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Nest architecture of *Nasutitermes* termites in a white water floodplain forest in central Amazonia, and a field key to species (Isoptera, Termitidae)

Dedicated to Prof. LUDWIG BECK honoring his invaluable support of my scientific career

Abstract

The architectural features of the five *Nasutitermes* species occurring in a Neotropical floodplain (várzea) forest on Ilha de Marchantaria in central Amazonia are described: external nest and runway architecture, nest volume, nest height above ground, nesting trees, degree of polycalism). These characteristics are used to build a tentative field key to the nest-building termite species which should be tested for its usefulness for ecological studies of central Amazonian termites.

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Key words

Termites, *Nasutitermes*, Amazonia, identification key, nest architecture

1. Introduction

Termites are important decomposer organisms in tropical ecosystems. Unlike solitary living decomposers, they are social insects living in colonies found in the soil, within dead wood and in nest mounds above the ground, often attached to trees. Tree-inhabiting makes nest-building termites ideal candidates for the colonization of floodplain forests. Here, termites have a very low diversity but their density is often similar to that in dryland rainforests (MARTIUS 1997; cf. below). Floodplains occupy about 100,000 km² or roughly 2 % of the Amazon basin, the world's largest rainforest area. These "várzea" floodplains, dominated by the white water of the Amazon river, are flooded once a year, the water generally covering the forest floor up to a height of several meters (JUNK 1997). Only a few ground-dwelling species have managed to survive under these conditions, apparently because they developed specific adaptations (MARTIUS 1997). Of the twelve termite species recorded in the várzea of central

Amazonia (MARTIUS 1989, MARTIUS 1997), nine are nest-building species belonging to the family Termitidae, and among these, the most dominant are five wood-feeding species belonging to the genus *Nasutitermes* (BUSTAMANTE & MARTIUS 1998). The *Nasutitermes* community of Ilha de Marchantaria, an island in the Amazon (03°14'17"S / 59°57'09"W) that has served as a case study site for the Max-Planck Work Group on Tropical Ecology (JUNK 1997), has been extensively studied by MARTIUS (1989, 1994a, b, 1997). Here, I present general descriptive data for the nests of these five species and a key to the species of *Nasutitermes* at this study site which should allow their identification in the field.

2. Material and Methods

Ilha de Marchantaria is an island in the Amazon (Solimões) River upstream of the city of Manaus. It is covered by a typical white water floodplain forest (JUNK 1997) that has grown for 20-80 years (WORBES 1986, WORBES et al. 1992). Nests of the local termite assemblage of one 1.4 ha plot on Ilha de Marchantaria (plot P; site description in MARTIUS 1989, 1997) were censused during 1985 and 1986. In total, 151 nests were assessed. Outside this plot, termite nests were sampled on Marchantaria island and elsewhere (Ilha de Careiro, Costa do Marrecão) near the city of Manaus. The censuses included observations of nest structure, external architecture, position on the nesting tree and also measurements of nest size parameters (see below). Termites were collected from the nests and preserved in 70% alcohol. They were identified by WILLIAM SANDS (Natural History Museum London, NHM) in comparison with specimens in the termite collection of NHM. Samples of the identified material were deposited at the museum in London as well as in the Entomological Collection of Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus. Nomenclature follows CONSTANTINO (1998).

Termite nests were mapped on a plot that measured 280 m along its main axis (E-W), the margins being determined by the margins of the forest. A central line was marked with wooden stakes, and the distance of the forest margin to the central line was measured with a tape. Nest size parameters (height, two diameters, height above ground, gallery width) were recorded and nest volume was calculated (cf. MARTIUS et al. 1994b for formulas used). The trees on which the termite mounds were sitting (nesting trees) were identified on the spot by the botanist LUIS COELHO (Departamento de Botânica,

Table 1. Some structural characteristics of *Nasutitermes* nests in the várzea. "Attachment" indicates how the nest is attached to the tree/liana. "Orientation" gives the cardinal point towards which the nests are directed, and "Gallery width" gives the range and typical values for each species. Difference to total N is based on nests where the attachment point was not discernible from the ground.

