

A GENERIC REVISION AND
PHYLOGENETIC STUDY OF
THE FAMILY KALOTER-
MITIDAE (ISOPTERA)

KUMAR KRISHNA

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NETIC STUDY OF THE FAMILY
KALOTERMITIDAE (ISOPTERA)

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INTRODUCTION

THE FAMILY Kalotermitidae consists of 353 living and fossil species, grouped under 24 genera in the present revision. The family is primitive in its morphology, nesting behavior, and social organization. The species found and maintain their colonies strictly in wood, without necessary soil connections, often in sound damp or dry wood. They do not construct definite nests, as do the higher termites, but instead excavate an irregular system of galleries with constructed partitions. Because of such an ecology, they have escaped competition with higher termites. The Kalotermitidae have intestinal flagellates but do not have any staphylinid beetles as guests.

The family Kalotermitidae consists of a number of living genera, which have existed presumably since Cretaceous times or earlier, even though they have given rise to phylogenetic series of advanced genera. Also, the transitional forms in the phylogenetic sequence have persisted to a remarkable degree to the present time, so that we have "living fossils" or connecting links between many genera. Because of the presence of such transitional forms, it is possible to theorize with considerable assurance about the derivation of a particular living genus from another living genus. For these reasons, the family is exceptionally satisfactory for the analysis of evolutionary history.

The objectives of this study are: (1) the regrouping of the formerly classified species into several genera consistent with the modern concept of the genus unfolded by the studies of the imago mandibles and their associated structural patterns in all castes and redescription and illustration of the various new and old genera; (2) the formulation of a hypothetical phylogeny; and (3) a synthesis of taxonomic, phylogenetic, and biogeographical data, in an attempt to elucidate the evolutionary history of the group.

The basic method of taxonomy is to compare and evaluate the characteristics of the structure by morphological comparisons and interpret them in the light of comparative genetics, biochemistry, embryology, behavior, ecology, and geography.

Michener and Sokal (1957) have criticized

the traditional classical practice of weighting characters. They argue that the procedure of assigning significance to either adaptive or non-adaptive characters brings in subjectivity in classification. They have proposed what they consider to be a more objective, quantitative approach in grouping 97 species of megachilid bees. Their basic procedure consisted of measuring correlations in 122 characters weighted equally. They thus arrived at a classification by grouping species according to the extent to which the characters are correlated. They claim that the resulting classification is closely similar to the one previously established by classical methods.

Inger (1958) attacked the quantitative methodology of Michener and Sokal and strongly objected to their practice of giving equal weight to all characters. He states that their method has no advantage over the more traditional taxonomic approaches, as their technique also rests on a subjective base.

Emerson (*in* Schmidt and Emerson, 1960) states: "The tendency to give equal importance to all comparative characters of organisms often leads to bias and to errors of judgment. Because the order of taxonomic classification is based upon homology through descent, principles of evolution are both substantiated by taxonomic data, and in turn, may be used for taxonomic interpretation. For example, it is possible to distinguish homology from analogy and both from fortuitous resemblance, strongly adaptive from weakly adaptive or nonadaptive characters, primitive from derivative characters, rapidly evolving from slowly evolving characters, persistent conservative characters from labile changing characters, progressively functional characters from regressed vestiges, relatively complex from relatively simple characters, and individually acquired characters from hereditary characters." All characters are not equivalent in their genetic control and in their development and ecological effects, and therefore cannot be treated equally (Inger, 1958). A competent taxonomist after long training and experience can determine which characters are constant, which are variable, and which are more important for generic classification. That character weighting has been

used injudiciously by poor taxonomists is not sufficient reason for rejecting the method.

Stroud (1953) used the technique of multiple factor analysis in the evaluation of characters, the elucidation of evolutionary processes by detection of adaptive trends, the detection of phylogenies, and the definition of categories. By this quantitative technique he analyzed correlations of 14 characters for soldiers of 48 species and imagoes of 43 species of the genus *Kaloterмес*. The application of multiple factor analysis as used by Stroud in establishing categories has limitations, because in his study of the genus *Kaloterмес* he selected characters in such a way that homologous dimensions of soldier and imago anatomy could be measured. He limited himself to only 14 characters found in both imagoes and soldiers and thus omitted important characters such as wing venation, imago-nymph mandible, arolium, anterior margin of soldier pronotum, and tibial spines. The statistical approach used by Stroud failed to correct the errors resulting from earlier investigations. The phylogenetic analysis used in the present paper conforms more closely to classical methods than did that of Stroud (1953). The method of multiple factor analysis used by Stroud when applied to the categories distinguished by the method used in this paper may indicate more subtle relationships and correlations of characters here treated as independent units. (Also see under the genus *Kaloterмес*.)

Inger (1958) suggests a biological approach to the delimitation of genera. He outlines a method for establishing genera on the basis of adaptive characters. He thinks that the use of adaptive characters has more advantages than the use of non-adaptive conservative characters. Many errors have been made because of convergence, when adaptive trends were used as the basis for classification. Also, many characters of importance in the classification of genera and higher taxonomic categories do not have known functions.

In termites, we have the soldier caste, which is adaptive for defense, and the imago, a more conservative reproductive caste. The ability to contrast slowly evolving, relatively conservative, weakly adaptive characters with strongly adaptive characters in the

different castes with the same basic genetic system corrects the errors due to the confusion of convergence with homology and provides excellent data for generic classification and phylogenetic analysis. In the present study, I have conformed to the traditional approach of character weighting in defining categories. I have studied a number of morphological characters—wing venation, imago-nymph mandible, arolium, eye size, pigmentation, pilosity, tibial spines, and other characters in the imago, and head shape, size, and pronotum in the soldier—and have defined genera based on a constellation of conservative, adaptive, and regressed characters.

The imago mandible is a conservative character which has been found valuable in generic classification. In a number of supergeneric groups within the family Kalotermitidae, the genera show no differences in the imago mandible. Yet it has been possible to recognize genera by other sets of characters, both in the imago and the soldier caste. An animal can retain primitive characters and at the same time have obvious derivative modifications. Different portions of the same individual may show conservative characters with little evolutionary change and also have more rapidly evolving adaptive specializations.

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I am greatly indebted to Dr. Alfred E. Emerson for suggesting the problem and taking keen interest in the progress of the work. My wife, Valerie Krishna, has provided editorial assistance. This work was done during tenures of a University Fellowship, John M. Prather Fellowship, and Chicago Natural History Museum Fellowship of the University of Chicago.

The author is also grateful to Mr. Rupert Wenzel of the Chicago Natural History Museum and to Mr. Victor Harris of the British Museum (Natural History), London, for the loan of specimens.

MATERIAL AND TECHNIQUE

This study is based primarily on the termites in the collection of the American Museum of Natural History, now in the custody of Alfred E. Emerson, the University

of Chicago. The majority of species were represented by primary types.

A total of 344 species was studied in alcohol under a binocular dissecting microscope. The imago-nymph mandibles were dissected. The drawings were made by two methods. Most were drawn with the help of a camera lucida. The drawings of wings were made with a microprojector. All drawings are of the type species of the different genera.

TERMINOLOGY

The morphological terms and measurements used in this paper are explained in Emerson (1945, 1952b) and Ahmad (1950). In this paper, the first plus second left marginal tooth and third left marginal tooth are equal to the first left marginal tooth and second left marginal tooth, respectively, as referred to by Ahmad (1950).

