

REVISTA BRASILEIRA DE ZOOLOGIA

Revista brasileira de Zoologia, S. Paulo 3 (8): 503-531

31.V.1987

MORPHOLOGY OF THE ALATE AND WORKER MANDIBLES OF THE SOIL-FEEDING NASUTE TERMITES (ISOPTERA, TERMITIDAE, NASUTITERMITINAE) FROM THE NEOTROPICAL REGION

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ABSTRACT. The morphology of the mandibles of the alates and workers of the 8 soil-feeding genera with nasute soldiers from the Neotropical Region is studied. Three mandibular patterns are recognized : (1) Convexitermes, Atlantitermes, Araujotermes, Coatitermes, Subulitermes and Agnathotermes have mandibles with complete marginal dentition and no reduced teeth, (2) Angularitermes has mandibles with complete marginal dentition but two teeth are vestigial, and in (3) Cyronotermes the marginal dentition is incomplete. A set of other characteristics is associated with each of these mandibular patterns. Intraspecific variation are registered, either between the alate and the worker castes of all genera, as between the worker types of the dimorphic worker caste of the genera with complete and developed marginal dentition. Such dimorphism was previously unreported for the soil-feeding Nasutitermitinae; the soldier arises from one worker type.

The mandibular morphology is highly adaptive to the soil diet, in a similar way either in the soil-feeding nasutes as in other soil-feeding termites. The function of the molar tooth in the soil-feeding termites is discussed, and new characteristics of the molar regions are presented.

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I. INTRODUCTION

The morphology of alate and worker mandibles has played an important role in termite systematics. It was used for the classification and phylogeny of the Isoptera, proposed respectively by Holmgren (1911, 1912) and Hare (1937), and since Ahmad's (1950) extensive phylogenetic study it has been a prominent part of all larger works on taxonomy and phylogeny (e. g. Krishna, 1961, 1968; Sands, 1965, 1972; Sen-Sarma, 1969) and in most descriptions of new genera and species.

The aim of this work is to describe the morphology of the dentition and molar regions of the alate and worker mandibles of the eight soil-feeding genera with nasute soldiers from the Neotropical region, in order to recognize mandibular patterns and adaptations to the soil-feeding habit. Comparisons have been made to the mandibles of the six genera of soil-feeding nasutes from the Ethiopian region, which were adequately described in the revisions of Emerson (1960b) and Sands (1965), and to a lesser extent to the mandibles of other soil-feeding Termitidae, of the subfamilies Apicotermitinae, Termitinae and Nasutitermitinae. Mandibular morphology proved to be highly adaptive to soil diet.

II. TERMINOLOGY

II.1. Mandibles

The mandibles of the alates are similar to those of the workers. Each mandible bears an apical tooth, two marginal teeth, and a molar region at the base. The parts are named according to the nomenclature utilized by Emerson (1933) and Ahmad (1950:46), with the modifications introduced by Krishna (1968: 265), for the dentition, and by Sands (1972 : 6), for the molar regions:

LEFT MANDIBLE (fig. 1) : apical tooth (A); first + second marginal tooth (M1 + 2); third marginal tooth (M3); molar tooth (Mt); molar prominence (mpr), with or without ridges on crushing surface.

RIGHT MANDIBLE (figs. 2-3): apical tooth (A); first marginal tooth (M1); second marginal tooth (M2); molar plate (mpl), with basal notch (bn) and apical thickenings (at), and with or without ridges on crushing surface.

The nomenclature adopted for the parts of the molar regions deserves a word of explanation. The term "ridges" was used by Sands (1965 : 10) to designate the transverse grinding processes which may be present on the crushing surface of the molar regions of both mandibles, and is applied in the same sense in this paper. The notch originated by the sinuate course of the dorsal margin of the molar plate of the right mandible, readily recognizable in front (and sometimes also in side) view of the plate, was previously treated as "indentation near basal end of anterior margin of molar plate" (Sands, 1965: 51) and as "basal indentation" (Sands & Lamb, 1975: 191), and is here designated basal notch (fig. 2, bn). Finally,

the prominent apical swellings of the dorsal and ventral margins of the right molar plate, previously unnamed, in this paper are designated apical thickenings (fig. 2, at.).

Other structures requiring further explanation are discussed in the following sections, when necessary.

The development of the apical teeth compared to the marginals, within a caste, is expressed through the left mandible index, defined by Emerson (1960a: 5-6) as the linear distance between the tips of the apical and first + second marginal teeth divided by the linear distance between the tips of the first + second marginal and third marginal teeth.

II.2. Workers

The worker caste is dimorphic in the genera *Convexitermes*, *Atlantitermes*, *Araujotermes*, *Coatitermes*, *Subulitermes* and *Agnathotermes*. The two worker types, very similar in morphology, differ in the mandibles, especially in the width of the gap between the third marginal tooth and the molar prominence of the left mandible (fig. 1, M3, mpr), and are referred to as "worker with narrow gap" and "worker with broad gap".

III. METHODS

Specimens were studied under ethanol 80%.

The study of the mandibles is easier if they are not detached from the head, but just opened enough in order to expose their dentition and molar regions. To achieve this, the inner muscles that connect each mandible to the head were cut out (preferably from the ventral face of the head) with sharp pincers, the outer muscles being kept intact, and the mandibles then opened by their bases with fine needles or pincers. The mandibles then remained steady in an open position, and moved freely when touched. The head was not separated from the body, and the labrum, maxillae and antennae were removed when necessary.

Quality steel pincers with slender points were used in cutting out mandibular muscles for the opening of the mandibles. The arm's point edges have been sharpened with a commercial abrasive oilstone, thus acting like small knives. Such cutting pincers are somewhat laborious to construct and have to be handled with care because the points are easily broken, but are very precise and easy to operate.

A small Petri dish half filled with clean beach sand has served to the aim of immobilizing the specimens in study. White sand was used for drawings, but for other purposes dark sand is more comfortable to the eyes. All figures have been drawn with the aid of a camera lucida coupled to a Zoom binocular (maximum helpful magnification 200X). Workers whose mandibles showed signs of wear by use were avoided. The masticatory ridges on the crushing surface of the molar regions, if not absent, are poorly developed and very difficult to see at the binocular; when enough specimens were available, the mandibles were dissected out and the molar regions electromicrographed.

The left mandible index was calculated for a single specimen of each caste (one of each worker type, in the genera with dimorphic worker caste). Measurements were taken from the rough drafts of the drawings, which are considerably larger and thus more adequate for measurements than the figures shown. When available, the mandibles of up to ten other specimens were compared to that of the one measured, with the aid of a Zoom binocular.

IV. MATERIAL

The eight nasute genera of soil-feeding termites from the Neotropical region have a total of 27 described species. The number of species in each genera is given in parentheses: *Agnathotermes* (1), *Angularitermes* (3), *Araujotermes* (3), *Atlantitermes* (7), *Coatitermes* (4) *Convexitermes*, (4) *Cyranotermes* (1) and *Subulitermes* (4). Complete bibliography for each taxon is given in Araujo (1977) and Fontes (1983).

Thirteen nest-series representing 1 species of each genus were studied. Type-species were selected whenever possible, but species studied are preferably those for which more specimens of both alate and worker castes became available. The alate caste of *Convexitermes* sp is unknown, so that the mandibles of the alates of *C. manni*, a close species for which scanty material was available, were studied. Alates of *Angularitermes orestes*, or of any of the 2 other species of this genus, were also not available; the mandibles of the workers of *A. orestes* are usually strongly worn. Much of the material is deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP). One nest-series came from the British Museum (Natural History) (BMNH), through the courtesy of Dr. William A. Sands and Mr. Solomon S. Bacchus.

Agnathotermes glaber. Brazil, State of Minas Gerais: Curvelo, 14.XI.1972, R.L. Araujo col., nest-series nr 5784 (MZSP), alates and workers.

Angularitermes orestes. Brazil, State of Minas Gerais: Curvelo, 10.II.1972, R.L. Araujo col., nest - series nr 5018 (MZSP), workers.

Araujotermes caissara. Brazil, State of São Paulo: Itanhaém, 23.III.1978, L.R. Fontes col., nest-series nr 7606 (MZSP), 1 king, 1 queen, workers; State of Santa Catarina: Itapema, 19.VII.1978, R.L. Araujo & L.R. Fontes col., nest-series nr 7685 (MZSP), alates and workers.

Atlantitermes quarinim. Brazil, State of São Paulo: Itanhaém, 23.II.1978, L. R. Fontes & F. S. Berchez col., nest-series nr 7598 and 7599 (MZSP), 2 kings, 2 queens, workers.

Convexitermes manni. Guyana, Orenoque River, 30.VII.1936, N. Weber col., nest-series nr 3500 (MZSP), 2 alates.

Covexitermes sp. Brazil, State of Mato Grosso: Utiariti (Rio Papagaio), 24.X.1966, K. Lenko col., nest-series nr 8057 (MZSP), workers.

Cyranotermes timuassu. Brazil, State of Minas Gerais: Bocaiuva, 25.VII.1975, R.L. Araujo col., nest-series nr 5936 (MZSP), workers; Distrito Federal : Brasília, 14.IX.1976, R. L. Araujo col., nest-series nr 6868 (MZSP), alates and workers.