	N	Attachment			Laterally attached to tree trunk	Orientation					Gallery width (cm)	
		In branch bifurcation	Branch bifurcation + lianas	Trunk and liana crossing		None	N	S	O	W	Variability	Typical width
<i>N. corniger</i>	92	71	12	1	0	62	20	7	2	1	0.5-10	1-4
<i>N. tatarendae</i>	21	3	14	2	0	13	2	2	3	1	1-5	2-3
<i>N. macrocephalus</i>	27	7	2	8	0	15	9	2	1	0	1-10	2-4
<i>N. surinamensis</i>	5	2	0	0	1	0	4	1	0	0	1-15	² 10
<i>N. ephratae</i>	6	3	0	0	1	1	4	0	0	1	0.5-10	1-5

Table 2. Average nest volume of *Nasutitermes* species of the várzea and average height of the nests above ground in the study site, Ilha de Marchantaria, Central Amazonia (means \pm 99 % confidence interval; data from MARTIUS et al. 1994b).

	All nests	<i>N. corniger</i>	<i>N. macrocephalus</i>	<i>N. surinamensis</i>	<i>N. ephratae</i>	<i>N. tatarendae</i>
n	130	92	6	5	6	21
Volume (l nest ⁻¹)	69.75 \pm 27.84	35.36 \pm 41.40	350.80 \pm 121.52	405.41 \pm 323.92	118.59 \pm 89.97	46.34 \pm 67.85
Height above ground (m)	5.11 \pm 0.50	4.92 \pm 0.58	7.13 \pm 2.03	7.60 \pm 3.12	3.77 \pm 0.99	5.33 \pm 1.24



Figure 1. Surface structure of a nest of *Nasutitermes corniger* ("simple" type).

INPA). Some of the termite species from the várzea are not yet described, the "codes" attributed to them in the key (preliminary morphospecies classifications) are identical to those under which they are deposited in the INPA collection.

3. Results and discussion

3.1 Nest architecture of *Nasutitermes* termites

All *Nasutitermes* nests of the várzea floodplain are arboreal, but they typically differ in architecture, size, and height above ground at which they are attached to trees. Two basic architectural models can be distinguished, the "simple" and the "envelope" type. Nests of *Nasutitermes corniger* and *N. tatarendae* belong to the simple type, where the external nest wall is identical with the outer wall of the outermost single nest chambers. Thus, the surface of these nests is "bumpy" (fig. 1). The termites extend their nest by simply adding new chambers on the top of existing chambers.

In contrast, in the case of *N. ephratae*, *N. macrocephalus* and *N. surinamensis*, the external nest wall is a thin cartonaceous sheet that is only loosely attached to the underlying nest structure. The underlying chambers are open to the external side, and only covered by the sheet. Therefore, parts of this sheet can be removed in large "plaques" from the nest without effort (fig. 2), and the nests of this type exhibit typical "growth zones" (fig. 3). In this nest type, apparently, nest growth is achieved by adding new external chambers under the protective external sheet, or the sheet is opened before along some ridges, the growth zones. Here, the wall is then added to.

The differences between the two groups appear to be species-specific, although deviations from this pattern may be seen in nests that have survived larger external injuries from falling branches, attack by parrots or ants, flooding, etc. (MARTIUS 1989). In most nests, however, these nest characteristics can be used for field identification of the nest-building species. In two species, *N. corniger* and *N. ephratae*, the morphological differences between soldiers are very weak, and identification based on the characteristic nest surface is often more reliable. THORNE (1980) and BECKER (1972) have made similar observations for other species. Therefore, a field key to the species of Ilha de Marchantaria, the studied várzea island, was developed based on nest characteristics (see below).

