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**THE DISTRIBUTION OF *NASUTE TERMITES*  
(ISOPTERA, TERMITIDAE, NASUTITERMITINAE)  
IN THE ETHIOPIAN ZOOGEOGRAPHICAL REGION**

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INTRODUCTION

The Ethiopian Zoogeographical Region consists of the African continent south of the Sahara Desert, and those adjacent parts of the Arabian peninsula where the climate permits the survival of African species. Extensive collections of termites are now available from Africa and a detailed revision of the subfamily Nasutitermitinae as it occurs in this region has recently been made. The subfamily Nasutitermitinae is characterized in the « Old World » by the adaptation of the head capsule of the soldier caste to a chemical mode of defence. The mandibles are reduced to vestiges, and the frons and vertex of the head capsule drawn out into a tubular nose terminating in the opening of the frontal gland from which a sticky fluid is ejected upon any attacker.

In the course of revision 120 previously described species were reduced by synonymy to 40, and 8 new species were described, bringing the total of valid species to 48, belonging to 14 genera. These conclusions were based on a study of 2410 nest series from all parts of Africa. As a result the distribution patterns of the genera and species have become clearer and it is now possible to relate them to the zonation of the vegetation types, which provide the best ecological basis for defining biotic subdivisions of the Ethiopian Zoogeographical Region (*Fig. 1*).

RELATIONSHIPS OF *NASUTE TERMITE* GENERA

The distribution of genera and species is most readily appreciated in the context of their probable relationships, and an outline of these is needed before proceeding with the discussion of distribution. AHMAD (1950) postulated the division of the subfamily into two branches at an early stage in its evolution. Subsequent studies (SANDS, 1957, 1965) have supported this fundamental division, which appears to have arisen because one branch became adapted to feeding on soil humus, whilst the other, and larger section of the subfamily was originally less

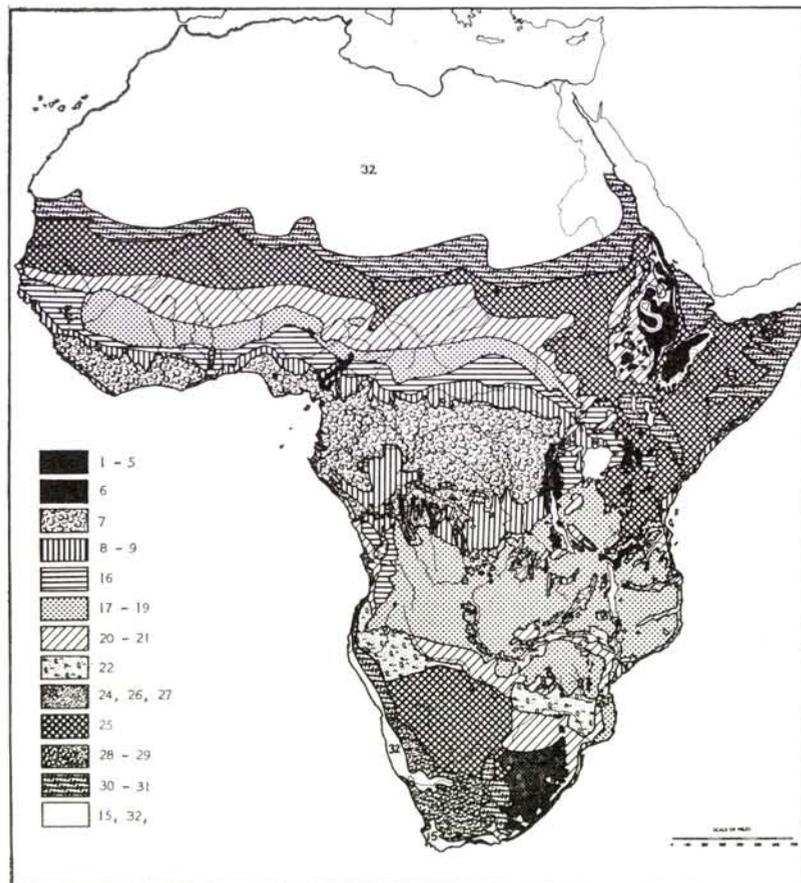


FIGURE 1.