Subulitermes microsoma. Brazil, State of Mato Grosso: Jaraguá, 25.X.1953, R.L. Araujo col., nest-series nr 3919 (MZSP), alates and workers; Chapada dos Guimarães, 6.II.1976, R.L. Araujo col., nest-series nr 6642 (MZSP), workers.

V. MORPHOLOGY OF THE MANDIBLES OF THE NEOTROPICAL SOIL-FEEDING NASUTES

The genera can be separated into 3 groups, according to the mandibular pattern:

Group 1. Marginal dentition complete and without reduced teeth: *Convexitermes*, *Atlantitermes*, *Araujotermes*, *Coatitermes*, *Subulitermes* and

Agnathotermes. Left mandible index 0.66-1.91, marginal teeth developed and presence of vestigial ridges in the molar regions (found at least in the left mandible). Presence of a dimorphic worker caste, recognizable only by the mandibles ("worker with narrow gap" and "worker with broad gap").

Group 2. Marginal dentition complete and with two reduced teeth: *Angularitermes*. Left mandible index (unknown in the alate) of worker 1.46, third marginal tooth of left mandible and second marginal tooth of right mandible reduced but distinct, and molar regions without ridges. Presence of a monomorphic worker caste.

Group 3. Marginal dentition incomplete: *Cyranotermes*. Left mandible index of alate 2.00 and of worker 2.64, third marginal tooth of left mandible reduced but distinct, second marginal tooth of right mandible absent, and no ridges in the molar regions. Presence of a monomorphic worker caste.

V.1. Dentition

V.1.a. Group 1 : Marginal dentition complete and without reduced teeth (figs. 1-54)

The mandibles of each worker type and of the alate have about the same size. Those of the alates are similar in both sexes.

Left mandible, general characteristics: apical tooth with posterior margin concave (more marked in *Subulitermes* and *Agnathotermes*); first + second marginal tooth with anterior margin straight; third marginal tooth with posterior margin convex, smaller than the first + second marginal tooth and a little smaller in the "worker with broad gap"; molar tooth as developed as or larger than the third marginal tooth and mostly hidden beneath the molar prominence.

Right mandible, general characteristics: apical tooth with posterior margin concave (more marked in *Subulitermes* and *Agnathotermes*); first marginal tooth with anterior and posterior margins straight; second marginal tooth with rounded point and smaller than the first marginal tooth, a little smaller in *Agnathotermes* than in the remainder genera; posterior margin of second marginal tooth concave.

"Worker with narrow gap", left mandible: cutting edge between the first + second marginal tooth and the third marginal tooth sinuate in *Convexitermes*, *Atlantitermes*, *Araujotermes* and *Subulitermes* (figs. 4, 13, 22, 40), weakly or not sinuate in *Coatitermes* (fig. 31), and not sinuate in *Agnathotermes* (fig. 49); gap between the third marginal tooth and the molar prominence narrower than the width of the basis of the third tooth (more marked in *Subulitermes*, fig.40).

"Worker with narrow gap", right mandible: point of second marginal tooth at about half distance between the point of the first marginal tooth and the molar plate.

"Worker with broad gap", left mandible: gap between the third marginal tooth and the molar prominence only a little wider than in the "worker with narrow gap" in *Convexitermes* and *Agnathotermes* (figs. 7, 52), and notably wider in the remainder genera; gap about as wide as the basal width of the third marginal tooth in *Convexitermes*, *Coatitermes*, *Subulitermes* and *Agnathotermes* (figs. 7, 34, 43, 52), and markedly wider in *Atlantitermes* and *Araujotermes* (figs. 16, 25).

"Worker with broad gap", right mandible: point of second marginal tooth closer to the point of the first marginal tooth than to the molar plate in *Convexitermes* and *Atlantitermes* (figs. 9, 18) and at about half distance between the point of the first marginal tooth and the molar plate in the remainder genera.

Alate, left mandible: cutting edge between the first + second marginal tooth and the third marginal tooth not sinuate in *Atlantitermes* (fig. 10); width of gap between the third marginal tooth and the molar prominence intermediate between

the width in each of the worker types; molar tooth more hidden beneath the molar prominence than in the workers.

Alate, right mandible: point of second marginal tooth closer to the point of the first marginal tooth than to the molar plate in *Covexitermes* and *Atlantitermes* (fig. 3, 12; as in the "worker with broad gap", figs. 9, 18), and at about half distance between the point of the first marginal tooth and the molar plate in the remainder genera (as in both worker types).

V.1.b. Group 2: Marginal dentition complete and with two reduced teeth (figs. 55-57)

From the description and figure of Mathews (1977 : 233-234, fig. 166), it seems that the dentition of the mandibles of the alate of *Angularitermes orestes* is similar to that of the worker.

Left mandible (fig.55) : apical tooth with posterior margin strongly concave; cutting edge between the first + second marginal tooth and the third marginal tooth sinuate; third marginal tooth very reduced and visible as a pointed projection in front of the molar tooth; gap between the third marginal tooth and the molar prominence narrow; molar tooth developed and mostly hidden beneath the molar prominence.

Right mandible (fig. 57) . apical tooth with posterior margin strongly concave; second marginal tooth visible as a rounded projection at about half distance between the point of the first marginal tooth and the molar plate; posterior margin of the second marginal tooth concave.

V.1.c Group 3: Marginal dentition incomplete (figs. 58-63)

The mandibles of the alate are similar in both sexes, and considerably smaller and less sclerotised than in the worker.

Worker, left mandible (fig. 61) : apical tooth with posterior margin strongly concave; cutting edge between the first + second marginal tooth and the third marginal tooth regularly concave; third marginal tooth very reduced and visible as a rounded projection anterior to the molar tooth, gap between the third marginal tooth and the molar prominence wide; molar tooth developed, just a small part hidden beneath the molar prominence (the point of the molar tooth is visible in the gap between the third marginal tooth and the molar prominence).

Worker, right mandible (fig. 63) : apical tooth with posterior margin strongly concave; cutting edge between the first marginal tooth and the molar plate concave.

Alate, left mandible (fig. 58) : cutting edge between the first + second marginal tooth and the third marginal tooth sinuate; third marginal tooth very reduced, visible as a pointed projection in front of the molar tooth; gap between the third marginal tooth and the molar prominence wider than in the worker.

Alate, right mandible (fig. 60) : as in the worker.

V.2 Development of the Apical Tooth (table 1)

Before presenting our data, it is convenient to point out that: (1) only one specimen of each caste of the studied species was measured for estimation of the left mandible index, so that the ranges of index variation are unknown, (2) in the smaller mandibles it is difficult to make precise measurements and therefore 0.10 or 0.20 variations in the value of the indices are not necessarily significant, as already noted by Emerson (1960a: 6), and (3) by being three-dimensional structures, the mandibles have to be carefully positioned to be strictly comparable, but

TABLE 1 — Left mandible index of the alate and worker castes of the soil-feeding nasute genera from the Neotropical Region

	Alate	Worker	
		"narrow gap"	"broad gap"
<i>Convexitermes</i>	0.66	0.77*	0.78
<i>Atlantitermes</i>	0.81	0.77*	0.68
<i>Araujotermes</i>	0.82	0.83*	0.80
<i>Coatitermes</i>	0.85	1.13*	1.00
<i>Subulitermes</i>	1.17	1.02	1.12*
<i>Agnathotermes</i>	1.67	1.91	1.88*
<i>Angularitermes</i>	—		1.46
<i>Cyranotermes</i>	2.00		2.64

* more frequent worker type

slight variation is inevitable in the smaller ones. By these reasons, strict comparisons of the estimated indices, either between genera or between the castes of a species, would be worthless and could lead to misleading conclusions.

As can be drawn from table 1, the left mandible index: (1) is higher in the worker than in the alate in *Cyranotermes*, and in this genus considerably higher than in the alates and workers of the remainder genera, (2) is higher in the worker of *Angularitermes* than in the alates and workers of *Subulitermes*, *Araujotermes*, *Atlantitermes* and *Convexitermes*, (3) is higher in the alate and worker of *Agnathotermes* than in the alates and workers of the genera (in supposed sequence of decreasing mandibular indices) *Subulitermes*, *Coatitermes*, *Araujotermes*, *Atlantitermes* and *Convexitermes* and (4) is higher in the alate and worker of *Subulitermes* than in the alate and worker of *Convexitermes*.

The genus *Angularitermes* still deserves a word of explanation, as the index of the alate left mandible is unknown. Mathews (1977 : 233) gives a value of about 0.77 for the left mandible index of the alate of *A. orestes*, but this was obtained by dividing the distance between the apical tooth and first + second marginal tooth by the distance between the first + second marginal tooth and the molar prominence (this was called "modified left mandible index" by Mathews), instead of dividing the first measurement above by the distance between the first + second marginal tooth and the third marginal tooth (index of Emerson), as adopted in this paper. The "modified left mandible index" for the worker of *A. orestes*, the sole caste studied in this paper, is approximately 1.15 and therefore considerably higher than in the alate.

Form the comparisons above (table 1), it is clear that the apical teeth are larger in the genera of group 3, and in group 2 (at least in the worker.) larger than in most of the genera of group 1.

V.3. Molar Tooth

The particular condition of the molar tooth in each of the studied genera was described in section V.1.

