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The Nasute Termites (Isoptera: Nasutitermitinae) of Papua New Guinea

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Abstract

The Nasutitermitinae fauna of Papua New Guinea is revised, based on collections from most regions of the country. A total of 22 species is reported, 12 of which are new. The genus *Nasutitermes* Dudley is represented by the following species: *N. triodiae* (Froggatt), *N. torresi* (Hill), *N. motu*, sp. nov., *N. princeps* (Desneux), *N. koiari*, sp. nov., *N. pinocchio*, sp. nov., *N. novarumhebridarum* (N. & K. Holmgren), *N. nomadensis*, sp. nov., *N. polygynus* Roisin & Pasteels, *N. bikpelanus*, sp. nov., *N. gracilirostris* (Desneux), *N. leponcei*, sp. nov., *N. muli*, sp. nov., *N. seghersi*, sp. nov., and *N. seghersi malangganus*, subsp. nov. *Niuginitermes*, gen. nov., is created for two species: *N. variratae*, sp. nov., and *N. liklik*, sp. nov. *Diwaitermes*, gen. nov., includes *D. kanehirae* (Oshima), comb. nov., *D. foi*, sp. nov., and *D. castanopsis*, sp. nov. A single species of *Tumulitermes* Holmgren, *T. marcidus* (Hill), is newly reported from mainland New Guinea. *Grallatotermes* Holmgren and *Hospitalitermes* Holmgren are each represented by one species, *G. grallator* (Desneux) and *H. papuanus* Ahmad. All known imagos (18 species) as well as soldiers and workers of all species are described and illustrated. For each species, the known geographic distribution within Papua New Guinea is reported. An identification key, based on soldiers and workers, is also provided.

Introduction

The termite fauna of New Guinea has never been the subject of systematic collections or specific studies, and is still one of the least known in the world. The eastern half of the island, together with the Bismarck Archipelago, the northernmost islands of the Solomon Archipelago (Bougainville and Buka), and a constellation of small islands, forms the Independent State of Papua New Guinea, whose fauna is the focus of the present work.

The Nasutitermitinae constitute one of the most widespread termite taxa. However, since Hill's (1942) revision, very little has been published on the Nasutitermitinae fauna of the Papuan zoogeographic region, except for a few descriptions or redescriptions of single species (Ahmad 1947; Roonwal and Maiti 1966; Gay 1971; Roisin and Pasteels 1985*a*). In this work, we present an extensive revision of the Nasutitermitinae from Papua New Guinea, mostly based on material from the Australian National Insect Collection (ANIC), the American Museum of Natural History (AMNH) and our own collection. This material represents such a sum of collecting efforts that only rare or locally distributed species are likely to have been missed. The present revision also includes a critical reappraisal of the generic assignment of each species, which led us to describe two new genera, *Niuginitermes* and *Diwaitermes*.

Materials

The present survey of Papua New Guinea termites started in 1978. The sites visited by at least one of us, with the special purpose of collecting termites and termitophiles, are shown in Fig. 1. These collections

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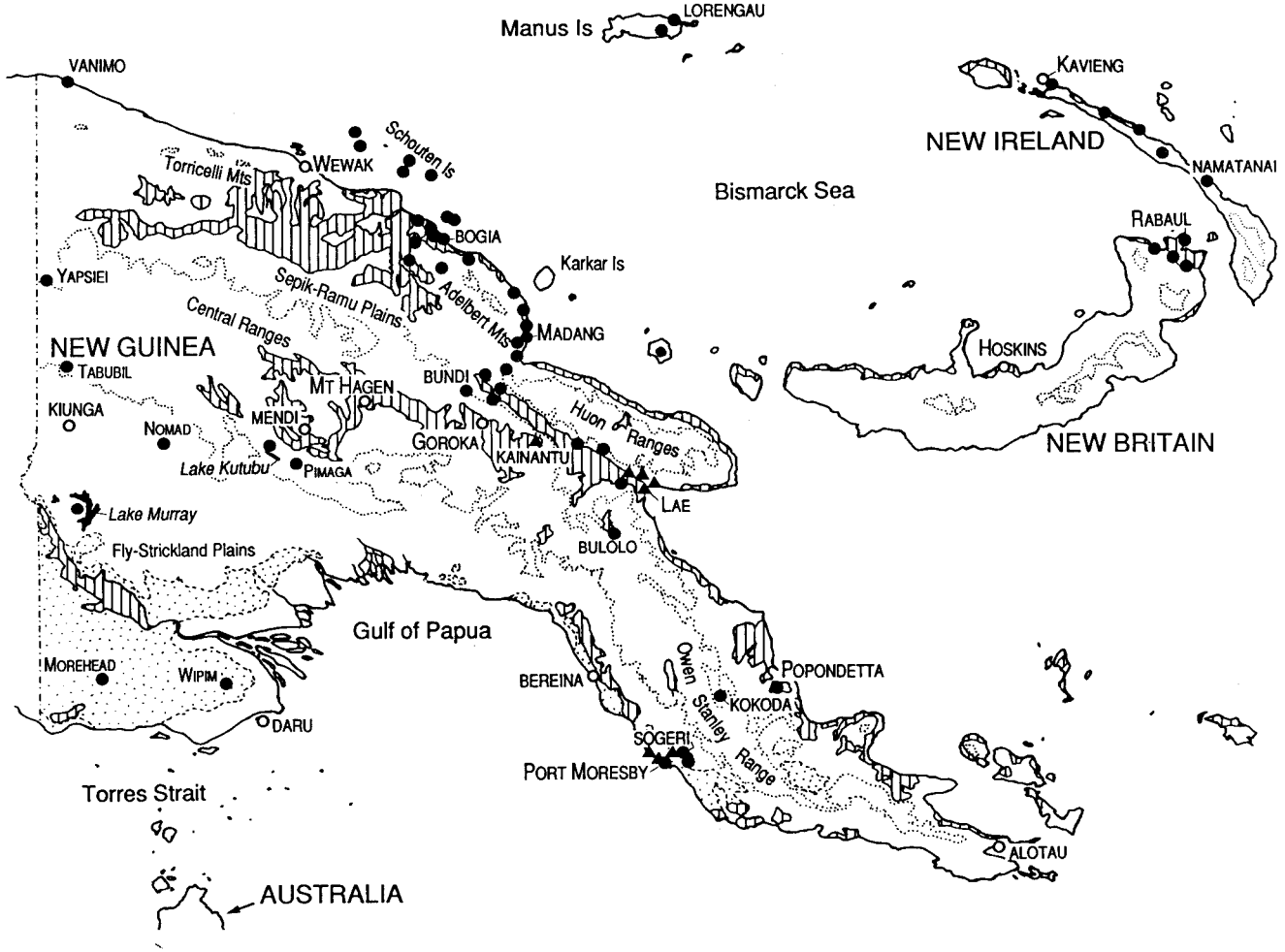


Fig. 1. Map of Papua New Guinea (excluding the North Solomons Prov.) showing major towns, collecting spots and geographic features. Vegetation types are represented on all maps as follows (modified from Robbins 1974). Unshaded: lowland and hill forest, mangrove; montane forest (limited by dotted line) or alpine vegetation (not detailed, only present on highest mountains. Stippled, limited by dashed line: savanna, open woodlands, dry sclerophyllous forest. Hatched: grasslands. Filled symbols indicate spots visited by at least one of the authors between 1978 and 1994 (●) or by A. and E. Emerson in 1962–1963 (▲), with the specific purpose of collecting termites.

cover most regions of the country, except the following: (1) the easternmost part of New Guinea (Milne Bay Province), (2) lowlands of the Gulf of Papua, (3) western New Britain and (4) the North Solomons (Bougainville and Buka islands). Most samples were collected in Bouin's fixative or in FAA (formol: alcohol: acetic acid) and preserved in 70% ethanol.

The ANIC possessed a number of undetermined termite samples collected by various entomologists when Papua and New Guinea were territories under Australian administration. During 1962–63, Alfred and Eleanor Emerson made a trip around the world to collect termites, visited the regions of Port Moresby and Lae (Fig. 1), and deposited their collections in the AMNH. Those ANIC and AMNH series, most of which were still unidentified, were loaned to us for study. In addition, some samples of undetermined nasutes from Papua New Guinea were provided to us directly by the collectors. Nest series are designated by the collection's abbreviation followed by the nest series' accession number.

Collectors

A. E.	Alfred E. Emerson
E. E.	Eleanor Emerson
J. M. P.	Jacques M. Pasteels
M. L.	Maurice Leponce
P. A.	P. Aloma
P. C. H.	P. C. Heyligers
P. P. D.	Phille P. Daur
Y. R.	Yves Roisin

Collections

AMNH	American Museum of Natural History, New York, USA
ANIC	Australian National Insect Collection, Canberra, Australia
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MCZC	Museum of Comparative Zoology, Cambridge (Massachusetts), USA
MZEL	Museum of Zoology and Entomology, Lund, Sweden
NHMB	Naturhistorische Museum, Basel, Switzerland
NHRM	Naturhistoriska Riksmuseet, Stockholm, Sweden
NMVM	National Museum of Victoria, Melbourne, Australia
PNGT	Authors' collection, Université Libre de Bruxelles, Belgium

The authors' collection, including type specimens designated from it in the present study, will be deposited at the IRSN. Paratypes will be deposited in the Papua New Guinea National Insect Collection and ANIC.

Methods

Characters Used

Colour is often very useful to identify species, especially in the field. The colour scale proposed by Sands (1965) will be used here. Although we do not expect that all readers will interpret it exactly as we did, the use of this scale should at least provide a consistent basis for comparing different specimens or different body parts of a single individual.

The number of antennal segments varies from 11 to 17. Sometimes, the segmentation of the base of the flagellum is ambiguous: it can be interpreted as one segment incompletely divided, or as two segments incompletely separated. We will describe such cases according to the latter interpretation.

The colour, pilosity and shape of the soldiers' head capsule, the number of antennal segments and the length of the appendages provide useful taxonomic criteria. Measurements require the following explanations. In imagos, eye diameter is its largest diameter, including the thin hyaline border. Length of pronotum is the distance between lines drawn tangentially to the foremost and the rearmost margins of the pronotum. Length of forewing is measured from the suture to the tip, thus excluding the stump. In soldiers, measurements were taken as in Pasteels *et al.* (1988): the head is positioned in dorsal view so as to focus simultaneously on the tip of the rostrum and on the rear margin of the head capsule. Total length of head capsule is measured in this position. The length of the rostrum is measured in the sagittal plane, from its tip to the line joining the fore margin of the antennal sockets. The distance, along the sagittal plane, between the hind margin of the head capsule and the line joining the sides of the head capsule where widest is defined as 'back of head' distance. The width of the rostrum is measured halfway along its length. Depth of head capsule excludes the postmentum. The chemical composition of the soldiers' defensive secretion is mentioned whenever available.

Workers are dimorphic in all *Nasutitermes* species studied: large workers are female, small ones are male (Noirot 1955; Pasteels 1965; Roisin and Pasteels 1986*a*, 1987). In addition, in each category, two or more successive instars occur, usually showing increasing size and pigmentation. The other New Guinean genera display a worker dimorphism or polymorphism parallel to that of *Nasutitermes*. First-instar large workers were used whenever possible for anatomical observations, but anatomical variations between different worker categories in a nest seem to be negligible.

Worker mandibles are widely used as taxonomic criteria, especially at the genus level. The left mandible index (Emerson 1960) is the ratio between the distance separating the apical tooth (A) from the fused first and second marginal teeth (M_{1+2}) and the distance separating M_{1+2} from the third marginal (M_3). Molar areas are called molar prominence (left mandible) and molar plate (right mandible).

The digestive tract often provides useful taxonomic criteria in termite workers (Sands 1972; Johnson 1979). The digestive tract of an unidentified African *Nasutitermes* species was described by Kovoor (1969) and the *in situ* configuration of the gut of *N. arborum* by Johnson (1979). The following characteristics seem constant throughout the genus (see Fig. 14): gizzard well-armed; mixed segment long; P1 (first segment of the proctodeum) tubular; enteric valve (P2) armed with spines; P3 forming a broad paunch; no distinct sphincter between P3 and P4; P4 (colon) originates anterodorsally from P3, proceeds to the right side of the paunch and then to the rectum (P5). All Papua New Guinean nasutes display basically the same configuration, but the following criteria were found to be of some taxonomic value.

(1) The configuration of the proctodeum *in situ*.

(2) The position of the mixed segment. The mesenteric part of the mixed segment can be oriented in various positions. In some species, it is linked to the remainder of the mesenteron by a wide mesenteric peduncle (see Fig. 14); in others, the two parts of the mesenteron are completely separated by proctodeal folds (see Fig. 49).

(3) There are always four malpighian tubules, swollen in their basal part, but constricted at their point of attachment to the mesentero-proctodeal junction. In most species, they are attached as two pairs separated by a gap (see Figs 54–57); in the others, they are all attached contiguously (see Figs 68–70). The malpighian tubules usually form a dense interlacing applied along the mesenteric part of the mixed segment.

(4) The enteric valve can be positioned *in situ* transversally, obliquely or longitudinally. Its armature typically consists of two rings of six spiny areas; each ring shows basically a trilateral symmetry, three major areas alternating with three minor ones (see Fig. 113). These rings are hereafter referred to as 'upper' and 'lower', the lower being closer to the paunch, and, in some species, penetrating into it. Asymmetries can affect both rings, especially the upper one when situated in a curve of the proctodeum.

Description Procedure

Under the heading of each genus or species name, the list of citations will be limited to the original author of the name, the author of the present combination, and authors of substantial revisions or descriptions providing useful information for species identification, complementary to the present work. As the purpose of this paper is not to discuss generic taxonomy on a worldwide basis, generic descriptions will focus on the diagnostic features allowing genus allocation of Papua New Guinean species. Full descriptions will be given of all species, except those for which adequate descriptions are readily available in the literature (Hill 1942; Ahmad 1947; Gay 1971; Roisin and Pasteels 1985*a*). We will nevertheless complement previous descriptions and pinpoint diagnostic traits allowing species identification. In addition, descriptions of worker digestive tract and data on worker polymorphism will be provided for all species.

Illustrations

Drawings of imago head and pronotum were made with the help of a camera lucida at 50× magnification, omitting pilosity. During the preparation of soldiers for scanning electron microscopy, their frontal gland often strongly adhered to the head capsule and caused its collapse under vacuum during metallisation. To prevent this, soldiers were treated by 6% KOH overnight before dehydration. This treatment partly dissolved the frontal gland. After washing with distilled water and dehydration by increasing concentrations of ethanol, the specimens were left in hexamethyldisilazane for at least 12 h before being air dried and sputter coated with gold. Microphotographs were taken with an ISI DS-130 scanning electron microscope. Mandibles and enteric valves of workers were dissected, then dehydrated and mounted on microscope slides. The digestive tube of large workers was observed *in situ* after removal of the abdominal wall and fat tissue under a dissecting microscope, then drawn at 50× magnification with the help of a camera lucida.

Subfamily **NASUTITERMITINAE** Hare

Type genus: *Nasutitermes* Dudley, 1890.

Soldiers in this subfamily are characterised by a well-developed frontal gland, opening through a pore situated at the tip of a more or less developed rostrum. This subfamily comprises three major groups of genera. In the 'mandibulate' nasutes (*Syntermes*-group), the soldiers possess functional mandibles and combine chemical and mechanical defences. This group is strictly neotropical. The other Nasutitermitinae possess soldiers with vestigial mandibles and a very elongated rostrum, relying solely on chemical weapons ('full' nasutes). They are pantropical. Among them, two groups can be recognised on the basis of worker anatomy and diet. These groups were long considered to represent divergent phyletic lines (Ahmad 1950), but nowadays, their phylogeny is subject to revision (Miller 1986). The following distinction may prove unnatural in the future, but is still convenient for identification purposes.

1. Left mandible index < 0·7; apical tooth equal to or shorter than M_{1+2}. Molar plate with prominent ridges. Long mixed segment (much longer than diameter of mesenteron) ..... Xylophagous nasutes (*Nasutitermes*-group)

   Left mandible index > 0·7; apical tooth longer than M_{1+2}. Molar plate concave, ridges weak, vestigial or absent. Mixed segment absent or very short (shorter than diameter of mesenteron) ..... Humivorous nasutes (*Subulitermes*-group)

Thus far, no humivorous nasute has been collected from New Guinea. *Oriensubulitermes* Emerson and related genera reach Borneo (Thapa 1982), but have not been reported east of Wallace's line. *Subulitermes undecimus* Kemner, from Ambon, was reassigned to *Nasutitermes* by Emerson (1960). However, *Macrosubulitermes* Emerson and *Australitermes* Emerson are present in Northern Australia (Emerson 1960; Miller 1984), suggesting that humivorous nasutes of Australian origin could be discovered in New Guinea in the future.

In total, 22 species of xylophagous nasutes are herein reported from Papua New Guinea (see Appendix). They represent six genera: *Nasutitermes* (14 species), *Niuginitermes* (new genus, 2 species), *Diwaitermes* (new genus, 3 species), *Tumulitermes* (new record, 1 species), *Grallatotermes* and *Hospitalitermes* (1 species each).

Genus *Nasutitermes* Dudley

Nasutitermes Dudley, in Dudley and Beaumont, 1890: 158.

Type species, by subsequent designation (Snyder 1949): *Termes cornigera* Motschulsky, 1855.

For a nomenclatorial discussion regarding authorship of this genus, see Sands (1965); regarding the type species, see Watson *et al.*, in press.

The most abundant and widespread nasute genus in New Guinea. Soldier variable in size, pilosity and pigmentation. Head capsule yellow to very dark sepia brown, not constricted behind antennae. Antennae of 12–14 segments. Workers variable in size and pigmentation. First instar of both sexes always with pale head capsule and translucent abdominal wall. Antennae of 14–15 segments. Mixed segment of gut long, with mesenteric part positioned on its upper and outer side. Malpighian tubules attached as two pairs separated by a space, usually very wide (the insertions of the two pairs being almost diametrally opposed) but sometimes small (very narrow in some populations of *N. gracilirostris*). Upper ring of spiny areas of enteric valve asymmetrical. Short space between upper and lower ring. Minor spiny areas of lower ring very reduced or absent. Valve armature not penetrating into the paunch.

Two groups of species can be recognised among New Guinean *Nasutitermes*. The first group comprises the species described hereunder from *N. triodiae* to *N. polygynus*. The soldiers are of medium to large size, with a darkly pigmented head capsule (chestnut brown to very dark sepia, without yellow tinge) and antennae of 13–14 segments. The other group comprises the species described from *N. bikpelanus* to *N. seghersi malangganus*. Soldiers possess a yellow to orange–brown head capsule, antennae of 12–13 segments, and are usually smaller than in the other

group. Worker polymorphism tends to be more pronounced in the first group, but varies from species to species. The enteric valve shows the same pattern in the two groups. The configuration of the digestive tract is almost identical in the two groups, apart from the mesenteric part of the mixed segment, which is in continuity with the remainder of the mesenteron in the first group but isolated from it by proctodeal folds in the second. In our opinion, this peculiarity alone would not justify splitting the genus.

Nasutitermes triodiae (Froggatt)

Eutermes triodiae Froggatt, 1897 (actually published in 1898, see Watson *et al.* in press): 745–747, pl. 35 (Fig. 8). Imago (error), soldier, worker, nest.

Eutermes triodiae. — Hill, 1942: 269–273, figs 175, 176, pls 13–15, pl. 16 (fig. 1). Imago, soldier, worker, biology, nest.

Nasutitermes triodiae. — Snyder, 1949: 299.

Material Examined

Authors' collection (PNGT). #1407, 1413, 1428, 1429, 1458, 1459: Morehead, Western Province (8°43′S, 141°38′E), 22–27.iii.1989 (Y. R., M. L.). #1477, 1493, 1510: Wipim, Western Province (8°47′S, 142°53′E), 30.iii–1.iv.1989 (Y. R., M. L.).

ANIC. #10 10367: Rouku, Western Distr., Apr. 1962 (W. Brandt). #10 10368: Dauan I. (Torres Strait), 2.vi.1962 (W. Brandt). #10 10388: Port Hedland, Western Australia, 10.vi.1962 (D. H. Perry). #10 13962: between Rouku and Weam (Western Distr.), 28.viii.1970 (K. H. L. Key, J. Balderson).

Imago (Fig. 2)

The largest Papua New Guinean species, especially distinguishable from all other species by the length of its appendages. Head capsule very dark chestnut brown, contrasting with orange postclypeus and antennae. Pronotum ferruginous. Antennae 16-segmented.

	Measurements (in mm)			
	ANIC#10 10388	PNGT#1429	PNGT#1459	PNGT#1493
	Alate ♂	Dealated ♀	Alate ♀	Queen
Head width across eyes	2·11	2·040	1·993	2·094
Largest diameter of eye	0·738	0·735	0·703	0·712
Ocellus length	0·242	0·243	0·218	0·226
Eye to ocellus	0·078	0·080	0·062	0·068
Pronotum width	2·06	2·007	1·960	2·079
Pronotum length	1·22	1·171	1·161	1·213
Hind tibia length	2·95	2·75	–	2·75
Forewing length	19·3	–	18·7	–

Soldier (Fig. 3)

A large, dark chestnut, hairy species with very long appendages. Antennae 14-segmented, segment 3 elongated, 2–3× as long as wide, well-separated from segment 4 and almost as long as it.

	Measurements (in mm)		
	ANIC#10 10388	PNG specimens (18 soldiers, from 6 colonies)	
		Range	Mean
Head capsule total length	2·10	1·764–2·009	1·857
Rostrum length	0·887	0·723–0·858	0·798
'Back of head' distance	0·583	0·430–0·540	0·480
Head width	1·23	0·983–1·234	1·103
Rostrum width (at half length)	0·164	0·144–0·177	0·161
Head depth	0·869	0·693–0·925	0·775
Hind tibia length	1·938	1·701–2·040	1·840

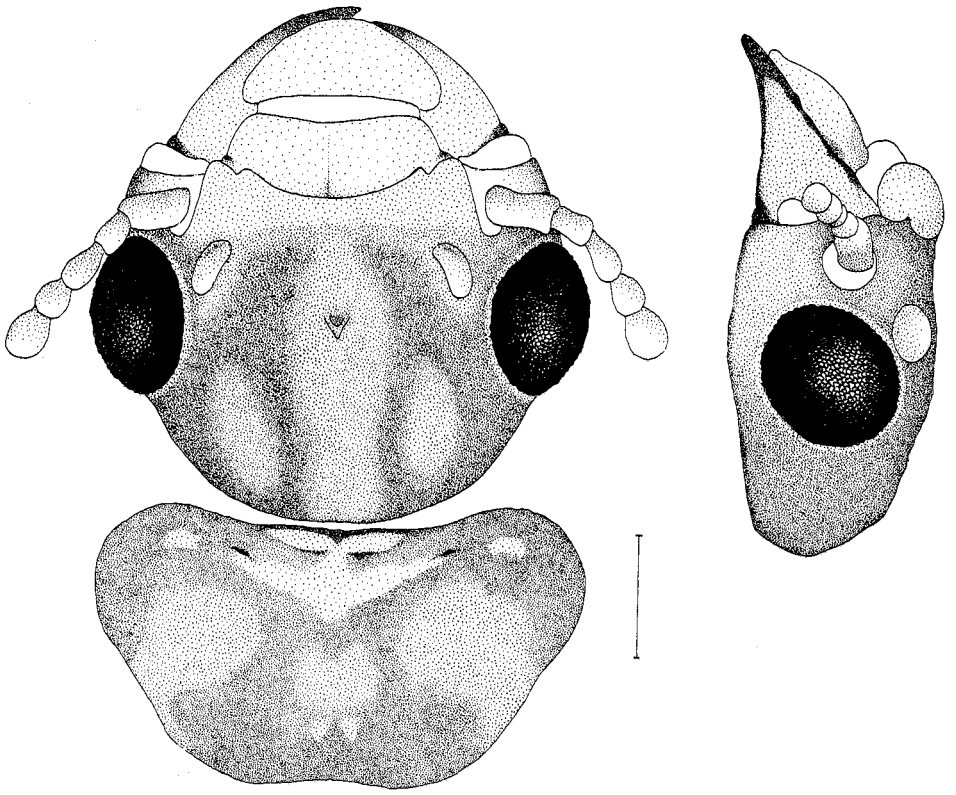


Fig. 2. *Nasutitermes triodiae* (Froggatt), female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Worker (Figs 4, 5)

Head capsule from pale yellow to chestnut. Large workers much larger than small ones. Large workers widely polymorphic, due to substantial growth between successive instars and conspicuous increase in sclerotisation. Mandibles as in Fig. 4. Short space between apical tooth and first marginal. On right mandible, first marginal much broader than notch between apical and first marginal. Molar areas somewhat sinuous. Configuration of the digestive tube very similar to that of *N. motu*, sp. nov., described below (see Fig. 14). Mesenteric part of mixed segment attached to main part of mesenteron by wide dorsal peduncle. Malpighian tubules attached as two well-separated pairs. Enteric valve weakly armed (Fig. 5): upper ring of ill-defined spiny areas in curve of proctodeum, spines short and asymmetrically distributed, much more numerous on outer side of curve. Lower ring of three unsclerotised areas with 5–12 short spines.

Head width of workers from nest PNGT#1493: small workers, first instar, 0·99–1·03 (mean = 1·01, n = 10); large workers, first instar, 1·32–1·37 (mean = 1·35, n = 25); instar 2 and older, 1·49–1·74 (mean = 1·62, n = 65).

Distribution (Fig. 15)

Widespread in Australia: Western Australia, Northern Territory, Queensland, Torres Strait (see Hill 1942; Watson and Abbey 1993). In Papua New Guinea, only recorded from southern savannas. Mounds presumably built by this species were also seen near the airstrips of Bensbach and Suki, Western Province.

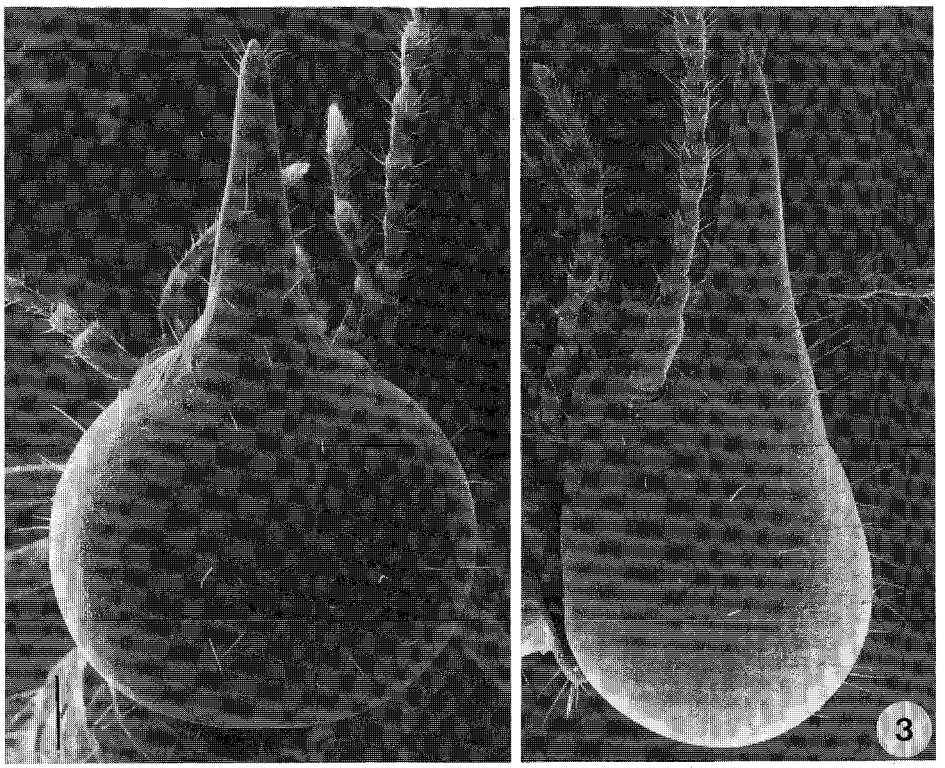


Fig. 3. *Nasutitermes triodiae* (Froggatt): soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Biology

Nasutitermes triodiae is famous in Australia for building huge epigeal mounds of varying size and shape (Hill 1942). The nests we observed in Papua New Guinea in March–April 1989 were of the 'columnar' type (as in Hill 1942, pl. 13, Fig. 1). They contained large amounts of stored food, as pieces of straw about 1 cm long. The queen of nest PNGT#1493 was found above ground level; there was no defined nursery or royal cell. The epigeal part of this nest was connected to underground chambers by a wide, central tunnel.

Nasutitermes torresi (Hill)

Eutermes torresi Hill, 1942: 303–305, figs 223–225. Imago, soldier, worker, nest.
Nasutitermes torresi. — Snyder, 1949: 299.

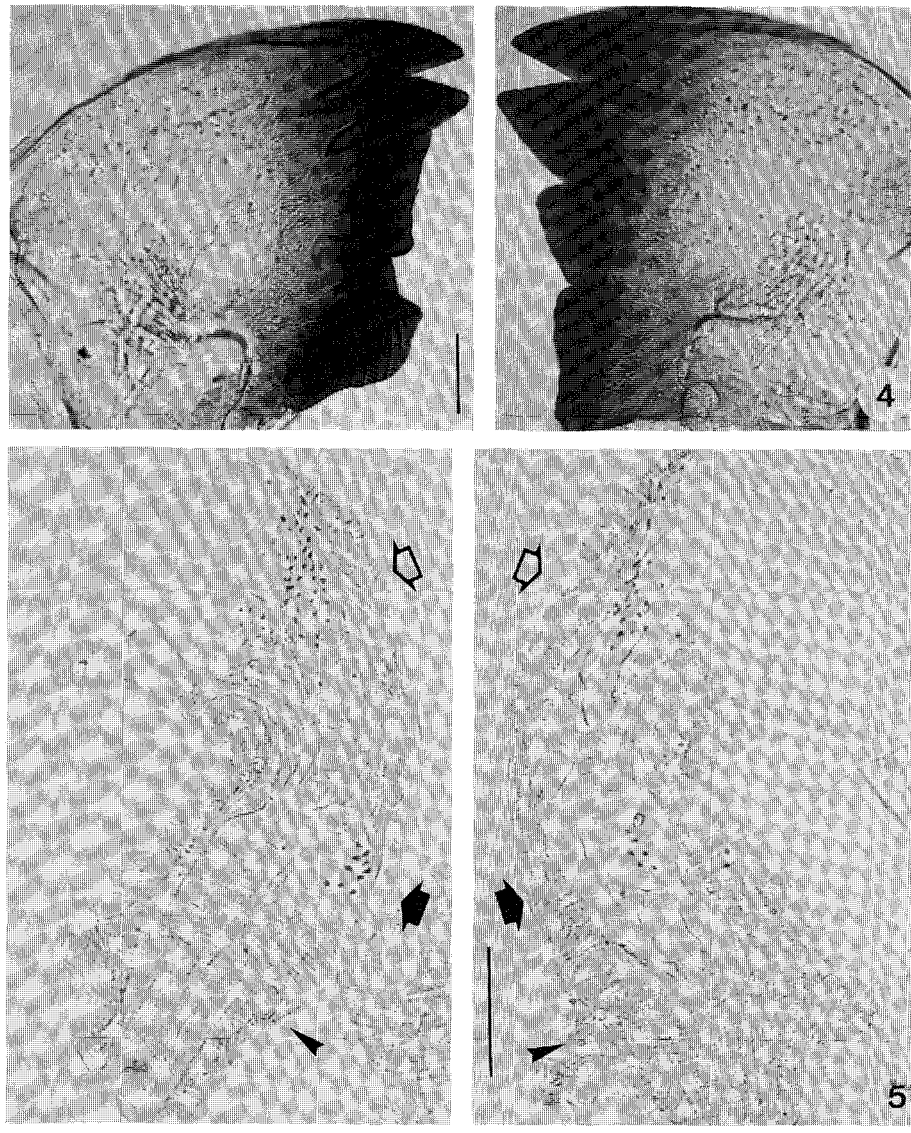
Material Examined

Type material. Two alates from type colony (ANIC#10 17707): Thursday I., Torres Strait, 1936 (H. N. Hockings). Soldiers and workers from paratype colony (ANIC#10 17708): *ibid.*, 17.x.1935 (H. N. Hockings).

Authors' collection (PNGT). #1437, 1461, 1463: Morehead, Western Province (8°43′S, 141°38′E), 24–27.iii.1989 (Y. R., M. L.).

Imago (Fig. 6)

Smaller than *N. triodiae*. Postclypeus and antennae darker, chestnut brown.



Figs 4, 5. *Nasutitermes triodiae* (Froggatt), large worker: *4*, mandibles; *5*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

	Measurements (mm)		
	PNGT#1461, queen	Type colony, alate ♂	
Head width across eyes	1·757	1·71	1·75
Largest diameter of compound eye	0·620	0·625	0·617
Ocellus length	0·215	0·214	0·198
Eye to ocellus	0·047	0·045	0·045
Pronotum width	1·703	1·62	1·57
Pronotum length	1·028	0·99	0·96
Hind tibia length	2·27	2·36	2·36
Forewing length (without stump)	–	15·5	–

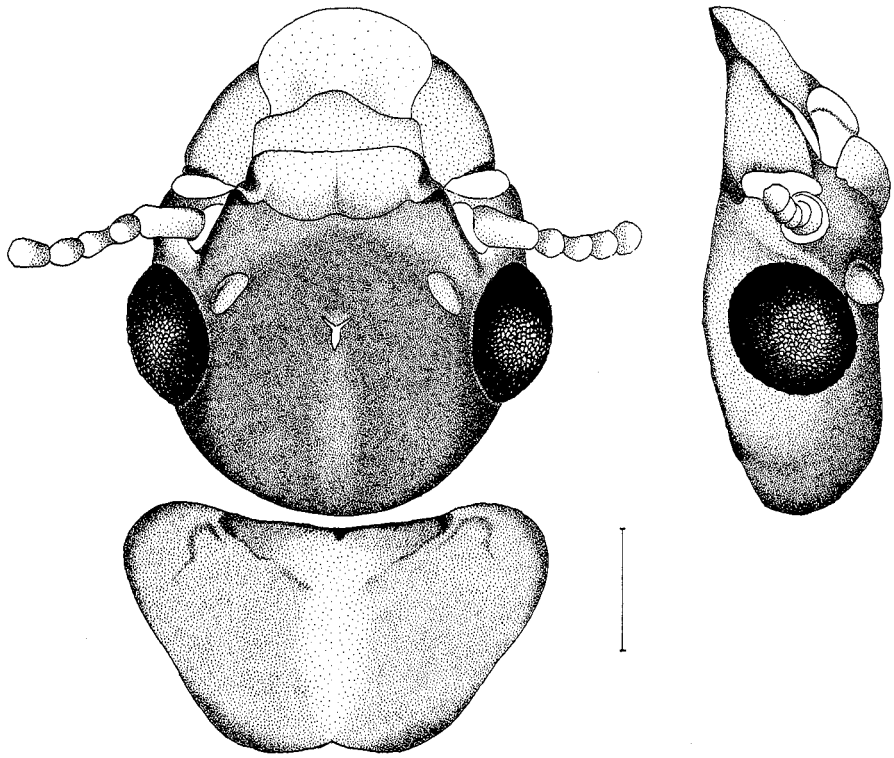


Fig. 6. *Nasutitermes torresi* (Hill), queen: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Soldier (Fig. 7)

Closely allied to *N. triodiae*, but clearly distinguished from it by its sepia brown abdominal tergites and antennae, contrasting with orange–yellow legs. Antennae almost as dark as head capsule. Third antennal segment shorter than in *N. triodiae*, less than twice as long as wide. Legs much shorter than in *N. triodiae*.

	Measurements (mm)		
	Paratype colony (3 soldiers)	PNG specimens (9 soldiers, from 3 colonies)	
	Mean	Range	Mean
Head capsule total length	1·849	1·724–1·906	1·794
Rostrum length	0·762	0·722–0·790	0·757
'Back of head' distance	0·510	0·458–0·508	0·484
Head width	1·143	0·977–1·158	1·052
Rostrum width (at half length)	0·156	0·150–0·162	0·156
Head depth	0·833	0·650–0·823	0·740
Hind tibia length	1·378	1·242–1·338	1·277

Worker (Figs 8, 9)

Closely allied to *N. triodiae*, but with brown abdominal tergites. Mandibles (Fig. 8) and digestive tract as in *N. triodiae*. Lower spiny areas of enteric valve slightly swollen, with 5–10 spines (Fig. 9).

Head width of workers from nest PNGT#1461: small workers, first instar, 0·901–0·940 (mean = 0·914, n = 8); large workers, first instar, 1·120–1·161 (mean = 1·146, n = 8); instar 2 and older, 1·218–1·327 (mean = 1·287, n = 16).

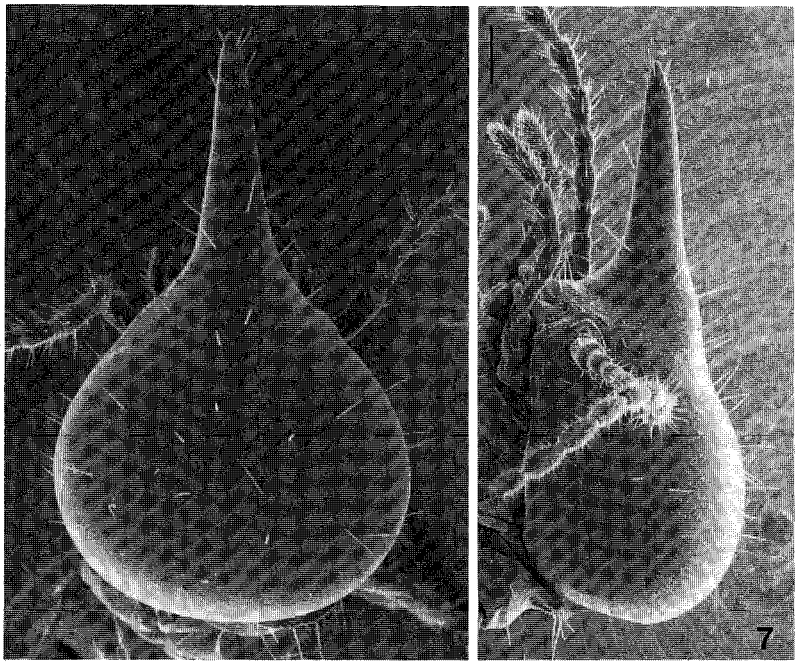


Fig. 7. *Nasutitermes torresi* (Hill): soldier head from above (left), in profile (right). Scale bar = 0·2 mm.

Distribution (Fig. 15)

Reported from Torres Strait Islands: Thursday I. (type locality), Prince of Wales I. (De Baar 1988). Also known from Northern Australia (Watson and Abbey 1993). In Papua New Guinea, found only in Morehead, Western Province.

Biology

The three nests encountered in Morehead were built on or close to pieces of dead wood, on which the termites presumably fed. Very little grass, if any, was stored in the nests.

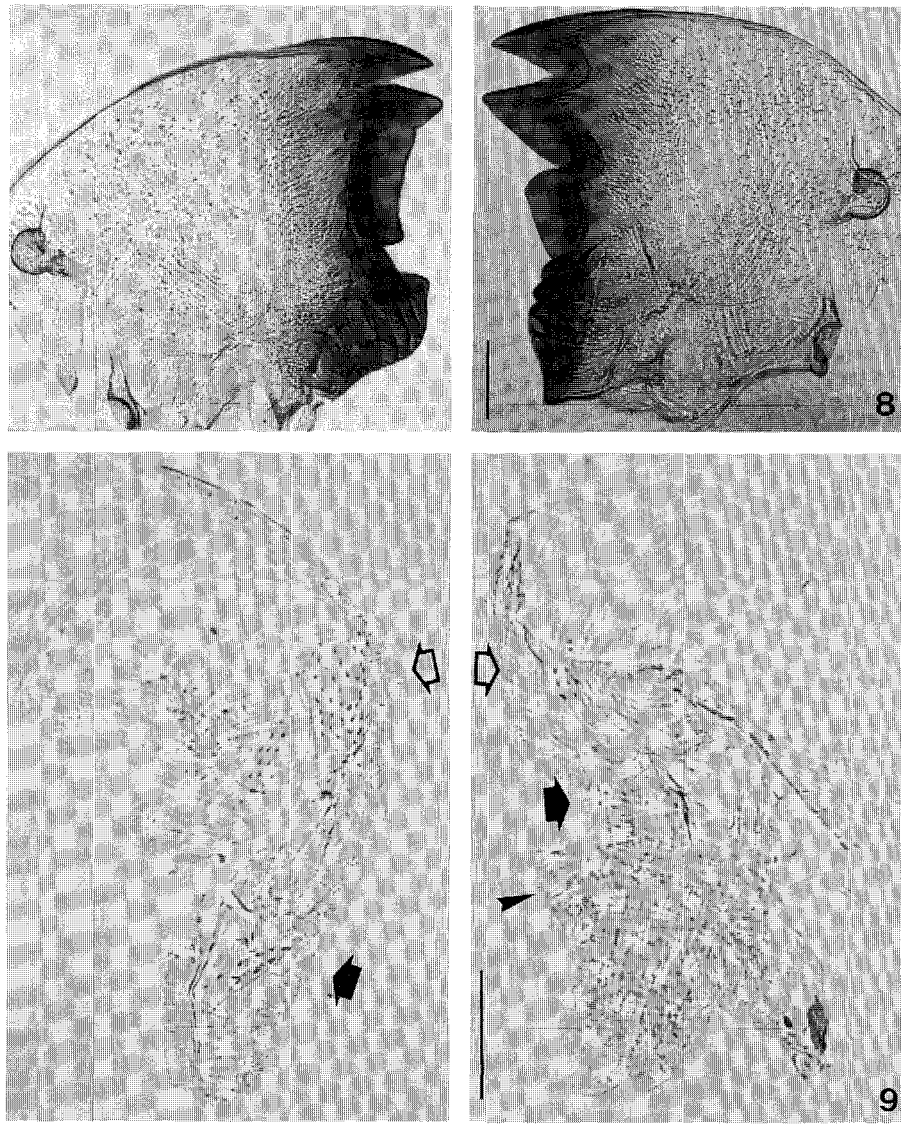
Nasutitermes motu, sp. nov.

Material Examined

Type colony (PNGT#936). Sirinumu Dam (Central Province), 9.iii.1985. Very large mound. One queen found, but seemed small to be lone reproductive in such a nest. No definite royal cell (J. M. P., Y. R.). Holotype: soldier.

Authors' collection (PNGT). #58–59: Port Moresby (Jackson's Airport), 7.ii.1979 (J. M. P.). #720–724: Waigani (Port Moresby), 12–13.vii.1984 (Y. R.). #732: Sogeri, Central Province, 14–15.vii.1984 (Y. R.). #856: Sogeri, 4.ii.1985 (J. M. P., Y. R.). #933, 942: Sirinumu Dam (Central Province), 9–10.iii.1985 (J. M. P., Y. R.). #948: Port Moresby (Jackson's Airport), 12.iii.1985 (J. M. P., Y. R.). #1339, 1343: University of PNG campus, Port Moresby, 4–5.xii.1988 (Y. R.). #1350, 1356: Varirata National Park, Central Province, 6.xii.1988 (Y. R., P. P. D.). #1409, 1432, 1454, 1460: Morehead, Western Province, 22–27.iii.1989 (Y. R., M. L.). #1478, 1479, 1494: Wipim, Western Province, 30–31.iii.1989 (Y. R., M. L.).

ANIC. #10 9922–9924: 21–27 km NNE Port Moresby, 24–25.ix.1961 (F. J. Gay). #10 10364: Rouku, Western Distr., Apr. 1962 (W. Brandt). #10 10411: Ilogo Plantation, Central Distr., alt. 500 m, 2.iii.1961 (A. Catley). #10 10450: 2 km NE Waima, Central Distr., 6.ix.1962 (P. C. H.). #10 10451: 3 km S Delena, Central Distr., 24.viii.1962 (P. C. H.). #10 10452: 5 km W Kanosia Plantation, Central Distr., 17.viii.1962



Figs 8, 9. *Nasutitermes torresi* (Hill), large worker: *8*, mandibles; *9*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowhead, attachment of paunch. Scale bars = 0·1 mm.

(P. C. H.). #10 10453: Bisianumu, Central Distr., 6.viii.1962 (P. C. H.). #10 10454: Araidabu, Central Distr., 1.viii.1962 (P. C. H.). #10 10455: 12 km NE Port Moresby, 21.vii.1962 (P. C. H.). #10 10456: 1 km N Papa, 19.vii.1962 (P. C. H.). #10 10457: 2 km N Gaile, 13.vii.1962 (P. C. H.). #10 10458: 13 km E Port Moresby, 5.vii.1962 (P. C. H.). #10 10459: Kido, 3.x.1962 (P. C. H.). #10 10460: 6 km W Inawi, 8.ix.1962 (P. C. H.). #10 10461: 5 km NNW Inawabui, 29.viii.1962 (P. C. H.). #10 10462: 15 km NE Port Moresby, 2.vii.1962 (P. C. H.). #10 13133–13135: Port Moresby, 4–11.iii.1969 (K. R. Norris). (no accession number): three samples from Taurama, Port Moresby, Apr. 1952 (Anderson).

Other collection. J. W. Turner. Dauan I., Torres Strait, 15.iv.1983. Saibai I., Torres Strait, 18.iv.1983.

AMNH. #E10, 17, 30–32, 34, 36: within 26 km of Port Moresby, 16–18.xi.1962 (A. E., E. E., J. J. H. Szent-Ivany).

Imago (Fig. 10)

Head capsule dark chestnut. Postclypeus chestnut brown. Labrum, antennae, legs and thoracic sclerites ferruginous. Abdominal tergites chestnut brown. Sternites orange. Wing membrane brown, turning yellow near its anterior border.

Posterior margin of the head regularly rounded. Fontanelle hyaline, short and narrow, Y-shaped. Eyes large, almost circular. Ocelli large, very close to eyes. Antennae 16-segmented, segments 3 and 4 subequal and incompletely separated.

Measurements of females (mm)

	Eastern Papua (7 queens, 5 alates)		Fly Plains (2 queens: PNGT)	
	Range	Mean	#1478	#1494
Head width across eyes	1·71–1·80	1·75	1·86	1·86
Largest diameter of eye	0·584–0·645	0·618	0·658	0·686
Ocellus length	0·210–0·262	0·231	0·240	0·242
Eye to ocellus	0·020–0·054	0·044	0·036	0·022
Pronotum width	1·60–1·76	1·69	1·79	1·83
Pronotum length	0·96–1·06	1·00	1·10	1·09
Hind tibia length	2·03–2·28	2·19	2·35	2·44
Forewing length	15·6–16·6	16·0	–	–

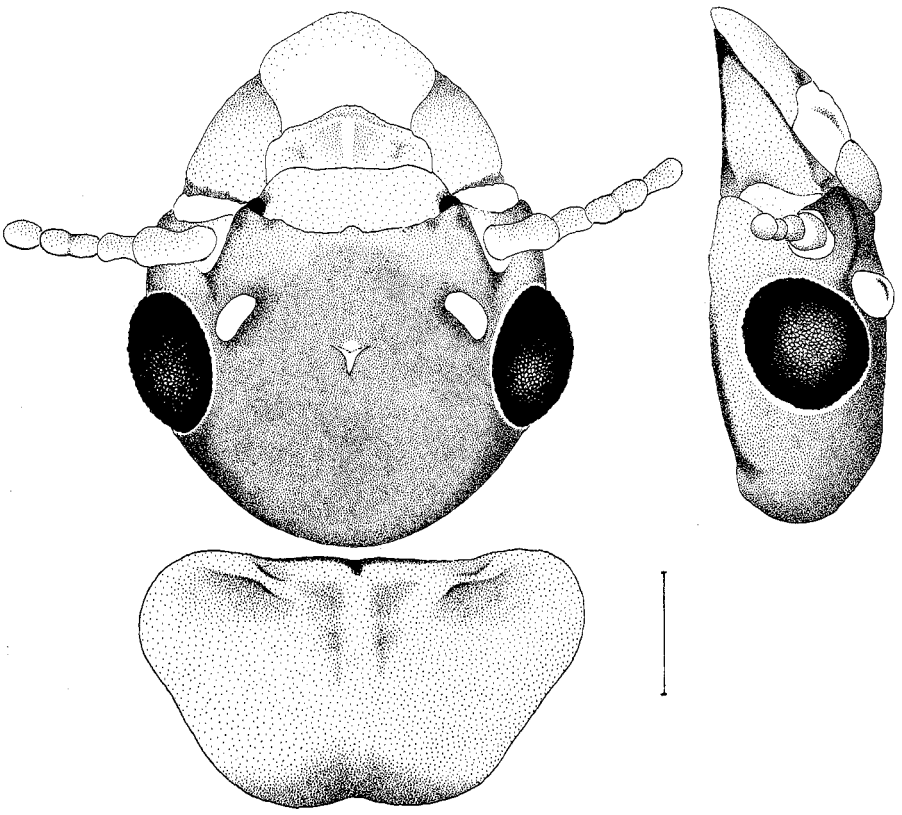


Fig. 10. *Nasutitermes motu*, sp. nov., female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Measurements of males (mm)

	Eastern Papua PNGT#59 (2 alates)		Fly Plains Taurama (ANIC, no accession No.) (king)	PNGT#1432 (alate)
Head width across eyes	1·68	1·71	1·69	1·71
Largest diameter of eye	0·618	0·613	0·612	0·604
Ocellus length	0·237	0·212	0·215	0·223
Eye to ocellus	0·026	0·029	0·040	0·026
Pronotum width	1·53	1·50	1·50	1·47
Pronotum length	0·93	0·925	0·91	0·96
Hind tibia length	2·19	2·14	2·20	2·13
Forewing length	14·5	14·2	–	–

Soldier (Fig. 11)

Head capsule dark chestnut, paler around and in front of antennal sockets. Thoracic nota, antennae and abdominal tergites yellow-brown. Legs and abdominal sternites very pale brown.

Head capsule rounded, often with a slight notch at the back, in profile slightly concave. Rostrum conical. Antennae 14-segmented, segments 3 and 4 incompletely separated. Head capsule pilose, with many long, stiff setae. Abdominal tergites with two rows of numerous stiff setae (10–15 per row on tergites 3–5).