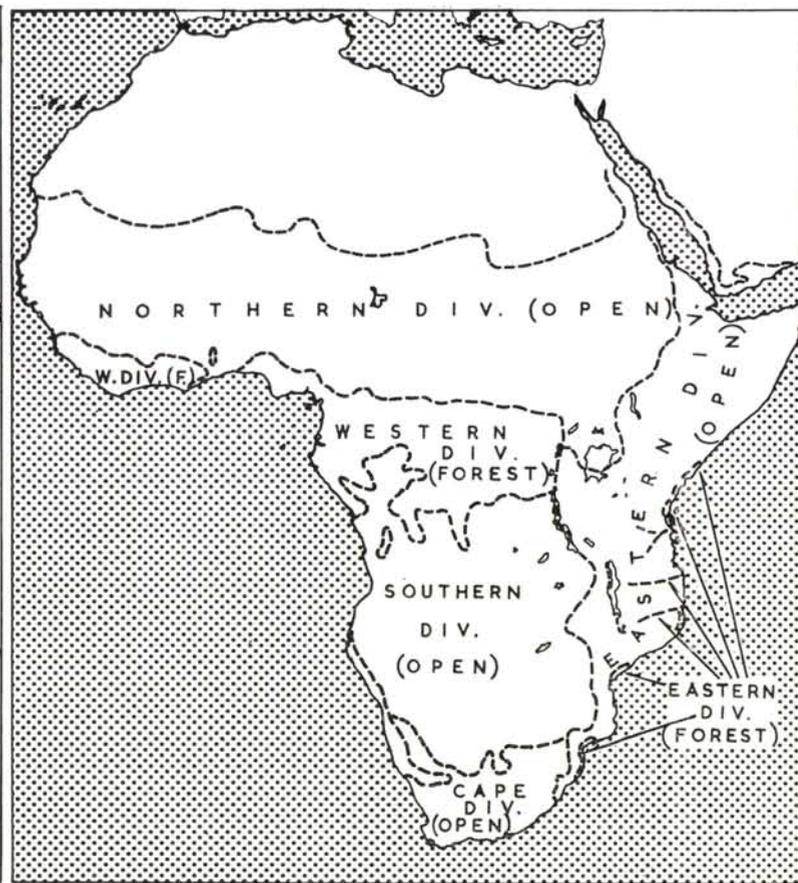


FIGURE 2.

specialised, and its members diverged to fit many ecological niches. Early division is indicated because all the stages in the development of the nasus and the reduction of the mandibles of the soldier caste are represented by extant species in both branches. It is customary to refer to each branch by the name of its most « primitive » genus : these are the Neotropical *Procornitermes* and *Paracornitermes*, the latter being the humus-feeding branch. The probable relationships of the Ethiopian species are shown as a dendrogram in figure 3. This is based on morphological, biological, and ecological similarities and differences, but it is qualitative in nature and does not attempt to quantify degrees of relatedness beyond the level of « more » or « less ». Genera from other regions are omitted for simplicity, so that some relationships appear more direct than they are in reality. The possible polyphyletic origin of *Nasutitermes* is suggested because the genus includes markedly different species resembling several subsidiary divisions of the « *Procornitermes* » branch. Some of them show traces of polymorphism in the derivation of the soldier caste from different instars. In a recent paper, SEN-SARMA (1966) has rearranged the genus *Grallatotermes* into what he terms the « *Grallatotermes*-complex », consisting of three monotypic genera and one with two species. Only *G. admirabilis* Light (« *Philippinitermes* ») is left in the « *Procornitermes* » branch, the other four species being assigned to the « *Paracornitermes* » branch. This was done because in these four the left mandible of the imago and worker castes bears an indentation in the cutting edge between first and third marginal teeth, just distal to the latter. This character has been shown (SANDS, 1965) to be invalid in this context, and the two phylogenetic branches were re-defined as indicated above, on the basis of feeding habits and molar structure. The theoretical diphyletic descent of the subfamily is an interesting and useful speculation. However, it can only lead to confusion if such arbitrary changes are made without reference to current opinion or understanding of the wider phylogenetic background of the subfamily as a whole. The subdivision of the genus *Grallatotermes* is moreover scarcely justified on taxonomic grounds. All the species previously included are clearly closely related, although exhibiting different specialisations such as might be expected in a widely disper-

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FIG. 1. — Vegetation of Africa south of the Sahara Desert (slightly modified from Keay et al., 1959). Vegetation types 1-5, Montane; 6, subtropical grassland; 7, tropical lowland forest; 8, 9, savanna-forest mosaic; 16, moist savanna; 17-19, moist savanna-woodland (*Isoberlinia* in N., *Brachystegia-Julbernardia* in S.); 20, 21, dry savanna-woodland; 22, dry savanna-woodland with *Colophospermum mopane*; 24, 26, 27, dry grass steppe; 25, dry wooded steppe with *Acacia* and *Commiphora*; 28, 29, Karroo steppe; 30, 31, subdesert steppe; 32, desert.

FIG. 2. — Biotic subdivisions of the Ethiopian Zoogeographical Region, based on distribution of termites.

sed and somewhat primitive genus. The generic name *Grallatotermes* is therefore retained here for the single african species, and there is no doubt of its correct assignment to the "*Procornitermes*" branch of the subfamily along with the remaining four species of the genus.