The molar tooth is similarly well developed in both alate and worker castes. The molar tooth is joined to the molar prominence through almost all the tooth length, by a palte-like projection of the molar prominence, more or less perpendicular to the tooth (figs. 66, 70, 72,). Consequently, a rounded, spoon-like chamber, opened posteriorly, is constructed at the distal portion of the left molar region.

V.4. Molar Regions

V.4.a. Molar prominence

In all genera the apex of the molar prominence extends well beyond the point of the molar tooth, and the inner surface is concave, tapering posteriorly and terminating in a narrow and somewhat tooth-like basal process.

In the genera with marginal dentition complete and without reduced teeth (- group 1) the molar prominence of the "worker with broad gap" is a little narrower than in the "worker with narrow gap". The molar prominence of the alate can be as wide as or narrower than in the workers, and its apex is pointed in *Convexitermes* and *Coatitermes* (figs. 1, 28).

In *Angularitermes* (group 2) the molar prominence of the alate (cf. Mathews, 1977, fig. 166) seems to be narrower than in the worker, in which it is very wide and has a rounded apex (fig. 55).

In *Cyranotermes* (group 3) the molar prominence of the alate (fig. 58) tapers more regularly towards the apex than in the worker (fig.61).

V.4.b. Molar plate

In all genera the molar plate is longer than its width and has a distinctly concave surface, due to the development of rounded and prominent margins on both sides. In Profile, the dorsal margin is concave, and the ventral margin convex. In frontal view, the dorsal margin (right side of the figures) is sinuate, and the ventral margin convex.

In the genera of group 1 the molar plate of the "worker with broad gap" is about as wide as in the "worker with narrow gap" in *Convexitermes* and *Atlantitermes* (figs. 5, 8, 14, 17), a little narrower in *Araujotermes*, *Subulitermes*, and *Agnathotermes* (figs. 23, 26, 41, 44, 50, 53), and much narrower in *Coatitermes* (figs. 32, 35). The molar plate is narrower in the alate than in the "worker with narrow gap" in all genera, and narrower in the alate than in the "worker with broad gap" in *Convexitermes*, *Atlantitermes*, *Subulitermes* and *Agnathotermes*; in *Araujotermes* and *Coatitermes* the molar plate has about the same width in the alate and "worker with broad gap".

In *Angularitermes* (group 2) the molar plate of the worker seems to be as wide as in the alate (cf. Mathews, 1977: 234).

In *Cyranotermes* (group 3) the molar plate is much narrower in the alate than in the worker (figs. 59, 62).

The apical thickenings are always well developed; the ventral one is visible even in dorsal view of the mandibles.

The basal notch, in profile, is weakly recognizable in the worker in *Atlantitermes*, *Agnathotermes* and *Cyranotermes* (figs. 15, 18, 51, 54, 63), and weakly recognizable or unrecognizable in the alate in all genera.

V.4.c. Ridges (figs. 64-73; table 2)

Rudimentar, present only in the mandibles with complete marginal dentition and without reduced teeth (group 1).

Molar prominence. Ridges are present in the alate and worker castes of all genera. Basal ridges are more developed than the apical ones. The smallest number of ridges (around three) is found in *Subulitermes* (figs. 37, 40, 43, 68).

Molar plate. Ridges are present at least in the worker caste, and do not cross the whole surface of the molar plate. The ridges, at least the apical ones, disappear near the ventral margin (left side of the figures) of the molar plate in *Convexitermes*, *Atlantitermes* and *Araujotermes* (figs. 2, 5, 8, 11, 14, 17, 20, 23, 26, 65, 67). They are present only in the dorsal half (right side of the figures) of the molar plate, and are also apparently less numerous, in *Coatitermes*, *Subulitermes* and *Agnathotermes* (figs. 29, 32, 35, 41, 44, 50, 53, 69); no ridge is present in the molar plate of the alate in *Subulitermes* and *Agnathotermes* (figs. 38, 47, 71).

VI. DISCUSSION

The Neotropical genera of soil-feeding nasutes can be separated into three groups, according to the mandibular pattern. The main characteristics of each group were given when introducing section V.

VI.1. Comparison to the Mandibles of other soil-feeding Termites

The soil-feeding nasutes from the Ethiopian Region (Emerson, 1960b; Sands, 1965) have two patterns of mandibles, corresponding exactly to groups 1

TABLE 2 — Number of ridges in the molar regions of the mandibles of the alate and worker castes of the soil-feeding nasute genera from the Neotropical Region

	Alate		Worker			
	mpr	mpl	"narrow gap"		"broad gap"	
			mpr	mpl	mpr	mpl
<i>Convexitermes</i>						
<i>Atlantitermes</i>	5 or +	5-6	5 or +	5-6	5 or +	5-6
<i>Araujotermes</i>						
<i>Coatitermes</i>	5 or +	4-5	5 or +	4-5	5 or +	4-5
<i>Subulitermes</i>	± 3	0	± 3	4-5	± 3	4-5
<i>Agnathotermes</i>	4 or +	0	4 or +	4-5	4 or +	4-5
<i>Angularitermes</i>	0	0			0	
<i>Cyranotermes</i>	0	0			0	

mpr, molar prominence; mpl, molar plate

and 3 described in the preceding section; no genus has mandibles like those of *Angularitermes* (group 2). The range of left mandible index variation is similar in the Ethiopian and Neotropical genera, and the indices are higher in those having mandibles with incomplete dentition (group 3). A comparison of the mandibles of Neotropical and Ethiopian nasutes is given in table 3.

The Ethiopian genera *Afosubulitermes*, *Eutermellus* and *Verrucositermes* are included in group 1. Their left mandible indices range from 0.89 (alate of *Afosubulitermes*) to 1.62 (worker of *Eutermellus*). Vestigial ridges are present at least in the left molar prominence. Like in *Convexitermes*, *Araujotermes* and *Subulitermes*, in both alate and worker castes of *Eutermellus* and *Verrucositermes* the cutting edge between the first + second marginal tooth and the third marginal tooth of the left mandible is sinuate, and like in *Atlantitermes*, in *Afosubulitermes* the cutting edge is sinuate in the worker, but not in the alate.

A dimorphic worker caste, each worker type differing by the mandibles, has not been reported for any of the Ethiopian genera belonging to group 1, but this requires investigation. Concerning the ridges of the molar regions (table 2), in the Neotropical genera of group 1 there appears to be a tendency towards a reduction in the length and number of ridges in the right molar plate, associated with an enlargement of the apical teeth. Thus, *Coatitermes*, *Subulitermes* and *Agnathotermes*, with indices higher than in *Covexitermes*, *Atlantitermes* and *Araujotermes*, have ridges crossing only half width, or less, of the molar plate; in *Subulitermes* and *Agnathotermes*, with the highest indices in the group, there are no ridges at all in the molar plate of the alates.

The Ethiopian genera *Postsubulitermes*, *Mimeutermes* and *Tarditermes* are included in group 3. Their left mandible indices range from 2.00 to 3.59 (respectively alate and worker caste of *Mimeutermes*). Ridges are completely absent in the molar regions of both mandibles. Like in *Cyranotermes*, in *Mimeutermes* the index of the left mandible is markedly higher in the worker than in the alate, and in *Mimeutermes* and *Tarditermes* (and possibly also in *Postsubulitermes*) the molar plate of the right mandible is narrower in the alate than in the worker. The worker caste is monomorphic.

There are eight genera with mandibulate soldiers in the subfamily Nasutitermitinae, all from the Neotropical region. Four of them, *Paracornitermes*, *Labiatermes*, *Armitermes* (some species) and *Curvitermes*, feed on soil. The mandibles of the alates and workers of these four genera (Mathews, 1977 : 205, 207, 210, 221, figs. 160-165; and personal observation) present developed apical tooth (left mandible index 0.8-2.3), larger than the first marginals, and concave molar plate devoid of ridges and with developed apical thickenings and clear basal notch; they are thus similar to the mandibles of the soil-feeding nasutes.

The remainder genera of the Nasutitermitinae, with either mandibulate or nasute soldiers, do not feed on soil. Their mandibles have apical teeth less developed than (or at most as developed as the smallest ones of) in the mandibles of the soil-feeding genera, the indices being around 0.5; some species of *Armitermes*, however, which appear to feed on decaying organic matter, have larger apical teeth (left mandible indices around 0.8; Mathews, 1977 : 210, figs. 161-163), what might represent an adaptation to exploit their particular sources of food. The second marginal tooth is usually more developed than in the soil-feeding nasutes. The molar regions have always prominent ridges, variously developed. In *Nasutitermes* (Sands & Lamb, 1975: 191, figs. 1-4; Mathews, 1977, plate 14; Fontes & Terra, 1981, figs. 12-14) a nasute genus whose species feed on hard woody materials, the molar regions are strongly ridged; the molar plate of the right mandible is flat and has 9-12 ridges across its whole width, a poorly developed or absent basal notch, and no apical thickening. In *Leptomyxotermes* (Sands, 1965: 51-53, figs. 163-165), *Kaudernitermes* (Sands & Lamb, 1975 figs. 8-11) and

TABLE 3 — Main characteristics of the mandibles of the alate and worker castes of the soil-feeding nasute genera from the Neotropical and Ethiopian Regions

	Marginal dentition	Ridges on the molar regions	Left mandible index	
			Alate	Worker
<i>Convexitermes</i>				
<i>Atlantitermes</i>				
<i>Araujotermes</i>				
<i>Coatitermes</i>				
<i>Subulitermes</i>	complete and developed	rudimentar	0.66-1.67	0.68-1.91
<i>Agnathotermes</i>				
<i>Eutermellus</i>				
<i>Afrosulitermes</i>				
<i>Verrucositermes</i>				
<i>Angularitermes</i>	complete, M2 and M3 reduced	absent		1.46
<i>Cyranotermes</i>				
<i>Postsubulitermes</i>	incomplete (M2 absent), M3 reduced			
<i>Mimeutermes</i>		absent	2.00-3.17	2.63-3.59
<i>Tarditermes</i>				

Caetetermes (Fontes, 1981: 135-136, figs. 9-12), nasute genera whose species feed on well rotten wood, the molar plate, unlike that of *Nasutitermes*, is concave and has usually less ridges, which are also less prominent, and a clear basal notch like that seen in the soil-feeding nasutes; the apical ridges are also more prominent and appear to be homologous to the apical thickenings seen in the molar plate of the soil-feeding nasutes.