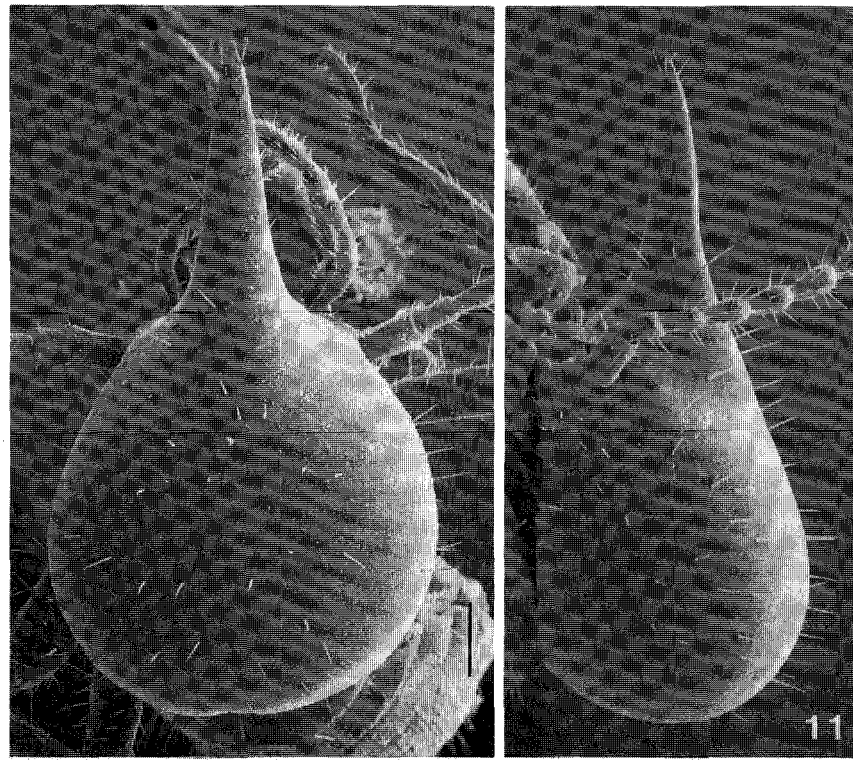


Fig. 11. *Nasutitermes motu*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Measurements (mm) 30 individuals from 10 colonies

	Range	Mean
Head capsule total length	1·476–1·892	1·684
Rostrum length	0·596–0·793	0·722
'Back of head' distance	0·381–0·525	0·448
Head width	0·828–1·146	0·968
Rostrum width (at half length)	0·135–0·165	0·150
Head depth	0·607–0·858	0·703
Hind tibia length	1·217–1·557	1·389

The diterpene content of the defensive secretion of this species was studied by Dupont *et al.* (1981), who called it *Nasutitermes* sp. A.

Worker (Figs 12–14, 54)

Head capsule yellow–white to dark chestnut. Tergites translucent to pale brown. Antennae 15-segmented, with segments 3 and 4 usually partly fused. Substantial growth and increase in pigmentation between successive instars in small and large workers.

Mandibles (Fig. 12) and gut (Fig. 14) very similar to those of *N. triodiae*. Mesenteric part of mixed segment attached to remainder of mesenteron by wide dorsal peduncle. Malpighian tubules attached as two well-separated pairs. Enteric valve weakly armed (Fig. 13): upper ring of ill-defined spiny areas in curve of proctodeum, spines short and asymmetrically distributed, much more numerous on outer side of curve. Lower spiny areas of enteric valve slightly sclerotised, with short spines.

Head width of workers from type colony: small workers, first instar, 0·91–1·01 (mean = 0·98, n = 14); large workers, first instar, 1·24–1·31 (mean = 1·27, n = 26); instar 2 and older, 1·36–1·56 (mean = 1·48, n = 61).

Distribution (Fig. 15) *and Biology*

Recorded from savannas and woodlands of Eastern Papua and Fly Plains. This is so far the only epigeal mound-building nasute found in the Port Moresby area, where it is very common. Sympatric with *N. triodiae*, *N. torresi* and *Tumulitermes marcidus* in Southern Fly savannas.

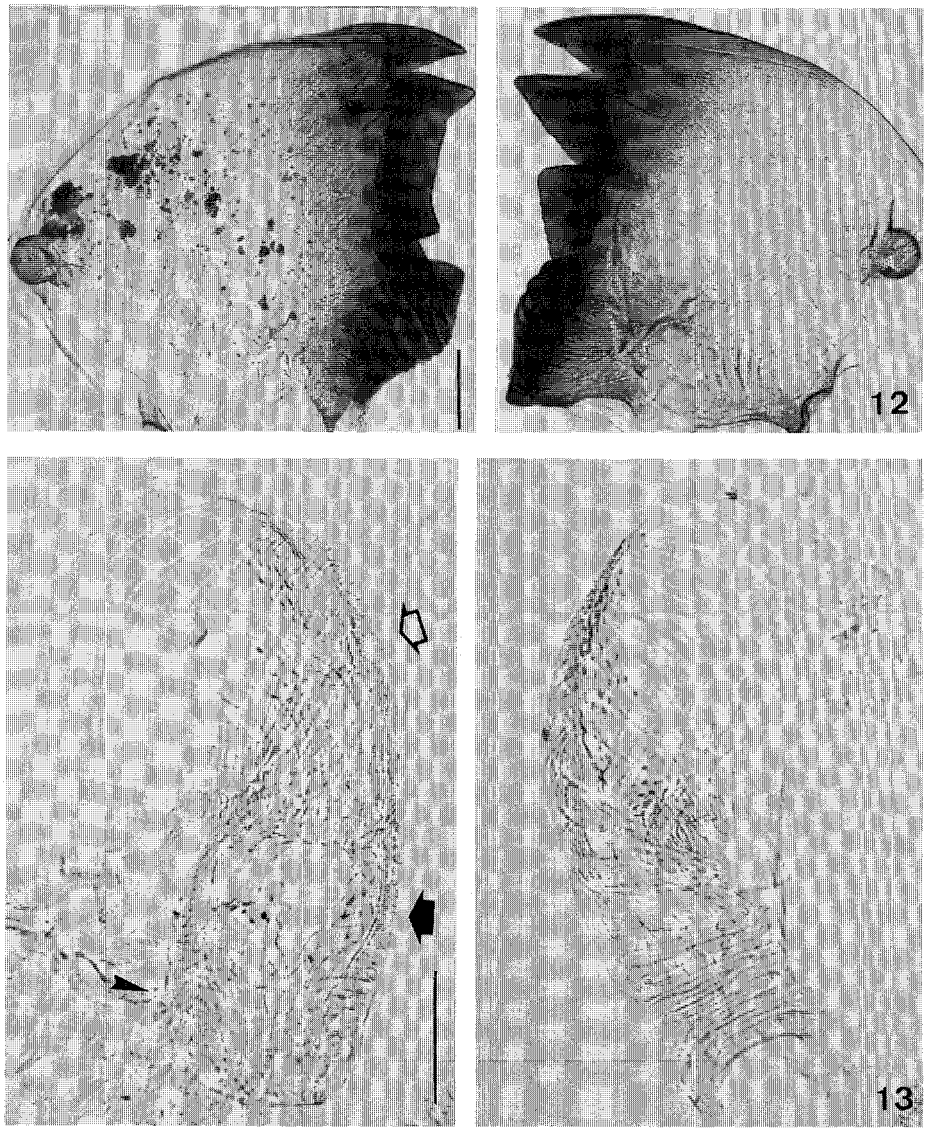
Nests of *N. motu* are dome-shaped (*v.* columnar in *N. triodiae*). Chambers extend below ground level without discontinuity, must be dug out with a shovel (whereas nests of *N. triodiae* can be overturned without tools if not too heavy). Stores small grass 'flakes', unlike *N. triodiae* which stores long pieces of grass. Polygyny seems frequent in this species, at least in the Eastern Papuan savannas. Of seven nests from this region in which sexuals were found, five were polygynous. By contrast, two nests from the Fly savannas contained a single queen.

Termitophiles

Kistner (1972) described a new species of termitophilous staphylinid, *Austrointhus papuanus*, from nest AMNH#E10. The termite species was then called *Nasutitermes* n. sp. I. (det. A. Emerson 1970).

Affinities

Similar to the other two epigeal nesting *Nasutitermes*, *N. triodiae* and *N. torresi*, by the number of antennal segments: 16 in alate, 14 in soldier, 15 in worker. The three species have large, wide-eyed imagos and dark-headed, very hairy soldiers. The alate of *N. motu* is smaller than that of *N. triodiae* and has much shorter legs. *N. motu* differs from *N. torresi* by its incompletely separated antennal segments 3–4; legs are of the same colour as antennae in *N. motu*, antennae are much darker than legs in *N. torresi*. The soldier of *N. motu* has diagnostic antennae, with segments 3–4 incompletely separated. It has shorter appendages than that of *N. triodiae*. *N. torresi* stands out by its darkly pigmented antennae and abdominal tergites. The smallest specimens of *N. motu* can be confused with the largest *Tumulitermes marcidus*, but the latter have a slightly constricted head capsule.



Figs 12, 13. *Nasutitermes motu*, sp. nov., large worker: *12*, mandibles; *13*, armature of enteric valve. Open arrow, upper ring of spiny areas; closed arrow, lower ring. Arrowhead, attachment of paunch. Scale bars = 0·1 mm.

Etymology

Named after the Motu people from the Port Moresby area, whose idiom forms the basis of a vehicular language in Southern Papua New Guinea.

Nasutitermes princeps (Desneux)

Termes (Eutermes) princeps Desneux, 1905: 375–376. Alate, soldier, worker.
Eutermes princeps. — Holmgren, 1911: 464, figs 6–7 (alate, soldier, worker); Hill, 1942: 261–263, figs 167–169 (alate, soldier, worker, biology).
Nasutitermes princeps. — Snyder, 1949: 294.

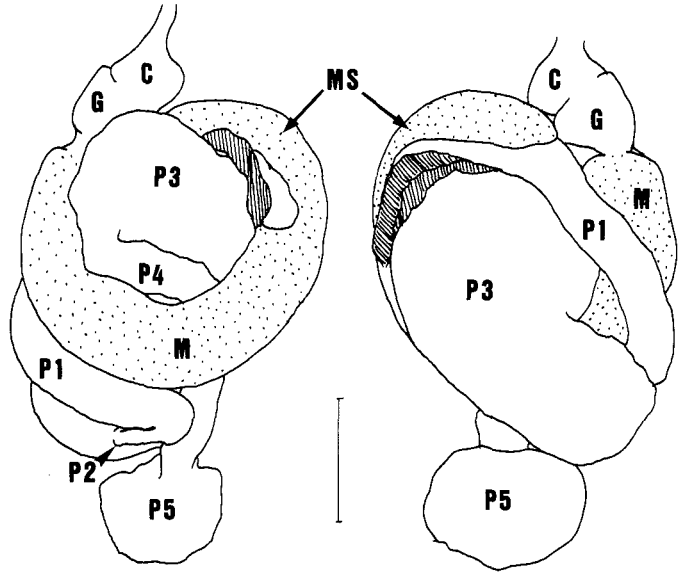


Fig. 14. *Nasutitermes motu*, sp. nov., large worker: dorsal and ventral view of gut *in situ*. C, crop. G, gizzard. M, mesenteron (stippled). MS, mixed segment. P1–P5, successive sections of the proctodeum, as in Noirot and Noirot-Timothée (1969): first section (P1), enteric valve (P2), paunch (P3), colon (P4), rectum (P5). Malpighian tubules hatched. Scale bar = 0·5 mm.

Material Examined

IRSN. Lectotype soldier (designated here), paralectotype alates, soldiers, workers and larvae: Friedrich-Wilhelmshafen (now Madang), 12.i.1901. Two vials with alates, soldiers, workers, larvae (L. Biró). #I.G.26373: Awar, Hansa Bay, 24.vii.1981 (PNG'81 - No. 507). One soldier from pitfall (M. Magap, J. Van Goethem).

Authors' collection (PNGT). Many series collected from coastal coconut plantations from Madang to Hansa Bay, and forests in the lower Ramu valley, Madang Province, since Nov. 1978. Other material: #5–7: Boisa I., 18.xi.1978 (B. Tursch). #95: Boisa Is., 23.vi.1981 (J. M. P.). #191: Kaiapit, 19.ii.1983 (J. M. P., Y. R.). #218: Akio (on Madang–Lae Road, in hills south of Madang), 23.ii.1983 (J. M. P., Y. R.). #810–811: Boisa I., 6.ix.1984 (Y. R.). #835–836: Tabele, Manam I., 19.ix.1984 (Y. R.). #1008b: Karkar I., 10.viii.1985 (S. W. Luxford). #1193, 1200, 1201: Braham Mission (5°45′S, 145°23′E), 5–6.v.1988 (Y. R.). #1214, 1215: Sira Sira (Leron River Valley, 6°20′S, 146°28′E, alt. 650 m), 14.v.1988 (Y. R.). #1252, 1253: Boisa I., 7.vii.1988 (Y. R.). #1256: Bieng, Manam I., 16.vii.1988 (Y. R.). #1277: Lower Gogol valley, 16.ix.1988 (Y. R.). #1330: Ramu valley, Madang–Bundi Road, 18.xi.1988 (Y. R.). #1379: Madang–Lae Road , in Ramu valley, 7.i.1989 (M. L.). #1571: Lake Murray, 23.v.1990 (Y. R., M. L.). #1720, 1721, 1737: Yapsiei, Sandaun Province, 10–11.iii.1994 (Y. R., M. L.).

ANIC. #10 9919, 9920: Bubia (Lae), 13.ix.1961 (J. H. Ardley). #10 15356: Black Forest Station (Madang), 6.ix.1974 (J. Simpson).

AMNH. #E16, 76, 81, 104, 113, 125: within 32 km from Lae, 30.xi.–28.xii.1962 (A. E., E. E., P. A.).

Imago (Figs 16, 17)

Polymorphic: beside normal imagos, short-winged individuals (microimagos) resulting from a precocious imaginal moult are commonly encountered (Roisin and Pasteels 1985*b*). Microimagos often become functional replacement reproductives (Roisin and Pasteels 1986*a*, 1986*b*). Normal (long-winged) alates (Fig. 16) are large, with 15-segmented antennae and bulging eyes. Apart from being smaller and with less bulging eyes, microimagos (Fig. 17) are usually of a lighter pigmentation.

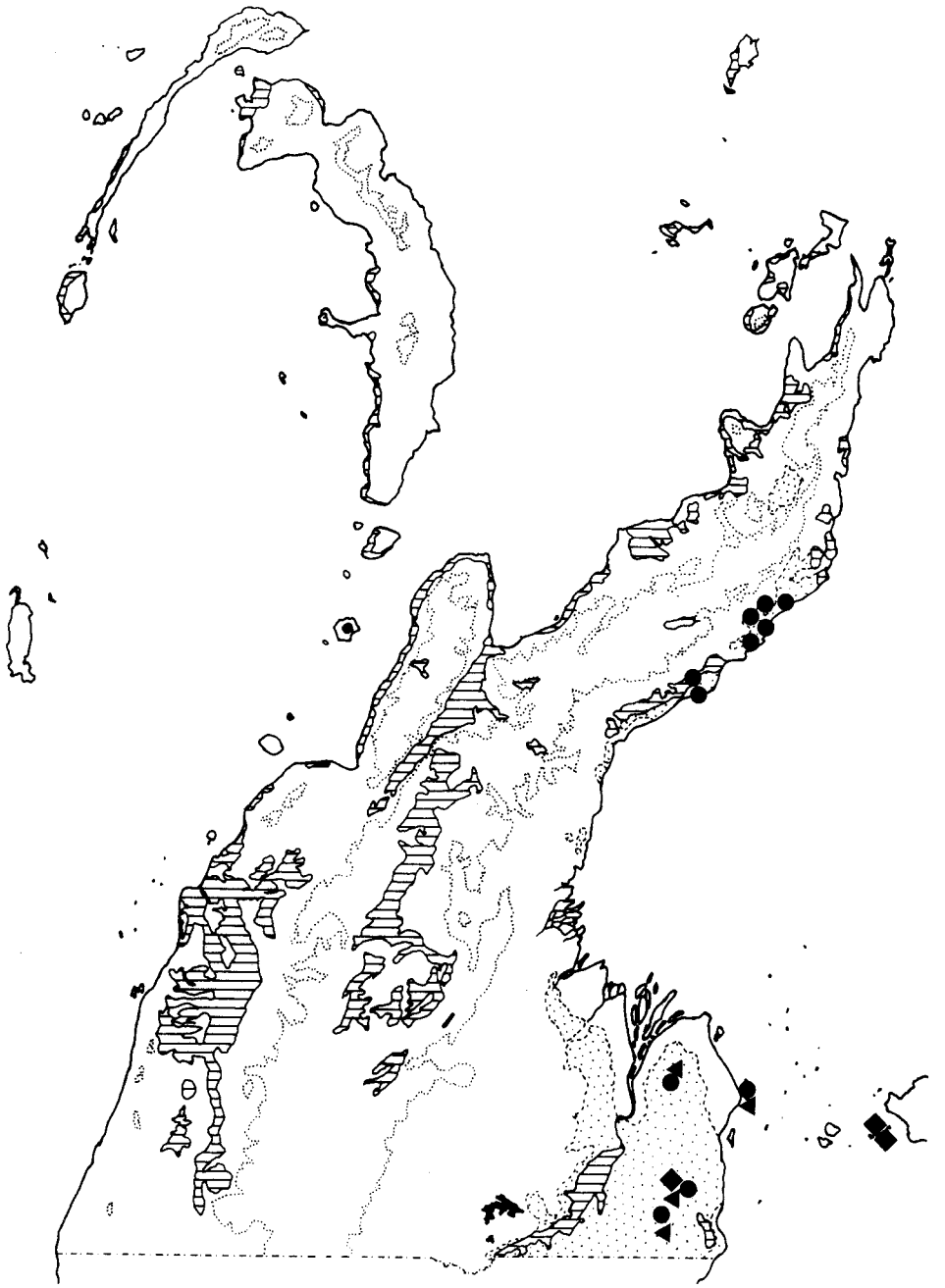


Fig. 15. Known distributions within Papua New Guinea and Torres Strait of *Nasutitermes triodiae* (▲), *N. torresi* (◆) and *N. motu* (●).

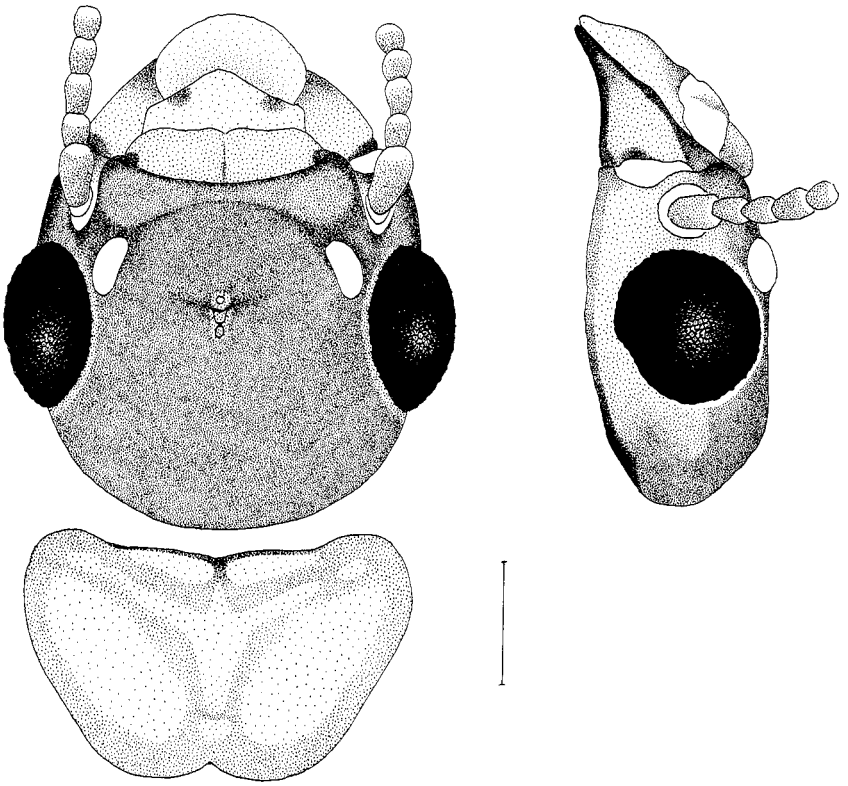


Fig. 16. *Nasutitermes princeps* (Desneux), normal female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

	Measurements (mm)			
	Normal alate females (10 from 5 colonies)		Normal alate males (11 from 6 colonies)	
	Range	Mean	Range	Mean
Head width across eyes	1·74–1·88	1·81	1·71–1·82	1·79
Largest diameter of eye	0·614–0·766	0·700	0·606–0·703	0·673
Length of ocellus	0·212–0·272	0·231	0·207–0·247	0·226
Eye to ocellus	0·031–0·057	0·041	0·028–0·067	0·047
Pronotum width	1·49–1·66	1·56	1·44–1·59	1·54
Pronotum length	0·96–1·04	0·99	0·87–1·02	0·94
Hind tibia length	2·08–2·29	2·15	2·08–2·27	2·17
Forewing length	12·9–16·3	14·9	11·9–15·0	13·9

	Microimaginal females (4 from 2 colonies)		Microimaginal males (8 from 2 colonies)	
	Range	Mean	Range	Mean
Head width across eyes	1·63–1·67	1·65	1·60–1·69	1·64
Largest diameter of eye	0·566–0·631	0·601	0·580–0·629	0·604
Length of ocellus	0·201–0·245	0·223	0·187–0·231	0·215
Eye to ocellus	0·040–0·061	0·049	0·058–0·077	0·065
Pronotum width	1·33–1·44	1·39	1·34–1·43	1·38
Pronotum length	0·82–0·86	0·84	0·78–0·89	0·82
Hind tibia length	1·91–1·95	1·93	1·90–2·02	1·97
Forewing length	6·1–8·1	7·1	5·8–8·9	7·6

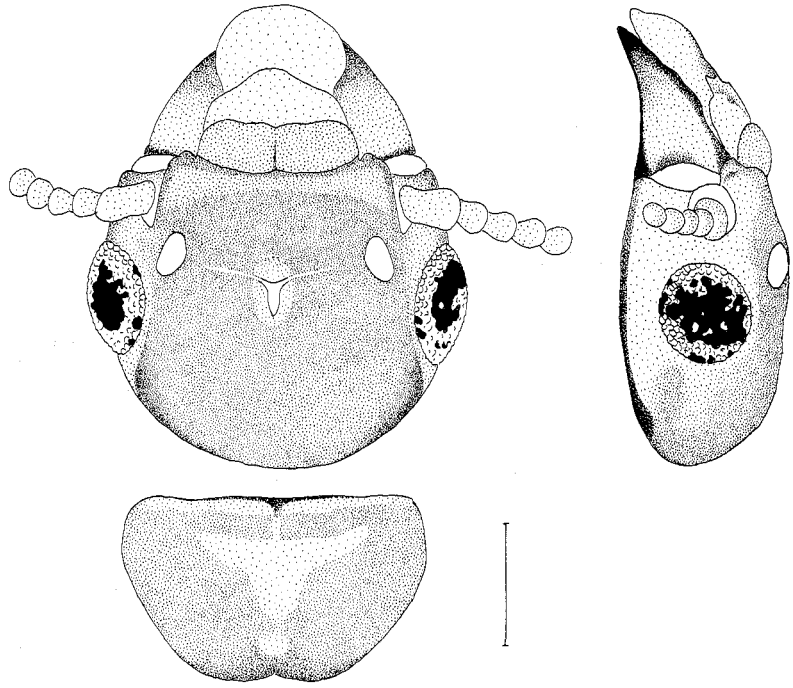


Fig. 17. *Nasutitermes princeps* (Desneux), microimaginal queen: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Soldier (Fig. 18)

A large, very dark sepia species. Antennae 13-segmented. As hairy as the epigeal nesting *Nasutitermes*, much hairier than the other large arboreal nasutes. Abdominal tergites with two rows of numerous (usually 12–16) erect setae.

Measurements (mm) of 35 individuals from 12 colonies

	Range	Mean
Head capsule total length	1·700–1·857	1·779
Rostrum length	0·700–0·830	0·773
'Back of head' distance	0·410–0·505	0·455
Head width	0·997–1·196	1·077
Rostrum width (at half length)	0·150–0·193	0·177
Head depth	0·650–0·823	0·753
Hind tibia length	1·399–1·623	1·497

The diterpene content of the soldiers' defensive secretion was studied by Braekman *et al.* (1980), Dupont *et al.* (1981) and Roisin *et al.* (1987). Among the monoterpenes, (+)-α-pinene is the dominant compound (80–90%), followed by limonene (5–10%) (Everaerts *et al.* 1988, 1990). Besides its role in the defensive properties of the frontal gland secretion, as a solvent and as an irritant, (+)-α-pinene serves as an alarm/recruitment pheromone (Roisin *et al.* 1990).

Worker (Figs 19, 20)

Head capsule pale yellow–brown to dark sepia. Increase in size and pigmentation between successive large-worker instars. Antennae 14-segmented. Mandibles as in Fig. 19. Distance between apical tooth and first marginal larger than in the epigeal nesting species *N. triodiae*,

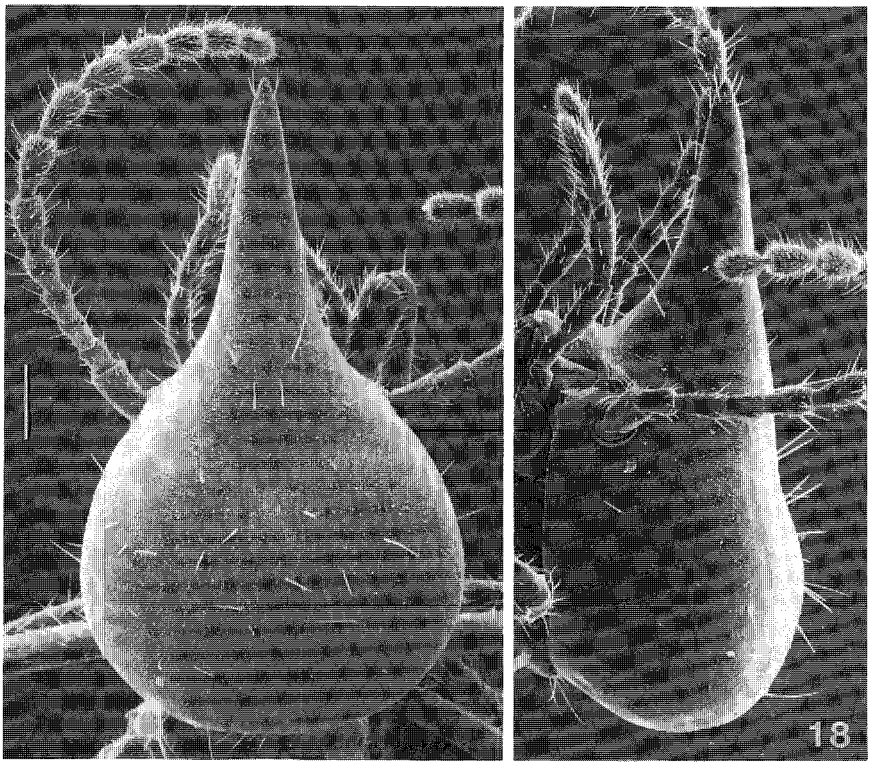


Fig. 18. *Nasutitermes princeps* (Desneux): soldier head from above (left), in profile (right). Scale bar = 0·2 mm.

N. torresi and *N. motu*. First marginal tooth of right mandible approximately equal to the notch between apical and first marginal. Molar plate almost straight. Digestive tract very similar to that of *N. motu*. Enteric valve (Fig. 20) transversal: upper ring strongly asymmetrical, with many short spines; lower ring of three distinctly sclerotised, swollen areas, bearing larger spines; a few small spines between sclerotised areas.

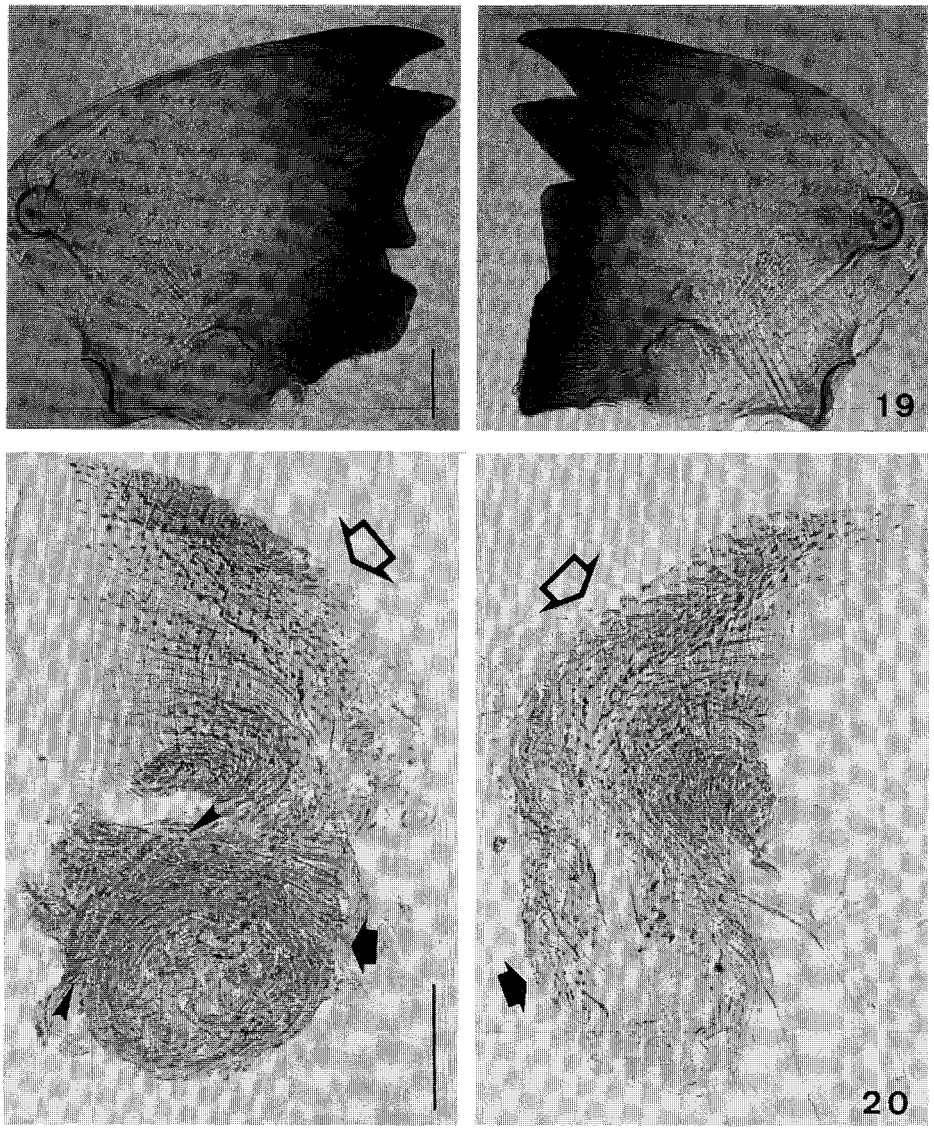
Head width (in mm) in workers from nest PNGT#7: small workers, first instar, 0·89–0·95 (mean = 0·92, n = 10); large workers, first instar, 1·22–1·28 (mean = 1·26, n = 15); instar 2, 1·39–1·44 (mean = 1·41, n = 10); instar 3 or older, 1·44–1·55 (mean = 1·50, n = 25).

Termitophiles

Nest E16 of the AMNH collection contained a termitophilous staphylinid (Perinthini) determined to be *Lauella palauensis* Seevers by Kistner (1972). Four species of Corotocini (Staphylinidae) were described from nests of this species in Madang Province: *Nasutiptochus kistneri*, *Neoguinella thierryi*, *Neoguinella valeriae* and *Termitoptocinus roisini* (Pasteels and Jacobson 1984; Jacobson and Pasteels 1985, 1992).

Distribution (Fig. 31)

Very common in coconut plantations along the coast of Madang Province. Widely distributed along the Madang–Lae Road. Recorded from Manam, Boisa and Karkar Islands, but not from smaller Schouten Islands. Never found on large Bismarck Islands, despite extensive prospecting in Gazelle Peninsula (East New Britain) and New Ireland. Common near Irian Jaya



Figs 19, 20. *Nasutitermes princeps* (Desneux), large worker: *19*, mandibles; *20*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

border on the north side of the Central Ranges (Yapsiei); a single record from southern New Guinea (Lake Murray). Unconfirmed reports from Parando (Dutch New Guinea, now Irian Jaya) (Holmgren 1911) and the Aru Islands (John 1925).

Biology

This species builds large arboreal nests in forests and coconut plantations. Nests are often polycalic and polygynous. The reproductive biology of this species has been widely studied (Roisin and Pasteels 1985*b*, 1986*a*, 1986*b*; Roisin 1987; Leponce *et al.* 1995, 1996).

Nasutitermes koiari, sp. nov.

Material Examined

Type colony (PNGT#917). Sirinumu Dam, Central Province, 7.iii.1985. Very large nest on dead tree in woodlands. Many non-physogastric sexuals, immatures, no alates. No definite royal cell (J. M. P., Y. R.). Holotype: soldier.

Authors' collection (PNGT). #734-735: Sogeri, Central Province, 15.vii.1984 (Y. R.). #911: Sirinumu Dam, Central Province, 6.iii.1985. #1148: Motupore I. (Bootless Bay, SE Port Moresby), Nov. 1987 (P. Grootaert). #1415: Morehead, Western Province, 22.iii.1989 (Y. R., M. L.). #1497: Wipim, Western Province, 31.iii.–2.iv.1989 (Y. R., M. L.). #1549, 1564, 1584, 1601: Lake Murray, Western Province, 22–27.v.1990 (Y. R., M. L.).

ANIC. #10 10378: Oriomo R., 50 km N Daru, Western Province (B. J. O'Hagan). #10 10449: 5 km N Hisiu, Central Province, 19.viii.1962 (P. C. H.). #10 16290: Thursday I., Torres Strait, 6.xii.1976 (R. Paton). #10 16292: Sue I., Torres Strait, 14.vi.1977 (R. Paton). #10 19487: Mt Ernest I., Torres Strait, 5.iv.1984 (J. W. Turner). #(no accession number): Port Moresby, Apr. 1962 (Anderson).

Other collection. J. W. Turner (all localities in Torres Strait). Hammond I., 12.iv.1983. St Paul, Moa I., 13.iv.1983. Boigu I., 14.iv.1983. Dauan I., 15.iv.1983 (3 series). Yam I., 21.iv.1983 (2 series).

AMNH. #E18: 19 km NW Port Moresby, 22.xi.1962 (A. E.).

Imago (Fig. 21)

Head capsule dark chestnut brown, postclypeus orange. Labrum, antennae, legs and thoracic sclerites orange–yellow. Sharp contrast between head capsule and pronotum. Abdominal tergites yellow–brown, sternites yellow. Wing membrane pale brown, turning pale yellow near its anterior margin.

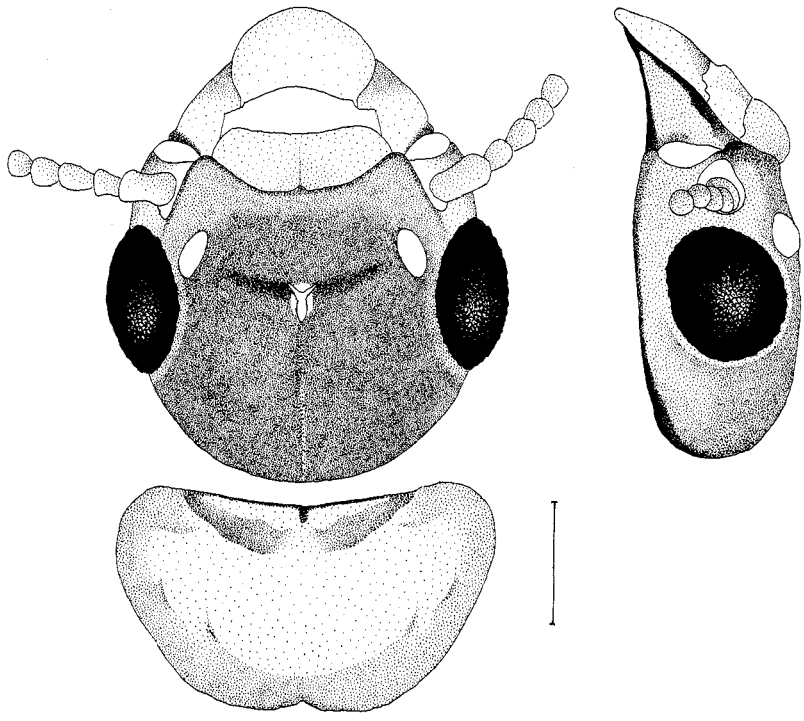


Fig. 21. *Nasutitermes koiari*, sp. nov., female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Posterior margin of head capsule regularly rounded. Eyes large, slightly prominent. Fontanelle Y-shaped, hyaline, medium-sized, almost as long as ocellus. Antennae of 15 segments, segment 3 slightly longer than segment 4, segment 4 longer than segment 2.

This species is closely related to *N. princeps*, which has polymorphic alates (Roisin and Pasteels 1985*b*). In the type series of *N. koiari* (nest PNGT#917), which contained many young dealated imagos, one specimen was probably a microimago of the kind described in *N. princeps*, as suggested by the measurements given below.

Measurements of normal imagos (mm)

	Females (4 alates, 2 dealates) (3 colonies)		Males (4 alates, 1 dealate) (3 colonies)	
	Range	Mean	Range	Mean
Head width across eyes	1·61–1·66	1·64	1·56–1·65	1·62
Largest diameter of eye	0·603–0·661	0·642	0·574–0·639	0·610
Length of ocellus	0·152–0·206	0·189	0·152–0·167	0·160
Eye to ocellus	0·025–0·056	0·044	0·044–0·062	0·052
Pronotum width	1·47–1·62	1·54	1·40–1·54	1·45
Pronotum length	0·90–0·96	0·92	0·86–0·94	0·89
Hind tibia length	1·96–2·14	2·05	1·88–2·07	1·98
Forewing length	13·2–15·2	14·2	12·5–13·8	13·2

Measurements of dealated females, type colony

	Normal females (n = 11)		Microimago?
	Range	Mean	
Head width across eyes	1·63–1·68	1·65	1·50
Largest diameter of eye	0·610–0·645	0·626	0·554
Ocellus length	0·182–0·209	0·194	0·160
Eye to ocellus	0·037–0·080	0·050	0·058
Pronotum width	1·50–1·63	1·58	1·37
Pronotum length	0·87–0·98	0·94	0·82
Hind tibia length	2·0–2·12	2·09	1·99
Forewing scale length	0·861–0·944	0·905	0·795

Soldier (Fig. 22)

Head capsule dark sepia brown, rostrum darker with paler tip. Antennae, legs, thorax and abdominal tergites yellow, sternites pale yellow. Overall appearance of body brightly coloured.

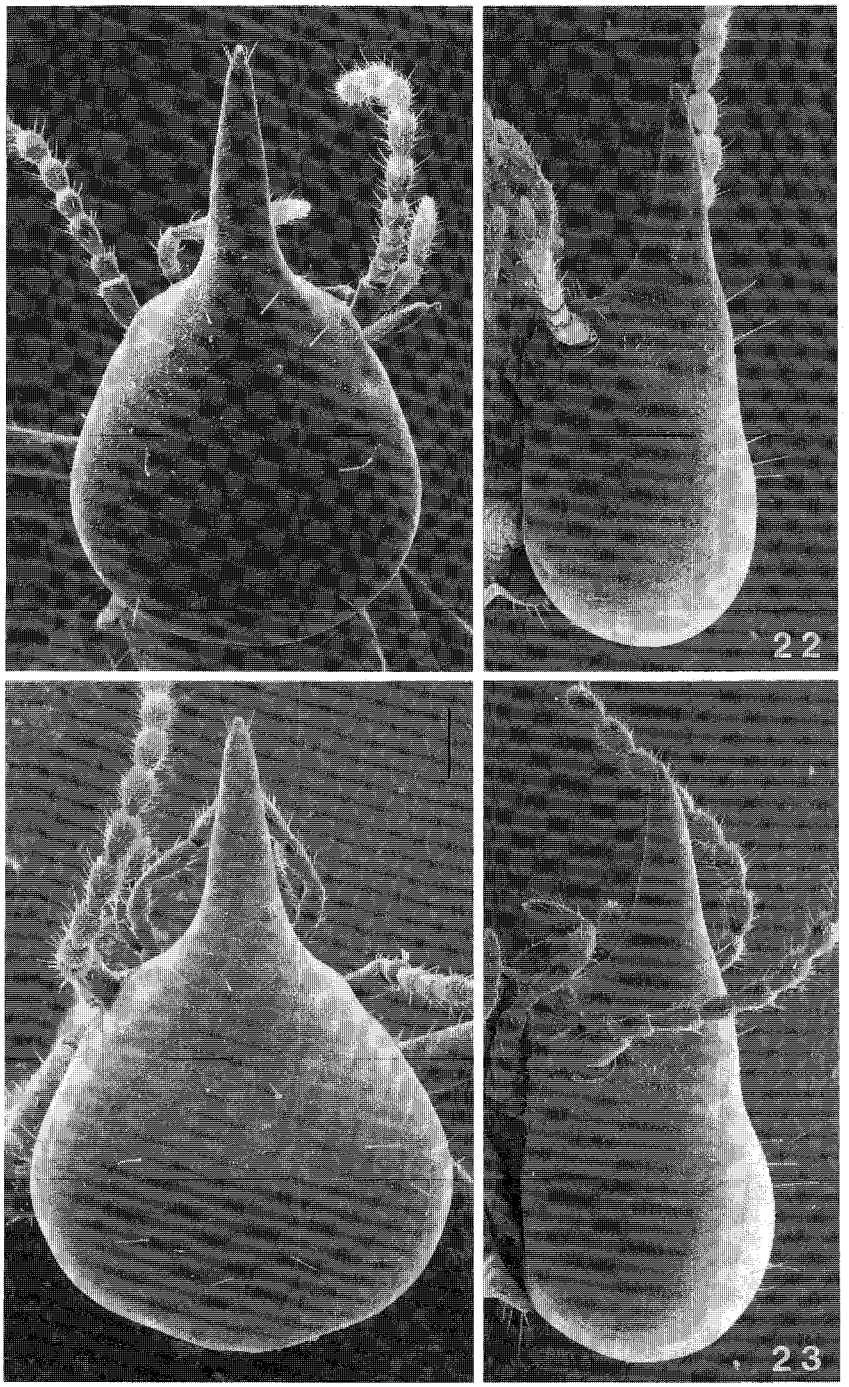
Head capsule slightly flattened laterally and posteriorly, in profile nearly straight. Rostrum narrow, conical. Antennae 13-segmented, segment 3 longest of all, segment 4 about as short as segment 2. Pilosity of head capsule as follows: 1 row of 4 setae at base of rostrum, 4 setae forming a rectangle on vertex, sometimes 2 additional setae on sides. Abdominal tergites pilose, with two rows of about 12 erect setae.

Measurements (mm) of 36 individuals from 12 colonies

	Range	Mean
Head capsule total length	1·396–1·775	1·614
Rostrum length	0·585–0·752	0·658
'Back of head' distance	0·366–0·495	0·418
Head width	0·825–1·146	1·006
Rostrum width (at half length)	0·122–0·159	0·144
Head depth	0·574–0·749	0·679
Hind tibia length	1·023–1·366	1·254

Worker (Figs 24–26, 55)

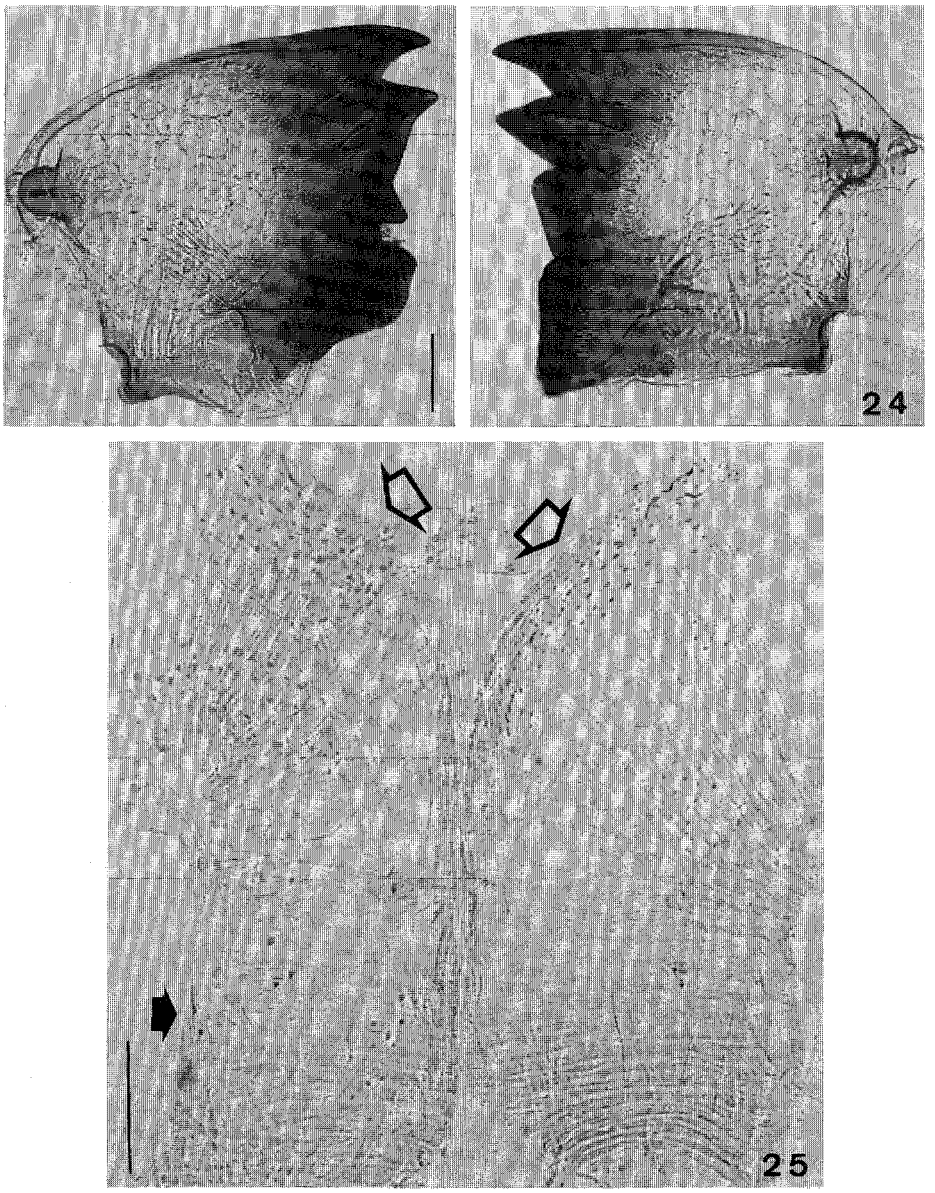
Head capsule from pale yellow to dark sepia. Antennae 14-segmented. Increase in size and pigmentation between successive large-worker instars. Mandibles (Fig. 24) very similar to those of *N. princeps*. Digestive tract (Fig. 26) very similar to that of *N. motu*. Pairs of malpighian



Figs 22, 23. Soldier heads from above (left) and in profile (right). *22*, *Nasutitermes koiari*, sp. nov.; *23*, *Nasutitermes graveolus* (Hill). Scale bar = 0·2 mm.

tubules separated by a wide space (Fig. 55). Enteric valve (Fig. 25) transversal: upper ring strongly asymmetrical, with many short spines; lower ring of 3 distinctly sclerotised areas, slightly swollen, each bearing 3–8 spines, slightly longer and thinner than those of upper ring; a few small spines between sclerotised areas.

Head width of workers from nest PNGT#1511: small workers, first instar, 0·84–0·91 (mean = 0·89, n = 8); large workers, first instar, 1·20–1·26 (mean = 1·23, n = 8); instar 2 and older, 1·40–1·58 (mean = 1·49, n = 16).



Figs 24, 25. *Nasutitermes koiari*, sp. nov., large worker: *24*, mandibles; *25*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrow, lower ring. Scale bars = 0·1 mm.

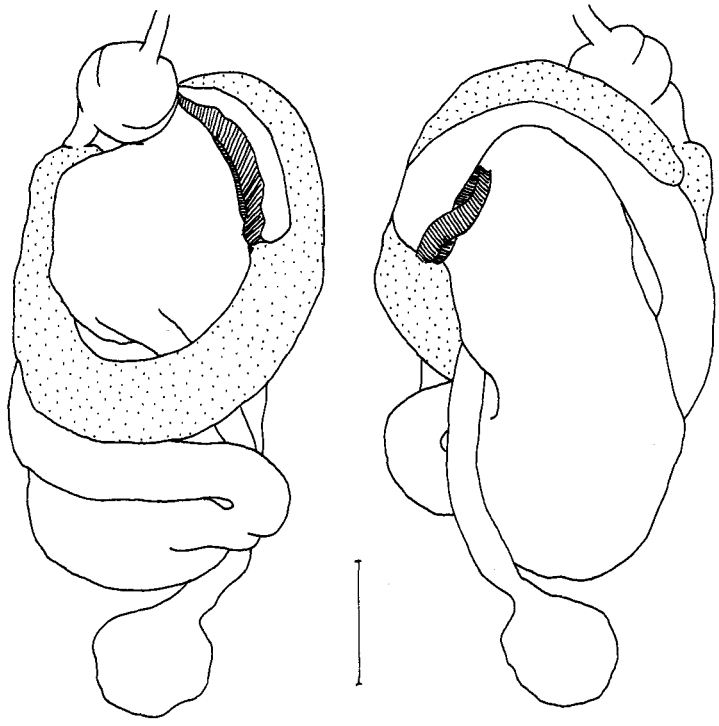


Fig. 26. *Nasutitermes koiari*, sp. nov., large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

Distribution (Fig. 31)

Savannas and woodlands in the Fly Plains and Eastern Papua. *N. koiari* reaches forests in southern Papua New Guinea (Lake Murray), where its range overlaps with those of *N. princeps* and *N. polygynus*. Also present on several Torres Strait islands.

Termitophiles

Recently, Jacobson and Pasteels (1992) described a new termitophilous staphylinid, *Termitoptocinus papuanus*, from nests of this species in the Sogeri (Eastern Papua) region.

Affinities

Closely related to *N. princeps*. The alate of *N. koiari* is distinguished from that of other arboreal species by its deep yellow pronotum, contrasting with dark head capsule. The soldier of *N. koiari* has a sparser pilosity than *N. princeps*, but is more pilose than *N. novarumhebridarum* and *N. polygynus*, especially on vertex (4 setae *v.* 2) and abdominal tergites. Its rostrum is thinner than that in either of these species.

Etymology

Named after the Koiari people from the Sogeri area, who are famous for building houses high up in trees.

Related Allopatric Species

Nasutitermes graveolus (Hill)

Eutermes graveolus Hill, 1925: 226–228, pls 25–26 (figs 36–42). — Hill, 1942: 225–227, figs 120–122, pl. 7. Imago, soldier, worker, biology, nest.
Nasutitermes graveolus. — Snyder, 1949: 278.

This species is widely distributed in Australia. Its imago caste seems to be polymorphic, like that of *N. princeps* and probably *N. koiari*: short-winged imagos, then considered as abnormal specimens, were present in the original series of *N. graveolus* (Hill 1925). The alate of *N. graveolus* resembles that of *N. koiari*, but is slightly smaller and has a more brown pronotum. The soldier of *N. graveolus* is slightly more pilose than that of *N. koiari*, and its head capsule is more flattened on its posterior sides (Fig. 23).

Nasutitermes pinocchio, sp. nov.

Material Examined

Type colony (AMNH#E22). Brown River, 35 km NW Port Moresby, 22.xi.1962. From log on ground in forest. Dealated female, eggs, 8 nanitic soldiers, 3 normal soldiers, 10 workers (A. E.). Holotype: normal soldier. This colony was at an early stage of foundation, which explains the presence of nanitic individuals.

