Paraconvexitermes acangapua (Isoptera: Termitidae, Nasutitermitinae), a new genus and new species of the so-called "small Neotropical soil-feeding nasutes" from South America

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Résumé – Paraconvexitermes acangapua (Isoptera: Termitidae, Nasutitermitinae), un nouveau genre et une nouvelle espèce de « petits nasuti humivores Neotropicaux». – Le nouveau genre Paraconvexitermes comprend P. acangapua n. sp., P. nigricornis (Holmgren) et P. junceus (Emerson), ces deux dernières espèces étant précedemment incluses dans le genre Convexitermes Holmgren. Convexitermes comprend maintenant C. manni Emerson et C. convexifrons (Holmgren). Le tube digestif des ouvriers de ces deux genres, ainsi que de plusieurs genres voisins (en particulier Atlantitermes) a permis de préciser la définition de ces genres. On donne des illustrations du tube digestif et des mandibules des ouvriers, de la tête du soldat, de la tête des ailés et d'une reine de remplacement. Les relations phylogénétiques avec les autres genres sont discutées ainsi que la définition des termites « humivores».

Abstract – A new genus *Paraconvexitermes* is described, comprising *Paraconvexitermes acangapua*, new species, *P. nigricornis* (Holmgren) and *P. junceus* (Emerson), both previously in *Convexitermes* Holmgren. Now, *Convexitermes* comprises *C. manni* Emerson and *C. convexifrons* (Holmgren). The worker's digestive tube of both genera along with those of *Atlantitermes* species allowed to get a better definition of these three genera. Illustrations on the digestive tube and mandibles of workers, soldier's head, alate's head and secondary reproductive female of the new genus and species are provided. The phylogenetic relationships with the other nasute genera are discussed along with the "soil feeding" concept.

H olmgren (1910) described the genus *Convexitermes* as a subgenus of *Eutermes*. The genus comprised four species (Constantino 1998): *C. convexifrons* (Holmgren), *C. junceus* Emerson, *C. manni* (Emerson) and *C. nigricornis* (Holmgren).

Holmgren (1906) described *C. nigricornis* from Chaquimayo, Peru. Emerson (1925) re-described *C. nigricornis* based on material collected by him in Guyana. Emerson (in Snyder 1949) then proposed the subspecies *C. nigricornis junceus*, based on the material previously determined by himself as *C. nigicornis* in 1925. We have had the opportunity to examine both materials (Holmgren's type material and *C. nigricornis* determined by Emerson) and we have concluded that the material determined by Emerson is not *C. nigricornis* (Holmgren). Constantino (1998) treated the subspecies *C. nigricornis junceus* as a full species: *Convexitermes junceus*. Examining material determined by Emerson as *C. nigricornis junceus*, we confirm Constantino's opinion.

Based on the worker's digestive tube, soldier characters and alate characters we decided to separate these two species, *C. nigricornis* and *C. junceus* previously included in *Convexitermes*, in a new genus named *Paraconvexitermes*, along with a new species herein described, *Paraconvexitermes acangapua*.

We are aware that the so-called "soil-feeding" group of nasutes, that comprises both *Convexitermes* and *Paraconvexitermes*, is in a very confused taxonomical situation and we do not intend to resolve the problem, although we hope to contribute to a better understanding of this important group.

Material and methods

The morphometric characters used in this paper, and their correspondence with Roonwal's system (Roonwal 1970) are as follows:

a) for soldiers: (LH) length of head with nasus = $n^{\circ}12$; (WH) width of head = $n^{\circ}17$; (WP) width of pronotum = $n^{\circ}68$; (LN) length of nasus = $n^{\circ}13$; (LT) length of hind tibia = $n^{\circ}85$.

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b) for reproductives: (LH) length of head = $n^{\circ}8$; (WH) width of head = $n^{\circ}17$; (E-E) inter-eye distance = $n^{\circ}52$; (ED) diameter of eye = $n^{\circ}48$; (min. OD) minimum diameter of ocellus = $n^{\circ}56$; (max. OD) maximum diameter of ocellus = $n^{\circ}55$; (WP) width of pronotum = $n^{\circ}68$; (LP) length of pronotum = $n^{\circ}65$; (LT) length of hind tibia = $n^{\circ}85$.