#### DISTRIBUTION OF NASUTITERMITINAE IN THE BIOTIC SUBDIVISIONS OF THE ETHIOPIAN ZOOGEOGRAPHICAL REGION

The biotic zones based by CHAPIN (1923, 1932) on the distribution of birds and some mammals have been found to be applicable to a number of other animal groups. Minor changes in this system were made by MOREAU (1952, 1963) in his studies of the birds. The outlines used by MOREAU were modified by DAVIS (1962) for conformity with a recently published vegetation map (KEAY et al. 1959) but he retained Moreau's names for the sub-regions, and was able to relate the distribution of certain rodents (Muridae) to these boundaries. CARCASSON (1964) in surveying the zoogeography of African butterflies subdivided some of these biotic zones and classified the major divisions somewhat differently from Moreau and Davis. His classification agrees in some respects with the distribution patterns that have been found to occur in certain groups of termites (SANDS, 1957 a, 1959) but, as might be expected, the distribution of the Nasutitermitinae does not conform exactly to any of these systems. For present purposes the main boundaries are taken to be those at which genera are separated, and subsidiary divisions those between recognisable groups of species. The resulting biotic zones have features in common with those of both MOREAU and CARCASSON. The upper altitude limit of the subfamily appears to be at about 5000 feet above sea level in tropical Africa, and it is not represented in the montane evergreen forests or the tropical montane grasslands. These are therefore omitted from further consideration. The biotic subdivisions of the Ethiopian region used here (Fig. 2) are as follows : —

##### **Forest subregion**

- (1) Western division
  - (a) Upper Guinean forests
  - (b) Congo and lower Guinean forests.
- (2) Eastern division-East African coastal forests.

##### **Open subregion**

- (1) Northern division-Moist Guinean savanna-woodlands to Sahel steppe ("Sudan arid" of Moreau).

(2) Eastern division-Moist "Miombo" savanna-woodland to arid steppe ("Somali arid" of Moreau).

(3) Southern division-Moist savanna and savanna-woodland including "Miombo", to arid steppe. ("Zambezi" and "Kalahari" of Carcasson).

(4) Cape division-Temperate and sub-tropical grassland "High Veldt", Karroo steppe, and Cape Macchia.

### Forest subregion.

The common feature of all systems is the fundamental division of the fauna between forests and more open vegetation types, which also holds good in the Nasutitermitinae. In the "*Procornitermes*-branch" this division is complete at generic level, whereas in the "*Paracornitermes*-branch" of humus-feeders it is less so, several genera including both savanna and forest species. This is probably because in the latter branch, species are entirely subterranean and less exposed to microclimatic differences.

