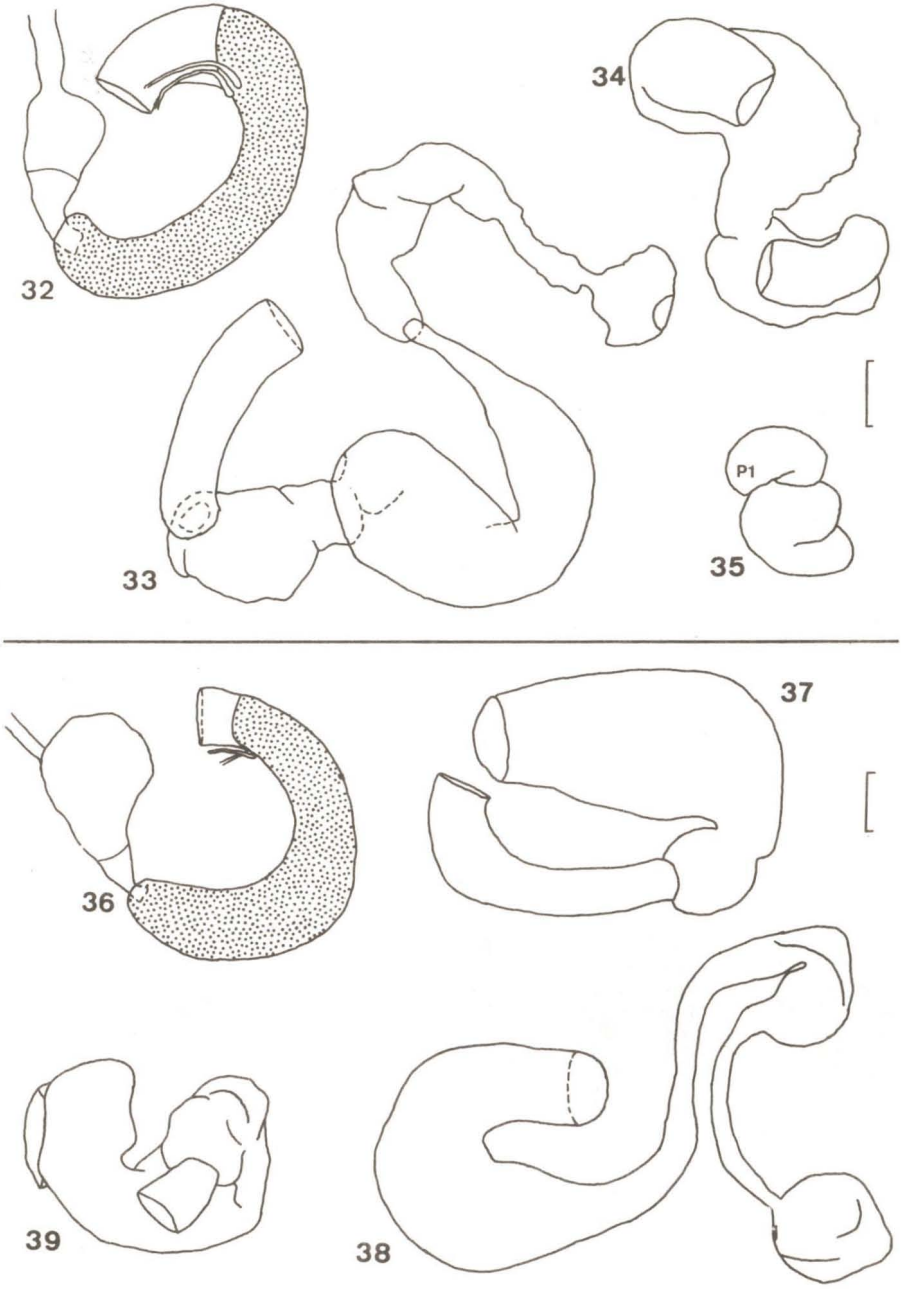




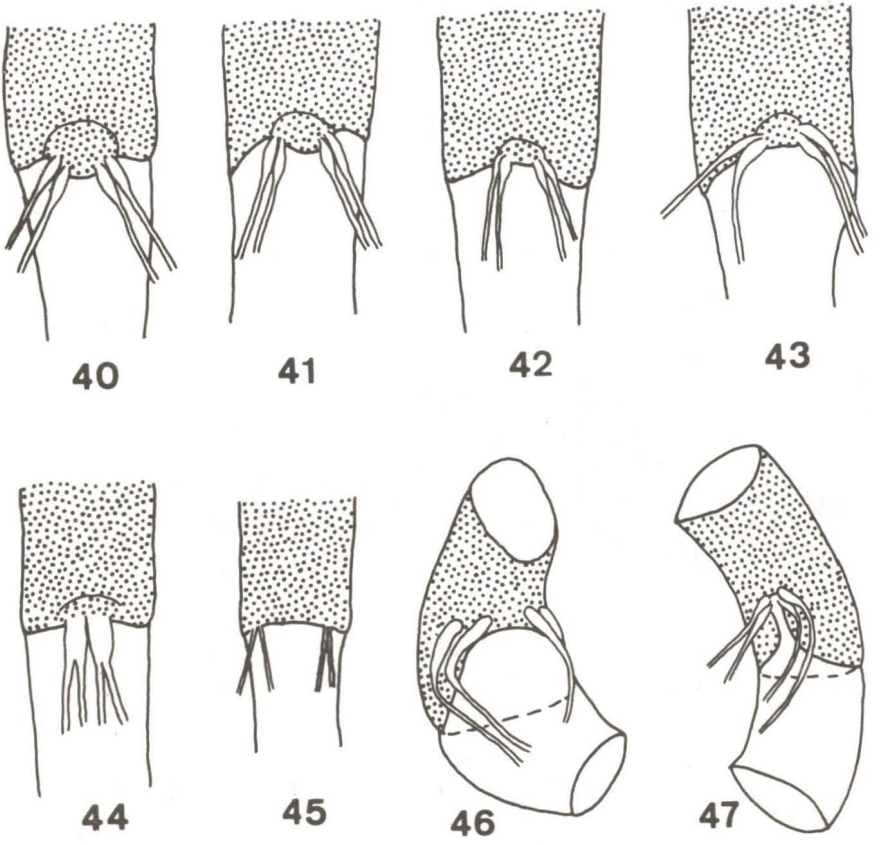
Parts of worker digestive tube. *Subulitermes microsoma* : 14-15, dorsal view; 16-17, lateral and ventro-lateral view of paunch, respectively. *Convexitermes sp* : 18-20, dorsal view; 21, lateral view of paunch. Scales 0.50 mm.



