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HUMIVOROUS NASUTE TERMITES (ISOPTERA : *NASUTITERMITINAE*) FROM THE PANAMA CANAL AREA

by

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SUMMARY

The taxonomic status of five species of humivorous nasutes from the Panama Canal area is examined. The following species are recognized : *Subulitermes zeteki* (Snyder, 1924), *Subulitermes denisae*, new species, *Atlantitermes kirbyi* (Snyder, 1926), *Ereymatermes panamensis*, new species, and *Coatitermes clevelandi* (Snyder, 1926). Their descriptions are herein given or complemented with emphasis on worker anatomy, diagnostic characters are provided and generic assignments are discussed.

Key words : Termitidae, taxonomy, new species, Neotropical Region.

INTRODUCTION

The Nasutitermitinae comprise a large array of fully nasute genera showing, to a variable extent, adaptations towards a humivorous diet. AHMAD (1950) hypothesized that the full nasute soldier (characterized by a pear-shaped head capsule with a long nasus and reduced mandibles) evolved twice : once from a primitive form related to *Procornitermes*, which gave rise to a lineage comprising, among others, the genus *Nasutitermes* ; and once from a primitive form related to *Paracornitermes*, which gave rise to another lineage comprising, among others, the genus *Subulitermes*. Although the phylogeny proposed by AHMAD (1950) has been recently widely criticized (see MILLER, 1986), it is clear that the two lineages of full nasutes he proposed correspond to ecologically distinct groups : the former (the *Nasutitermes* group) comprises sound wood or grass feeding genera, whereas the latter (the *Subulitermes* group) comprises genera showing variously developed adaptations to a diet of soft vegetable matter or humus, such as an increase in the concavity of the molar areas and a reduction of the molar ridges of the worker mandibles

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(SANDS 1965, DELIGNE 1966). The two groups are therefore traditionally referred to as, respectively, xylophagous and humivorous nasutes.

Three species of humivorous nasutes were described from Panama by SNYDER (1924, 1926) : *Nasutitermes (Subulitermes) zeteki, Nasutitermes (Subulitermes) kirbyi* and *Nasutitermes (Convexitermes) clevelandi.* Since then, no further species has been added to this list (NICKLE and COLLINS, 1992), although the generic taxonomy went through several changes. The subgenera *Subulitermes* and *Convexitermes* were erected to generic status (FULLER, 1921 ; SNYDER, 1949). Later, FONTES (1979, 1982) created several new genera and the new combinations *Araujotermes zeteki, Atlantitermes kirbyi* and *Coatitermes clevelandi.* He subsequently published comparative studies of the digestive tube (FONTES, 1987a) and mandibles (FONTES, 1987b) of all Neotropical humivorous nasute genera, represented by their type species. The denominations proposed by FONTES were recently adopted by NICKLE and COLLINS (1992).

Collections made in 1990-1991 in Barro Colorado Nature Monument and Parque Nacional Soberanía yielded two additional species of humivorous nasutes. The need for a clear taxonomic context to describe the new taxa led me to re-examine the status of the three previously known species. In this paper, I describe the new species as *Subulitermes denisae* and *Ereymatermes panamensis* and discuss their generic assignment together with that of the other three species formerly described by SNYDER (1924, 1926).

MATERIAL AND METHODS

The new material examined in this study comes either from the island of Barro Colorado in the Panama Canal (9° 10'N, 79° 50'W) or from Parque Nacional Soberanía, on the north side of the Canal, west of the town of Gamboa. Specimens were collected and fixed in FAA (formol-alcohol-acetic acid) and preserved in 70 % ethanol. Camera lucida drawings of digestive tubes were made after removal of abdominal walls, fat tissues and malpighian tubules. Pictures of mandibles and enteric valves were taken after dissection, dehydration by ethanol and toluene and mounting on microscope slides in balsam. Pictures of soldier heads and molar areas of worker mandibles were taken with a ISI-DS 130 scanning electron microscope after ethanol dehydration, immersion for at least 12 h in hexamethyldisilazane, air drying at 60° C, and metallization with gold. Soldier heads were treated by 6 % KOH for 2-6 h at 60° C before dehydration, as this method was found to clean the head capsule both externally and internally, especially from remnants from the frontal gland, and preclude deformation during dessication and metallization.

The terminology used for describing the mandibles follows that of SANDS (1972) : the left mandible index is L_a/L_1, where L_a is the distance separating the apical tooth from the fused first and second marginals, and L_1 the distance separating the fused first and second marginals from the third marginal. The molar areas are called molar prominence (left mandible) and molar plate (right mandible). Each

genus or species heading is followed by a short bibliography, limited to the original description and publications of new combinations.

Abbreviations :
BCI : Barro Colorado Island, Panama.
IRSN : Institut Royal des Sciences Naturelles, Brussels, Belgium.
NMNH : U.S. National Museum of Natural History, Washington D.C., U.S.A.
STRI : Smithsonian Tropical Research Institute, Panama.

DESCRIPTIONS

Genus *Subulitermes* Holmgren, 1910

Eutermes subgenus *Subulitermes* : HOLMGREN, 1910, pp. 208, 218.

Type species : *Eutermes microsoma* Silvestri, 1901.

Soldier monomorphic, fully nasute ; rostrum thin, mandibles without points ; head capsule little or not constricted behind antennae.

Worker (according to FONTES, 1987a, b) : around 3 vestigial molar ridges on molar prominence, 4-5 on molar plate ; left mandible index 1.02-1.12 ; gizzard with complete armature, but weakly sclerotized ; mesentero-proctodeal junction oblique, no distinct mixed segment ; malpighian tubules in two pairs, separated by a short space at their point of attachment to the mesentero-proctodeal junction ; paunch not constricted after junction of enteric valve ; armature of enteric valve composed of six subequal swellings with small spines ; colon long and narrow.

Subulitermes zeteki (Snyder, 1924)
(Figs 1, 6, 11, 16, 20)

Nasutitermes (Subulitermes) zeteki : SNYDER, 1924, p. 32 (soldier).

Subulitermes zeteki (Snyder) : SNYDER, 1949, p. 342.