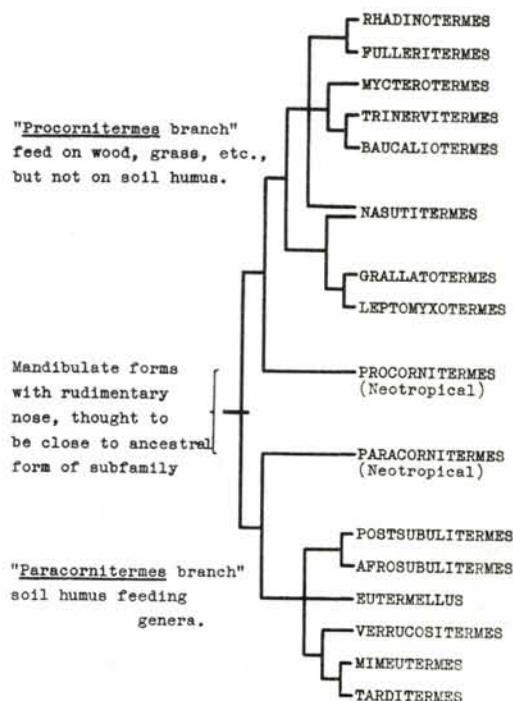


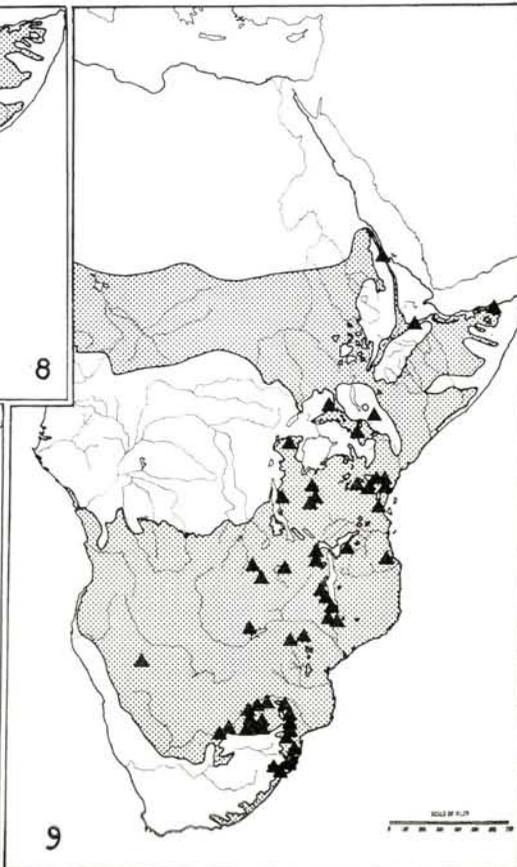
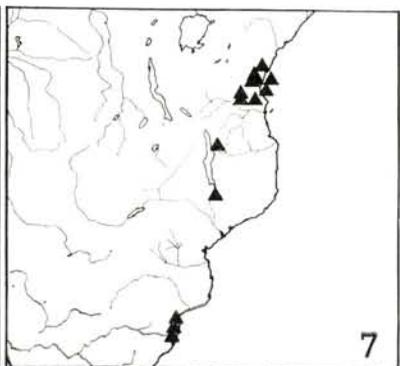
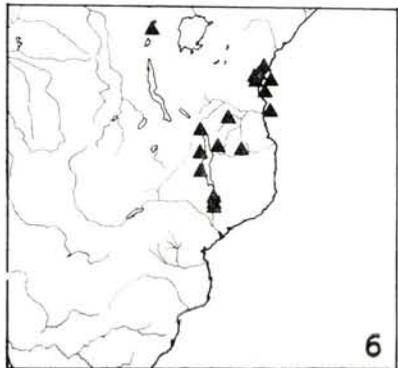
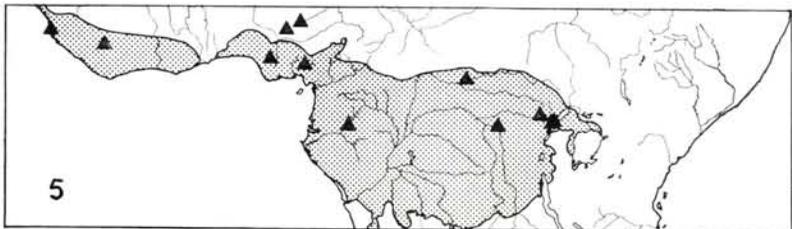
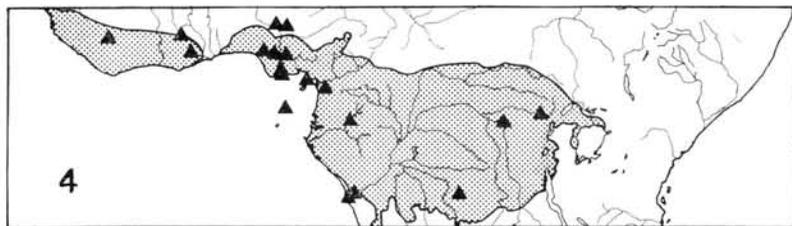
FIG. 3. — Dendrogram of probable relationships among the genera of Nasutitermitinae of the Ethiopian Zoogeographical Region. (Genera from other regions omitted for simplicity).

The forest subregion comprises all the lowland evergreen forests of the continent. The greater part of these is represented by the Western division which included the Guinean and Congo forests. These have varied considerably in extent even in recent geological time, during the several pluvial periods of the Pleistocene. The present phase is one of regression, and human agencies have also contributed largely to the destruction of forest areas in recent memory. Relic patches of forest once part of the main Congo block remain in Uganda and as far east as the Imatong mountains in the southern Sudan. The Eastern division of evergreen forests consists of small remnants scattered along the east coast of Africa from Kenya to Natal, with inland extensions along the major rivers such as the Ruvuma in Tanzania, and around the shores of Lake Nyassa. According to Moreau, the biological evidence suggests that the East African forests have remained separated from the Western division, at least since early in the Pleistocene.

The forest-limited genera of the "*Procornitermes*" branch are three in number: *Nasutitermes*, *Leptomyxotermes*, and *Grallatotermes*. *Nasutitermes* has twelve African species, of which ten are entirely confined to the Western division and two to the Eastern division. The paucity of the Eastern fauna is a reflection of the small size of the forest patches that form its environment. CARCASSON (*loc. cit.*) observed a similar reduction in the butterfly fauna and suggested that it was due to extinction of species during extreme interpluvial contractions of the forests. However, to apply this explanation to the termites of the Eastern division raises certain difficulties. Two species of *Nasutitermes* in the Western division, *N. elegantulus* (Sjöst.) (*fig. 4*) and *N. fulleri* Em. (*fig. 5*), closely resemble the Eastern pair, *N. kempae* HARRIS (*fig. 7*) and *N. infuscatus* (Sjöst.) (*fig. 6*) in their morphology and habits except that they are much smaller and comparatively rare. They appear to be restricted to minor ecological niches in the inner rain forest by more abundant competitors. Some of these are "marginal species" in the sense of WILSON (1965), also being found in habitats only capable of supporting one or two species in the few suitable ecological niches. These marginal habitats consist of small relic forest patches and even moist woodland well beyond the present limits of the Western division of rain forest. Such conditions are similar to those prevailing in the Eastern division, and had any related species existed there in times past, they might be expected to have survived the interpluvial contractions in preference to the two now found there.