All measurements are presented in millimeters.

For worker mandibles the "left mandibular index" (Fontes 1987b) was used.

The terms "bristles" and "hairs" are used in a comparative way, as in Emerson (1925). We use "very short hairs" for those visible at 12 X magnification and microscopic hairs for those visible at 60 X magnifications.

The terminology adopted for the parts of the worker mandibles follows Fontes (1987b).

For the digestive tube the techniques and terminology used are described by Noirot (1995, 2001).

Material examined – Most of the studied material is in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, state of São Paulo, and we also examined material from the American Museum of Natural History (AMNH), New York, from Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, state of Amazonas, from Museu Paraense Emílio Goeldi (MPEG), Belém, state of Pará, and from Universidade Federal de Goiás, state of Goiás (UFG).

We have examined material from localities not recorded before (Constantino 1998). They are: – *Paraconvexitermes junceus*: BRAZIL, Amazonas, Rio Negro (31' S 60°48' W). – *Convexitermes manni*: BRAZIL, Amazonas, Anavilhanas, Rio Negro (2°31'S - 60°48' W); Pará, Benevides (Faz. Morelandia-1°29' S 48°13' W); Pará, Vigia (00° 51' S 48° 08' W); Pará, Tucuruí, Rio Tocantins (4° 19' S 49° 32' W); Piauí, Corrente (8° 18' S 44° 05' W); Bahia, Ilhéus (14° 47' S 39° 03' W); Mato Grosso, Utiariti, Rio Papagaio; Goiás, Goiânia. – *Convexitermes convexifrons*: COLOMBIA, Meta, Villavicencio (4° 09' N 73° 38' W). BRAZIL, Mato Grosso (12° 00' S 59° 30' W); Amazonas, Anavilhanas, Rio Negro (2° 31' S 60° 48' W).

(For localities of *Paraconvexitermes acangapua*, n. sp., see under the species description)

RESULTS

Paraconvexitermes n. gen. (figs. 1, 2, 4-8)

Type-species: Paraconvexitermes nigricornis (Holmgren).

Description – **Alate** (figs. 5, 6). Known only from *Paraconvexitermes junceus*: Head elongate, fontanelle slit-shaped, long, in a depressed area. Eyes very large and very close to the lower margin of head. Ocelli large, nearly round, almost touching the eyes. Postclypeus inflated, anterior margin near straight and posterior convex. Antennae broken in the examined material (Emerson, 1925, did not mention the exact number of the antennae articles). The third article of antennae very small and 2nd almost equal to 4th. Pronotum narrower than head width



Figure 1 Paraconvexitermes acangapua, soldier head, dorsal view.

(with eyes), and sub-rectangular, posterior margin slightly emarginate, sides somewhat round. Posterior margin of mesonotum and metanotum widely emarginate. Head with many short hairs, many bristles oriented in different directions, and a few long bristles; anteclypeus and postclypeus with some bristles and short hairs; labrum with two long bristles and some short hairs. Postmentum and palpi very hairy. Pronotum with many short hairs and many bristles, and only a few long bristles on the margins. Tergites and sternites with many short hairs. Head capsule pale brown, labrum and postclypeus lighter, fontanelle pale yellow, with a row of four circular areas lighter in front of the fontanelle opening. Two ellipsoid marks larger than ocelli, in front of them and many lighter marks (sockets of bristles) variable in size; pronotum, mesonotum and metanotum pale yellow.

Soldier (figs 1, 2): small-sized nasutes. Head rounded with a conical nasus variable in size, and variable in thickness at base. Vestigial mandibles without points. Antennae with 10-11 articles. Head and nasus densely covered by many hairs and bristles along with a few long bristles. Tergites densely covered by short hairs and bristles on posterior margin and sternites densely covered by short hairs and bristles perpendicular to body length. Many small "pits" (visible only under SEM) on the base of nasus and along its length, variable in density, according to species.



Figure 2 Paraconvexitermes acangapua, soldier head, profile.



Figure 3 Convexitermes manni, soldier head, dorsal view.