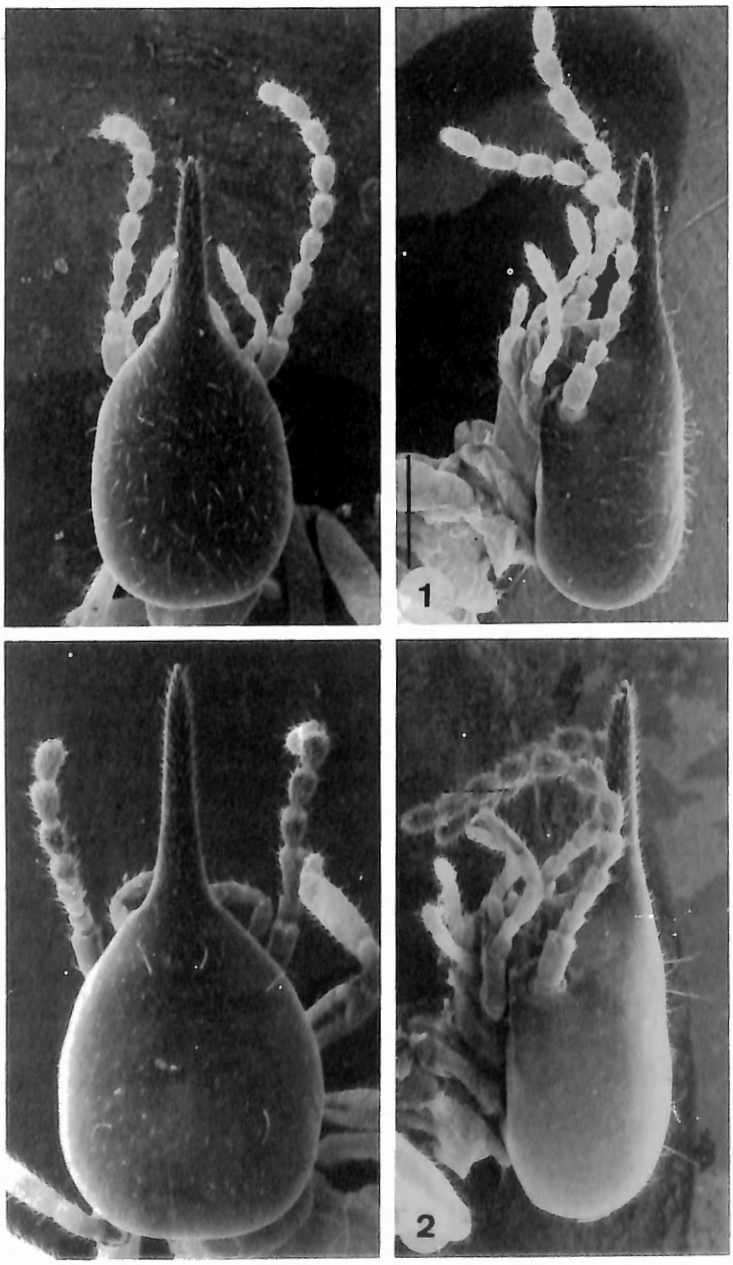
Araujotermes zeteki (Snyder) : FONTES, 1982, p. 100.

Material examined :

NMNH. # Z1731 : soldiers and workers from type series. Summit, Canal Zone, Panama, 29.vii.1922. Coll. J. Zetek and I. Molino, det. T.E. Snyder. One soldier, kept separately with two workers, possibly holotype, but not so designated on label. # Z2479 : 5 soldiers, 3 workers, 3 reproductive nymphs. BCI, 3.x.1924. Coll. J. Zetek, det. T.E. Snyder.

Coll. J.M. Pasteels. # 71 : BCI, 10.viii.1969. Large sample with soldiers, workers, larvae and reproductive nymphs, from old log.

Coll. Y. Roisin. # PANT7 : BCI, 8.xii.1990. Soldiers, workers and a few nymphs in small earth nest nearby stump occupied by *Embiratermes chagresi* (Snyder). # PANT12 : BCI, 10.xii.1990. Soldiers, workers and two nymphs from rotten stump. # PANT42 : BCI, 27.xii.1990. Soldiers, workers, larvae and reproductive nymphs, next to a nest of *Microcerotermes* sp. in dead palm tree on the ground. # PANT84 : BCI, 7.v.1991. Soldiers, workers, larvae and nymphs in decayed log. # PANT112 : BCI, 5.vi.1991. Soldiers and workers. # PANT118 : BCI, 12.vi.1991. Soldiers and workers under log in forest.



Figs 1-2. — Scanning electron micrographs of soldier heads, dorsal view (left) and profile (right). 1. *Subulitermes zeteki*. — 2. *S. denisae*, paratype. Scale bar = 0.25 mm.

PANT125 : BCI, 15.vi.1991. Soldiers and workers. # PANT155 : BCI, 23.viii.1991. Soldiers, workers, larvae and 1 nymph under bark of log on forest floor.

Imago unknown. Fourth instar nymphs possess antennae with 12 articles, with article 3 presenting two constrictions, suggesting that the alate possesses 14-jointed antennae.

The soldier is the smallest Panamanian humivorous nasute (Table 1). Most specimens have unequivocally 11-jointed antennae, but in some colonies, article 3 tends to be constricted. Head capsule yellow, reddish on rostrum, elongated, almost straight in profile, bearing numerous hairs of various lengths (Fig. 1).

The worker has mandibles (Figs 6, 11) with five to seven ridges on molar prominence, at least 4 on molar plate ; left mandible index 0.90-0.95. Antennae 12-jointed. Digestive tract (Fig. 16) as described for *Subulitermes*. Enteric valve armature composed of six swellings bearing about 25 short spines (Fig. 20). Rudimentary lobes at junction between enteric valve and paunch. Head width unimodal, 0.48-0.57 mm (mean = 0.535 mm ; based on 2 × 100 individuals from colonies # PANT84 and 155).

Subulitermes denisae sp. nov.
(Figs 2, 7, 12, 17, 21)

Material examined :

Type colony : # PANT173 : Pipeline Road, near Limbo Camp, Parque Nacional Soberanía, Panama, 19.ix.1991. Large sample from rotten stump in forest, with soldiers, workers, larvae and reproductive nymphs. Holotype : soldier, in the collection of the IRSN.