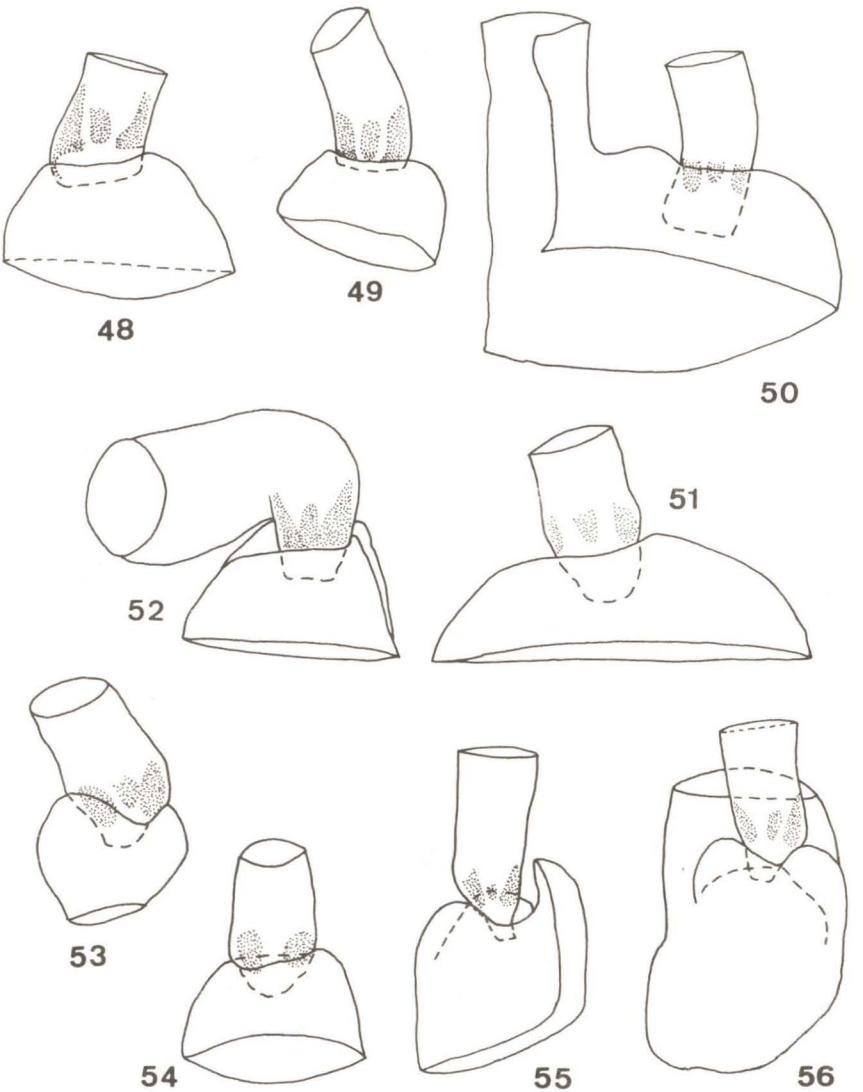
Parts of worker digestive tube. *Atlantitermes guarinim:* 22-24, dorsal view; 25-26, 27-28, lateral view of paunch of two workers. *Agnathotermes glaber:* 29-30, dorsal view; 31 , lateral view of paunch. Scales 0.50 mm.