SYSTEMATIC REVISION

- FAMILY **KALOTERMITIDAE** BANKS, 1919
- > <Subfamily Calotermitinae FROGGATT, 1896, p. 516.
 - > <Subfamily Glyptotermitinae FROGGATT, 1896, p. 518.
 - <Subfamily Calotermitinae SILVESTRI, 1901, p. 1 (no description).
 - <Subfamily Calotermitinae SILVESTRI, 1903, pp. 16, 17.
 - <Subfamily Calotermitinae DESNEUX, 1904b, p. 284.
 - <Tribe Calotermitini DESNEUX, 1904b, p. 285.
 - <Subfamily Calotermitinae DESNEUX, 1904d, pp. 9, 11.
 - > <Tribe Calotermitini DESNEUX, 1904d, p. 20.
 - <Tribe Termopsis DESNEUX, 1904d, p. 12.
 - > <Subfamily Calotermitinae FROGGATT, 1905, pp. 17, 19.
 - > <Subfamily Glyptotermitinae FROGGATT, 1905, pp. 17, 23.
 - <Subfamily Calotermitinae HANDLIRSCH, 1908, p. 697 (no description).
 - <Suborder Cryptoclidoptera ENDERLEIN, 1909, p. 171.
 - Family Calotermitidae ENDERLEIN, 1909, p. 172 (no description).
 - <Subfamily Calotermitinae WASMANN, 1909, pp. 170, 171.
 - <Tribe Calotermitini WASMANN, 1909, pp. 171, 172.
 - <Family Protermitidae HOLMGREN, 1909, p. 100 (no description).
 - <Family Protermitidae HOLMGREN, 1910a, p. 285 (no description).
 - <Subfamily Calotermitinae HOLMGREN, 1910a, p. 285 (no description).
 - > Genus *Calotermes* HOLMGREN, 1910a, p. 285 (no description).
 - <Family Protermitidae HOLMGREN, 1910b, p. 137.
 - <Subfamily Calotermitinae HOLMGREN, 1910b, p. 137.
 - > Genus *Calotermes* HOLMGREN, 1910b, p. 137 (no description).
 - <Family Protermitidae HOLMGREN, 1911a, pp. 10, 13, 14, 33, 34.
 - > <Subfamily Calotermitinae HOLMGREN, 1911a, pp. 10, 34, 35, 48, 49, 51, 61.
 - <Subfamily Hodotermitinae HOLMGREN, 1911a, pp. 34, 41, 42, 44, 45.
 - > Genus *Calotermes* HOLMGREN, 1911a, pp. 10, 49, 51, 52, 60, 61.
 - <Family Protermitidae HOLMGREN, 1911d, pp. 185, 189, 206, 209.
 - > Genus *Calotermes* HOLMGREN, 1911d, p. 209.
 - > Genus *Calotermes* HOLMGREN, 1913a, p. 36 (no description).
 - <Family Kalotermitidae BANKS, 1919, p. 475.
 - <Family Kalotermitidae BANKS AND SNYDER, 1920, pp. 10, 77.
 - = Subfamily Kalotermitinae BANKS AND SNYDER, 1920, pp. 10, 16, 77.
 - Family Kalotermitidae LIGHT, 1921, p. 29 (no description).
 - > <Group *Kalotermes* FULLER, 1921, pp. 15, 16.
 - Family Kalotermitidae LIGHT, 1924, pp. 52, 53.
 - <Family Kalotermitidae EMERSON, 1925, pp. 312, 316.
 - <Subfamily Kalotermitinae EMERSON, 1925, pp. 312, 316.
 - > Genus *Kalotermes* EMERSON, 1925, pp. 298, 316.
 - Family Calotermitidae JOHN, 1925, p. 380 (no description).
 - Family Kalotermitidae SNYDER, 1925d, p. 158.
 - > Genus *Calotermes* HILL, 1925b, p. 86.
 - <Family Calotermitidae SJÖSTEDT, 1926, pp. 7, 8, 22.
 - <Family Calotermitidae TILLYARD, 1926, pp. 104, 105.
 - > Genus *Calotermes* HILL, 1926b, p. 144.
 - <Family Protermitidae BATHELLIER, 1927, p. 126.
 - > Genus *Calotermes* BATHELLIER, 1927, pp. 126, 127.
 - Subfamily Calotermitinae PONGRÁČZ, 1928, pp. 110, 114, 115.
 - <Family Kalotermitidae EMERSON, 1928, pp. 410, 420.
 - > Genus *Kalotermes* EMERSON, 1928, p. 421.
 - <Subfamily Calotermitinae HANDLIRSCH, 1930, p. 856.
 - <Tribe Calotermitini HANDLIRSCH, 1930, p. 857.
 - Family Kalotermitidae LIGHT, 1930, pp. 15–17.
 - <Family Calotermitidae HILL, 1932a, pp. 9, 10.
 - > Genus *Calotermes* HILL, 1932a, p. 12.
 - = Family Calotermitidae BRUES AND MELANDER, 1932, pp. 94, 95.
 - <Family Kalotermitidae LIGHT, 1933, pp. 82, 83.
 - = Subfamily Kalotermitinae LIGHT, 1933, p. 82.
 - > Genus *Kalotermes, sensu lato*, LIGHT, 1933, p. 83.
 - <Family Kalotermitidae LIGHT, 1934, pp. 121, 130.
 - Family Calotermitidae SILVESTRI, 1934, pp. 32, 33 (no description).

<Family Kalotermitidae KEMNER, 1934, pp. 29, 179.

Family Kalotermitidae WU, 1935, p. 217 (no description).

Subfamily Kalotermitinae WU, 1935, p. 217 (no description).

Family Kalotermitidae HARE, 1937, pp. 460, 461, 474.

Subfamily Kalotermitinae HARE, 1937, pp. 460, 461.

<Family Protermitidae MARTYNOV, 1937, pp. 86, 87, 89, 96, 102, 103, 104, 113, 115–117, 119, 129, 131.

>Genus *Calotermes* MARTYNOV, 1937, pp. 88, 113, 116, 117, 149.

<Subfamily Calotermitinae STATZ, 1939, pp. 35–37, pl. 4.

=Tribe Calotermitini STATZ, 1939, p. 38, pl. 4.

<Family Calotermitidae HILL, 1942, pp. 6, 7.

>Genus *Calotermes* HILL, 1942, pp. 7, 11, 14, 36.

<Family Kalotermitidae EMERSON, 1942, p. 10.

>Subfamily Kalotermitinae EMERSON, 1942, pp. 9, 10.

><Subfamily Electrotermitinae EMERSON, 1942, pp. 9, 10.

<Family Kalotermitidae KIRBY, 1944, p. 195.

<Family Calotermitidae KELSEY, 1944, p. 236.

>Genus *Calotermes* KELSEY, 1944, p. 236.

<Family Kalotermitidae SNYDER, 1948, pp. 227, 228, 230.

<Family Kalotermitidae SNYDER, 1949, pp. 5, 10, 356.

>Subfamily Kalotermitinae SNYDER, 1949, pp. 5, 11, 356.

><Subfamily Electrotermitinae SNYDER, 1949, pp. 7, 356.

<Family Calotermitidae GRASSÉ, 1949, p. 530.

>Subfamily Calotermitinae GRASSÉ, 1949, pp. 530, 531.

><Subfamily Electrotermitinae GRASSÉ, 1949, p. 530.

Family Calotermitidae CACHAN, 1949, p. 192.

<Family Kalotermitidae AHMAD, 1950, pp. 44, 48–50.

<Family Calotermitidae IMMS, 1951, p. 291.

<Family Calotermitidae RATCLIFFE, GAY, AND GREAVES, 1952, pp. 49, 63.

>Genus *Calotermes* RATCLIFFE, GAY, AND GREAVES, 1952, pp. 55, 63–66.

=Family Kalotermitidae AHMAD, 1955, p. 203.

<Family Kalotermitidae WEIDNER, 1955a, pp. 9, 18, 20, 38, 39, 45, 68, 74, 76, 77.

<Subfamily Kalotermitinae WEIDNER, 1955a, pp. 9, 46, 68, 75.

><Subfamily Electrotermitinae WEIDNER, 1955a, pp. 45, 46, 68.

<Family Kalotermitidae WEIDNER, 1955b, pp. 60, 61, 64, 70.

>Subfamily Kalotermitinae WEIDNER, 1955b, p. 61.

><Subfamily Electrotermitinae WEIDNER, 1955b, pp. 61, 64, 70.

<Family Kalotermitidae EMERSON, 1955, pp. 506–508, 516, 517.

>Subfamily Kalotermitinae EMERSON, 1955, p. 507.

><Subfamily Electrotermitinae EMERSON, 1955, p. 507.

=Family Kalotermitidae AHMAD, 1958, pp. 34, 35.

TYPE GENUS: *Kalotermes* Hagen, 1853.

The subfamily "Calotermitinae" was originally named by Froggatt in 1896, who placed it in the family Termitidae and included the genus *Calotermes* and seven other genera. *Glyptotermes* (now placed in the family Kalotermitidae) he included with *Heterotermes* (now in the family Rhinotermitidae) in a separate subfamily, Glyptotermitinae.

Silvestri (1901, 1903) followed the classification of Froggatt. Desneux (1904d) divided the subfamily Calotermitinae into three tribes and included the genera *Calotermes* and *Psammotermes* (now placed in the family Rhinotermitidae) in the tribe Calotermitini. Wasmann (1909) followed the classification of Desneux, but included the genera *Calotermes*, *Glyptotermes*, and *Psammotermes* in the tribe Calotermitini.

Enderlein (1909) included the families Calotermitidae and Termitidae in the suborder Cryptoclidoptera. As he gave no description, his concept of the family is unknown.

Holmgren (1911a) discarded all the previous classifications and divided the order Isoptera into four families: the Mastotermitidae, Protermitidae, Mesotermitidae, and Metatermitidae. He divided the family Protermitidae into four subfamilies, namely, the Termopsinae, Hodotermitinae, Stotermitinae, and Calotermitinae. In the subfamily Calotermitinae he included the genera *Calotermes* Hagen, *sensu lato*, and *Porotermes*, the latter now placed in the family Hodotermitidae. He further subdivided the genus *Calotermes* Hagen, *sensu lato*, into a number of subgenera, which have been given generic rank by Banks and Snyder (1920), Emerson (1942, 1955), Snyder (1949), and others. Holmgren (1911a) also placed the genus

Pterotermes, now placed in the family Kalotermitidae, in the subfamily Hodotermitinae.

The family Kalotermitidae was first described by Banks in 1919. Banks and Snyder (1920) changed the family names Protermitidae, Mesotermitidae, and Metatermitidae, as used by Holmgren (1911a), because the names were not based on any included generic names and therefore did not conform to the accepted rules of nomenclature. With this change, the Kalotermitidae became equivalent to the Protermitidae of Holmgren (1911a). Banks and Snyder (1920) further subdivided the family Kalotermitidae into the subfamilies Mastotermitinae, Stolotermitinae, Termopsinae, and Kalotermitinae. The changes made by Banks and Snyder were accepted by Light (1921, 1924, 1933) and Emerson (1925). Snyder (1925d) and Sjöstedt (1926) separated the family Hodotermitidae from the Kalotermitidae of previous workers, and this change was adopted by Emerson (1928).

The classification of Handlirsch (1930), which was followed by Statz (1939), is essentially the same as that of Desneux (1904d); these authors divide the subfamily Calotermitinae into the tribes Termopsini, Hodotermitini, and Calotermitini, but also include the tribe Stolotermitini in the subfamily.