Paratype colonies. # PANT19 : BCI, 13.xii.1990. Soldiers, workers and one reproductive nymph from stump of palm tree. # PANT176 : BCI, 27.ix.1991. Soldiers, workers and a few larvae from tree stump. Paratypes will be deposited in the IRSN, STRI and the University of Panama.

Name derivation : this species is dedicated to Denise Thorin, for her continuous support since we met in Panama.

Imago unknown. Nymphs of the fourth instar possess 13-jointed antennae, with article 3 presenting a constriction, suggesting that the alate possesses 14-jointed antennae.

Soldier larger than that of *S. zeteki* (Table 1). Antennae 12-segmented. Overall aspect not so elongated as *S. zeteki*. Head capsule yellow, reddish on rostrum, elongated, almost straight in profile, with 4 long setae at base of rostrum and 2 on vertex, and numerous very small hairs (Fig. 2).

Worker less elongated than in *S. zeteki*. Antennae 13-jointed. Mandibles (Figs 7, 12) very similar to those of *S. zeteki*. Molar prominence with 5-6 ridges, molar plate with at least 5 ridges. Left mandible index 0.75-0.97 (N = 10 workers from type colony). Digestive tube (Fig. 17) very similar to that of *S. microsoma* (see FONTES 1987a, figs 86-89). Enteric valve swellings (Fig. 21) garnished with 5-10 spines. Head width unimodal, 0.59-0.65 mm (mean = 0.62 mm ; based on 2 × 100 individuals from colonies # PANT173 and 176).

Genus *Atlantitermes* Fontes, 1979

Atlantitermes : FONTES, 1979, pp. 220-222.

Type species : *Atlantitermes guarinim* Fontes, 1979.

The original description does not provide diagnostic criteria for this genus. The following peculiarities were mentioned in subsequent papers (FONTES, 1987a, b).

Soldier with slightly, yet distinctly constricted head. Worker mandibles with at least 5 ridges on molar prominence, 4-5 on molar plate. Left mandible index 0.68-0.77, lower than in *Subulitermes*. Digestive tube configuration resembling that of *Subulitermes*. Enteric valve armature composed of six cushions (three large ones alternating with smaller ones), all garnished with small spines on their surface and larger ones on their edge. Weak constriction at junction between enteric valve and paunch.

Atlantitermes kirbyi (Snyder, 1926)
(Figs 3, 8, 13, 18, 22)

Nasutitermes (Subulitermes) kirbyi : SNYDER, 1926, pp. 14-15 (soldier).

Subulitermes kirbyi (Snyder) : SNYDER, 1949, p. 340.

Atlantitermes kirbyi (Snyder) : FONTES, 1982, p. 107.

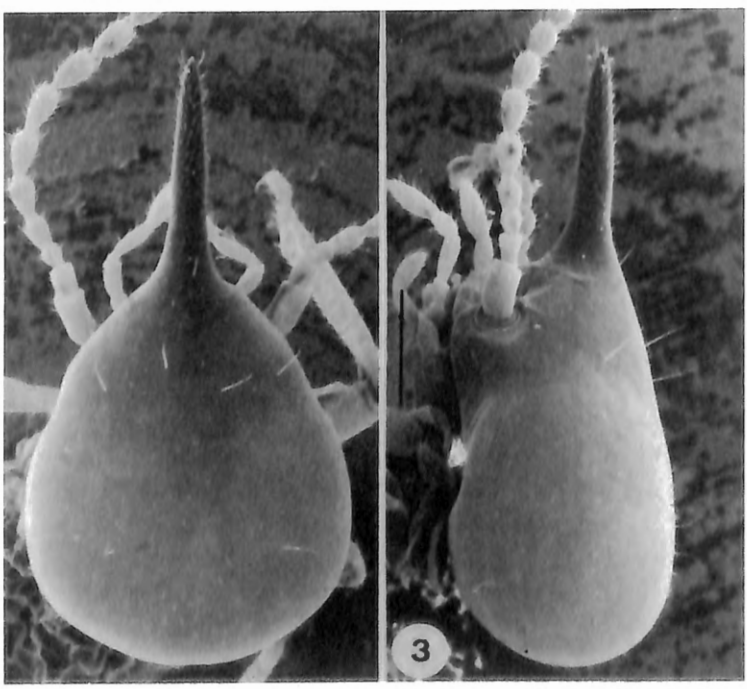


Fig. 3. — *Atlantitermes kirbyi*. Paratype soldier : head in dorsal view (left), in profile (right). Scale bar = 0.25 mm.

Material examined :

NMNH. Holotype soldier, BCI, Canal Zone, Panama, 3.ix.1925. Coll. H. Kirby. Paratype soldiers and workers, same data as holotype.

Soldier with 12-jointed antennae. Head capsule yellow, rostrum reddish. Head capsule (Fig. 3) slightly longer and distinctly wider than in *S. denisae* (Table 1), rostrum shorter and thicker, elevated. Four long setae near base of nose, two on vertex, and many minute hairs.

Worker with 13-jointed antennae. Mandibles as in Figs 8 and 13. Molar prominence and molar plate were worn on the two specimens examined, but the molar prominence showed at least 5 vestigial ridges. No ridge could be seen on the molar plate. Left mandible index difficult to calculate with precision due to mandible wear, but obviously high, near 1.4, on the two specimens examined. Digestive tube (Fig. 18) broader than in *A. guarinim*, paunch more voluminous. Enteric valve preceded by a slight, but distinct constriction. Armature (Fig. 22) as in generic description. Head width, 0.736-0.756 mm (based on 3 individuals from type colony).

Genus *Ereymatermes* Constantino, 1991

Ereymatermes : CONSTANTINO, 1991, pp. 1-7, figs 1-18.

Type species : *Ereymatermes rotundiceps* Constantino, 1991.

This genus was created to accommodate a new species from Brazilian Amazonia.