Worker: head round, fontanelle region slightly depressed, antennae of 10-11 articles, with mandible dimorphism: broad gap vs. narrow gap (Fontes 1987b). Pilosity as in the soldiers, and tergites and sternites very hairy. Head pale yellow (or yellow whitish), antennae and legs withish and abdomen completely translucent. Mandibles dimorphic: complete marginal dentition (fig. 7): apical tooth larger than marginal teeth, with posterior margin concave in left and right mandibles. Left mandible: cutting edge between M1 +2 and M3 slightly or strongly sinuous and M3 smaller or much smaller than M1 +2. The gap between M3 and molar prominence in the "workers with narrow gap" is very narrow and in those "with broad gap" is much wider. Molar prominence with ridges (more or less marked). Right mandible: Apical concave larger than M1. M2 small or inconspicuous, the posterior margin slightly concave. Point of the M2 closer to the first marginal than to the molar plate in both kinds of workers. Molar tooth mostly hidden beneath the molar prominence in the "workers with narrow gap" and visible in the "workers with broad gap". Molar plate with ridges.

Digestive tube (fig. 8): gizzard relatively small but with a complete poorly sclerotized cuticular armature; columnar belt short, pulvillar belt much more developed, pulvilli I overlapping about 2/3 of the columns. Junction midgut-hindgut circular (no mixed segment). Malpighian tubules four in number, slightly dilated at their base, attached individually but closely adjacent in pairs on a small nodule (d = $80-100 \ \mu m$) at the mesentericproctodeal junction (fig. 8F). P1 (ileum) long but very narrow. P2 (enteric valve) with a conspicuous armature on six ridges of two sizes in alternation. The larger (fig. 8K, L) are more or less triangular with the posterior part bulging in the gut lumen as a strongly sclerotized shield bearing a row of 15-30 huge spines maximally developed at the tip. The smaller ridges (fig. 8I) are more bulbous, not so prominent and unsclerotized except for a various number (5-18) of shorter spines on the posterior half. The symmetry is approximately triradial but both types of ridges bear some intraspecific variations (especially in the spine number). Paunch (P3) voluminous (fig. 8C) divided in two compartments, P3a and P3b. P3b is especially developed, very prominent in dorsal view, above the midgut ring. The narrow constriction between P3a and P3b is a true sphincter with a distinct circular musculature, but the most distinctive feature is a dense cover of thin sclerotized bristles of variable length (up to 100μ m). The sphincter is a short curved tube, with the bristles inserted on its inner (convex) face; they are oriented backwards and thus oppose the return of the gut content from P3b to P3a. P4 (colon) is long (anterior position of the U-turn) and very narrow so that the elongated sphincter (isthmus) separating P3 from P4 is not very distinct.

Comparison – The alates of this new genus are known only from *P. junceus* (figs. 5, 6). The alates of *Paraconvexitermes* are different from the alates of *Convexitermes* in the following characters: head longer and narrower, eyes much larger and prominent, ocelli much larger and near the eyes, postclypeus larger and much more inflated, anterior part of the fontanelle different in shape, pronotum larger and with different shape (with sides almost parallel, while in *Convexitermes* they converge towards the rear).

The soldiers are very similar to those of *Convexitermes* (*C. manni* and *C. convexifrons*). *Convexitermes* soldiers have a different pattern of pilosity (see figs. 1-3) with a mat of microscopic hairs on head and nasus (hardly visible in fig. 3) along with just two long bristles on the vertex and zero, two or four bristles at the base of the nose. *C. manni* has a longer and thinner nasus, and *C. convexifrons* contour of head is similar to *Paraconvexitermes acangapua* n. sp., that is, almost round.