AMNH. #E20: *ibid.*, 21.xi.1962 (A. E.).

Authors' collection (PNGT). #852: Sogeri, Central Province, 4.ii.1985 and 22.iii.1985 (J. M. P., Y. R.). #1632: Nomad R., Western Province, 31.v.1990 (M. L., Y. R.).

ANIC. #10 13131: Nunumai, Amazon Bay (Central Distr.), Jul. 1969 (R. Pullen).

Imago (Fig. 27)

Only known from one dealated female, from an incipient colony (type series). Head capsule dark chestnut brown. Postclypeus, labrum, thoracic sclerites chestnut brown. Antennae and legs pale brown. Abdominal tergites chestnut brown, sternites paler.

Posterior margin of head regularly rounded. Eyes medium-sized, slightly bulging. Fontanelle hyaline, 0·116 mm long by 0·050 mm wide. Antennae mutilated, presumably 15-segmented in alate. Segments 2–4 of approximately equal length.

Measurements (mm)	
Head width across eyes	1·75
Largest diameter of eye	0·595
Ocellus length	0·236
Eye to ocellus	0·053
Pronotum width	1·52
Pronotum length	0·93
Hind tibia length	2·10
Forewing scale length	0·964

Soldier (Fig. 28)

Head capsule dark chestnut brown. Thoracic nota and abdominal tergites chestnut brown. Appendages and abdominal sternites paler.

Head capsule elongated, triangular with rounded posterior angles, hind margin straight or sometimes slightly notched in middle. In profile with a hump at base of rostrum. Rostrum conical, thin and extremely long. Antennae 13-segmented, segments 2 and 4 each a little more than half the length of segment 3. Four long setae at base of rostrum, 2 on vertex. A row of about 6 long setae along border of abdominal tergites. The type colony contained nanitic soldiers, with 11-segmented antennae, besides normal ones.

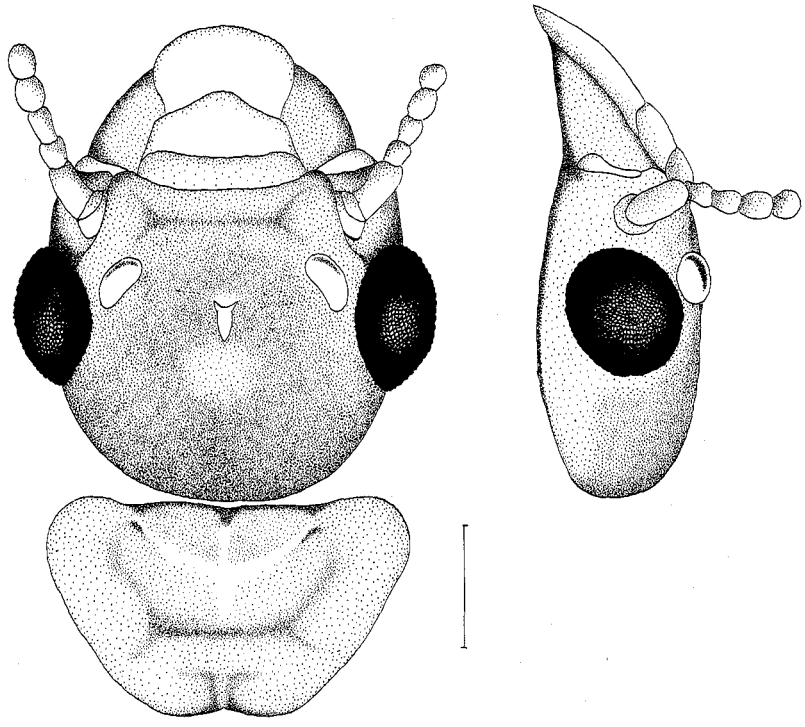


Fig. 27. *Nasutitermes pinocchio*, sp. nov., queen from type colony: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

	Measurements (mm)		
	Normal soldiers (15 from 5 colonies)		Nanitic soldiers (3 from type colony)
	Range	Mean	Range
Head capsule length	1·923–2·179	2·041	1·484–1·517
Rostrum length	0·957–1·108	1·023	0·744–0·765
'Back of head' distance	0·390–0·440	0·415	0·300–0·308
Head capsule width	0·984–1·135	1·050	0·722–0·768
Rostrum width (at half length)	0·133–0·155	0·142	0·125–0·140
Head depth	0·658–0·768	0·725	0·511–0·540
Hind tibia length	1·206–1·399	1·319	0·796–0·817

Worker (Figs 29, 30, 56)

Head capsule pale yellow-brown to dark chestnut. Antennae 14-segmented. Moderate increase in size and pigmentation between successive large-worker instars. Mandibles (Fig. 29) similar to those of *N. princeps*. Configuration of gut *in situ* similar to *N. koiari*. Mesenteric part of mixed segment connected to main body of mesenteron by short, thin, dorsal peduncle. Malpighian tubules attached in two well-separated pairs (Fig. 56). Enteric valve oblique. Upper ring of spiny areas long and asymmetrical, with many short spines (Fig. 30). Lower ring of three weakly sclerotised swellings, bearing about 8 spines, slightly longer and thinner than those of upper ring. Small spines present between swellings.

Head width (mm) in workers from nest PNGT#1632: small workers, first instar, 0·91–0·96 (mean = 0·94, n = 6); large workers, first instar, 1·22–1·29 (mean = 1·25, n = 10); instar 2 or older, 1·26–1·35 (mean = 1·32, n = 15).

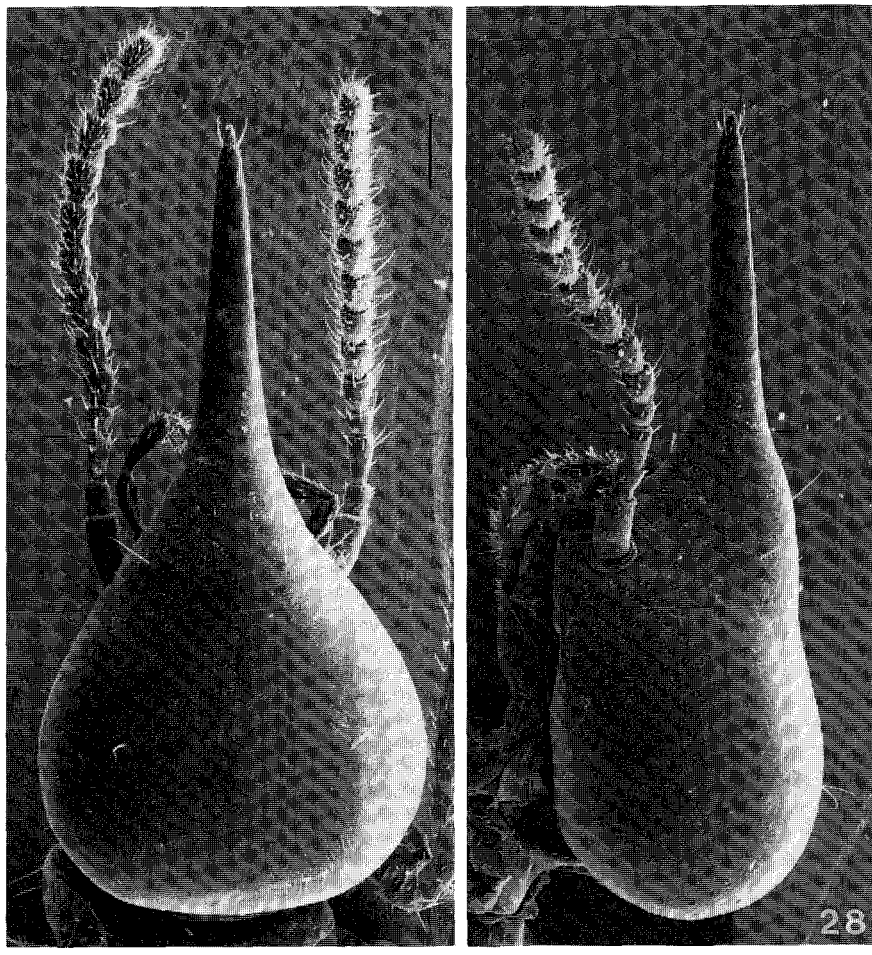


Fig. 28. *Nasutitermes pinocchio*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Distribution (Fig. 31) *and Biology*

A forest-dwelling species, widely spread south of the central mountains, but apparently rather uncommon. Uses wood carton for construction.

Affinities

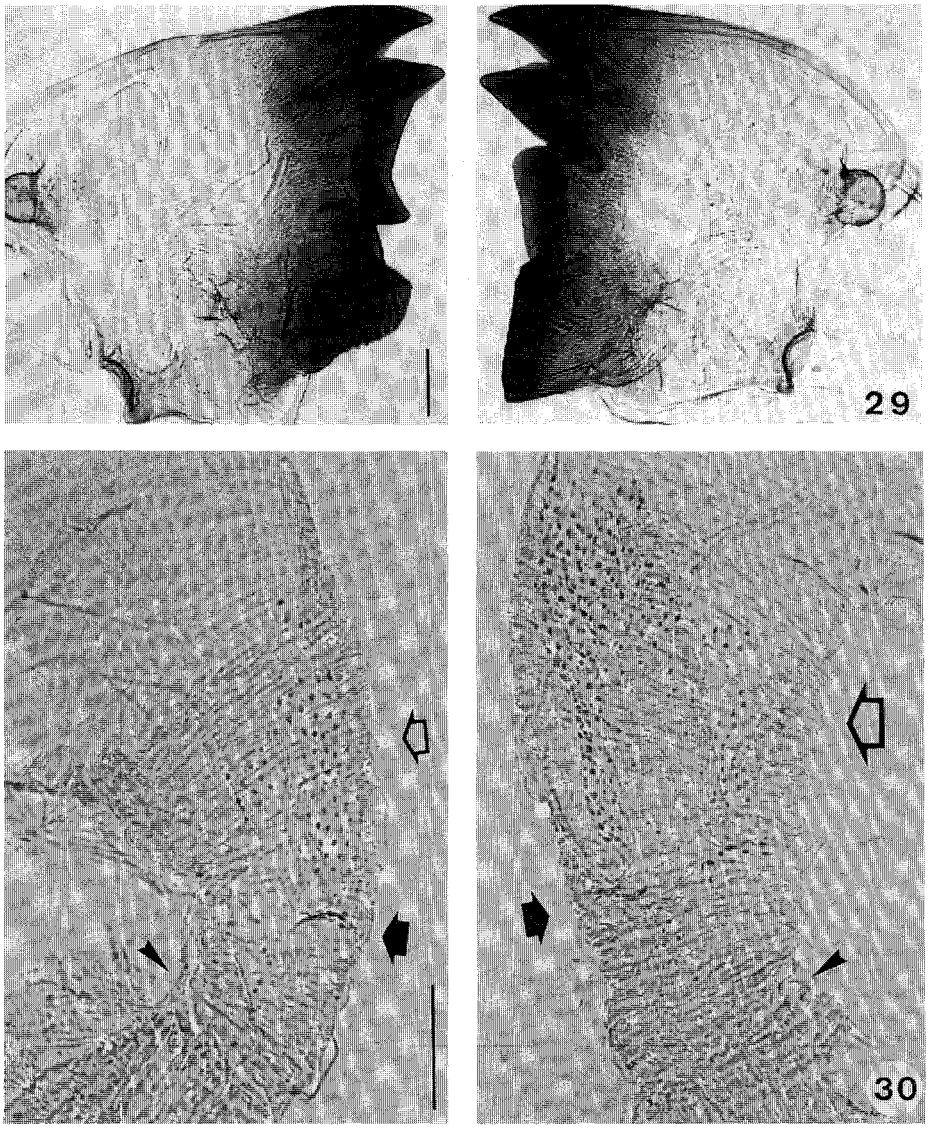
Imago larger than *N. koiari* and *N. novarumhebridarum*, about as large as *N. princeps* but with smaller, less bulging eyes. Soldier unmistakable by the length of its rostrum and shape of its head capsule.

Etymology

The name refers to the elongated nose of Pinocchio, hero of Collodi's famous tale.

Nasutitermes novarumhebridarum (N. Holmgren & K. Holmgren)

Eutermes (Eutermes) novarum hebridarum Holmgren and Holmgren, 1915: 92–93. Alate.
Nasutitermes (Grallotermes) oceanicum Snyder, 1925: 439–440. Soldier, nymph, worker.



Figs 29, 30. *Nasutitermes pinocchio*, sp. nov., large worker: *29*, mandibles; *30*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

Eutermes yandiniensis Hill, 1927: 25–28, pl. I (figs 22–26), pl. V (fig. 157), pl. VIII (fig. 158). Alate, soldier, worker.

Eutermes novarum-hebridarum. — Hill, 1942: 242–244, figs 140–141. Alate, soldier, worker, biology.

Nasutitermes novarum hebridarum. — Snyder, 1949: 290–291.

Material Examined

From Vanuatu (formerly New Hebrides)

NHMB. Holotype, female alate: Ambrym, Jun. 1911. *NMVM.* #WWF23: Vila, 10.vi.1913 (W. W. Froggatt). *ANIC.* #10 11826: Vaté I., Aug. 1966 (P. Cochereau).

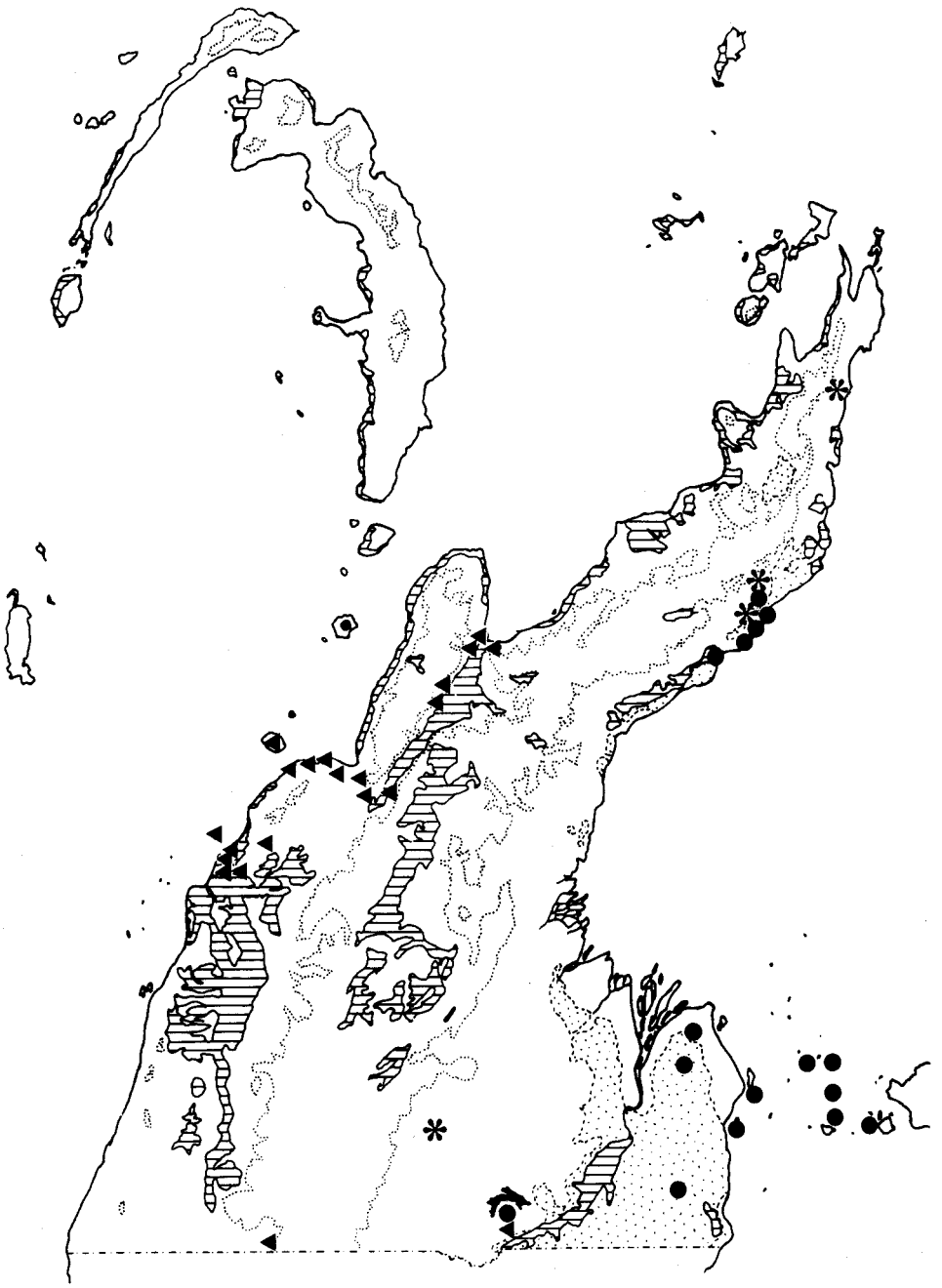


Fig. 31. Known distributions within Papua New Guinea and Torres Strait of *Nasutitermes princeps* (▲), *N. koiari* (●) and *N. pinocchio* (*).

From the Solomon Archipelago

NHMB. #Auki, Malaita I., 14.iv.1929. Male alate (labeled 'homotype'), with one soldier and one worker (K. P. Schmidt). These collection data match those given by Seevers (1937) in his original description of the physogastric termitophilous staphylinid *Thyreoxenus solomonensis*: the termites examined thus probably belonged to the colony that housed the holotype of this species.

NMVM. Syntypes of *Eutermes yandiniensis* Hill: Yandini, near Cape Mark, Bougainville I., Dec. 1923. With alates (G. M. Heydon). #WWF21: Banaka Estate, Solomon Is.

ANIC. #10 1585: Tulagi, 12.iv.1934 (R. Lever). #10 4506: Honiara Dist., Guadalcanal I., 17.i.1956 (E. S. Brown). #10 8639: Numa Numa Plantation, Bougainville I., 21.vi.1957 (J. H. Barrett). #10 9761: Konga, Bougainville I., Mar. 1961 (W. Brandt). #10 12253-12254: Buka I., 13.xi.1967 (R. E. Halpin). #10 12761: Honiara Dist., Guadalcanal I., 17.xi.1955 (E. S. Brown). #10 17707: Honiara Distr., Guadalcanal I., 17.i.1956. 3 alates only (E. S. Brown).

From Papua New Guinea (excluding the North Solomon Islands) and Torres Strait

Authors' collection (PNGT). Many series collected from coastal coconut plantations and villages from Hansa Bay to Bogia, Madang Province, since Dec. 1978, and the following additional material. #14–17: Blup Blup I., 22.xi.1978 (B. Tursch). #69: *ibid.*, 16.vi.1981 (J. M. P.). #76: Vokeo I., 18.vi.1981 (J. M. P.). #79, 88: Koil I., Jun. 1981 (J. M. P.). #81, 86: Bam I., 19.vi.1981 (J. M. P.). #96: Boisa I., 23.vi.1981 (J. M. P.). #98–100: Manam I., 23.vi.1981 (J. M. P.). #156: Bulolo, 10.ii.1983 (J. M. P., Y. R., G. Seghers). #180, 188: Oomsis, 20 km from Markham bridge on Lae–Bulolo Road (J. M. P., Y. R., G. Seghers). #520: Marangis (mouth of Ramu R.), 25.i.1984 (J. M. P., Y. R.). #554, 557: Bai (Rabaul, New Britain), 18.v.1984 (J. M. P., Y. R.). #565: Warongoi, New Britain, 19.v.1984 (J. M. P., Y. R.). #583: Keravat, 21.v.1984 (J. M. P., Y. R.). #592: 30 km W Keravat, 23.v.1984 (J. M. P., Y. R.). #614: Konos, New Ireland, 28.v.1984 (J. M. P., Y. R.). #639: Lemakot, New Ireland, 31.v.1984 (J. M. P., Y. R.). #648-649: Lorengau, Manus I., 3.vi.1984 (J. M. P., Y. R.). #733: Sogeri, Central Province, 14.vii.1984 (Y. R.). #812: Boisa I., 6.ix.1984 (Y. R.). #834: Tabele, Manam I., 19.ix.1984 (Y. R.). #983: Popondetta, 18.iii.1985 (J. M. P., Y. R.). #1004: Brown R., 30 km N Port Moresby, 21.iii.1985 (J. M. P., Y. R.). #1007a, 1008a: Karkar I., 10.viii.1985 (S. W. Luxford). #1050–1051: Boroi (near Ramu mouth), 29.i.1987 (J. M. P.). #1239: Lae–Bulolo Road, 27 km from Markham bridge, 24.v.1988 (Y. R.). #1245: Yoro, Madang Province, 1.vi.1988 (Y. R.). #1249–1251: Boisa I., 7.vii.1988 (Y. R.). #1298: Pimaga, Southern Highlands, alt. 800 m, 15.x.1988 (Y. R.). #1374: Mirap, Madang Province, 22.xii.1988 (M. L.). #1563, 1607: Lake Murray, Western Province, 23–27.v.1990 (Y. R., M. L.). #1706, 1714: 3 km W Vanimo, 8.iii.1994 (Y. R., M. L.). #1722, 1755, 1756: Yapsiei, Sandaun Province, 10.iii.1994 (Y. R., M. L.).

ANIC. #10 813: Rabaul, New Britain, 29.v.1930 (J. L. Froggatt). #10 8600: Kwato, nr Samarai (Milne Bay), Aug. 1944 (H. F. C. Davis). #10 8624: Karakakual Plantation, Rabaul, 11.v.1952 (J. H. Barrett). #10 8640: Keravat, New Britain, 15.vi.1957 (J. H. Barrett). #10 9921: Lae, 20.ix.1961 (F. J. Gay). #10 10733: Hargita Plantation, Milne Bay, Jun. 1963 (T. Martin). #10 11151: Keravat, 8.ix.1965 (F. J. Gay). #10 11152: Rabaul, 8.ix.1965 (F. J. Gay). #10 11276: Tavilo Plantation, Gazelle Peninsula, New Britain, 29.vi.1961 (B. Gray, E. Lamai). #10 12250–12252, 12255–12257: Madang, 2–11.iv.1968 (R. E. Halpin). #10 15338: Lake Wisdom, Long I., 25.xi.1972. Alates only (E. Ball). #10 19471: Yam I., Torres Strait, 23.x.1979 (R. L. Paton). #10 19472: Saibai I., Torres Strait, 27.x.1979 (R. L. Paton).

NMVM. Two vials from Namatanai, New Ireland (R. Rigby). Kaewieng (now Kavieng), New Ireland, 2.xii.1923 (N. Wallace).

Other collection. J. W. Turner: two series from Stephens I., Torres Strait, 20.iv.1983.

AMNH. #E3–6: within 22 km from Lae, 22–30.xi.1962 (A. E., E. E., P. A.). #E27: 58 km NE Port Moresby, 500 m elevation, 24.xi.1967. #E29, 35: within 24 km from Port Moresby, 17–22.xi.1962. (A. E., E. E.). #E61, 65–67, 74, 80, 91, 96, 110, 114, 115, 119, 120, 124: within 33 km from Lae, 28.xi–31.xii.1962 (A. E., E. E., P. A.). #131, 132: Selimun Village near Namatanai, New Ireland, 3°40′S, 152°25′E, 9.xii.1962 (A. Catley). #133: Kunaie Village, Lihir I., 12.xii.1962 (A. Catley).

From New Caledonia

ANIC. #10 11825: Nouméa, Feb. 1966 (P. Cochereau).

Imago (Fig. 32)

A medium-sized species, with large eyes. Antennae of 15 segments. Smaller than *N. princeps*. Thorax smaller than in *N. koiari*, with brown pronotum (distinctly tinged with

yellow in *N. koiari*). Almost identical to the imago of *N. bikpelanus*, *N. gracilirostris* and *N. leponcei*, described below.

	Measurements (mm)				
	Holotype ♀ (NHMB)	Females (18 alates, 5 dealates) (13 colonies)		Males (20 alates, 7 dealates) (14 colonies)	
		Range	Mean	Range	Mean
Head width across eyes	1·57	1·52–1·68	1·60	1·41–1·64	1·56
Largest diameter of eye	0·607	0·543–0·634	0·592	0·505–0·632	0·590
Length of ocellus	0·182	0·159–0·217	0·189	0·152–0·235	0·188
Eye to ocellus	0·042	0·026–0·088	0·049	0·015–0·067	0·043
Pronotum width	1·24	1·22–1·41	1·30	1·10–1·35	1·26
Pronotum length	0·76	0·74–0·86	0·79	0·63–0·80	0·74
Hind tibia length	1·66	1·66–1·85	1·74	1·56–1·85	1·76
Forewing scale length	0·823	0·760–0·876	0·834	0·716–0·872	0·808
Forewing length	–	11·7–14·1	13·1	9·7–13·4	12·3

Soldier (Fig. 33)

A large, dark chestnut, sparsely pilose species: reddish tinge diagnostic in the field, compared with *N. princeps* or *N. koiari*, which appear almost black. Antennae 13-segmented. Closely resembles *N. polygynus*, but head capsule wider, not as dark, and more regularly rounded or elliptical behind (somewhat flattened posteriorly in *N. polygynus*). Four long setae at base of rostrum, 2 on vertex (4 in *N. koiari*). Abdominal tergites with one row of sparse (usually 6) setae.

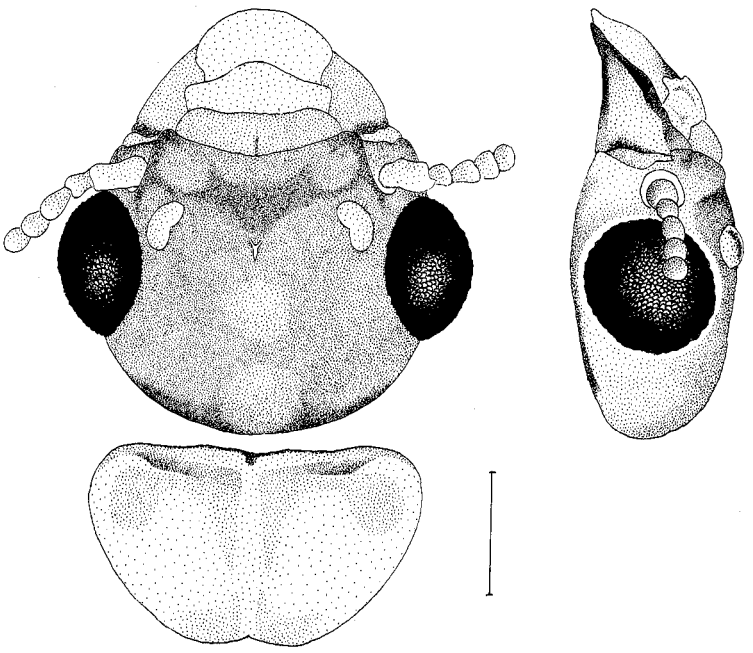


Fig. 32. *Nasutitermes novarumhebridarum* (N. & K. Holmgren), female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

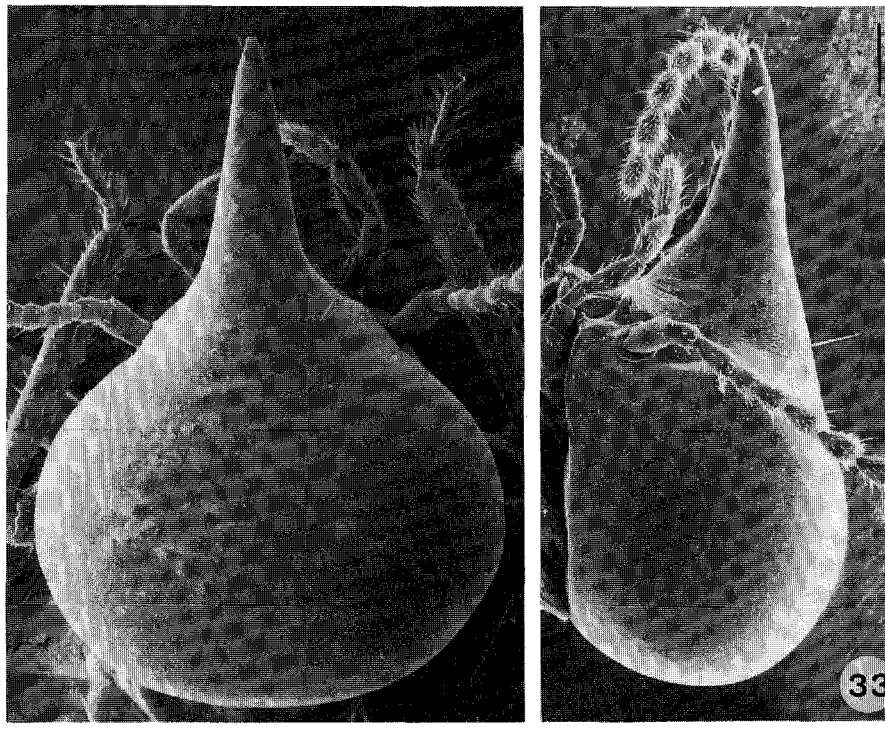


Fig. 33. *Nasutitermes novarumhebridarum* (N. & K. Holmgren): soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

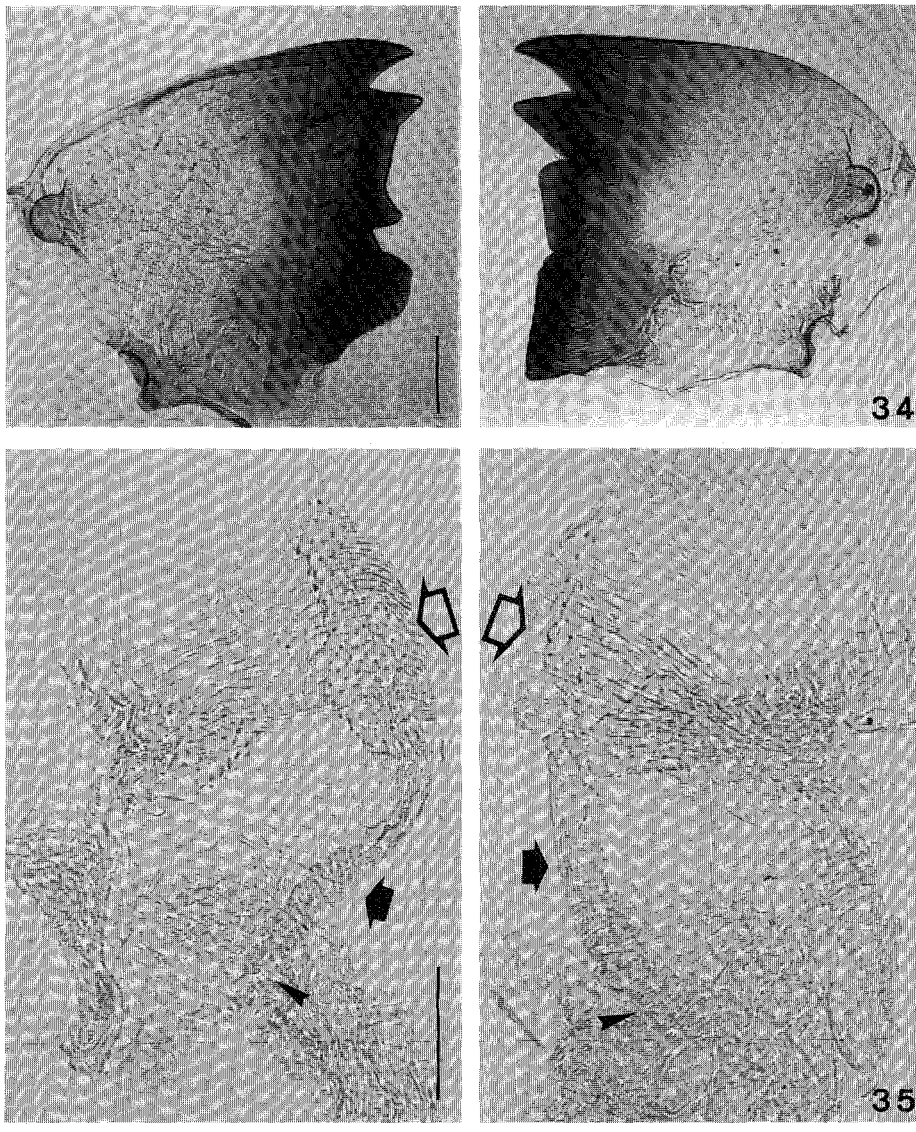
Measurements (mm) of 69 individuals from 23 colonies

	Range	Mean
Head capsule total length	1·520–1·920	1·707
Rostrum length	0·645–0·890	0·768
'Back of head' distance	0·350–0·530	0·426
Head width	0·900–1·400	1·090
Rostrum width (at half length)	0·150–0·220	0·176
Head depth	0·610–0·900	0·733
Hind tibia length	1·070–1·590	1·316

The chemical composition of the soldiers' defensive secretion has been studied in detail. The diterpene fraction is unique among the New Guinean nasutes studied, in containing large amounts of propionate derivatives (*Nasutitermes* sp. C in Dupont *et al.* 1981). The monoterpene content is dominated by myrcene (80%), followed by limonene (7%) (Everaerts *et al.* 1988). The secretion also contains relatively large amounts of sesquiterpenes, especially epi-α- and epi-β-selinene (Everaerts *et al.* 1993).

Worker (Figs 34, 35)

Head capsule from pale brown to dark chestnut. Substantial growth and marked increase in pigmentation between successive large- and small-worker instars. Antennae of 14 segments. Mandibles (Fig. 34) similar to those of *N. princeps*. Configuration of digestive tract very similar to that of *N. koiari*. Enteric valve (Fig. 35) transversal: upper spiny areas sclerotised and swollen, forming protruding plates, bearing multiple spines. Lower ring of non-sclerotised areas with few spines.



Figs 34, 35. *Nasutitermes novarumhebridarum* (N. & K. Holmgren), large worker: *34*, mandibles; *35*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

Head width (in mm) of workers from colony PNGT#45: small workers, first instar, 0·94–1·00 (mean = 0·96, n = 29); second instar, 1·00–1·08 (mean = 1·05, n = 15); large workers, first instar, 1·11–1·17 (mean = 1·14, n = 43); instar 2, 1·25–1·33 (mean = 1·28, n = 31); instar 3 or older, 1·34–1·42 (mean = 1·38, n = 23).

Distribution (Fig. 44)

Very common and widespread from New Guinea to the Solomon Archipelago, Santa Cruz and New Hebrides. Also present on many small islands off the coast of New Guinea (Schouten Is). Reaches New Caledonia eastward.

Biology

Nasutitermes novarumhebridarum is common in coconut plantations, where it is preferentially found on dead or injured trees (Szent-Ivany 1956; Roisin and Pasteels 1987; Leponce *et al.* 1995). This species seems almost always monogynous (Roisin 1987, 1993). In New Guinea, nests were always found on trees, but epigeal nests are sometimes encountered in the Solomon Islands (Harris and Brown 1958). The queen cell is formed of hard carton and situated in the central part of the nest, or within the wood of the supporting tree. Alates were found in nests from mid-August to December in the Hansa Bay region, in April near Madang, in March in Popondetta, in June in Milne Bay Distr. Queen-removal experiments invariably led to the differentiation of ergatoid (i.e. worker-derived) replacement reproductives (Roisin and Pasteels 1987).

Termitophiles

Nests AMNH#E3–E6, formerly determined to be *N. brevirostris* (Oshima) by A. E. Emerson, contained termitophilous staphylinids determined by Kistner (1972) to be *Lauella palauensis* Seevers. The physogastric staphylinid *Thyreoxenus solomonensis* Seevers, described from a single specimen from the Solomon Islands, also occurs with *N. novarumhebridarum* in New Guinea (Pasteels and Jacobson 1984).

Related Allopatric Species

Nasutitermes matangensis (Haviland)

Termes matangensis Haviland, 1898: 427–428. Imago, soldier, worker.
Eutermes (Eutermes) matangensis. — Holmgren, 1913: 183–184, pl. VII (figs 17, 21, 22). (imago, soldier, worker); John, 1925: 398, pl. XIX (fig. 12), pl. XX (fig. 13) (imago, soldier, worker, nest).
Eutermes (Eutermes) matangensis f. *matangensioides* Holmgren, 1913. Imago, soldier, worker.
Eutermes (Eutermes) matangensis (Haviland) var. *matangensioides*. — Bathellier, 1927: 173–175, 221–241, 279 sqq., figs 9, 44–62, pl. IV–VI, VII (colour), X. Imago, soldier, worker, nest, biology, castes.
Nasutitermes matangensis. — Snyder, 1949: 287.

Nasutitermes matangensis is widely distributed in Southeast Asia: its range extends from Viet-Nam to Borneo, through the Malay Peninsula, Sumatra and Java. On the basis of published descriptions, it appears very similar to *N. novarumhebridarum*. Syntype soldiers of the form *matangensioides* (Holmgren collection, NHRM) were examined; they closely resemble *N. novarumhebridarum*. In addition, the soldier defensive secretion of *N. matangensis* is almost identical to that of *N. novarumhebridarum* (termed *Nasutitermes* sp. C in Dupont *et al.* 1981): both contain the same two major propionate diterpene derivatives, and myrcene (77–88%) and limonene (12–21%) as major monoterpenes (Chuah *et al.* 1989). Sesquiterpenic compounds, present in *N. novarumhebridarum* (Everaerts *et al.* 1993), have thus far not been searched for in *N. matangensis*. The biology of *N. matangensis* was described extensively by Bathellier (1927), and also resembles that of *N. novarumhebridarum*, particularly in the ability to produce ergatoid replacement reproductives. *N. matangensis* and *N. novarumhebridarum* are thus obviously closely related, and it is even possible that these names designate allopatric populations of a single species, spreading from Southeast Asia to New Caledonia. Unfortunately, there is still a dearth of material from the Wallace Line area, where the ranges of the two taxa probably come into contact. We therefore consider it wiser to retain the taxon *N. novarumhebridarum* as a distinct species.

Nasutitermes brevirostris (Oshima)

Eutermes (Grallatotermes) brevirostris Oshima, 1917: 198–200, figs 3–4. Alate, soldier, small worker.
Nasutitermes (Nasutitermes) brevirostris. — Light and Wilson, 1936: 476.

This species described from Ponapi, Palau Islands, might be a junior synonymous or a subspecies of *N. matangensis* or *N. novarumhebridarum*, as judged by the description alone. The samples #E3–E6 of the AMNH collection were determined to be *N. brevirostris* (Oshima)

by A. E. Emerson (AMNH collection labels), who examined a syntype of this species; these specimens are herein reassigned to *N. novarumhebridarum*.

Nasutitermes amboinensis (Kemner)

Eutermes amboinensis Kemner, 1931: 38–43, figs 13–14. Alate, soldier, worker, biology (after Weyer).
Nasutitermes amboinensis. — Snyder, 1949: 266.

Soldiers of this species, described from Ambon, come very close to *N. novarumhebridarum* by their pilosity and head shape. However, by its ability to form polycalic colonies and to produce imaginal replacement reproductives (Weyer 1930), *N. amboinensis* resembles *N. polygynus* more. Measurements (mm) of an alate female from the type series (MZEL): head width across eyes, 1·58; eye diameter, 0·483; ocellus length, 0·183; pronotum width, 1·37; pronotum length, 0·85; forewing length, 12·8; forewing scale length, 0·828. *N. amboinensis* comes thus close to *N. novarumhebridarum* by its measurements, although the latter has larger eyes.

***Nasutitermes nomadensis*, sp. nov.**

Material Examined

Type colony (PNGT#1658). Nomad River (6°18′S, 142°14′E), 3.vi.1990. Nest about 4 m up a big tree in almost undisturbed forest. Neighbouring trees were attacked as well. Three imaginal queens and one king (Y. R., M. L.). Holotype: soldier.

PNGT #1640: *ibid.*, 1.vi.1990 (Y. R., M. L.).

Imago (Fig. 36)

Only known from three queens and one king, from the type colony. Head capsule chestnut brown, postclypeus, labrum and antennae ferruginous, legs paler, thoracic nota and abdominal tergites brown, sternites paler.

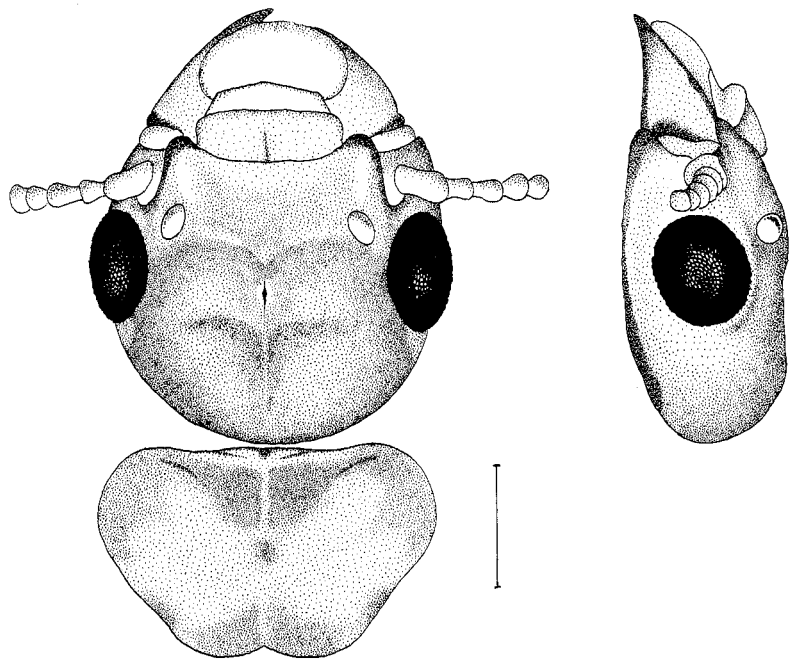


Fig. 36. *Nasutitermes nomadensis*, sp. nov., queen from type colony: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Posterior margin of head regularly rounded. Fontanelle slit-like, very narrow, pale brown. Eyes medium-sized, not prominent. Ocelli rather large, distant from eyes by about half their own diameter.

Measurements (mm) of the three queens and one king from the type colony

	Queen	Queen	Queen	King
Head width across eyes	1·42	1·47	1·47	1·42
Largest diameter of eye	0·478	0·503	0·494	0·477
Ocellus length	0·182	0·174	0·181	0·170
Eye to ocellus	0·069	0·099	0·080	0·086
Pronotum width	1·26	1·38	1·37	1·32
Pronotum length	0·76	0·84	0·87	0·82
Hind tibia length	1·70	1·74	1·62	1·82
Forewing scale length	0·816	0·840	0·837	0·837

Soldier (Fig. 37)

Head capsule dark to very dark chestnut brown. Thoracic and abdominal tergites chestnut brown, other thoracic sclerites, legs and antennae ferruginous.

Head capsule rounded, in profile with a slight hump at base of rostrum. Rostrum conical, thinner than in *N. novarumhebridarum*. Antennae of 13 segments, with segment 3 longer than segments 2 and 4. Head capsule with four long setae at base of rostrum and four forming a rectangle on vertex, as in *N. koiari*. Abdominal tergites with small hairs and one posterior row of, usually, 6 long setae.

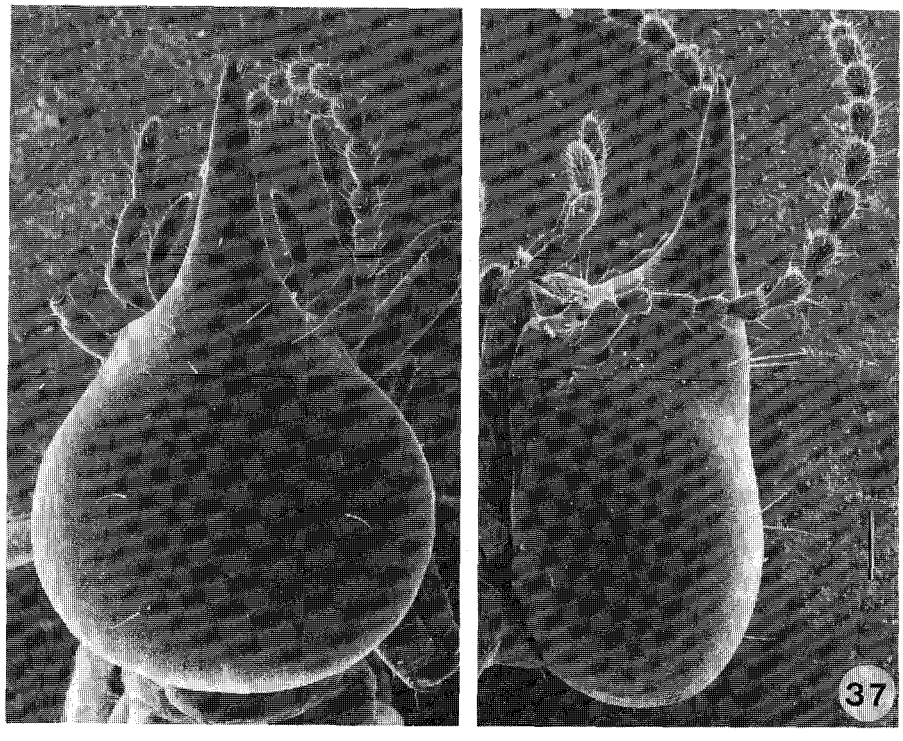


Fig. 37. *Nasutitermes nomadensis*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Measurements (mm) of 8 individuals from 2 colonies

	Range	Mean
Head capsule total length	1·657–1·730	1·692
Rostrum length	0·690–0·746	0·719
'Back of head' distance	0·399–0·461	0·431
Head width	1·053–1·161	1·100
Rostrum width (at half length)	0·151–0·165	0·157
Head depth	0·670–0·718	0·694
Hind tibia length	1·335–1·409	1·356

Worker (Figs 38, 39)

Head capsule chestnut to dark chestnut brown. Increase in size and pigmentation between successive instars. Tergites and abdominal membranes pigmented, giving the body an overall ferruginous to dark chestnut appearance. Antennae of 14 segments. Mandibles (Fig. 38) similar to those of *N. princeps*.

Gut very similar to that of *N. koiari*. Mixed segment: mesenteric part connected to remainder of mesenteron by wide dorsal peduncle. Malpighian tubules attached as two widely separated pairs. Enteric valve oblique. Upper ring of spiny areas comprising three unsclerotised swellings and intervening areas, all bearing small spines. Lower ring comprising three unsclerotised areas with many short spines (Fig. 39).

Head width of workers from type colony (PNGT#1658): small workers, first instar, 0·91–0·99 (mean = 0·95, n = 8); large workers, first instar, 1·16–1·18 (mean = 1·17, n = 8); instar 2 and older, 1·24–1·34 (mean = 1·29, n = 16).

Distribution (Fig. 44) *and Biology*

Only known from type locality. The single nest collected was polygynous; further collections are needed to determine whether this species has a reproductive biology similar to that of *N. princeps*.

Affinities

The small, non-prominent eyes of the imagos described here seem diagnostic. However, one must bear in mind the possibility of an imaginal polymorphism as in the related species *N. princeps*, *N. graveolus* and, probably, *N. koiari*. Polygyny and the fact that the imagos of *N. nomadensis* described above possess such small eyes suggest that these sexuals might be microimagos, and that a larger, darker and wider-eyed normal form might exist, awaiting discovery.

The soldier of *N. nomadensis* comes very close to that of *N. koiari* by the shape and pilosity of its head capsule, but differs by a conspicuous dark reddish tinge on head and body, and less pilose abdominal tergites. *N. novarumhebridarum* has a broader head capsule with a thicker, more conical rostrum and only two setae on vertex.

Etymology

Named after Nomad River, the type locality.

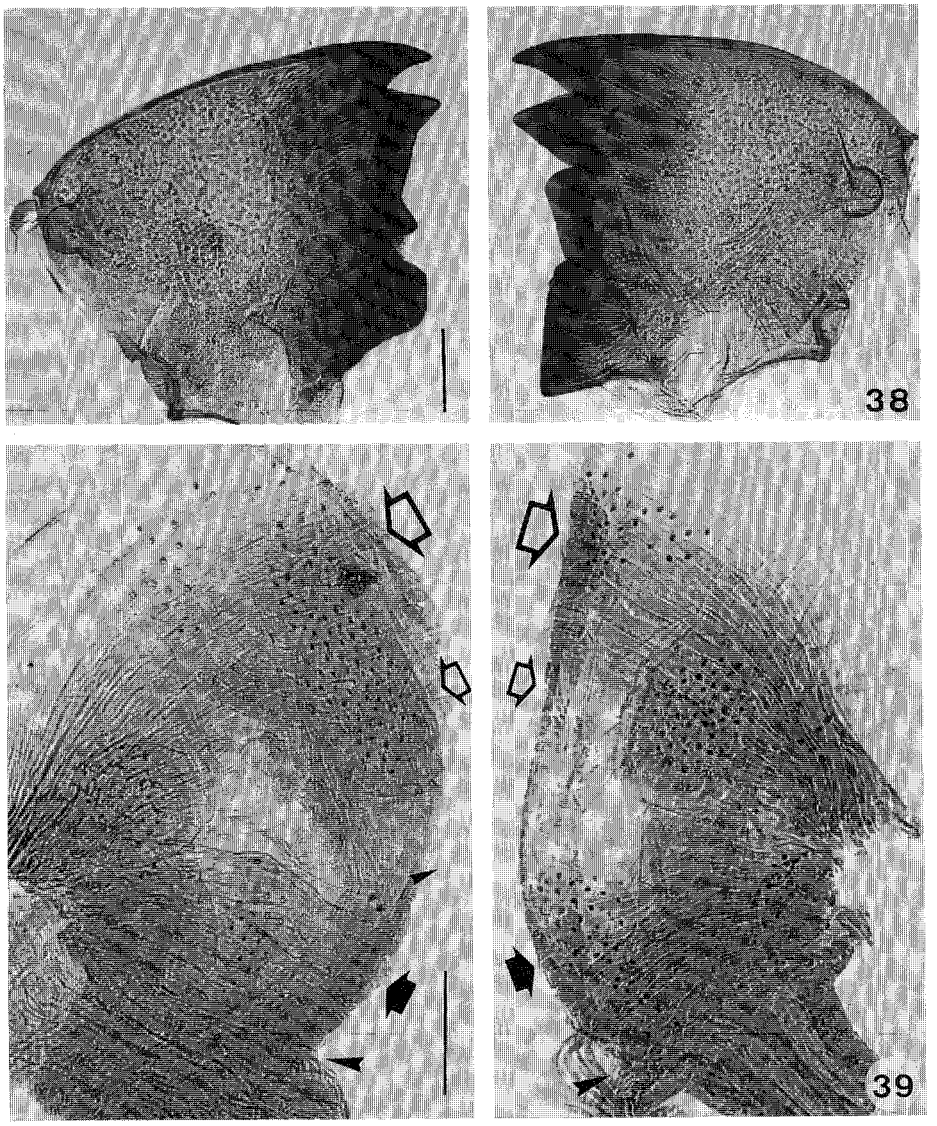
Nasutitermes polygynus Roisin & Pasteels

Nasutitermes polygynus Roisin & Pasteels, 1985*a*: 325–329, figs 1–2. Alate, soldier, worker, biology.

Material Examined

Numerous samples from Bogia Distr., Madang Province (see Roisin and Pasteels 1985*a*), and the following additional material.