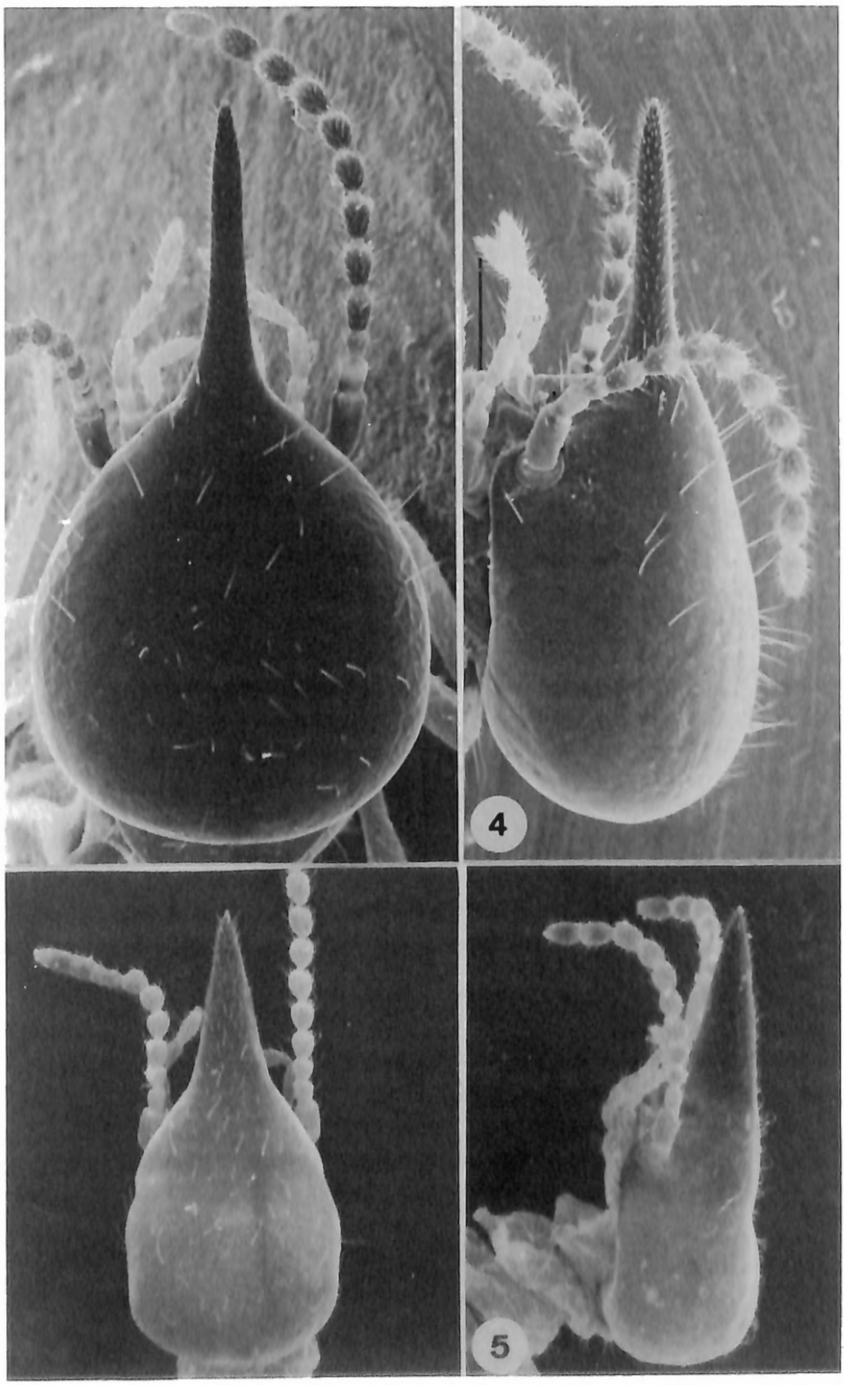
Soldier monomorphic, fully nasute ; rostrum thin, mandibles without points. Head capsule little or not constricted behind antennae ; antennae 12-segmented.

Worker remarkable for the configuration of its digestive tract. Enteric valve situated in a distinctive pocket and constituted by 6 equal flattened protrusions edged with numerous large spines, preceded by 6 dome-shaped swellings with 0-5 tiny spines. First section of the paunch U-shaped, delimited anteriorly by the enteric valve on the left and an almost symmetrical, yet unarmed, constriction to the right.

Ereymatermes panamensis sp. nov.
(Figs 4, 9, 14, 19, 23)

Material examined :

Type colony : # PANT138 : BCI, 24.vi.1991. Soldiers, workers and larvae from underground chambers. Holotype : soldier, in the collection of the IRSN.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Coll. Y. Roisin. # PANT13 : BCI, 10.xii.1990. Soldiers and workers from dead wood on forest floor. # PANT22a : BCI, 14.xii.1990. Soldiers and workers from stump of palm tree.

Imago unknown.

Soldier with 12-jointed antennae. Head capsule yellow, rostrum reddish. Head capsule not constricted behind antennae, pilose, regularly rounded posteriorly, nose thin, cylindrical, slightly upturned (Fig. 4). Very similar to the soldier of *E. rotundiceps*, except for being substantially smaller and having a relatively narrower head capsule. Distinguished from *S. denisae* by larger size (Table 1), wider, more rounded head capsule, covered with more numerous long setae, nasus very thin, slightly elevated. Distinguished from *A. kirbyi* by unconstricted and much more pilose head capsule, and more cylindrical, less elevated nose.

Worker with antennae of 13 segments. Mandibles as in Figs 9 and 14, with numerous but weak molar ridges ; left mandible index 1.5-1.7. General configuration of digestive tube (Fig. 19) and enteric valve (Fig. 23) indistinguishable from those of *E. rotundiceps* (compare with figs 13-17 in CONSTANTINO, 1991). Head width unimodal, 0.65-0.73 mm (mean = 0.695 mm ; based on 100 individuals from colony # PANT138). Distinguished from sympatric *Subulitermes* species by larger apical tooth and left mandible index, weaker molar ridges, and different digestive tract configuration and enteric valve armature. Difficult to distinguish from *A. kirbyi* : in this latter species, the paunch does not show a ventral constriction on the right side of the abdomen, and the enteric valve armature is different.

Genus *Coatitermes* Fontes, 1982

Coatitermes : FONTES, 1982, pp. 104-105.

Type species : *Nasutitermes (Convexitermes) clevelandi* Snyder, 1926.

Soldier monomorphic, fully nasute, with very broad, conical rostrum.

