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New Genera of Termites Related to *Subulitermes* from the Oriental, Malagasy, and Australian Regions (Isoptera, Termitidae, Nasutitermitinae)[1]

By Alfred E. Emerson[2]

INTRODUCTION

In the following pages, several new genera of nasute termites from the Orient, Madagascar, and Australia are distinguished. The species have already been named and, for the most part, adequately described, so that the emphasis here is on the generic diagnoses and the phylogenetic relations. The author plans to publish another article in the near future on several new species and genera belonging to the *Subulitermes* branch of the Nasutitermitinae that he collected in Africa. He is presently engaged in a study of the species and genera of the *Subulitermes* branch that are confined to South and Central America, and he hopes that the descriptions of the new Neotropical genera allied to *Subulitermes* will be published within a year or so.

PHYLOGENY OF THE GENERA WITH NASUTE SOLDIERS

Prior to about 1935, no student of the phylogeny of termites was

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aware of the probable diphyletic origin of the nasute soldier from the primitive genera with mandibulate soldiers confined to the Neotropical zoogeographical region. A series of publications by Emerson (1945, 1949, 1952, 1955) and his associates (Hare, 1937; Ahmad, 1950) provide the evidence for the separate origin of the nasute soldier in two major branches of the phylogenetic tree of the Nasutitermitinae. The major clue to the convergent evolution of the adaptively similar nasute soldiers was found in the characters of the imago-worker mandibles, rather than in the characters of the soldier caste with its regressed and functionless mandibles. The imago-worker mandibles are evidently very conservative, slowly evolving characters compared to the more rapidly evolving and highly adapted protective characters of the soldier, and consequently are more trustworthy for use in the distinguishing of higher taxonomic categories than are any adaptive characters under high selection pressures. Although the imago-worker mandibles are adaptive in their biting and chewing functions, the morphological differences in the imago-worker mandibles in different genera and higher taxonomic categories are non-adaptive or at most weakly adaptive. The dentition of the mandible does not change much when the food is shifted from wood to dead leaves, grass, or humus, but does evolve at the generic, subfamily, or family levels with the changes in the general complex genetic constitution. It may be postulated that many genes that influence the development of the imago-worker mandibles have pleiotropic effects. Selection for these multiple effects gradually produces evolutionary changes in the imago-worker mandibles. At the same time, much of the genetic pattern probably does not change during long periods of time, and this highly conservative pattern gives us a clue to basic phylogenetic relationships.

Holmgren (1909, 1911a, 1912) was the first investigator of termite systematics and phylogeny to use the imago-worker mandible as one basis for some of his phylogenetic groups, although he was not always consistent in his interpretations, and he missed some of the refinements of classification that in part were possible only with the added knowledge of the fauna of the world that has become available in recent years.

Silvestri (1914) used characters of the imago-worker mandible for the diagnosis of some of his systematic groups, but he did not make any phylogenetic interpretations. Hill (1942) made drawings of the imago-worker mandibles of the new Australian genera described in this article, but he decided to place the species in the polyphyletic *"Eutermes"* that included many other groups now given generic status. The old

generic name *"Eutermes"* is invalid from a nomenclatural viewpoint, and is also polyphyletic as used by Hagen, Holmgren, Silvestri, Hill, and other early termite systematists.

Since the general review of the phylogeny of termite genera by Ahmad (1950) with the emphasis placed upon the imago-worker mandibles, we are now able to correct many errors of identification and phylogenetic arrangement. Many termite taxonomists in the past assumed that imagoes collected with soldiers and workers in the same vial belonged to the same species. In numerous instances two or more genera were mixed together by the collector. It is now a relatively simple matter to examine the mandibles of the associated imagoes and workers. Numerous errors thus may be avoided, and it is hoped that all modern investigators will make use of the growing body of evidence linking the imago-worker mandible characters with the other characters already found valuable in taxonomic and phylogenetic interpretations.

The imago-worker mandibles show a high degree of consistency within the species and genus. The worker mandible is usually a little smaller than that of the imago, and it may be secondarily worn by use, with some consequent alteration of points and edges of the teeth. The mandibles of the larger nymphs of the imagoes also have consistent characters and do not show wear. Different species of the same genus usually have essentially the same characters in the imago-worker mandibles, while the mandibles of the mandibulate soldiers are usually valuable for species diagnoses. In those genera with nasute soldiers, the specific distinctions are usually found in the pilosity and the shapes of the heads rather than in the vestigial mandibles. If there is a marked difference between the imago-worker mandibles of one species and those of other species classified in a single genus, it is highly likely that more than one genus is involved. The author and several other modern termite taxonomists are now engaged in dividing several named genera on the basis of differences in the imago-worker mandibles. The present paper is an attempt to arrange related species formerly classified in a more inclusive generic category by subdividing the group into several genera consistent with the modern concept of the genus as unfolded by the studies of the imago-worker mandibles and their associated structural patterns in all castes. It is confidently believed that greater order of systematic arrangements, phylogenetic sequences, geographical distribution, and ecological associations will ensue from such studies. At the same time, the imago-worker mandibles should not be used exclusively, but many patterns of associated characters of all the castes

should be sought. In a number of supergeneric groups within the same family or subfamily, the genera do not show any differences in the imago-worker mandibles, yet it is possible to recognize quite valid genera by other sets of characters both in the imago and in the soldier castes.

As already postulated by Emerson (1945, 1949, 1952, 1955) and Ahmad (1950), the study of the Nasutitermitinae provides evidence that indicates that this subfamily arose in the Neotropical region, probably early in the Cretaceous period. Several genera with mandibulate soldiers (*Syntermes, Procornitermes, Cornitermes, Rhynchotermes*) have highly similar imago-worker mandibles. Derived genera in this branch remain closely similar in the characters of the imago-worker mandibles after the origin of the nasute soldier. There is a trend in some derived genera (i.e., *Constrictotermes*) towards a proportionately smaller apical tooth in the imago-worker mandibles. These genera on the *Nasutitermes* branch are characterized by the possession of an apical tooth that is close in size or smaller than the first marginal tooth in both the right and left mandibles, and the cutting edge of the fused first and second marginal teeth of the left mandible is comparatively evenly concave and without a deep notch in front of the third marginal tooth (see figures in Ahmad, 1950). Some slight exceptions in some genera of the *Nasutitermes* branch make the description of the branch difficult, but the general pattern is fairly consistent, particularly among the more primitive genera on the branch. In contrast, several Neotropical genera with mandibulate soldiers (*Paracornitermes, Labiotermes, Armitermes, Curvitermes*) typically have the apical teeth of the right and left imago-worker mandibles larger than the first marginal teeth, and the cutting edge of the fused first and second marginal teeth of the left mandible is often undulating with convex and concave portions of the edge. Often there is a rounded notch immediately in front of the third marginal tooth. This branch of the Nasutitermitinae seems to have independently evolved genera possessing a nasute soldier with reduced functionless mandibles. This phylogenetic branch may be called the *Subulitermes* branch, and the most primitive genus at the base of the branch is the Neotropical *Paracornitermes.*

Because of the similar appearance of the convergent adaptive enlargement of the frontal tube or projection on the head of the soldier and the convergent reduction of the soldier mandibles to vestiges, the analogous nasute soldiers in the genera in the separate branches of the Nasutitermitinae have been erroneously treated as monophyletic. Thus Holmgren (1910, 1912) described *Subulitermes* as a subgenus of

"Eutermes," a group of species that contained many modern genera, including *Nasutitermes.* Subsequent investigators placed several Old World species in the genus *Subulitermes* that clearly belong to the *Nasutitermes* branch. Also many species in the Old World have been given separate generic status without a clear recognition of their relationship to the *Subulitermes* branch (*Occasitermes, Mimeutermes, Eutermellus*).