Authors' collection (PNGT). #1025: Yoro, 14.vi.1986 (Y. R., C. Everaerts). #1055: Makarup (Lower Ramu plains), 1–3.ii.1987 (J. M. P.). #1132: Yoro, 22.viii.1987 (Y. R.). #1182–1183: Laing I., 19.iv.1988 (Y. R.). #1274: Gogol River valley, 35 km from Madang–Lae Road, 16.ix.1988 (Y. R.). #1375: Mirap (North Coast Hwy), 22.xii.1988 (M. L.). #1376: Wasab, 24.xii.1988 (M. L.). #1566: Lake Murray, 23.v.1990 (Y. R., M. L.).



Figs 38, 39. *Nasutitermes nomadensis*, sp. nov., large worker: *38*, mandibles; *39*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

ANIC. #10 8599: Madang, Jul. 1944 (J. E. Cummins). #10 10410: Matupit Plantation, Madang, 6.ix.1962 (J. J. H. Szent-Ivany). #10 10448: Berebei (Central Distr.), 2.viii.1962 (P. C. H.).

The following sample probably belongs to this species as well: ANIC#10 10463: Deria (Amazon Bay), alt. 200 m, Dec. 1962. Alates only (W. Brandt).

Imago (Fig. 40)

A medium-sized species, with diagnostic small eyes and ocelli. Antennae 15-segmented. Alate with uniform dark sepia brown wings.

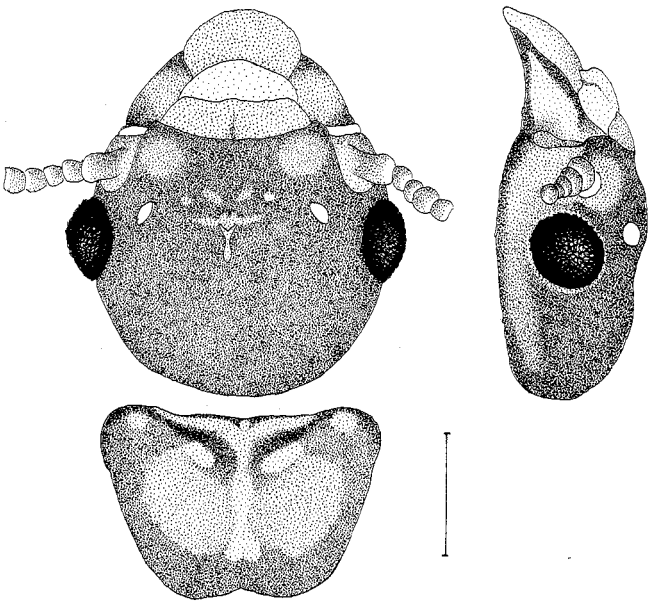


Fig. 40. *Nasutitermes polygynus* Roisin & Pasteels, female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Measurements (after original description) of 18 alates from 4 colonies and 23 dealated reproductives from 6 other colonies

	Range	Mean
Head width across eyes	1·28–1·44	1·34
Largest diameter of eye	0·31–0·35	0·335
Length of ocellus	0·10–0·14	0·12
Eye to ocellus	0·12–0·19	0·15
Pronotum width	0·97–1·25	1·10
Pronotum length	0·61–0·81	0·725
Hind tibia length	1·52–1·72	1·61
Forewing length	9·2–10·8	9·9

Soldier (Fig. 41)

A very dark chestnut brown species, slightly smaller than the other arboreal nasutes. Rostrum stout, conical, pilosity sparse. Antennae 13-segmented. Closely resembles *N. novarumhebridarum*, but head capsule darker and somewhat flattened posteriorly.

Measurements (mm) of 39 individuals from 13 colonies

	Range	Mean
Head capsule total length	1·380–1·645	1·490
Rostrum length	0·570–0·659	0·610
'Back of head' distance	0·350–0·455	0·390
Head width	0·840–1·120	0·953
Rostrum width (at half length)	0·140–0·198	0·172
Head depth	0·570–0·713	0·632
Hind tibia length	0·970–1·276	1·128

The diterpene content of the defensive secretion of this species was studied by Dupont *et al.* (1981), who termed it *Nasutitermes* sp. B. The monoterpene content is dominated by terpinolene (83%), followed by limonene (9%) and minor constituents (Everaerts *et al.* 1988).

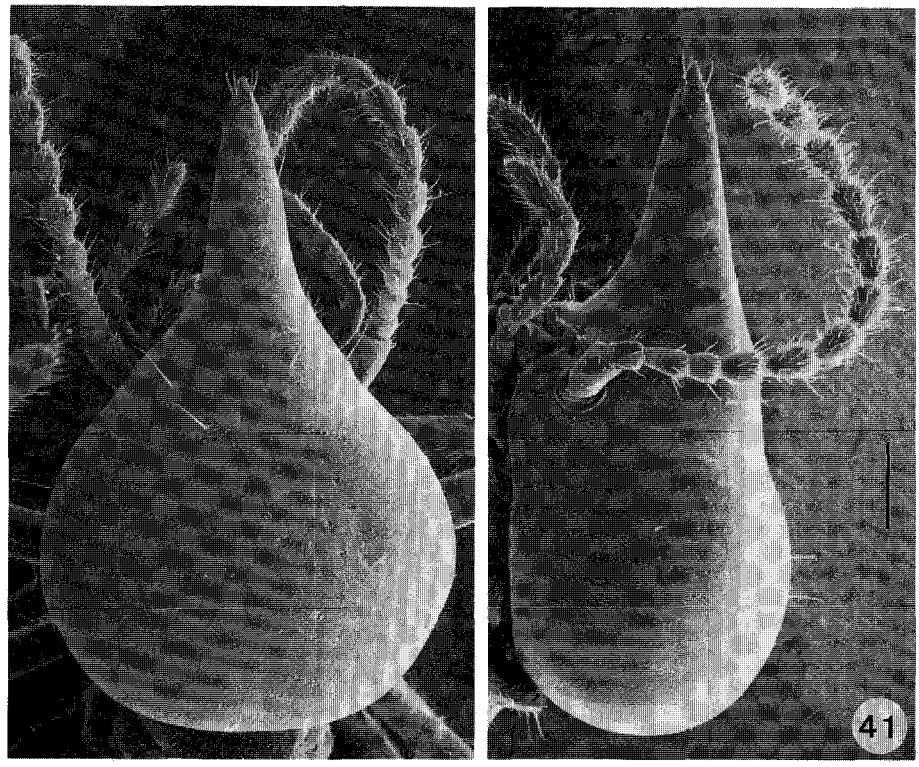


Fig. 41. *Nasutitermes polygynus* Roisin & Pasteels: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Worker (Figs 42, 43)

Head capsule from very pale brown to dark sepia. Moderate growth and marked increase in pigmentation between successive large- and small-worker instars. Antennae of 14 segments. Mandibles (Fig. 42) as in *N. princeps*. Configuration of digestive tube very similar to that of *N. koiari*. Enteric valve (Fig. 43): upper spiny areas sclerotised and swollen, forming protruding plates, bearing multiple spines. Lower ring of non-sclerotised areas with few spines.

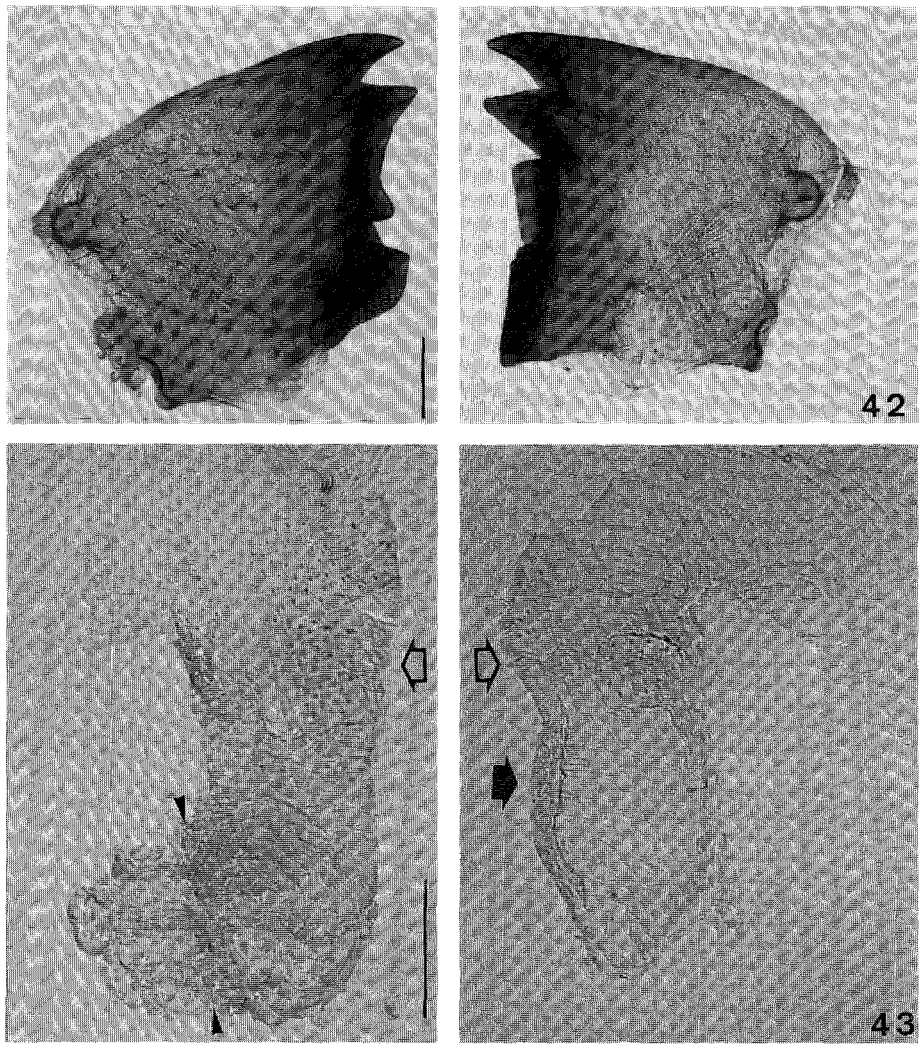
Head width (in mm) of workers from type colony (after original description): small workers, first instar, 0·78–0·88 (mean = 0·83, n = 15); second instar, 0·84–0·94 (mean = 0·89, n = 15); large workers, first instar, 1·00–1·10 (mean = 1·05, n = 15); second instar, 1·08–1·18 (mean = 1·15, n = 15); third instar, 1·08–1·20 (mean = 1·14, n = 15).

Distribution (Fig. 44)

More widespread in New Guinea than previously reported, but less common than the other arboreal nasutes. The distribution of this species in southern New Guinea remains largely unknown. Not reported from the Schouten or Bismarck Islands.

Biology

This is a highly polygynous species forming polycalic systems of arboreal nests (see Roisin and Pasteels 1986*c*). Two swarming events were observed on Laing Island at sunset, the first rainy days of the wet season (November) (Roisin and Pasteels 1985*a*).



Figs 42, 43. *Nasutitermes polygynus* Roisin & Pasteels, large worker: *42*, mandibles; *43*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrow, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

Nasutitermes bikpelanus, sp. nov.

Material Examined

Type colony (PNGT#2). Nubia–Bunapas Road, Madang Province, 16.xi.1978. Small arboreal nest 1 m from ground, in crevice in trunk of live tree. With royal pair and 1 nymph (J. M. P.). Holotype: soldier.

Authors' collection (PNGT). #113, 140, 249, 270, 279, 293, 368, 400, 428, 455, 519, 533, 548, 679, 698, 699, 707, 744, 745, 780, 825, 845, 869, 878, 1070, 1099, 1121, 1129, 1133, 1136, 1171, 1174, 1265: from Bogia to Guam R. and lower Ramu, 26.vi.1981–29.viii.1988 (J. M. P., Y. R., M. L.). #31: Boisa I., 3.xii.1978 (J. M. P.). #66: Manam I., 12–13.vi.1981 (J. M. P.). #82, 84: Bam I., 19.vi.1981 (J. M. P.). #83: Blup Blup I., 16.vi.1981 (J. M. P.). #94: Boisa I., 23.vi.1981 (J. M. P.). #173: Wampit (40 km after Markham bridge on Lae–Bulolo Road), 16.ii.1983 (J. M. P., Y. R.). #186: Oomsis R., (20 km after Markham bridge on Lae–Bulolo Road), 17.ii.1983 (J. M. P., Y. R.). #189, 195: Kaiapit, 19.ii.1983 (J. M. P., Y. R.). #309, 312-313, 344: Yagaum Hospital, Madang, 10.iv.–13.v.1983 (Y. R.). #601: Kolonoboi, New Ireland, 25.v.1984 (J. M. P., Y. R.). #616: Konos, New Ireland, 29.v.1984 (J. M. P., Y. R.). #632: Lemakot,

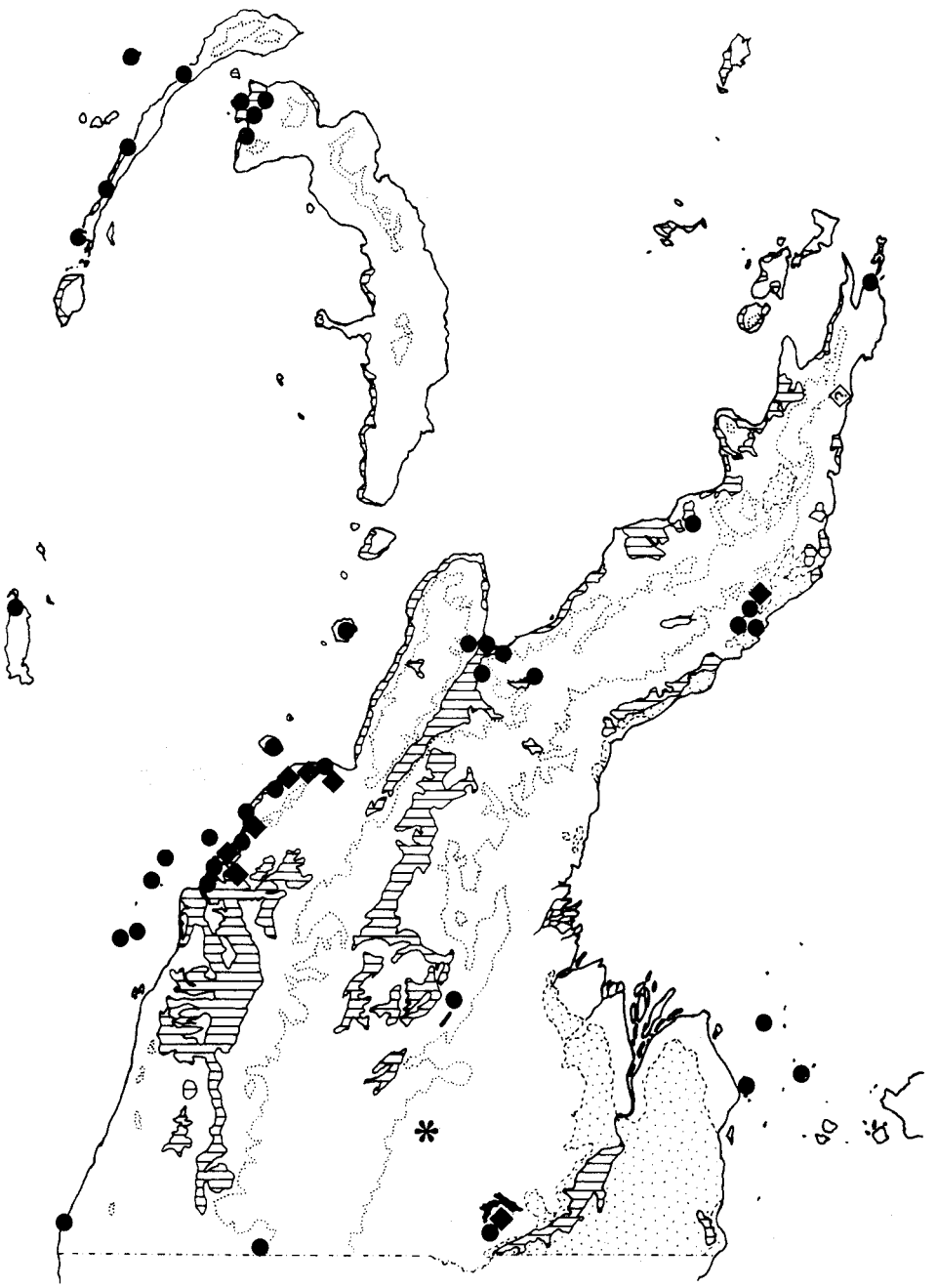


Fig. 44. Known distributions within Papua New Guinea (excluding the North Solomons Prov.) and Torres Strait of *Nasutitermes novarumhebridarum* (●), *N. nomadensis* (*) and *N. polygynus* (◆).

New Ireland, 31.v.1984 (J. M. P., Y. R.). #641: 14 km SE Kavieng, 2.vi.1984 (J. M. P., Y. R.). #656, 657, 676, 677: Manus I., 32 km from Lorengau on road to south coast, 4–6.vi.1984 (J. M. P., Y. R.). #813, 818: Boisa I., 6.ix.1984 (Y. R.). #963, 967, 973, 974: Kokoda, 15–16.iii.1985 (J. M. P., Y. R.). #984: Popondetta, 18.iii.1985 (J. M. P., Y. R.). #1008c: Karkar I., 10.viii.1985 (S. W. Luxford). #1086–1088: Bulolo, Mount Susu Nature Reserve, alt. 950 m, 23.v.1987 (Y. R., P. P. D.). #1092, 1093, 1097: Oomsis Forest Station, 25.v.1987 (Y. R.). #1194: Braham Mission (middle Ramu), 5.v.1988 (Y. R.). #1208: Bundi, alt. 1000 m, 10.v.1988 (Y. R.). #1223, 1224: Bulolo, Manki Ridge, alt. 1300 m, 18.v.1988. #1229, 1230: Bulolo, Mount Susu Nature Reserve, alt. 950–1000 m, 19.v.1988 (Y. R.). #1240: Lae–Bulolo Road, 27 km after Markham Bridge, 24.v.1988 (Y. R.). #1272: 50 km from Madang on North Coast Road, 15.ix.1988 (Y. R.). #1290: Lake Kutubu, Southern Highlands, alt. 850–900 m, 11.x.1988 (Y. R.). #1299, 1309: Pimaga, Southern Highlands, alt. 800 m, 16–17.x.1988 (Y. R.). #1326: Braham Mission, 17.xi.1988 (Y. R.). #1575: Lake Murray, 24.v.1990 (Y. R., M. L.). #1613, 1618, 1639: Nomad R., 29.v.–1.vi.1990 (Y. R., M. L.). #1715– 1717: 3 km W Vanimo, 8.iii.1994 (Y. R., M. L.). #1723, 1745: Yapsiei, Sandaun Province, 10–12.iii.1994 (Y. R., M. L.). Amboin, Karawari Lodge, East Sepik Province, March 1983 (A. C. Messer).

ANIC. #10 10952: Bulolo, 24.vii.1963 (J. Tomani). #10 12923: Lugos, Manus I., 21.iv.1969 (B. Gray). #10 13234: Pimaga, Southern Highlands, 25.xi.1969 (B. Gray). #10 13236: Bulolo, 6.xii.1969 (F. R. Wylie).

AMNH. #E11–15, 48, 51, 53–55, 57, 58, 69, 93, 101: within 32 km from Lae, 5–31.xii.1962 (A. E., E. E., P. A.). #E38: Brown R., 32 km NW Port Moresby, 15.xi.1962 (A. E.). #E59, 82: Bulolo, alt. 725 m, 14.xii.1962 (A. E.). #E116: Bulolo, alt. 700 m, 29.xi.1962 (A. E.). #E130: Wanuma, Adelbert Range, alt. 670 m (R. Zweifel).

Imago (Fig. 45)

Head capsule sepia brown, paler on vertex. Labrum and postclypeus yellow–brown, pronotum sepia, with paler T- or Y-shaped mark. Legs and antennae yellow–brown. Thoracic sclerites and abdominal tergites sepia, sternites paler, pale yellow in middle. Wings brown, paler along distal costal-subcostal part.

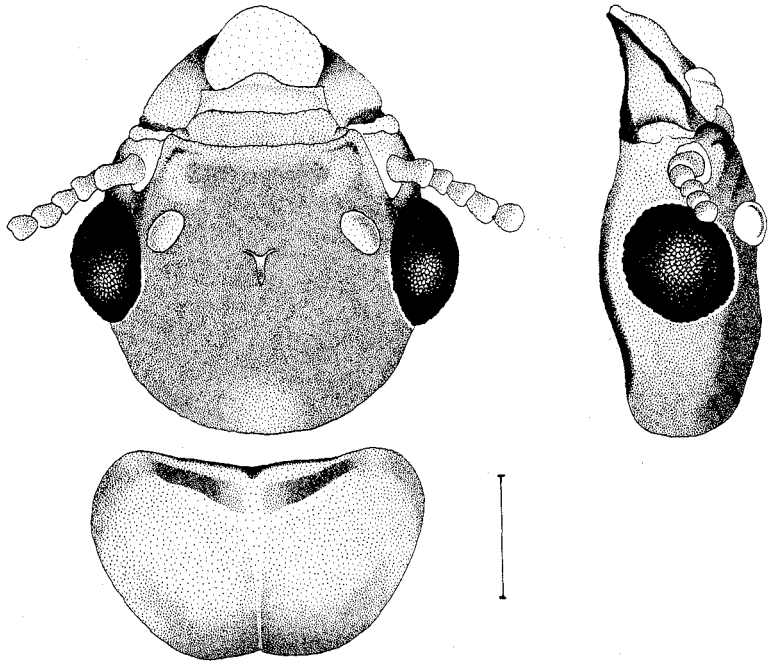


Fig. 45. *Nasutitermes bikpelanus*, sp. nov., female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Eyes large, prominent, ocelli medium to large, close to eye. Fontanelle distinct, narrow, with parallel sides, *c.* 0·120 mm long by 0·030 mm wide, hyaline at least in anterior half, often turning light brown posteriorly. Antennae 15-segmented, segment 3 the smallest, slightly smaller than segment 2 and conspicuously smaller than segment 4, segment 4 slightly larger than segment 5.

	Measurements (mm)			
	Females (6 alates, 5 queens) (5 colonies)		Males (12 alates, 1 king) (7 colonies)	
	Range	Mean	Range	Mean
Head width across eyes	1·44–1·59	1·53	1·46–1·57	1·51
Largest diameter of eye	0·454–0·565	0·514	0·492–0·544	0·514
Length of ocellus	0·188–0·218	0·202	0·160–0·203	0·182
Eye to ocellus	0·017–0·110	0·055	0·029–0·085	0·051
Pronotum width	1·18–1·35	1·27	1·20–1·29	1·24
Pronotum length	0·73–0·87	0·81	0·73–0·80	0·76
Hind tibia length	1·63–1·82	1·75	1·72–1·85	1·79
Forewing scale length	0·743–0·851	0·795	0·735–0·840	0·795
Forewing length	10·5–12·3	11·7	10·4–12·1	11·2

Soldier (Fig. 46)

Head capsule from orange–yellow to ferruginous-orange, more reddish on rostrum. Antennae and thoracic sclerites orange–yellow, abdominal tergites ferruginous, legs and sternites very pale.

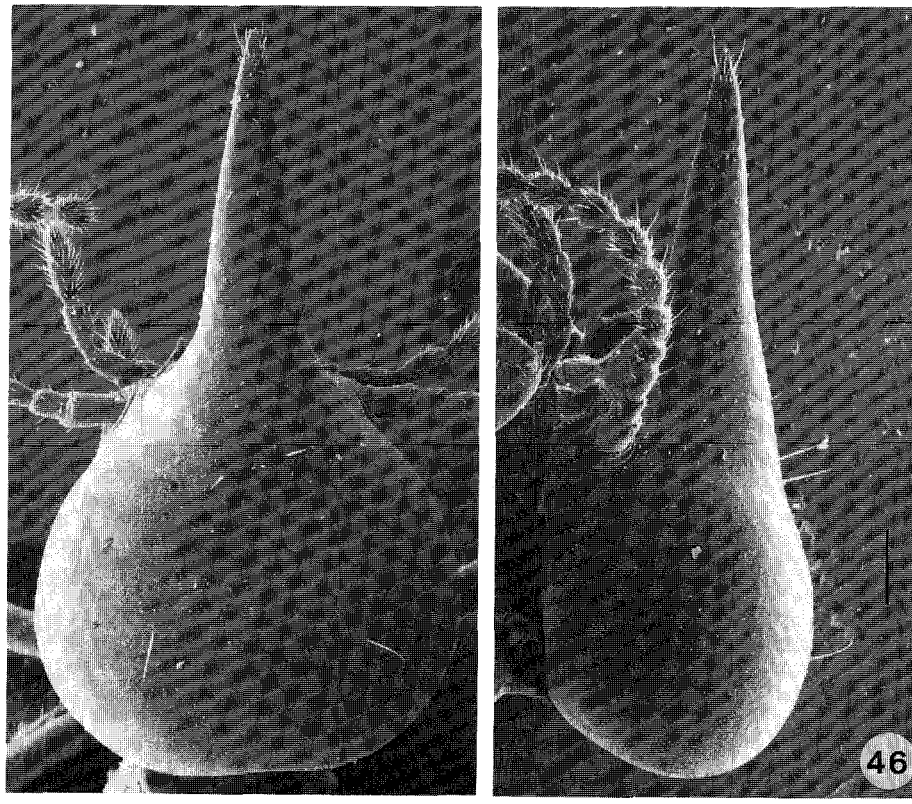


Fig. 46. *Nasutitermes bikpelanus*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Head regularly rounded behind, in profile nearly straight, with slight hump at base of rostrum. Rostrum long, thick, conical. Antennae of 13 segments, lengths of segments 2:3:4 in approximate ratio 5:9:6. Pilosity sparse: a few setae on rostrum tip, 4 at base of rostrum, 2 on vertex. One row of 4–6 long setae along posterior margin of abdominal tergites.

Measurements (mm) of 371 individuals from 87 colonies

	Range	Mean
Head capsule total length	1·39–1·98	1·70
Rostrum length	0·59–1·00	0·85
'Back of head' distance	0·30–0·46	0·38
Head width	0·69–1·14	0·91
Rostrum width (at half length)	0·13–0·21	0·17
Head depth	0·48–0·79	0·62
Hind tibia length	0·85–1·33	1·14

The major monoterpenes contained in this species' defensive secretion are α-pinene (60%), limonene (13%) and α-terpinene (*Nasutitermes* sp. F in Everaerts *et al.* 1988).

Worker (Figs 47–49)

Head capsule from pale yellow to ferruginous. Abdominal tergites translucent to very pale brown. Increase in pigmentation between successive worker instars, slight increase in size from first to second large worker. Antennae of 14 segments. Mandibles (Fig. 47) as in *N. princeps*.

Configuration of the digestive tract as in Fig. 49. Mesenteric part of mixed segment separated from remainder of mesenteron, only connected to it through narrow dorsal peducle formed by proctodeal folds. Malpighian tubules attached as two separated pairs at the mesentero-proctodeal junction. Upper ring of enteric valve asymmetrical, with many small spines. Lower ring of three swellings bearing a few larger spines (Fig. 48).

Head width (in mm) of 50 workers from colony PNGT#869: Small workers, first instar, 0·960–0·980 (mean = 0·939, n = 9); second instar, 0·950 (n = 1); large workers, first instar, 1·152–1·190 (mean = 1·175, n = 6); second instar, 1·195–1·281 (mean = 1·244, n = 28); third instar and older, 1·206–1·288 (mean = 1·240, n = 6).

Distribution (Fig. 78)

Widespread throughout Eastern New Guinea: present on northern and southern sides of the Central Ranges, up to 1300 m in mountains. Reaches New Ireland and Manus, but not recorded from New Britain.

Biology

This species typically nests within hollow tree trunks, stumps or branches, where it builds alveolar constructions. When not completely enclosed within the supporting tree itself, these constructions are protected by an envelope resembling that of other arboreal nasute nests. Appears to be monogynous usually, but one polygynous nest was found near Kavieng, New Ireland.

Affinities

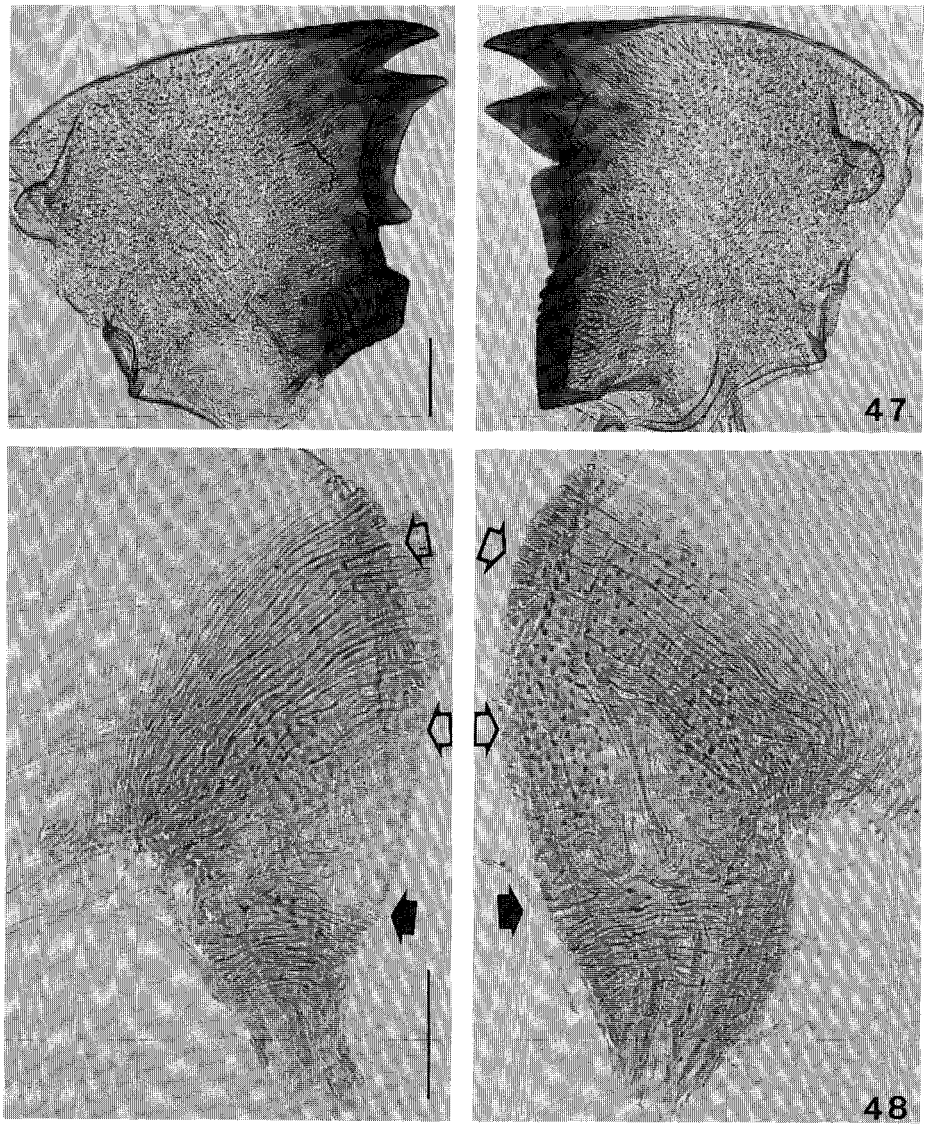
The soldier of *N. bikpelanus* is unique for its long and thick rostrum.

Termitophiles

Two species of aleocharine staphylinids (tribe Perinthini), *Lauella aenigma* and *L. alomai*, were reported from nests of this species (AMNH#E12, 15) in the Lae area (Kistner 1972).

Etymology

The name is derived from Neo-Melanesian *bikpela nus*, meaning big nose.



Figs 47, 48. *Nasutitermes bikpelanus*, sp. nov., large worker: *47*, mandibles; *48*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

Nasutitermes gracilirostris (Desneux)

Termes (Eutermes) gracilirostris Desneux, 1905: 376–377, fig. 5. Soldier.
Eutermes gracilirostris. — Hill, 1942: 221–223, figs 117–118. Soldier, worker.
Nasutitermes gracilirostris. — Snyder, 1949: 278.

This species seems to be rather variable from one locality to another, and even within a single locality. The possibility exists that the samples grouped here under *N. gracilirostris* actually represent several closely related species.

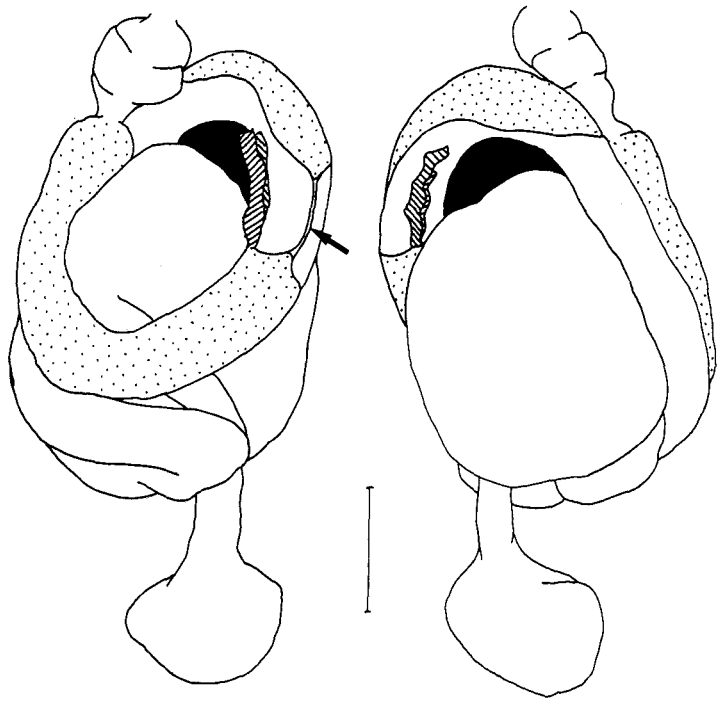


Fig. 49. *Nasutitermes bikpelanus*, sp. nov., large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched. Arrow: proctodeal folds linking mesenteric part of mixed segment to main body of mesenteron.

Material Examined

IRSN. Lectotype soldier (designated here), paralectotype soldiers and workers (#11813): Friedrich-Wilhelmshafen (now Madang), 13.i.1901 (L. Biró). Paralectotype soldiers and workers: *ibid.*, 8.i.1901, (L. Biró).

Authors' collection (PNGT). #68b: Blup Blup I., 16.vi.1981 (J. M. P.). #106, 109, 139, 456, 476, 549, 682, 684, 696, 879, 1053, 1098, 1135, 1143, 1161, 1187, 1188, 1190, 1523: Bogia Distr., between Ramu R. and coast, 26.vi.1981–25.iv.1989 (J. M. P., Y. R., M. L.). #174: Wampit, 40 km from Markham Bridge on Bulolo Road, 16.ii.1983 (J. M. P., Y. R.). #200, 203: Kaiapit, 20.ii.1983 (J. M. P., Y. R.). #211: Usino, 22.ii.1983 (J. M. P., Y. R.). #370: Yoro, 20.v.1983 (Y. R.). #964, 968, 970, 990: Kokoda, 15–19.iii.1985 (J. M. P., Y. R.). #1209: Bundi, road to Kobum cardamom plantation, alt. 1000 m. (Y. R.). #1216–1218: Sira Sira, Leron River valley, Wantoat Road, alt. 650 m (Y. R.). #1243: Yoro, 1.vi.1988 (Y. R.). #1276: Gogol River, 38 km from Madang–Lae Road, 16.ix.1988 (Y. R.). #1325, 1331: Braham Mission, 17–18.xi.1988 (Y. R.). #1724: Yapsiei, Sandaun Province, 10.iii.1994 (Y. R., M. L.).

ANIC. #10 9819: Lae, 14.vi.1961 (J. S. Womersley). #10 10489: Lae, 26.x.1960 (J. S. Womersley).

AMNH. #E7–9, 40, 41, 44–47, 56, 60, 62, 68, 75, 77, 79, 86, 87, 95, 97, 105, 106, 111: within 40 km of Lae, 1–31.xii.1962 (P. A., A. E., E. E.).

Imago (previously undescribed) (Fig. 50)

Described here from two nest series collected near Lae, one with a royal pair and the other with alates. Almost indistinguishable from *N. bikpelanus*. *N. gracilirostris* seems a little paler, but this might be due to preservation. The fontanelle of *N. gracilirostris* may be diagnostic: large, hyaline, about 0·120 mm long by 0·075 mm wide, with two short and thin anterior extensions. Shape ovoid, with widest part at posterior third (*v.* narrow, with parallel sides in *N. bikpelanus*).

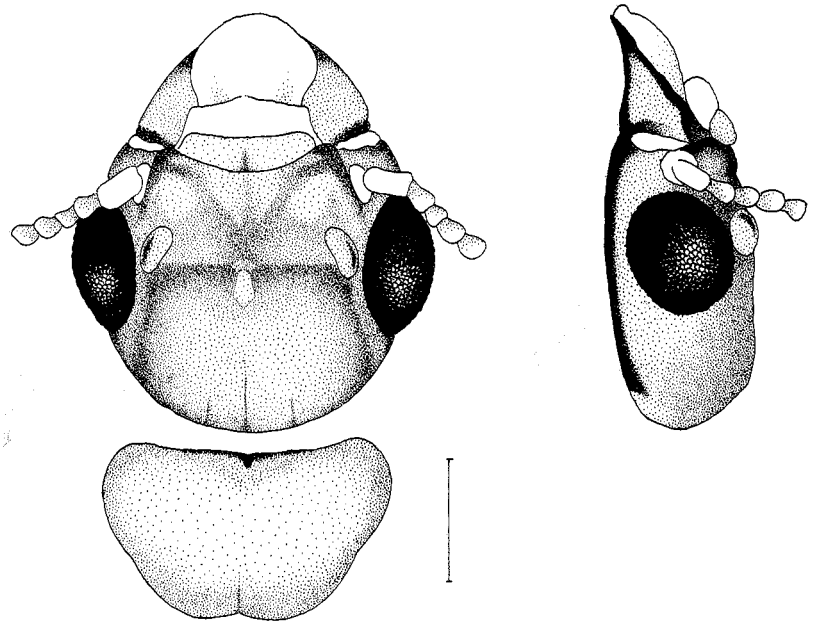


Fig. 50. *Nasutitermes gracilirostris* (Desneux), female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Measurements (mm) of royal pair of sample AMNH#E7 and 4 alates of each sex from AMNH#E40

	Females		Males	
	Range	Mean	Range	Mean
Head width across eyes	1·50–1·54	1·52	1·43–1·47	1·45
Largest diameter of eye	0·549–0·566	0·556	0·536–0·563	0·547
Length of ocellus	0·193–0·209	0·204	0·192–0·217	0·204
Eye to ocellus	0·031–0·042	0·035	0·038–0·058	0·044
Pronotum width	1·193–1·254	1·224	1·168–1·212	1·186
Pronotum length	0·732–0·801	0·761	0·697–0·722	0·712
Hind tibia length	1·84–1·91	1·86	1·73–1·85	1·80
Forewing scale length	0·784–0·837	0·802	0·758–0·796	0·772
Forewing length	11·5–12·3	12·0	9·5–10·9	10·4

Soldier (Fig. 51)

A medium-sized, thin-nosed, orange–yellow to orange species. Distinguished from *N. bikpelanus* by smaller size and much shorter and narrower rostrum. Pilosity sparse: 4 setae at base of rostrum, 2 on vertex. A row of up to six long setae on border of abdominal tergites, but those setae are missing on anterior segments in some series. Antennae variable, as described by Desneux (1905), usually of 13 segments but of 12 segments in some individuals.

Measurements (mm) of 95 individuals from 26 colonies

	Range	Mean
Head capsule total length	1·366–1·695	1·503
Rostrum length	0·634–0·780	0·691
'Back of head' distance	0·310–0·420	0·364
Head width	0·724–0·894	0·827
Rostrum width (at half length)	0·096–0·129	0·109
Head depth	0·465–0·660	0·582
Hind tibia length	0·854–1·091	0·963

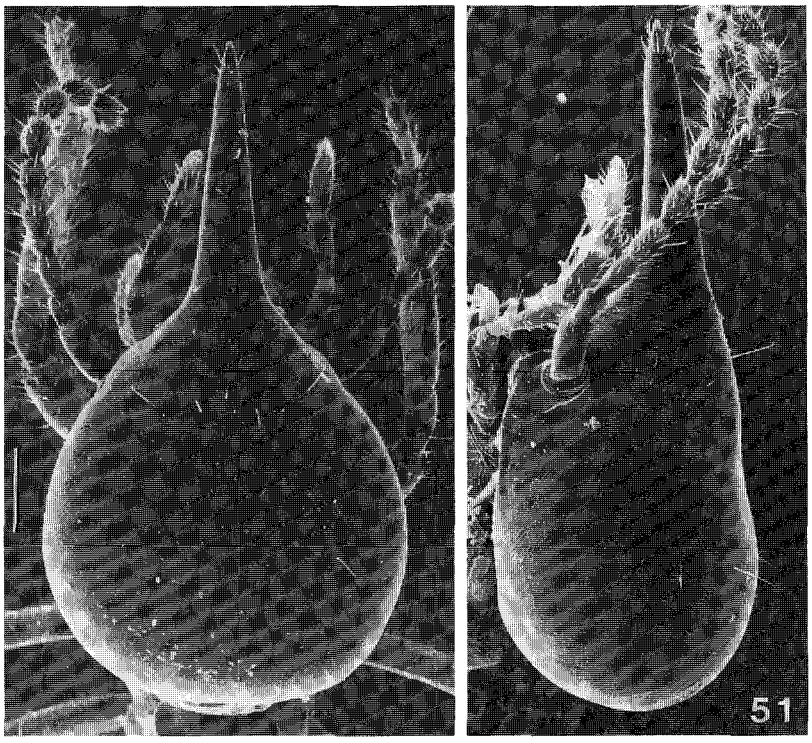


Fig. 51. *Nasutitermes gracilirostris* (Desneux): soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

The defensive secretion of this species is rich in α-phellandrene (69% of the monoterpene content), limonene (22%), and contains terpinolene (5%) as well (Everaerts *et al.* 1988).

Worker (Figs 52, 53, 58–62)

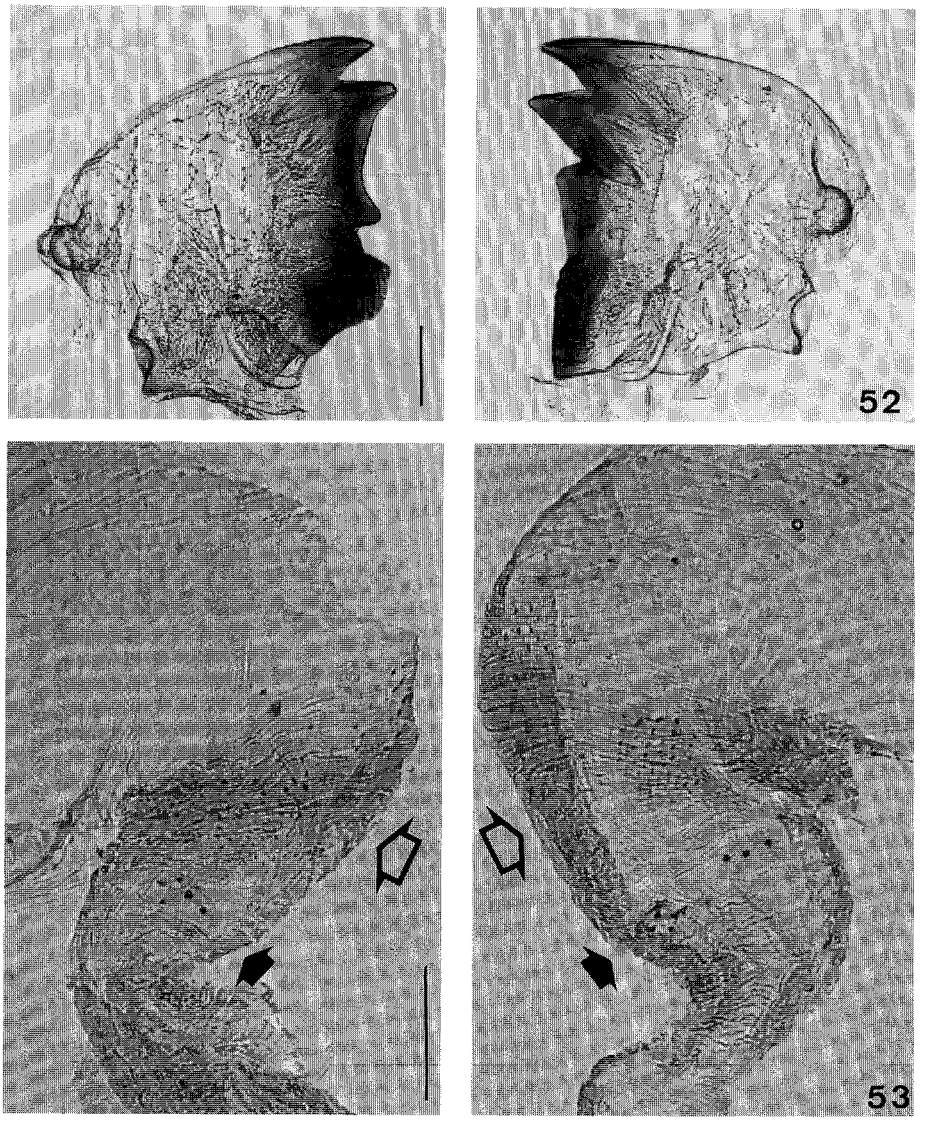
Head capsule yellow–white to ferruginous. Antennae of 14 segments, segments 3–5 often incompletely separated but always distinct, especially visible in older instars. Little growth from large-worker instar 1 to 2, or none at all. Mandibles (Fig. 52) as in *N. princeps*.

Mixed segment and enteric valve (Fig. 53) very similar to those of *N. bikpelanus*. Malpighian tubules variable: usually attached to the gut as two separated pairs (Figs 58–60), but sometimes one pair is markedly curved in its proximal part and reaches the gut almost jointly with the other one. This phenomenon affects specimens from the Lae area (Fig. 61) and even more those from Kokoda (Fig. 62).

Head width (in mm) of workers from colony PNGT#1188: small workers, 0·795–0·870 (mean = 0·840, n = 8); large workers, first instar, 1·065–1·120 (mean = 1·099, n = 12); second instar and older, 0·990–1·130 (mean = 1·086, n = 12).

Distribution (Fig. 101) *and Biology*

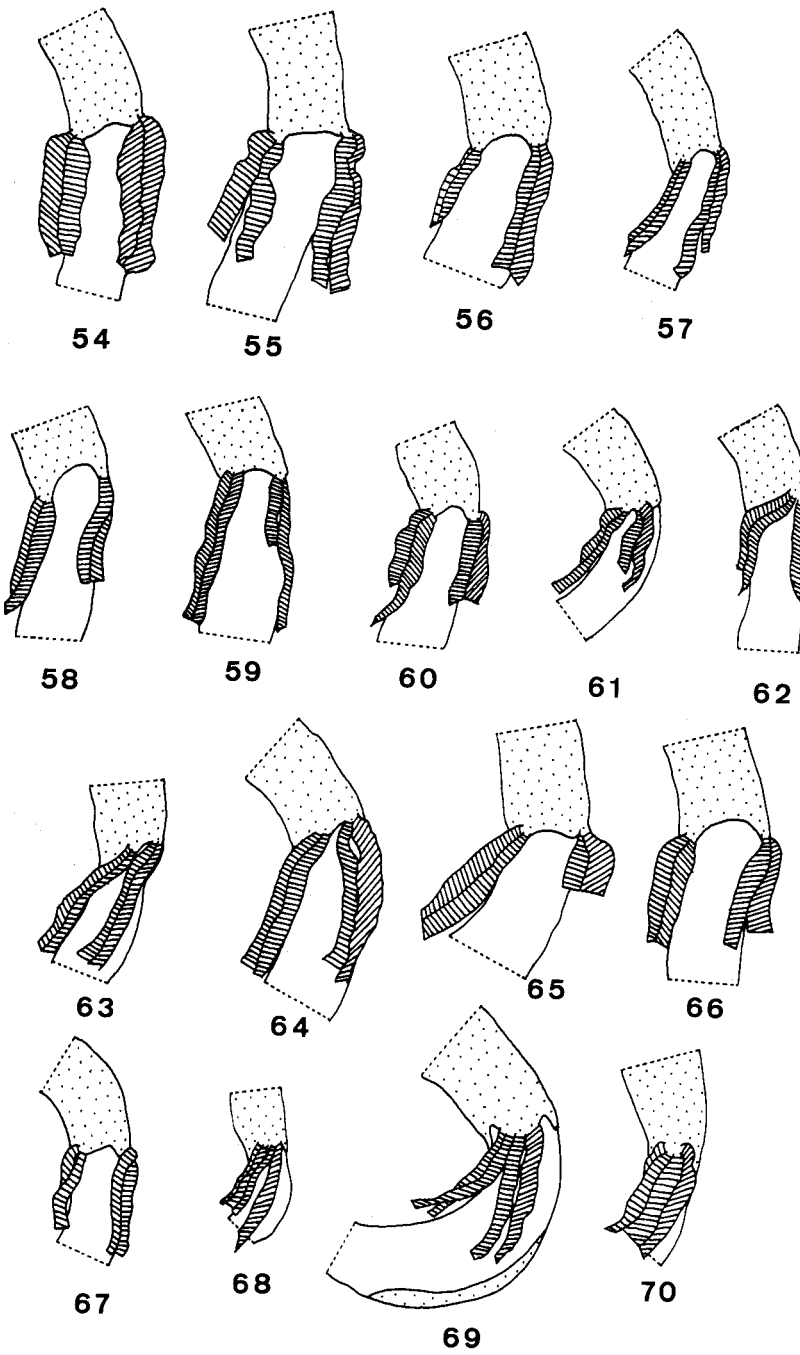
Recorded from northern mainland New Guinea, from the upper Sepik to Kokoda. Foragers are frequently encountered in dead wood on forest floor, but the nest was found only once, on top of a stump in forest near Lae (A. Emerson).



Figs 52, 53. *Nasutitermes gracilirostris* (Desneux), large worker: *52*, mandibles; *53*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

Termitophiles

The following species of termitophilous staphylinids (Aleocharinae, Perinthini) were found with *N. gracilirostris* in the Lae area (Kistner 1972): *Lauella alomai*, *L. gigantea*, *L. minuta* and *Paralauella manni*. AMNH#E7 was the host colony for holotype and 23 paratypes of the staphylinid *Lauella alomai*, unique specimen of *L. gigantea* and types (2 specimens) of *Paralauella manni*. This series was considered by Emerson (collection label and *in* Kistner 1972) as representing an undescribed species (*Nasutitermes* sp. IV), but we did not find any consistent criteria to distinguish it from the other series determined to be *N. gracilirostris*. AMNH#E9 was the host colony for the types (3 specimens) of *Lauella minuta*.