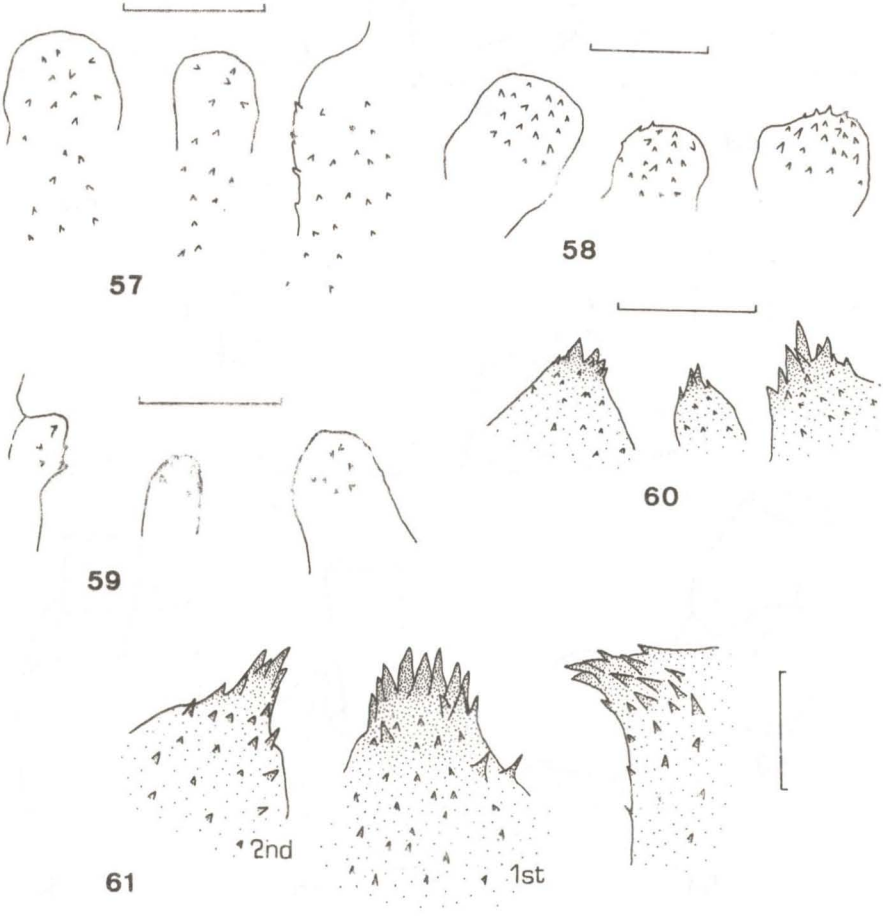
Parts of worker digestive tube. *Angularitermes orestes:* 32-33, dorsal view; 34 lateral view of paunch; 35, insertion of enteric valve into paunch. *Cyranotermes timuassu:* 36-38, dorsal view; 39, lateral view of paunch. Scales 0.50 mm.