A reëxamination of many species of Old World nasute genera indicates that the *Subulitermes* branch, paralleling the *Nasutitermes* branch, had differentiated in the New World and spread to all tropical regions, probably by mid-Cretaceous times (Emerson, 1955). So far, no species on the *Subulitermes* branch has been recorded from the Papuan region, which possesses a termite fauna sufficiently distinct from that of the Australian region to deserve full regional status. It is likely that more complete collections will disclose Papuan species on this branch. It is impossibe to give a detailed picture of the evolution and dispersion of the genera on the basis of a study of modern derived forms only and in the absence of any fossils. We can say, however, that the movement probably was from the Neotropical region to the Orient, and thence to Australia on the one hand, and to Africa and Madagascar on the other hand. At present there are insufficient data to indicate whether one or several genera of the *Subulitermes* branch invaded these regions in early times, but it seems probable that several genera with nasute soldiers invaded each region more or less at the same time, and that a fair amount of evolution occurred before and during the Tertiary period after some of the tropical land connections or land approximations between the zoogeographical regions and subregions had been effectively broken. The genera arising after geographical and climatic barriers had been established are now derivative types confined to such areas as Australia, Madagascar, Africa, and the Orient. During this Old World differentiation, the basic stock left in the New World was also undergoing further evolution in the area of origin, so that many derived genera now occur in the Neotropical region along with the primitive genera little changed from the original Cretaceous ancestors.

The phylogenetic trend of the imago-worker dentition (fig. 1) in the *Subulitermes* branch seems to have been towards the further proportional enlargement of the apical teeth compared to the first marginal teeth of both mandibles. This proportionate relation may be expressed by a left mandible index, which is the linear distance between the pointed tips of the apical and first marginal teeth divided by the linear

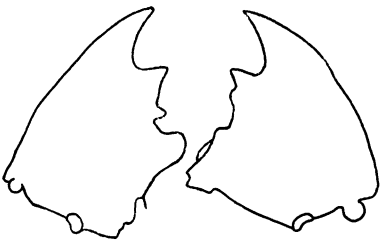

FIG. 1. Mandibles of worker of *Subulitermes microsoma* (Silvestri). Cotype from Coxipo, Mato Grosso, Brazil.

distance between the pointed tips of the first marginal and third marginal teeth. The second marginal tooth of the left mandible is reduced and fused with the posterior cutting edge of the first marginal tooth (see Ahmad, 1950). A left mandible index of 1.0 would mean that the distance between the tips of the apical and first marginal teeth is equal to the distance between the tips of the first and third marginal teeth. A left mandible index of 0.50 would mean that the distance between the apical and first marginal teeth is half of that between the first and third marginal teeth. The primitive genera on the *Subulitermes* branch and all the genera on the *Nasutitermes* branch have comparatively low indices. A high index indicates a derivative condition in nearly every genus on the *Subulitermes* branch, although a very low index indicates a derivative condition among the genera of the *Nasutitermes* branch, and it is probable that occasionally a genus with a lower index has evolved from one with a higher index, even on the *Subulitermes* branch. Other characters must be used in forming these phylogenetic hypotheses. (Also it must be noted that each detected character used for systematic distinction is not statistically equivalent to every other character, but that principles formulated from objective evidence from structure, development, genetics, behavior, biogeography, and ecology must be used in broad perspective for an understanding of evolutionary events and processes.) In a few genera (see Ahmad, 1950), the third marginal tooth of the left imago-worker mandible is reduced, and the measurements cannot be made with accuracy for the computation of the left mandible index. It is surmised that all such genera are derived from more primitive forms that possessed a well-defined third marginal tooth.

Many of the genera on the *Subulitermes* branch are very small, and the smaller the mandible, the more difficult it is to make accurate measurements. Variations in the index of 0.10 or even of 0.20 are not necessarily of generic value. However, other characters, including char-

acters of the molar portion of the right or left imago-worker mandible, may indicate generic distinction between species with close left mandible indices.

When one takes into account the morphological evidence from many genera on the *Subulitermes* branch in various zoogeographical regions, it appears probable that an enlarged apical tooth in the imago-worker mandible associated with a high left mandible index, and occasionally accompanied by a reduction of the third marginal tooth of the left mandible, has independently evolved a number of times in various isolated geographical regions. Left mandibles with equally high indices are not necessarily closely related because of this character alone. The explanation of this evolutionary trend in independent generic groups remains obscure, but there is no indication that a functional adaptation of the imago-worker mandible is involved.

The primitive genera of Nasutitermitinae in both of the main branches of the subfamily possess mandibulate soldiers. The evolutionary sequence is obviously from the genera with mandibulate soldiers to the genera with nasute soldiers in both the *Nasutitermes* branch and the *Subulitermes* branch. As the frontal projection of the soldier head evolved progressively into a "squirt-gun" adaptation, the mandibles became proportionately smaller and ultimately became functionless in the nasute soldier. The primitive nasute soldiers retain the apical point. Some genera even show a marginal tooth on the soldier mandible (Hare, 1937). The vestigial mandibles of the soldier in the most advanced genera in both branches have lost the apical points (i.e., *Trinervitermes* in the *Nasutitermes* branch and *Subulitermes* in the *Subulitermes* branch). In some genera (i.e., *Nasutitermes*), apical points on the soldier mandibles may be present in some species and absent in other species of the same genus. In a few genera (i.e., *Leucopitermes, Malagasitermes, Occasitermes,* and *Australitermes*), the apical points may be present in one mandible and absent in the other mandible of the same individual soldier, or present in some individuals and absent in other individuals of the same species or the same colony. This variation in the presence and absence of the apical points on the soldier mandibles seems to be an example of different developmental thresholds of genetic penetrance, and it may be assumed that the genetic potentiality for producing apical points on the soldier mandibles is present in such species, even though the mandibles lack the points in some individuals. The taxonomist and evolutionist must take into account such genetic and physiological principles in forming their phylogenetic hypotheses.

ORIENTAL GENERA

LEUCOPITERMES, NEW GENUS

< Subgenus *Subulitermes* HOLMGREN, 1914, p. 252.
< Genus *Subulitermes* KEMNER, 1934, p. 116.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Leucopitermes* EMERSON, 1955, pp. 502, 514 (no adequate description).

TYPE SPECIES: *Leucopitermes leucops* (Holmgren) [= *Eutermes (Subulitermes) leucops* Holmgren].

The single species *Leucopitermes leucops* (Holmgren) now constitutes this monotypic genus. An examination of the type specimens of *"Subulitermes undecimus"* Kemner (1931, pp. 33, 34) from Amboina, Moluccas, shows that it belongs to the genus *Nasutitermes* on the *Nasutitermes* branch of the Nasutitermitinae, and not in *Leucopitermes* as tentatively suggested by Emerson (1955, p. 502).