Figs 54–70. Insertion of malpighian tubules (hatched) in New Guinean Nasutitermitinae. Mesenteron stippled. *54*, *Nasutitermes motu*, sp. nov.; *55*, *N. koiari*, sp. nov.; *56*, *N. pinocchio*, sp. nov.; *57*, *N. seghersi*, sp. nov., subsp. *seghersi*. *58–62*, *N. gracilirostris* (Desneux): *58*, from Bundi; *59*, from Yoro; *60*, from Kaiapit; *61*, from Wampit; *62*, from Kokoda. *63*, *64*, *N. leponcei*, sp. nov.: *63*, from Tabubil; *64*, from Nomad River. *65*, *66*, *N. muli*, sp. nov., two samples from Nomad River; *67*, *Niuginitermes variratae*, sp. nov.; *68*, *Diwaitermes kanehirae* (Oshima); *69*, *D. castanopsis*, sp. nov.; *70*, *Tumulitermes marcidus* (Hill).

Other Probably Conspecific Material

Sample PNGT#1027

A single sample from Yoro, Madang Province, was formerly considered to be a distinct, undescribed species (*Nasutitermes* sp. H: Everaerts *et al.*, 1988, p. 440, tables 2–3. Monoterpenes of soldier defensive secretion). Its description is given below.

Material Examined

PNGT#1027: Yoro, Madang Province, 14.vi.1986 (Y. R., C. Everaerts). Two alates were obtained in a piece of wood cut from the source log and kept in the laboratory until June 24.

Imago

Only known from two, incompletely pigmented alates, obtained in the laboratory.

Matches the description of *N. bikpelanus* and *N. gracilirostris*, apart from fontanelle, which is hyaline, with parallel sides, about 0.035 mm wide on a length of about 0·090 mm from posterior edge, then widening and turning pale brown in front.

Measurements (in mm) of two females

Head width across eyes	1·45	1·39
Largest diameter of eye	0·486	0·466
Ocellus length	0·203	0·176
Eye to ocellus	0·048	0·058
Pronotum width	1·09	1·03
Pronotum length	0·73	0·68
Hind tibia length	1·59	1·57
Forewing scale length	0·760	0·703
Forewing length	11·4	–

Soldier

Rostrum conical at base, tapering to cylindrical shape towards apex. Long setae present from abdominal tergite 5 to 7 backwards, in a row of 2–4 on tergite edge. Antennae of 13 segments.

Measurements (in mm) of 5 individuals

	Range	Mean
Head capsule total length	1·65–1·70	1·68
Rostrum length	0·74–0·77	0·75
'Back of head' distance	0·43–0·44	0·44
Head width	0·91–1·03	0·99
Rostrum width (at half length)	0·12–0·14	0·13
Head depth	0·66–0·75	0·72
Hind tibia length	1·01–1·07	1·05

The monoterpene fraction of the defensive secretion of these specimens contains the following constituents: sabinene (30%), terpinolene (30%), limonene (13%), myrcene (9%), β-pinene (7%), α-pinene and α-phellandrene (6% each), and traces of other compounds (Everaerts *et al.* 1988).

Worker

Indistinguishable from specimens of other series assigned to *N. gracilirostris*.

Comparisons

Soldier slightly larger than most specimens of *N. gracilirostris*, but otherwise indistinguishable from them. In the alate, the fontanelle might be diagnostic, but as the imago of *N. gracilirostris* is known only from one distant locality, the validity of this criterion is uncertain. Differences in the chemical composition of the defensive secretion of the soldier led

us to consider sample PNGT#1027 to be a distinct species (Everaerts *et al.* 1988). However, cases of high intraspecific variation of the monoterpene content have been described in other nasutes (*Longipeditermes longipes*, Goh *et al.* 1984; *Nasutitermes ephratae*, Valterová *et al.* 1989). We therefore consider that there is presently too little evidence to substantiate the description of sample PNGT#1027 as a new species.

Nasutitermes leponcei, sp. nov.

Material Examined

Type colony (PNGT#1536). Tabubil, Western Province, alt. 500 m, 19.v.1990. Wood carton nest on the ground at edge of secondary forest. With queen (Y. R., M. L.). Holotype: soldier.

Authors' collection (PNGT). #925, 944, 946: Sirinumu Dam, Central Province, 8–10.iii.1985 (J. M. P., Y. R.). #1537, 1546: Tabubil, 19–20.v.1990 (Y. R., M. L.). #1625, 1631, 1647, 1652, 1654: Nomad River, 31.v.–2.vi.1990 (Y. R., M. L.).

Imago (Fig. 71)

Almost identical to that of *N. gracilirostris*. Specimens examined have a large hyaline fontanelle (0·125–0·165 mm long by 0·050–0·065 mm wide). In queen of type colony (PNGT#1536), antennae are mutilated and segment 4 is constricted in middle. In series PNGT#946, antennal segment 3 is about the same size as segment 4.

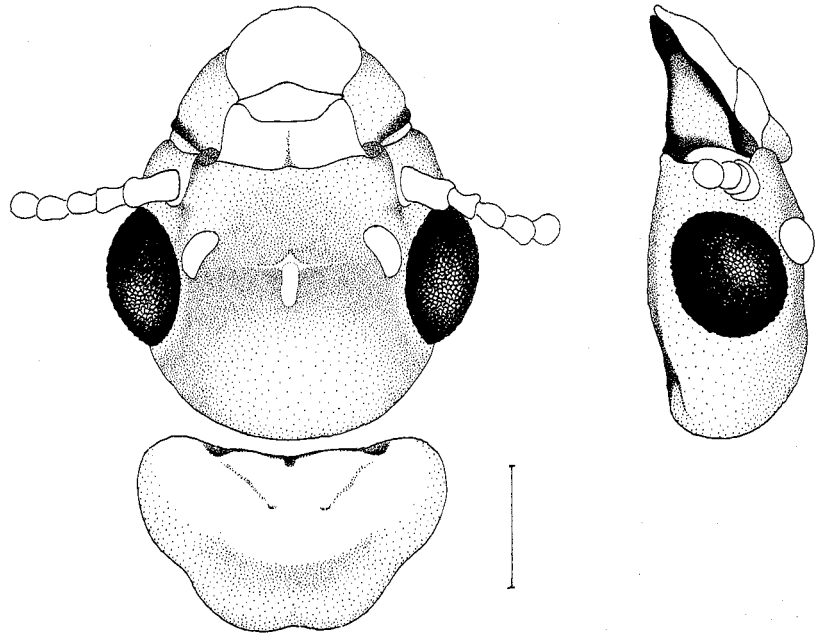


Fig. 71. *Nasutitermes leponcei*, sp. nov., queen from type colony: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

	Measurements (in mm)		
	PNGT#1536 Queen	PNGT#946 (4 alates of each sex)	
		Females	Males
Head width across eyes	1·51	1·53–1·57	1·48–1·51
Largest diameter of eye	0·585	0·557–0·563	0·545–0·574
Ocellus length	0·214	0·209–0·229	0·196–0·207
Eye to ocellus	0·038	0·022–0·035	0·018–0·027
Pronotum width	1·25	1·33–1·42	1·23–1·29
Pronotum length	0·82	0·81–0·84	0·72–0·77
Hind tibia length	1·85	1·78–1·91	1·75–1·85
Forewing scale length	0·872	0·880–0·900	0·815–0·861
Forewing length	–	13·7–14·0	12·6–12·9

Soldier (Fig. 72)

Head capsule orange to ferruginous-orange, rostrum darker. Antennae, thoracic and abdominal tergites orange, legs pale yellow, abdominal sternites orange–yellow.

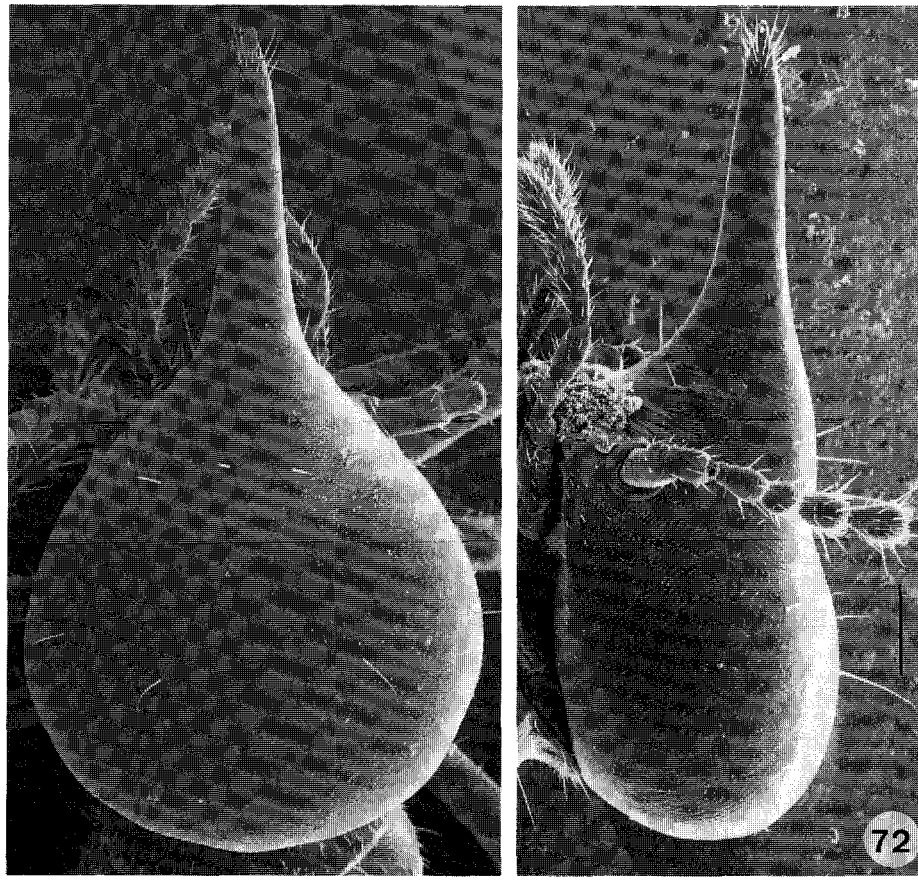


Fig. 72. *Nasutitermes leponcei*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Head capsule slightly pyriform, rostrum narrow, conical, angle widening progressively towards base. In profile, hump at base of rostrum. Four long setae at base of rostrum, two on vertex, two on sides. Abdominal tergites with one row of usually 6 long setae, numerous smaller oblique hairs (about one-fourth the length of the larger setae) on tergite surface. Antennae of 13 segments, segment 3 much longer than segments 2 and 4.

Measurements (in mm) of 39 individuals from 11 colonies

	Range	Mean
Head capsule total length	1·506–1·750	1·636
Rostrum length	0·719–0·840	0·774
'Back of head' distance	0·316–0·420	0·375
Head width	0·839–1·050	0·945
Rostrum width (at half length)	0·116–0·150	0·128
Head depth	0·547–0·690	0·619
Hind tibia length	0·988–1·198	1·111

Worker (Figs 63, 64, 73, 74)

Head capsule yellow–white to yellow–brown. Antennae 14-segmented. Mandibles (Fig. 73) as in *N. princeps*. Configuration of digestive tract similar to that of *N. bikpelanus*. Malpighian tubules attached as two pairs separated by a narrow gap (Figs 63, 64). Enteric valve (Fig. 74): upper ring asymmetrical, long and with many short spines, major areas slightly swollen; lower ring with 3 swellings bearing 8–15 longer spines, minor areas elongated with a few very small spines.

Head width of workers from type colony (PNGT#1536): small workers, first instar, 0·89–0·94 (mean = 0·90, n = 8); large workers, first instar, 1·17–1·24 (mean = 1·20, n = 8); instar 2 and older, 1·15–1·25 (mean = 1·18, n = 16).

Distribution (Fig. 78) *and Biology*

Found in forested areas on the southern side of the central ranges. Wood carton nests were built on the ground in Tabubil.

Affinities

See under *N. muli*, described below.

Etymology

This species is dedicated to Maurice Leponce for his invaluable help during collecting trips.

Nasutitermes muli, sp. nov.

Material Examined

Type colony (PNGT#1643). Nomad R. (6°18′S, 142°14′E, alt. 150 m), 1.vi.1990. Covered runway on trunk of live tree in high rainforest. Alveolar wood carton structure at foot of trunk, but no real nest (Y. R., M. L.). Holotype: soldier.

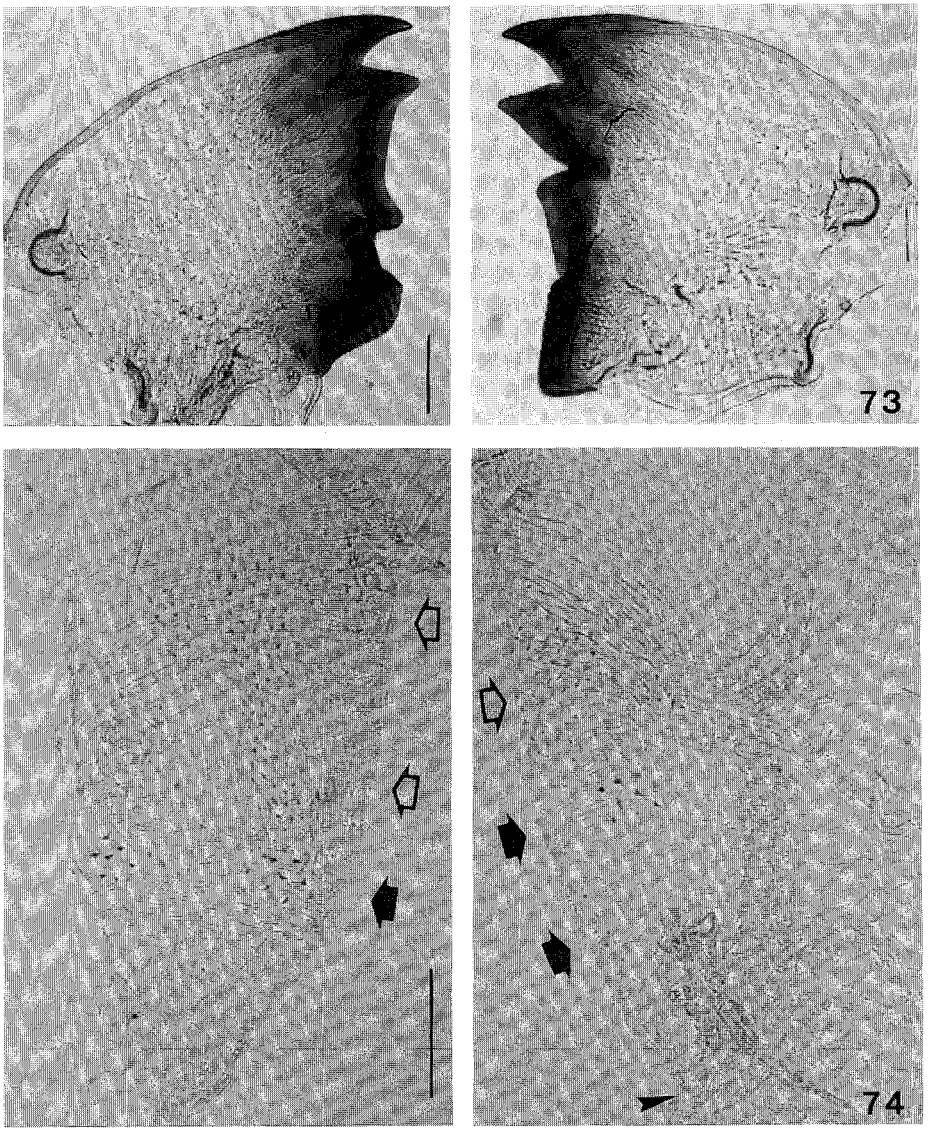
Authors' collection (PNGT). #1644: same data as #1643, possibly same colony (Y. R., M. L.). #1664, 1665: *ibid.*, 3.vi.1990 (Y. R., M. L.).

Imago

Unknown.

Soldier (Fig. 75)

A rather large, dark species with long, thin rostrum. Head capsule ferruginous to chestnut, rostrum darker. Antennae and thoracic sclerites ferruginous, abdominal tergites brown, sternites yellow–brown, legs paler.



Figs 73, 74. *Nasutitermes leponcei*, sp. nov., large worker: *73*, mandibles; *74*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowhead, attachment of paunch. Scale bars = 0·1 mm.

Head capsule slightly pyriform, rounded behind, rostrum narrow, conical, angle widening progressively towards base. In profile, no hump at base of rostrum, which is slightly elevated. Four long setae at base of rostrum, sometimes two additional setae lateral to this anterior row, two on vertex. Abdominal tergites with one row of, usually, 6 long setae, numerous smaller oblique hairs (about one-third the length of the larger setae) on tergite surface. Antennae of 13 segments, segment 3 much longer than segments 2 and 4.

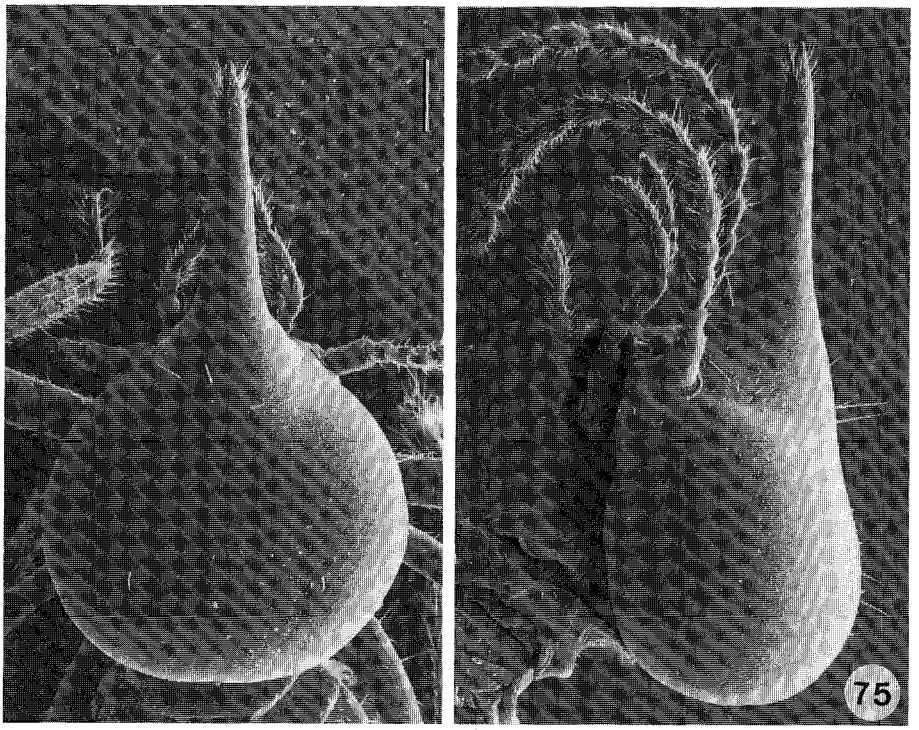


Fig. 75. *Nasutitermes muli*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Measurements (mm) of 12 individuals from 4 nest series

	Range	Mean
Head capsule total length	1·689–1·780	1·741
Rostrum length	0·796–0·855	0·821
'Back of head' distance	0·403–0·420	0·411
Head width	0·952–1·026	0·988
Rostrum width (at half length)	0·120–0·138	0·130
Head depth	0·651–0·695	0·672
Hind tibia length	1·084–1·130	1·112

The chemical composition of the defensive secretion is unknown; a strong odour of lemon emanates from the soldiers when seized.

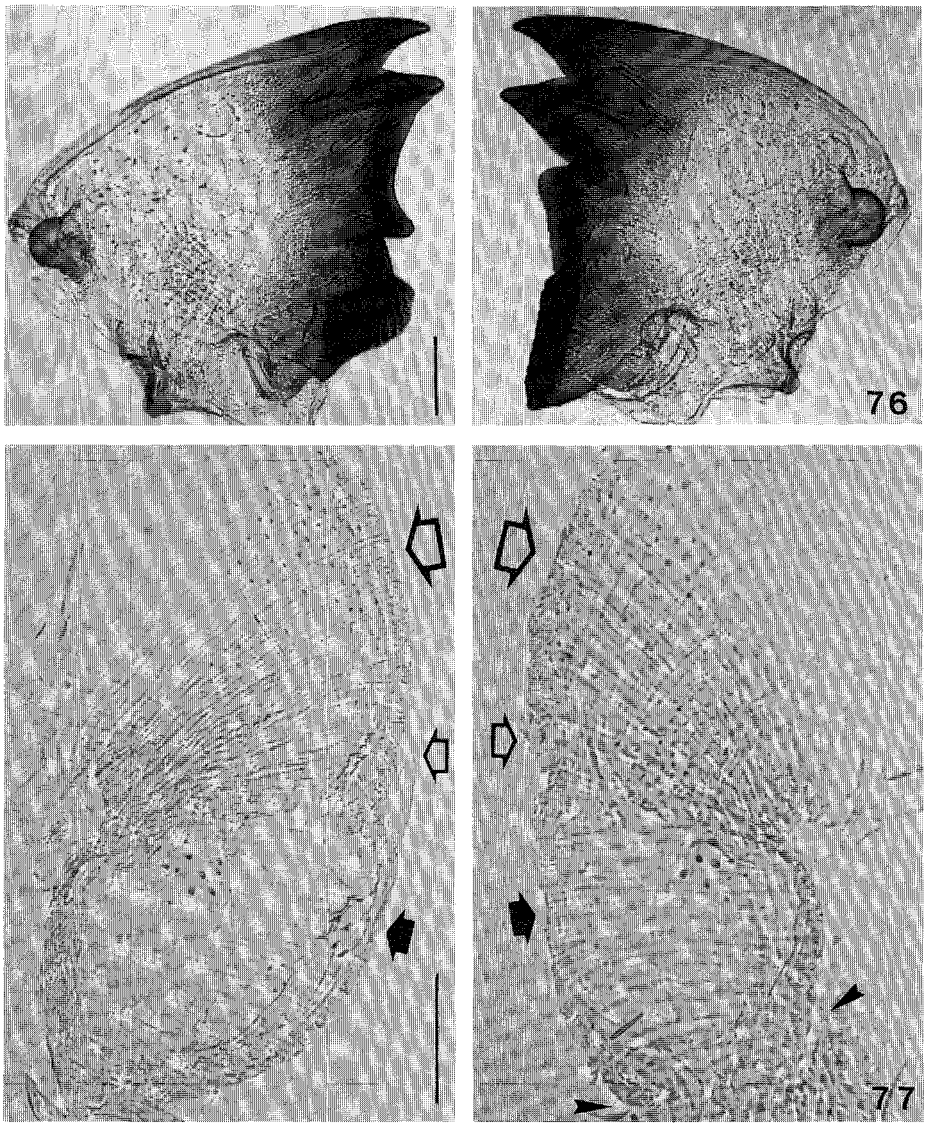
Worker (Figs 65, 66, 76, 77)

Head capsule yellow–white to chestnut. Increase in pigmentation between successive large-worker instars. Antennae 14-segmented. Mandibles (Fig. 76) as in *N. princeps*. Configuration of the digestive tract and armature of enteric valve (Fig. 77) very similar to those of *N. leponcei*, but pairs of malpighian tubules constantly separated by a wide space at their point of insertion (Figs 65, 66).

Head width of workers from nest PNGT#1644: small workers, first instar, 0·89–0·94 (mean = 0·90, n = 8); large workers, first instar, 1·15–1·20 (mean = 1·17, n = 8); instar 2 and older, 1·13–1·24 (mean = 1·19, n = 16).

Distribution (Fig. 78) *and Biology*

Only known from type locality. Samples were found in almost undisturbed rainforest, where this species builds wood carton structures.



Figs 76, 77. *Nasutitermes muli*, sp. nov., large worker: *76*, mandibles; *77*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

Affinities

Nasutitermes gracilirostris, N. leponcei and *N. muli* have medium-sized, orange-coloured, thin-nosed soldiers. *N. gracilirostris* is recorded only from northern New Guinea and its worker differs from those of *N. leponcei* and *N. muli* by its enteric valve armature. *N. leponcei* and *N. muli* are present in southern New Guinea. The soldier head capsule of *N. leponcei* possesses lateral setae. That of *N. muli* is more darkly coloured than in the other two species. It is less humped in profile than that of *N. leponcei*, and lacks lateral setae. Workers of these two species differ by the insertion of malpighian tubules.

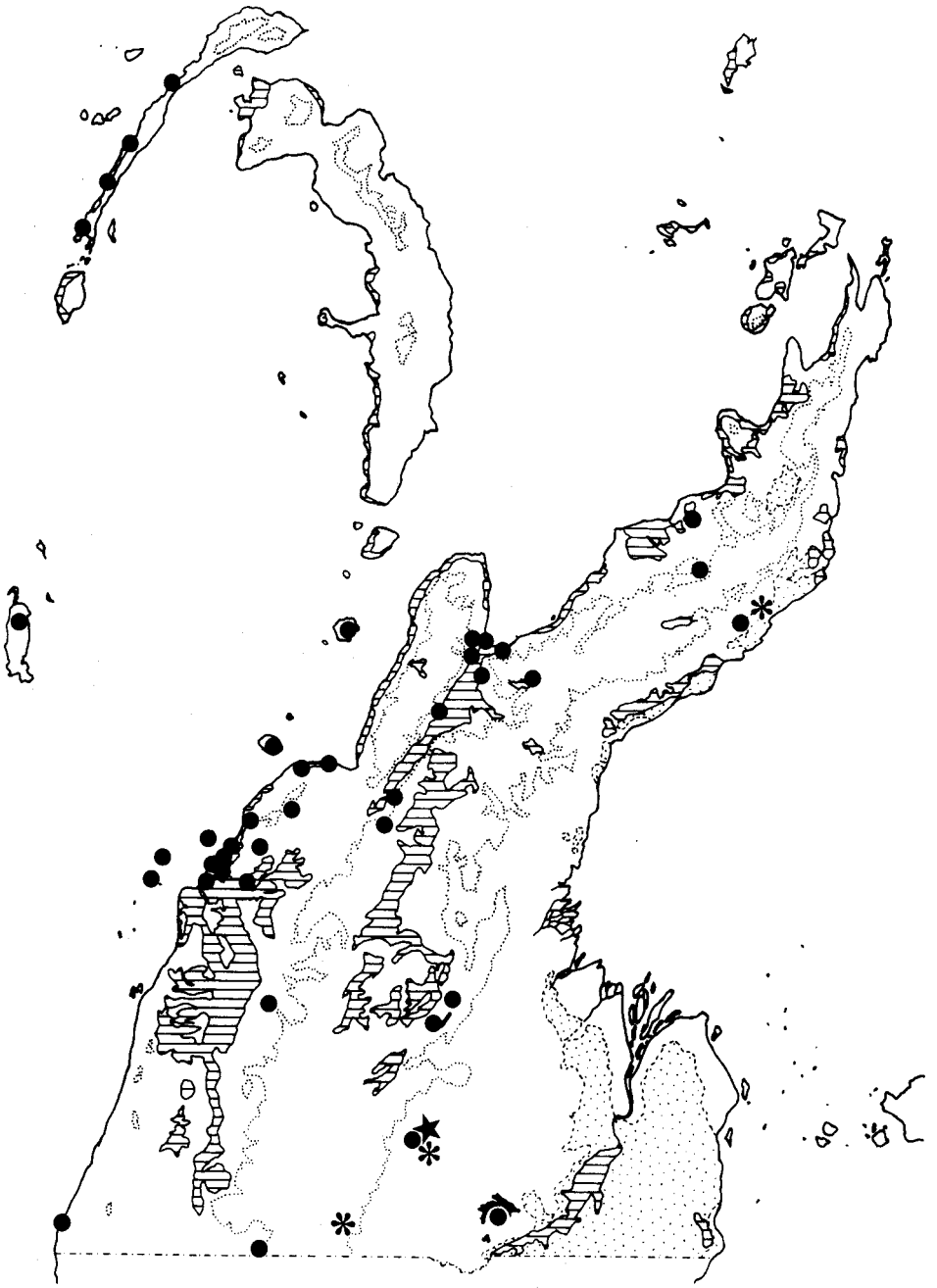


Fig. 78. Known distributions of *Nasutitermes bikpelanus* (●), *N. leponcei* (*) and *N. muli* (★).

Etymology

Neo-Melanesian *muli*, meaning generic name for all *Citrus* fruits and referring to the soldiers' strong lemon smell.

Nasutitermes seghersi, sp. nov.

The following description is based on New Guinean specimens, which constitute the nominotypical subspecies, *N. seghersi seghersi*. Specimens from New Ireland consistently display slightly different features, which justify their assignment to a distinct subspecies, described below.

Material Examined

Type colony (PNGT#366). Yoro, Madang Province, 20.v.1983. Soldiers and workers from dead wood on forest floor (Y. R.). Holotype: soldier.

Authors' collection (PNGT). #123: Madang–Lae Road, *c.* 30 km from Madang, 4.vii.1981 (J. M. P.). #206: Usino, 22.ii.1983 (J. M. P., Y. R.). #296: Makarup Road, 1·5 km from Potsdam plantation, Hansa Bay, 30.iii.1983 (Y. R.). #301, 302, 307, 339, 342: 1 km from Yagaum Hospital, Madang, 7.iv.–13.v.1983 (Y. R.). #1195–1197, 1202: Braham Mission, 5–6.v.1988 (Y. R.). #1526: Nubia–Bunapas Road, 25.iv.1989 (M. L.). #1746, 1747: Yapsiei, Sandaun Province, 12.iii.1994 (Y. R., M. L.).

IRSN. #I.G.25848 (PNG'78-No.37): 4 km NW Bogia, 9.v.1978 (J. Van Goethem).

Imago

Unknown.

Soldier (Fig. 79)

Head capsule orange–yellow to ferruginous-orange, with deeper reddish tinge on rostrum. Antennae pale orange, tergites pale yellow–brown, sternites lighter.

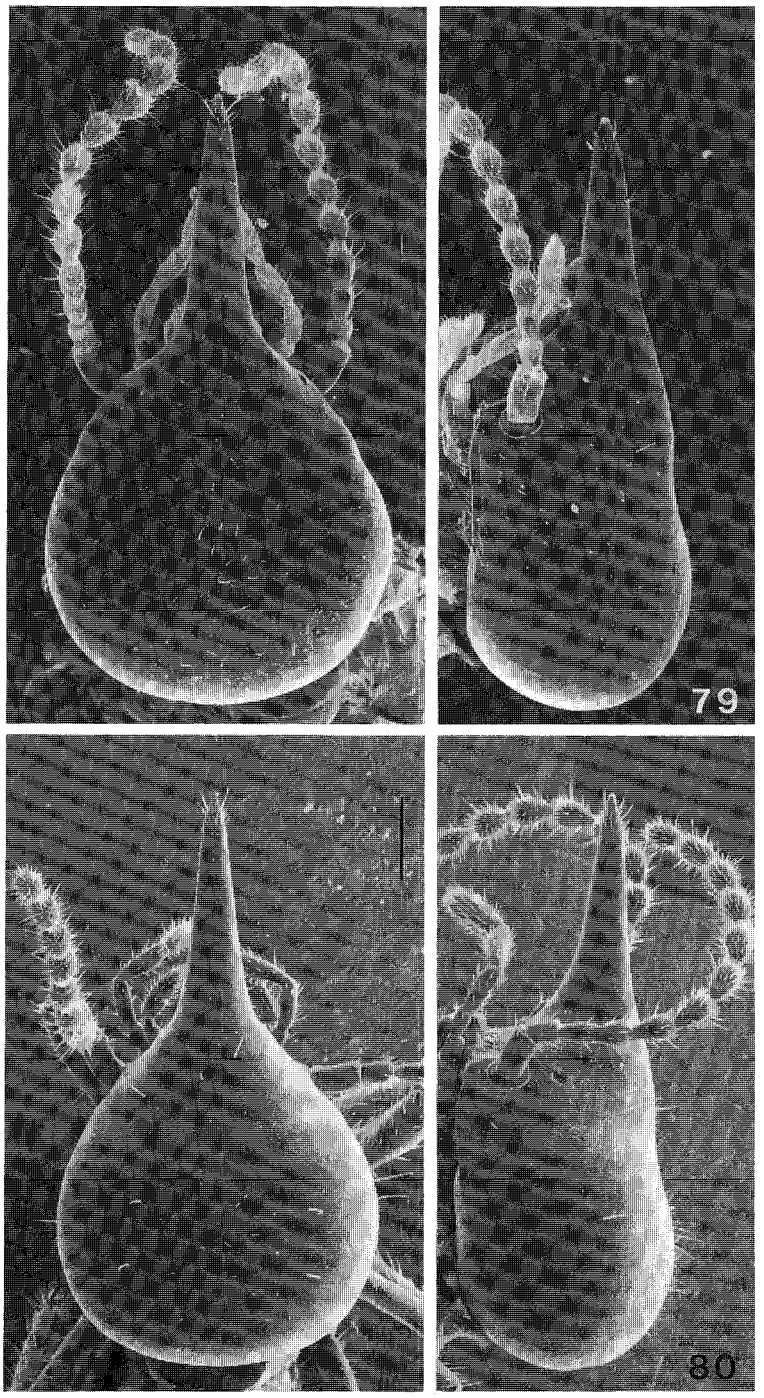
Head capsule slightly flattened on sides, rounded behind, in profile slightly humped at base of rostrum. Rostrum conical, thicker than in *N. gracilirostris* but much narrower than in *N. bikpelanus*. Antennae of 12 segments, with segments 2 and 4 of approximately equal length, segment 3 tending to be slightly longer and thinner, sometimes partially subdivided. Usually four long setae on head capsule at base of rostrum, four on vertex, two on sides; many smaller, oblique hairs of increasing length from rostrum to vertex, reaching about half the length of the major setae. Abdominal tergites with one row of 6 long setae and many small oblique hairs about one-quarter to one-third the length of the long setae.

Measurements (in mm) of 40 individuals from 14 colonies

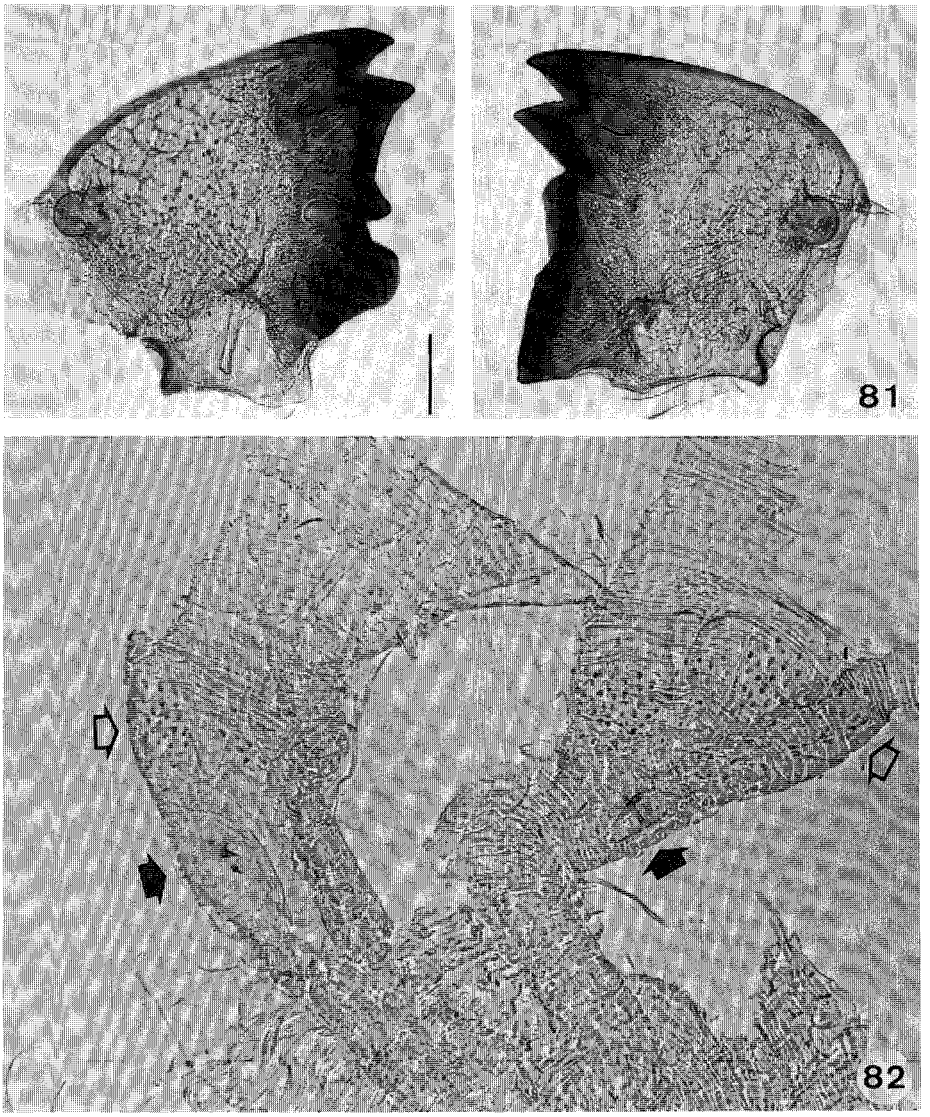
	Range	Mean
Head capsule total length	1·311–1·525	1·419
Rostrum length	0·566–0·672	0·624
'Back of head' distance	0·325–0·404	0·354
Head width	0·757–0·938	0·828
Rostrum width (at half length)	0·108–0·129	0·119
Head depth	0·500–0·614	0·555
Hind tibia length	0·809–0·936	0·861

Worker (Figs 57, 81–83)

Head capsule whitish to yellow-brown. Slight increase in pigmentation between successive large-worker instars, no increase in size. Antennae of 14 segments, with segments 3–5 often incompletely separated in the youngest instars. Mandibles (Fig. 81) similar to those of *N. princeps*. Configuration of the digestive tube (Fig. 83) very similar to that of *N. bikpelanus*. Malpighian tubules inserted as two well-separated pairs (Fig. 57). Upper spiny areas of enteric valve asymmetrical, wide, with numerous small spines; lower ring of three slightly thickened areas usually bearing strong spines (Fig. 82).



Figs 79, 80. *Nasutitermes seghersi*, sp. nov.; soldier head from above (left) and in profile (right). *79, N. s. seghersi*; *80, N. s. malangganus*, subsp. nov. Scale bar = 0·2 mm.



Figs 81, 82. *Nasutitermes seghersi* sp. nov., subsp. *seghersi*, large worker: *81*, mandibles; *82*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

Head width of workers from type colony (PNGT#366): small workers, first instar, 0·799–0·826 (mean = 0·815, n = 8); large workers, first instar, 1·014–1·088 (mean = 1·053, n = 13); instar 2 and older, 0·988–1·080 (mean = 1·035, n = 11).

Nasutitermes seghersi malangganus, subsp. nov.

Material Examined

Type colony (PNGT#598). Kolonoboi, New Ireland, 25.v.1984. Dead wood on ground on path in secondary growth, leading to food gardens (J. M. P., Y. R.). Holotype: soldier.

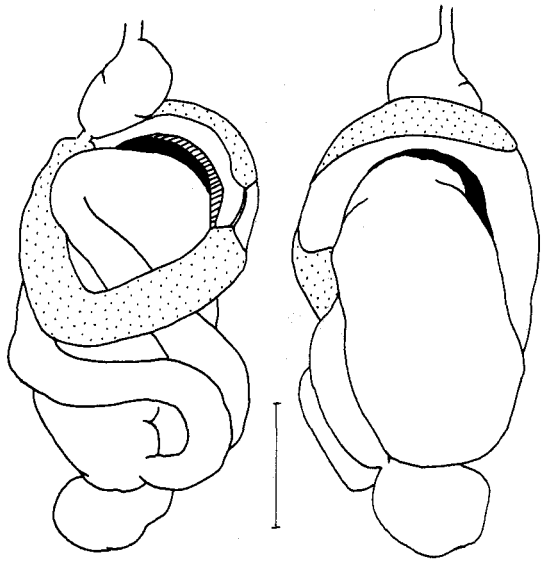


Fig. 83. *Nasutitermes s. seghersi*, subsp. nov., large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

Authors' collection (PNGT). #606–608: Lelet Plateau, alt. 900 m, 27.v.1984 (J. M. P., Y. R.). #619: Konos, 29.v.1984 (J. M. P., Y. R.). #631, 640: Lemakot, 30–31.v.1984 (J. M. P., Y. R.). #642: 14 km from Kavieng, 2.vi.1984 (J. M. P., Y. R.).

Imago

Unknown.

Soldier (Fig. 80)

Distinguished from the nominotypical subspecies by relatively narrower head, longer rostrum and longer legs. Pilosity of head capsule as in *N. s. seghersi*, but small hairs on vertex shorter, about one-third the length of major setae. Antennae 12-segmented, segments 3 and 4 longer than segment 2.

Measurements (mm) of 40 individuals from 14 colonies

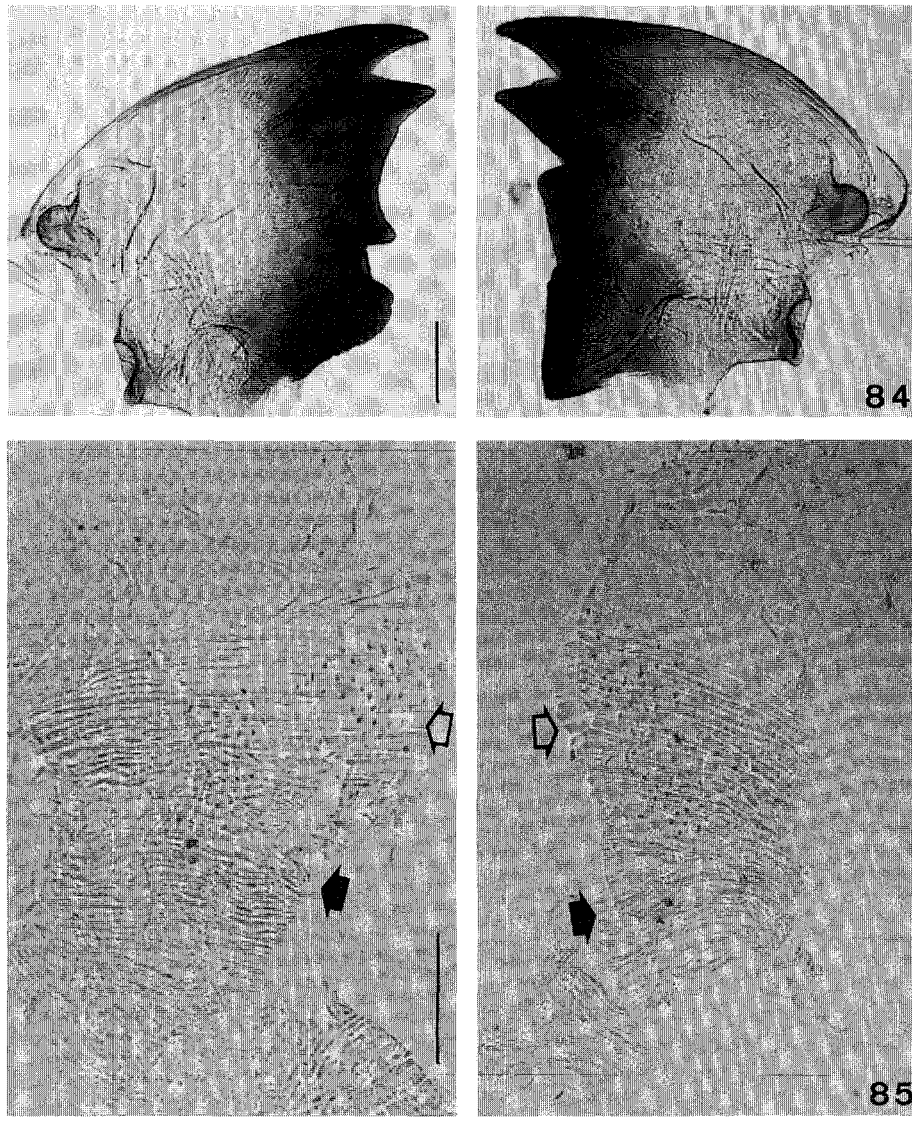
	Range	Mean
Head capsule total length	1·309–1·600	1·463
Rostrum length	0·585–0·727	0·662
'Back of head' distance	0·332–0·392	0·358
Head width	0·701–0·842	0·786
Rostrum width (at half length)	0·100–0·126	0·115
Head depth	0·478–0·593	0·545
Hind tibia length	0·782–1·010	0·904

Worker (Figs 84, 85)

Indistinguishable from that of *N. s. seghersi.*

Distribution (Fig. 101) *and Biology*

Nasutitermes seghersi seghersi is known from the upper Sepik and middle and lower Ramu valley in northern New Guinea, *N. s. malangganus* from several localities in New Ireland, from sea level to an altitude of 900 m on Lelet Plateau. Foraging groups of either subspecies were always encoutered in dead wood; nest unknown.



Figs 84, 85. *Nasutitermes seghersi malangganus*, subsp. nov., large worker: *84*, mandibles; *85*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

Etymology

This species is dedicated to Guy Seghers, for his assistance throughout our research programme in Papua New Guinea. The subspecific name *malangganus* derives from the *Malanggan* ritual of New Ireland.

Affinities

Nasutitermes seghersi (either subspecies) is most easily confused with *N. gracilirostris*, which occurs sympatrically with *N. s. seghersi* in New Guinea. Soldiers of *N. seghersi* can be distinguished by their more pilose head capsule. They also possess a more conical rostrum and shorter legs. Soldiers of *N. bikpelanus* possess a longer, thicker rostrum, and 13-segmented antennae. *Nasutitermes leponcei* and *N. muli*, apparently confined to southern New Guinea, also have soldiers with antennae of 13 segments.

Related Allopatric Species

Nasutitermes retus (Kemner)

Eutermes retus Kemner, 1931: 43–45, fig. 15. Soldier, worker, biology (after Weyer).
Nasutitermes retus. — Snyder, 1949: 295.

The examination of syntypes (MZEL) revealed that this species, described from Ambon, is similar to *N. seghersi* with its 12-segmented antennae (soldier) and mixed segment of the gut (worker). The state of preservation of these syntypes was such that the shape and pilosity of the head capsule of soldiers could not be examined in detail. There is, however, no doubt that *N. retus* belongs to the same group of species as *N. seghersi*.

Genus ***Niuginitermes***, gen. nov.

Type species: *Niuginitermes variratae*, sp. nov., by present designation.

Imago

Small to medium-sized species, with 14-segmented antennae. So far, the number of antennal segments (14) seems to constitute the only consistent criterion that distinguishes imagos of *Niuginitermes* from those of New Guinean *Nasutitermes*.

Soldier

Small to medium-sized nasutes, closely allied to *Nasutitermes*. Soldier caste monomorphic. Head capsule without constriction behind antennae. Antennae 12-segmented. Mandibles with points. The two included species are orange coloured.

Worker

Dimorphic: large workers show variable pigmentation by instar. Antennae of 13 segments. Mandibles (Figs 88, 99) very similar to those of *Nasutitermes*. Left mandible index: 0·38–0·53. Gut configuration diagnostic (Fig. 90). Mixed segment long, mesenteric extension on external side of gut curve, attached to remainder of mesenteron by wide dorsal peduncle. Malpighian tubules inserted as two well-separated pairs (Fig. 67). Colon long, starting backwards from top of paunch, then following a three-dimensional S formed by two 180° curves, forward then downwards, followed by an almost straight segment towards the rectum. Enteric valve oblique, almost symmetrical, upper and lower rings of spiny areas widely separated (Figs 89, 100). Upper ring of 6 areas bearing numerous small spines. Lower ring of 3 swellings bearing spines whose size decreases towards paunch. The armature does not penetrate into the paunch.

Comparisons

This genus comes close to *Nasutitermes*, but the worker possesses a longer colon and different enteric valve structure. In all New Guinean species of *Nasutitermes*, workers have antennae of at least 14 segments.

Because the Indo-Malayan genus *Leucopitermes* Emerson superficially resembles *Niuginitermes*, we examined material of *L. leucops* (Holmgren) (syntypes of *Subulitermes javanellus* Kemner, 1934, synonymized with *L. leucops* by Emerson 1960). The general configuration of the worker digestive tract is very similar (Fig. 93) in the two genera. However, *Leucopitermes* workers possess a larger left mandible index (0·56–0·64; Fig. 91) and a distinct enteric valve (Fig. 92): upper ring made of diffuse areas with many tiny spines; lower ring with 3 major swellings bearing 5–10 long, sharp spines in their upper part and tiny ones in their lower part, and 3 elongated minor areas with about 10 small spines.

Although originally thought to be related to *Subulitermes* (Ahmad 1968), the monotypic genus *Eleanoritermes* Ahmad (Figs 94–96), from Borneo, also resembles *Niuginitermes*, but differs from it by the enteric valve positioned more anteriorly, weakly armed with few small spines on 3 swellings (Fig. 95), and malpighian tubules inserted contiguously. In addition, the soldier of *E. borneensis* Ahmad has 11-segmented antennae and mandibles without points, the worker 12-segmented antennae.

Etymology

From *Niugini*, Neo-Melanesian spelling for New Guinea.

Niuginitermes variratae, sp. nov.

Material Examined

Type colony (PNGT#1347). Varirata National Park, Central Province, alt. 800 m, 6.xii.1988. Nesting in dead wood on ground in woodlands. With alates, larvae and eggs (Y. R., P. P. D.). Holotype: soldier.

Authors' collection (PNGT). #854, 920, 924, 938: Sogeri and Sirinumu Dam area, 4.ii.–9.iii.1985 (J. M. P., Y. R.). #1300, 1313, 1317: Pimaga, Southern Highlands, alt. 900 m, 15–19.x.1988 (Y. R.). #1353: Varirata Natl Pk, 6.xii.1988 (Y. R., P. P. D.). #1540: Tabubil, Western Province, alt. 500 m, 20.v.1990 (Y. R., M. L.). #1593: Lake Murray, 25.v.1990 (Y. R., M. L.). #1649, 1653, 1662: Nomad R., 2–3.vi.1990 (Y. R., M. L.).

Imago (Fig. 86)

Head capsule very dark chestnut brown, postclypeus orange, antennae ferruginous, pronotum ferruginous with paler transversal anterior mark, thoracic and abdominal tergites brown, legs yellow-brown, abdominal sternites brown on sides, yellow in middle. Wings sepia brown, smoky, slightly paler along costal veins.

Head capsule rounded behind, eyes and ocelli medium-sized, ocellus close to eye. Fontanelle very small, punctual. Antennae of 14 segments, segments 3 and 4 smaller than segments 2 and 5.

	Measurements (mm)		
	Sogeri–Pimaga (3 colonies) (4 alates of each sex, 1 queen)		PNGT#1593 (Lake Murray)
	Females	Males	Queen
Head width across eyes	1·069–1·116	1·056–1·097	0·981
Largest diameter of eye	0·294–0·327	0·316–0·334	0·303
Ocellus length	0·124–0·154	0·130–0·135	0·121
Eye to ocellus	0·058–0·083	0·058–0·073	0·059
Pronotum width	0·818–0·922	0·810–0·852	0·768
Pronotum length	0·574–0·636	0·568–0·582	0·533
Hind tibia length	1·371–1·422	1·355–1·429	1·086
Forewing scale length	0·609–0·653	0·594–0·648	0·533
Forewing length	9·56–10·68	9·33–9·41	–

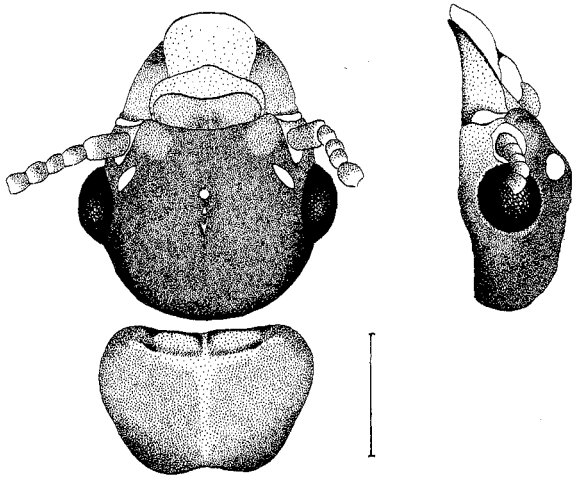


Fig. 86. *Niuginitermes variratae*, sp. nov., male alate from type colony: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Soldier (Fig. 87)

Head capsule yellow to ferruginous-orange, with deeper reddish tinge on rostrum. Antennae orange, abdominal wall translucent with slight yellow shade.