Most of the Termitinae and all of the Apicotermitinae, of the family Termitidae, are soil-feeders; this diet does not occur in the subfamily Macrotermitinae and in the remainder of the families of Isoptera (Noirot & Noirot-Timothee, 1969: 51). The mandibles of the soil-feeding Termitinae (Deligne, 1966: 1323-1324; Mathews, 1977: 112, 119, 123, 124, 128, 130, 134, 140, figs. 59-65, 67-70) present well developed apical tooth (left mandible index 0.8-4.5 in the Neotropical genera; Mathews, 1. c.), usually reduced or incomplete marginal dentition, and concave molar plate without ridges. Conversely, the mandibles of the Termitinae that do not feed on soil have smaller apical tooth and present ridges on the molar regions (these are flat or concave, the former bearing more developed ridges); the genus *Termes*, however, contains a number of elements which requires separate generic treatment (as pointed out by Krishna, 1970: 145) and the various mandibular patterns presented may be correlated to several feeding habits, a matter which is poorly understood in the Neotropical species. The soldierless Apicotermitinae of Africa were

revised by Sands (1972) and two genera from the Neotropics were described by Mathews (1977: 94-103); their mandibles have a concave molar plate devoid of ridges but the development of the apical and marginal teeth is variable. In both subfamilies the presence of developed apical thickenings and a clear basal notch in the right molar plate appear to be always associated with soil diet (personal observation on some Neotropical genera).

VI.2. Intraspecific Variation

Comparing alate and worker mandibles, differences in the morphology of the mandibles of each caste, within a species, had already been mentioned by Sands (1965; 1972), Ahmad (1968), Mathews (1977) and Fontes (1979; 1982), for several genera with various diets. The main differences registered, which are also observed in some of the soil-feeding species studied in this paper, are alate mandibles with apical teeth a little smaller and molar regions less developed than in worker mandibles. My opinion is in agreement with that of Sands (1980, personal communication), that the set of characteristics found in the mandibles of the worker caste reflects a better adaptation for food collecting.

VI.3. Function of the Molar Tooth

The molar tooth is well developed in all genera of soil-feeding termites. The term molar tooth was proposed by Krishna (1968: 265) to designate the toothlike process found on the underside of the molar prominence. Sands & Lamb (1975: 190) argued that the molar tooth, when well developed, may have only an incisory function, working together with the third marginal tooth against the second marginal tooth of the right mandible, and that in some wood-eating termites it seems to constitute the principal cutting element of the left mandible; for this reason, they proposed the name of fourth marginal tooth instead of molar tooth. Deligne (1966: 1325) explained the working mechanism of the molar regions of Isoptera mandibles, without making reference to the molar tooth: in the wood-feeding genera the strongly developed molar ridges grind the still poorly decomposed and compact food, like the molar teeth of ruminant mammals, while in the soil-feeding genera the soil, a soft food, is gathered and pressed in the oral cavity by the concave and

smooth molar regions. At least in the soil-feeding species studied in this paper, it is clear from figures 1-63 that the molar tooth of the left mandible faces the molar plate of the right mandible, lying exactly in the space between the apical thickenings of the dorsal and ventral margins of the molar plate; as the molar tooth is connected to the molar prominence through almost all the tooth length, the resulting spoon-like chamber constructed at the distal end of the left molar prominence (figs. 66, 70, 72) probably helps in driving the food from the molar regions towards the oral cavity. Further, the narrow and prominent process that basally terminates the left molar prominence (see drawings and scanning pictures number 64, 66, 68,) opposing to the narrow base of the right molar plate, may press the food further backward, enabling the termite to ingest the food. Thus, although it is possible to suppose also an incisory function, if the just proposed working mechanism is correct it seems more convenient to use the term molar tooth instead of fourth marginal tooth, in order to emphasize the simultaneous action of this tooth and the opposite molar plate of the right mandible. Similarities in the molar regions of the mandibles of other soil-feeding Termitidae suggest that they work in the same way.

VI.4. The Dimorphic Worker Caste of the Genera With Complete and Developed Marginal Dentition

The most noteworthy fact observed in the soil-feeding nasutes studied in this paper is the existence of a dimorphic worker caste in the genera *Convexitermes*, *Atlantitermes*, *Araujotermes*, *Coatitermes*, *Subulitermes* and *Agnathotermes*, all of them presenting mandibles with complete and developed marginal dentition (group 1). Recognizing the worker types with confidence requires inspection of the mandibles (hence the designations "worker with narrow gap" and "worker with broad gap", referring to the width of the interval between the left mandible third molar tooth and the molar prominence, the main differential feature of the mandibles), as they appear to be identical in other aspects. The frequency of one worker type was found to be consistently lower than the other (1-2 specimens among 30 workers examined); for the species studied in this paper, the "worker with narrow gap" is the type more frequently found in *Convexitermes*, *Atlantitermes*, *Araujotermes* and *Coatitermes*, and the "worker with broad gap" in *Subulitermes* and *Agnathotermes*.

The ontogeny of Termitidae workers and soldiers has been extensively reviewed by Noirot (1969) and complemented by Noirot (1974) and Brian (1979). With respect to the soil-feeding nasutes, the ontogenetic development of the castes has been investigated only in *Eutermellus* and *Mimeutermes* (Noirot, 1955: 463-465), from the Ethiopian region. In these genera there is only one stage of workers, of both sexes, developed through two immature stages; sexual dimorphism is very slight, expressed by the length of the antenna, and recognition of the sex on the basis of this character is often difficult or impossible. The soldiers, which are mostly males, arise from the workers. The development of various soil-feeding Termitinae (Noirot, 1969: 328-329) is similar, but most the soldiers are female.

The Neotropical soil-feeding genera with nasute soldiers are poorly represented in collections, so that a brief ontogenetic study was carried out on *Araujotermes caissara*, *Atlantitermes guarinim*, and on a new species of *Subulitermes* (collected in Itanhaém, State of São Paulo), from which some molting specimens became available; the sexual status of the studied specimens was not determined. The results are: (1) *Araujotermes caissara*: 2 "workers with narrow gap" molting to presoldiers, and 2 "workers with narrow gap" molting to "workers with narrow gap"; (2) *Atlantitermes guarinim*: 6 "workers with narrow gap" molting to presoldiers, 1 "worker with narrow gap" molting to a "worker with narrow gap", and 2 "workers with narrow gap" molting to undetermined worker types; (3) *Subulitermes* sp. n.: 1 "worker with narrow gap" molting to a presoldier, 3 "workers

with narrow gap" molting to "workers with narrow gap", 3 "workers with narrow gap" molting to undetermined worker types, and 1 "worker with broad gap" molting to a "worker with broad gap". These results show clearly that the ontogeny of the neuters of the Neotropical genera of soil-feeding nasutes with complete and developed marginal dentition in the mandibles is similar to that of *Eutermellus* and *Mimeuterme*s, in that the soldiers arise from the workers (although apparently only from the "workers with narrow gap"). The worker caste of the Neotropical genera, however, is particular in that , besides being dimorphic, each worker type molts at least once, giving rise to an older worker instar with similar mandibular pattern.

VII. CONCLUSIONS

The studies on the morphology of Isoptera alate and worker mandibles started with the work of Ahmad (1950), and have been then developed mainly in papers devoted to termite taxonomy and phylogeny. Two opposite predictions have arose with mandible studies. On one hand, Ahmad (*l. c.*:76), Emerson (1960a: 2) and Sen-Sarma (1969: 19) are of the opinion that the morphological differences seen in the mandibles of different genera are the results of pure evolutionary process deprived of direct adaptive value, as they observed that termites eating the same kind of food may have different types of mandibular dentition, while termites which feed on different materials may present similar dentition. On the other hand, Sands (1965 : 10) and Deligne (1966: 1323-1325) concluded that the mandibular morphology is highly adapted to alimentary regime, based on the fact that the molar regions of the mandibles of the soil-feeding termites are concave and have no (or at most rudimentar) ridges, while those of the genera which utilize other kinds of food are either concave or flat but always present developed ridges; Deligne (p. 1325) also commented briefly the greater development of the apical teeth and the reduction of the marginal dentition seen in the mandibles of the soil-feeding termites. According to the latter proposition, genera adapted to exploit the same food source can have different marginal dentition, but the molar regions are always characteristic; supporting this opinion Sands & Lamb (1975: 191) and Sands (1980, personal communication) reported that the occurrence in some of the non-soil-feeding termites of a concave molar plate, with more or less reduced ridges, seems to be associated to the habit of eating plant residues or well rotten wood, and therefore soft alimant.