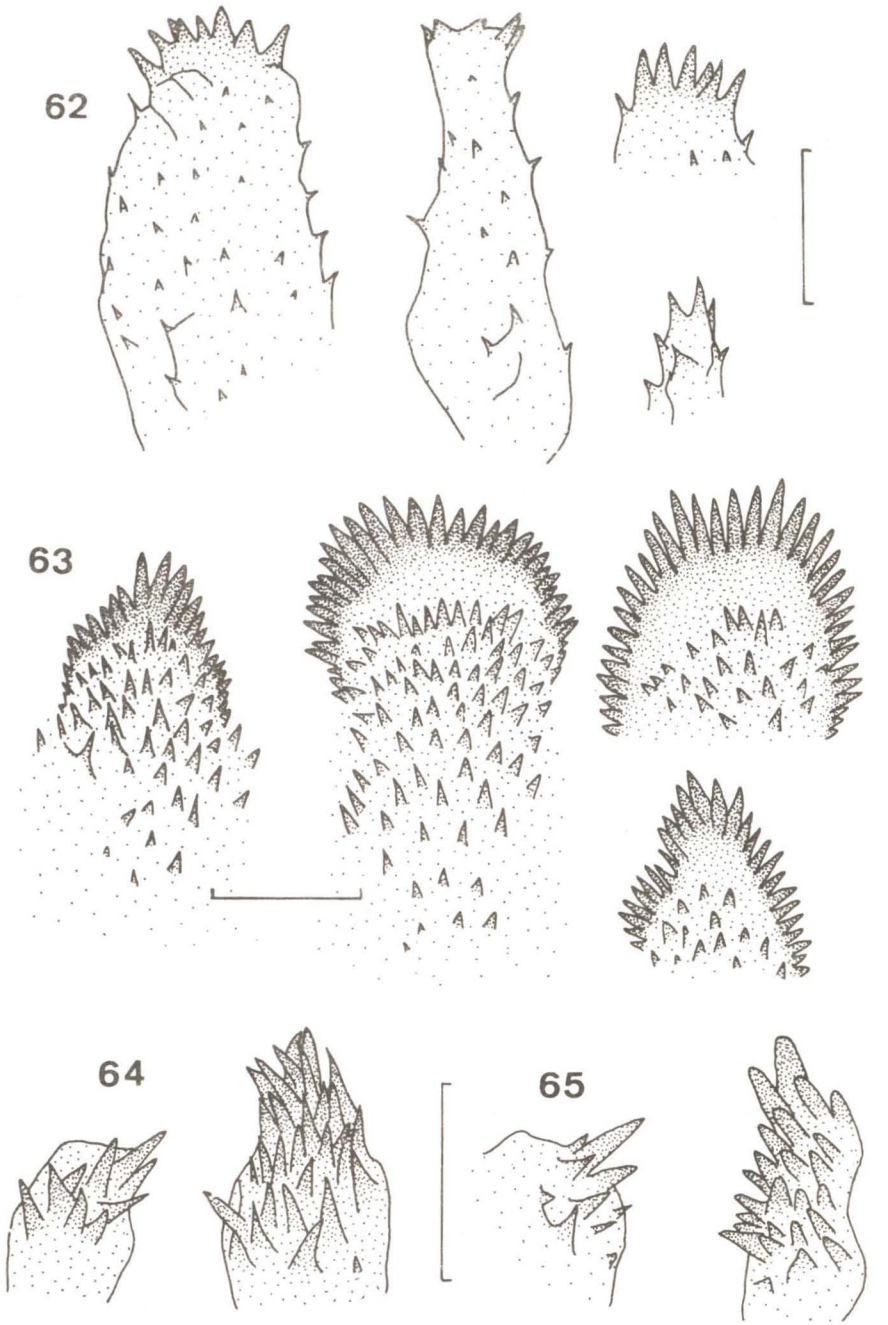
Mesenteron-proctodeal junction and Malpighian tubules: 40, *Coatitermes clevelandi*; 41,*Atlantitermes guarinim*; 42, *Araujotermes caissara*; 43, *Subulitermes microsoma*; 44, *Convexitermes sp*; 45, *Agnathotermes glaber*; 46, *Angularitermes orestes*; 47, *Cyranotermes timuassu*.