Head capsule rounded on sides, slightly flattened posteriorly, in profile nearly straight. Rostrum narrow, conical. Antennae of 12 segments, with segment 3 thinner than segment 4, segments 3 and 4 longer than segment 2. Four long setae on head capsule at base of rostrum, usually 4 forming a rectangle on vertex and 2 lateral ones. Abdominal tergites with a posterior row usually of 6 long setae, many smaller oblique hairs about one-third the length of the longer setae.

Measurements (mm) of 21 individuals from 7 colonies

	Range	Mean
Head capsule total length	1·313–1·550	1·398
Rostrum length	0·566–0·724	0·632
'Back of head' distance	0·306–0·404	0·356
Head width	0·733–0·847	0·769
Rostrum width (at half length)	0·088–0·121	0·102
Head depth	0·491–0·569	0·526
Hind tibia length	0·799–0·955	0·865

Worker (Figs 67, 88–90)

Head capsule yellow–white to orange–yellow. Antennae 13-segmented. Little increase in pigmentation between successive instars, no size increase. Digestive tube (Figs 67, 90) as in generic diagnosis, mandibles and enteric valve as in Figs 88 and 89.

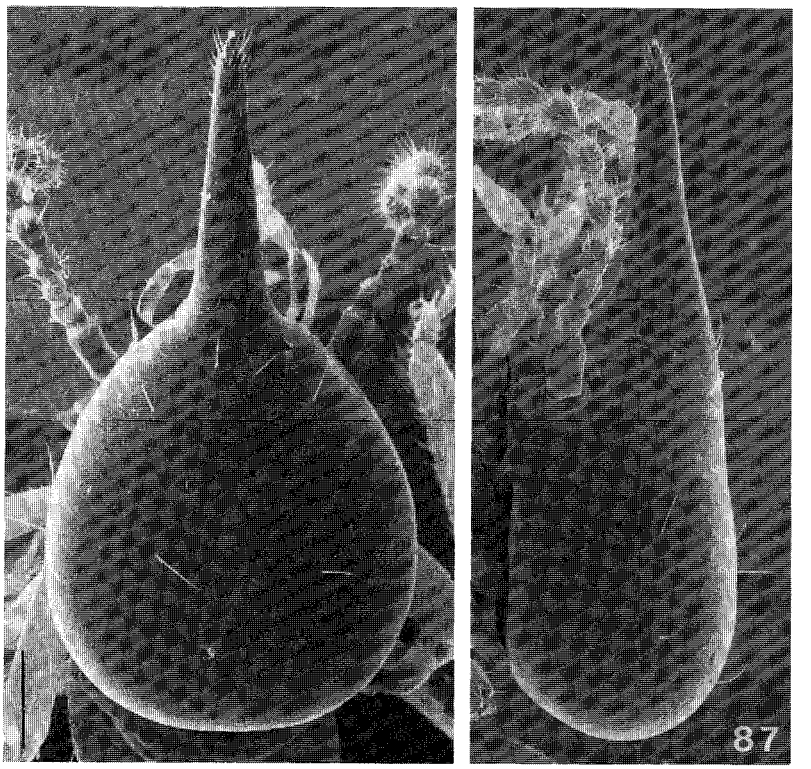
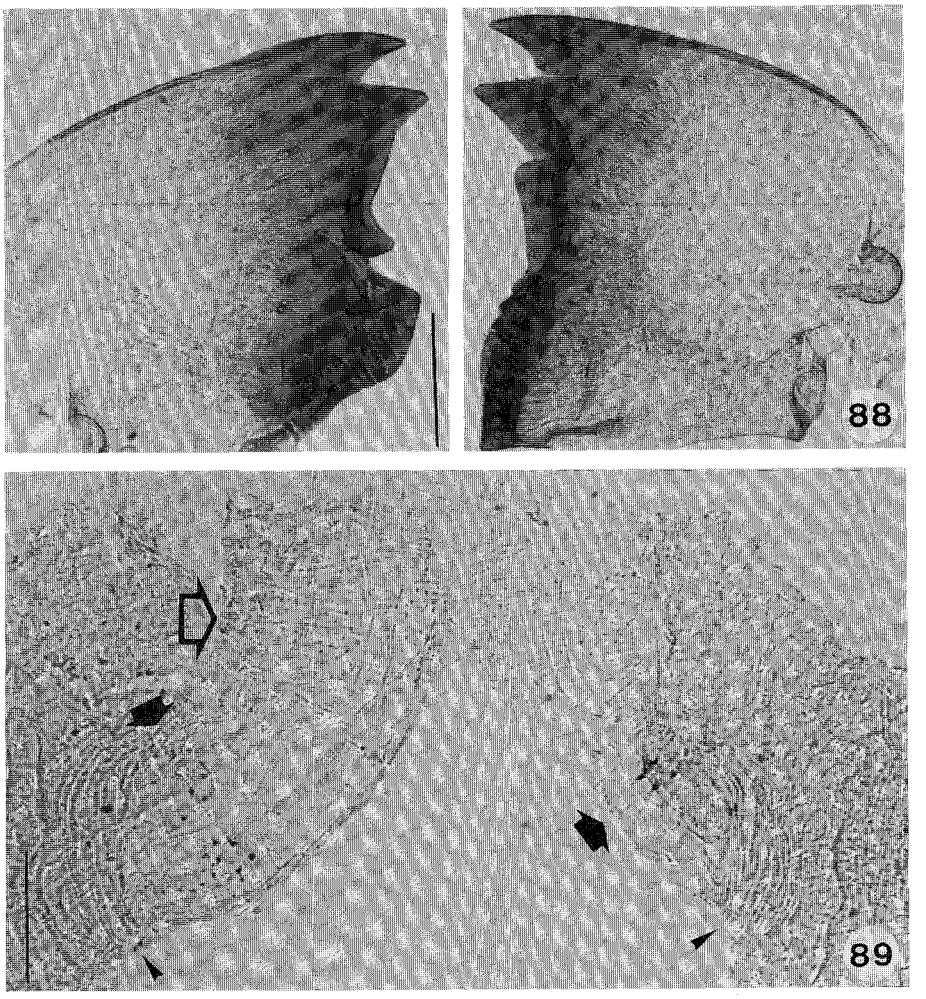


Fig. 87. *Niuginitermes variratae*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.



Figs 88, 89. *Niuginitermes variratae*, sp. nov., large worker: *88*, mandibles; *89*, armature of enteric valve. Open arrow, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

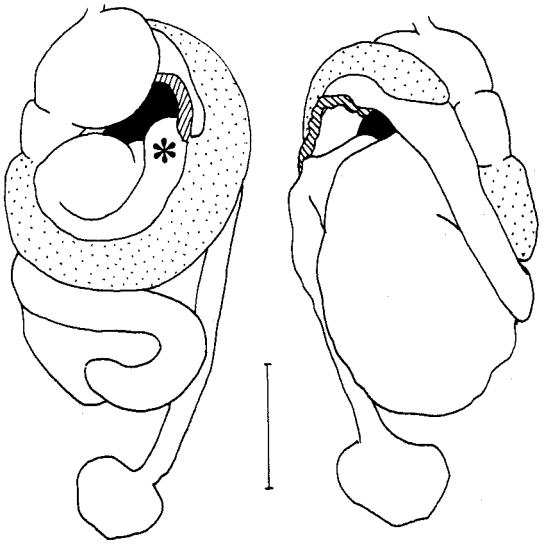
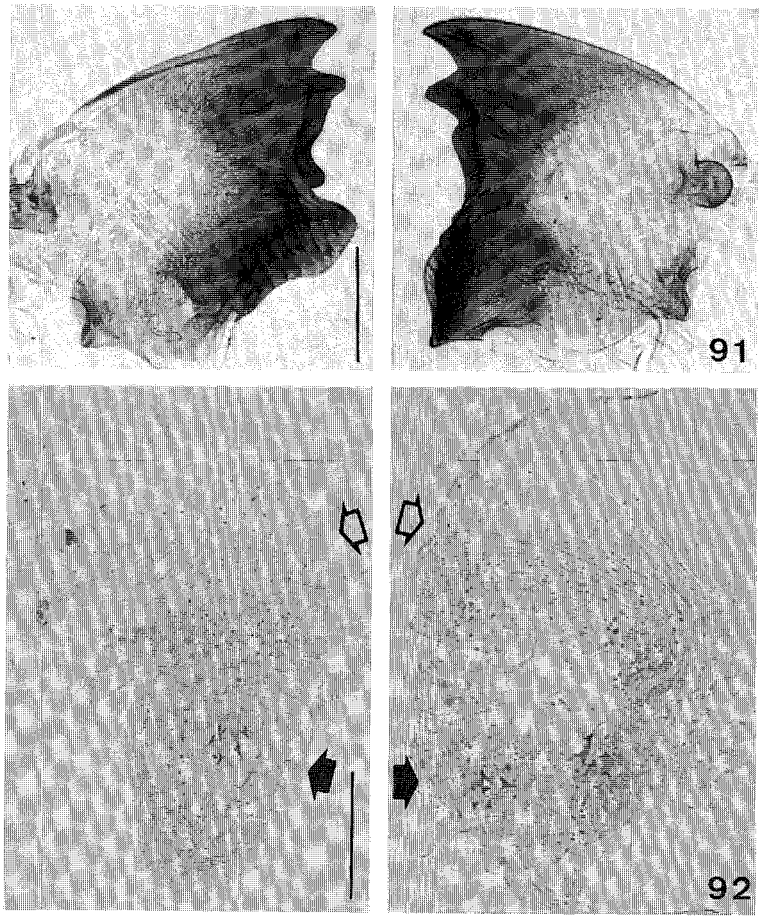


Fig. 90. *Niuginitermes variratae*, sp. nov., large worker: dorsal and ventral view of gut *in situ*, showing forward-directed loop formed by colon (*). Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.



Figs 91, 92. *Leucopitermes leucops* (Holmgren), worker: *91*, mandibles; *92*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

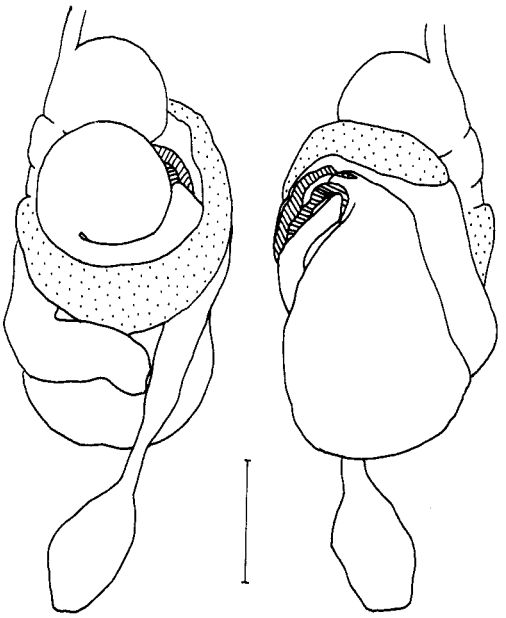
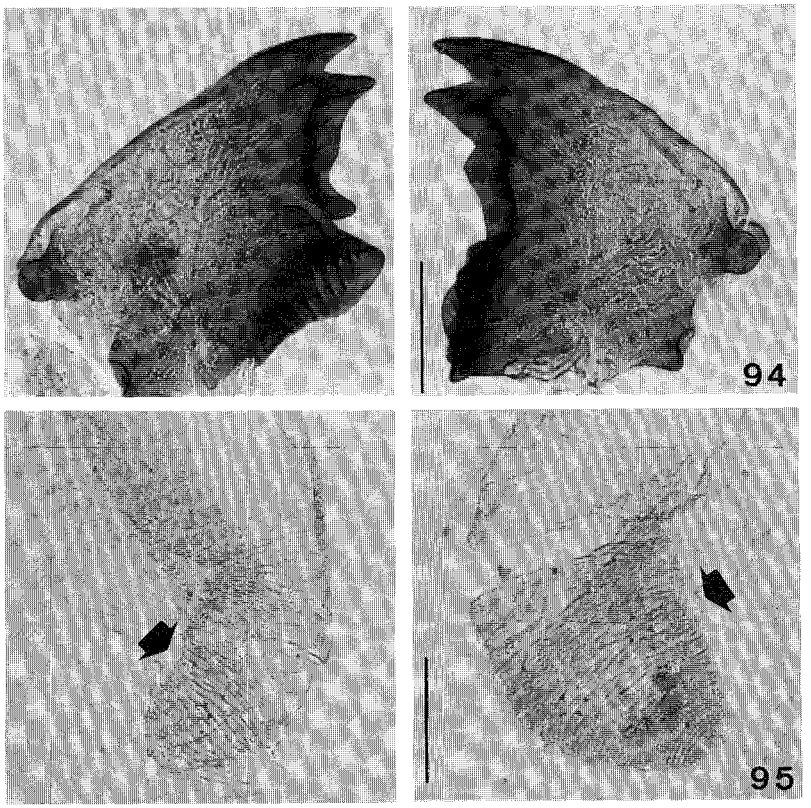


Fig. 93. *Leucopitermes leucops* (Holmgren), worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.



Figs 94, 95. *Eleanoritermes borneensis* (Ahmad), worker: *94*, mandibles; *95*, armature of enteric valve. Arrows, ring of spiny areas. Scale bars = 0·1 mm.

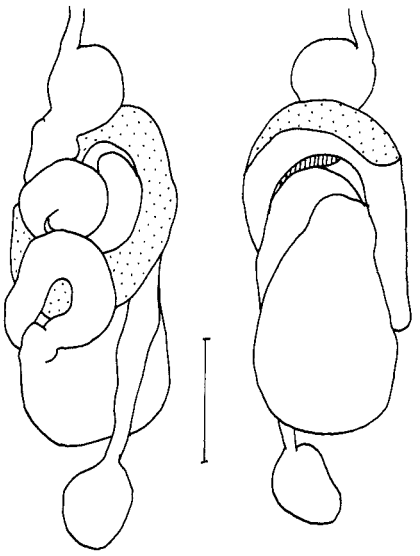


Fig. 96. *Eleanoritermes borneensis* Ahmad, worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

Head width of workers from type colony (PNGT#1347): small workers, first instar, 0·80–0·82 (mean = 0·81, n = 8); large workers, first instar, 0·90–0·93 (mean = 0·91, n = 8); instar 2 and older, 0·88–0·93 (mean = 0·90, n = 16).

Distribution (Fig. 101) *and Biology*

Only known from southern New Guinea. Nests were found in rather hard dead wood in forest.

Affinities

The antennal structure (13-segmented) and digestive tract of the worker are the best criteria to distinguish *N. variratae* from *Nasutitermes* species with very similar soldiers, such as *N. gracilirostris*, *N. seghersi* and *N. leponcei*. See also under *Niuginitermes liklik*, described below.

Etymology

Named after Varirata National Park, where the type series was collected.

Niuginitermes liklik, sp. nov.

Material Examined

Type colony (PNGT#1445). Morehead, Western Province (8°43′S, 141°39′E), 25.iii.1989. Standing dead wood in woodlands. Alates, soldiers, workers (Y. R., M. L.). Holotype: soldier.

Authors' collection (PNGT). #1483, 1498, 1508: Wipim, Western Province, 30.iii.–1.iv.1989 (Y. R., M. L.). #1550, 1551: Lake Murray, 22.v.1990 (Y. R., M. L.).

ANIC#10 10370: Rouku, Apr. 1962 (W. Brandt).

Imago (Fig. 97)

Head capsule brown, postclypeus pale yellow–brown, antennae, pronotum, abdominal tergites and legs pale brown, meso- and metanotum pale yellow–brown. Abdominal sternites pale brown on sides, yellow-white in middle. Wings brown, smoky, paler along costal veins.

Head capsule rounded behind, eyes and ocelli medium-sized, ocellus close to eye. Fontanelle small but clearly distinct, *c.* 0·045 mm long by 0·015 mm wide, hyaline, with parallel sides. Antennae of 14 segments, segment 3 smaller than segment 4, segment 4 smaller than segment 5, segments 2 and 5 approximately equal. Pronotum long and relatively narrow.

Measurements (mm) of 6 male alates, from the type colony

	Range	Mean
Head width across eyes	0·818–0·832	0·823
Largest diameter of eye	0·259–0·277	0·268
Ocellus length	0·110–0·116	0·113
Eye to ocellus	0·036–0·048	0·041
Pronotum width	0·588–0·620	0·606
Pronotum length	0·415–0·431	0·419
Hind tibia length	0·949–1·006	0·983
Forewing scale length	0·455–0·488	0·471
Forewing length	6·34–6·70	6·56

Soldier (Fig. 98)

Head capsule yellow to orange–yellow, with deeper reddish tinge on rostrum. Antennae yellow, abdominal wall translucent.

Head capsule slightly flattened on sides and posteriorly, straight in profile. Rostrum narrow, conical. Antennae of 12 segments, segment 3 the thinnest, segments 2–4 of about equal length. Four long setae at base of rostrum, 4 forming a rectangle on vertex, 2 laterally situated, and many shorter hairs, some of which reach more than half the length of the major setae, especially on vertex. Abdominal tergites with an apical row of usually 6 long setae, tergite surface with many oblique hairs, some of them more than half the length of the major setae.

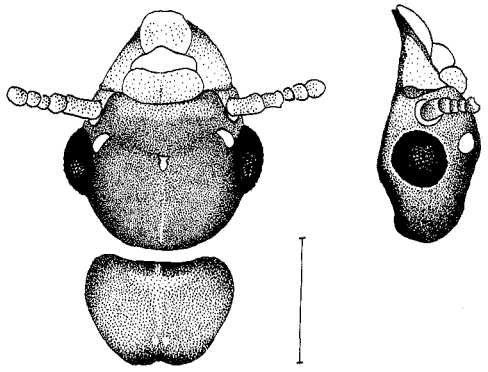


Fig. 97. *Niuginitermes liklik*, sp. nov., male alate from type colony: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

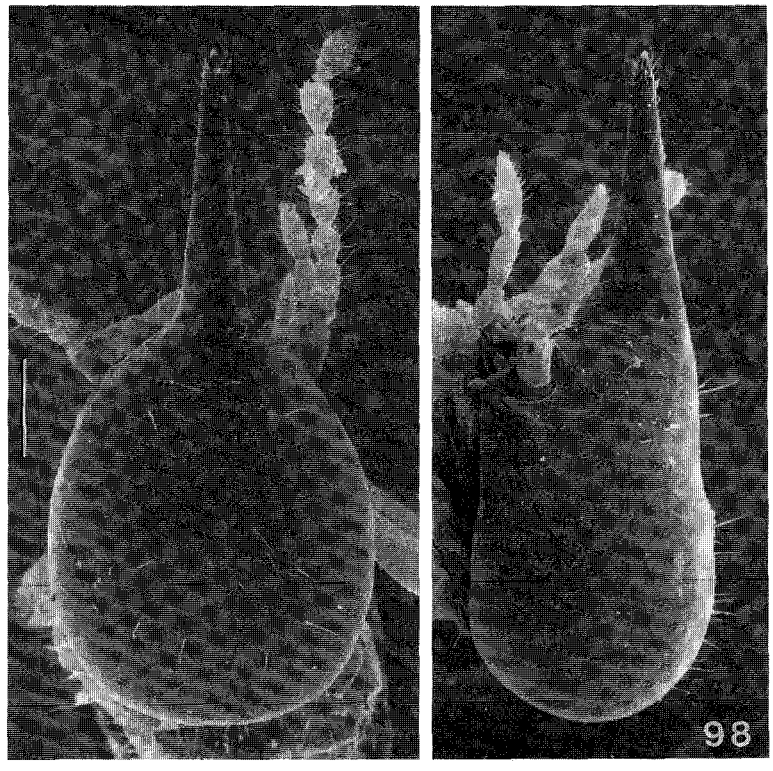


Fig. 98. *Niuginitermes liklik*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Measurements (mm) of 18 individuals from 6 colonies

	Range	Mean
Head capsule total length	1·151–1·289	1·226
Rostrum length	0·480–0·579	0·527
'Back of head' distance	0·284–0·352	0·315
Head width	0·621–0·701	0·669
Rostrum width (at half length)	0·080–0·096	0·088
Head depth	0·428–0·514	0·480
Hind tibia length	0·694–0·766	0·734

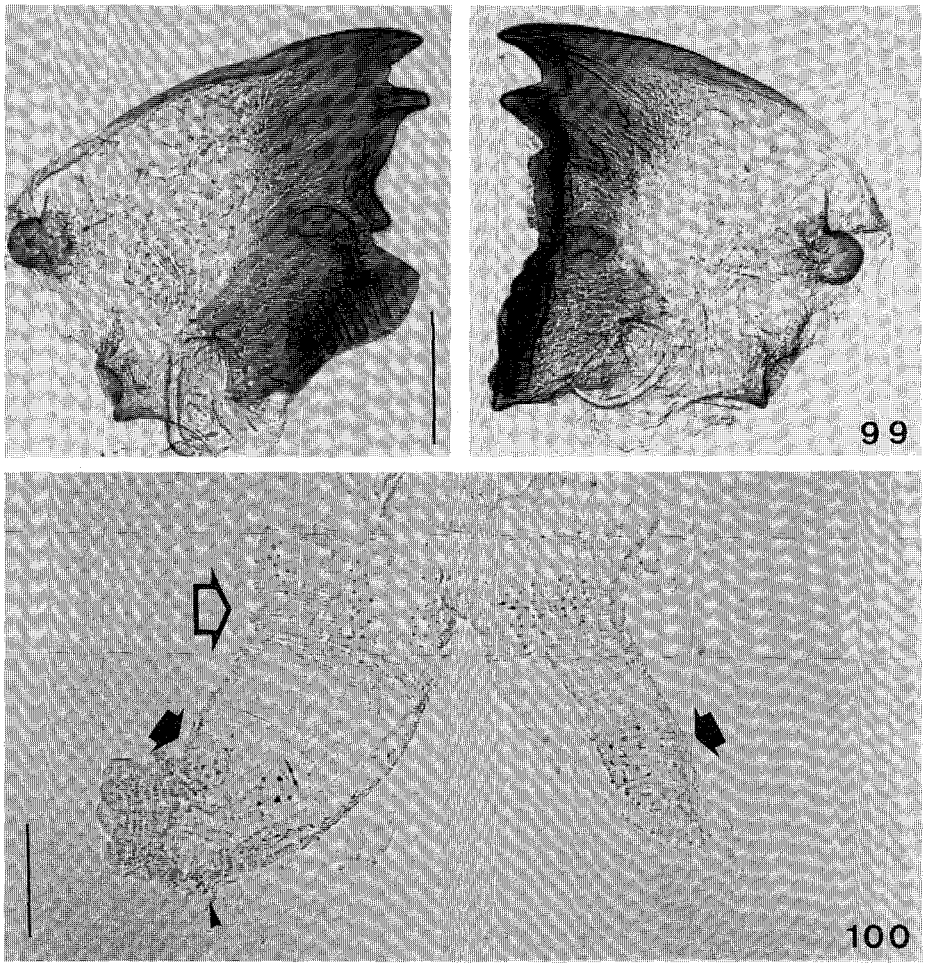
Worker (Figs 99, 100)

Head capsule yellow–white to orange. Antennae 13-segmented. Increase in pigmentation between successive instars. Mandibles (Fig. 99), general configuration of the digestive tract and armature of the enteric valve (Fig. 100) as in *N. variratae*.

Head width of workers from nest PNGT#1498: small workers, first instar, 0·683–0·713 (mean = 0·700, n = 5); large workers, first instar, 0·770–0·792 (mean = 0·780, n = 12); instar 2 and older, 0·790–0·804 (mean = 0·797, n = 12).

Distribution (Fig. 101) *and Biology*

Found in woodlands of southern New Guinea. Compared with *N. variratae*, *N. liklik* was found in more open habitats.



Figs 99, 100. *Niuginitermes liklik*, sp. nov., large worker: *99*, mandibles; *100*, armature of enteric valve. Open arrow, upper ring of spiny areas; closed arrows, lower ring. Arrowhead, attachment of paunch. Scale bars = 0·1 mm.

Affinities

Alates of *N. liklik* are conspicuously smaller and paler than those of *N. variratae*, and have a more developed fontanelle. Soldiers of *N. liklik* are smaller and more hairy than those of *N. variratae*. *N. liklik* superficially resembles *Diwaitermes kanehirae* (see below), but has one additional antennal segment in all castes: alates (14 *v.* 13), soldiers (12 *v.* 11) and workers (13 *v.* 12).

Etymology

From Neo-Melanesian *liklik*, meaning small.

Genus ***Diwaitermes***, gen. nov.

Type species: *Nasutitermes (Subulitermes) orientis* Snyder, 1925, by present designation.

This species is almost certainly a junior synonym of *Eutermes kanehirae* Oshima, 1914, and is hereunder treated as such. However, since the syntypes of *E. kanehirae* available for study are too few and not adequately preserved for fine anatomical studies, the generic description is based on *N. orientis*. We therefore thought it safer to designate *N. orientis* as type species, because if later studies of *E. kanehirae* revealed it to be distinct from *N. orientis*, the designation of the latter as type species of *Diwaitermes* would preserve the concordance between genus name and diagnosis.

Imago

Only known in the type species. The number of antennal segments will probably prove diagnostic in the future to distinguish this genus from *Nasutitermes* and *Niuginitermes*.

Soldier

Fully nasute, related to *Nasutitermes*. Head not constricted behind antennal sockets. Soldier caste monomorphic, small to medium sized. Antennae of 11 or 12 segments; if of 12 segments, third one very short and incompletely separated from the fourth (Fig. 111). Head capsule hairy, with many setae of various lengths. Points on mandibles small, sometimes missing.

Worker

Antennae of 12 or 13 segments; if of 13 segments, third one very short and incompletely separated from the fourth. Mandibles (Fig. 104) very similar to those of *Nasutitermes*. Left mandible index, 0·45–0·55. Digestive tract as in Figs 106, 114. Mesenteric part of mixed segment attached to remainder of mesenteron by wide peduncle positioned laterodorsally on inner side of gut curve. The four malpighian tubules converge towards their attachment to the mesentero-proctodeal junction (Figs 68–69). Upper ring of spiny areas of enteric valve slightly asymmetrical, lower ring with spines penetrating into the paunch. Worker caste dimorphic. Size distribution of large workers unimodal: no growth and slight increase in pigmentation with instar among large workers.

Comparisons

Xylophagous nasutes related to *Nasutitermes* and *Niuginitermes*. The worker digestive tract presents several peculiarities that justify the creation of a new genus.

The genus *Eleanoritermes* (Ahmad), from Borneo, resembles *Diwaitermes*, differing from it in the worker caste by mandibles with more concave molar areas (Fig. 94), enteric valve positioned more anteriorly, weakly armed with few small spines on three swellings (Fig. 95), and longer colon (Fig. 96).

Etymology

From Neo-Melanesian *diwai*, meaning wood.

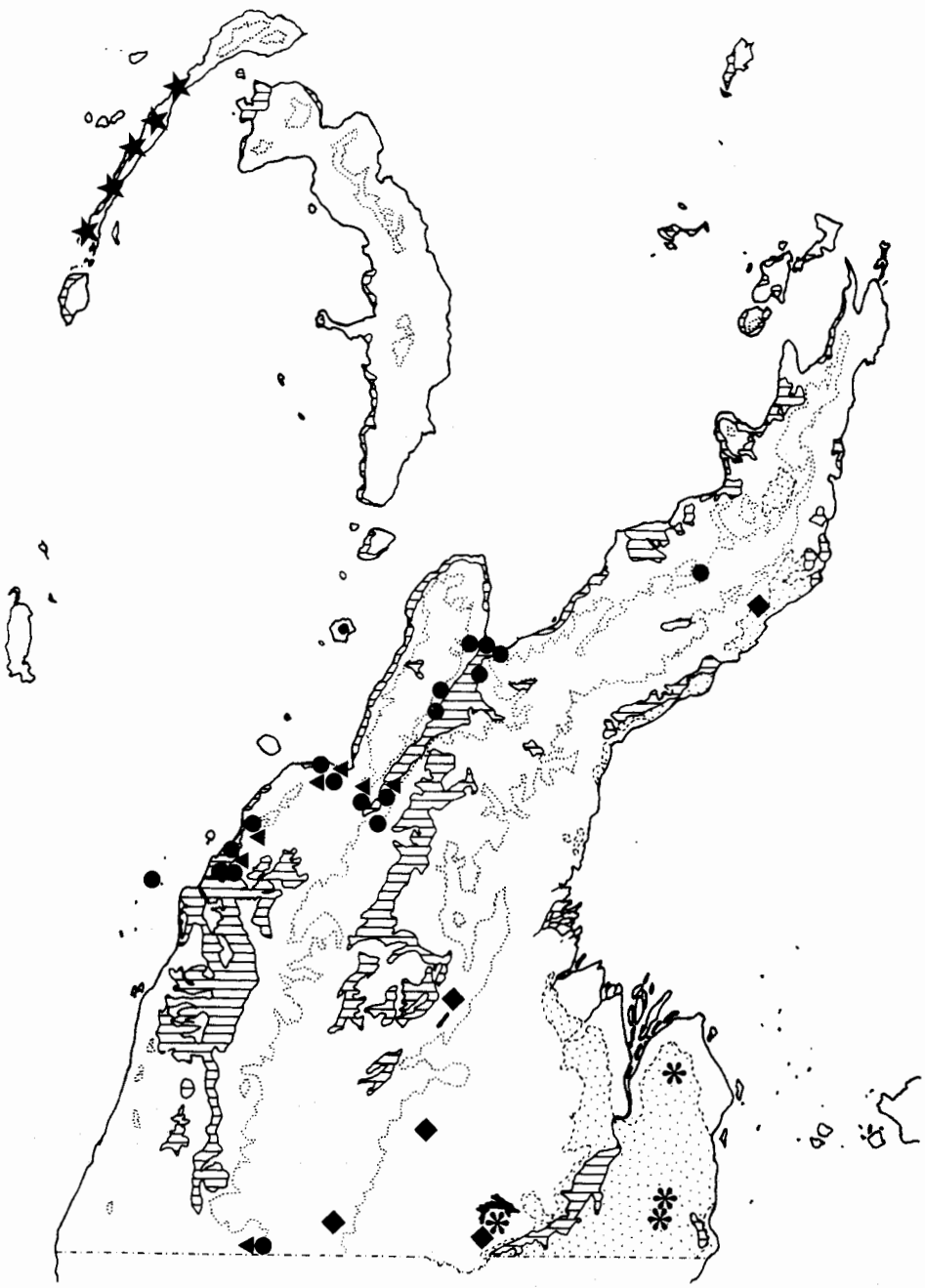


Fig. 101. Known distributions of *Nasutitermes graciliorostris* (●), *N. seghersi seghersi* (▲), *N. seghersi malangganus* (★), *Niuginitermes variratae* (♦) and *N. liklik* (*).

Diwaitermes kanehirae (Oshima), comb. nov.

Eutermes (Sublitermes) kanehirae Oshima, 1914: 578, pl. X (fig. 14: error). Soldier, worker.
Nasutitermes kanehirae. — Snyder, 1949: 281.

New Synonymy

Nasutitermes (Subulitermes) orientis Snyder, 1925: 440–441. Imago, soldier, worker.

Nasutitermes (Subulitermes) orientis, var. *tulagiensis* Snyder, 1925: 441–442. Soldier, worker.

Nasutitermes (Subulitermes) sanctae-crucis Snyder, 1925: 442–443. Imago, soldier.
Nasutitermes sanctae-crucis. — Snyder, 1949: 296.

Eutermes rufirostris Hill, 1927: 24–25, pl. I (figs 19–21). Soldier, worker.
Nasutitermes rufirostris. — Snyder, 1949: 296.

Eutermes kaewiengensis Hill, 1927: 28–31, pl. I (figs 27–28), pl. V (fig. 159), pl. VIII (fig. 160). Imago, nymph, soldier, worker.
Nasutitermes kaewiengensis. — Snyder, 1949: 281.

Subulitermes undecimus Kemner, 1931: 34–38, figs 11 and 12. Imago, soldier, worker, biology (after Weyer).
Nasutitermes undecimus. — Emerson, 1960: 8.

Material Examined

Samples from which soldiers were measured and submitted to principal component analysis (see below) are marked by an asterisk (*).

AMNH. Syntypes*. 1 soldier, 7 workers from type colony, Dobo, Aru I., 7.v.1913 (R. Kanehira). #E1: Brown R. forest, 35 km NW Port Moresby, 21.xi.1962 (A. E., E. E.). #E2*: 14 km N Lae, 1.xii.1962 (A. E., E. E.). #E19, 21, 23, 24, 25*, 26, 28*, 33, 37, 39*: within 35 km from Port Moresby, 15–23.xi.1962 (A. E., E. E.). #E42*, 49, 50, 52, 71–73, 78, 83, 84, 88, 90, 92, 94, 98, 100, 102, 103, 107–109, 117, 121, 123, 126–129: within 32 km from Lae, 27.xi.–31.xii.1962 (A. E., E. E., P. A.).

MCZC. #15294*. Syntypes of *Nasutitermes orientis* Snyder: Auki, Malaita I. (Solomon Is), May–Jun. 1916 (W. M. Mann). #15295*: syntypes of *Nasutitermes orientis* Snyder, var. *tulagiensis* Snyder: Tulagi I. (Solomon Is), May 1916 (W. M. Mann). #15296: syntypes of *Nasutitermes sanctaecrucis* Snyder: Graciosa Bay, Santa Cruz Archipelago, Jul. 1916 (W. M. Mann).

MZEL. Syntypes of *Subulitermes undecimus* Kemner: 5 slides with imagos, soldiers, workers. Amboina (now Ambon), 1929–1930 (F. Weyer).

Authors' collection (PNGT). #68b: Blup Blup I., 16.vi.1981 (J. M. P.). #82, 85: Bam I., 19.vi.1981 (J. M. P.). #89, 91: Koil I., 17.vi.1981 (J. M. P.). #107, 110, 134, 137, 138, 271, 280, 295, 326, 358, 474*, 477, 496, 497, 683, 697, 702, 875, 891, 1100, 1118, 1134, 1153, 1189, 1264, 1527*, 1704*: Bogia Distr., along roads to Ramu R., 26.vi.1981–26.x.1990 (J. M. P., Y. R., M. L.). #122*: 30 km from Madang on Lae Road, 4.vii.1981 (J. M. P.). #181*: Oomsis, 20 km from Highlands Hwy on Bulolo Road, 17.ii.1983 (J. M. P., Y. R.). #199, 201*, 202: Forest on river bank near Kaiapit, 20.ii.1983 (J. M. P., Y. R.). #205*, 210, 212: Usino, 22.ii.1983 (J. M. P., Y. R.). #226: Akio (Usino–Madang Road), 23–24.ii.1983 (J. M. P., Y. R.). #250–251: Marangis (Ramu mouth), 7.iii.1983 (J. M. P., Y. R.). #314, 347, 348: Yagaum Hospital, Madang, 12.iv.–13.v.1983 (Y. R.). #555*, 556*: Bai, near Rabaul (East New Britain), type locality of *Eutermes rufirostris* Hill, 18.v.1984 (J. M. P., Y. R.). #560*, 564, 566, 569*, 570, 576, 578, 580*: Warongoi (East New Britain), 19–20.v.1984 (J. M. P., Y. R.). #584*, 587, 588: Keravat, 22.v.1984 (J. M. P., Y. R.). #589–591: 30 km E Keravat, 23.v.1984 (J. M. P., Y. R.). #597*, 599, 600, 605: Kolonoboi (New Ireland), 25.v.1984 (J. M. P., Y. R.). #615*, 617, 618: Konos, 29.v.1984 (J. M. P., Y. R.). #633, 634*: Lemakot, 30.v.1984 (J. M. P., Y. R.). #643*, 644: 14 km from Kavieng along north coast, 2.vi.1984 (J. M. P., Y. R.). #658, 660*, 663, 664*: Manus I., 32 km from Lorengau on road to south coast, 4–5.vi.1984 (J. M. P., Y. R.). #738: Sogeri, 15.vii.1984 (Y. R.). #846: Yoro Road, 23.ix.1984 (Y. R.). #851*: Sogeri, 4.ii.1985 (J. M. P., Y. R.). #894: Yoro Road, 22.ii.1985 (J. M. P., Y. R.). #915, 928: Sirinumu Dam, 6–8.iii.1985 (J. M. P., Y. R.). #994, 1000*, 1002: Brown R. (35 km NW Port Moresby), 21.iii.1985 (J. M. P., Y. R.). #1091*, 1096: Oomsis Forest Station (near Lae), 25–26.v.1987 (Y. R.). #1203: Braham Mission, Middle Ramu Valley, 6.v.1988 (Y. R.). #1205*: Bundi Road, first climb from Kausi Village (5°44′S, 145°14′E), alt. 600 m, 7.v.1988 (Y. R.). #1211*: Sira Sira, Leron River Valley (6°20′S, 146°28′E), alt. 550 m, 14.v.1988 (Y. R.). #1244: Yoro Road, 1.vi.1988 (Y. R.). #1275*: Lower Gogol Valley, 16.ix.1988 (Y. R.). #1278, 1279: Wasab (north of Madang), 17.ix.1988 (Y. R.). #1324: Braham Mission, 17.xi.1988 (Y. R.). #1440*, 1442: Morehead, Western Province, 25.iii.1989 (Y. R., M. L.). #1472*, 1502: Wipim, Western Province, 29–31.iii.1989 (Y. R., M. L.). #1544, 1547*: Tabubil, Western Province, alt. 500 m,

20.v.1990 (Y. R., M. L.). #1585, 1595, 1599*, 1602*: Lake Murray (7°01′S, 141°30′E), 24–27.v.1990 (Y. R., M. L.). #1611, 1616*, 1645*, 1648, 1657: Nomad River Station (6°18′S, 142°14′E), alt. 150 m, 29.v.–3.vi.1990 (Y. R., M. L.). #1707, 1708: 3 km W Vanimo, 8.iii.1994 (Y. R., M. L.). #1725, 1726, 1748: Yapsiei, Sandaun Province, 10–12.iii.1994 (Y. R., M. L.).

ANIC. #10 17706*: syntype of *Eutermes rufirostris* Hill. Bai, near Rabaul, New Britain, Jun. 1922. One soldier (G. F. Hill). #10 8598: Labu Lagoon (Lae), Oct. 1944 (H. F. C. Davis). #10 9913: 27 km NNE Port Moresby, 24.ix.1961 (F. J. Gay). #10 11015*: Sinaeda Plantation (Milne Bay Distr.), 13.viii.1963 (L. Smee). #10 11281: Keravat, 27.vi.1966 (B. Gray). #10 12924: Naringil, Manus I., 21.iv.1969 (B. Gray). #10 12760*: Rennell I., Solomon Is, 23.xi.1955. One soldier (E. S. Brown). The status of this specimen is doubtful: its larger size suggests that it might represent a distinct subspecies or species. Nevertheless, we mention it here because it is clearly more related to this species than to any other.

Imago (Fig. 102)

A small, dark species, distinguished from all other known Papua New Guinean species by its 13-segmented antennae.

	Measurements (mm)			
	Females (14 alates, 9 dealates from 15 colonies)		Males (16 alates, 6 dealates from 13 colonies)	
	Range	Mean	Range	Mean
Head width across eyes	0·938–1·064	0·997	0·923–1·088	1·001
Largest diameter of eye	0·272–0·335	0·310	0·280–0·341	0·309
Length of ocellus	0·091–0·120	0·103	0·093–0·117	0·103
Eye to ocellus	0·046–0·079	0·063	0·044–0·082	0·066
Pronotum width	0·698–0·814	0·745	0·652–0·793	0·733
Pronotum length	0·452–0·545	0·499	0·428–0·537	0·480
Hind tibia length	0·960–1·144	1·026	0·950–1·185	1·047
Forewing scale length	0·452–0·538	0·498	0·430–0·558	0·518
Forewing length	7·42–8·10	7·78	6·76–7·92	7·49

Soldier (Fig. 103)

Smaller than any other New Guinean nasute, except *Niuginitermes liklik*, from which it is distinguished by its 11-segmented antennae. Head capsule very variable in colour, even between neighbouring colonies, from yellow–brown to sepia, paler on vertex and with reddish tinge towards the tip of the rostrum.

The photograph illustrating the original description of the species (Oshima 1914, pl. X, fig. 14) features a soldier with a thick, conical rostrum, in contradiction with the description and

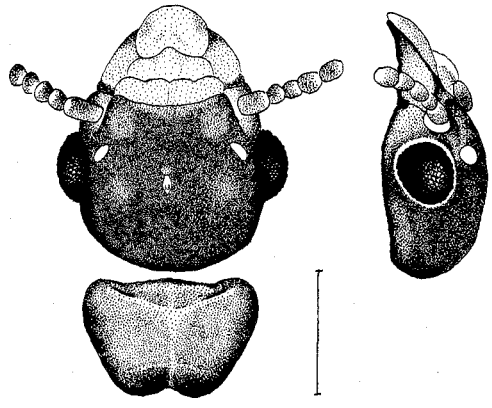


Fig. 102. *Diwaitermes kanehirae* (Oshima), female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

the type material available. An error almost certainly occurred in this paper, possibly a transposition with the sympatric species, *E. doboensis*, described as having a conical rostrum, but pictured with a very thin one (Oshima 1914: 576–77, pl. X, fig. 12).

Measurements (in mm) of 120 individuals from 41 colonies

	Range	Mean
Head capsule length	1·077–1·288	1·189
Rostrum length	0·447–0·584	0·521
'Back of head' distance	0·251–0·360	0·296
Head capsule width	0·606–0·772	0·690
Rostrum width (at half length)	0·064–0·098	0·084
Head depth	0·402–0·529	0·459
Hind tibia length	0·604–0·800	0·676

Worker (Figs 68, 104–106)

Head capsule whitish to light brown, body translucent. Antennae of 12 segments. Head capsule of older instar large workers more pigmented than in first instar. Mandibles as in Fig. 104.

Configuration of the digestive tract as in Figs 68, 106: P1 long, enteric valve situated longitudinally, entering paunch posteriorly. Upper ring of spiny areas slightly asymmetrical, with many short spines; lower ring penetrating into the paunch, narrow, garnished with elongated strips of small spines (Fig. 105).

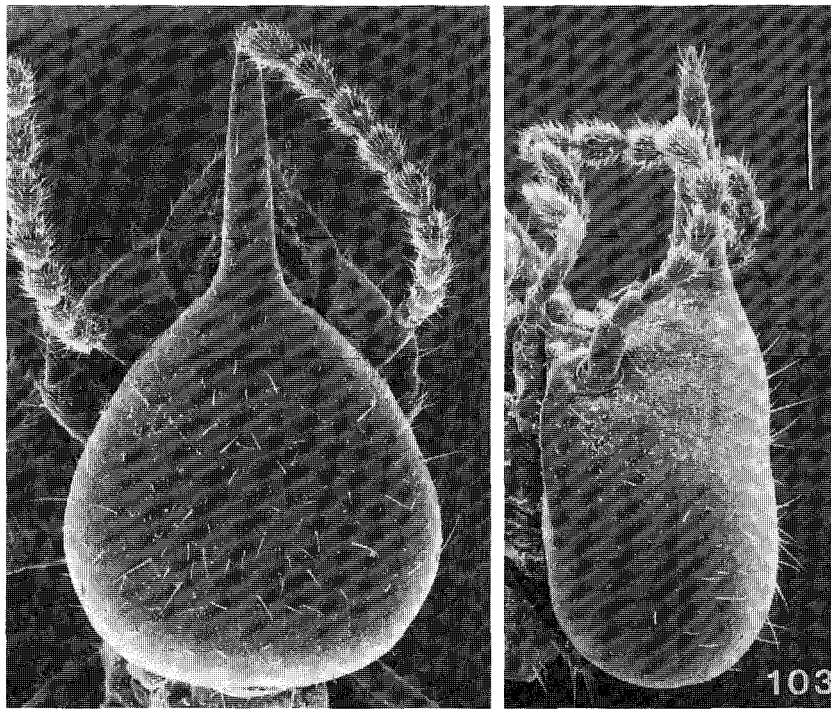


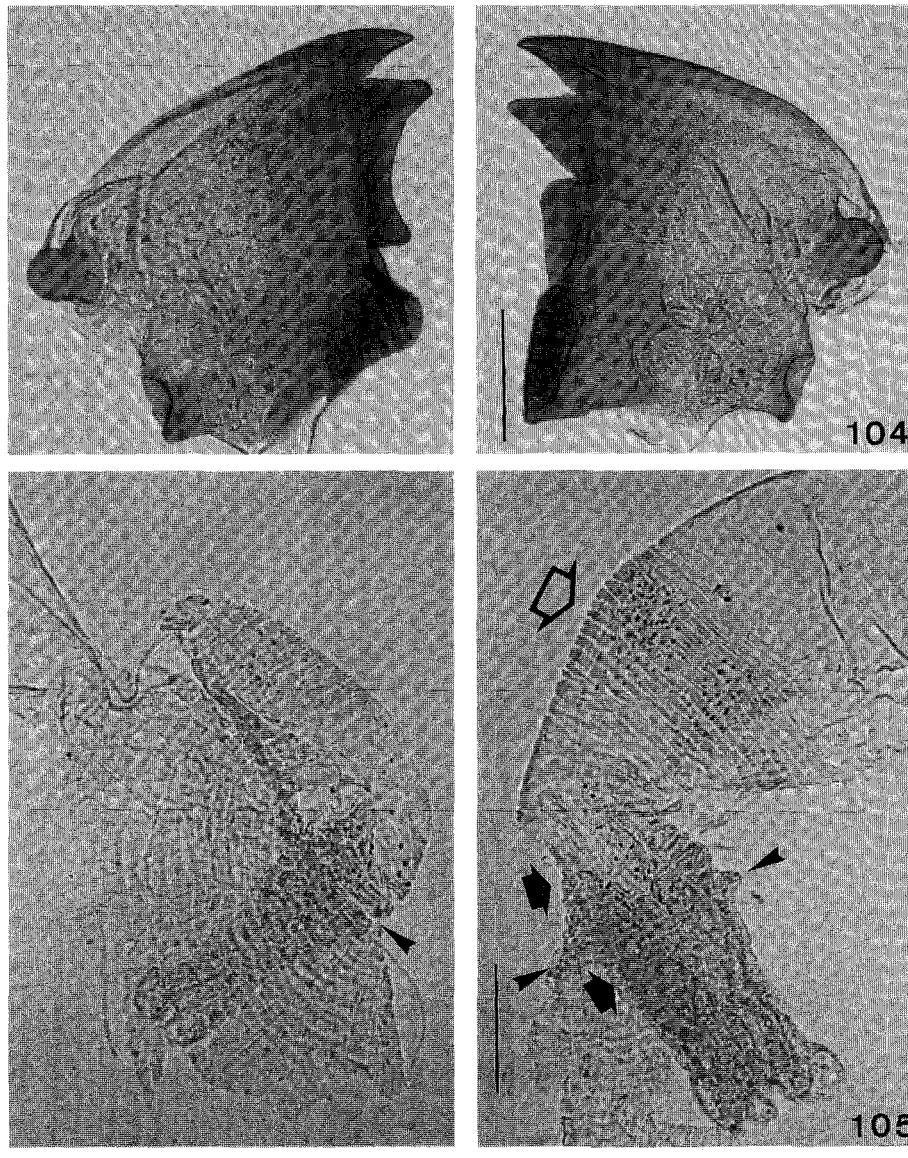
Fig. 103. *Diwaitermes kanehirae* (Oshima): solider head from above (left) and in profile (right). Scale bar = 0·2 mm.

Termitophiles

The staphylinid *Lauella snyderi* was described from a nest (AMNH#E2) of this species (then called *Nasutitermes orientis*) collected near Lae (Kistner 1972).

Distribution and Geographical Variation

Hill (1942) already suggested that *E. kaewiengensis*, *N. orientis*, *E. rufirostris* and *N. sanctaecrucis* could actually constitute local races of a single species. All were described from different islands situated to the north or east of New Guinea, but none had been reported from New Guinea itself. Observations of newly collected nest series from many localities in New



Figs 104, 105. *Diwaitermes kanehirae* (Oshima), large worker: *104*, mandibles; *105*, armature of enteric valve. Open arrow, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

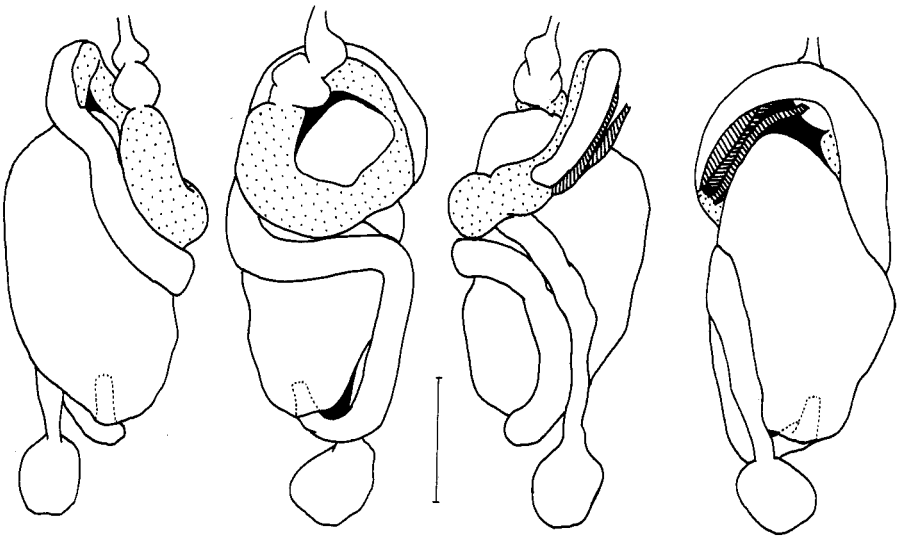


Fig. 106. *Diwaitermes kanehirae* (Oshima), large worker; gut *in situ* viewed successively from left, above, to right, below. Scale bar = 0·5 mm.

Guinea and the Bismarck Islands revealed no consistent morphological character that would justify maintaining these taxa as separate species. In addition, observation of type material of *E. kanehirae* and *S. undecimus*, described from islands situated to the southwest and west of New Guinea, supports their inclusion within the same species.