Worker (after FONTES, 1987a, b) with at least 5 ridges on molar prominence, 4-5 on molar plate ; left mandible index 1.00-1.13. Configuration of worker digestive tract similar to that of *Subulitermes*. Enteric valve armature diagnostic, consisting of three major swellings alternating with minor ones, all bearing stout spines of various lengths (see FONTES, 1987a, fig. 60).

Figs 4-5. — Scanning electron micrographs of soldier heads, dorsal view (left) and profile (right). — 4. *Ereymatermes panamensis*, paratype. — 5. *Coatitermes clevelandi*. Scale bar = 0.25 mm.

Coatitermes clevelandi (Snyder, 1926)
(Figs 5, 10, 15, 24)

Nasutitermes (Convexitermes) clevelandi : SNYDER, 1926, pp. 15-16 (soldier, nymph).

Convexitermes clevelandi (Snyder) : SNYDER, 1949, p. 342.

Coatitermes clevelandi (Snyder) : FONTES, 1982, pp. 104-105, figs 9-16 (alate, soldier, worker).

Material examined :

Coll. Y. Roisin. # PANT3 : BCI, 5.xii.1990. Nest in rotten stump in forest. # PANT16 : BCI, 12.xii.1990. From terrestrial mound also occupied by *Anoplotermes parvus* Snyder. # PANT55 : Gigante Peninsula, 21.i.1991. Earth nest around tree stump, with queen, workers, soldiers, larvae and nymphs. # PANT60 : Gigante Peninsula, 29.i.1991. Nest in and under piece of dead wood on the ground, with queen. # PANT106 : Gigante Peninsula, 21.iii.1991. Nest at foot of *Astrocaryum* palm. Mixed with *Anoplotermes parvus*. # PANT128 : BCI, 15.vi.1991. Soldiers, workers, nymphs and alates from earthen sheeting running over crack in live tree, from ground to a height of at least 1.5 m. # PANT183 : Gigante Peninsula, 2.x.1991. Earthen construction about 1.5 cm thick on tree stump, with soldiers, workers, larvae and nymphs. Queen found in cell against the stump. This nest of *C. clevelandi* was contiguous to a nest of *Embiratermes chagresi* (Snyder) ; no aggression was observed between the two species as they came into contact when the nest was dissected.

The description of the imago by FONTES (1982) is adequate and needs few complements. The antenna is 14-segmented in the alate and tends to be so in the last two nymphal instars as well, although segments 3-5 are not completely separated.

Soldier almost as small as in *S. zeteki*. Unmistakable among Panamanian small nasutes for the broad conical shape of its rostrum (Fig. 5). Head capsule yellow, rostrum ferruginous, head capsule and rostrum covered with numerous short setae. Antennae 11-segmented.

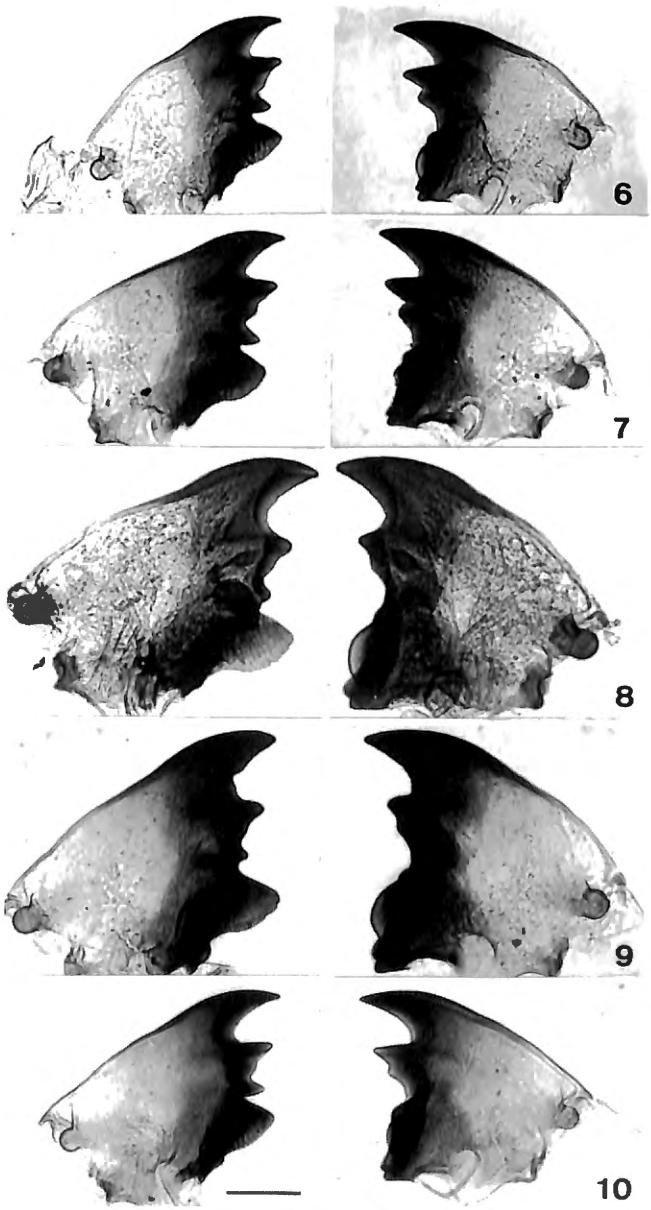
Worker with 12-segmented antennae, as in *S. zeteki*, but overall appearance much less elongated. Mandibles as in Figs 10 and 15. Both molar areas with 5 well-marked ridges and some faint ones. Left mandible index 1.07-1.37 (N = 10 individuals from colony # PANT183). The description of the digestive tract of workers by FONTES (1987a) fits the Panamanian specimens perfectly. Enteric valve armature diagnostic among Panamanian nasutes (Fig. 24). Head width unimodal, 0.57-0.64 mm (mean = 0.60 mm ; based on 3 × 100 individuals from colonies # PANT55, 60 and 183).