SOLDIER: Minute hairs occur on the frontal tube and vertex that are not so long nor so abundant as in *Malagasitermes milloti.* The tergites have short hairs and bristles, shorter than those on *Malagasitermes.* The profile of the head is convex, and the back of the head is not so elevated nor so wide as in *Malagasitermes.* A small but distinct constriction at the sides of the head behind the bases of the antennae is visible from above. The mandibles may be with or without points. The front margin of the pronotum is weakly indented. The profile of the pronotum shows a sharp angle between the front and rear portions, the angle being about equal to a right angle.

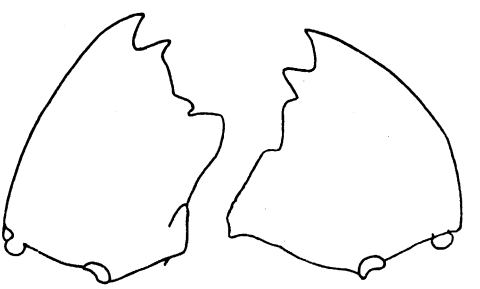

FIG. 2. Mandibles of worker of *Leucopitermes leucops* (Holmgren). Cotype from Selangor Gap, Malacca.

WORKER (FIG. 2): The mandibles of the worker show a rather generalized condition compared to those of related genera. The apical tooth of each mandible is only a little larger than the first marginal tooth. The angle between the apical tooth and the first marginal tooth

is rather sharp. The mandibular index of the left mandible is 0.56. The first marginal tooth of the left mandible has a rather sharp angle separating it from the cutting edge at the position of the regressed second marginal tooth, and the notch in front of the third marginal tooth is wide but distinct. The third marginal tooth is proportionately rather wide. The right mandible has a distinct second marginal tooth, with a fairly sharp angle a little less than a right angle separating the first and second marginal teeth. The outline of the molar plate of the right mandible is fairly straight.

RELATIONS: *Ceylonitermellus hantanae* worker-nymph mandibles (fig. 4) have proportionately somewhat larger first marginal teeth in both mandibles, and the cutting edge of the first plus second marginal tooth of the left mandible is less undulated. The left mandible index is 0.62. The soldier mandibles are without points.

Aciculitermes aciculatus worker mandibles (fig. 3) have less of a notch immediately behind the first marginal tooth of the left mandible, the third marginal tooth is narrower, and the molar plate of the right mandible is more concave in outline. The left mandible index is 0.73. The soldier lacks points on the mandibles.

Oriensubulitermes inanis worker-nymph mandibles (fig. 5) have proportionately larger apical teeth, with a left mandible index of 1.06. The cutting edge of the first plus second marginal tooth in the left mandible is fairly evenly concave, without notches either behind the first marginal tooth or in front of the third marginal tooth. The second marginal tooth of the right mandible is so reduced as to be barely visible, and the outline of the molar plate is moderately concave. The soldier lacks points on the mandibles.

The Australian *Occasitermes occasus* seems to be the closest genus in both imago-worker mandibles (fig. 7) and in the presence or absence of points on the soldier mandibles. The major distinction is in the rounded notch in front of the third marginal tooth of the left mandible. The left mandible index is 0.50. The soldier of *Occasitermes* has a conspicuously thicker frontal projection. The pilosity is similar to that of *Leucopitermes*.

The generalized imago-worker mandibles and the retention of the points on the soldier mandibles in some specimens indicate that *Leucopitermes* is the most primitive of the Oriental genera of this branch of the Nasutitermitinae and is probably derived from the same base that gave rise to *Occasitermes* in Australia and to *Malagasitermes* in Madagascar.

Leucopitermes leucops (Holmgren), new combination

Termes aciculatus HAVILAND, 1898, p. 426 (soldier, worker) [part only].
Eutermes (Subulitermes) leucops HOLMGREN, 1914, p. 252 (soldier, worker, biology), pl. 7, fig. 12 (soldier).
Subulitermes javanellus KEMNER, 1934, pp. 115, 120 (soldier, worker), fig. 27 (soldier).
Subulitermes javanellus SNYDER, 1949, p. 340 (synonymy).
Subulitermes leucops SNYDER, 1949, p. 340 (synonymy).

An examination of two vials from Marudi, Sarawak, each with the label "*Termes aciculatus* Cotype" determined and collected by G. D. Haviland shows that two species were mixed together in the original material of *Aciculitermes aciculatus*. Both the worker mandibles and the soldiers conform to the two species now placed in two different genera. One vial contains specimens from which Holmgren (1913, p. 156) redescribed "*Eutermes (Subulitermes) aciculatus*," and these specimens are now in the collection of the American Museum of Natural History with the label "*Aciculitermes aciculatus* (Haviland) COTYPE," followed by the above data. Haviland (1898) gives the number 447 in his description of "*Termes aciculatus*," and this number should be considered his type colony. I am assuming that it belongs to *Aciculitermes aciculatus* until the specimens are reëxamined. Altogether, the generic description of *Leucopitermes* has been drawn from four vials of cotypes of *Leucopitermes leucops* determined by N. Holmgren as "*Eutermes (Subulitermes) leucops*" from Selangor Gap, Malacca; Maxwell's Hill, Taiping, Malacca; and Tandjong Slamat, eastern Sumatra. Also two vials contain the specimens removed from the cotype material of "*Termes aciculatus*" from Marudi, Sarawak, referred to above, and two vials contain soldiers and workers from the type colony of "*Subulitermes javanellus* Kemner" from Buitenzorg, Java. I have been unable to find any consistent differences between specimens from Java and those from the other localities and am placing "*Subulitermes javanellus* Kemner" tentatively in synonymy with *Leucopitermes leucops* (Holmgren). It is possible that imagoes, when described, will enable us to distinguish taxonomically some of the populations now placed together under one species.

ACICULITERMES, NEW GENUS

< Subgenus *Subulitermes* HOLMGREN, 1912, pp. 59, 61, 64.
< Subgenus *Subulitermes* HOLMGREN, 1913, p. 153.
< Subgenus *Subulitermes* JOHN, 1925, p. 391.
< Genus *Subulitermes* KEMNER, 1931, p. 33.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Aciculitermes* EMERSON, 1955, p. 515 (no description).

TYPE SPECIES: *Aciculitermes aciculatus* (Haviland) (= *Termes aciculatus* Haviland, part only).

The cotype material of *"Termes aciculatus"* Haviland (1898, p. 426) from Marudi, Sarawak, contains two species. One of these is the type species of *Aciculitermes*, and the other is the type species of *Leucopitermes*. I consider that Holmgren's (1914) description of *"Eutermes (Subulitermes) leucops"* constitutes a selection of *Aciculitermes aciculatus* as here defined to carry the specific name. If Haviland's type no. 447 is not *A. aciculatus*, this nomenclature may have to be changed.

IMAGO: John (1925) and Kemner (1931) described the imago from Sumatra and Singapore, but no specimens are available to the present author for the description of the genus or for the verification of the species.

SOLDIER: The soldier of *Leucopitermes leucops* is more robust and larger. Haviland (1898) described the third antennal article as shorter than the second, a character that seems to refer to *Aciculitermes aciculatus* only. His measurement of the width of the head at 8.0 mm. is obviously incorrect. The soldier of *Aciculitermes* lacks points on the mandibles.