This study on the mandibles of the eight Neotropical soil-feeding nasute genera, with comparison to the mandibles of other Termitidae, supports Sands' and Deligne's conclusion on the adaptive value of mandibular morphology to feeding habit. The following are the conclusive remarks which arise from this study, concerning the morphology of the mandibles of the soil-feeding termites :

1. The mandibles of the termites that feed on soil have molar regions with rudimentar or no ridges. The molar plate of the right mandible is strongly concave and has a pair of developed apical thickenings and a clear basal notch; these characteristics can be less developed in the molar plate of the alate right mandible. The development of the marginal dentition in variable, but the apical teeth are usually larger, and the second marginal tooth of the right mandible usually smaller, than those of the genera with other diets.

2. General morphology of the mandibles of soil-feeding nasutes: developed apical teeth (index of left mandible 0.66-3.59), as large as, but commonly larger, than the first marginal tooth of each mandible; marginal dentition either developed, reduced or incomplete (in this case, the second marginal tooth of the right mandible is absent); when present, second marginal tooth with rounded apex and smaller than the first marginal tooth; angle between the posterior margin of the apical tooth and the anterior margin of the first marginal tooth of each mandible

close to or higher than 45° ; angle between the posterior margin of the first marginal tooth and the anterior margin of the second marginal tooth close to or higher than 90° ; molar tooth developed as much as or more than the third marginal tooth; molar plate with developed apical thickenings and basal notch.

3. The soil-feeding nasutes can be separated into three groups, according to their mandibles :

Group 1. Marginal dentition complete and without reduced teeth. Left mandible index 0.66-1.91, marginal teeth developed and presence of vestigial ridges at least in the left molar region. The worker caste of the Neotropical genera is dimorphic; worker types are recognized by mandibles. This group includes the genera *Convexitermes*, *Atlantitermes*, *Araujotermes*, *Coatitermes*, *Subulitermes* and *Agnathotermes*, from the Neotropical region, and *Eutermellus*, *Afrosbulitermes* and *Verrucositermes*, from the Ethiopian region.

Group 2. Marginal dentition complete and with two reduced teeth. Left mandible index of worker 1.46, third marginal tooth of left mandible and second marginal tooth of right mandible reduced, and molar regions without ridges. An accurate determination of the left mandible index of the alate remains to be done. The worker caste is monomorphic. This group includes only the genus *Angularitermes*, from the Neotropical region.

Group 3. Marginal dentition incomplete. Left mandible index 2.00-3.59, third marginal tooth of left mandible reduced, second marginal tooth of right mandible absent, and no ridge in the molar regions. The worker caste is monomorphic. This group includes the genera *Cyranotermes*, from the Neotropical region, and *Postsubulitermes*, *Mimeutermes* and *Tarditermes*, from the Ethiopian region.

4. The largest apical teeth (and therefore the highest values for the left mandible index) are found in the mandibles of the genera of group 3, with incomplete marginal dentition. In group 2 (at least in the worker) the apical teeth are larger than in most of the genera of group 1.

5. Ridges are present only in the mandibles of the genera of group 1, with marginal dentition complete and without reduced teeth. In the Neotropical genera it is seen that simultaneously to the gradual enlargement of the apical tooth, the ridges show a tendency to reduce in length (thus becoming shorter than the width of the molar region) and to occur in lower number.

6. The development of the apical tooth, expressed through the left mandible index, can show variation within a species, according to the caste concerned. Similar variation occur in several other genera of Nasutitermitinae (Fontes, unpublished) either between the alate and the worker caste, as among the worker types; this fact deserves the special attention of termite taxonomists, as the left mandible index has been largely utilized in the taxonomy and phylogeny of the termite genera.

7. Minor intraspecific variation are also observed in the morphology of other components of the mandibles of the soil-feeding nasutes, either when comparing alate and worker caste, or worker instars. These also deserves the attention of termite taxonomists.

8. The molar tooth of the left mandible of the soil-feeding termites works against the molar plate of the right mandible, probably driving the food towards the oral cavity. The tooth works as an incisor in the wood -, grass - and litter-feeding termites, but a similar action of the tooth against the right molar plate in these groups can not be discarded.

9. The Neotropical genera of group 1 have a dimorphic worker caste, worker types being recognized by the mandibles. Each worker type molts at least once,

giving rise to an older worker instar with similar mandibular pattern, and the soldiers arise from the workers (as far as known, only from the "workers with narrow gap"). A similar dimorphism is found in several other genera of Nasutitermitinae (Fontes, unpublished), with other diets; this should prove to be valuable for future ontogenetic studies to be carried on the subfamily.

ACKNOWLEDGEMENTS

I would like to thank the Trustees of the Museu de Zoologia da Universidade de São Paulo for permission to examine material in the termite collection and facilities allowed during my work in the Museu, and the Fundação de Amparo à Pesquisa do Estado de São Paulo and the Conselho Nacional de Desenvolvimento Científico e Tecnológico for the financial assistance for the development of this study (Proc. FAPESP number 78/1149r, 80/0064 and 82/0346-4, and CNPq number 40.2963/79).

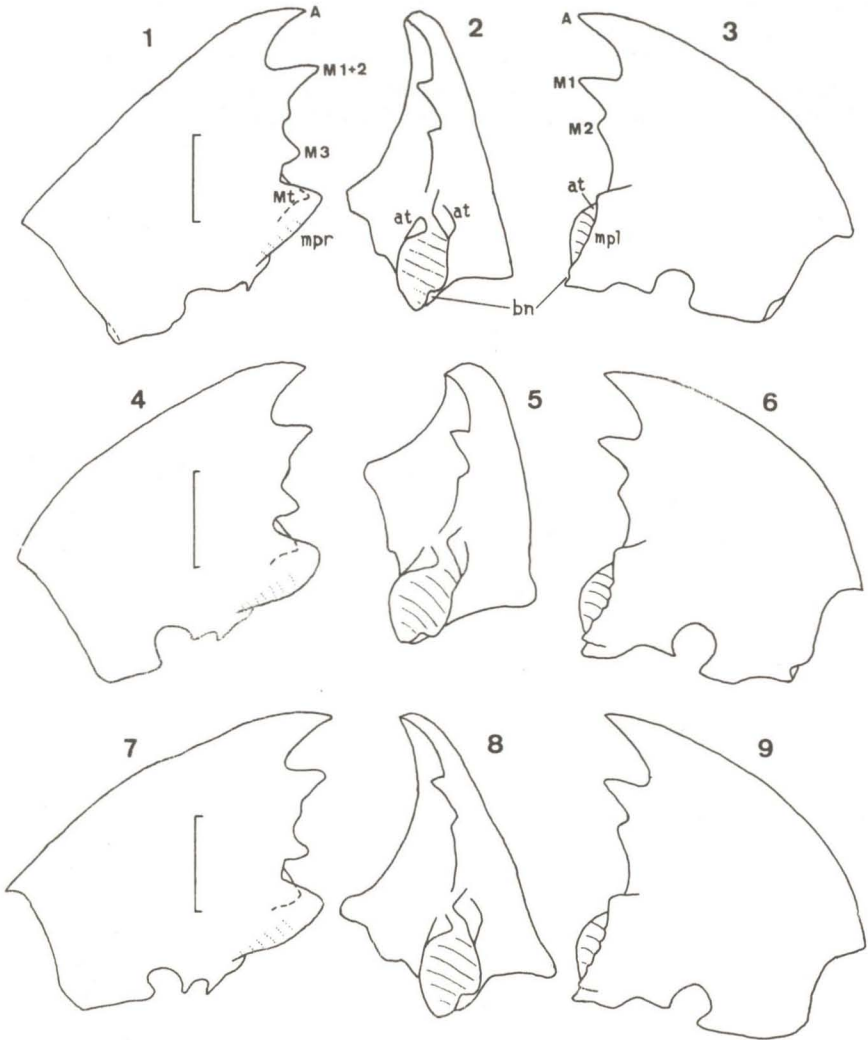
Dr. William A. Sands generously contributed with extensive and delightful discussions in the fields of mandibular morphology and anatomy of worker digestive tube, during my visit to the British Museum (Natural History) and Centre for Overseas Pest Research, in January and February of 1980, and with valuable information in letters. He also criticized a first manuscript of this paper. I hope to have made adequate references to his personal observations, whenever necessary in the text. Dr. Charles Noirot, in the opportunity of this visit to São Paulo, in July of 1983, contributed with a valuable discussion on the question of the worker dimorphism in the soil-feeding nasutes. Much criticism and encouragement has arose from my colleagues of the Universidade de São Paulo, especially Dr. Nelson Papavero, Ubirajara R. Martins, Maria E. Jorge, Sérgio A. Vanin, Paulo S. Terra, Walter A. Neves and Solange M. F. Ribeiro. Scanning micrographies were prepared in the Faculdade de Saúde Pública by Dr. José M. S. Barata and Mr. Carlos A. Paula Leite, to whom I am also very grateful.