Other structural characteristics of the nests also show species-specific differences (tab. 1). Generally, nests of *N. ephratae* and *N. surinamensis* are laterally attached to large trees, whereas the nests of *N. corniger*, *N. tatarendae* and *N. macrocephalus* are associated with a bifurcation of branches in smaller trees (fig. 4). The mechanism by which the royal couple selects these bifurcations during nest establishment is not known, but one can speculate that ridges and other bark irregularities or detritus accumulated in such bifurcations provide a better shelter than the plain tree trunk. Also, the bifurcation provides a better mechanical hold for the nest which in these species is often only loosely attached to the stem surface. Additional features are lianas that may run through the nest (tab. 1). Often, nests were found that were not sitting in a bifurcation but on a spot where a liana crossed the unbranched tree trunk. I have listed these cases separately because lianas are abundant and seem to play a role in linking nests together (calies, see below).

Laterally attached nests may actually surround the trunk when they grow to adult size. They are much more firmly attached to the tree surface.

In black water floodplains (igapó, JUNK 1997), *Nasutitermes* nests were found in trees containing central voids in their stems (MARTIUS 1989). However, this was not the case in the várzea, maybe due to the fact that very few such trees were found in the investigated sites.

Galleries

In all species, differences in size were observed in the galleries leading downward and upward from the nest. The galleries leading upward generally consisted only of one runway which was 0.5 to 1.0 cm wide in the smaller species, and up to 2 cm wide in the larger species, whereas the downward leading galleries often consisted of several parallel runways. The latter was the case in *N. surinamensis*, where the parallel runways were over- and undersecting each other in a 10-15 cm wide extension of the nest (tab. 1). Width



Figure 2. Surface structure of a nest of *Nasutitermes ephratae* ("envelope" type).

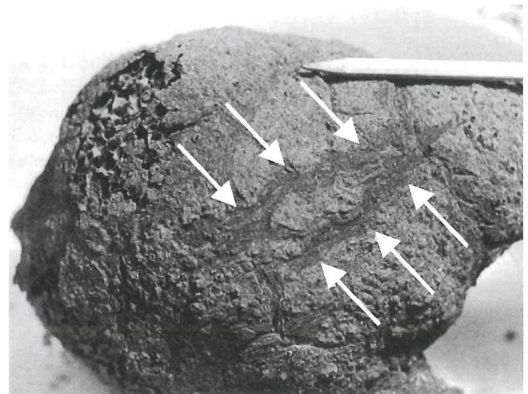


Figure 3. "Growth zone" on surface of a nest of the "envelope" type".

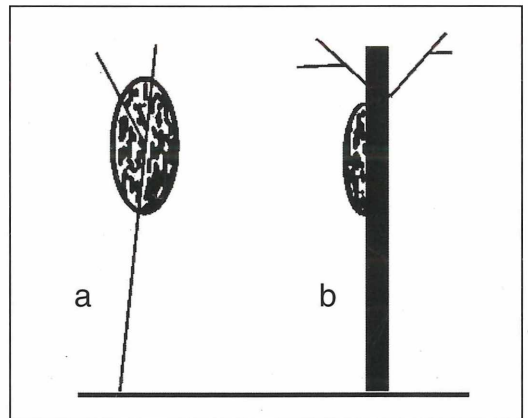


Figure 4. Central (a) and lateral (b) attachment of termite nests to trees.