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FIGS. 4-10. — Distribution of representative species of Nasutitermitinae. (Shade areas show the extent of the vegetation types from which each species has been recorded). 4, *Nasutitermes elegantulus*; 5, *N. fulleri*; 6, *N. infuscatus*; 7, *N. kempae*; 8, *Trinervitermes bettonianus*; 9, *T. dispar*; 10, *T. rapulum*.



A more acceptable interpretation of the present distribution would seem to be that the four species mentioned are derivatives of the original colonisers belonging to this genus, already adaptively "committed" to woodfeeding. *N. elegantulus* and *N. kempae* both have features resembling the *Diversitermes-Trinervitermes* group of genera and so may be morphologically more primitive than their congeners. DARLINGTON (1959) argued that if large area and favourable climate increase population size, and with it, the availability of mutations for selection, then adaptation and the evolution of dominant animals should be accelerated. However, he also pointed out that the availability of variation due to gene-recombination should be greatest if a population is divided into sub-populations which are partially isolated from each other but interbreed occasionally. This should result in more efficient adaptation than can occur in single populations.

Each of these sets of conditions seems to have occurred in Western and Eastern divisions respectively. In the Western, speciation and possibly later invasion have produced competitors, constricting the little changed derivatives of the older species to minor niches. In the Eastern, adaptation to drier conditions appears to have been more efficient, but speciation restricted by the limitations of the marginal habitats. The presence of extant species in East African Pleistocene gum copal perhaps provides further evidence of restricted speciation in that area. *N. kempae* and *N. infuscatus* are found in moist *Bra-chystegia* woodland around Lake Nyassa. *N. infuscatus* extends to Rwindi on the borders of the Congo, following the track of the probable most recent connection between Eastern and Western divisions along the shores of the Rift Valley lakes.

In the Western division, *N. diabolus* (Sjöst.) and *N. ferranti* (Wasm.) have not been collected from the Upper Guinean Forest, and so may have more recent origins than the remaining species for which the distributions are known, namely *N. arborum* (Smeath.), *N. latifrons* (Sjöst.), *N. lujae* (Wasm.), and *N. schoutedeni* (Sjöst.). These are common to both the Upper and Lower Guinean and the Congo forests.

The other two genera already mentioned have one species each. The monotypic *Leptomyxotermes doriae* (Silv.) is found in the Western and *Grallatotermes africanus* HARRIS in the Eastern division. They appear to be most closely related to a group of constricted-headed genera found mainly in the Indo-Malayan Region, and their separate existence in the two divisions of the forest subregion in Africa must be of ancient origin. According to MOREAU (*loc. cit.*) an evergreen forest connection between Africa and Asia is unlikely to have occurred later than the early Pliocene. EMERSON (1955) has suggested that *Grallatotermes* arose in Indo-Malaya in the Cretaceous and reached Africa in the Cretaceous or early Tertiary. *Leptomyxotermes* appears morphologically and biologically somewhat more primitive, and so may have become separated from its Indo-Malayan relations even earlier.

The "Paracornitermes-branch" is represented in the Western division by the monotypic genera *Verrucositermes*, *Tarditermes*, *Afrosubulitermes* and *Postsubulitermes*, and by species of *Eutermellus* and *Mimeutermes*. *M. giffardii* Silv. is one of the few species that appears to be confined to the Upper Guinean forest, west of the Dahomey gap. No member of this branch has been found in the Eastern division of the Forest subregion.

### Open subregion.

This comprises all the remaining vegetation types of the continent. They range from subdesert steppe on the fringes of the true deserts, to the moist derived savannas and savanna-woodlands adjacent to the rain forest. In all of these open types, grasses form an important part of the vegetation, and the grass-feeding genus *Trinervitermes* is the dominant member of the "Procornitermes-branch". *Fulleritermes* is found in a subsidiary wood-feeding ecological niche, and the similar genus *Rhadinotermes* occurs in parts of the subregion. Humus-feeding members of the "Paracornitermes-branch" are confined to the moister savannas and are restricted to a few species of *Eutermellus* and *Mimeutermes*. As conditions become drier, both northwards and southwards towards the deserts, the faunae become more restricted. Fewer species of *Trinervitermes* are found, and *Fulleritermes* persists, but the humus-feeding genera are not found beyond the limits of the *Isoberlinia* and *Brachystegia-Julbernardia* savanna-woodlands, vegetation types 17 to 19. On the fringes of the deserts there are very few species; one or two *Trinervitermes* still occur, and the small related genera *Mycterotermes* and *Baucaliotermes* are found in these types in Arabia and South-West Africa respectively.