The most recent classification is that of Emerson (1942), which has been adopted by Snyder (1949), Grassé (1949), Weidner (1955a, 1955b), and Emerson (1955). Emerson (1942) divided the family Kalotermitidae into two subfamilies, the Electrotermittinae and Kalotermitinae. He placed all the fossil genera, *Eotermes*, *Proelectrotermes*, *Prokalotermites*, and *Electrotermes*, in the subfamily Electrotermittinae, and the living genera, *Kalotermes*, *Neotermes*, *Paraneotermes*, *Rugitermes*, *Procryptotermes*, *Cryptotermes*, *Eucryptotermes*, *Glyptotermes*, and *Calcaritermes*, in the subfamily Kalotermitinae. Emerson (1942) separated the fossil subfamily Electrotermittinae from the subfamily Kalotermitinae on the basis of the primitive condition of the cerci, which are four- to five-segmented, and of the spines on the middle tibia. I have examined the cerci of some fossil species and made the following observations: The fossil of *Prokalotermes hageni* is poorly preserved, and the number of articles of the cercus is highly

questionable. In the amber fossil *Electrotermes affinis* the cercus, although mentioned by Weidner (1955b) as being four- to five-segmented, is definitely two-segmented, which is characteristic of all the living genera of the family Kalotermitidae. Also, the spines of the middle tibia in the fossil and living genera are present in various combinations which form a connected series: two outer tibial spines and one inner tibial spine in *Proelectrotermes*; two outer tibial spines in *Electrotermes*; and only one outer spine in the living genus *Postelectrotermes*, new genus.

In view of the above facts, it seems that the distinctions between the subfamilies Electrotermittinae and Kalotermitinae are not sufficiently sharp to warrant systematic distinction or names.

Statz (1939) described the fossil genus *Eotermes* from Rott on Siebengebirge, upper Oligocene of Germany, and tentatively placed it, with the genus *Ulmeriella* Meunier, in the tribe Termopsini. Emerson (1942) transferred the genus *Ulmeriella* from the tribe Termopsini to the subfamily Hodotermitinae, family Hodotermitidae, because it has a four-segmented tarsus, small eyes, probably no ocelli, and the branches of the radial sector running inward to join the lower margin of the wing. The above-mentioned characteristics are typical of the subfamily Hodotermitinae. *Ulmeriella* is described by Statz (1939) as having the pronotum either wider or narrower than the head. Emerson (1952) doubted this and stated that a reexamination of the fossil species may show that the pronotum is always narrower than the head—a characteristic of the family Hodotermitidae. The description and figures of the genus *Eotermes*, as given by Statz (1939), are poor, and therefore the classification of this genus should be considered with great caution. He mentioned that this genus has a *Hodotermes*-like imago mandible, small eyes, 22-segmented antenna, pronotum broader than head, and a four-segmented tarsus. He gives an illustration of the forewing in which the upper and lower edges of the wing are for the most part parallel; the apical edge is nearly straight; the subcosta is short; the radius (R_1) is simple; the radial sector is forked, the upper branch forking repeatedly and the branches joining the costal margin and the

upper part of the straight apical edge; the lower branch runs straight for a short distance, forking several times, the branches bending down to join the lower part of the straight apical edge. The figures of the head and leg, as given by Statz, show that the ocelli and arolium are absent.

Emerson (1942) placed the genus *Eotermes* in the subfamily Electrotermatinae, family Kalotermitidae. I am of the opinion that *Eotermes* does not belong to the family Kalotermitidae and that it should be placed tentatively in the family Hodotermitidae. In the Kalotermitidae, the radial sector runs straight and gives off branches only to the costal margin, the ocelli are present, and the imago mandible is different from that in the Hodotermitidae.

Statz (1939) states that *Eotermes* is related to the genus *Ulmeriella*, as there is a fundamental similarity in the wing venation. I am of the opinion that the wing venation of *Eotermes* is unique and is not related to that of *Ulmeriella*, as in *Ulmeriella* and all other genera of the subfamily Hodotermitinae the radial sector definitely joins the lower margin. Also, *Eotermes* cannot be placed in any other subfamily (the Termopsinae, Stolotermitinae, or Porotermitinae of the family Hodotermitidae) and should therefore be placed only in the family Hodotermitidae, without its being assigned to any subfamily until more characters are discovered.

DIAGNOSIS OF THE FAMILY KALOTERMITIDAE

IMAGO: Fontanelle absent. Ocelli present. Antenna with 11 to 21 articles. Imago-nymph mandible as in the family Mastotermitidae. Left mandible with an apical tooth, two distinct marginal teeth, and a molar plate; second marginal tooth fused with first marginal tooth; first plus second marginal tooth separated from third by a wide-angled notch; first plus second marginal tooth equal to or smaller than third. Right mandible with two marginal teeth and a molar plate; posterior margin of second marginal tooth subequal or longer than molar plate. Pronotum flatly arched and as broad as or wider than head. Forewing scale large and overlapping hind wing scale. In the forewing, subcosta short and sclerotized; radius (R_1) sclerotized, short, and simple; radial sector heavily sclerotized,

running parallel to costal margin and having a number of branches which join costal margin (except in the genera *Glyptotermes* and *Calcaritermes*, in which it is unbranched); media either weak or strong, variable in position and joining wing tip or radial sector either close to wing scale or far from it; cubitus weak and unsclerotized, large number of branches to inner margin of wing. Anal vein absent. In hind wing, subcosta absent; short anal vein present. Tarsi four-segmented. Arolium present or absent. Tibial spurs 3:3:3, with additional spines in a few genera. Cerci two-segmented.

SOLDIER: Head robust, long, in some species subtruncate or phragmotic. Eyes rudimentary, in some pigmented. Y suture always present. Antenna with 10 to 19 articles. Mandibles usually robust; dentition variable. Left mandible with an apical tooth and three marginal teeth, all gradations of reduction to complete reduction of the three marginal teeth present. Right mandible with an apical tooth and two marginal teeth, in some species the two marginal teeth completely reduced.

WORKER: A true worker caste is absent.

GENERA INCLUDED: *Proelectrotermes*¹ von Rosen; *Electrotermes*¹ von Rosen; *Postelectrotermes*, new genus; *Neotermes* Holmgren; *Rugitermes* Holmgren; *Eucryptotermes* Holmgren; *Prokalotermes*¹ Emerson; *Kalotermes* Hagen; *Paraneotermes* Light; *Ceratokalotermes*, new genus; *Comatermes*, new genus; *Glyptotermes* Froggatt; *Calcaritermes* Snyder; *Pterotermes* Holmgren; *Incisitermes*, new genus; *Allotermes* Wasmann; *Marginitermes*, new genus; *Tauritermes*, new genus; *Proneotermes* Holmgren; *Bifiditermes*, new genus; *Bicornitermes*, new genus; *Epicalotermes* Silvestri; *Procryptotermes* Holmgren; and *Cryptotermes* Banks.

KEY TO THE GENERA OF THE FAMILY KALOTERMITIDAE

BASED ON THE CHARACTERS OF THE IMAGO

1. Forewing with media and cubitus arising from a common stem outside the wing scale: arolium absent (fig. 64) 2
Forewing with media and cubitus arising from

¹ Fossil.

- inside the wing scale; arolium present or absent (fig. 21) 3
2. Left imago-nymph mandible with anterior margin of third marginal tooth longer than one and one-half times the length of the posterior margin of first plus second marginal tooth (fig. 70) *Epicalotermes*
Left imago-nymph mandible with anterior margin of third marginal tooth clearly longer but usually not more than one and one-half times longer than the posterior margin of first plus second marginal tooth (figs. 63, 67) *Bifiditermes*, *Bicornitermes*
3. Middle tibia with three apical spurs and additional spines (figs. 2, 4, 6) 4
Middle tibia with three apical spurs only, additional spines absent 6
4. Middle tibia with two outer spines and one inner spine; fossil only (fig. 2)
 *Proelectrotermes*
Middle tibia with one or two outer spines, inner spine absent 5
5. Middle tibia with two outer spines; fossil only (fig. 4) *Electrotermes*
Middle tibia with one outer spine; living (fig. 6) *Postelectrotermes*
6. Left imago-nymph mandible with anterior margin of third marginal tooth equal to the posterior margin of first plus second marginal tooth (fig. 20) 7
Left imago-nymph mandible with anterior margin of third marginal tooth clearly longer than posterior margin of first plus second marginal tooth (fig. 46) 15
7. Forewing with media unsclerotized, weak, and running midway between radial sector and cubitus to tip of wing (fig. 21) 8
Forewing with media sclerotized (figs. 5, 9, 13, 25) 9
8. Wings dark, with pimple-like nodules (fig. 21); arolium present. *Kalotermes*
Wings hyaline with no nodules (fig. 43); arolium absent *Pterotermes*
9. Forewing with media sclerotized, but not so strongly as radial sector (figs. 25, 29, 32) 10
Forewing with media as strongly sclerotized as radial sector (figs. 9, 13, 17, 36) 12
10. Head and pronotum densely covered with very long and wavy hairs (fig. 31)
 *Comatermes*
Head and pronotum covered with short bristles; long hairs absent 11
11. Left imago-nymph mandible with distinct dent in posterior margin of first plus second marginal tooth; base of first plus second marginal tooth slightly larger than base of third marginal tooth (fig. 24)
 *Paraneotermes*
Left imago-nymph mandible with no dent in posterior margin of first plus second marginal tooth, evenly rounded; base of first plus second marginal tooth equal to base of third marginal tooth (fig. 28)
 *Ceratokalotermes*
12. Radial sector without branches; media running close to radial sector to tip of wing (fig. 36) *Glyptotermes*, *Calcaritermes*
Radial sector with branches 13
13. Media very small, coalescing with radial sector very close to suture (fig. 13)
 *Rugitermes*
Media running close and parallel to radial sector to tip of wing (figs. 9, 17) 14
14. Anterior margin of forewing scale convex (fig. 9); eye diameter, 0.46-0.78 mm.
 *Neotermes*
Anterior margin of forewing scale almost straight (fig. 17); eye diameter, 0.43 mm. *Eucryptotermes*
15. Media slightly sclerotized and running closer to radial sector than to cubitus (fig. 60) *Proneotermes*
Media not sclerotized and running midway between radial sector and cubitus (figs. 47, 54, 75) 16
16. Media bending up and joining radial sector in middle or beyond middle of wing (figs. 75, 79) *Procryptotermes*, *Cryptotermes*
Media running clear to tip of wing (figs. 47, 54) 17
17. Arolium always absent
 *Marginitermes*, *Allotermes*
Arolium usually present; occasionally absent *Incisitermes*, *Tauritermes*
- BASED ON THE CHARACTERS OF THE SOLDIER
1. Middle tibia with one outer spine
 *Postelectrotermes*
Middle tibia with no spine 2
2. Front tibia with a thick conspicuous spur near apex of outer side, much larger than two apical spurs (fig. 40) *Calcaritermes*
Front tibia with an apical spur not enlarged 3
3. Head short and highly phragmotic (figs. 18, 69, 76, 80) 4
Head long or short, not phragmotic, sloping in front at an approximate angle of 20 to 45 degrees; with or without anterolateral prominences (figs. 10, 14, 22, 26, 30, 33, 37, 48, 55, 61, 65) 8
4. Anterior margin of pronotum serrated (figs. 18, 69, 80) 5