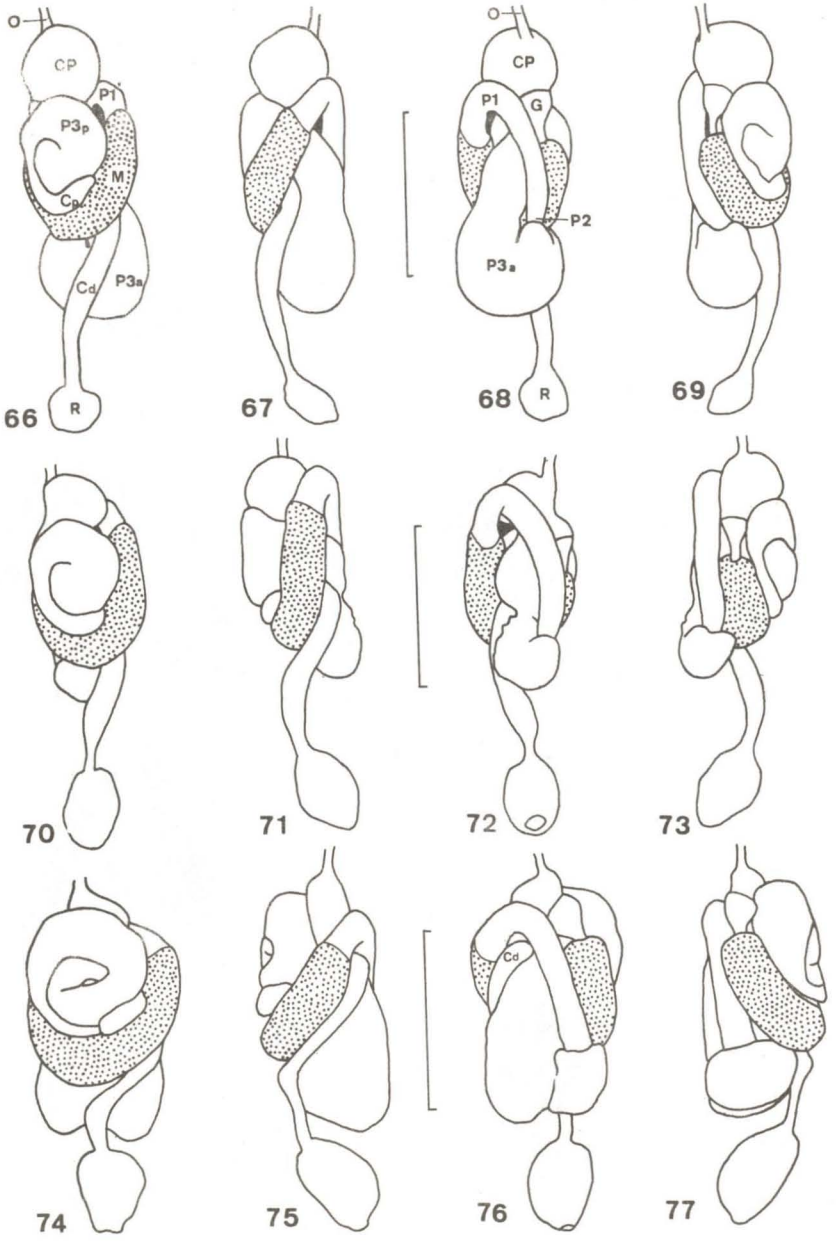
Insertion of enteric valve into paunch: 48, *Atlantitermes guarinim;* 49, *Cyranotermes timussu;* 50, *Subulitermes microsoma;* 51, *Convexitermes sp;* 52, *Angularitermes orestes;* 53, *Agnathotermes glaber;* 54, *Coatitermes clevelandi;* 55-56, *Araujotermes caissara.*