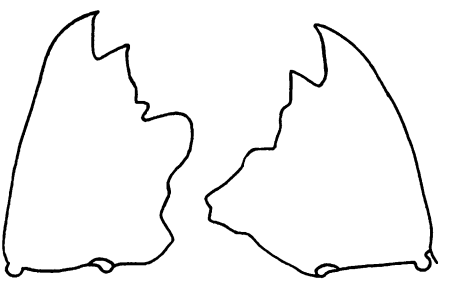

FIG. 3. Mandibles of worker of *Aciculitermes aciculatus* (Haviland). Cotype from Marudi, Sarawak.

WORKER (FIG. 3): The left mandibular index is 0.73, while it is 0.56 for *Leucopitermes* and 1.33 for *Subulitermes*. The apical teeth of both mandibles are proportionately larger than in *Leucopitermes* (fig. 2), there is no notch immediately posterior to the first marginal tooth of the left mandible, and the third marginal tooth is narrower. The second marginal tooth of the right mandible is a rounded hump, and the outline of the molar plate is somewhat concave.

Aciculitermes aciculatus (Haviland), new combination

Termes aciculatus HAVILAND, 1898, p. 426 (soldier, worker) [part only].
Eutermes (Subulitermes) aciculatus HOLMGREN, 1912, p. 64.

Eutermes (Subulitermes) aciculatus HOLMGREN, 1913, p. 156 (soldier, worker).
Eutermes (Subulitermes) aciculatus JOHN, 1925, p. 392 (imago, biology).
Subulitermes aciculatus KEMNER, 1931, pp. 33, 34 (imago).
Subulitermes aciculatus SNYDER, 1949, p. 339 (synonymy).

SOLDIER: Head and frontal projection with many short microscopical hairs. Vertex and base of head projection with a few bristles. Head proportionately wider than that of *Subulitermes microsoma.* Profile of head from tip of projection to the vertex almost straight or slightly concave, with a slight hump at the base of the projection. Projection thin and more conical than that of *Subulitermes microsoma.* Antenna with 12 articles, the third article shorter than the second and about equal to the fourth. Head length, 1.13 mm.; head width, 0.58 mm.

The description is taken from a single cotype soldier with workers from Marudi, Sarawak. The known localities are given under the heading for the genus.

CEYLONITERMELLUS, NEW GENUS

< Subgenus *Subulitermes* HOLMGREN, 1912, pp. 59, 61, 64.
< Subgenus *Subulitermes* HOLMGREN, 1913, p. 153.
< Genus *Subulitermes* KEMNER, 1931, p. 33.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Ceylonitermellus* EMERSON, 1955, p. 515 (no description).

TYPE SPECIES: *Ceylonitermellus hantanae* (Holmgren) (= *Eutermes hantanae* Holmgren).

ADDITIONAL SPECIES: *Ceylonitermellus kotuae* (Bugnion) (= *Eutermes Kotuae* Bugnion).

IMAGO: I have not had an opportunity to study the imagoes described by Bugnion (1914a, 1914c).

SOLDIER: The mandibles lack apical points.

WORKER-NYMPH (FIG. 4): The left mandible has a characteristically long first plus second marginal tooth. The left mandible index is 0.62. The third marginal tooth is proportionately small compared to that of *Leucopitermes.* The right mandible has a concave outline of the molar plate. The angles between the apical teeth and the first marginal teeth of both mandibles are wider than those of any other related genera in the Oriental region.

Ceylonitermellus hantanae (Holmgren), new combination

Eutermes hantanae HOLMGREN, 1911b, p. 198 (soldier, worker), p. 211 (soldier), pl. 3, figs. P_1, P_2 (soldier).

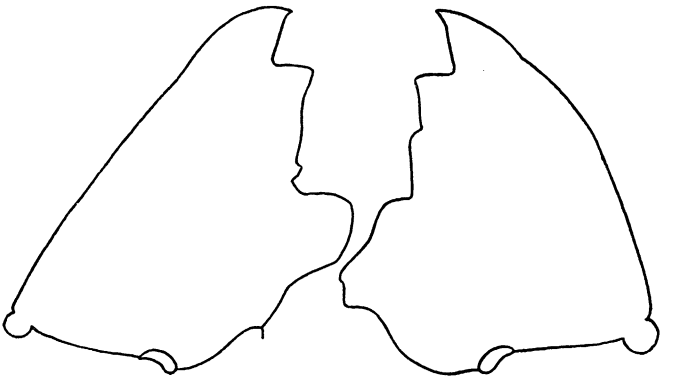

FIG. 4. Mandibles of worker-nymph of *Ceylonitermellus hantanae* (Holmgren). Cotype from Hantana, Ceylon.

Eutermes hantanae ESCHERICH, 1911, p. 133 (biology).
Eutermes Hantanae BUGNION, 1912, p. 504 (soldier).
Eutermes (Subulitermes) Hantanae HOLMGREN, 1913, pp. 153, 155 (soldier, worker), pl. 7, fig. 3 (soldier).
Eutermes hantanae GREEN, 1913, p. 14 (locality).
Eutermes Hantanae BUGNION, 1914b, p. 184 (locality, biology).
Eutermes Hantanae BUGNION, 1914c, p. 155 (imago, soldier, worker, nymph), pl. 24, figs. 1–2 (imago), figs. 3–5 (worker), pl. 25 (soldier).
Eutermes Hantanae BUGNION, 1933, p. 11 (synonymy).
Subulitermes hantanae SNYDER, 1949, p. 339 (synonymy).

The species is known only from Hantana, Ceylon.

Ceylonitermellus kotuae (Bugnion), new combination

Eutermes Kotuae BUGNION, 1914a, p. 193 (imago, soldier, worker, nymph), pl. 12 (soldier), pl. 13 (soldier, worker), pl. 14 (imago, nymph).
Eutermes Kotuae BUGNION, 1914b, p. 184 (locality, biology).
Eutermes Kotuae (sic) BUGNION, 1933, p. 11 (synonymy).
Subulitermes kotuae SNYDER, 1949, p. 340 (synonymy).

This species is recorded only from Kotua, 8 miles north of Point Galle, Ceylon. The author has not had an opportunity to examine any specimens, but the description is sufficient to place the species in the same genus with *Ceylonitermellus hantanae*.

ORIENSUBULITERMES, NEW GENUS

< Subgenus *Subulitermes* HOLMGREN, 1912, pp. 59, 61, 64.
< Subgenus *Subulitermes* HOLMGREN, 1913, p. 153.
< Genus *Subulitermes* KEMNER, 1931, p. 33.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Oriensubulitermes* EMERSON, 1955, p. 515 (no description) .

TYPE SPECIES: *Oriensubulitermes inanis* (Haviland) (= *Termes inanis* Haviland).

ADDITIONAL SPECIES: *Oriensubulitermes inaniformis* (Holmgren) [= *Eutermes* (*Subulitermes*) *inaniformis* Holmgren].

SOLDIER: The mandibles are without points.

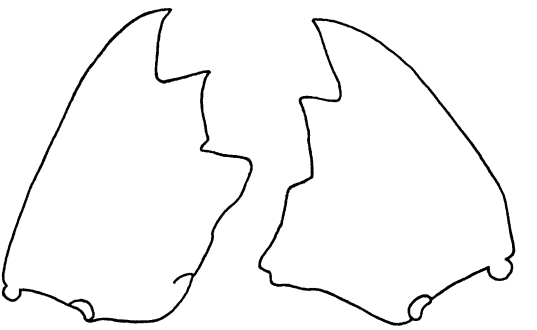

FIG. 5. Mandibles of worker-nymph of *Oriensubulitermes inanis* (Haviland). Homotype from Kuala Lumpur, Malaya.