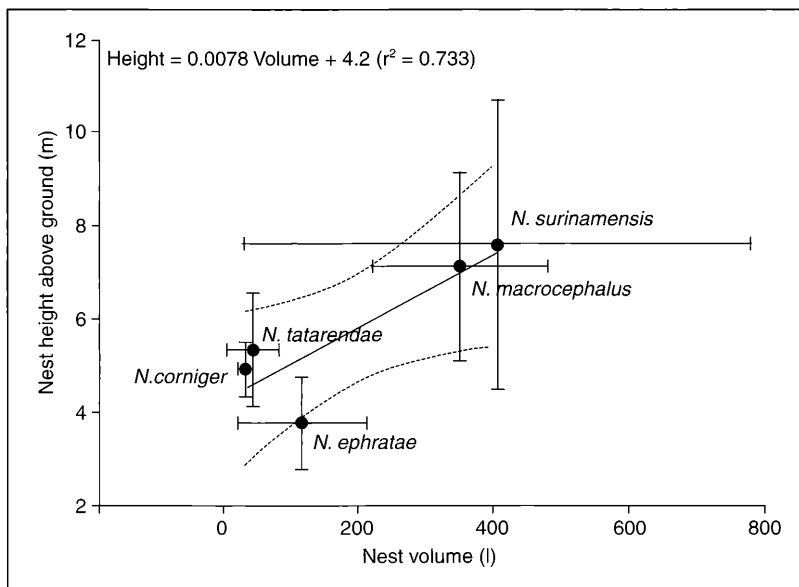


Figure 5. Correlation between average nest volume of each species (l) and the average height above ground in nests of five *Nasutitermes* spp. of the study site, Ilha de Marchantaria.

Table 3. Tree species with nests of *Nasutitermes* spp. in the study site, Ilha de Marchantaria and frequency of use by termites. Trees on which several nests were found were counted only once. Importance Value Indices (IVI) of the tree species were determined in a near-by stand (WORRES et al. 1992)

Tree taxon	n	IVI
<i>Laetia corymbulosa</i>	18	35.3
<i>Allophylus amazonicus</i>	16	
<i>Crataeva benthamii</i>	16	56.8
<i>Guarea trichiloides</i>	9	
<i>Casearia aculeata</i>	5	9.5
<i>Zanthoxylum compactum</i>	3	
<i>Tabebuia barbata</i>	3	
<i>Vatairea</i> sp.	3	
<i>Gustavia augusta</i>	2	
<i>Cecropia latiloba</i>	2	17.2
<i>Vitex cymosa</i>	2	23.8
<i>Pithecolobium</i> sp.	2	
<i>Pseudobombax munguba</i>	1	
<i>Astrocaryum jauary</i>	1	
<i>Crescentia amazonica</i>	1	
<i>Crudia amazonica</i>	1	
<i>Cordia</i> sp.	1	
<i>Ficus</i> sp.	1	
<i>Ilex</i> sp.	1	
<i>Luehea</i> sp.	1	24.0
<i>Rheedia</i> sp.	1	
Liana (undet.)	4	
Undet. spp.	13	5.5
Dead tree (undet.)	4	
Sum (140 nests)	111	

and height of the galleries seem to depend on the size of the termites, because galleries of 0.5 cm width were only found in the smaller species, *N. corniger* and *N. ephratae*.

Most (50 - 70 %) of the nests of *N. corniger*, *N. tatarendae* and *N. macrocephalus* were not orientated towards any compass cardinal point ("none" in table 1). Most of the nests of all five species showing an orientation were directed towards the north, but in *N. tatarendae* all cardinal points were equally frequent. Orientation to north may be related with less solar exposure of the nest.

Nest size

Nasutitermes corniger and *N. tatarendae* had small nests (volumes below 50 litres per nest), nests of *N. ephratae* were somewhat larger on average, and *N. macrocephalus* and *N. surinamensis* had very large nests with volumes around 350-400 l (tab. 2). THORNE & NOIROT (1982) recorded values for 129 nests of *N. corniger* in Panama, their largest nest having a volume of 54 l, much below the volumes recorded for the largest nests in the present study (2 nests with a volume of 210 l).

Nest height above ground

Nest height above ground is linearly correlated to nest volume ($R^2 = 0.733$; fig. 5). The nests of *Nasutitermes ephratae* are generally positioned lower in the forest than the other nests; those of *N. surinamensis* and *N. macrocephalus* are highest up in the trees.