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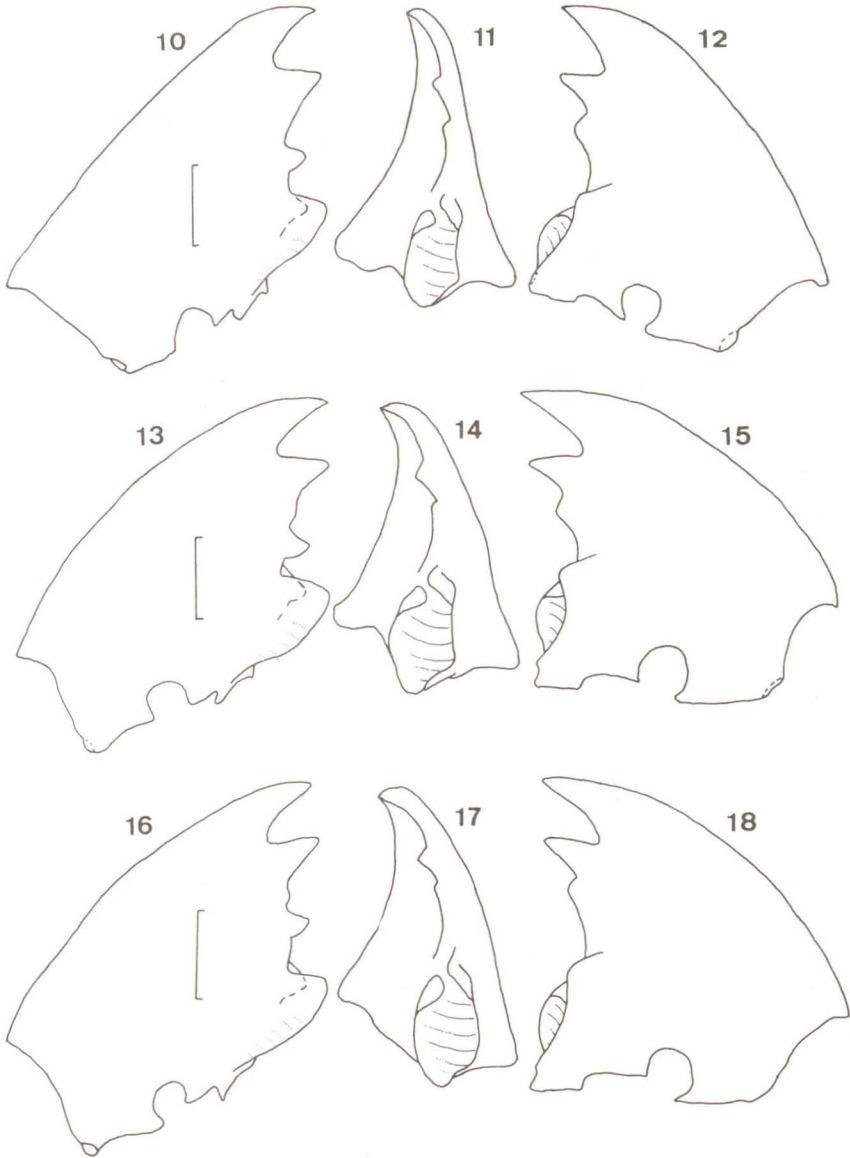
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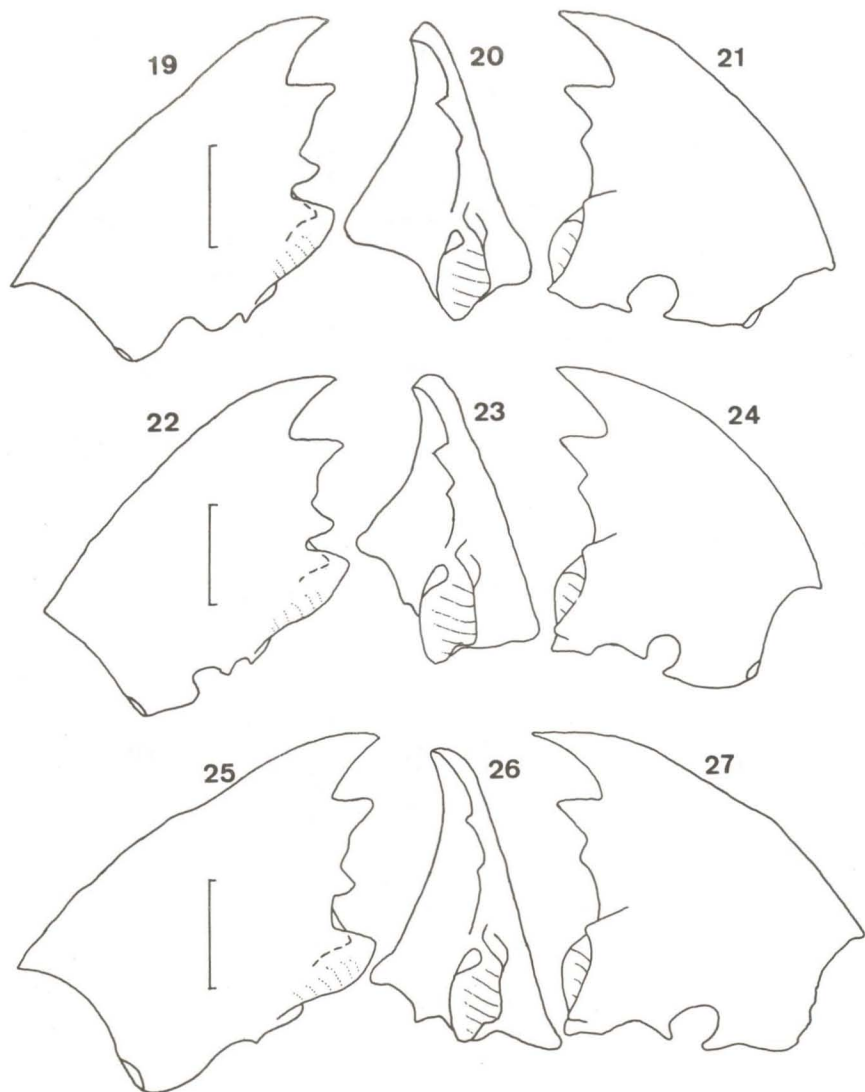
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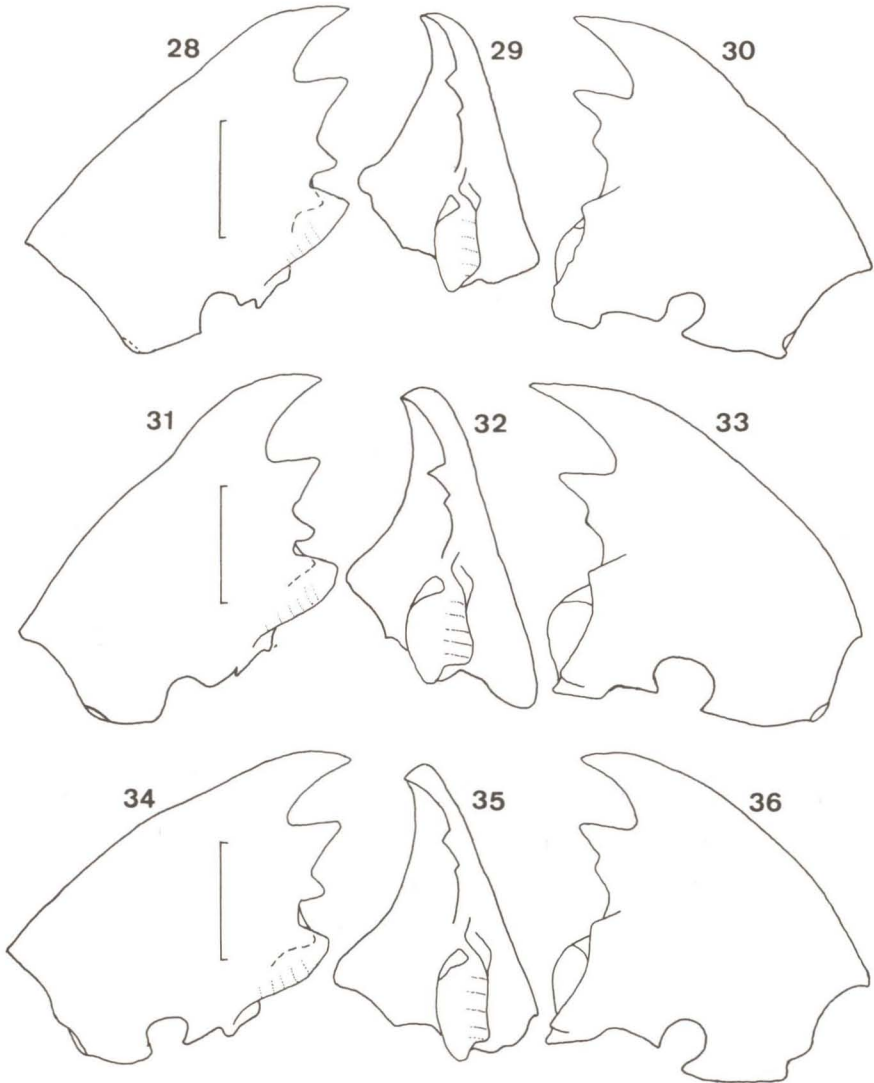
Mandibles of *Convexitermes manni*: 1-3, glate. Mandibles of *Convexitermes* sp.: 4-6, worker with narrow gap; 7-9, worker with broad gap. A, apical tooth; M1, first marginal tooth; M1+2, first plus second marginal tooth; M2, second marginal tooth; M3, third marginal tooth; Mt, molar tooth; mpr, molar prominence; mpl, molar plate; at, apical thickening; bn, basal notch. Scales 0.10 mm.