WORKER-NYMPH (FIG. 5): The index of the left mandible is 1.06. The cutting edge of the first plus second marginal tooth is evenly concave, with no notch in front of the third marginal tooth. The second marginal tooth of the right mandible is almost completely regressed, and the outline of the molar plate is somewhat concave. The lack of a distinct third marginal tooth on the left mandible and the reduced second marginal tooth on the right mandible distinguish this genus from all others in the *Subulitermes* branch in the Oriental region.

Oriensubulitermes inanis (Haviland), new combination

Termes inanis HAVILAND, 1898, p. 425 (soldier, worker).

Eutermes (*Subulitermes*) *inanis* HOLMGREN, 1913, pp. 153, 154 (soldier, worker), pl. 7, fig. 2 (soldier).

(?) *Eutermes inanis* GREEN, 1913, p. 14 (locality). This record from Ambalangoda, Ceylon, is almost surely a mistaken identification.

Eutermes (*Subulitermes*) *inaniformis* JOHN, 1925, p. 391 (biology). The imago in this collection from Kota Baroe, Sumatra, is *Capritermes nemorosus* (Haviland). Soldiers and workers have been redetermined as *Oriensubulitermes inanis* by A. E. Emerson.

Subulitermes inanis SNYDER, 1949, p. 340 (synonymy).

The known localities for this species include Perak, Malaya (type locality); Kuala Lumpur, Malaya; Bukit Timah, Singapore; Tandjong Slamat, eastern Sumatra; Kota Baroe, eastern Sumatra.

Oriensubulitermes inaniformis (Holmgren), new combination

Eutermes (Subulitermes) inaniformis HOLMGREN, 1912, p. 64, pl. 3, fig. 10 (soldier).

Eutermes (Subulitermes) inaniformis HOLMGREN, 1913, pp. 153, 154 (soldier, worker, nymph), pl. 7, fig. 1 (soldier).

Subulitermes inaniformis SNYDER, 1949, p. 340 (synonymy).

Unfortunately no exact locality is known for this species. The type material has a label of "East Indies," and the species has not been rediscovered since the original collection by G. D. Haviland.

MALAGASY GENUS

MALAGASITERMES, NEW GENUS

< Genus *Eutermes* CACHAN, 1949, pp. 189, 248.

= Genus *Malagasitermes* EMERSON, 1955, pp. 489, 501, 514 (no adequate description).

TYPE SPECIES: *Malagasitermes milloti* (Cachan) (= *Eutermes Milloti* Cachan).

SOLDIER: The head has short hairs on the frontal tube and on the vertex, but there are few hairs at the base of the frontal tube. The vertex has a few bristles. The tergites and sternites have abundant, proportionately rather long hair, and each tergite and sternite has a posterior marginal row of bristles about twice as long as the hairs. The head has a distinct constriction and a rather bulbous rear portion. The frontal tube is conic. The antenna has 12–13 articles. The single soldier of *Malagasitermes milloti* examined has a distinct but short, sharp, apical point on the right mandible and no apical point on the left mandible. Other genera on the *Subulitermes* branch with apical points present or absent on the mandibles are *Leucopitermes, Occasitermes,* and *Australitermes.* The profile of the pronotum has a sharp angle between the front and rear portions that is less than a right angle.

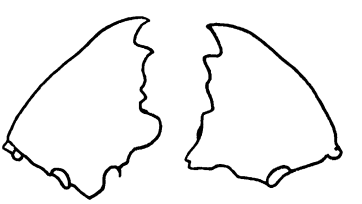

FIG. 6. Mandibles of worker of *Malagasitermes milloti* (Cachan). Paratype from type colony from Ambohitantely, Madagascar.

WORKER (FIG. 6): The worker mandibles clearly show that *Malagasitermes* belongs to the *Subulitermes* branch of the Nasutitermitinae.

Both mandibles have proportionately large apical teeth compared to the first marginal teeth, and the cutting edge of the first plus second marginal tooth of the left mandible is undulated. A distinct notch is retained in front of the third marginal tooth of the left mandible. The right mandible has a somewhat rounded second marginal tooth. The mandibular index of the left mandible is 0.66.

RELATIONS: All the known nasute genera of the *Subulitermes* branch in Africa (including four new genera yet to be described) have higher left mandible indices, the smallest of which is *Eutermellus* with an index of 1.12. Of the new Oriental genera, *Leucopitermes* seems to be the closest. Compared to *Leucopitermes* (fig. 2), *Malagasitermes* has a proportionately larger apical portion of the left mandible, with a slightly concave outer margin at the base of the apical tooth. The angle between the apical tooth and the first marginal tooth of the left mandible is a little wider, the undulation between the first marginal tooth and the notch in front of the third marginal tooth is more distinct, the notch is sharper, and the third marginal tooth is proportionately smaller. The apical tooth of the right mandible is proportionately larger, and the upper edge of the molar plate is distinctly more concave in outline. Although rather different in a number of characters, *Malagasitermes* seems to be closer to *Leucopitermes* from the Oriental region than to any of the genera from the Ethiopian region.

The description is taken from a single paratype soldier and two workers determined by P. Cachan as *"Eutermes Milloti"* from Ambohitantely, Madagascar, 1947, collected by J. Millot. The specimens were kindly sent to me by Dr. R. Paulian.

The discovery of this genus in Madagascar helps to substantiate the theory of the Mesozoic northern dispersal of this group of termites from a Neotropical ancestry and followed by Tertiary isolation in the various major zoogeographical regions during which endemic genera differentiated (Emerson, 1955). The fact that *Malagasitermes* is more closely related to *Leucopitermes* in the Oriental region than to *Mimeutermes*, the only other Ethiopian genus of this branch with points on its soldier mandibles, may be explained by extinction of the African ancestry or by our incomplete knowledge of the African fauna that may yet be shown to have a close relative.

Malagasitermes milloti (Cachan), new combination

Eutermes Milloti CACHAN, 1949, p. 189 (soldier), p. 248 (soldier, worker, biology), fig. 31 (soldier, worker).

Malagasitermes milloti EMERSON, 1955, p. 501 (soldier, worker).

The species is known only from the type locality of Ambohitantely (*"tampoketsa d'Ankasobe"*), Madagascar.

AUSTRALIAN GENERA

OCCULTITERMES, NEW GENUS

< Genus *Mirotermes* HILL, 1927, p. 92.
< Genus *Eutermes* HILL, 1942, pp. 8, 9, 12, 13, 14, 202.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Occultitermes* EMERSON, 1955, p. 515 (no description).

TYPE SPECIES: *Occultitermes occultus* (Hill) (= *Mirotermes occultus* Hill).

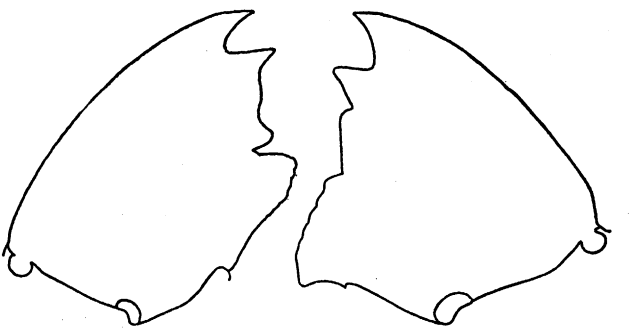

FIG. 7. Mandibles of imago of *Occasitermes occasus* (Silvestri). Homotype colony from Mundaring, southwestern Australia.