The Open subregion is clearly separable into four faunistic divisions. These are similar to those suggested in connection with a revision of the genus *Amitermes* (SANDS, 1959), but there appears to be less overlapping at the limits of these divisions in the Nasutitermitinac.

#### 1) NORTHERN DIVISION.

This division includes all the savanna and steppe vegetation from the Atlantic coast of West Africa, north of the Guinean forests, to Uganda north of the Equator and the foothills of the Ethiopian Massif. The south-western part of Arabia should probably be included in this division, but it is at the meeting point with the Eastern division and the Palaearctic Region, and has also a few endemic species. Leaving aside South-West Arabia, the Northern division has more species of *Trinervitermes* than any other, five in all, namely *T. geminatus* (Wasm.), *T. occidentalis* (Sjöst.), *T. oeconomus* (Träg.), *T. togolensis* (Sjöst.), and *T. trinervius* (Ramb.). MOREAU (*loc. cit.*) stated that

the savanna vegetation belts stretching across the entire continent were probably broken up several times by the expanding forests and lakes of the Pleistocene pluvials, and this would have provided ideal conditions of frequent geographical isolation for rapid speciation of savanna forms. These five species (SANDS, 1961, 1961 a) show all stages from a primitive shade dwelling species, *T. occidentalis* feeding on dead leaves and wood as well as grass, and lacking any foodstorage habit, to a savanna species feeding almost entirely on grass, with the storage habit well developed, namely *T. geminatus*. *T. oeconomus* and *T. trinervius* are intermediates, and *T. togoensis* is an offshoot with a harvesting habit similarly developed to *T. geminatus* but nesting almost entirely in the mounds of other species. The storage habit probably originated at the western end of their range, with *T. trinervius* itself or a similar ancestral form, after the more primitive species had spread throughout the division. *T. trinervius* reaches its greatest abundance in the moist savannas of that area, and its life history is adapted to the climatic conditions (SANDS, 1965). It is limited in northward spread by the boundary of the *Isoberlinia* savanna-woodland. *T. geminatus* is more abundant and widely distributed, reaching the drier areas of the Sudan. The *Fulleritermes* species of this division is *F. tenebricus* (Silv.) which is tolerant of the full range of climatic conditions. In the "Paracornitermes-branch", two species of *Eutermellus* and two of *Mimeutermes* have been recorded from the western part of this division, but not from further east than Northern Nigeria.

## 2) EASTERN DIVISION.

The Eastern division is less well defined than the Northern, partly because its boundaries often do not coincide exactly with the limits of particular vegetation types, and partly because it is delimited by the distribution of fewer species. Its north-eastern boundary appears to approximate to the Great Rift Valley from Asmara in Eritrea southwards through Ethiopia to the Kenya highlands and Lake Victoria. In western Uganda, the northern limit of the division approximates to the Equator, where the recent degradation of a forest barrier to savanna has not yet led to the mingling of species of the Northern and Eastern divisions on each side of it. From the Equator southwards, the boundary is the Albertine Rift Valley, as far as the southern tip of Lake Tanganyika. The Luangwa Rift Valley in Zambia appears of greater significance than the Nyassa Rift to the east, and from here southwards to Natal there is considerable mingling of the faunae, so that the limits of the divisions become indistinct.

The "*Procornitermes*-branch" is represented by four species of *Trinervitermes* and *Rhadinotermes coarctatus* (Sjöst.), which closely resembles *Fulleritermes* in general appearance but to judge from the imago and worker mandibles has probably different feeding habits,

showing similarity in this respect to the grass feeding *Trinervitermes*. *R. coarctatus* has been recorded from the drier savannas and the coastal savanna-forest mosaic which has similar rainfall (vegetation types 20 and 9 respectively). Of the *Trinervitermes* species, *T. dispar* (Sjöst.) (fig. 9) has the widest geographical range, from Mount Kullo in Eritrea to Pietermaritzburg in Natal and Grootfontein in South-West Africa. It is found in vegetation ranging from savanna-woodland to steppe (types 9, 18, 19, 20, 25, and 26), and has thus spread into the Southern division on a broad front, though not recorded from the extreme western part. It has also been found a short distance into the Northern division in Uganda, but it appears to occupy an ecological niche very closely similar to *T. togoensis* as a predominantly mound-sharing species. It has probably therefore been restricted by biotic as well as geographical barriers in that area. *T. rapulum* (Sjöst.) (fig. 10) has a more restricted range, being mainly confined to the drier savannas (types 9, 20, and 22), from north-eastern Tanzania to South-West Africa, but it is unknown from western Tanzania.