- Anterior margin of pronotum even and not serrated (fig. 76) 7
5. Anterior margin of pronotum sharply serrated; head bilobed, with region between lobes depressed; ridge between vertex and frons absent (fig. 69) *Bicornitermes*
- Anterior margin of pronotum wavy, weakly or finely serrated; ridge between frons and vertex present (figs. 18, 80) 6
6. Head in front strongly scooped out; antennal socket at one-third to half of the length of head from front (fig. 18) *Eucryptotermes*
- Head in front vertical and not so strongly scooped out; antennal socket close to side base of mandibles (fig. 80) *Cryptotermes*
7. Ridge between vertex and frons distinct; head in front not vertical; third joint of antenna large and club-shaped (fig. 76) *Procryptotermes*
- Ridge between vertex and frons absent; head in front vertical; third joint of antenna not large *Glyptotermes* (some spp.), *Kalotermes* (some spp.)
8. Anterior margin of pronotum not deeply concave or incised 9
- Anterior margin of pronotum deeply concave or incised 13
9. Head with a prominent ridge in front formed by a continuation of the dorsal antennal margin medially (fig. 14) *Rugitermes*
- Head without the prominent ridge 10
10. Head usually with distinct anterolateral prominences, sometimes phragmotic (fig. 37) *Glyptotermes*
- Head long, without prominent anterolateral prominences (figs. 26, 33) 11
11. Mandibles short in proportion to rest of head capsule (figs. 26, 33) 12
- Mandibles long, not so short in proportion to rest of head capsule (figs. 10, 22) *Kalotermes*, *Neotermes*
12. Postmentum very broad in front (fig. 26); nymph mandible as in figure 24 *Paraneotermes*
- Postmentum not very broad in front (fig. 33); head slope in front concave (fig. 33) *Comatermes*
13. Sides of head distinctly and clearly rounded (fig. 44); sclerotized swelling at base of postmentum *Pterotermes*
- Sides of head almost straight; no swelling at base of postmentum 14
14. Third segment of antenna very large, as long as next five to seven segments together; head with a ridge between vertex and frons (fig. 55) *Marginitermes*
- Third segment of antenna not so long as next five to seven segments together 15
15. Head dorsoventrally flat (figs. 48, 72) 16
- Head thick (figs. 30, 51, 56, 61) 17
16. Head sloping anteriorly from near middle; mandibles long in proportion to rest of head capsule and strongly curved (fig. 72); femur not swollen *Epicalotermes*
- Head not sloping anteriorly from near middle; mandibles short in proportion to rest of head capsule (figs. 48, 49); femur strongly swollen *Incisitermes*
17. Head with a horn-like projection below and in front of antennal socket (fig. 51) *Allotermes*
- Head without horn-like projection 18
18. Head with distinct anterolateral prominences (figs. 30, 56) 19
- Head with indistinct anterolateral prominences 20
19. Third segment of antenna modified, longer and darker than fourth; anterior margin of pronotum distinctly wavy (fig. 56) *Tauritermes*
- Third segment of antenna not modified, equal to fourth; anterior margin of pronotum faintly wavy (fig. 30) *Ceratokalotermes*
20. Femur swollen; head in front dark; faint ridge between vertex and frons (fig. 61) *Proneotermes*
- Femur not swollen; ridge between vertex and frons absent (fig. 65) *Bifiditermes*
- GENUS **PROELECTROTERMES** VON ROSEN, 1913
- <Genus *Kalotermes* HAGEN, 1854, p. 223.
- <Gruppe *Kalotermes* PICTET AND HAGEN, 1856, p. 49.
- <Genus *Calotermes* HAGEN, 1858a, pp. 31-38.
- <Genus *Calotermes* HAGEN, 1858b, p. 1.
- <Genus *Kalotermes* HAGEN, 1862, p. 58.
- =Subgenus *Proelectrotermes* VON ROSEN, 1913, p. 331.
- =Genus *Proelectrotermes* EMERSON, 1942, pp. 9, 10.
- =Genus *Proelectrotermes* SNYDER, 1949, p. 356.
- =Genus *Proelectrotermes* GRASSÉ, 1949, p. 530.
- =Genus *Proelectrotermes* WEIDNER, 1955a, pp. 46, 68.
- =Genus *Proelectrotermes* WEIDNER, 1955b, pp. 64, 65, 70.
- =Genus *Proelectrotermes* EMERSON, 1955, p. 507.
- TYPE SPECIES: *Proelectrotermes berendtii* (Pictet).
- The type species of this genus, *Proelectrotermes berendtii*, was described by Pictet in 1854, and the holotype specimen was depos-

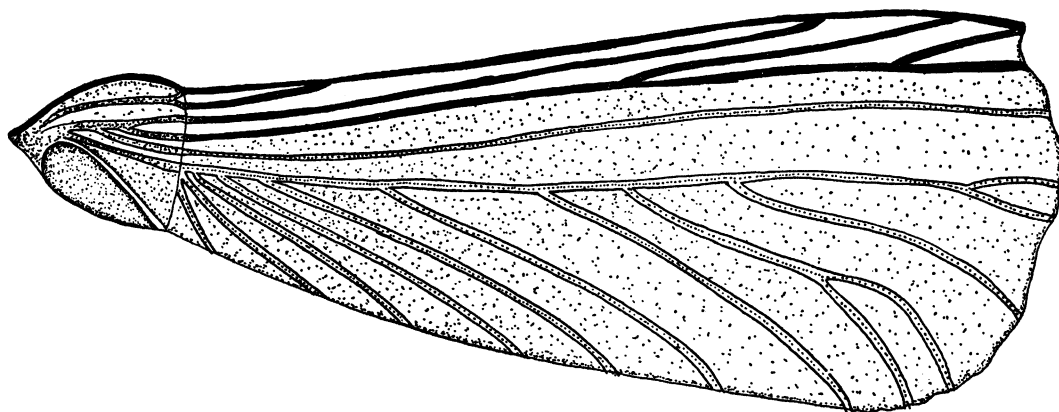


FIG. 1. Forewing of *Proelectrotermes berendtii* (Pictet). Baltic amber.

ited in the collection of Berendt in Danzig. Weidner (1955b) states that at present its depository is unknown, and perhaps the type is lost. In addition to the type specimen, Hagen had two additional specimens at that time which were probably deposited in the Munich Museum. Emerson in 1926 studied two specimens in the Munich Museum, one labeled "*Termes berendtii* Pict. (? belongs to Königsberg Museum) No. 14681, No. 61," the other, "K7808, collected by Dr. Klebs." Weidner states that these specimens were lost during the Second World War (personal

communication). Recently, I have discovered a specimen of *Proelectrotermes berendtii* Pictet in the Kohlman collection of arthropods in Baltic amber acquired by the Chicago Natural History Museum in 1953 (Wenzel, 1953). If the type specimens and the other specimens are lost, as suspected, then this is the only existing specimen of *Proelectrotermes berendtii* (Pictet), and I am tentatively selecting it as a neotype.

IMAGO: Color generally dark, probably owing to preservation. Eyes large; diameter, 0.52 mm. Ocellus about 0.03 mm. from eye. Antenna with 19 to 20 articles. Pronotum wider than head; anterior margin concave. Forewing with all major veins arising independently at wing suture; radius (R_1) simple; media weak, running slightly closer to radial sector than to cubitus; cubitus weak (fig. 1). Tibial spurs 3:3:3. Fore tibia with no additional spines; middle tibia with two spines on outer edge and one spine on inner edge near the apical spur (fig. 2); hind tibia with one inner spine. Arolium present.

SPECIES INCLUDED

Proelectrotermes berendtii (Pictet), 1854

GEOGRAPHICAL DISTRIBUTION: Baltic amber of East Prussia.

GEOLOGICAL DISTRIBUTION: Upper Eocene.

GENUS **ELECTROTERMES** VON ROSEN, 1913

<Genus *Kalotermes* HAGEN, 1854, p. 223.