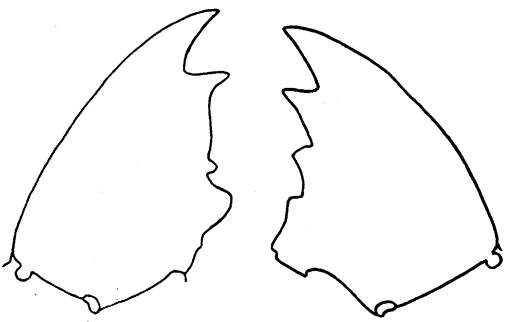

FIG. 8. Mandibles of imago of *Occultitermes occultus* (Hill). Stapleton, Northern Territory, Australia.

IMAGO (FIG. 8): Numerous bristles and short hairs occur on the head and pronotum. Tergites with many short hairs and a few bristles on the sides tending to form a marginal row. Fontanelle distinctly forked at the anterior end. Postclypeus much longer than half of the width (length, 0.22 mm.; width, 0.32 mm.). The mandibles of the imago

(fig. 8) clearly indicate that this genus belongs to the *Subulitermes* branch of the Nasutitermitinae. The generic distinctions include the prominent second marginal tooth on the right mandible, the long cutting edge of the first plus second marginal tooth of the left mandible, and the proportionately long apical tooth of the left mandible. The left mandible index is 0.68. The mandibles differ from those of *Occasitermes occasus* (fig. 7) in the proportionately longer apical tooth of the left mandible, and they differ from those of *Subulitermes microsoma* (fig. 1) in having a much longer cutting edge between the first and third marginal teeth of the left mandible. The pronotum has flatly rounded sides not converging towards the rear so much as in *Australitermes* and *Macrosubulitermes*. The mesonotum and metanotum each has a wide, shallow indentation. Tibial spurs 2:2:2.

SOLDIER: Dimorphic. The mandibles are without points.

RELATIONS: The relationship of this genus to others in the *Subulitermes* branch is not clear. The genera with a close or lower index of the left mandible of the imago-worker include *Occasitermes* (0.50), *Leucopitermes* (0.56), *Convexitermes* (0.57), *Ceylonitermellus* (0.62), *Malagasitermes* (0.66), and *Aciculitermes* (0.73). Of these, *Occasitermes*, *Leucopitermes*, and *Malagasitermes* have points on the soldier mandibles in at least some of the specimens. Points on the mandibles of the soldier are obviously primitive compared to their absence, but points may be lost in several independent lines of evolution, so those soldiers without points are not necessarily closely related. It should also be emphasized that the loss of a character such as points on the soldier mandibles is probably much less complex genetically than their original acquisition, and it is for this reason that a character once regressed in the course of evolution seldom undergoes progressive evolution (Emerson, 1949). The dimorphic soldier is a specialization, in all probability. All other genera on this branch of the Nasutitermitinae have monomorphic soldiers. Several genera on the *Nasutitermes* branch have dimorphic or trimorphic soldiers. When the various characters are taken into account, *Aciculitermes* seems to be the closest genus, but the phylogenetic relations must remain somewhat speculative until a more thorough study has been made.

The nasute soldier is a highly advanced type in the evolution of termite genera, and the occurrence of nasute soldiers in several genera on both branches of the phylogenetic tree of the Nasutitermitinae in Australia, together with the large proportion of endemic genera among these adaptively specialized groups, can be interpreted only as an indication of the advanced evolution of termites by mid-Cretaceous times

when access to Australia from the eastern Oriental region was broken for animals with low vagility (Emerson, 1949, 1955). No fossils are known in Mesozoic rocks that would verify this hypothesis based on the distribution and ecology of living species, but the circumstantial evidence makes any other explanation of the facts far less probable. This does not mean that termites have not evolved important adaptations since Mesozoic times. The endemic genera probably arose during Tertiary times and give an indication that termites are continuing to evolve important adjustments, although their progressive evolution is very slow in comparison with that of mammals and birds.

Occultitermes occultus (Hill), new combination

Mirotermes occultus HILL, 1927, p. 112 (imago), pl. 4, figs. 147–149, pl. 6, fig. 215 (imago, wing).

Eutermes occultus HILL, 1942, pp. 9, 12, 245 (imago, major soldier, minor soldier, worker, biology), figs. 144–149 (imago, major soldier, minor soldier).

Subulitermes occultus SNYDER, 1949, p. 341 (synonymy).

The species has been adequately described and figured by Hill. It is the only species assigned to *Occultitermes*. It has been collected at Koolpinyah (type locality) and Stapleton, Northern Territory, Australia.

MACROSUBULITERMES, NEW GENUS

< Genus *Eutermes* HILL, 1942, pp. 8, 9, 12, 13, 14, 202.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Macrosubulitermes* EMERSON, 1955, pp. 503, 515 (no description).

TYPE SPECIES: *Macrosubulitermes greavesi* (Hill) (= *Eutermes greavesi* Hill).

ADDITIONAL SPECIES: *Macrosubulitermes perlevis* (Hill) (= *Eutermes perlevis* Hill).

IMAGO (FIG. 9): The apical articles of the antennae are light, while the basal articles are as dark as the lighter portions of the head, in *Macrosubulitermes greavesi*. The darker parts of the pronotum are equal to the dark-colored head, while in *Subulitermes microsoma* the pronotum is lighter. The tibia and the apical portion of the femur are darker than the middle portion of the femur. The wings of *Macrosubulitermes greavesi* are darker than those of *Subulitermes microsoma* owing to the more dense punctations. The sternites of *Macrosubulitermes greavesi* have dark lateral spots, and the middle of each sternite is light. Head and pronotum have bristles and short hairs, the short hairs almost forming a mat. Both *Macrosubulitermes greavesi* and

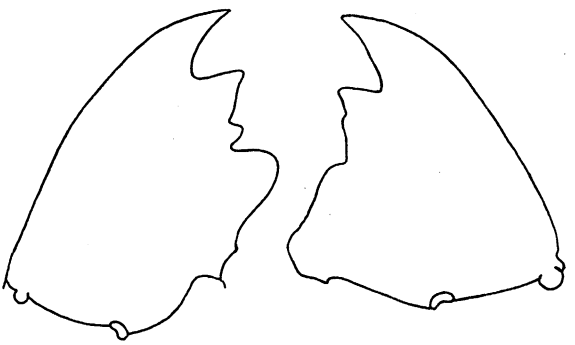

FIG. 9. Mandibles of imago of *Macrosubulitermes greavesi* (Hill). Paratype from type colony from Gadgarra, northern Queensland, Australia.