A principal component analysis (Fig. 107) was carried out on the measurements of soldiers presumed to belong to this species, from various regions of Papua New Guinea and the Solomon Islands. The seven measurements routinely taken to substantiate the descriptions were used as variables, and reduced to zero mean and unit variance. The first two principal axes account for 82% of the total variance. Most specimens fit into an elliptic scattercloud that contains the syntypes of *E. kanehirae*, *N. orientis*, *N. orientis* var. *tulagiensis* and *E. rufirostris*. Some geographic variation appears here, as specimens from the Bismarck Archipelago tend to be, on average, larger than those from mainland New Guinea, although there is a large overlap in the measurements of soldiers from these populations. A single soldier from Rennell Island (ANIC#10 12760) stands out because of its larger size. Two samples from Lake Kutubu and Pimaga (PNGT#1293 and #1308) separate widely from the others by their more elongated head capsule. As these two samples come from the same high valley of the Southern Highlands, there is little doubt that they were part of a single, well-isolated population. The distinctiveness of these specimens, compared with the relative morphological constancy observed in samples from all coastal areas of New Guinea, Aru, Bismarck, Admiralty and Solomon Islands, is such that we think it appropriate to describe them below as a distinct species.

Diwaitermes kanehirae is common throughout the lowlands of Papua New Guinea (Fig. 115). Its absence from all collections from higher hills (> 700 m elevation) is noteworthy. With the inclusion of samples formerly referred to as *N. kaewiengensis*, this species now appears to range from Ambon to Vanuatu and to reach northern Australia (Watson *et al.*, in press).

Biology

Diwaitermes kanehirae was always encountered in dead wood, commonly under the bark of dead trees. This species apparently does not build any nest or foraging tunnels. Many foraging parties comprise only soldiers and workers, but fourth-instar nymphs commonly occur among them. Incipient colonies were found in logs. When reproductives could be found in mature colonies, they were located deep within a piece of dead wood. This species is able to produce ergatoid replacement reproductives.

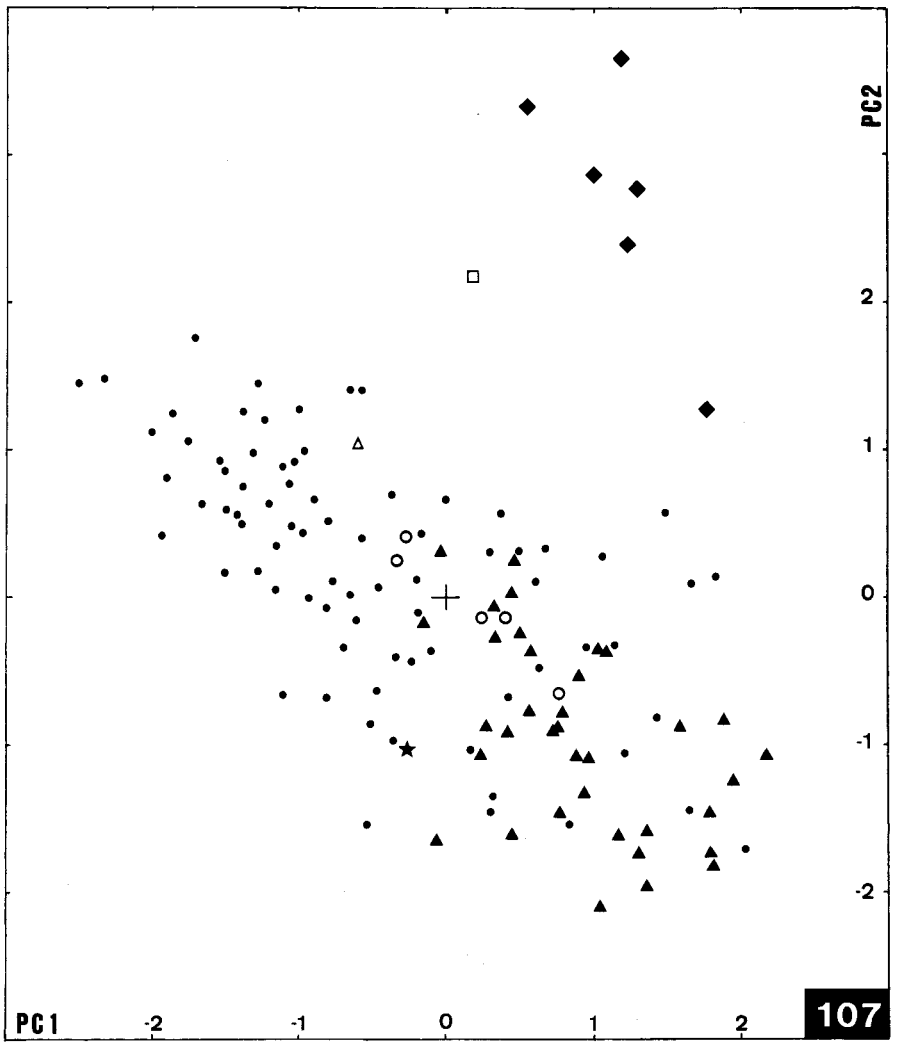


Fig. 107. Principal component analysis based on 7 measurements of soldiers of the *Diwaitermes kanehirae* group. Principal axes 1 (PC1) and 2 (PC2). ★, *D. kanehirae* (Oshima), syntype from Aru Island. ○, syntypes of *N. orientis* (Snyder) and *N. orientis* var. *tulagiensis* (Snyder), from the Solomon Islands. △, syntype of *N. rufirostris* (Hill) from New Britain. ●, *D. kanehirae* (Oshima) from mainland New Guinea. ▲, *D. kanehirae* (Oshima) from New Britain, New Ireland and Manus Island. □, dubious specimen from Rennell Island. ◆, *D. foi*, sp. nov., paratypes from Pimaga and Lake Kutubu.

Diwaitermes foi, sp. nov.

Material Examined

Type colony (PNGT#1293). Lake Kutubu (6°21′S, 143°17′E), 900 m elevation, 13.x.1988. From rotten stump in forest (Y. R.). Holotype: soldier.

PNGT#1308: Pimaga (6°30′S, 143°30′E), alt. 800 m, 17.x.1988 (Y. R.).

Imago

Unknown.

Soldier (Fig. 108)

Head capsule yellow, darker in front, rostrum ferruginous. Antennae orange–yellow, thoracic and abdominal sclerites pale yellow, translucent, legs yellow–white.

Posterior part of head capsule rounded, slightly flattened in middle, anterior sides flattened and converging towards base of rostrum. Head capsule almost straight in profile, with slight hump above antennae. Rostrum evenly conical, relatively narrow, rather long. Mandible points very small, sometimes missing. Antennae of 11 segments, segment 3 distinctly longer than segment 2, slightly longer than segment 4.

Head capsule pilose, with numerous setae of various sizes, whose length tends to increase from base of rostrum to vertex. Abdominal tergites bearing many setae on their whole surface, longer ones along posterior margin of tergites.

Measurements (in mm) of 6 individuals from 2 colonies

	Range	Mean
Head capsule total length	1·377–1·479	1·437
Rostrum length	0·616–0·697	0·665
'Back of head' distance	0·342–0·366	0·354
Head width	0·765–0·799	0·785
Rostrum width (at half length)	0·095–0·110	0·103
Head depth	0·521–0·544	0·530
Hind tibia length	0·759–0·851	0·795

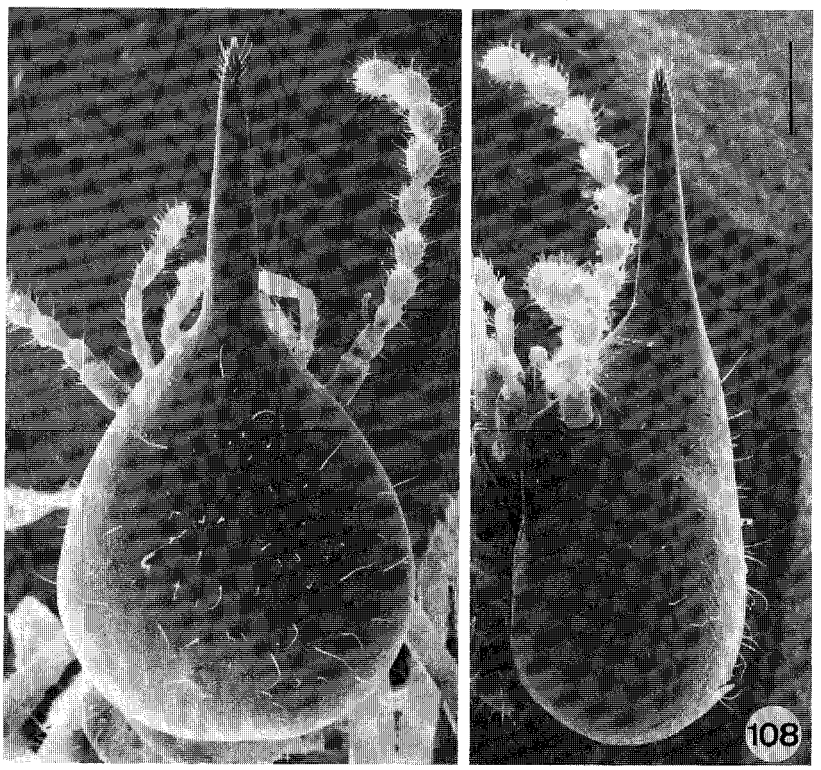
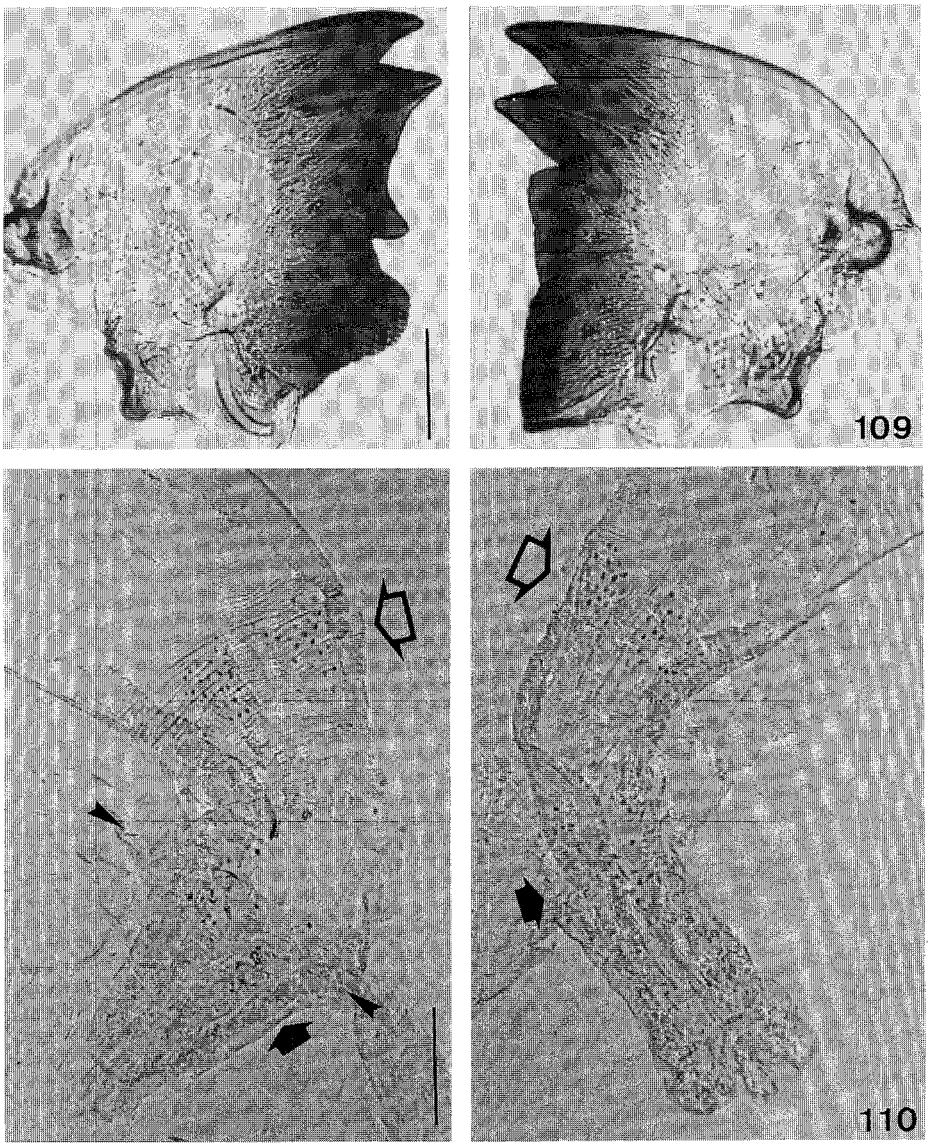


Fig. 108. *Diwaitermes foi*, sp. nov.: soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

These measurements were incorporated in the principal component analysis described under *D. kanehirae* (Fig. 107).

Worker (Figs 109, 110)

Head capsule yellow–white to orange–yellow, body translucent. Antennae of 12 segments. Head capsule of older instar large workers more pigmented and slightly narrower than in first instar. Mandibles (Fig. 109) similar to those of *D. kanehirae*. Configuration of the digestive tract as in *D. kanehirae*. Part of enteric valve penetrating into the paunch slightly wider than in *D. kanehirae*, with longer spines (Fig. 110).



Figs 109, 110. *Diwaitermes foi*, sp. nov., large worker: *109*, mandibles; *110*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

Head width of workers from nest PNGT#1498: small workers, first instar, 0·759–0·803 (mean = 0·777, n = 15); large workers, first instar, 0·866–0·905 (mean = 0·877, n = 12); instar 2 and older, 0·834–0·882 (mean = 0·858, n = 8).

Distribution (Fig. 115) *and Biology*

Only known from humid hill forest in the region of Lake Kutubu and Pimaga, Southern Highlands, where foragers were found in rotten wood.

Affinities

Head capsule of soldier distinctly larger, more elongated and generally paler than in *D. kanehirae*. Superficially resembles *N. variratae*, *N. gracilirostris* and *N. seghersi*, but distinguished from them by paler colour, denser pilosity and 11-segmented antennae.

Etymology

Named after the Foi people from the region of Lake Kutubu and Pimaga, in the Southern Highlands.

Diwaitermes castanopsis, sp. nov.

Material Examined

Type colony (PNGT#1225). Bulolo, Manki Ridge (7°15′S, 146°36′E), alt. 1300 m, 18.v.1988. From dead wood on ground in *Castanopsis* forest (Y. R.). Holotype: soldier.

ANIC. #10 9057: Tairora Ck, Abiera Road, Kainantu Distr., alt. 1500 m, 18.vii.1958 (J. H. Barrett).

AMNH. #E63, 85, 118: Upper Ramu Ck, 1·5 km N of Kainantu, Eastern Highlands, alt. 1550 m, 4.i.1963 (A. E., E. E., J. H. Barrett).

Imago

Unknown.

Soldier (Fig. 111)

Head capsule orange–yellow, brownish on sides, darker on rostrum. Antennae orange–yellow, thoracic and abdominal sclerites pale yellow, translucent, legs yellow–white.

Head capsule slightly pyriform, flattened posteriorly, in profile almost straight, with slight hump at base of rostrum. Points on mandibles very small, sometimes missing. Rostrum conical, narrow. Antennae of 12 segments, segment 3 small, shorter than segment 2 and incompletely separated from segment 4 (Fig. 111).

Head capsule pilose, with 4 long setae at base of rostrum, several other long setae on vertex and numerous smaller setae of various sizes, of increasing length from base of rostrum to vertex. Abdominal tergites bearing many setae on their whole surface, longer ones along posterior margin of tergites.

Measurements (in mm) of 9 individuals from 3 colonies

	Range	Mean
Head capsule total length	1·577–1·624	1·597
Rostrum length	0·715–0·755	0·741
'Back of head' distance	0·363–0·425	0·397
Head width	0·900–0·963	0·929
Rostrum width (at half length)	0·114–0·121	0·118
Head depth	0·610–0·639	0·625
Hind tibia length	0·916–1·013	0·970

Worker (Figs 69, 112–114)

Head capsule yellow–white to orange–yellow, body translucent.

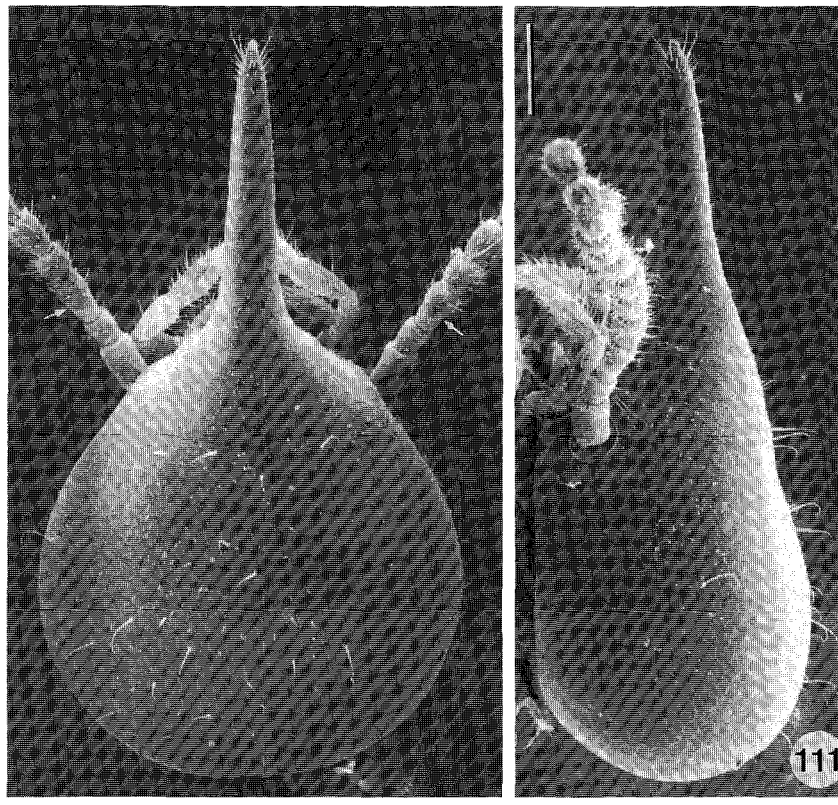


Fig. 111. *Diwaitermes castanopsis*, sp. nov.: soldier head from above (left) and in profile (right). Arrows, incomplete separation between antennal segments 3 and 4. Scale bar = 0·2 mm.

Antennae of 13 segments, with segment 3 very small and incompletely separated from segment 4. Small workers scarce in our samples. Little variation in size and pigmentation of large workers. Mandibles (Fig. 112) as in *D. kanehirae*. General configuration of the digestive tract (Figs 69, 114) similar to that of *D. kanehirae*, but P1 shorter. Enteric valve oblique. Upper ring asymmetrical, of 6 well-defined areas bearing many small spines; lower ring well distant from upper ring, wholly inside the paunch, wide, with three short spiny areas alternating with elongated ones, all bearing 10–20 spines (Fig. 113).

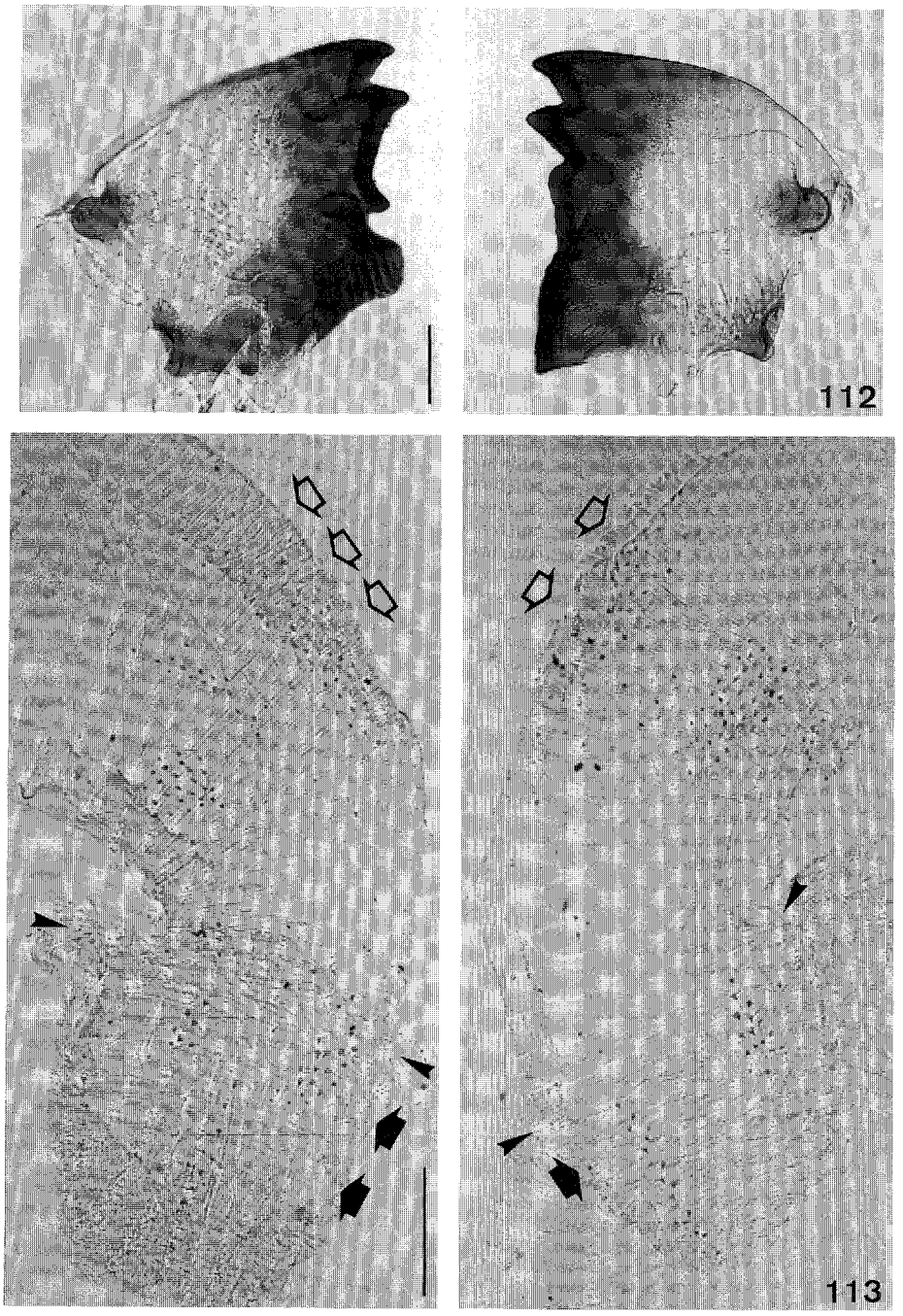
Head width (mm) of workers from type colony (PNGT#1225): small workers, 0·91–0·92 (n = 2); large workers, 1·02–1·09 (mean = 1·05, n = 79).

Distribution (Fig. 115) *and Biology*

Only reported from two collection sites in the mountains of northern New Guinea, near Bulolo and Kainantu. Both are located in *Castanopsis* (southern oak) forests between 1300 and 1550 m elevation. This is the species whose presence in the New Guinea Highlands was reported by Barrett (1965). Thus far, this is the only nasute recorded at such an elevation in New Guinea. Further research is needed to determine whether this species is specialised on this remarkable habitat and to establish its geographical range.

Affinities

Antennal structure diagnostic. In addition, soldiers easily distinguished from those of *D. kanehirae* and *D. foi* by larger size; head capsule hairier than that of *N. gracilirostris*,



Figs 112, 113. *Diwaitermes castanopsis*, sp. nov., large worker: *112*, mandibles; *113*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Arrowheads, attachment of paunch. Scale bars = 0·1 mm.

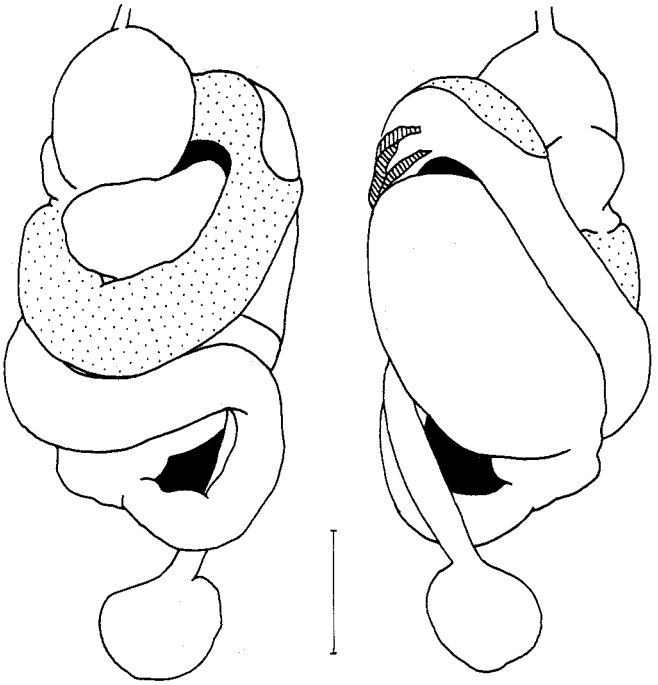


Fig. 114. *Diwaitermes castanopsis*, sp. nov., large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

N. seghersi, *N. leponcei* and *N. bikpelanus*. Larger than *N. gracilirostris*, rostrum much narrower than that of *N. bikpelanus*.

Etymology

The name refers to the discovery of this species in *Castanopsis* forests.

Genus ***Tumulitermes*** Holmgren

Eutermes subgenus *Tumulitermes* Holmgren, 1912: 59–61, 64.
Tumulitermes. — Snyder, 1949: 301.
Type species, by monotypy: *Eutermes tumuli* Froggatt, 1898.

Formerly considered an Australian endemic, this genus is very similar to *Nasutitermes* in its general appearance. It is characterised by the constricted head of the soldier. Several Australian species of this genus possess dimorphic soldiers, but this seems not to be the case in the New Guinean species. The worker gut differs from that of *Nasutitermes* by the Malpighian tubules inserted contiguously (Kovoor 1969; see Fig. 70 herein) and the enteric valve armature (Fig. 119).

Tumulitermes marcidus (Hill)

Eutermes marcidus Hill, 1942: 290, 291, figs 202, 203. Queen, soldier, worker, biology.
Tumulitermes marcidus. — Snyder, 1949: 302.

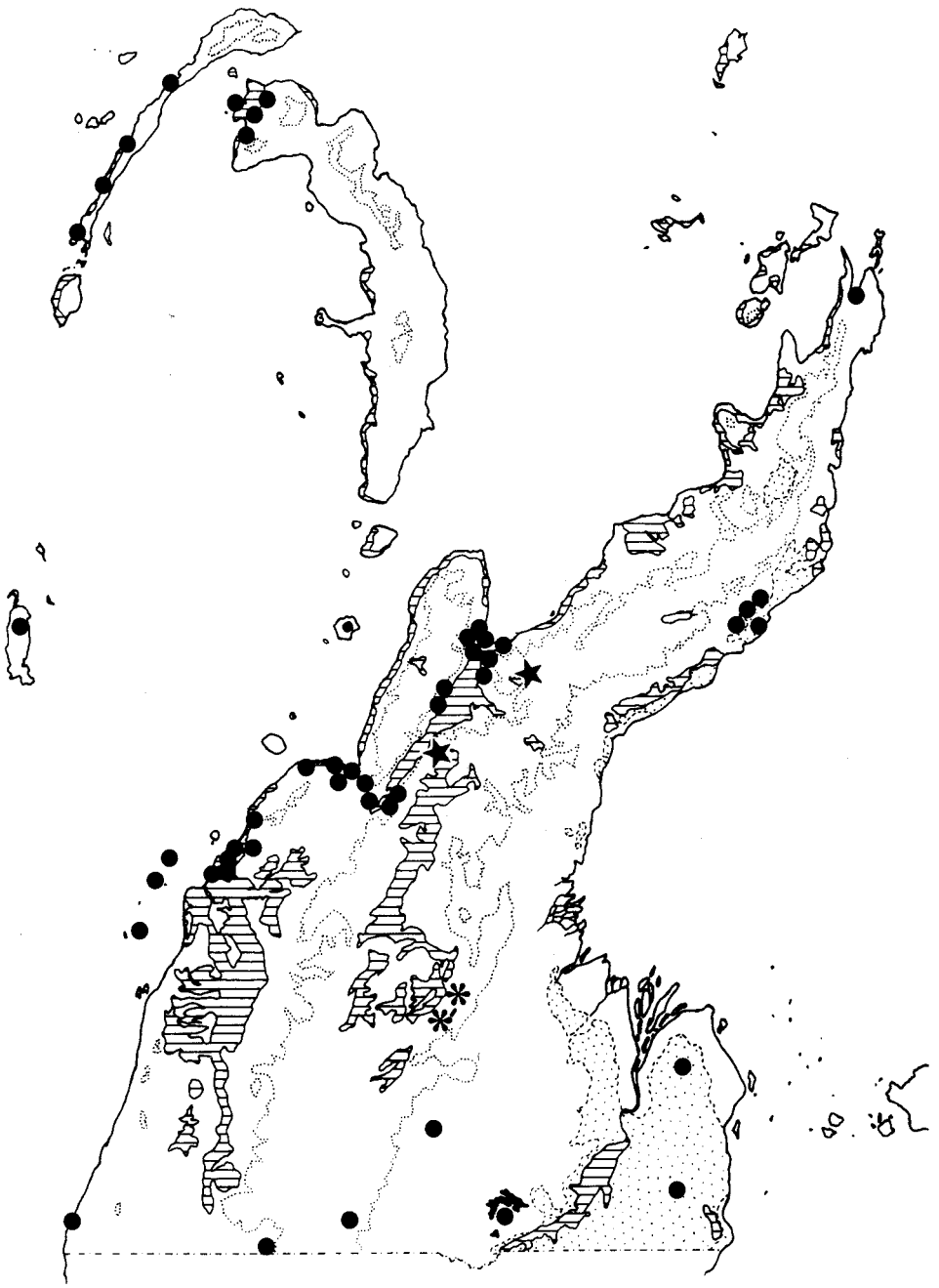


Fig. 115. Known distributions within Papua New Guinea (excluding the North Solomons Prov.) of *Diwaitermes kanehirae* (●), *D. foi* (*) and *D. castanopsis* (★).

Material Examined

ANIC. Paratype colony (#10 2104): 2·8 km S of Millungera Station, N Queensland, 29.v.1936. Two soldiers, 2 workers, 1 nymph (G. F. Hill). #10 20026: Cape York Peninsula, (12°40′S, 142°40′E), 6.xi.1978 (L. R. Miller).

Authors' collection (PNGT). #1430, 1451, 1457: Morehead, Western Province, 24–26.iii.1989 (Y. R., M. L.).

Imago (Fig. 116)

Head capsule very dark sepia brown, almost black. Postclypeus dark sepia, mandibles ferruginous on sides. Thoracic tergites dark sepia, other thoracic and abdominal sclerites, legs and antennae sepia. Wing membrane almost hyaline, costal and radial veins ferruginous, sepia line below radial vein.

Head capsule rounded posteriorly. Eyes small, not prominent, ocelli small, distant from eyes by about own largest diameter. Postclypeus very large and bulging. Antennae of 15–16 segments, with incomplete separation between segments 3 and 4; sometimes segment 5 also partially divided. Fontanelle small, hyaline, narrow (0·050 × 0·015 mm).

	Measurements (in mm)		
	Females	Males	
	(1 alate, 3 queens)	alate	king
Head width across eyes	1·23–1·26	1·23	1·23
Largest diameter of eye	0·310–0·355	0·325	0·343
Ocellus length	0·103–0·122	0·096	0·100
Eye to ocellus	0·091–0·119	0·114	0·115
Pronotum width	1·08–1·18	1·05	1·06
Pronotum length	0·71–0·75	0·68	0·69
Hind tibia length	1·45–1·55	1·53	1·51
Forewing scale length	0·664–0·769	0·684	0·733
Forewing length	9·6	8·7	–

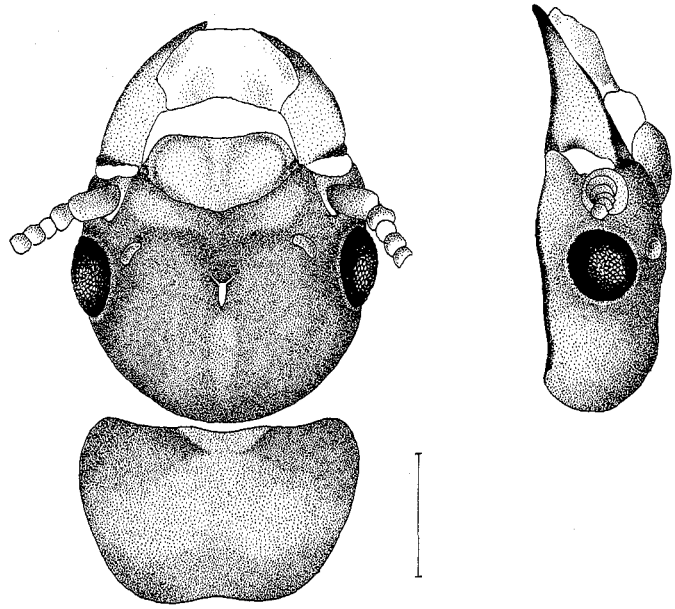


Fig. 116. *Tumulitermes marcidus* (Hill), queen: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

Soldier (Fig. 117)

A medium-sized species, with a very dark chestnut brown head capsule, slightly constricted behind antennal sockets. Soldier caste monomorphic, unlike several other species of this genus. Usually 14 antennal segments, sometimes 13.

Measurements (in mm) of 13 individuals from 5 colonies

	Range	Mean
Head capsule total length	1·371–1·620	1·494
Rostrum length	0·590–0·724	0·654
'Back of head' distance	0·311–0·392	0·356
Head width	0·727–0·860	0·795
Rostrum width (at half length)	0·099–0·143	0·123
Head depth	0·503–0·609	0·559
Hind tibia length	0·965–1·102	1·030

Worker (Figs 118–120)

Head capsule with four broad, longitudinal lines of pigmentation, from pale brown to sepia. Increase in size and pigmentation between successive large-worker instars.

Antennae 15-segmented. Mandibles (Fig. 118) resembling those of *N. triodiae*, with narrow gap between apical tooth and first marginal. General configuration of digestive tube (Fig. 120) resembling that of *Nasutitermes*, except for malpighian tubules inserted contiguously at most anterior point of mesentero-proctodeal junction (Fig. 70). Mesenteric part of mixed segment attached to remainder of mesenteron by wide peduncle. Enteric valve (Fig. 119): upper ring of 3

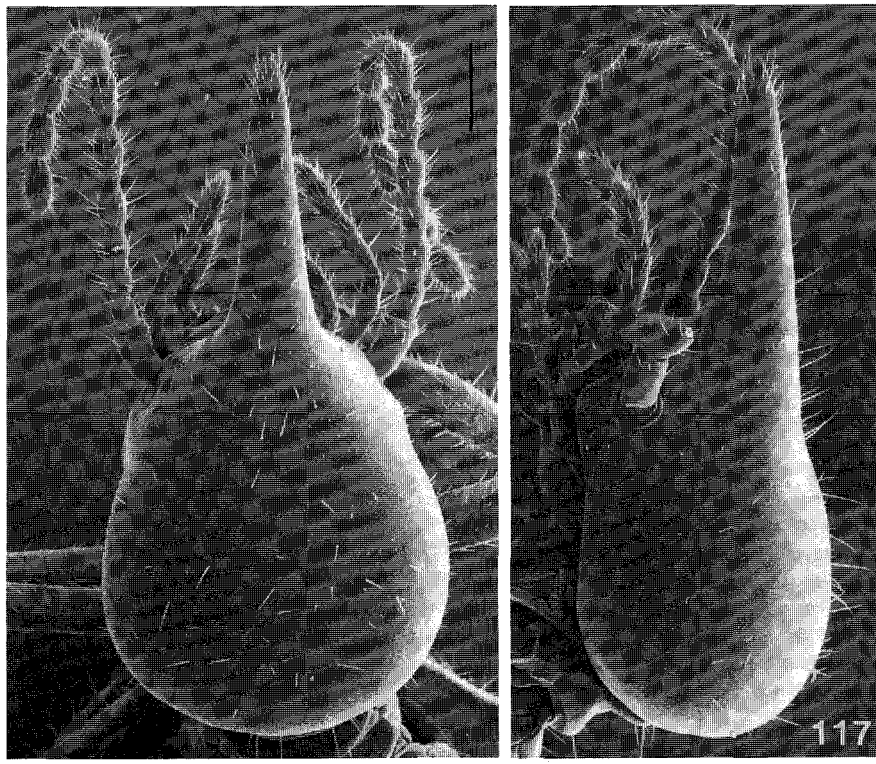
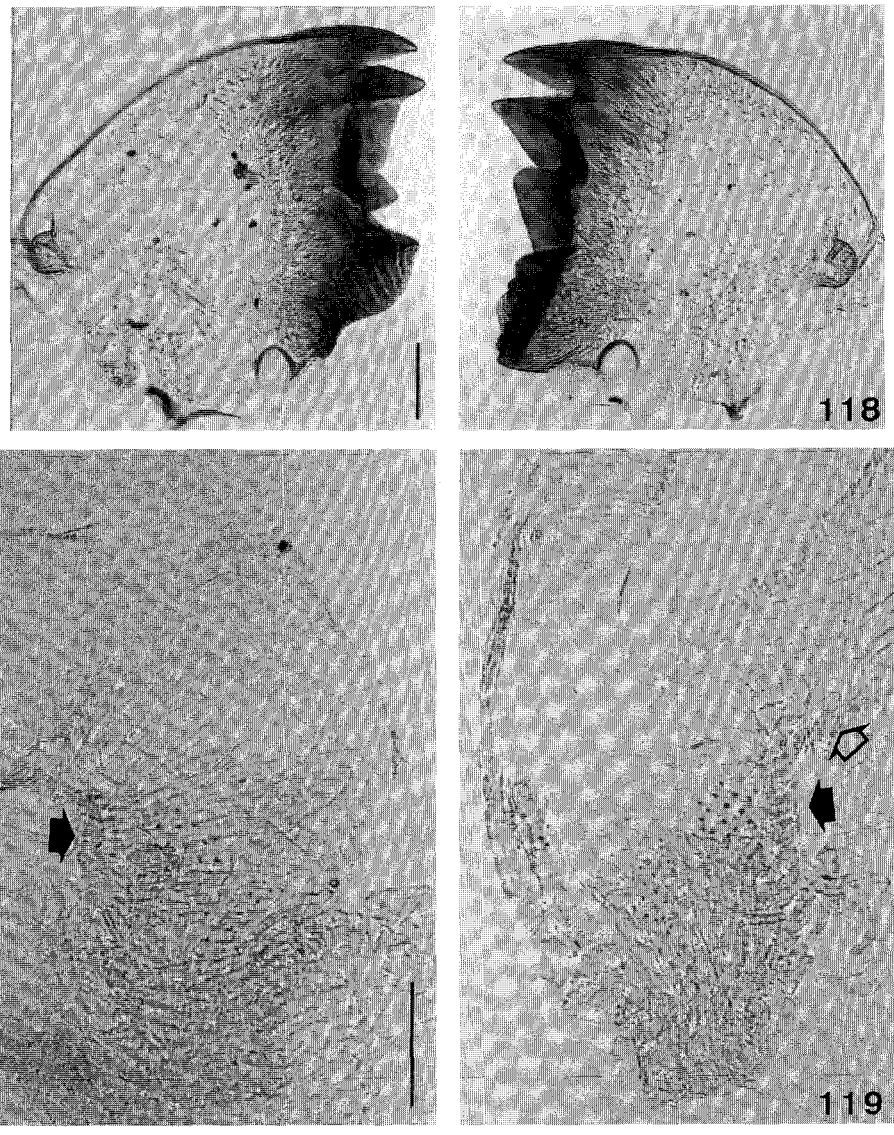


Fig. 117. *Tumulitermes marcidus* (Hill): soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.



Figs 118, 119. *Tumulitermes marcidus* (Hill), large worker: *118*, mandibles; *119*, armature of enteric valve. Open arrow, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

barely delimited areas bearing numerous tiny spines; lower ring of 3 distinct swellings bearing about 12–16 small, pointed spines, alternating with more elongated areas garnished with numerous tiny spines.

Head width of workers from nest PNGT#1430: small workers, first instar, 0·803–0·851 (mean = 0·825, n = 8); large workers, first instar, 1·062–1·084 (mean = 1·071, n = 9); instar 2 and older, 1·122–1·243 (mean = 1·178, n = 16).

Distribution (Fig. 131) *and Biology*

Type locality is Moa (= Banks) Island, Torres Strait. Also reported from northern Queensland (Hill 1942; Watson *et al.*, in press). In Papua New Guinea, found only in grasslands near Morehead, where this species builds small pointed epigeal mounds of the kind described by Hill (1942). Small stores of chaffed grass were found in the nests.

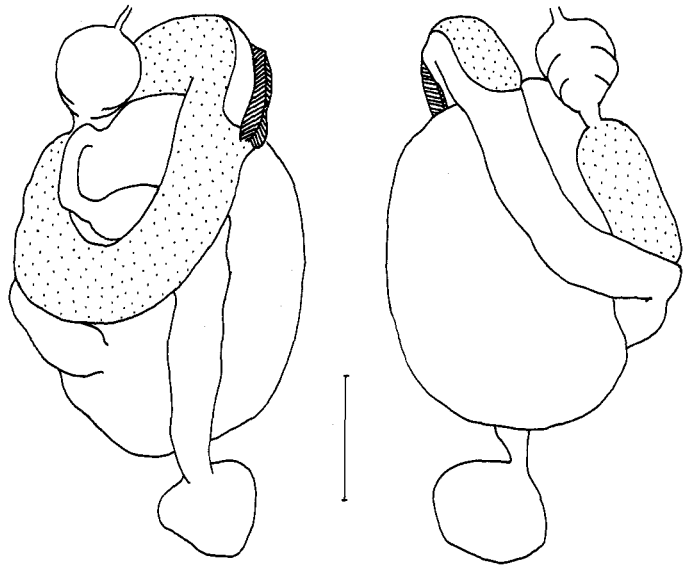


Fig. 120. *Tumulitermes marcidus* (Hill), large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

Genus *Grallatotermes* Holmgren

Eutermes subgenus *Grallatotermes* Holmgren, 1912: 59–61, 65.
Grallatotermes. — Light, 1930: 16, 17, 19, 40; Gay, 1971: 45–47.
Type species, by monotypy: *Termes (Eutermes) grallator* Desneux, 1905.

Grallatotermes and *Hospitalitermes* are heavily pigmented, long-legged species that commonly forage without cover at daytime in rainforests. Both genera differ from *Nasutitermes* by their very dark abdominal tergites (workers and soldiers), their constricted head capsule (soldier) and their worker mandibles, characterised by a large molar region and a deflected apical tooth. *Grallatotermes* is unmistakable for its stout, conical rostrum.

Grallatotermes grallator (Desneux)

Termes (Eutermes) grallator Desneux, 1905: 374–375, fig. 4. Soldier, worker, biology.

Grallatotermes grallator. — Snyder 1949: 314; Gay, 1971: 41–45, figs 1, 2 (alate, soldier, worker, biology).

Gay (1971) provided excellent descriptions of all castes, which need few additional details.

Material Examined

IRSN#11813. Lectotype soldier (designated here) and paralectotype soldiers and workers: Graget I. (most probably the island now known as Kranket, alongside Madang Harbour), 1901 (L. Biró).

Authors' collection (PNGT). #700: Nubia–Bunapas Road, 3·5 km, 18–20.vi.1984 (Y. R.). #793: Yoro, 25.viii.1984 (Y. R.). #1242: Yoro, 1.vi.1988. (Y. R.). #1530: Nubia–Bunapas Road, 7·6 km, 25.v.1989 and 26.x.1990 (Y. R., M. L.). #1634: Nomad R., 1.vi.1990 (Y. R., M. L.). #1739, 1740: Yapsiei, Sandaun Province (4°38'S, 141°06'E), 11.iii.1994.

ANIC. #10 9063: Bulolo, Dec. 1958 (D. Halpin). #10 10379, 10380: Oriomo R., 48 km N Daru, Western Province, 1.xi.1961 (B. J. O'Hagan). #10 11878: Bulolo, 15.x.1967 (L. T. Clifford). #10 13232: Bulolo, 6.xi.1969 (Teng, Anton). #10 13853: Bulolo, Dec. 1958 (D. Halpin).

Imago (Fig. 121)

Larger than all other New Guinean species except *N. triodiae*, which is lighter coloured. Its description by Gay (1971) is applicable to our specimens from nest PNGT#1739, except that in the latter, alates have antennae of 17 or (seldom) 16 segments.

	Measurements (in mm)			
	Females (4 alates from nest PNGT#1739)		Males (4 alates from nest PNGT#1739)	
	Range	Mean	Range	Mean
Head width across eyes	1·918–1·959	1·938	1·827–1·845	1·837
Largest diameter of eye	0·632–0·677	0·653	0·669–0·679	0·676
Length of ocellus	0·212–0·239	0·229	0·206–0·223	0·216
Eye to ocellus	0·058–0·083	0·068	0·050–0·078	0·063
Pronotum width	1·726–1·832	1·782	1·663–1·692	1·677
Pronotum length	1·089–1·157	1·116	1·059–1·080	1·070
Hind tibia length	2·61–2·68	2·64	2·48–2·55	2·52
Forewing scale length	1·050–1·069	1·061	1·034–1·064	1·045
Forewing length	17·4–18·0	17·7	16·2–16·5	16·3

Soldier (Fig. 122)

Superficially similar to that of *N. novarumhebridarum*, but distinguished from it by head capsule constricted behind antennae, stouter rostrum, much longer legs and antennae and darker pigmentation.

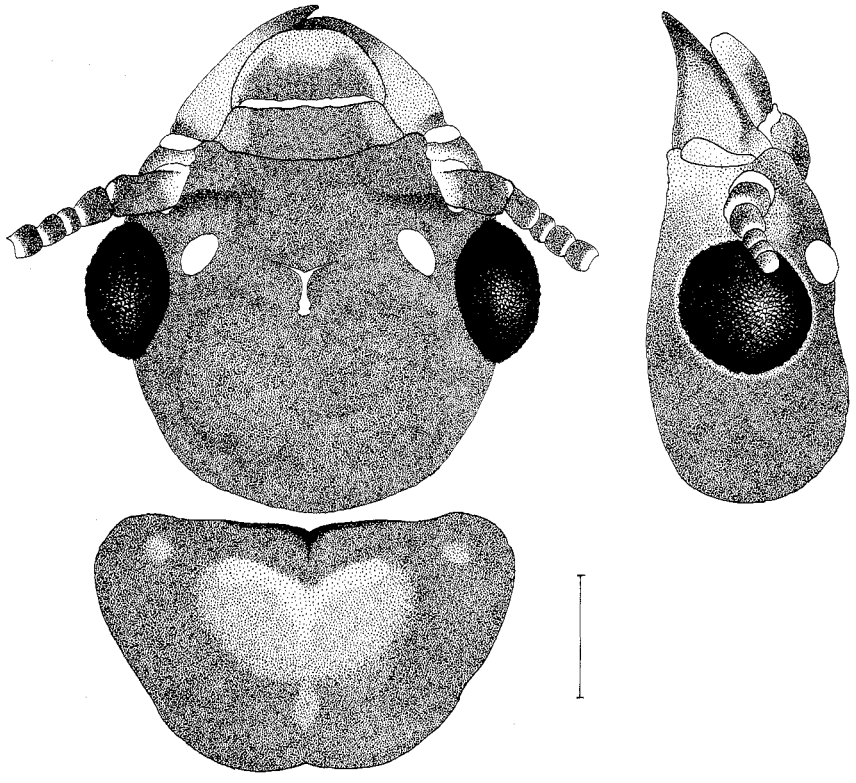


Fig. 121. *Grallatotermes grallator* (Desneux), female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

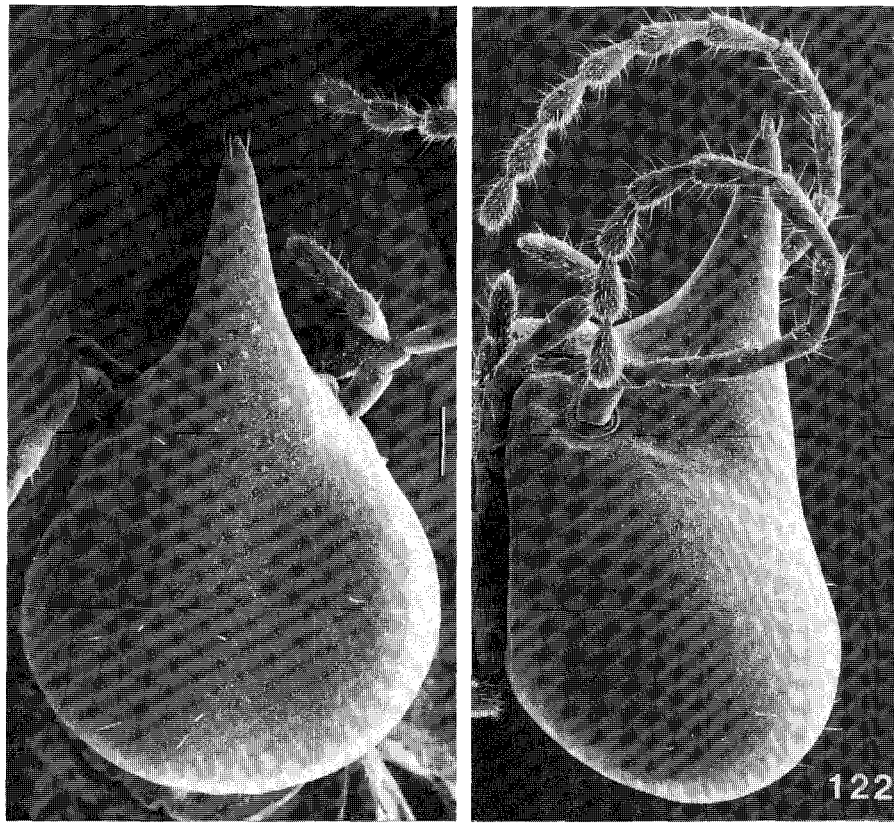


Fig. 122. *Grallatotermes grallator* (Desneux): soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Measurements (in mm) of 25 individuals from 8 colonies

	Range	Mean
Head capsule total length	1·656–2·154	1·863
Rostrum length	0·591–0·816	0·719
'Back of head' distance	0·441–0·626	0·508
Head width	1·078–1·564	1·219
Rostrum width (at half length)	0·180–0·293	0·218
Head depth	0·812–1·191	0·924
Hind tibia length	1·80–2·99	2·20

The monoterpene fraction of the soldiers' defensive secretion is dominated by α-pinene (58%), with smaller amounts of limonene (18%) and sabinene (11%) (Everaerts *et al.* 1988).