Nesting trees

Fifty-nine of the 111 investigated nesting trees belonged to only four species (tab. 3). We did not



Figure 6. Polydomous nest of *Nasutitermes tatarendae*, the parts being linked by galleries on a liana.

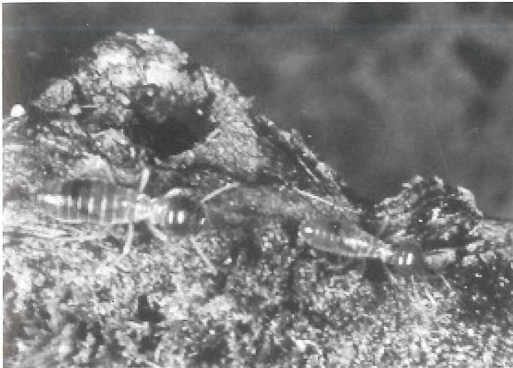


Figure 7. Soldiers and workers of *Nasutitermes macrocephalus*.

assess the tree species density on that site, but the Importance Value Indices (IVI) of the tree species in a near-by stand (WORRES et al. 1992; given in table 3) indicate that although the tree species with the highest IVI, *Crataeva benthamii* and *Laetia corymbulosa* are among the four most termite colonized, the termite distribution on the trees does not totally reflect tree dominance. This may indicate that founding couples actively select trees. The difference between termite occupation on *L. corymbulosa* and *C. benthamii*, for example, could be due to the fact that the former, although less dominant in the stand, has a rougher bark structure, which could facilitate the survival of the royal couple on this tree.

Polycalism

Interactions between the termites of neighboring nests were not observed, but evidence from other studies suggests that a strong intraspecific aggression between termites from different colonies exists (cf. ESENTER 1980, LEVINGS & ADAMS 1984, STUART 1963). Therefore, I assumed nests occurring on the same

tree or on neighboring trees linked with lianas (fig. 6) as belonging to one colony. This is also based on the observation that these nests were always linked with galleries. table 4 lists all nests from one census of the assemblage (June 17, 1985) for which those links could be confirmed. At least 57 of 100 nests were not autonomous but represented parts (calies) of polycalic nests. In *N. corniger* alone, the percentage was higher (43 of 69 nests, 62.3 %) indicating that this species in particular often develops polycalic nests. On average, 3.2 calies belong to one colony (2.9 in *N. corniger*). Most often double nest colonies were observed ($n = 8$), i.e. colonies consisting of two calies occurring on one tree. One colony of *N. tatarendae* consisted of 10 calies on several trees that were connected by one liana; two of the calies were found directly at the point where the liana, making loops, touched itself. This is a much lower number than the 37 nests of *N. corniger* recorded by LEVINGS & ADAMS (1984) and ADAMS & LEVINGS (1987) that belonged to one colony covering 0.8 ha in a mangrove forest in Panama. However, all gallery connections between calies in the mangrove forest with its open canopy were on the ground, making it easier for these authors to document all links between different calies. In the Marchantaria forest

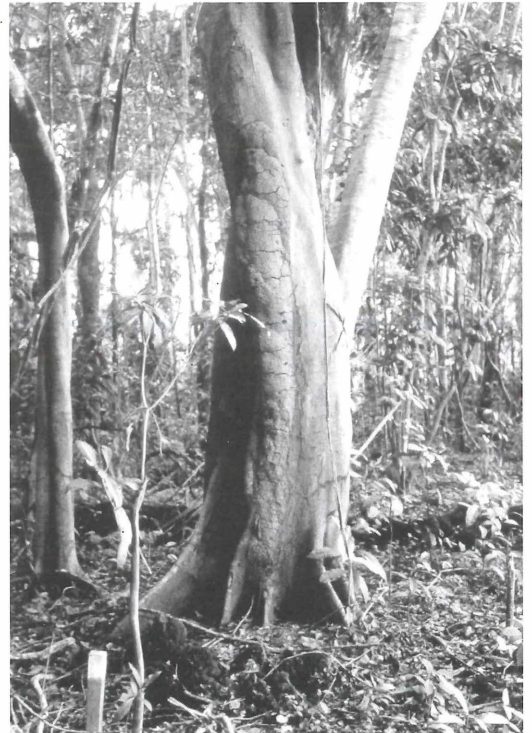


Figure 8. Nest architecture of *Anoplotermes* sp. "A" (cf. MARTIUS 1997).