Subulitermes microsoma have scattered short hairs on the membranes and veins of the wings. The tergites of *Macrosubulitermes greavesi* have short hairs, and the posterior margins have longer hairs without marginal bristles. The sternites have both bristles and hairs, the hairs being longer than those on the tergites. The top of the head between the ocelli is more flatly arched than in *Subulitermes microsoma.* The profile of the head is strongly arched, with the peak above the ocelli, while in *S. microsoma* the profile of the head is not so strongly arched and the peak is behind the ocelli. The fontanelle is a light slit with a forked front margin, inconspicuous, shorter in length than the ocellus. A light spot occurs immediately in front of the fontanelle but is not joined to it. In *Subulitermes microsoma* the fontanelle is more conspicuously forked, with the branches enclosing a light spot; the length of the slit including the forks is about the same as the length of the ocellus. Antenna with 15 articles in both species. In *Macrosubulitermes greavesi* the third article is a little longer than the second or fourth and also has a more bulbous apical part, while in *Subulitermes microsoma* the second, third, and fourth articles are about equal and the third article does not have so much of a bulbous tip. The postclypeus is shorter than half of its width (0.20–0.22 mm. long and 0.47 mm. wide), with a light longitudinal line in the middle. The postclypeus of *Subulitermes microsoma* is longer than half of its width (0.20 mm. long and 0.35 mm. wide). The imago mandibles (fig. 9) are fairly close to the worker mandibles of *Subulitermes microsoma* (fig. 1). The major differences are the sharper angles between the apical and first marginal teeth of both mandibles in *Macrosubulitermes greavesi.* The left mandible index is 1.07 in *Macrosubulitermes greavesi* and 1.29–1.33 in *Subulitermes microsoma.* The pronotum of *Macrosubulitermes greavesi*

is more angular, with the sides converging towards the rear, as compared to *Subulitermes microsoma,* but is not so deeply indented in the rear as in figure 199 in Hill (1942). *Australitermes* has more converging sides of the pronotum. The tibial spurs are 2:2:2 in *Macrosubulitermes,* as in all genera with nasute soldiers in both branches of the phylogenetic tree. Indices of possible generic importance are: the length of the postclypeus divided by its width, which is 0.47 in *Macrosubulitermes greavesi* and 0.54 in *Subulitermes microsoma;* the width of the head divided by the length of the hind tibia, which is 0.75 in *Macrosubulitermes greavesi* and 0.87 in *Subulitermes microsoma;* the length of the pronotum divided by the length of the hind tibia, which is 0.47 in both species; and the length of the forewing from the suture divided by the length of the hind tibia, which is 6.13 in *Macrosubulitermes greavesi* and 7.95 in *Subulitermes microsoma.*

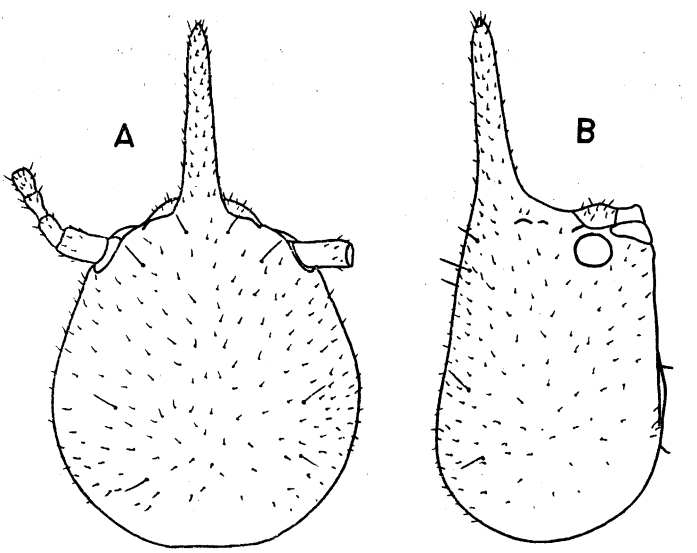

FIG. 10. Soldier of *Macrosubulitermes greavesi* (Hill). A. Head from above. B. Head from side. Morphotype from type colony from Gadgarra, northern Queensland, Australia.

SOLDIER (FIG. 10): Head with eight bristles at the base of the frontal projection and on the vertex. Frontal projection and head are sparsely covered with fairly short hairs. The abdominal tergites have fairly thick hair that is only a little shorter than the marginal bristles. *Subulitermes microsoma* has six bristles on the head, proportionately shorter hair on the head, and proportionately shorter hair on the ter-

gites. *Macrosubulitermes greavesi* has a larger head than *Subulitermes microsoma* and also has a proportionately wider and more bulbous posterior portion of the head. The head length divided by the head width is 1.49–1.63 in *Macrosubulitermes perlevis*, 1.71 in *M. greavesi*, and 2.27 in *Subulitermes microsoma*. The head of *Macrosubulitermes greavesi* is very slightly constricted, with lateral humps just posterior to the base of the frontal projection. The head of *Subulitermes microsoma* is not constricted nor does it have lateral humps. The frontal tube or projection is nearly cylindrical in *Macrosubulitermes greavesi* but is slightly conical and not upturned in profile, while in *Subulitermes microsoma* it is more cylindrical and upturned. The antenna has 12 articles in *Macrosubulitermes perlevis*. The second, third, and fourth articles are about equal in length in *Macrosubulitermes*. The third article is narrower at the base than the second or fourth, and is somewhat bulbous at the anterior end in *M. greavesi* as compared to *Subulitermes microsoma*, but is not so bulbous in *Macrosubulitermes perlevis*. The mandibles are without points in both *Macrosubulitermes* and *Subulitermes*. The fore tibia of *Macrosubulitermes greavesi* is nearly as wide as the femur and is somewhat swollen in appearance. The tibial spurs are 2:2:2 in this and all other nasute genera. The abdomen is thick, wide, and rounded compared to the long cylindrical abdomen of *Subulitermes microsoma*.

Macrosubulitermes greavesi (Hill), new combination

Eutermes greavesi HILL, 1942, pp. 9, 12, 287 (imago, soldier [part], worker), fig. 199 (imago).

Subulitermes greavesi SNYDER, 1949, p. 339 (synonymy).

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF PARATYPE FEMALE IMAGO OF *Macrosubulitermes greavesi* (HILL)

Width of head	1.06
Diameter of eye	0.36
Length of ocellus	0.13
Ocellus from eye	0.05
Length of postclypeus	0.22
Width of postclypeus	0.47
Length of pronotum	0.67
Width of pronotum	0.96
Length of hind tibia	1.41
Length of forewing from suture	8.65
Width of forewing	2.44

IMAGO (FIG. 9): The specific characters are given in the generic description and in the original description (Hill, 1942).

SOLDIER (FIG. 10): The unique morphotype soldier is in the collection sent to the present author by Hill and is now in the American Museum of Natural History. It is one of the soldiers mentioned in the original description, but is the one "allied to *E. perlevis*" rather than to *"E. pluvialis."* The major characters are described above in the generic diagnosis. The size is somewhat smaller than that of *M. perlevis*, but the species is otherwise very close in generic and specific characters.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF MORPHOTYPE SOLDIER OF *Macrosubulitermes greavesi* (HILL)

Length of head	1.47
Width of head	0.86
Length of hind tibia	0.96

The descriptions and measurements were taken from one paratype female imago and one morphotype soldier determined as *"Eutermes greavesi"* by G. F. Hill from the type colony collected at Gadgarra on the Atherton Tableland, northern Queensland, Australia, by T. Greaves, June 11, 1939, No. 2659.

Macrosubulitermes perlevis (Hill), new combination

Eutermes perlevis HILL, 1942, pp. 9, 12, 293 (soldier, biology), figs. 206, 207 (soldier).

Subulitermes perlevis SNYDER, 1949, p. 341 (synonymy).

SOLDIER: The soldiers agree in all substantial generic characters with those of *Macrosubulitermes greavesi*, and I have no hesitation in assigning the two species to the same genus. The pilosity is similar in the two species. The head is larger and proportionately wider in *M. perlevis* than in *M. greavesi*. The antenna has 12 articles and is in general similar to that of *M. greavesi*, except that the third article does not have the bulbous end found in the single specimen of *M. greavesi*.