TABLE 1

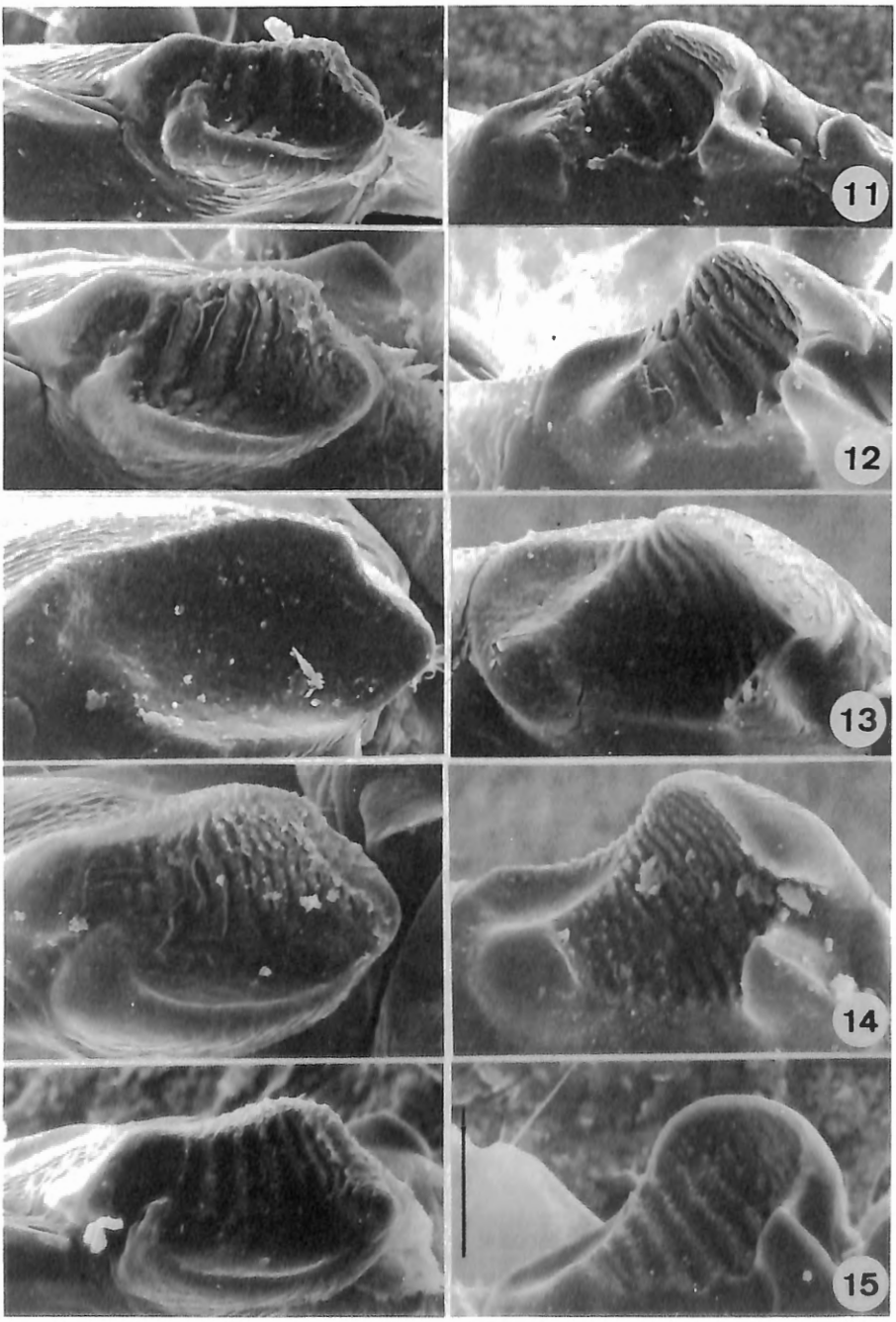
Measurements of soldiers (in mm) of Subulitermes zeteki, S. denisae, Atlantitermes kirbyi *and* Ereymatermes panamensis.

	Subulitermes zeteki 12 soldiers from 4 colonies		*Subulitermes denisae* 9 soldiers from 3 colonies		*Atlantitermes kirbyi* 6 soldiers from type colony		*Ereymatermes panamensis* 9 soldiers from 3 colonies	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
HL	0.985-1.155	1.038	1.175-1.284	1.233	1.272-1.310	1.291	1.338-1.465	1.384
RL	0.376-0.510	0.416	0.504-0.562	0.530	0459-0.488	0.477	0.525-0.577	0.555
HL-RL	0.604-0.645	0.622	0.671-0.722	0.703	0.793-0.825	0.814	0.813-0.888	0.829
HW	0.455-0.517	0.485	0.544-0.610	0.588	0.686-0.692	0.688	0.680-0.812	0.731
RW	0.059-0.070	0.064	0.067-0.072	0.070	0.078-0.090	0.083	0.062-0.075	0.069
HD	0.303-0.381	0.345	0.395-0.439	0.417	0.455-0.486	0.468	0.475-0.541	0.493
T3L	0.473-0.562	0.512	0.626-0.683	0.660	0.689-0.757	0.726	0.683-0.744	0.711
HL:HW	2.074-2.234	2.140	2.023-2.210	2.096	1.848-1.910	1.876	1.804-1.979	1.895
(HL-RL):HW	1.182-1.364	1.285	1.152-1.252	1.194	1.153-1.203	1.183	1.094-1.196	1.135