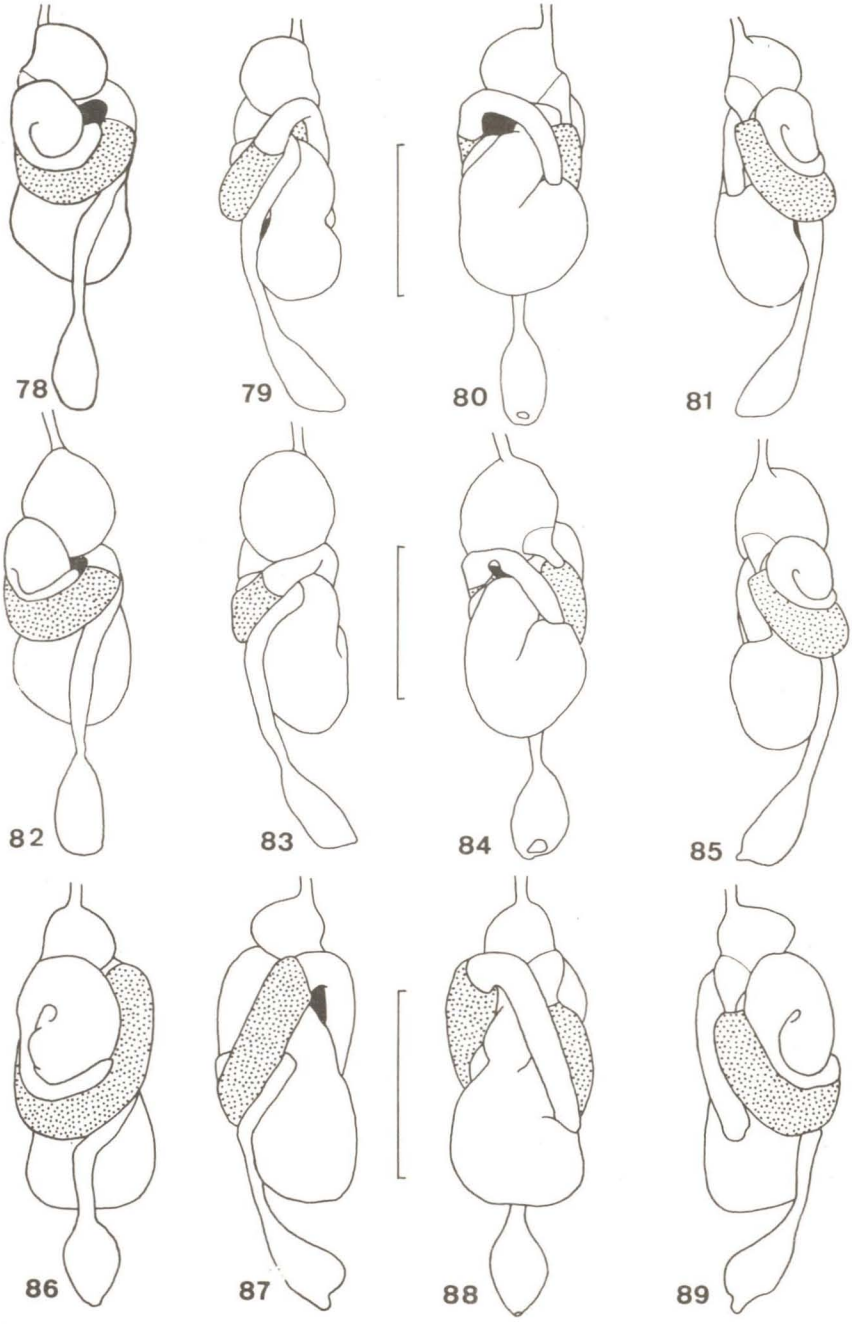
Armature of enteric valve: 57, *Convexitermes sp;* 58, *Araujotermes caissara;* 59, *Subulitermes microsoma;* 60, *Coatitermes clevelandi;* 61, *Atlantitermes guarinim.* 1st, 2nd, swellings of first and second orders, respectively. Scales 0.05 mm.