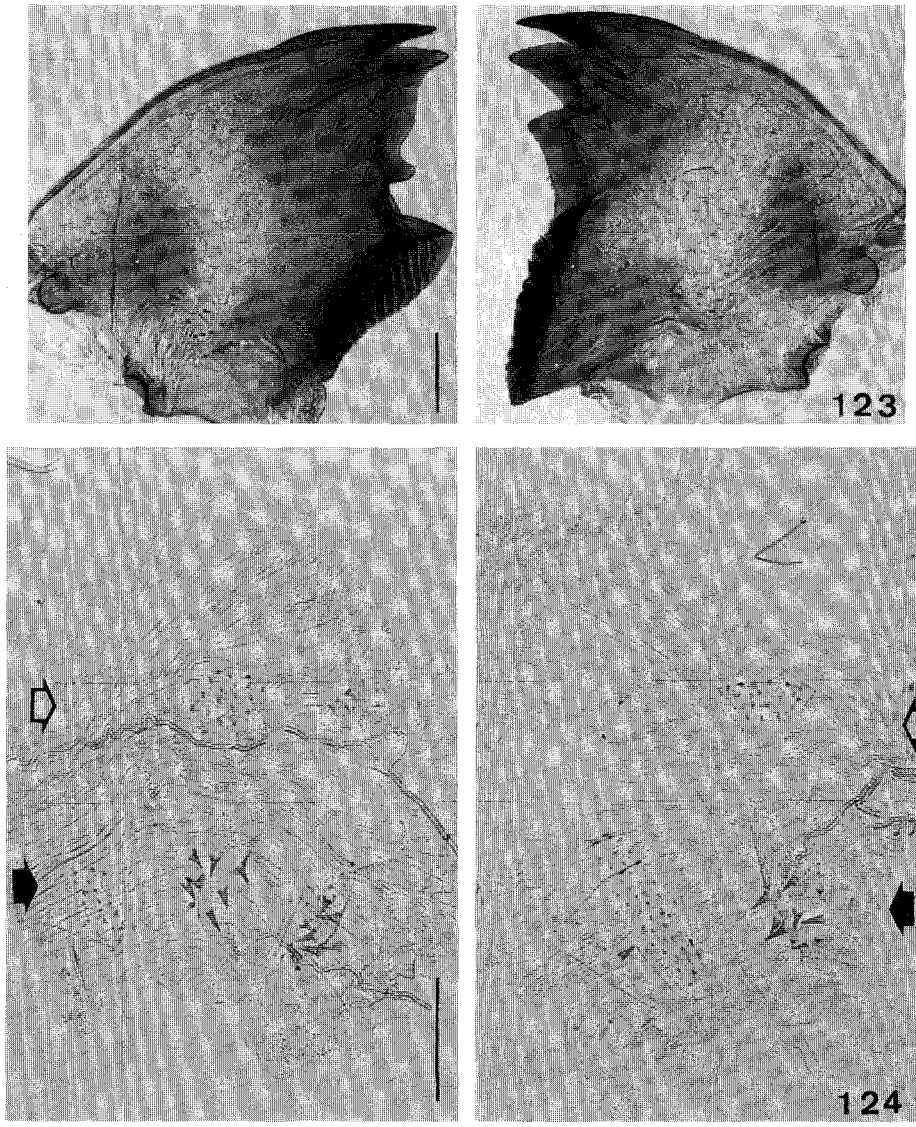
Worker (Figs 123–125)

Large difference in size between small and large workers. In *G. grallator*, even the youngest worker instars display a very dark pigmentation, contrary to the other nasute genera described above.

Antennae of 15 segments. Mandibles as in Fig. 123, with apical tooth strongly deflected downwards and long molar plate. General configuration of the digestive tract (Fig. 125) similar to that of *Nasutitermes*. Crop very voluminous. Mesenteric part of mixed segment attached to

remainder of mesenteron by wide peduncle. Enteric valve (Fig. 124) almost symmetrical: upper ring of 3 wide, slightly swollen areas, bearing numerous small spines; lower ring of 3 swellings each bearing 7–9 long, strong spines, alternating with elongated areas bearing numerous small spines.

Head width of workers from nest PNGT#1530: small workers, first instar, 0·907–0·972 (mean = 0·934, n = 10); large workers, first instar, 1·151–1·232 (mean = 1·196, n = 20); instar 2 and older, 1·306–1·364 (mean = 1·346, n = 10).



Figs 123, 124. *Grallatotermes grallator* (Desneux), large worker: *123*, mandibles; *124*, armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

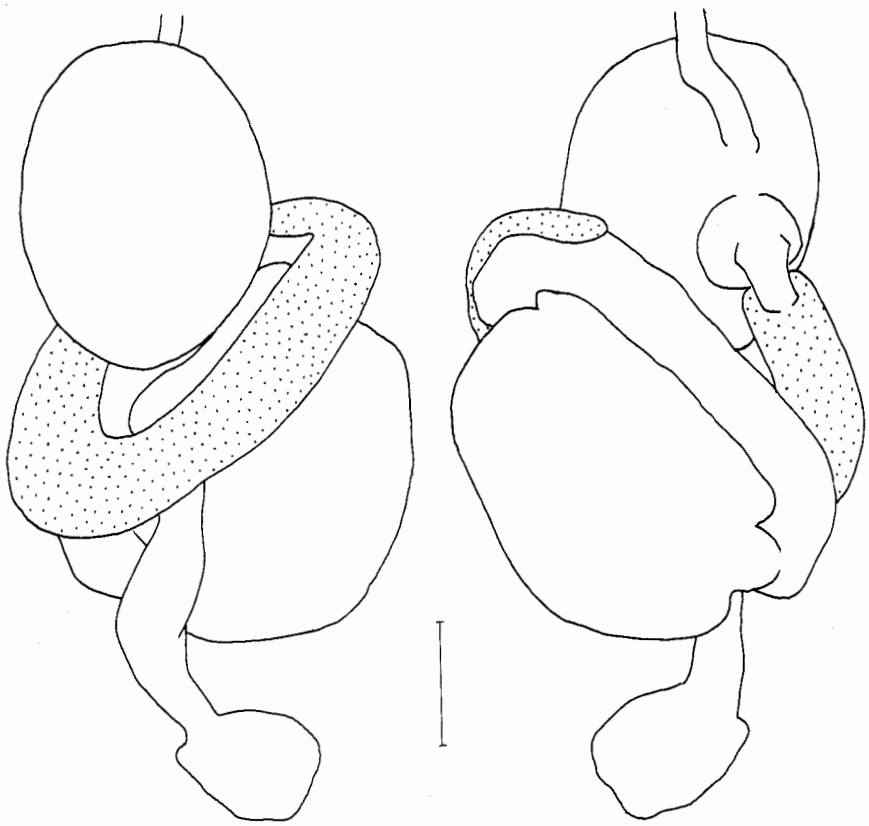


Fig. 125. *Grallatotermes grallator* (Desneux), large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

Distribution (Fig. 131) *and Biology*

In northern New Guinea, recorded from the upper Sepik to Bulolo; two records from southern New Guinea. This species commonly forages at daytime along open-air trails in rainforests. Workers apparently feed on algae and lichens on the trunk of living trees and return to the nest with large amounts of stored food in their crop. The strongly deflected apical tooth of their mandibles could constitute an adaptation for 'browsing' on tree trunks. A nest was found on a small tree in forest in Yapsiei (PNGT#1739). The queen was found among the nest debris, as there was no definite royal cell. Unlike all arboreal nests of *Nasutitermes* observed in New Guinea up to now, this nest of *G. grallator* was not connected to the ground by carton-covered runways.

Related Allopatric Species

Grallatotermes weyeri Kemner

Grallatotermes Weyeri Kemner, 1931: 46–50, fig. 16. Queen, soldier, worker, biology (after Weyer).

According to the original description, this species, known from Ambon and Saparua Islands, is smaller than *G. grallator*. Workers of *G. weyeri* possess 14-segmented antennae (15-segmented in *G. grallator*).

Genus *Hospitalitermes* Holmgren

Eutermes subgenus *Hospitalitermes* Holmgren, 1912: 59–62, 66.
Hospitalitermes. — Oshima, 1923: 18.
Type species, by subsequent designation (Snyder, 1949): *Termes hospitalis* Haviland, 1898.

Distinguished from *Grallatotermes* by thin rostrum, deeply constricted head capsule, darker pigmentation (especially on abdominal sternites) and longer appendages.

Hospitalitermes papuanus Ahmad

Hospitalitermes papuanus Ahmad, 1947: 4, 5, fig. 4. Soldier.

Material Examined

Authors' collection (PNGT). #1610, 1622, 1667: Nomad R., 29.v.–3.vi.1990 (Y. R., M. L.). #1727, 1728, 1738, 1749: Yapsiei (4°38′S, 141°06′E), 10–12.iii.1994 (Y. R., M. L.).

ANIC. #10 10361: Rouku, Western Distr., Apr. 1962 (W. Brandt). #10 13961: 1·5 km E Morehead, (6°43′S, 141°39′E), 27.viii.1970 (K. H. L. Key, J. Balderson).

Imago (previously undescribed) (Fig. 126)

Head capsule black, shining, very dark sepia brown around antennal sockets. Postclypeus black. Labrum dark ferruginous. Antennae very dark sepia on segments 1–2, sometimes on

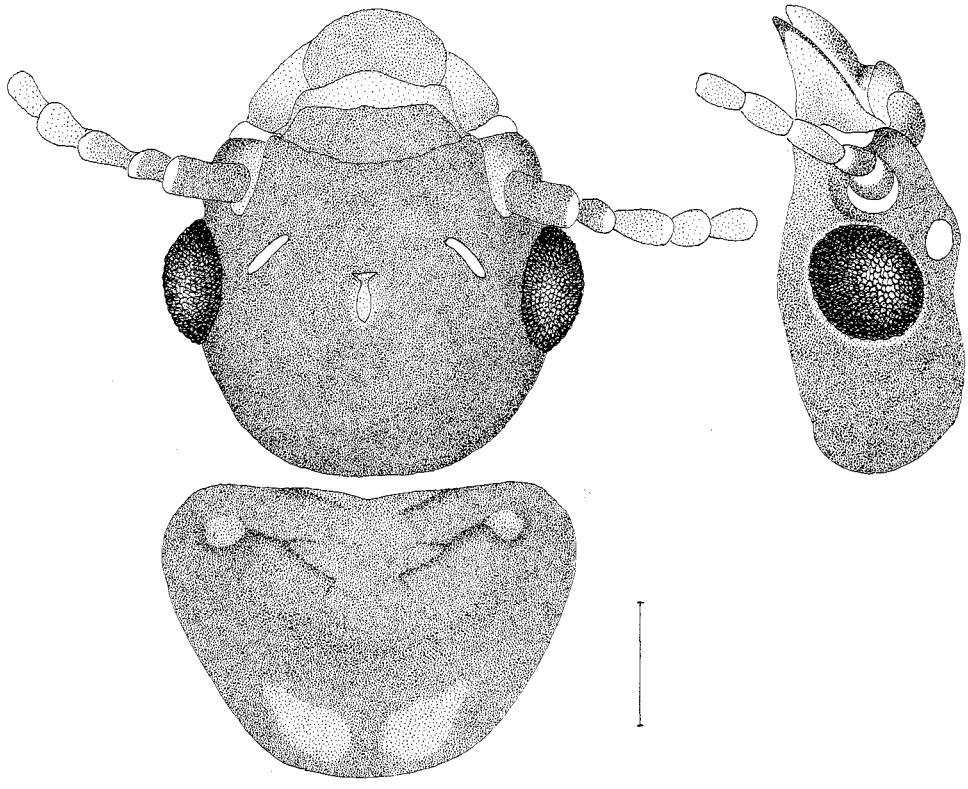


Fig. 126. *Hospitalitermes papuanus* (Ahmad), female alate: head capsule and pronotum from above, head capsule in profile. Scale bar = 0·5 mm.

segment 3, turning ferruginous orange on following segments. Pronotum very dark chestnut along anterior margin, chestnut in middle. Meso- and metanotum ferruginous orange. Lateral thoracic sclerites, coxae and femora sepia. Tibiae diagnostic: whitish except on both extremities, pale brown on femoral end, orange on tarsal end. Abdominal tergites very dark sepia brown, sternites dark sepia on sides, orange to sepia in middle. Wings brown, smoky, slightly paler along coastal margin.

Head capsule evenly rounded posteriorly, eyes medium-sized, moderately prominent. Fontanelle ovalate, shorter than ocelli, hyaline in females, tending to be smoky and narrower in males. Ocelli elongated, distant from eyes by more than smaller and less than larger own diameter. Antennae of 15 segments, segment 3 slightly longer than segments 2 and 4.

	Measurements (in mm)			
	Females (4 alates from nest PNGT#1728)		Males (4 alates from nest PNGT#1728)	
	Range	Mean	Range	Mean
Head width across eyes	1·716–1·764	1·731	1·748–1·777	1·762
Largest diameter of eye	0·548–0·564	0·559	0·564–0·579	0·572
Length of ocellus	0·188–0·220	0·203	0·227–0·246	0·235
Eye to ocellus	0·130–0·163	0·144	0·125–0·149	0·134
Pronotum width	1·665–1·717	1·702	1·558–1·584	1·571
Pronotum length	1·231–1·277	1·258	1·102–1·154	1·126
Hind tibia length	2·72–2·75	2·74	2·43–2·53	2·49
Forewing scale length	1·168–1·198	1·184	1·093–1·144	1·121
Forewing length	14·8–16·2	15·5	13·5–14·2	13·9

Soldier (Fig. 127)

Head capsule is pitch black in our specimens, with tip of rostrum ferruginous. Our samples match the original description of the species, apart from being darker coloured, but this difference may be due to colour fading in alcohol-preserved specimens.

Measurements (in mm) of 21 individuals from 7 colonies		
	Range	Mean
Head capsule total length	1·694–1·944	1·821
Rostrum length	0·666–0·783	0·715
'Back of head' distance	0·354–0·483	0·399
Head width	1·036–1·280	1·139
Rostrum width (at half length)	0·128–0·158	0·140
Head depth	0·808–0·996	0·880
Hind tibia length	2·313–2·655	2·473

Worker (previously undescribed) (Figs 128–130)

Head capsule pitch black, with neat pale sutures. Thorax and abdominal tergites dark sepia, sternites sepia brown. Legs and antennae extremely long, antennae 15-segmented. Mandibles as in Fig. 128, with apical tooth strongly deflected downwards and long molar plate. Digestive tract configured as in Fig. 130, conforming to description given by Kovoor (1969) for *H. ataramensis*. The crop can be very voluminous. Mesenteric part of mixed segment attached to main body of mesenteron by wide peduncle. Malpighian tubules attached as two widely separated pairs. Enteric valve (Fig. 129): upper ring wide and long, formed by diffuse areas garnished with numerous small spines, extending on a longer distance on the external side of the gut curve; lower ring formed by three strong swellings bearing short, stout spines on their upper part, alternating with non-sclerotised areas with a few tiny spines.

Head width of workers from nest PNGT#1728: small workers, first instar, 0·857–0·929 (mean = 0·896, n = 38); large workers, first instar, 1·017–1·121 (mean = 1·077, n = 83); instar 2 and older, 1·154–1·237 (mean = 1·203, n = 29).

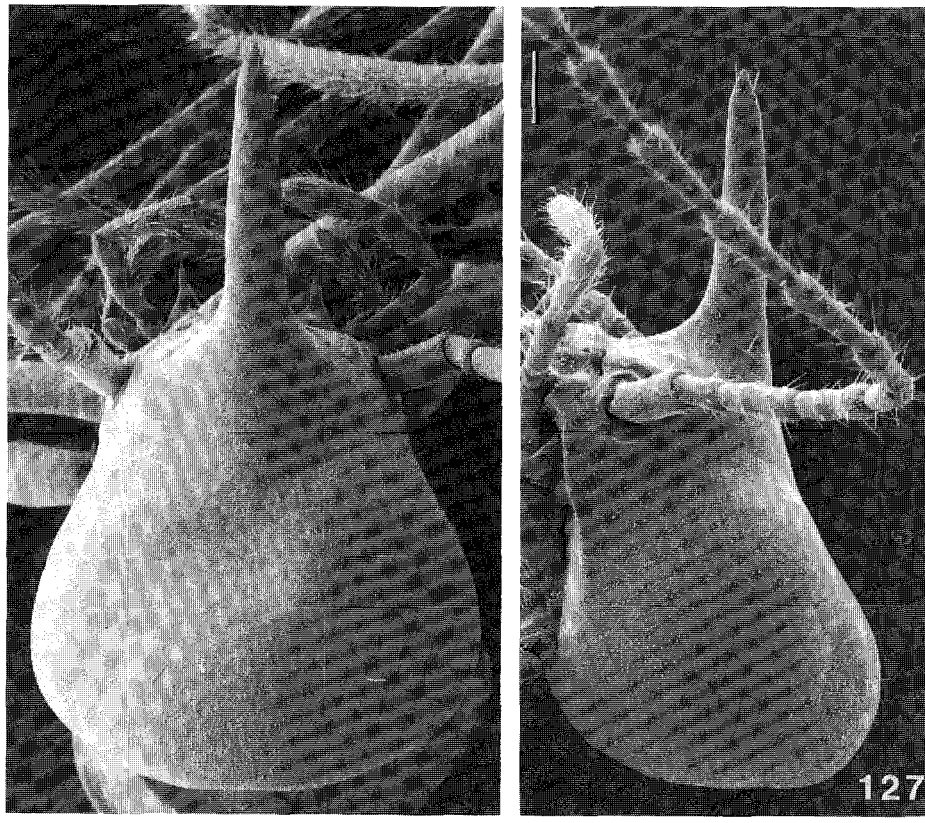


Fig. 127. *Hospitalitermes papuanus* (Ahmad): soldier head from above (left) and in profile (right). Scale bar = 0·2 mm.

Distribution (Fig. 131)

Type locality: Strickland River (no additional precision). Some of our samples come from Nomad River Station, situated about 16 km west of Strickland River. Also present in the Morehead area and on the north slope of the Central Ranges, in Yapsiei, near border with Irian Jaya.

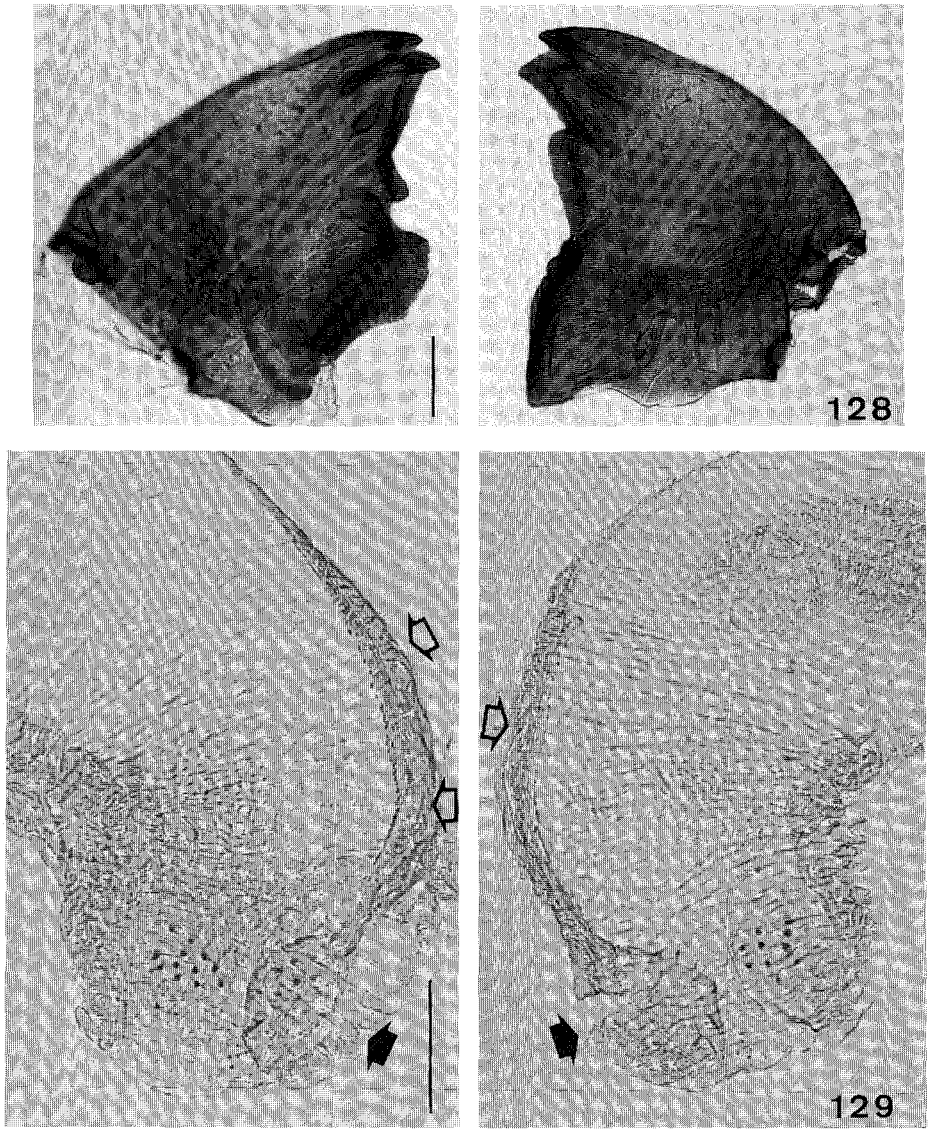
Biology

This species commonly forages along uncovered trails 1–3 cm wide in the daylight in the forest. Trails were observed on which some workers were carrying greyish green particles (probably lichens) between their mandibles. One nest was found in Yapsiei (PNGT#1728). Its location was discovered by following numerous collection trails, without carton cover, which converged towards the base of a dead tree and from there climbed towards an epiphytic bush, at a height of 15–20 m. The nest was made of brittle black carton intermingled with the roots of this epiphyte. There was no royal cell; the queen was found among debris in the central part of the nest.

Related Allopatric Species

Hospitalitermes irianensis Roonwal & Maiti

Hospitalitermes irianensis Roonwal and Maiti, 1966: 131–137, figs 11, 12, tables 11, 12. Soldier, major worker, minor worker.



Figs 128, 129. *Hospitalitermes papuanus* (Ahmad), large worker: *128*, mandibles; *129* armature of enteric valve. Open arrows, upper ring of spiny areas; closed arrows, lower ring. Scale bars = 0·1 mm.

Hospitalitermes irianensis is described from its type locality only: Meervlakte, Indenburg River, Irian Jaya, 3°20′S, 139°E. The following diagnostic features of the soldier were mentioned by Roonwal and Maiti (1966).

	H. irianensis	*H. papuanus*
Head profile	strongly concave	moderately concave
Low hump at rostrum base	absent	present
Head shape	drawn, narrowly rounded behind	not drawn, broadly rounded behind
Rostrum	cylindrical	almost conical
Apical portion of mandibles	long and slender	short and sharply pointed

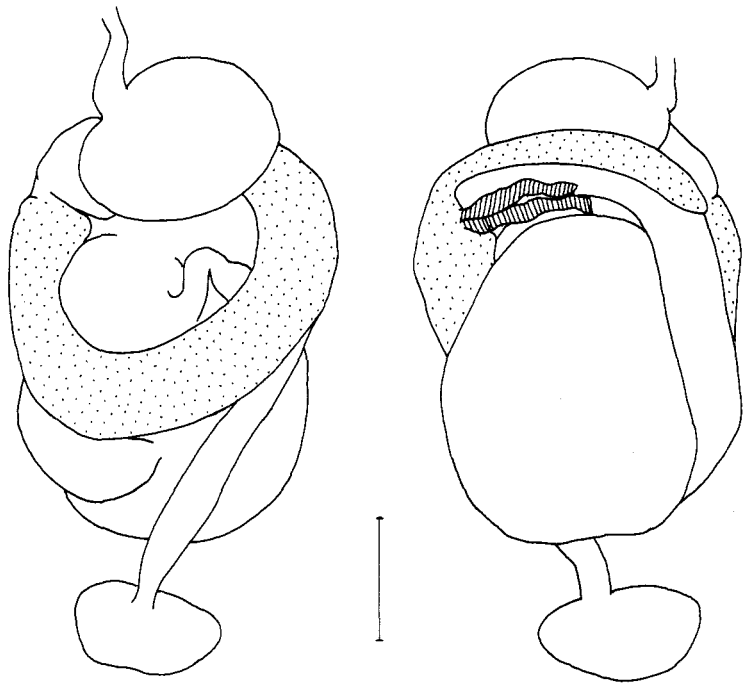


Fig. 130. *Hospitalitermes papuanus* (Ahmad), large worker: dorsal and ventral view of gut *in situ*. Scale bar = 0·5 mm. Mesenteron stippled, malpighian tubules hatched.

These criteria allow for much subjectivity in their interpretation. All our *Hospitalitermes* samples fit the description of *H. papuanus* at least as well as that of *H. irianensis*. Our specimens from Yapsiei, situated north of the Central Ranges and less than 300 km away from the type locality of *H. irianensis*, cannot be distinguished by any consistent criteria from those of the Fly Plains. For this reason, we assigned all our specimens to *H. papuanus*. *H. irianensis* might be a junior synonym of *H. papuanus*, but this hypothesis could only be tested when the types of *H. irianensis* and additional material from Irian Jaya are examined.

Key to the Nasutitermitinae from Papua New Guinea, Based on Soldiers and Workers

1. Soldier and all workers: head very dark sepia brown to black, thoracic and abdominal tergites sepia to dark sepia brown. Legs and antennae very long. Worker left mandible: apical tooth deflected downwards. Right mandible: molar plate convex and long. Often encountered by day, walking in huge columns along wide (1–3 cm), long (several metres) open-air trails in the forest 2

   Soldier head capsule from pale yellow to very dark (almost black) brown. Worker head colour variable, yellow–white to ferruginous in the first instar, darker in the older instars. Thoracic and abdominal tergites from translucent to brown. Worker left mandible: apical tooth not deflected. Right mandible: molar plate straight or slightly concave, and short. Rarely seen foraging in the daylight without cover, and always over short distances 3

2. Soldier: rostrum thin, almost cylindrical. Head capsule strongly constricted behind antennae (Fig. 127). Abdominal sternites sepia brown, almost as dark as tergites ..... *Hospitalitermes papuanus*

   Soldier: rostrum stout, broadly conical. Head capsule slightly constricted behind antennae (Fig. 122). Abdominal sternites pale brown, translucent, much paler than tergites ... *Grallatotermes grallator*

3. Soldier: antennae of 11 or 12 segments; if of 12 segments, segment 3 very short and not completely separated from segment 4 (Fig. 111). Worker digestive tract: mesenteric part of mixed segment on inner side of gut curve. The four malpighian tubules converging towards attachment to mesentero-proctodeal junction. Armature of enteric valve penetrating into the paunch .... *Diwaitermes* ... 4

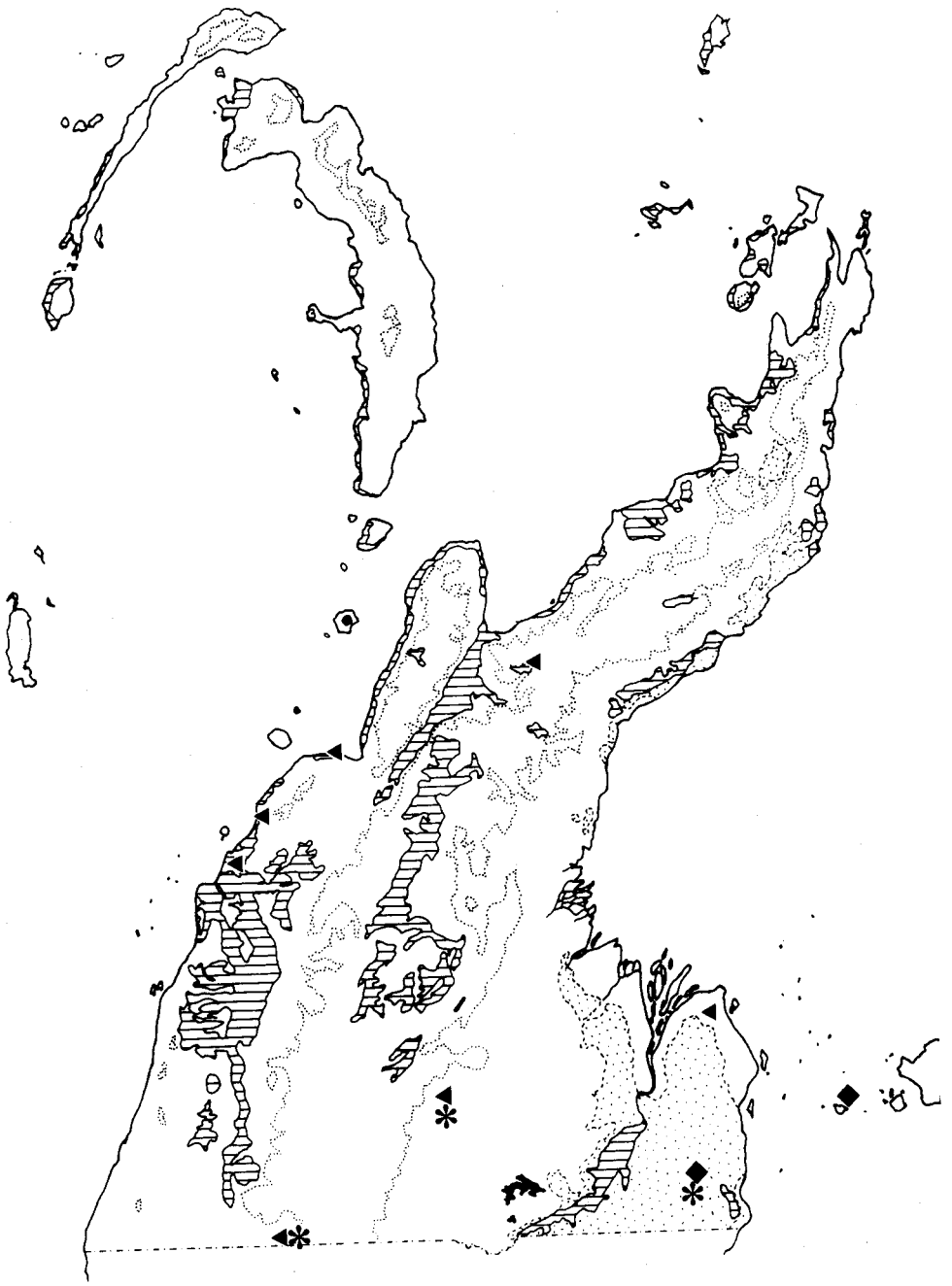


Fig. 131. Known distributions within Papua New Guinea and Torres Strait of *Tumulitermes marcidus* (◆), *Grallatotermes grallator* (▲) and *Hospitalitermes papuanus* (*).

Soldier with at least 12 well-separated antennal segments. Worker digestive tract: mesenteric part of mixed segment on outer or upper side of gut curve. Malpighian tubules running along the proctodeum as two separated pairs, usually attached separately; in a few cases, the two pairs of tubules converge and join the gut almost at the same point. Armature of enteric valve not penetrating into the paunch 6

4. Larger species: soldier head capsule length > 1·5 mm, width > 0·85 mm. Antennae of 12 segments, segment 3 very small and incompletely separated from segment 4 (Fig. 111). Lower montane forests ..... *Diwaitermes castanopsis*
   Smaller species, soldier head capsule length < 1·5 mm, width < 0·85 mm. Antennae of 11 segments ... 5
5. Soldier head capsule yellow, > 1·35 mm long. Hill forest, Southern Highlands ..... *D. foi*
   Soldier head capsule variable in colour, < 1·35 mm long. Lowlands and lower hills ..... *D. kanehirae*
6. Worker: colon long, forming a 3-dimensional S on top and right side of paunch, before proceeding towards the rectum (Fig. 90). Antennae 13-segmented. Soldier: small to medium-sized, orange, with 12-segmented antennae ..... *Niuginitermes* ... 7
   Worker: colon shorter, forming a smooth curve from paunch to rectum (Figs 14, 49). Antennae of 14–15 segments (segment 4 sometimes very small and incompletely separated from segments 3 and 5, especially in young instars). Soldier variable, with antennae of 12–14 segments 8
7. Smaller species, soldier head capsule length < 1·3 mm, width < 0·72 mm, with more than 10 long setae ..... *Niuginitermes liklik*
   Larger species, soldier head capsule length > 1·3 mm, width > 0·72 mm, with 10 or fewer long setae .. .. *N. variratae*
8. Soldier head capsule dark brown to blackish, with more than 10 long, erect setae. Antennae of 13–14 segments 9
   Soldier head capsule with 10 or fewer long setae; sometimes with distinct yellow tinge. Antennae of 12–13 segments ..... *Nasutitermes* ... 13
9. Soldier: head capsule constricted behind antennae (Fig. 117; if in doubt, tilt soldier's head backwards). Mandibles usually without points. Hind tibia length < 1·15 mm. Worker: all 4 malpighian tubules attached contiguously at mesentero-proctodeal junction ..... *Tumulitermes marcidus*
   Soldier: head capsule not constricted behind antennae. Mandibles with points. Hind tibia length > 1·15 mm. Worker: malpighian tubules attached at mesentero-proctodeal junction as two pairs, almost diametrally opposed ..... *Nasutitermes* ... 10
10. Soldier: antennae of 13 segments. Forested lowlands ..... *Nasutitermes princeps*
    Soldier: antennae of 14 segments (segment 3 sometimes incompletely separated from segment 4) Southern savannas 11
11. Appendages very long. Hind tibia length of soldier > 1·6 mm. Fly Plains ..... *N. triodiae*
    Appendages shorter. Hind tibia length of soldier < 1·6 mm 12
12. Soldier: antennae sepia brown, conspicuously darker than legs. Segments 3 and 4 well separated. Abdominal tergites sepia, without yellow tinge. Fly Plains ..... *N. torresi*
    Soldier: antennae yellow-brown, almost of the same colour as legs. Segment 3 incompletely separated from segment 4. Abdominal tergites yellow–brown. Fly Plains and Eastern Papuan savannas .... *N. motu*
13. Soldier head capsule chestnut brown, acute triangular, with extremely long rostrum (Fig. 28). Head capsule length > 1·9 mm, length/width > 1·85, width of rostrum at half length/head width < 0·15 .. .. *N. pinocchio*
    Soldier different 14
14. Soldier head capsule chestnut to dark sepia brown, without yellow tinge 15
    Soldier head capsule yellow to ferruginous, with distinct yellow tinge 19
15. Soldier head capsule with 4 long setae forming a rectangle on vertex. Southern New Guinea 16
    Soldier head capsule with 2 long setae on vertex 17
16. Soldier: abdominal tergites with two rows of numerous (about 12) erect setae. Body orange–yellow to ferruginous-orange, contrasting sharply with very dark (almost black) head capsule ..... *N. koiari*
    Soldier: abdominal tergites with one row of usually 6 erect setae. Body chestnut brown, only slightly paler than head capsule ..... *N. nomadensis*
17. Soldier: rostrum narrow, < 0·14 mm wide at half length. Southern New Guinea ..... *N. muli*
    Soldier: rostrum > 0·14 mm wide at half length 18
18. Soldier head capsule dark chestnut brown, broad, regularly rounded behind, body ferruginous ..... *N. novarumhebridarum*
    Soldier head capsule sepia brown, with reddish tinge on rostrum, slightly flattened posteriorly, body pale brown ..... *N. polygynus*
19. Soldier rostrum long and thick (Fig. 46). Rostrum width (at half length)/head width > 0·154. Two long setae on vertex ..... *N. bikpelanus*
    Soldier rostrum not so long and thick. Rostrum width (at half length)/head width < 0·155 20

20. Soldier head capsule with 4 long setae on vertex, 2 lateral ones, and many smaller hairs reaching >1/3 length of major setae. Northern New Guinea, New Ireland ..... *N. seghersi*
Soldier head capsule with 2 long setae on vertex, and sometimes 2 lateral ones. Shorter hairs hardly visible under dissecting microscope 21
21. Soldier head capsule with two long setae on vertex and two lateral ones. Southern New Guinea ..... *N. leponcei*
Soldier head capsule with two long setae on vertex and no lateral ones 22
22. Soldier head capsule orange. Rostrum length < 0·785 mm. Head width usually < 0·95 mm. Northern New Guinea ..... *N. gracilirostris*
Soldier head capsule ferruginous to chestnut brown. Rostrum length > 0·785 mm. Head width usually > 0·95 mm. Southern New Guinea ..... *N. muli*

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References

Ahmad, M. (1947). New termites from the Indo-Malayan and Papuan regions. *American Museum Novitates* **1342**, 1–7.

Ahmad, M. (1950). The phylogeny of termite genera based on imago-worker mandibles. *Bulletin of the American Museum of Natural History* **95**, 37–86.

Ahmad, M. (1968). Termites of Malaysia. I. Nasute genera related to *Subulitermes* (Isoptera, Termitidae, Nasutitermitinae). *Bulletin of the Department of Zoology University of the Panjab (New Series)* **3**, 1–34.

Barrett, J. H. (1965). The occurrence of termites in the New Guinea Highlands. *Papua and New Guinea Agricultural Journal* **17**, 95–8.

Bathellier, J. (1927). Contribution à l'étude systématique et biologique des termites de l'Indochine. *Faune des Colonies Françaises* **1**, 121–369.

Braekman, J. C., Daloze, D., Dupont, A., Pasteels, J., Tursch, B., Declercq, J. P., Germain, G., and Van Meersche, M. (1980). Secotrinervitane, a novel bicyclic diterpene skeleton from a termite soldier. *Tetrahedron Letters* **21**, 2761–2.

Chuah, C. H., Goh, S. H., and Tho, Y. P. (1989). Interspecific variation in defense secretions of Malaysian termites from the genus *Nasutitermes* (Isoptera, Nasutitermitinae). *Journal of Chemical Ecology* **15**, 549–63.

De Baar, M. (1988). Insects collected during a trip to Torres Strait 27 March to 10 April, 1987. *Entomological Society of Queensland News Bulletin* **15**, 107–17.

Desneux, J. (1905). Isoptera of New Guinea collected by L. Biró. *Annales Historico-Naturales Musei Nationalis Hungarici* **3**, 367–77.

Dudley, P. H., and Beaumont, J. (1890). Termites of the isthmus of Panama. Part II. *Transactions of the New York Academy of Sciences* **9**, 157–80.

Dupont A., Braekman, J.-C., Daloze, D., Pasteels, J. M., and Tursch, B. (1981). Chemical composition of the frontal gland secretions from Neo-Guinean nasute termite soldiers. *Bulletin des Sociétés Chimiques Belges* **90**, 485–99.

Emerson, A. E. (1960). New genera of termites related to *Subulitermes* from the Oriental, Malagasy, and Australian regions (Isoptera, Termitidae, Nasutitermitinae). *American Museum Novitates* **1986**, 1–28.

Everaerts, C., Pasteels, J. M., Roisin, Y., and Bonnard, O. (1988). The monoterpenoid fraction of the defensive secretion in Nasutitermitinae from Papua New Guinea. *Biochemical Systematics and Ecology* **16**, 437–44.

Everaerts, C., Roisin, Y., Le Quéré, J.-L., Bonnard, O., and Pasteels, J. M. (1993). Sesquiterpenes in the frontal gland secretions of nasute soldier termites from New Guinea. *Journal of Chemical Ecology* **19**, 2865–79.

Froggatt, W. W. (1897). Australian Termitidae. Part III. *Proceedings of the Linnean Society of New South Wales* **22**, 721–58.

Gay, F. J. (1971). Notes on *Grallatotermes grallator* (Desneux) and the taxonomic status of the genus *Grallatotermes* (Isoptera: Termitidae: Nasutitermitinae). *Pacific Insects* **13**, 41–8.

Goh, S. H., Chuah, C. H., Tho, Y. P., and Prestwich, G. D. (1984). Extreme intraspecific chemical variability in soldier defense secretions of allopatric and sympatric colonies of *Longipeditermes longipes*. *Journal of Chemical Ecology* **10**, 929–44.

Harris, W. V., and Brown, E. S. (1958). The termites of the Solomon Islands. *Bulletin of Entomological Research* **49**, 737–50.

Haviland, G. D. (1898). Observations on termites; with descriptions of new species. *Journal of the Linnean Society (Zoology)* **26**, 358–442.

Hill, G. F. (1925). Termites from the Australian Region: descriptions of new species and hitherto undescribed castes. *Proceedings of the Royal Society of Victoria (New Series)* **37**, 206–29.

Hill, G. F. (1927). Termites from the Australian Region. Part I. *Memoirs of the National Museum, Melbourne* **7**, 5–120.

Hill, G. F. (1942). 'Termites from the Australian Region.' (C.S.I.R.: Melbourne.)

Holmgren, N. (1911). Neu-Guinea Termiten. *Mitteilungen aus dem Zoologischen Museum in Berlin* **5**, 452–65.

Holmgren, N. (1912). Termitenstudien. 3. Systematik der Termiten. Die Familie Metatermitidae. *Kungliga Svenska Vetenskapsakademiens Handlingar* **48** (4), 1–166.

Holmgren, N. (1913). Termitenstudien. 4. Versuch einer systematischen Monographie der Termiten der Orientalischen Region. *Kungliga Svenska Vetenskapsakademiens Handlingar* **50** (2), 1–276.

Holmgren, N., and Holmgren, K. (1915). Termiten aus Neu-Caledonien und den benachbarten Inselgruppen. *Nova Caledonia Zoologie* **2**, 85–93.

Jacobson, H. R., and Pasteels, J. M. (1985). A new termitophilous species of *Termitoptocinus* Silvestri from New Guinea and a redescription of the genus (Coleoptera, Staphylinidae, Aleocharinae, Corotocini). *Indo-Malayan Zoology* **2**, 319–23.

Jacobson, H. R., and Pasteels, J. M. (1992). Staphylins termitophiles de Nouvelle-Guinée: une nouvelle espèce de *Termitoptocinus* et *Nasutiptochus* nn. nov. (Coleoptera, Staphylinidae, Corotocini). *Sociobiology* **20**, 49–55.

John, O. (1925). Termiten von Ceylon, der Malayischen Halbinsel, Sumatra, Java und den Aru-Inseln. *Treubia* **6**, 360–419.

Johnson, R. A. (1979). Configuration of the digestive tube as an aid to identification of worker Termitidae (Isoptera). *Systematic Entomology* **4**, 31–8.

Kemner, N. A. (1931). Die Termitenfauna von Amboina. *Lunds Universitets Årsskrift (N.F.) Avdeling 2* **27** (13), 1–53.

Kistner, D. H. (1972). Termitophiles from nests of *Nasutitermes* collected by Alfred E. Emerson in the Orient (Coleoptera: Staphylinidae). *Pacific Insects* **14**, 679–96.

Kovoor, J. (1969). Anatomie comparée du tube digestif des termites. II.- Sous-famille des Nasutitermitinae. *Insectes Sociaux* **16**, 195–234.

Leponce, M., Roisin, Y., and Pasteels, J. M. (1995). Environmental influences on the arboreal nesting community in New Guinean coconut plantations. *Environmental Entomology* **24**, 1442–52.

Leponce, M., Roisin, Y., and Pasteels, J. M. (1996). Structure and dynamics of the arboreal termite community in New Guinean coconut plantations. *Biotropica* **28**, in press.

Light, S. F. (1930). Notes on Philippine termites, IV. *Philippine Journal of Science* **42**, 13–58.

Light, S. F. and Wilson, F. J. (1936). The nasute termites of the Philippines. *Philippine Journal of Science* **60**, 461–520.

Miller, L. R. (1984). The Australian genera of the *Subulitermes* branch of the Nasutitermitinae (Isoptera: Termitidae). *Journal of the Australian Entomological Society* **23**, 119–25.

Miller, L. R. (1986). The phylogeny of the Nasutitermitinae (Isoptera: Termitidae). *Sociobiology* **11**, 203–14.

Noirot, C. (1955). Recherches sur le polymorphisme des termites supérieurs (Termitidae). *Annales des Sciences Naturelles, Zoologie* **17**, 399–595.

Noirot, C., and Noirot-Timothée, C. (1969). The digestive system. In 'Biology of Termites. Vol. I'. (Eds K. Krishna and F. M. Weesner.) pp. 49–88. (Academic Press: New York.)

Oshima, M. (1914). Notes on a collection of termites from the East Indian Archipelago. *Annotationes Zoologicae Japonicae* **8**, 553–85.

Oshima, M. (1917). Three new species of termites from the Caroline Islands. *Annotationes Zoologicae Japonicae* **9**, 195–200.

Oshima, M. (1923). Fauna Simalurensis Termitidae. *Capita Zoologica* **11** (3), 1–22.

Pasteels, J. M. (1965). Polyéthisme chez les ouvriers de *Nasutitermes lujae* (Termitidae Isoptères). *Biologia Gabonica* **1**, 191–205.

Pasteels, J. M., and Jacobson, H. R. (1984). The termitophilous Corotocina from Papua New Guinea (Coleoptera, Staphylinidae, Aleocharinae, Corotocini). *Indo-Malayan Zoology* **1**, 195–208.

Pasteels, J. M., Roisin, Y., Everaerts, C., Bonnard, O., Braekman, J.-C., and Daloze, D. (1988). Morphological and chemical criteria in the taxonomy of *Nasutitermes* in Papua New Guinea (Isoptera: Termitidae). *Sociobiology* **14**, 193–206.

Robbins, R. (1974). Vegetation. In 'Papua New Guinea Resource Atlas'. (Ed. E. Ford.) pp. 12–13. (The Jacaranda Press: Milton, Queensland.)

Roisin, Y. (1987). Polygyny in *Nasutitermes* species: field data and theoretical approaches. In 'From Individual to Collective Behavior in Social Insects'. (Eds J. M. Pasteels and J.-L. Deneubourg.) pp. 379–404. (Birkhäuser Verlag: Basel.)

Roisin, Y. (1993). Selective pressures on pleometrosis and secondary polygyny: a comparison of termites and ants. In 'Queen Number and Sociality in Insects'. (Ed. L. Keller.) pp. 402–21. (Oxford University Press: Oxford, UK.)

Roisin, Y., and Pasteels, J. M. (1985*a*). A new *Nasutitermes* species from New Guinea (Isoptera: Termitidae). *Indo-Malayan Zoology* **2**, 325–30.

Roisin, Y., and Pasteels, J. M. (1985*b*). Imaginal polymorphism and polygyny in the Neo-Guinean termite *Nasutitermes princeps* (Desneux). *Insectes Sociaux* **32**, 140–57.

Roisin, Y., and Pasteels, J. M. (1986*a*). Differentiation of worker-derived intercastes and precocious imagoes after queen removal in the Neo-Guinean termite *Nasutitermes princeps* (Desneux). *Journal of Morphology* **189**, 281–93.

Roisin, Y., and Pasteels, J. M. (1986*b*). Replacement of reproductives in *Nasutitermes princeps* (Desneux) (Isoptera: Termitidae). *Behavioral Ecology and Sociobiology* **18**, 437–44.

Roisin, Y., and Pasteels, J. M. (1986*c*). Reproductive mechanisms in termites: polycalism and polygyny in *Nasutitermes polygynus* and *Nasutitermes costalis*. *Insectes Sociaux* **33**, 149–67.

Roisin, Y., and Pasteels, J. M. (1987). Caste developmental potentialities in the termite *Nasutitermes novarumhebridarum*. *Entomologia Experimentalis et Applicata* **44**, 277–87.

Roisin, Y., Pasteels, J. M., and Braekman, J.-C. (1987). Soldier diterpene pattern in relation with aggressive behaviour, spatial distribution and reproduction of colonies in *Nasutitermes princeps*. *Biochemical Systematics and Ecology* **15**, 253–61.

Roisin, Y., Everaerts, C., Pasteels, J. M., and Bonnard, O. (1990). Caste-dependent reactions to soldier defensive secretion and chiral alarm/recruitment pheromone in *Nasutitermes princeps*. *Journal of Chemical Ecology* **16**, 2865–75.

Roonwal, M. L. and Maiti, P. K. (1966). Termites from Indonesia including West Irian. *Treubia* **27**, 63–140.

Sands, W. A. (1965). A revision of the termite subfamily Nasutitermitinae (Isoptera, Termitidae) from the Ethiopian Region. *Bulletin of the British Museum (Natural History) Entomology* Supplement 4, 1–172.

Sands, W. A. (1972). The soldierless termites of Africa (Isoptera: Termitidae). *Bulletin of the British Museum (Natural History) Entomology* Supplement 18, 1–244.

Seevers, C. H. (1937). New species of termitophilous Staphylinidae from tropical America and the Solomon Islands. *Annals of the Entomological Society of America* **30**, 1–23.

Snyder, T. E. (1925). New termites from the Solomon Islands and Santa Cruz Archipelago. II. *Journal of the Washington Academy of Sciences* **15**, 438–44.

Snyder, T. E. (1949). Catalog of the termites (Isoptera) of the world. *Smithsonian Miscellaneous Collections* **112**, 1–490.

Szent-Ivany, J. J. H. (1956). New insect pests and host plant records in the Territory of Papua and New Guinea. *Papua and New Guinea Agricultural Journal* **11**, 82–7.

Thapa, R. S. (1982). Termites of Sabah (East Malaysia). *Sabah Forest Record* **12**, 1–374.

Valterová, I., Křeček, J., and Vrkoč, J. (1989). Intraspecific variation in the defence secretions of *Nasutitermes ephratae* soldiers and the biological activity of some of their components. *Biochemical Systematics and Ecology* **17**, 327–32.

Watson, J. A. L. and Abbey, H. M. (1993). 'Atlas of Australian Termites.' (CSIRO: Melbourne.)

Watson, J. A. L., Miller, L. R., and Abbey, H. M. (in press). Isoptera. In 'Zoological Catalogue of Australia. Vol. 23. Archaeognatha, Thysanura, Blattodea, Isoptera, Mantodea, Dermaptera, Phasmatodea, Embioptera, Zoraptera'. (Ed. W. W. K. Houston.) (CSIRO: Melbourne.)

Appendix. Checklist of genera and species of Nasutitermitinae from Papua New Guinea

Asterisks indicate type species; indented species are synonyms; square brackets indicate related taxa of neighbouring areas

***Nasutitermes* Dudley, 1890**
N. triodiae (Froggatt, 1898)
N. torresi (Hill, 1942)
N. motu, sp. nov.
N. princeps (Desneux, 1905)
N. koiari, sp. nov.
[*N. graveolus* (Hill, 1925)]
N. pinocchio, sp. nov.
N. novarumhebridarum (N. Holmgren & K. Holmgren, 1915)
[*N. matangensis* (Haviland,1898)]
[*N. brevirostris* (Oshima, 1917)]
[*N. amboinensis* (Kemner, 1931)]
N. nomadensis, sp. nov.
N. polygynus Roisin & Pasteels, 1985
N. bikpelanus, sp. nov.
N. gracilirostris (Desneux, 1905)
N. leponcei, sp. nov.
N. muli, sp. nov.
N. seghersi, sp. nov.
N. seghersi malangganus, subsp. nov.
[*N. retus* (Kemner, 1931)]

***Niuginitermes*, gen. nov.**
**N. variratae*, sp. nov.
N. liklik, sp. nov.

***Diwaitermes*, gen. nov.**
D. kanehirae (Oshima, 1914), comb. nov.
[**Nasutitermes orientis* Snyder, 1925]
[*N. orientis tulagiensis* Snyder, 1925]
[*N. sanctaecrucis* Snyder, 1925]
N. rufirostris (Hill, 1927)
N. kaewiengensis (Hill, 1927)
[*N. undecimus* (Kemner, 1931)]
D. foi, sp. nov.
D. castanopsis, sp. nov.

***Tumulitermes* Holmgren, 1912**
T. marcidus (Hill, 1942)

***Grallatotermes* Holmgren, 1912**
**G. grallator* (Desneux, 1905)
[*G. weyeri* Kemner, 1931]

***Hospitalitermes* Holmgren, 1912**
H. papuanus Ahmad, 1947
[*H. irianensis* Roonwal & Maiti, 1966]

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