The other two species are even more restricted. *T. bettonianus* (Sjöst.) (fig. 8) is commonest in the *Acacia-Commiphora* steppe (type 25) and has been recorded from northern Uganda to the Zambezi valley. *T. graciosus* (Sjöst.) is confined to types 20, 25 and 26 in Kenya and Tanzania, and has been found in small patches of types 20, 24 (grass steppe on Kalahari sand) and 27 (grass steppe, Luanda type) scattered across the southern Congo and Angola to the Atlantic coast. The broken distribution of both this and *T. bettonianus* suggest that they are relict species that perhaps had wider ranges in past interpluvial periods. None of these Eastern division species has been recorded as having as well developed habit of food storage.

A new species of *Mimeutermes* (SANDS, 1965 a) is the sole representative of the "*Paracornitermes*-branch", and this is probably an overlap from the Southern division where Coaton (1957) has recorded the occurrence of undescribed species of both *Eutermellus* and *Mimeutermes*.

### 3) SOUTHERN DIVISION.

This division includes all the open vegetation south of the Congo forest, west of the Great Rift Valley and Luangwa Rift, to the edges of the subtropical "High Veldt" grassland and Karroo steppe of the Cape division. It has only one endemic *Trinervitermes* species, *T. rhodesiensis* (Sjöst.), which tolerates all vegetation and climatic conditions from the derived forest-savanna mosaic to subdesert steppe, apart from the *Colophospermum mopane* savanna-woodland (type 22). It overlaps in Southern Rhodesia and Transvaal with *T. rapulum* and *T. dispar* from the Eastern division, and with *T. trinervoides* (Sjöst.) from the Cape. *Fulleritermes* has two species in this division. *F. con-*

*tractus* (Sjöst.) is found in the derived and moist savannas (types 8, 16, 18 and 19). *F. coatoni* Sands is only found in the drier type 20 in Transvaal and Southern Rhodesia, and it does not overlap at all with its congener. On the basis of these two species, the separation by CARCASSON (1964) of the Southern division into two zones, the "Zambesian" for moister and "Kalahari" for drier savannas, seems to have some relevance to termite distribution also.

#### 4) CAPE DIVISION.

Although the Cape division is small in area, comprising only the Macchia, Karroo, and subtropical « High Veldt » grassland vegetation types, it has three endemic species, one belonging to a genus unknown elsewhere, namely *Baucaliotermes hainesi* (FULLEER). This is clearly allied to *Trinervitermes*, and is confined to the arid areas of subdesert steppe of South and South-West Africa. The single *Trinervitermes* species, *T. trinervoides* (Sjöst.) has a wide range of climatic tolerance, occurring throughout the division and extending to near Windhoek in South-West Africa and Salisbury in Southern Rhodesia. It is the most morphologically variable of all the species, perhaps owing to its adaptation to a wide variety of habitats, and is successful and abundant, reaching pest density at times. It has a well developed food-storage habit.

The other Cape species is *Fulleritermes mallyi* (FULLER), which is confined to the various modifications of Karroo steppe (types 28, 29 and 30), in the extreme south-west corner of Cape province. It differs considerably from its congeners, which closely resemble one another, and it has clearly been separated from them for a considerable period of time.

#### General discussion.

The present distribution of the nasute genera in the Ethiopian Zoogeographical Region appears to have arisen from several waves of immigration. The most ancient of these was probably that represented by the related relict constricted-headed forest genera *Leptomyxotermes* and *Grallatotermes*. EMERSON (1955) pointed out the lack of any related genera or species in the Malagasy region. If they were present in Africa in the Cretaceous of early Tertiary, when a connection with Madagascar still existed, their present absence can probably only be explained by subsequent extinction owing to competition from genera such as *Nasutitermes*. This may also account for their comparative rarity and paucity of species in Africa. The tropicopolitan genus *Nasutitermes* also requires a forest connection with other regions to explain its existence in Africa, as also do the ancestral forms of the « *Paracornitermes*-branch ».

The savanna-dwelling genera are probably more recent arrivals. *Fulleritermes* and *Rhadinotermes* are closely related to the Malagasy

genus *Coarctotermes*, and their constricted-headed polymorphic ancestors must have reached Africa before the separation of Madagascar, which according to EMERSON (*loc. cit.*) took place in the late Eocene. *Coarctotermes* occupies a similar ecological niche to *Trinervitermes*, which is absent from Madagascar, and so probably of more recent origin. The existence in South-West Arabia of *Mycterotermes*, a monotypic relict genus closely related and perhaps ancestral to *Trinervitermes*, suggests that the latter genus probably first arose in the north-eastern part of the Ethiopian Region. In the Eastern division, *Trinervitermes* is a relatively inconspicuous genus, never reaching high levels of population density. The reason for this may be that the species in that area have not developed the food-storage habit sufficiently to exploit fully the seasonal grasses of the savanna and steppe habitats. In the Southern division, *T. rhodesiensis* has been recorded as storing grasses to some extent, but it is only at the extremes of dispersion of the genus in the Northern and Cape divisions, that species have arisen with the habit fully developed, so enabling them to attain high levels of population density. It therefore appears that the food-storage habit may have arisen independently twice within the genus. This would not be surprising since related genera of Nasutitermitinae in other zoogeographical regions have convergently evolved this adaptation to life in savanna vegetation zones.