The general appearance of workers of both genera are very similar. The mandibles of *Paraconvexitermes* are very similar to those of *Convexitermes* (see Fontes 1987b: figs. 1-9), and the most conspicuous difference is the gap between the third marginal tooth and molar prominence of the left mandible in the two kinds of workers. While in *Convexitermes* the gap is only a little wider in the "workers with broad gap" in relation to "workers with narrow gap", in *Paraconvexitermes* it may be twice in the "workers with broad gap". In the left mandible the angle between the apical tooth and first plus second teeth is wider (larger) in *Paraconvexitermes* and the margin of apical tooth more concave. The right mandible apical



Figure 4

Paraconvexitermes acangapua, physogastric nymphoid female, total view. Scale bar = 0.1 mm.

tooth of Convexitermes is larger than that of Paraconvexitermes, and the second marginal tooth is more prominent in Convexitermes than in Paraconvexitermes. The molar plate is narrower in *Convexitermes manni* than in P. junceus and P. acangapua (all bear about 10 ridges, strongly marked or weakly marked). The gut of Paraconvexitermes differs from that of Convexitermes by three important characters: first, the attachment of the Malpighian tubules on a small but clearly distinct nodule (compare the figures 8F and 8G); second, by the conspicuous armature of its enteric valve (nearly unarmed in *Convexitermes*); and third, by the cuticular armature of the sphincter between P3a and P3b. The first character is shared by several other genera: Subulitermes, Coatitermes, Atlantitermes (Fontes 1987a), Ereymatermes (Constantino 1990), Anhangatermes (Constantino 1991), but only in the two latter genera is a short mixed segment also present. A strong armature of the enteric valve is observed in other soil-feeding Nasutitermitinae but that of Paraconvexitermes is idiosyncratic. The valve of Atlantitermes is the most similar but the larger ridges (fig. 8M, N) are rectangular, the spinose posterior shield is reflexed forward and several smaller spines are scattered on the surface of these ridges whereas in Paraconvexitermes the surface of the larger ridges is smooth (compare figures 8K and 8M). However the smaller ridges are very similar in both genera. Third, the armed sphincter between P3a and P3b has never been observed in any other termite until now. Admittedly, this part of the gut is rarely analyzed but we did not find this armed sphincter in Atlantitermes, Cyranotermes or Anhangatermes.

Paraconvexitermes acangapua n. sp. (figs. 1, 2, 4, 8)

Type material – **Holotype**: soldier, part of lot nr. MZUSP 11192 Brazil, Pará, Belém, Faz. Morelândia (1° 29' S 48° 13' W). 2.viii.1983. *Charles Noirot* coll.



Figure 5 *Paraconvexitermes junceus*, alate, dorsal view. Scale bar = 0.5 mm.



Figure 6 Paraconvexitermes junceus, alate, profile. Scale bar = 0.5 mm.

Field number BN-27. E. M. Cancello det. 2002. Obs. "in a decayed log on the ground, about 30 cm in diameter". - Paratypes: soldiers and workers of lot nr MZUSP 11192, with the same label of the holotype. MZUSP 8442 soldiers, workers and nymphoid females; Brazil, Pará, Belém, Faz, Morelândia; 18/viii/1980; A.G. Bandeira coll., E.M. Cancello det. 2002. MPEG 793 soldiers and workers; Brazil, Pará, Belém, Icoaraci (1° 17' S 48° 28' W); 22/vi/1979; Paulo Eremita coll., E.M. Cancello det. 2002. MPEG 958; Brazil, Pará, Benevides, Faz Morelândia (1° 29' S 48° 13' W), 18/viii/1980, A.G. Bandeira coll., E.M.Cancello det.. 2002. MPEG 982 soldiers and workers; idem; 16/ix/1980; A.G. Bandeira coll., E.M. Cancello det. 2002. MPEG 1010 soldiers and workers: idem. 27/i/1981; A.G. Bandeira & R. Bittencourt Neto coll., E.M. Cancello det. 2002. MPEG 1024 soldiers and workers; idem; 29/i/1981; A.G. Bandeira & R. Bittencourt Neto coll; E.M. Cancello det. 2002. MPEG 1163 soldiers and workers; idem. 27/vii/1982; A.G. Bandeira & R. Bittencourt Neto coll., E.M. Cancello det. 2002. MPEG 1446 soldiers and workers: idem. 2/viii/1983; A.G. Bandeira coll., E.M. Cancello det. 2002. MPEG 3407 soldiers and workers; Brazil, Pará, Belém, Mocambo, 27/vi/1989; R. Constantino coll., E.M. Cancello det. 2002. MPEG 3449; Brazil, Pará, Benevides. 29/i/1981. A.G. Bandeira coll., E.M. Cancello det. 2002.