<Gruppe *Kalotermes* PICTET AND HAGEN, 1856, p. 49.

<Genus *Calotermes* HAGEN, 1858a, pp. 31-38.

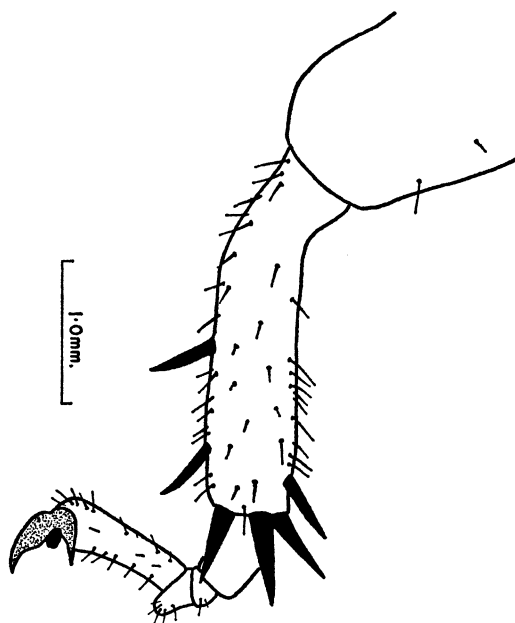


FIG. 2. Right middle leg of *Proelectrotermes berendtii* (Pictet). Baltic amber.

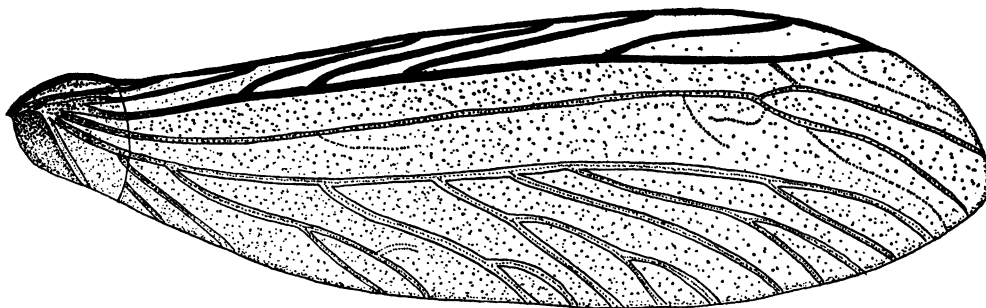


FIG. 3. Forewing of *Electrotermes affinis* (Hagen). Baltic amber.

- <Genus *Calotermes* HAGEN, 1858b, p. 1.
 <Genus *Kalotermes* HAGEN, 1862, p. 58.
 =Subgenus *Electrotermes* VON ROSEN, 1913, p. 331.
 =Genus *Electrotermes* EMERSON, 1942, pp. 9, 10.
 =Genus *Electrotermes* SNYDER, 1949, p. 357.
 =Genus *Electrotermes* GRASSÉ, 1949, p. 530.
 =Genus *Electrotermes* WEIDNER, 1955a, pp. 46, 68.
 =Genus *Electrotermes* WEIDNER, 1955b, pp. 58, 65, 66, 70, 71.
 =Genus *Electrotermes* EMERSON, 1955, p. 507.

TYPE SPECIES: *Electrotermes affinis* (Hagen).

IMAGO: Eyes small; diameter, 0.29 mm. Ocellus very close to eye, but not touching. Antenna with 15 to 18 articles. Pronotum broader than head. Forewing with all major veins arising independently at wing suture; radius (R_1) simple; occasionally a second branch of radius present; radial sector strongly sclerotized, with six to seven branches; media weak and running slightly closer to radial sector than to cubitus, branching near apical region of wing; cubitus weak and unsclerotized (fig. 3). Tibial spurs 3:3:3. Middle tibia with two outer spines (fig. 4). Arolium present.

SPECIES INCLUDED

Electrotermes affinis (Hagen), 1854
Electrotermes girardi (Giebel), 1856

GEOGRAPHICAL DISTRIBUTION: Baltic amber of East Prussia.

GEOLOGICAL DISTRIBUTION: Upper Eocene.

POSTELECTROTERMES, NEW GENUS

- <Genus *Calotermes* HAGEN, 1858a, pp. 31–38.
 <Genus *Calotermes* HAGEN, 1858b, p. 1.

- <Genus *Calotermes* WASMANN, 1897, p. 150.
 <Genus *Calotermes* SJÖSTEDT, 1900b, pp. 19–21, 35.
 <Genus *Calotermes* DESNEUX, 1904d, pp. 20–24.
 <Subgenus *Neotermes* HOLMGREN, 1911a, p. 54.
 <Subgenus *Glyptotermes* HOLMGREN, 1911a, p. 56.
 <Subgenus *Neotermes* HOLMGREN, 1913a, pp. 36, 37.
 <Genus *Neotermes* SJÖSTEDT, 1926, p. 33.
 <Genus *Glyptotermes* SJÖSTEDT, 1926, pp. 22, 23, 42.
 <Genus *Neotermes* CACHAN, 1949, pp. 190, 191, 196, 197.
 <Genus *Glyptotermes* CACHAN, 1949, pp. 190, 208.
 <Genus *Kalotermes* SNYDER, 1949, p. 11.
 <Genus *Neotermes* SNYDER, 1949, p. 21.
 <Genus *Proglyptotermes* COATON, 1950, p. 28.
 <Genus *Proneotermes* CACHAN, 1951, p. 1.

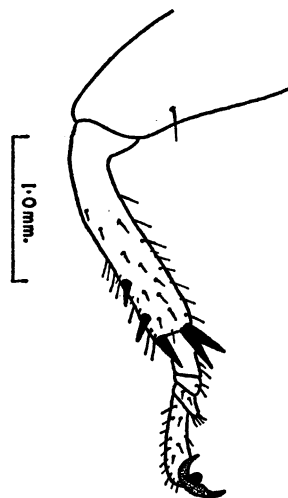


FIG. 4. Right middle leg of *Electrotermes affinis* (Hagen). Baltic amber.

<Genus *Proglyptotermes* STROUD, 1953, p. 88.

<Genus *Neotermes* AHMAD, 1958, p. 36.

TYPE SPECIES: *Postelectrotermes praecox* (Hagen) (= *Calotermes praecox* Hagen).

Most of the species that now constitute this new genus were placed by Snyder (1949) in the genera *Kalotermes* and *Neotermes*. This genus can be distinguished from *Neotermes* and other genera by the presence of a spine on the outer margin of the middle tibia, close to the outer apical spur, in both the imago and the soldier caste. The wing venation resembles that of the genus *Neotermes* but differs from it in having a more weakly sclerotized median vein.

IMAGO: Usually dark brown. Eyes usually small; diameter, 0.25–0.50 mm. Ocellus touching eye or approximately 0.01–0.04 mm. from eye. Antenna with 13 to 19 articles. Mandibles as in the genus *Kalotermes*, i.e., left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth; posterior margin of first plus second marginal tooth not

straight, convex at base. Right mandible with posterior margin of second marginal tooth equal to molar plate. Pronotum wider than head. Forewing with all major veins arising independently at wing suture; radius (R_1) in some species branched; radial sector with seven to eight branches, first branch arising at one-fifth of length of wing from suture; media sclerotized, but not quite so strong as radial sector, running closer to radial sector than to cubitus; many cross branches between radial sector and media; cubitus weak, unsclerotized (fig. 5). Tibial spurs 3:3:3; middle tibia with a distinct dark outer spine not quite so long as apical spur, close to outer apical spur (fig. 6). Arolium present.

SOLDIER: Head long, frons in some species with a medial depression which forms two slight prominences on each side, sloping downward in front towards anteclypeus at an angle of approximately 25 to 30 degrees. Eyes mostly unpigmented; in *Postelectrotermes pishinensis* (Ahmad) eyes slightly pigmented. Antenna with 11 to 18 articles; third article unspecialized and not highly sclerotized,

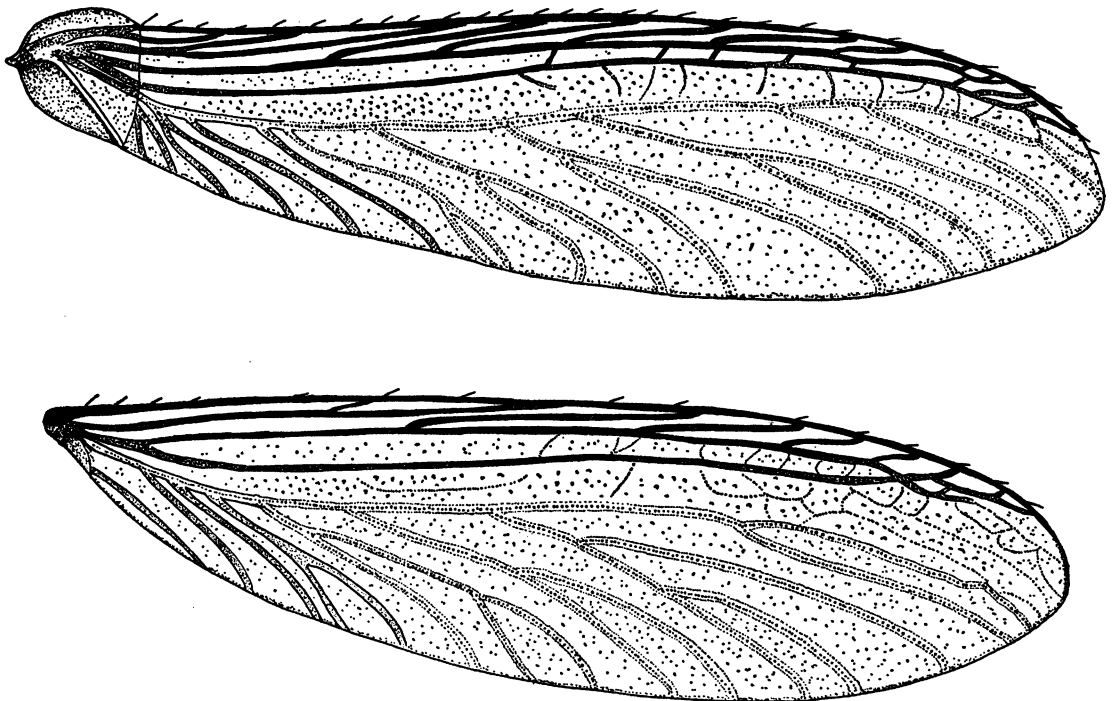


FIG. 5. Forewing and hind wing of *Postelectrotermes praecox* (Hagen). Homotype colony from Camancha, Madeira Island.