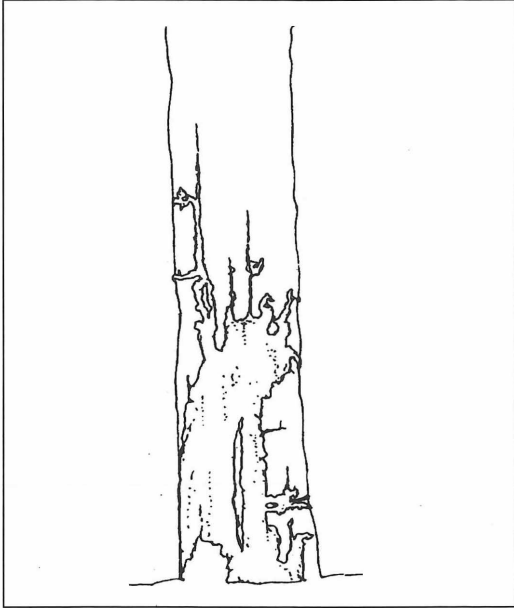


Figure 9. Nest architecture of Apicotermitinae, *Anoplotermes* sp. "D" (cf. MARTIUS 1989).



Figure 10. Habitus of a nest of *Nasutitermes corniger* that has an irregular shape due to attack by ants (*Dolichoderus bispinosus*; cf. MARTIUS 1994b).

where the canopy is closed many such connections occurred in the canopy, and the recorded numbers of calies per colony, based on confirmed connections, are to be considered minimum values. Based on nest mapping, further potential links are possible; e.g. it is possible that the two *N. tatarendae* colonies B and C, or even all 16 calies of this species (B, C, and C') belonged to one colony. If this is the case, this colony would have occupied an area of about 600 m². Much larger assemblages of calies have been observed in *Nasutitermes* species of Papua New Guinea by LEPONCE et al. (1997).

Polycalism seems to be genetically fixed (ROISIN & PASTEELS 1987), and one can hypothesize that this may have several adaptive advantages: The termites may be able to avoid the critical swarming phase through "vegetative budding", a colony separated in different nests may better survive attacks of raiding ants. The species more prone to polycalism, *N. corniger*, is dominant in the studied várzea plots, a pioneer ecosystem with high predatory pressure. Also, it may be an advantage to forage in a large territory from several dispersed nests instead of from one central nest. The larger multi-nest colonies occupy territo-

Table 4. Confirmed and potential polycalism in *Nasutitermes* colonies of the study site, Ilha de Marchantaria (only colonies in which polycalism was observed are listed here)

Species	Colony Code	no. of nests per one colony	
		confirmed	potential maximum colony Size
<i>N. ephratae</i>	A	2	
<i>N. tatarendae</i>	B	10	B+C: 12
<i>N. tatarendae</i>	C	2	B+C+C': 16
<i>N. tatarendae</i>	C'	4	
<i>N. corniger</i>	D	3	
<i>N. corniger</i>	E	2	
<i>N. corniger</i>	F	2	
<i>N. corniger</i>	G	2	G+H: 5
<i>N. corniger</i>	H	3	
<i>N. corniger</i>	I	3	I+K: 7
<i>N. corniger</i>	K	4	
<i>N. corniger</i>	L	4	
<i>N. corniger</i>	M	2	
<i>N. corniger</i>	N	3	
<i>N. corniger</i>	O	4	
<i>N. corniger</i>	P	2	
<i>N. corniger</i>	Q	4	
<i>N. corniger</i>	R	3	
<i>N. corniger</i>	S	2	
	All		<i>N. corniger</i> only
Sum of Nests	57		43
Sum of Colonies	18		15
Average nest no. per colony	3.17		2.87