Description – **Alate** unknown.

Female secondary reproductive (physogastric nymphoid female- fig. 4): head elongate, shorter than the alate of *P. junceus*, large eyes close to the ventral margin of head, ocellus semi-circular and separated from the eye by less than its diameter; antennae with 15 articles, the third smallest and 2nd almost equal to the 4th, 5th and 6th, from 7th to the last a little larger; pronotum narrower than head width (with eyes); abdomen very physogastric. Head and legs pale yellow, pronotum lighter, pleural



Figure 7 Paraconvexitermes junceus, worker mandibles.

region whitish. Head covered by many hairs; pronotum, meso and metanota with microscopic hairs and short hairs, abdominal tergites very hairy. Measurements of two secondary reproductive females from the same colony: (LH): 0.48-0.51; (WH): 0.70; (E-E): 0.45; (ED): 0.24; (min. OD): 0.06-0.08; (max. OD): 0.08; (WP): 0.51-0.54; (LP): 0.34; (LT): 0.93.

Soldier. Head round from above with a conical nasus about one third head length, thick at base. Some soldiers with the nose slightly downward oriented. Antennae with 11 articles, 3rd longer than 4th, the 4th as long as the 2nd. Tibial spur formula: 2:2:2. Many short hairs and bristles along with a few long bristles scattered on head, and on nasus. In SEM pictures (magnification about 300 X) there are some "pits" (which may be glands) on the surface of head and nasus. Head pale yellow to yellow, the distal 2/3 of nose brown to dark brown while the very end is a little lighter (forming a distinctive light brown tip). Antennae same color as the head. The entire frontal gland can be seen, by translucence, in some soldiers, even when they are very well pigmented. Measurements of 10 soldiers from two different colonies: (LH): 1.15 - 1.23; (WH): 0.72 - 0.80; (WP): 0.35 - 0.37; (LN): 0.37 - 0.42; (LT): 0.64 - 0.70.

Comparison – the soldier of *Paraconvexitermes acangapua* has a wider head than *P. junceus*, a shorter nasus, thicker at the base, and with the brown tip very marked. Although both are pilosous, *Paraconvexitermes acangapua* soldier has fewer long bristles on the cephalic capsule and they are shorter. The nose of *P. nigricornis* (Holmgren) is thicker at base and longer than in *P. acangapua* soldier. The pilosity of *P. nigricornis* is more similar to *P. junceus*, with much longer bristles than *P. acangapua*, and these bristles are even longer in *P. nigricornis*.

Worker: left mandibular index about 1.4-1.5 for workers with "narrow gap" and 1.25 for workers with "broad gap". Cutting edge sinuous between 1st plus 2nd and 3rd marginal tooth. The gap between M3 and molar prominence is much wider in workers with "broad gap" than those of "narrow gap". Second marginal tooth of right mandible inconspicuous in workers with "broad gap" and very small in workers with "narrow gap". Workers with "narrow gap" seem to be more frequent than those with "broad gap".

Digestive tube (fig. 8): if the digestive tube gives good generic characters it is, by contrast, very uniform inside the genus. Especially, the enteric valves of the three species cannot be distinguished, owing the intraspecific variability of their armature.

Etymology – from Tupi, an indian language, "acanga" means head and "pua" means round.

DISCUSSION

Paraconvexitermes is a new member of a group usually called "small Neotropical soil-feeding nasutes" which also includes the genera Convexitermes, Atlantitermes, Araujotermes, Coatitermes, Subulitermes, Agnathotermes, Angularitermes, Cyranotermes (see Fontes 1987a, b), Anhangatermes (Constantino 1990), Ereymatermes (Constantino 1991).

We are aware of the weakness of the genus concept in the systematics of this group of Nasutitermitinae (Roisin 1995; Constantino 1998). Even so, we think that it is better to point out the differences between two group of species (mainly their apomorphies) by describing another new genus, rather than hiding these differences by maintaining all the species in one "genus". We were able to identify two patterns in the soldier's pilosity, differences in the morphology of the alates' head, and in the worker's digestive tube, along with some differences in the worker's mandibles. Therefore, we decided to describe this new genus, *Paraconvexitermes*, with the aim of contributing to a better understanding of this difficult group.