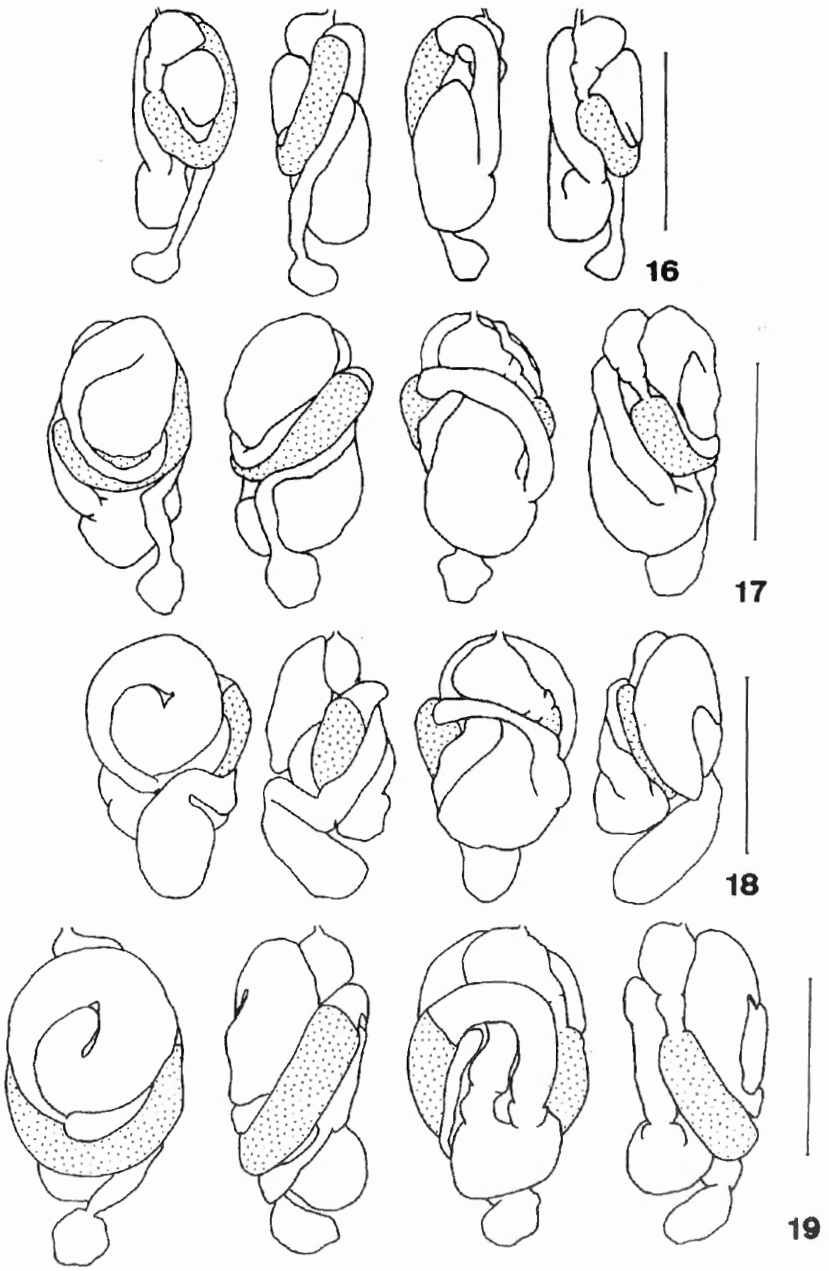
HL, head capsule length ; RL, rostrum length ; HW, head capsule width ; RW, rostrum width (at half length) ; HD, head capsule depth (excluding gula) ; T3L, length of hind tibia.



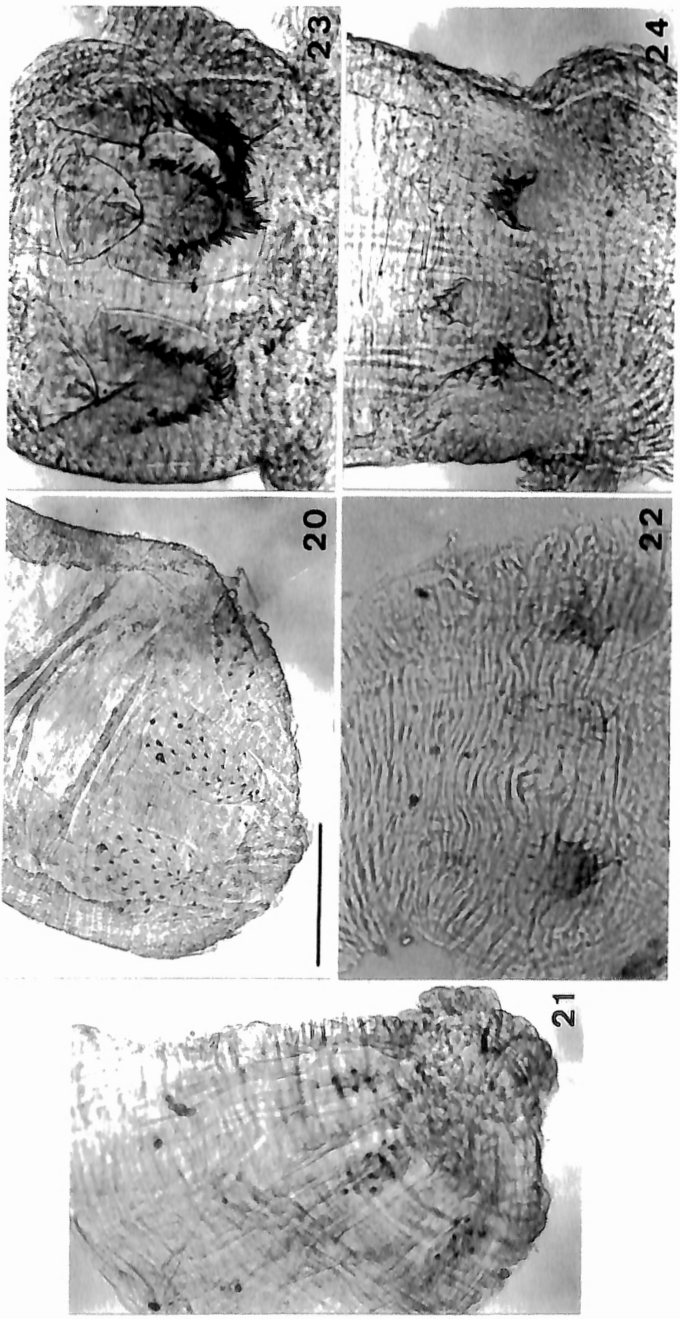
Figs 6-10. — Micrographs of worker mandibles, left and right. — 6. *Subulitermes zeteki.* — 7. *S. denisae*, paratype. — 8. *Atlantitermes kirbyi*, paratype. — 9. *Ereymatermes panamensis*, paratype. — 10. *Coatitermes clevelandi.* Scale bar = 0.1 mm. All left mandibles shown here are of the « narrow gap » type of FONTES (1987b), which is the more frequent; in some individuals (« broad gap »), there is a larger space between the third marginal tooth and the edge of the molar prominence. The meaning of these variations, without consequence for the identification of Panamanian nasutes, is under study.