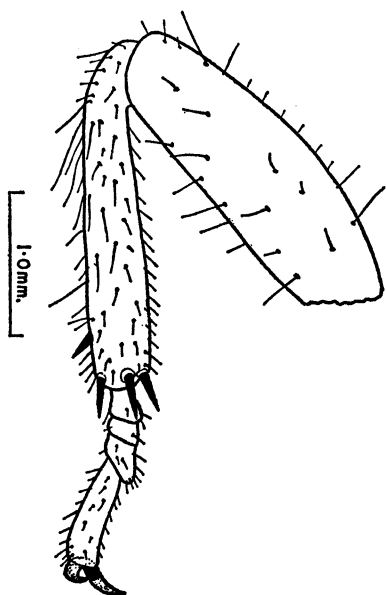


FIG. 6. Middle leg of *Postelectrotermes praecox* (Hagen). Homotype colony from Camancha, Madeira Island.

either longer or shorter than fourth. Pronotum narrower, as wide as or wider than head; anterior margin broadly and shallowly concave or angular. Tibial spurs 3:3:3. Middle tibia with an extra spine on outer margin, close to outer apical spur.

SPECIES INCLUDED

- P. amplus* (Sjöstedt), new combination = *Neotermes amplus* Sjöstedt, 1925
P. barretoii (Grassé), new combination = *Calotermes barretoii* Grassé, 1939
P. castaneiceps (Sjöstedt), new combination = *Calotermes castaneiceps* Sjöstedt, 1914
P. howa (Wasmann), new combination = *Calotermes howa* Wasmann, 1897
P. longiceps (Cachan), new combination = *Calotermes longiceps* Cachan, 1949
P. longus (Holmgren), new combination = *Calotermes (Glyptotermes) longus* Holmgren, 1910b
P. militaris (Desneux), new combination = *Calotermes militaris* Desneux, 1904a
P. pishinensis (Ahmad), new combination = *Neotermes pishinensis* Ahmad, 1955
P. praecox (Hagen), new combination = *Calotermes praecox* Hagen, 1858a
P. sordwanae (Coaton), new combination = ?
Glyptotermes sordwanae Coaton, 1949
P., new species, from Mare Longue, Réunion
P., new species, from near Ihosy, Madagascar

GEOGRAPHICAL DISTRIBUTION: Indo-Malayan: Ceylon, Pakistan. Ethiopian: Africa. Malagasy: Madagascar, Réunion. Palearctic: Maderé Island.

GENUS *NEOTERMES* HOLMGREN, 1911

- <Genus *Calotermes* HAGEN, 1858a, pp. 31–38.
 <Genus *Calotermes* HAGEN, 1858b, p. 1.
 <Genus *Calotermes* FROGGATT, 1896, pp. 517, 521.
 <Subgenus *Calotermes*, *sensu stricto*, WASMANN, 1897, p. 150.
 <Genus *Calotermes* HAVILAND, 1898, pp. 371, 373.
 <Genus *Calotermes* SJÖSTEDT, 1900b, pp. 19–21, 35.
 <Genus *Calotermes* SILVESTRI, 1903, pp. 20, 104.
 <Genus *Calotermes* DESNEUX, 1904d, pp. 20–24.
 <Subgenus *Neotermes* HOLMGREN, 1911a, pp. 53, 54, 57, 58, 61.
 <Genus *Neotermes* SILVESTRI, 1912, p. 212.
 <Subgenus *Neotermes* HOLMGREN, 1913a, pp. 36, 37.
 <Genus *Kalotermes* BANKS, 1919, pp. 476, 477.
 <Genus *Neotermes* BANKS, 1919, p. 476.
 <Genus *Kalotermes* BANKS AND SNYDER, 1920, pp. 16, 17.
 >Genus *Neotermes* BANKS AND SNYDER, 1920, pp. 16, 32.
 =Genus *Neotermes* FULLER, 1921, pp. 19, 23, 29.
 >Genus *Neotermes* SNYDER, 1922, p. 8.
 =Subgenus *Neotermes* EMERSON, 1925, pp. 312, 316.
 Subgenus *Neotermes* SNYDER, 1925c, p. 396.
 Subgenus *Neotermes* HILL, 1925b, p. 86.
 <Genus *Neotermes* SJÖSTEDT, 1926, pp. 22, 23, 33.
 Subgenus *Neotermes* EMERSON, 1928, pp. 405, 412, 418, 421.
 =Genus *Neotermes* LIGHT, 1930, pp. 15, 16, 18, 21.
 =Genus *Neotermes* LIGHT, 1931, p. 585.
 <Genus *Kalotermes* LIGHT, 1933, p. 83.
 =Subgenus *Neotermes* SNYDER, 1934b, pp. 24, 27.
 =Genus *Neotermes* KEMNER, 1934, pp. 30, 31.
 <Subgenus *Neotermes* HARE, 1937, pp. 474, 475.
 <Subgenus *Neotermes* HILL, 1942, pp. 7, 44, 45.
 >Subgenus *Neotermes* SNYDER, 1948, pp. 228, 232, 234, 235.
 <Genus *Kalotermes* SNYDER, 1948, pp. 228, 232.
 <Genus *Neotermes* CACHAN, 1949, pp. 180, 185, 196.

> <Genus *Neotermes* SNYDER, 1949, pp. 21, 359.

<Genus *Kalotermes* SNYDER, 1949, p. 11.

<Genus *Rugitermes* SNYDER, 1949, p. 34.

Genus *Neotermes* GRASSÉ, 1949, p. 531.

> <Genus *Neotermes* AHMAD, 1950, pp. 44, 50.

Genus *Neotermes* EMERSON, 1951, p. 156.

<Genus *Proglyptotermes* STROUD, 1953, p. 88.

<Genus *Neotermes* EMERSON, 1955, pp. 467, 468, 472, 478, 483, 490, 492, 507, 508.

<Genus *Neotermes* WEIDNER, 1955a, pp. 46-48, 68.

Genus *Neotermes* HARRIS, 1957, p. 25.

<Genus *Neotermes* AHMAD, 1958, pp. 36, 38.

TYPE SPECIES: *Neotermes castaneus* (Burmeister).

The species *Kalotermes mona* was described by Banks (1919), based on the soldier caste

alone. Banks (1920) also described *Kalotermes jouteli* from a dealate and soldier. The wing venations of these two species were unknown at that time. In the collection of A. E. Emerson there are associated series of imagoes and soldiers of both species. The wing venations of these two species are as in the genus *Neotermes*, and the imago mandibles are also *Neotermes*-like. The soldiers are as large as those of the genus *Neotermes* and closely resemble those of *Neotermes connexus* Snyder from Hawaii. In the present paper I am placing these two species in the genus *Neotermes*. I am also including *K. cubanus* Snyder, *N. gracilidens* Sjöstedt, and *N. arthur-mulleri* von Rosen. The first two species were included in *Kalotermes*, and the last one was