ries of up to 600 m² (tab. 4) which corresponds to the territory size controlled by the larger, non-polycalic species like *N. surinamensis* or *N. macrocephalus*. The construction of secondary nests can, however, also be a reaction to environmental stress as it occurs in a seasonally flooded floodplain. Sometimes, termite nests have been constructed below the high water level of the coming flood, and then, the construction of secondary nests higher up in the tree could be observed in several cases. When the waters cede, the old nest is often re-integrated into the colony system, and the colony has thus won a second nest. Often, the form of these secondary nests built under extreme circumstances differ considerably from the original design. In these cases, identification of the species based on nest characters alone might be misleading to the non-specialist.

3.2 Identification of termite species in the field

The analysis of the *Nasutitermes* assemblage of the várzea floodplain on Ilha de Marchantaria resulted in following findings:

- 1) The dominant species in terms of nest number is *Nasutitermes corniger*, in terms of nest volume *N. macrocephalus* and *N. surinamensis* gain more weight.
- 2) Nest architecture, size and height of the nests above the ground are species-specific characters that are useful for identification of the species in the field. The nests of *Nasutitermes corniger* and *N. tatarendae* are relatively small (about 50 l volume per nest); those of *N. macrocephalus*, *N. surinamensis* and *N. ephratae* are larger (120 - 400 l volume). Only secondary nests built after catastrophic events that destroyed the original nest, are of different, often simpler structure.
- 3) *Nasutitermes corniger* and *N. tatarendae* may form multi-nest (polycalic) colonies that generally consist of 2-3 but may comprise up to 10 or more nests, occupying territories of up to 600 m². This corresponds to the territory size controlled by the larger species, as determined by measurements of total gallery extension.

In the following, a key to the termite species on Ilha de Marchantaria was developed that is based on easily observable external characters and should allow identification of the original nest builder species in the field. Although the species composition in other floodplain forests of Amazonia can be quite different (e.g. in Juruá, CONSTANTINO 1992; cf. also MARTIUS 1994b) the key might be of help in future studies of termite ecology in white water inundation forests in central Amazonia, actually a center of research on the várzea ecosystem (JUNK 1997).

Finally, a few cautionary notes: the termite species found in a nest is not always the one which originally built it (APOLINÁRIO 1993, MARTIUS 1989). Nests and



Figure 11. Surface of a nest of *Nasutitermes macrocephalus* (diameter left to right about 30 cm).

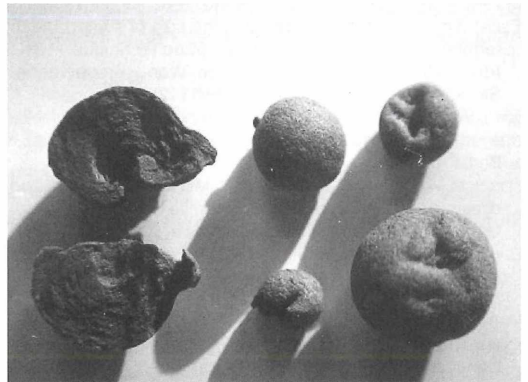


Figure 12. Roundly shaped conglomerates that are typically found in nests of *Nasutitermes macrocephalus* (cf. MARTIUS 1993).

termites should thus be identified separately. Other termites (*Rhinotermes* sp., *Coptotermes* sp.) do not build external nests but live within dead wood (MARTIUS 1997); these are not included to in the key. The following key is based on material collected during an inventory of termites in the years 1985 - 1992 on and around the island Ilha de Marchantaria.