Figs 11-15. — Scanning electron micrographs of molar areas of worker mandibles. Left, molar plate (right mandible); right, molar prominence (left mandible). — 11. *Subulitermes zeteki*. — 12. *S. denisae*, paratype. — 13. *Atlantitermes kirbyi*, paratype. — 14. *Ereymatermes panamensis*, paratype. — 15. *Coatitermes clevelandi*. Scale bar = 0.05 mm.



Figs 16-19. — Configuration of the worker digestive tube *in situ*. — 16. *Subulitermes zeteki*. — 17. *S. denisae*, paratype. — 18. *Atlantitermes kirbyi*, paratype. — 19. *Ereymatermes panamensis*, paratype. Viewed successively from above, right, below, left. Mesenteron stippled, malpighian tubules not represented. Scale bars = 1.0 mm. For adequate representations of the digestive tube of *Coatitermes clevelandi*, see FONTES (1987a : figs 74-77).



Figs 20-24. — Longitudinal sections of enteric valve. — 20. *Subulitermes zeteki*. — 21. *S. denisae*, paratype. — 22. *Atlantitermes kirbyi*, paratype. — 23. *Ereymatermes panamensis*, paratype. — 24. *Coatitermes clevelandi*. Sections shown on Figs 22 and 24 feature a minor spine-bearing swelling between two major ones. Scale bar = 0.1 mm.

DISCUSSION

FONTES (1982, pp. 100-101) created the genus *Araujotermes* (type species : *Araujotermes caissara* Fontes, 1982) and proposed to transfer *Subulitermes zeteki* to it. *Araujotermes* is distinguished by the following criteria (FONTES, 1982, 1987a, b) : soldier with longer hairs than *Subulitermes* or *Atlantitermes* ; head capsule not constricted (contrary to *Atlantitermes*), nose not elevated (contrary to *Subulitermes* and *Atlantitermes*) ; worker mandibles with at least 5 ridges on molar prominence and 4-5 on molar plate, left mandible index 0.80-0.83 ; apical tooth of mandibles less developed than in *Subulitermes* ; enteric valve armature very similar to that of *Subulitermes* ; two lobes at junction of enteric valve with paunch (none in *Subulitermes* and *Atlantitermes*).

The main argument to support the transfer of *S. zeteki* to *Araujotermes* is its worker mandible morphology, which appears closer to *A. caissara* than to *S. microsoma* by the number of molar ridges, although this number is often difficult to determine unambiguously (see figs 68-69 in FONTES, 1987b). However, the left mandible index of *S. zeteki* falls midway between the figures given by FONTES (1987b) for *Subulitermes* and *Araujotermes*. *S. microsoma* and *A. caissara* have very similar gut configurations and enteric valve armatures : a small difference is the presence of lobes at the junction between the enteric valve and the paunch in *A. caissara*. In this respect, *S. zeteki* is intermediate between these two species. By its number of enteric valve spines, *S. zeteki* resembles more *A. caissara*, but this number often varies between species wihin a single genus. The head profile of *S. zeteki* soldiers is almost straight, as in *A. caissara*. Finally, *S. zeteki* is unique for its 11-segmented antennae in the soldier, although in some colonies, the third antennal article shows signs of division. The worker of *S. denisae* comes close to *A. caissara* by its mandibular characters ; however, its digestive tube resembles more that of *S. microsoma* by the enteric valve armature, the shape of paunch and the complete absence of lobes at the junction between enteric valve and paunch. The soldier of *S. denisae* is much less hairy than that of *A. caissara*.

The soundness of the distinction between *Araujotermes* and *Subulitermes* is difficult to appreciate without comparative data on a large array of species. Unfortunately, FONTES' (1987a, b) anatomical work is limited to the type species of each genus. *S. zeteki* resembles more *A. caissara* than *S. microsoma*, but *S. denisae* is intermediate between these species in several respects. Gut configurations and left mandible indices do not allow a clear separation of the two genera. Minor variations in soldier head profile or pilosity can hardly be used as diagnostic characters at the genus level. The absence of unambiguous diagnostic criteria suggests that *Araujotermes* should be treated as a junior synonym of *Subulitermes*. I therefore propose to retain the combination *Subulitermes zeteki*.

The transfer of *Subulitermes kirbyi* to *Atlantitermes*, proposed by FONTES (1982), is supported by the constricted shape of the soldier's head capsule, very similar to that of *A. guarinim*. The enteric valve armature of the worker is well developed and

greatly resembles FONTES' (1987a : Fig. 61) drawings of *A. guarinim*. However, the worker gut of *A. kirbyi* appears broader than that of *A. guarinim* (compare Fig. 18 herein with figs 90-97 in FONTES, 1987a), and its left mandible index is considerably higher (1.4 vs 0.77 ; compare Fig. 8 herein with figs 13-15 in FONTES, 1987b). In addition, the molar plate of the two examined paratypes of *A. kirbyi* was completely devoid of ridges (compare Fig. 13 herein with figs 64-65 in FONTES, 1987b), although one cannot exclude that this condition was due to mandible wear. Mandibular characters thus favor the removal of *A. kirbyi* from *Atlantitermes*, but soldier morphology and worker enteric valve armature go against it. Thus far, for the sake of nomenclatorial stability, it seems wise to retain the combination *A. kirbyi*, although this implies an extension of the definition of the genus *Atlantitermes*.

Nowadays, characters of the worker mandibles (left mandible index, molar ridges) and digestive tube (general configuration, armature of enteric valve, etc.) are often considered diagnostic at the genus level in termite taxonomy. However, none of the three abovementioned species fits precisely within any existing genus when all those criteria are considered. Such discrepancies outline the need for reliable phylogenetic studies, which would allow an assessment of all characters traditionally used in the generic taxonomy of humivorous nasutes. Characters of the worker mandible seem especially subject to caution. The whole complex of genera related to *Subulitermes* might have to be revised when data on a sufficient number of species are available.

The remaining species of Panamanian humivorous nasutes belong to better defined genera. *Ereymatermes panamensis* is very similar to *E. rotundiceps* ; in particular, both species have almost identical mandibles, gut configurations and enteric valves, which leaves no doubt that they are congeneric. As to *Coatitermes clevelandi*, the present observations of Panamanian samples of this species, collected at or near the type locality, corroborate those of FONTES (1982, 1987a, b) on Brazilian specimens. They support the validity of the genus *Coatitermes*, created to accommodate this species (FONTES, 1982).

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