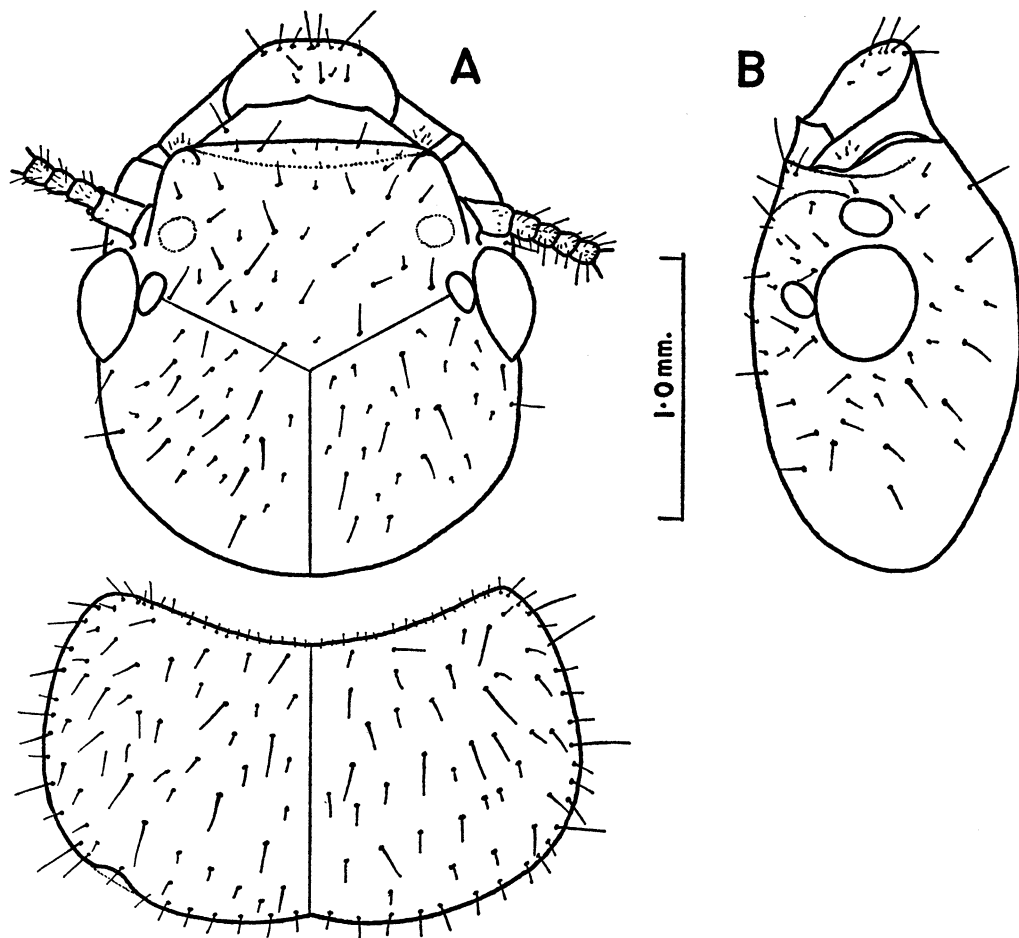


FIG. 7. Imago of *Neotermes castaneus* (Burmeister). A. Head and pronotum from above. B. Head from side. Punta de San Juan, Santa Clara Province, Cuba.



FIG. 8. Mandibles of imago of *Neotermes castaneus* (Burmeister).
Pine Crest, Monroe County, Florida.

placed in the genus *Rugitermes*, by Snyder (1949). In the present paper I am also excluding the following species from the genus *Neotermes* that were formerly included by Snyder (1949): *N. amplus*, *N. gracilignathus*, *N. perfectus*, *N. howa*, *N. militaris*, *N. pishinensis*, *N. praecox*, and *N. semilunaris*.

IMAGO (FIG. 7): Color ranging from light castaneous brown to dark brown. Eyes large; diameter, 0.46–0.78 mm. Ocellus touching eye or approximately 0.01 mm.–0.10 mm. from eye. Antenna with 12 to 21 articles. Mandi-

bles as in the genus *Kaloterмес*, i.e., left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth (fig. 8). Right mandible with posterior margin of second marginal tooth subequal to molar plate (fig. 8). Pronotum slightly narrower, as broad as, or broader than head. Forewing with all major veins arising independently at wing suture; radial sector with variable number of branches; media as strongly sclerotized as radial sector and running close and parallel to

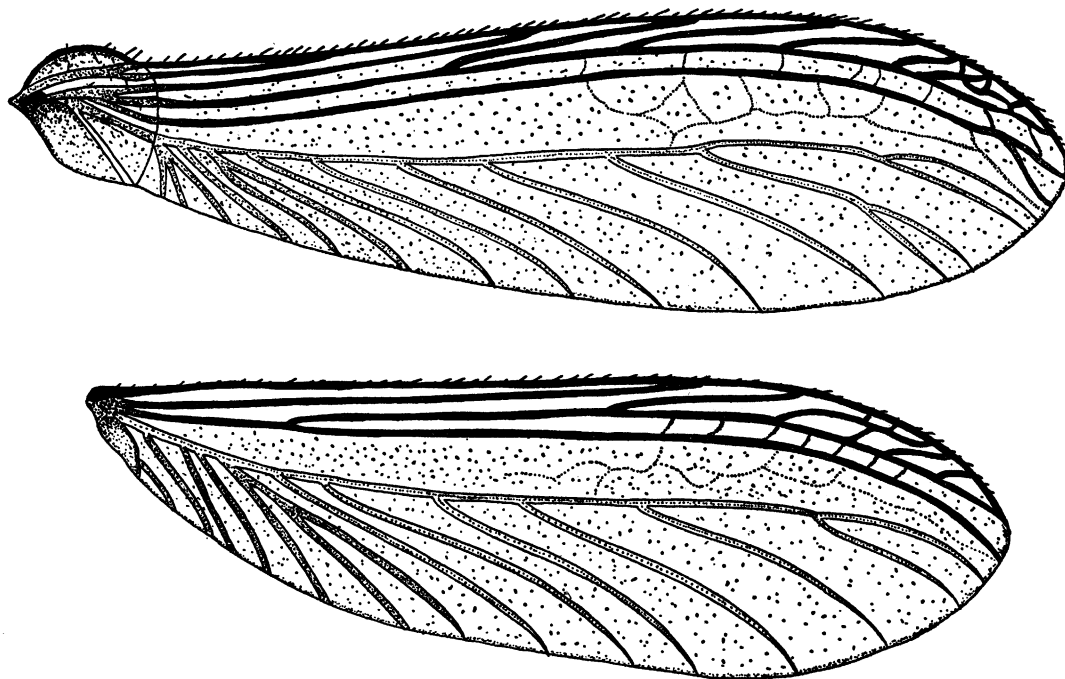


FIG. 9. Forewing and hind wing of *Neotermes castaneus* (Burmeister). Punta de San Juan, Santa Clara Province, Cuba.

radial sector; cubitus weak and unsclerotized (fig. 9). Tibial spurs 3:3:3. Arolium usually present, but absent in a few species.

SOLDIER (FIG. 10): Larger than that of the genus *Kaloterмес*. Head usually long, sides parallel; frons faintly depressed in middle, sloping less than 45 degrees; in some species antennal carinae large and projecting. Eyes usually unpigmented; pigmented in a few species. Antenna with 12 to 19 articles;

third article either shorter or longer than second or fourth. Mandibles long or short, strong, and with variable dentition. Pronotum as broad as head; anterior margin usually shallowly concave or widely emarginate. Femur in some species swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago closely resembles that of *Postelectrotermes* in wing venation, but differs from it in that the forewing has the

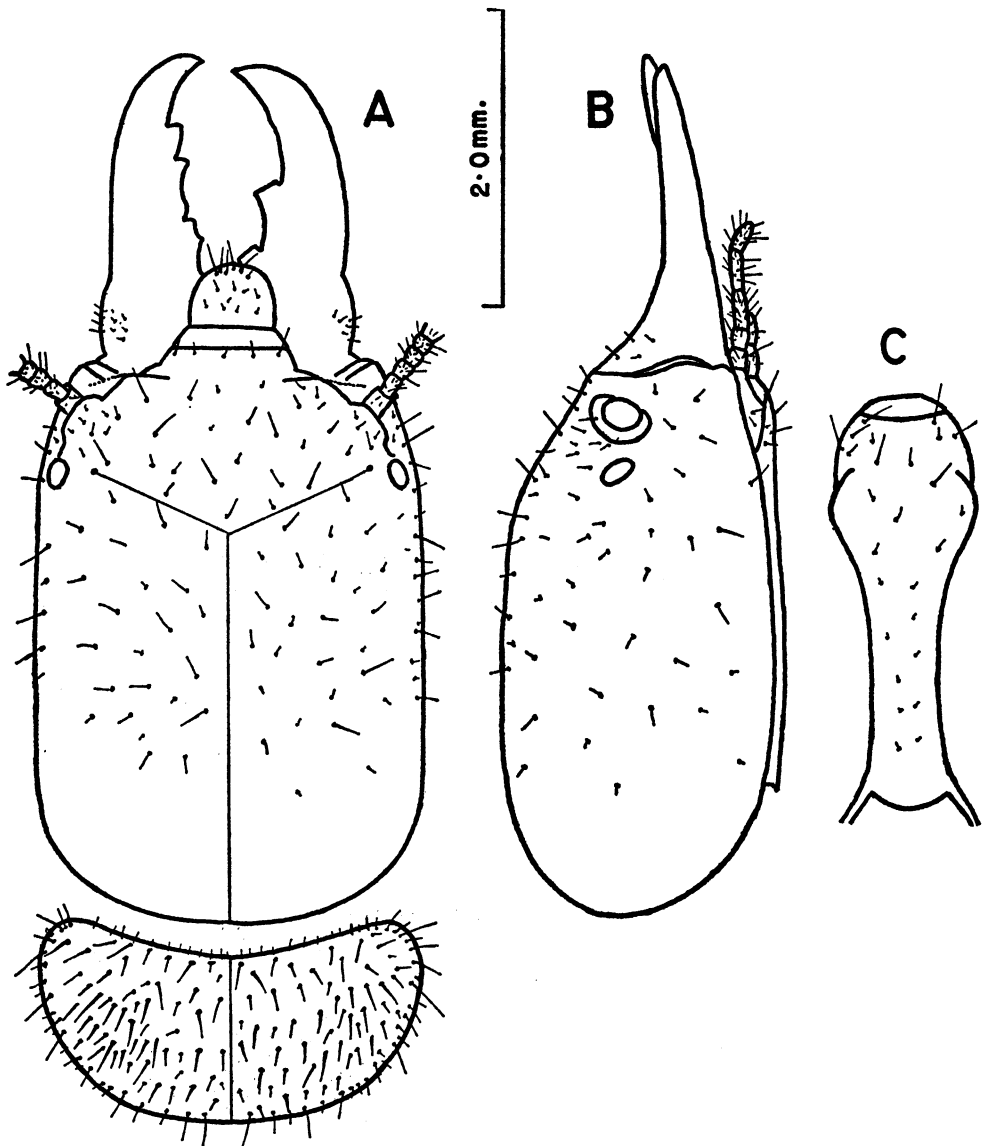


FIG. 10. Soldier of *Neoterмес castaneus* (Burmeister). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Miami, Florida.

median vein much more strongly sclerotized; spine in the middle tibia is absent. The soldier of *Kaloterme*s is smaller and usually has the frons sloping more steeply.