#### SUMMARY

The total number of species of Nasutitermitinae recorded from the Ethiopian Zoogeographical Region has been reduced by revision from 120 to 48, belonging to 14 genera. The distribution of the genera is related to the vegetation zones in two subregions. These are the Forest subregion, which is divided into Western and Eastern divisions, and the Open subregion, with four divisions, namely the Northern, Eastern, Southern, and Cape. The forest-limited faunae are probably of more ancient origin than those of the savannas. The divisions are based upon the separation of recognisable faunistic groups of species. The Western division of the Forest subregion contains the greater number of species of the forest-limited genus *Nasutitermes*. In the Open subregion, the greatest number of species of the savanna genus *Trinervitermes* is found in the Northern division, where the continent-wide vegetation belts of the savanna zones are thought to have been broken up during Pleistocene pluvial periods, resulting in recent speciation. In *Trinervitermes* the habit of food-storage in the mounds probably developed independently in the Northern and Cape divisions.

## REFERENCES

- AHMAD (M.), 1950: The phylogeny of termite genera based on imago-worker mandibles. *Bull. Amer. Mus. nat. Hist.*, 95, 2, 37-86.
- CARCASSON (R. H.), 1964: A preliminary survey of the zoogeography of African butterflies. *E. Afr. Wildl. J.*, 2, 122-157.
- CHAPIN (J. P.), 1923: Ecological aspects of bird distribution in tropical Africa. *Am. Nat.*, 57, 106-125. — 1932: Birds of the Belgian Congo. *Bull. Amer. Mus. nat. Hist.*, 65, 1-756.
- COATON (W. G. H.), 1957: *Report on investigations of the termite problem in the potential plantation areas of Northern Rhodesia*, unpublished.
- DARLINGTON (P. J.), 1959: Area, climate, and evolution. *Evolution*, 13, 488-510.
- DAVIS (D. H. S.), 1962: Distribution patterns of South African Muridae, with notes on some of their fossil antecedents. *Ann. Cape Prov. Mus.*, 2, 56-76.
- EMERSON (A. E.), 1955: Geographical origins and dispersions of termite genera. *Fieldiana, Zool.*, 37, 465-521.
- KEAY (R. W. J.) et al., 1959: *Vegetation map of Africa south of the Tropic of Cancer*. 24 p., 1 map. Oxford.
- MOREAU (R. E.), 1952: Africa since the Mesozoic: with particular reference to certain biological problems. *Proc. zool. Soc. Lond.*, 121, 4, 869-913. — 1963: Vicissitudes of the African biomes in the late Pleistocene. *Proc. zool. Soc. Lond.*, 141, 2, 395-421.
- SANDS (W. A.), 1957: The soldier mandibles of Nasutitermitinae (Isoptera, Termitidae). *Insectes Soc., Paris*, 4, 1, 13-24. — 1957 a: Revision of the East African Nasutitermitinae (Isoptera). *Bull. Brit. Mus. (Nat. Hist.) Ent.*, 5, 1, 1-28. — 1959: A revision of the termites of the genus *Amitermes* from the Ethiopian Region (Isoptera, Termitidae, Amitermitinae). *Bull. Brit. Mus. (Nat. Hist.) Ent.*, 8, 4, 127-156. — 1961: Nest structure and size distribution in the genus *Trinervitermes* (Isoptera, Termitidae, Nasutitermitinae) in West Africa. *Insectes Soc., Paris*, 8, 2, 177-188. — 1961 a: Foraging behaviour and feeding habits in five species of *Trinervitermes* in West Africa. *Ent. Exp. et Appl.*, 4, 277-288. — 1965: Alate development and colony foundation in five species of *Trinervitermes* (Isoptera, Nasutitermitinae) in Nigeria, West Africa. *Insectes Soc., Paris*, 12, 2, 117-130. — 1965 a: A revision of the termite subfamily Nasutitermitinae (Isoptera, Termitidae) from the Ethiopian Region. *Bull. Brit. Mus. (Nat. Hist.) Ent. Suppl.*, 4, 1-172. — 1965 b: A new species of *Mimeuterms* *Silvestri* and the imago of *Nasutitermes diabolus* (Sjöstedt) from Africa (Isoptera, Nasutitermitinae). *Proc. R. ent. Soc. Lond. (B.)*, 34, 9-10, 132-136.
- SEN-SARMA (P. K.), 1966: Three new genera of *Grallatotermes* complex (Isoptera: Termitidae: Nasutitermitinae). *J. Bombay nat. Hist. Soc.*, 63, 1, 167-184.
- WILSON (E. O.), 1965: The Challenge from Related Species. In: *The Genetics of Colonising Species*, pp. 7-24, 5 fig. Academic Press Inc., New York.