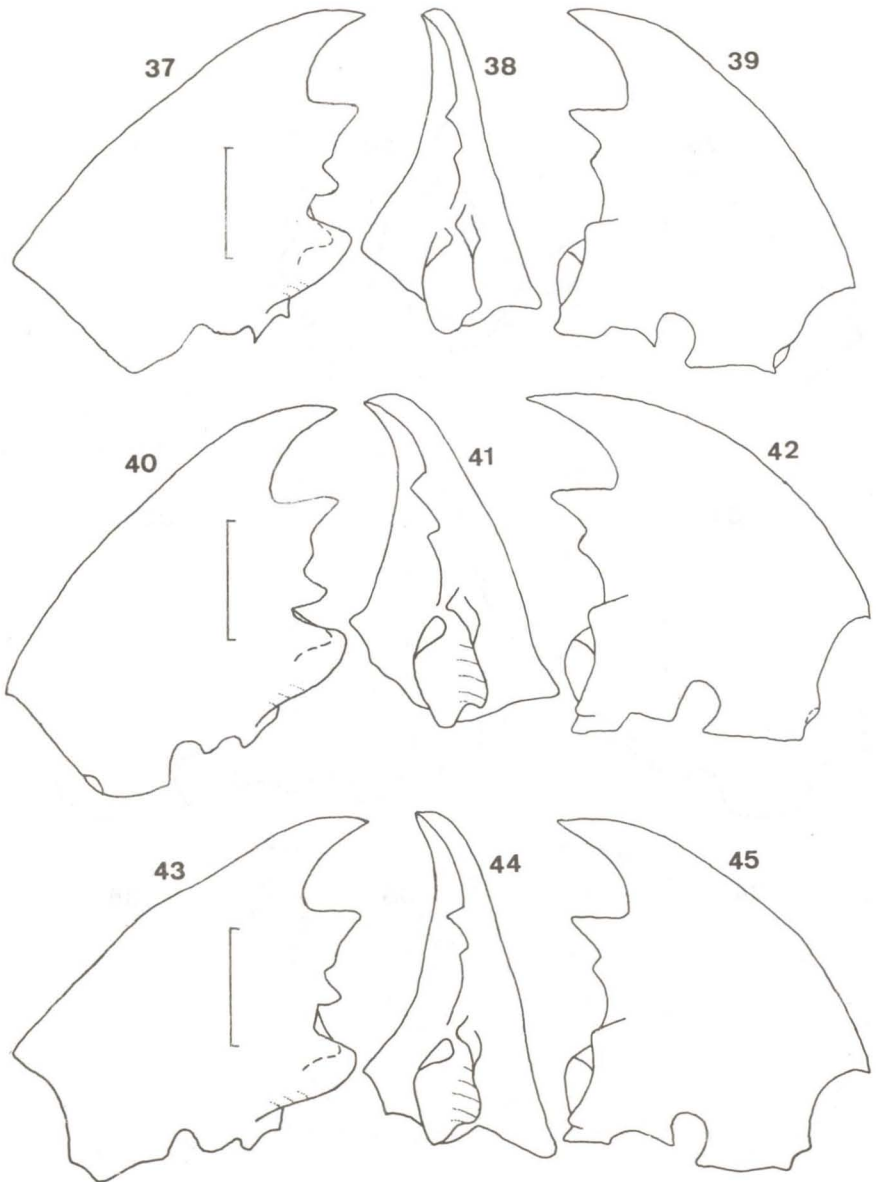
Mandibles of *Atlantitermes guarinim*: 10-12, alate; 13-15, worker with narrow gap; 16-18, worker with broad gap. Scales 0.10 mm.



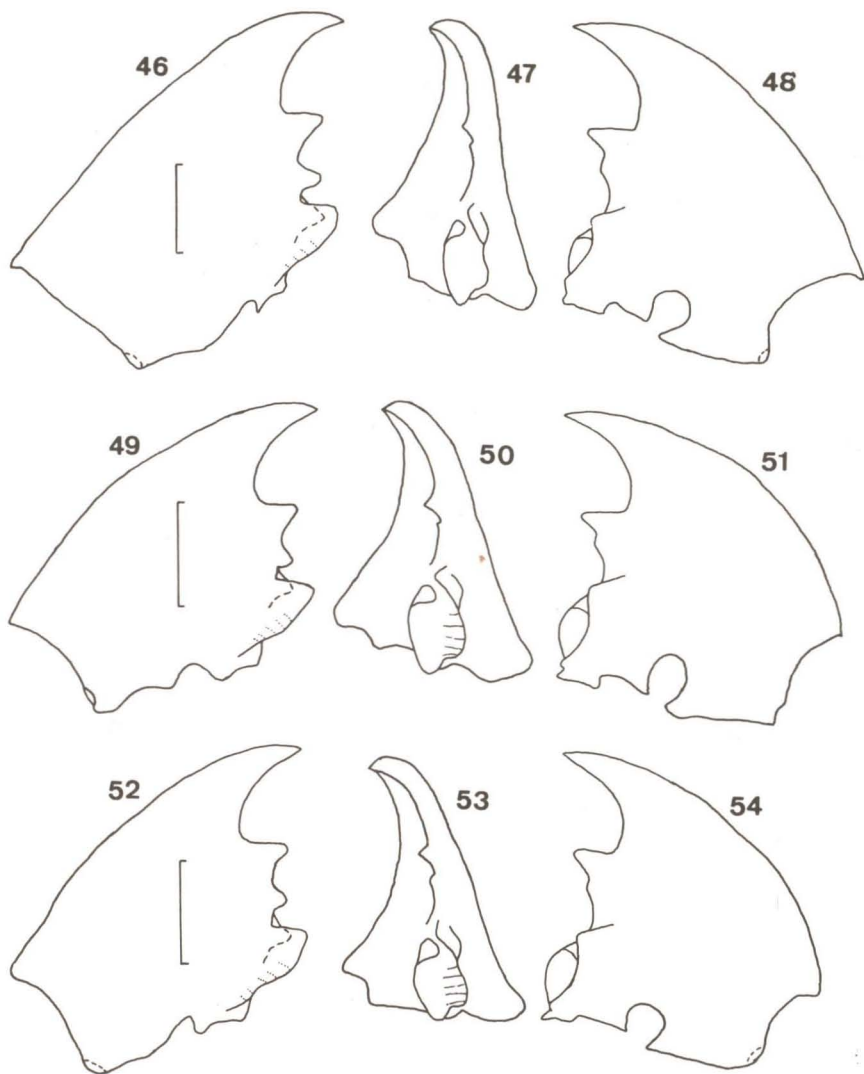
Mandibles of *Araujotermes caissara*: 19-21, alate; 22-24, worker with narrow gap; 25-27, worker with broad gap. Scales 0.10 mm.



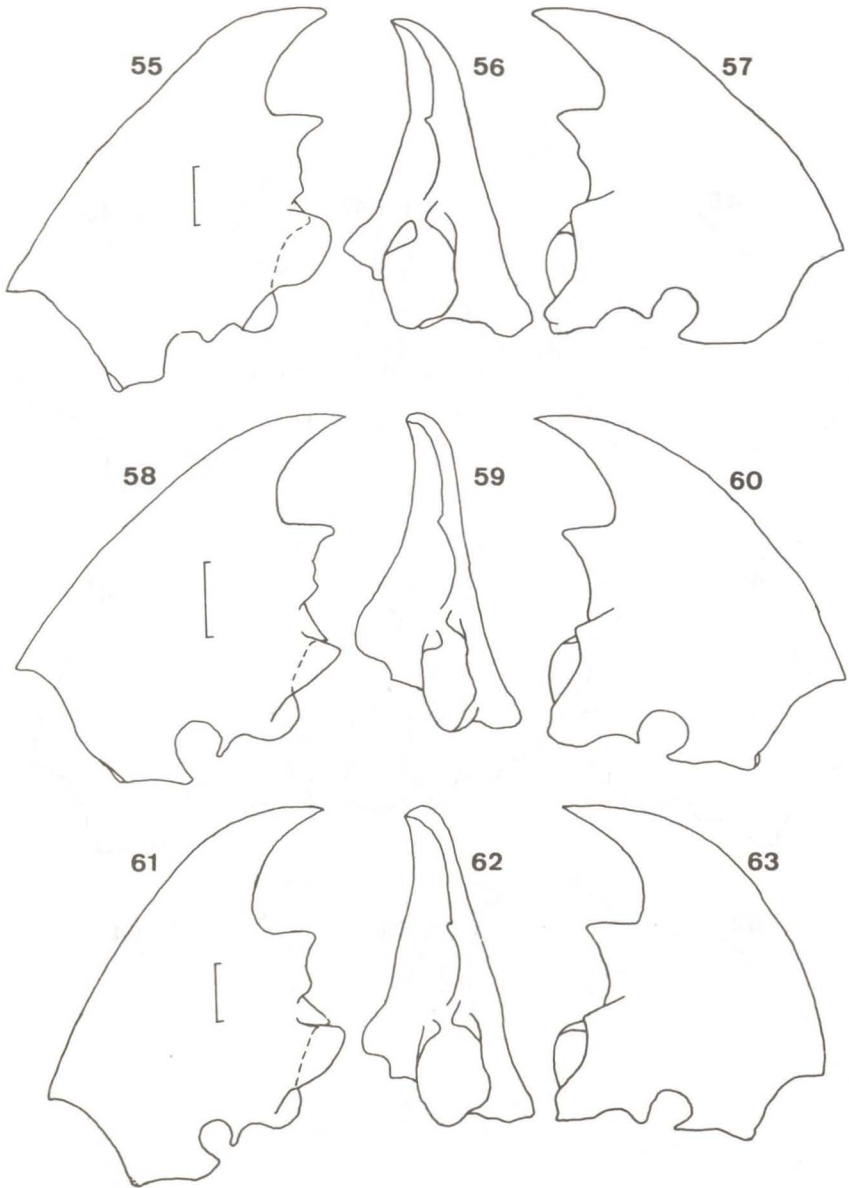
Mandibles of *Coatlitermes cleavelandi*: 28-30, alate; 31-33, worker with narrow gap; 34-36, worker with broad gap. Scales 0.10 mm.