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF PARATYPE SOLDIERS OF *Macrosubulitermes perlevis* (HILL)

	No.	Range	Mean
Length of head	13	1.53–1.67	1.62
Width of head	13	0.99–1.06	1.03
Length of hind tibia	13	0.91–1.00	0.94

The description is taken from 13 paratype soldiers from the type colony collected and determined by G. F. Hill as *"Eutermes perlevis,"* 34-mile siding on the N. T. Railway south of Port Darwin, Northern Territory, Australia, July 27, 1913, No. 72. No workers were in the vial received from Hill.

AUSTRALITERMES, NEW GENUS

< Genus *Eutermes* HILL, 1942, pp. 8, 9, 12, 13, 14, 202.
< Genus *Subulitermes* SNYDER, 1949, p. 338.
= Genus *Australitermes* EMERSON, 1955, p. 515 (no description).

TYPE SPECIES: *Australitermes dilucidus* (Hill) (= *Eutermes dilucidus* Hill).

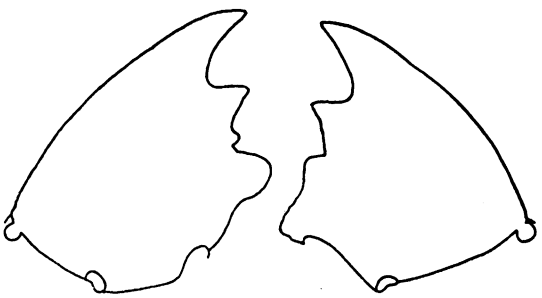

FIG. 11. Mandibles of king of *Australitermes dilucidus* (Hill). Paratype from type colony from near Aramara, Queensland, Australia.

IMAGO (FIG. 11): Head and pronotum with numerous short bristles and a few scattered short hairs. Tergites with short hairs and a few sparsely distributed bristles on the sides, but not forming a conspicuous marginal row. Sternites with a marginal row of long bristles and also with scattered shorter hairs. Eye and ocellus large, the ocellus less than its width from the ocular suture and longer (0.15 mm.) than the diameter of the basal socket of the antenna (0.12 mm.). Fontanelle long and narrowly oval, without a distinctly forked tip. Postclypeus much longer than half of its width (length, 0.32 mm.; width, 0.50 mm.). Antenna with 15 articles, the third article longer than the fourth and the fourth longer than the second. Mandibles (fig. 11) with the highest left mandible index (1.54) of any of the Australian genera of the *Subulitermes* branch of the Nasutitermitinae. The closest Australian genus is *Macrosubulitermes* (fig. 9), with an index of 1.07. The second marginal tooth of the right mandible is reduced to a vestige. The mandibles convergently resemble those of the genus *Termes* (Ahmad,

1950), but the imagoes of *Termes* have tibial spurs 3:2:2. The pronotum of *Australitermes* is proportionately wide, nearly as wide as the head, with the sides more extended and more strongly converging towards the rear than in *Macrosubulitermes*. The hind margin of the metanotum is about the same as that of the mesonotum except that the whole margin is narrower. The tibial spurs are 2:2:2.

SOLDIER: Monomorphic. With scattered hairs on the frontal projection and on the top of the head and a number of long bristles on the head. Tergites with many rather long hairs and no bristles. Sternites with marginal bristles and hairs the same length and abundance as on the tergites. Head with a small constriction visible from both the top and side. The profile of the pronotum has a sharp angle close to a right angle between the front lobe and the basal portion.

Australitermes dilucidus (Hill), new combination

Eutermes dilucidus HILL, 1942, pp. 9, 12, 285 (imago, soldier, worker, biology), figs. 195–198 (imago, imago mandibles, soldier).
Subulitermes dilucidus SNYDER, 1949, p. 339 (synonymy).

SOLDIER: The length of the head is 1.44–1.56 mm.

The specific characters have been described adequately by Hill from three colonies collected near Aramara in the Doongul State Forest, Queensland, Australia. The generic description is taken from paratype dealates and soldiers in the collection of the American Museum of Natural History.

SUMMARY

The relative values of adaptive characters, non-adaptive characters, regressive characters, progressive characters, conservative characters, and rapidly evolving characters for phylogenetic interpretation are discussed.

The diphyletic origin of the nasute soldier in the *Nasutitermes* branch and in the *Subulitermes* branch of the Nasutitermitinae (Termitidae) is indicated. After the origin of the nasute soldier with regressed mandibles in the Neotropical region in Cretaceous times, it is postulated that genera in both branches dispersed to the Oriental region and then to the Ethiopian and Malagasy regions on the one hand, and to the Australian region on the other. From these highly advanced termites, endemic genera evolved during Tertiary times in each major isolated zoogeographical region.

New genera are named and described on the *Subulitermes* branch from species already described and named. All were formerly placed

under other generic names. Following are the new genera and the new combinations of specific names:

Leucopitermes, new genus from the Oriental region, includes the type species, *Leucopitermes leucops* (Holmgren), a new combination for *Eutermes leucops* Holmgren, which was also placed in the subgenus and genus *Subulitermes.* Part of the cotype specimens of *Termes aciculatus* Haviland are placed in synonymy with *Leucopitermes leucops* (Holmgren).

Aciculitermes, new genus from the Oriental region, includes the type species, *Aciculitermes aciculatus* (Haviland), a new combination for *Termes aciculatus* Haviland later placed in *Eutermes* and *Subulitermes.*

Ceylonitermellus, new genus from the Oriental region, includes the type species, *Ceylonitermellus hantanae* (Holmgren), a new combination for *Eutermes hantanae* Holmgren later placed in *Subulitermes,* and one other species, *Ceylonitermellus kotuae* (Bugnion), a new combination for *Eutermes Kotuae* Bugnion later placed in *Subulitermes.*

Oriensubulitermes, new genus from the Oriental region, includes the type species, *Oriensubulitermes inanis* (Haviland), a new combination for *Termes inanis* Haviland later placed in *Eutermes* and *Subulitermes,* and one other species, *Oriensubulitermes inaniformis* (Holmgren), a new combination for *Eutermes inaniformis* Holmgren also placed in *Subulitermes.*

Malagasitermes, new genus from the Malagasy region, includes the type species, *Malagasitermes milloti* (Cachan), a new combination for *Eutermes Milloti* Cachan.

Occultitermes, new genus from the Australian region, includes the type species, *Occultitermes occultus* (Hill), a new combination for *Mirotermes occultus* Hill later placed in *Eutermes* and *Subulitermes.*

Macrosubulitermes, new genus from the Australian region, includes the type species, *Macrosubulitermes greavesi* (Hill), a new combination for *Eutermes greavesi* Hill later placed in *Subulitermes,* and one other species, *Macrosubulitermes perlevis* (Hill), a new combination for *Eutermes perlevis* Hill later placed in *Subulitermes.*

Australitermes, new genus from the Australian region, includes the type species, *Australitermes dilucidus* (Hill), a new combination for *Eutermes dilucidus* Hill later placed in *Subulitermes.*

Nasutitermes undecimus (Kemner), a new combination for *Subulitermes undecimus* Kemner from Amboina, Moluccas, in the Papuan region was also tentatively placed in *Leucopitermes* (Emerson, 1955, p. 502).

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