The phylogenetic relationships among this group, the so-called soil feeding nasutes, are far from being well understood. For a comprehensive understanding of the group it will be necessary to have much more material available, with large series of all described species, along with detailed descriptions of the digestive tube and the alates. Unfortunately, these are still unknown for many species.

All the genera of this group are considered to be soilfeeders but this assumption must be questioned. Their biology is poorly known but in several instances the specimens were collected in close connection with decayed wood. One of us (EMC) has collected *Convexitermes manni* in different localities and always from inside dead trunks, sometimes in a most humid and decayed part and even associated with *Heterotermes*, a genus well known as a xylophagous termite. The holotype and paratypes from the same sample of *Para*- *convexitermes acangapua*, n. sp., were also collected by Ch. N. in a decayed log on the ground, about 30 cm in diameter and the termites were mainly in the center of the log where the humidity was maximal. Also, Roisin (1995) found *Subulitermes zeteki* (Snyder) and *S. denisae* Roisin (including nymphs and larvae) in decayed wood, and soldiers and workers of *Ereymatermes panamensis* Roisin "in dead wood on forest floor" and "in a stump of palm tree". Constantino (1990) collected *Anhanga*- *termes macarthuri* Constantino "below a fallen rotten tree trunk".

On the other hand, the careful observation of the worker morphology, by comparison with undisputed humus-feeders (Apicotermitinae of the *Apicotermes* group, Termitinae of the *Cubitermes* group), suggests that the small nasutes are less adapted, to varing degrees, to the soil-feeding habit. Combining our observations with those of Fontes (1987a, b) and



Figure 8

Digestive tube. – **A**, **B**: *Paraconvexitermes acangapua*, gut *in situ* in dorsal (A) and ventral (B) view. – **C-E**: paunch in ventral view with its two compartments P3a and P3b: **C**, *P. acangapua*, the arrow points to the armed sphincter. **D**, *Convexitermes convexifrons*. **E**, *Atlantitermes raripilus* (Emerson). – **F-H**: attachment of the Malpighian tubules; **F**, *Paraconvexitermes acangapua*. **G**, *Convexitermes manni*. **H**, *Atlantitermes guarinim* Fontes. – **I-J**: enteric valve, smaller ridges. **I**, *Paraconvexitermes acangapua*. **J**, *Atlantitermes guarinim*. – **K-N**: enteric valves, larger ridges. **K**, *Paraconvexitermes acangapua*, en face view. **L**, *idem* in profile. **M**, *Atlantitermes guarinim*, en face view. **N**, *idem* in profile. Scale bars = 50 µm.

Constantino (1990, 1991), we can summarize this comparison. For the mandibles, the development of the apical tooth is always obvious but of variable importance, with *Cyranotermes* being the most extreme. The reduction of the third marginal on the left mandible and of the second in the right mandible is maximal in *Angularitermes, Anhangatermes* and *Cyranotermes.*. The absence of the transversal ridges in the molar region is only seen in *Cyranotermes* and *Anhangatermes* but a conspicuous reduction of these ridges is observed in all other genera.

In the gut, the cuticular armature of the gizzard is complete (although poorly sclerotized) except in *Agnathotermes* where the cushions of the third order are absent (this armature is strongly reduced in most, if not all, strict soil-feeders). The other gut characters seem not so well correlated with diet, except for an increase of the hindgut volume in all the soil-feeders *sensu lato*.

To sum up, the Neotropical small "soil feeders" are probably not eating at the end of the humification gradient, with *Cyranotermes, Anhangatermes* and possibly *Angularitermes* probably being the farthest down the gradient. Donovan *et al.* (2001) proposed a new feeding classification of termites based on observations of both the worker gut content and morphology. In this classification *Convexitermes* and *Paraconvexitermes* are assigned to group III whereas the true soil-feeders form group IV.