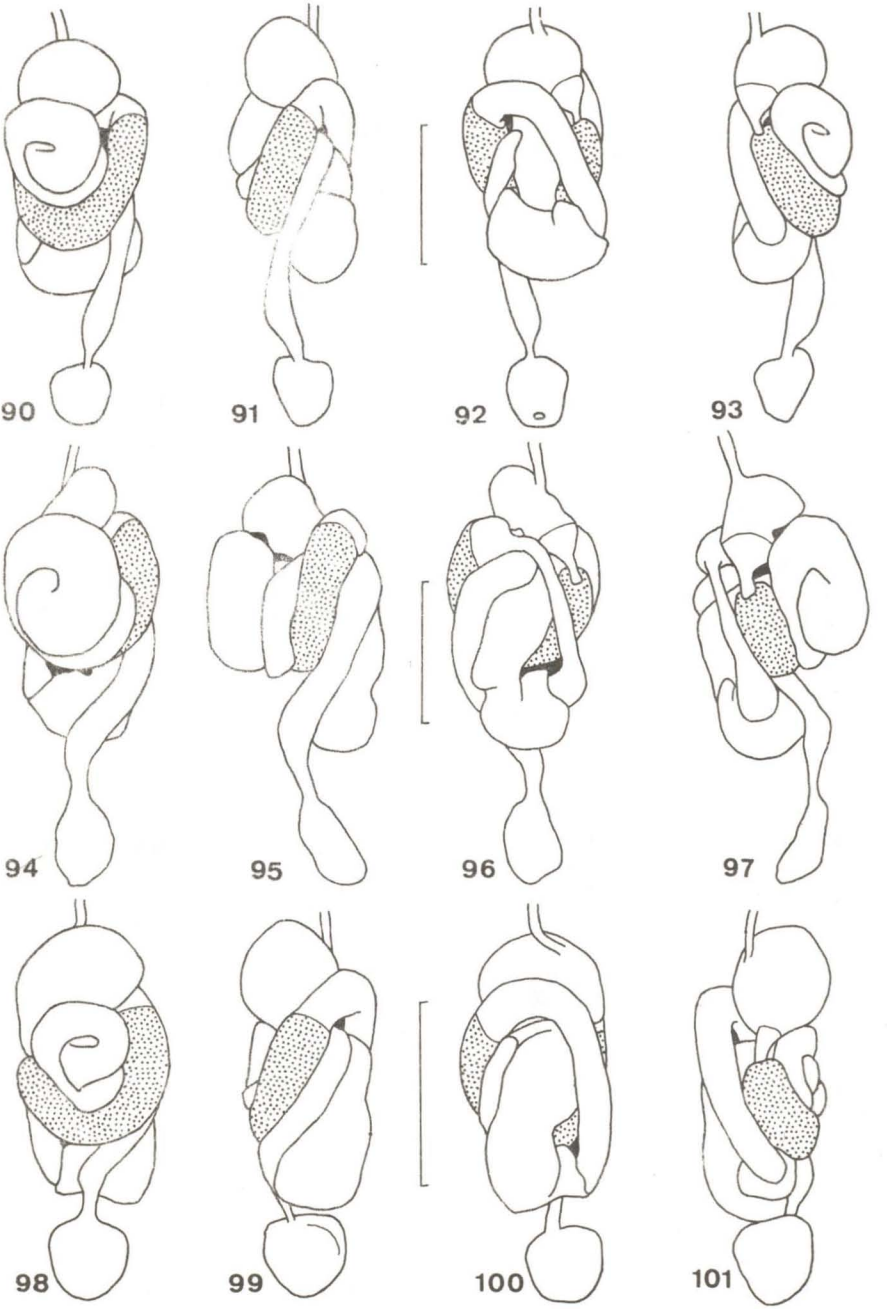
Armature of enteric valve: 62, *Angularitermes crestes;* 63, *Cyranotermes timuassu;* 64-65, *Agnathotermes glaber.* Scales 0.05 mm.