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Appendix

Field key to the nest-building termite species of central Amazonian várzea floodplains

1. Nest made of soil matter; long (up to a height of 6 m) "columns" of soil attached to one side of a tree trunk (fig. 8) or shallow soil sheath covering tree trunk entirely up to a height of 12 - 14 m (fig. 9). No termite soldiers (soldierless termites), worker termites are generally small and of dark grey color
 - Nest round or ellipsoid in shape, sometimes very irregularly so, but never as in (1). Nests generally made of "carton" (digested wood) (figs 1 - 3). When disturbed, small orange red- or dark-headed "nasute" soldiers (fig. 7) appear quickly
 - Anoplotermes* (Apicotermitinae) 2
 - Nasutitermes* (Nasutitermitinae) 3
2. Soil nest is a column attached to one side of a tree trunk, being up to 6 m high, 10 - 15 cm deep, 10 - 20 cm wide at breast height, the top of the column often broadening into a wider "head" which reaches beyond the (coming) flood level (nests are rarely found at the beginning of the dry season, termites are subterranean during the dry period and start the epigeal (above-soil) constructions before the coming flood; nests attain highest size shortly before the flood)
 - Soil constructions are shallow (0.5-0.8 cm thick) sheaths of soil which cover the lower parts of a tree trunk up to a height of 12 - 14 m (they probably are covered feeding places of bark-feeding termites which have subterranean nests during the dry season).
 - Anoplotermes* sp. "A" 4
 - Anoplotermes* sp. "D" 5
3. The outer nest wall is a thin cartonaceous coverage which can be easily lifted off the nest in large plaques ("envelope" type; see above; cf. fig. 2); the surface often shows "growth zones" (fig. 3); generally only one and often large nest
 - Nest surface cannot be lifted off as a thin sheet, appearance is "bumpy" ("simple" type; see above; cf. fig. 1) without any growth zones; often several nests on neighboring trees are connected by "galleries" (covered runways). Nests are generally (but not necessarily) small. 6
4. Small to moderately large nests, generally laterally attached to a tree trunk. Termites: small brown-headed nasute soldiers and small workers.
 - Nasutitermes ephratae* (HOLMGREN)
 - Moderately large to large (tab. 2) nests generally built in a branch bifurcation of a tree. Termites: orange- or red-headed nasute soldiers and relatively large workers 5
5. Nest of dark grey to brown color, often connected by a 10 - 15 cm wide "highway" gallery to the ground. External nest surface of the "envelope" type. Termites: Soldier head reddish brown, slender, long pointed nose; workers very large
 - Nasutitermes surinamensis* (HOLMGREN)
 - Nest of a light brown to reddish-brown color, only narrow (3-4 cm) galleries leading to the ground. Surface "envelope" type, as in figure 11. Inside sometimes compact concretions of fecal matter are found which are of lighter color than the surrounding nest material (fig. 12). Nests often on a single tree in the outermost area of the forest where the flood lasts longer. Termites: Soldier head of lighter orange color than *N. surinamensis*, head broadly rounded, nose stout (fig. 7), head covered with numerous bristles (detectable only at a higher magnification), workers smaller than in *N. surinamensis*
 - Nasutitermes macrocephalus* (SILVESTRI)
6. Soldier termites small, soldier head dark chestnut brown, head broadly rounded, nose stout (head very slightly broader and stouter than in *N. ephratae*); small workers. The most common termites found in the várzea forest. Occur often in "polycalic" colonies (colonies with several interconnected nests, fig. 6)
 - Nasutitermes corniger* (MOTSCHULSKY)
 - Soldier termites small, although somewhat larger than those of *N. corniger*; soldier head reddish brown, in shape similar to *N. corniger*; workers smaller than in *N. surinamensis* and *N. macrocephalus*. Rare species, although sometimes occurring in "polycalic" colonies
 - Nasutitermes tatarendae* (HOLMGREN)