The left mandible of the workers is dimorphic in most of the genera, the difference being in the gap between the third marginal and the molar prominence (workers with "narrow gap" vs. those with "broad gap", Fontes 1987b). However the workers are monomorphic

REFERENCES

- CONSTANTINO R. 1990 Anhangatermes macarthuri, new genus and species of soil feeding nasute termite from Amapá State, Brazil (Isoptera, Termitidae, Nasutitermitinae). – Goeldiana Zoologia, 3: 1-6.
- CONSTANTINO R. 1991 *Ereymatermes rotundiceps*, new genus and species of termite from the Amazon Basin (Isoptera, Termitidae, Nasutitermitinae). – *Goeldiana Zoologia*, **8**: 1-11.
- CONSTANTINO R. 1998. Catalog of the termites of the New World. Arquivos de Zoologia, 35: 135-230.
- DONOVAN S.E., EGGLETON P. & BIGNELL D.E. 2001 Gut content analysis and a new feeding group classification of termites. – *Ecological Entomology*, **26**: 356-366.
- EMERSON A.E. 1925. The termites of Kartabo, Bartica District, British Guiana. *Zoologica*, 6: 291-459.
- FONTES L.R. 1987a Morphology of the worker digestive tube of the soilfeeding nasute termites (Isoptera, Termitidae, Nasutermitinae) from the Neotropical Region. – *Revista brasileira de Zoologia*, **3**: 475-501.
- FONTES L.R. 1987b Morphology of the alate and worker mandibles of the soil-feeding nasute termites (Isoptera, Termitidae, Nasutitermitinae) from the Neotropical Region. – *Revista brasileira de Zoologia*, 3: 503-531.
- HOLMGREN N. 1906 Studien über südamerikanische Termiten. Zoologische Jahrbücher Abt. Systematik, 23: 521-676.

in Cyranotermes, Anhangatermes and Angularitermes, the three genera nearest to the strict soil-feeders. The observations of Roisin (1996) on Subulitermes and Coatitermes strongly suggest that the two morphs of workers represent successive instars, the "narrow gap" being first instar and the "broad gap" second instar workers. However, Fontes (1987b) observed that in Araujotermes, Atlantitermes and Subulitermes some workers with the narrow gap molted into workers again possessing the narrow gap. These observations show that in some genera the workers can molt again. All the strict soil-feeders for which the caste development has been studied show a simplified polymorphism, with only one monomorphic worker instar (review in Roisin, 2000), including the Ethiopian nasutes Mimeutermes and Eutermellus (Noirot 1955). It is therefore not surprising that the three Neotropical nasutes with monomorphic workers are those which apparently are the most adapted to soilfeeding as suggested by Roisin (1996).

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- HOLMGREN N. 1910 Versuch einer Monographie der americanische Eutermes- Arten. – Jahrbuch der Hamburgischen Wissenchaftlichen Anstalten, **27**: 171-325.
- NOIROT C. 1955 Recherches sur le polymorphisme des termites supérieurs (Termitidae). – Annales des Sciences naturelles, Zoologie, 17: 399-595.
- NOIROT C. 1995 The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. I. Lower Termites. – Annales de la Société entomologique de France (n.s.), 31: 197-226.
- NOIROT C. 2001 The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. II. Higher termites (Termitidae). Annales de la Société entomologique de France (n.s.), 37: 431-471.
- ROISIN Y. 1995 Humivorous nasute termites (Isoptera: Nasutitermitinae) from the Panama canal area. – *Belgian Journal of Zoology*, **125**: 283-300.
- ROISIN Y. 1996 Castes in humivorous and litter-dwelling neotropical nasute termites (Isoptera: Termitidae). – *Insectes Sociaux*, 43: 375-399.
- ROISIN Y. 2000 Diversity and evolution of caste patterns. In: Abe T., Bignell D.E., Higashi M. (eds), Termites: Evolution, Sociality, Symbiosis, Ecology, p. 95-119, Dordrecht: Kluwer.
- ROONWAL M. L. 1970 Measurement of termites (Isoptera) for taxonomic purposes. – Journal of the Zoological Society of India, 21: 9-66.
- SNYDER T.E. 1949 Catalog of the termites (Isoptera) of the world. Smithsonian Miscellaneous Collection, 112: 1-490.