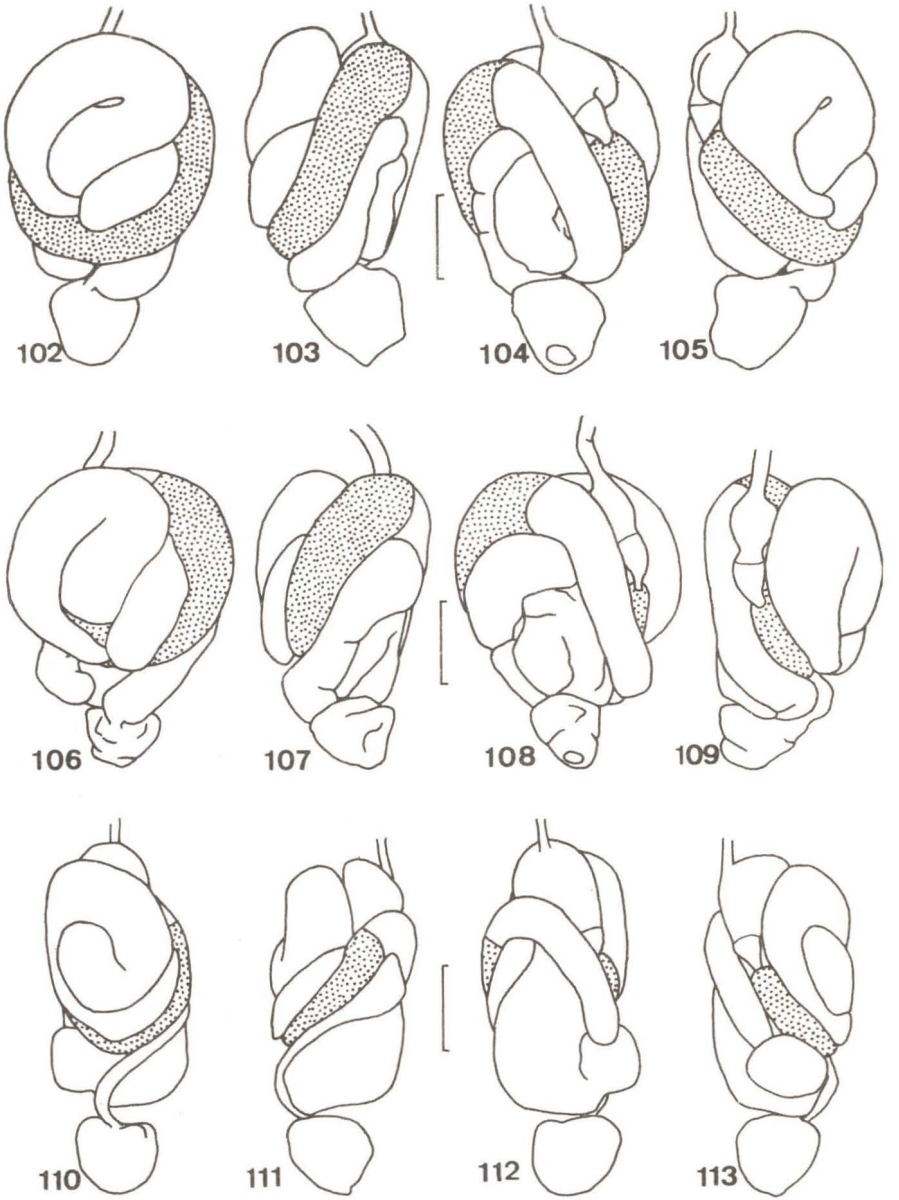
Coiling of worker digestive tube: 66-69, 70-73, *Araujotermes caissara;* 74-77, *Coatitermes clevelandi.* Dorsal, right, ventral and left views, respectively. Cd, distal colon; Cp, proximal colon; CP, crop; G, gizzard; M, mesenteron; O, oesophagus; P1, first proctodeal segment; P2, enteric valve; P3a, anterior part of paunch; P3p, posterior part of paunch; R, rectum. Scales 1.0 mm.



Coiling of worker digestive tube: 78-81, 82-85, *Convexitermes sp;* 86-89, *Subulitermes microsoma*. Dorsal, right, ventral and left views, respectively. Scales 1.0 mm



Coiling of worker digestive tube: 90-93, 94-97, *Atlantitermes guarinim;* 98-101, *Agnathotermes glaber*. Dorsal, right, ventral and left views, respectively. Scales 1.0 mm.



Coiling of worker digestive tube: 102-105, 106-109, *Angularitermes orestes;* 110-113, *Cyranotermes timuassu.* Dorsal, right, ventral and left views, respectively. Scales 1.0 mm.