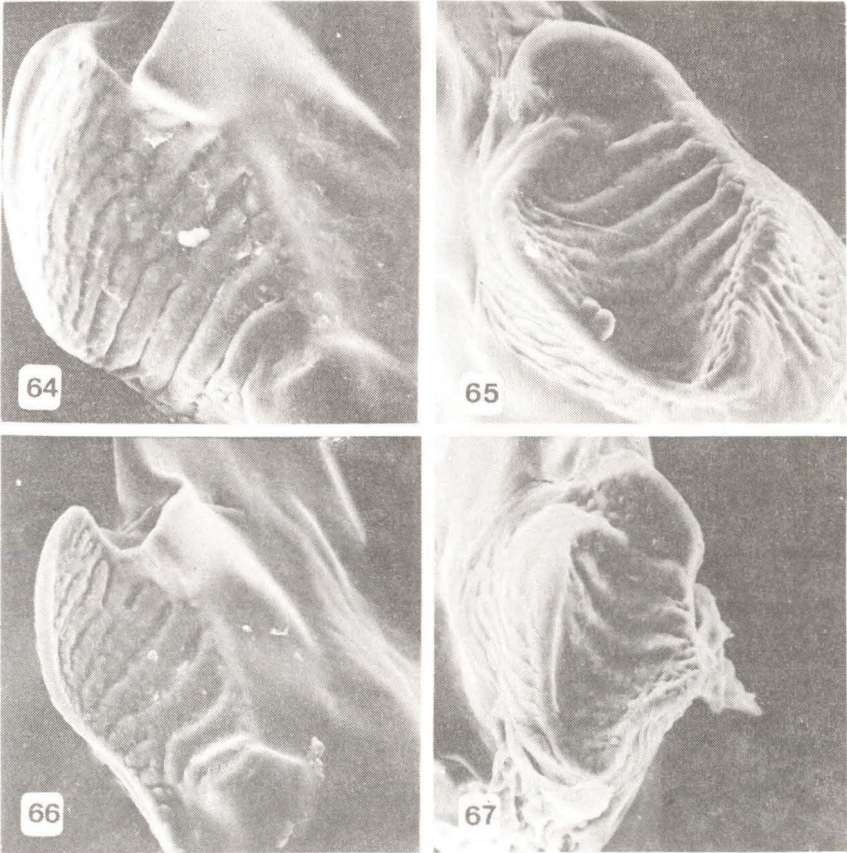
Mandibles of *Subulitermes microsoma*. 37-39, alate; 40-42, worker with narrow gap; 43-45, worker with broad gap. Scales 0.10 mm.



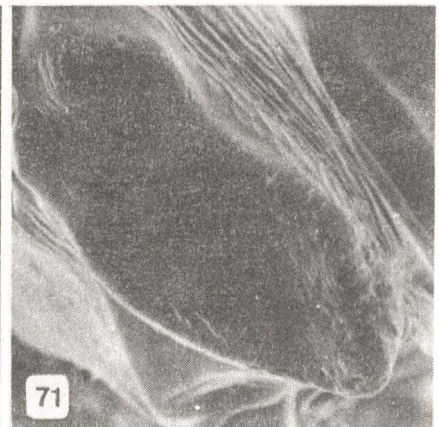
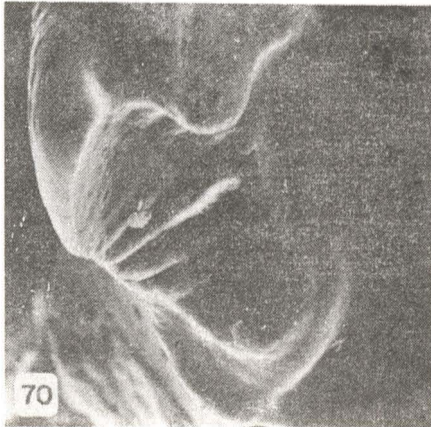
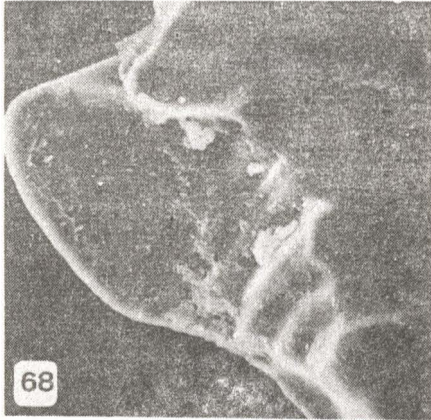
Mandibles of *Agnathotermes glaber*: 46-48, alate; 49-51, worker with narrow gap; 52-54, worker with broad gap. Scales 0.10 mm.



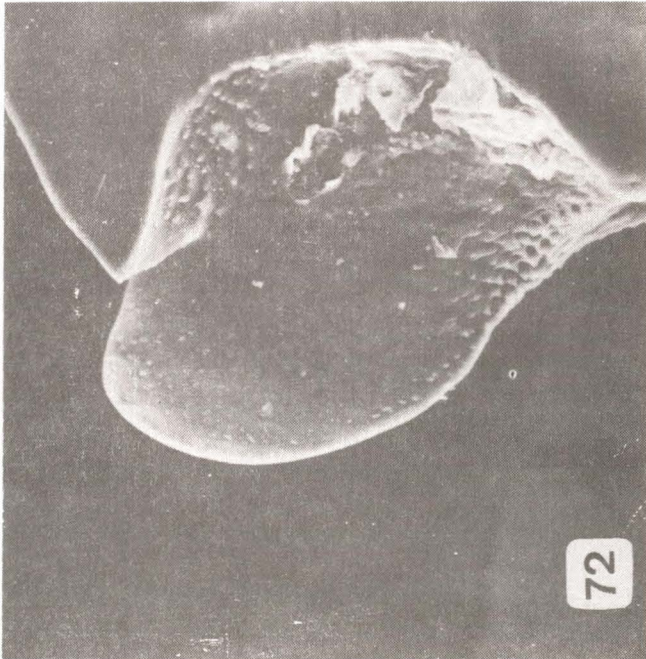
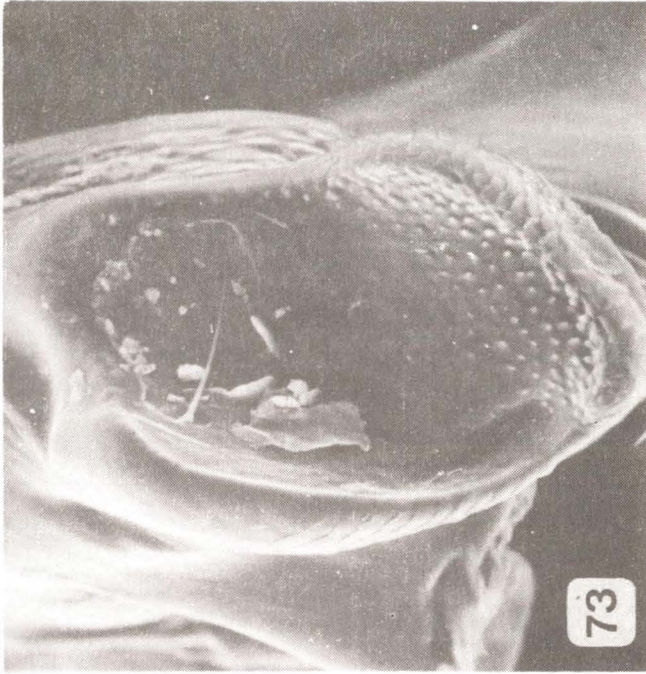
Mandibles of *Angularitermes orestes*: 55-57, worker. Mandibles of *Cyranotermes timuassu*: 58-60, alate; 61-63, worker. Scales 0.10 mm.



Atlantitermes guarinim, worker with narrow gap: 64, molar prominence; 65, molar plate.
Araujotermes caissara, worker with narrow gap: 66, molar prominence; 67, molar plate.



Subulitermes microsoma, worker with narrow gap: 68, molar prominence; 69, molar plate. *Agnathotermes glaber*, alate: 70, molar prominence; 71, molar plate.



Cyranotermes limuassu, worker: 72, molar prominence; 73, molar plate.