SPECIES INCLUDED

N. aburiensis Sjöstedt, 1926
N. agilis (Sjöstedt), 1902a
N. andamanensis Snyder, 1933a
N. araguaensis Snyder, 1959
N. arthur-mulleri von Rosen, 1912
N. artocarpi (Haviland), 1898
N. assmuthi Holmgren, 1913a
N. brevinotus Snyder, 1932
N. camerunensis (Sjöstedt), 1897
N. castaneus (Burmeister), 1839
N. chilensis (Blanchard), 1851
N. chilensis subsp. *cayutuensis*, Goetsch, 1933
N. chilensis subsp. *zaallarensis* Goetsch, 1933
N. collarti Coaton, 1955
N. connexus Snyder, 1922
N. cryptops (Sjöstedt), 1900a
N. cubanus (Snyder), new combination = *Kaloterme cubanus* Snyder, 1922
N. dalbergiae (Kalshoven), 1930
N. desneuxi (Sjöstedt), 1904
N. erythraeus Silvestri, 1918
N. europae (Wasmann), 1910
N. ferruginus Holmgren, 1911b
N. firmus (Sjöstedt), 1911
N. fletcheri K. and N. Holmgren, 1917
N. fulvescens (Silvestri), 1901
N. gardneri Snyder, 1933a
N. gestri Silvestri, 1912
N. gracilidens Sjöstedt, 1925
N. grandis Light, 1930
*N. grassei*¹ Piton, 1940
N. greeni (Desneux), 1908
N. hirtellus (Silvestri), 1901
N. holmgreni Banks, 1918
N. insularis (White), 1846
N. jouteli (Banks), new combination = *Kaloterme jouteli* Banks, 1920
N. kanehirae Oshima, 1917a
N. kartaboensis Emerson, 1925
N. ketelensis Kemner, 1932b
N. koshunensis Shiraki, 1909
N. lagunensis Oshima, 1920
N. larseni Light, 1935
N. laticollis (Holmgren), 1910b
N. lepersonneae Coaton, 1955
N. longipennis Kemner, 1930
N. magnoculus Snyder, 1926d
N. major Snyder, 1922
N. malatensis Oshima, 1917b

N. medius Oshima, 1923
N. meruensis (Sjöstedt), 1907b
N. microphthalmus Light, 1930
N. modestus (Silvestri), 1901
N. mona (Banks), new combination = *Kaloterme mona* Banks, 1919
N. nigeriensis (Sjöstedt), 1911
N. ovatus Kemner, 1931
N. pallidicollis (Sjöstedt), 1902b
N. papua (Desneux), 1905
N. paraensis da Costa Lima, 1942
N. parviscutatus Light, 1930
N. rainbowi Hill, 1926a
N. rouxi N. and K. Holmgren, 1915
N. saleierensis Kemner, 1932b
N. samoanus (Holmgren), 1912
N. sanctae-crucis Snyder, 1925c
N. sarasini N. and K. Holmgren, 1915
N. schultzei Holmgren, 1911b
N. sepulvillus Emerson, 1928
N. setifer Snyder, 1956
N. sinensis (Light), 1924
N. sjostedti (Desneux), 1908
N. sonneratae Kemner, 1932b
N. superans Silvestri, 1927
N. tectonae (Dammermann), 1915
N. voeltzkowi (Wasmann), 1897
N. wagneri (Desneux), 1904c
N. zuluensis Holmgren, 1913b

GEOGRAPHICAL DISTRIBUTION: Australian: Australia and New Zealand. Papuan: Amboina, Caroline Islands, Hawaii, New Guinea and adjoining islands, New Caledonia, New Hebrides, Samoa, Society Islands. Indo-Malayan: Andaman Islands, Celebes, Ceylon, south China, India, Java, Philippines, Sumatra. Ethiopian: Africa. Malagasy: Madagascar, Seychelles. Nearctic: Southern North America. Neotropical: Central and South America, Cocos Island, Mona Island, and the West Indies.

GEOLOGICAL DISTRIBUTION: Eocene, Recent.

GENUS *RUGITERMES* HOLMGREN, 1911

- <Genus *Caloterme*s HAGEN, 1858a, pp. 31–38.
- <Genus *Caloterme*s HAGEN, 1858b, p. 1.
- <Genus *Caloterme*s SILVESTRI, 1901, pp. 1–3.
- <Genus *Caloterme*s SILVESTRI, 1903, p. 20.
- <Genus *Caloterme*s DESNEUX, 1904d, pp. 20–24.
- =Subgenus *Rugiterme*s HOLMGREN, 1911a, pp. 53, 54, 57, 58, 61.
- =Subgenus *Rugiterme*s EMERSON, 1925, p. 320.
- =Subgenus *Rugiterme*s SNYDER, 1925e, p. 198.
- =Subgenus *Rugiterme*s EMERSON, 1928, p. 405.

¹ Fossil.

=Subgenus *Metaneotermes* LIGHT, 1932, p. 77.
 =Subgenus *Rugitermes* HARE, 1937, pp. 474, 475.

<Genus *Rugitermes* SNYDER, 1949, p. 34.

Genus *Rugitermes* GRASSÉ, 1949, p. 531.

Genus *Rugitermes* AHMAD, 1950, pp. 44, 50.

Genus *Rugitermes* WEIDNER, 1955a, p. 68.

<Genus *Rugitermes* EMERSON, 1955, pp. 478, 491, 492, 498, 508.

TYPE SPECIES: *Rugitermes nodulosus* (Hagen).

Snyder (1949) included the species *Neotermes arthur-mulleri* von Rosen in the genus *Rugitermes*. This species is an intermediate between *Neotermes* and *Rugitermes*. It has a *Neotermes*-like wing venation and imago mandible. The wing coloration and the eye size are similar to those of *Rugitermes*. The soldier also resembles in some respects that of

the genus *Rugitermes*. In the present paper, I am placing this species in the genus *Neotermes*, where it was originally included by von Rosen (1912).

IMAGO (FIG. 11): Usually dark brown, in some species pronotum yellowish. Eyes small; diameter, 0.29–0.43 mm. Ocellus not touching eye, 0.04–0.07 mm. from eye. Antenna with 15 to 20 articles. Mandibles as in the genus *Kalotermes*, i.e., left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth (fig. 12). Right mandible with posterior margin of second marginal tooth equal to molar plate (fig. 12). Pronotum broader than head. Wing membrane densely covered with small, pimple-like, pigmented nodules. Forewing with all major veins arising independently at wing suture; radius (R_1)

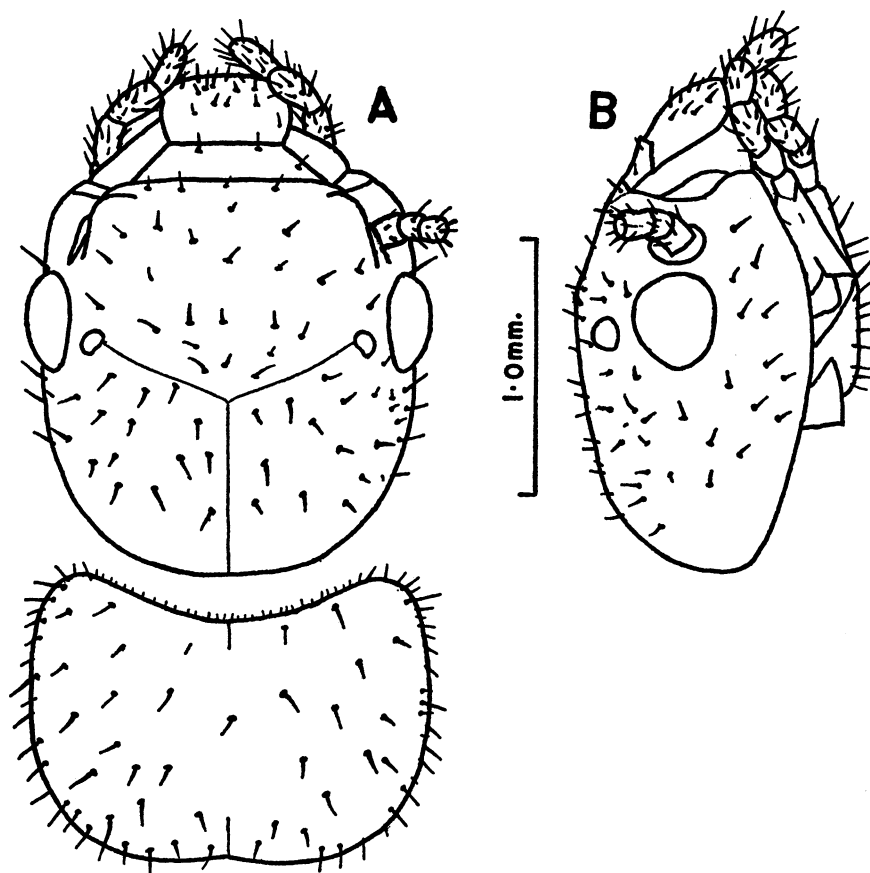


FIG. 11. Imago of *Rugitermes nodulosus* (Hagen). A. Head and pronotum from above. B. Head from side. Brazil.

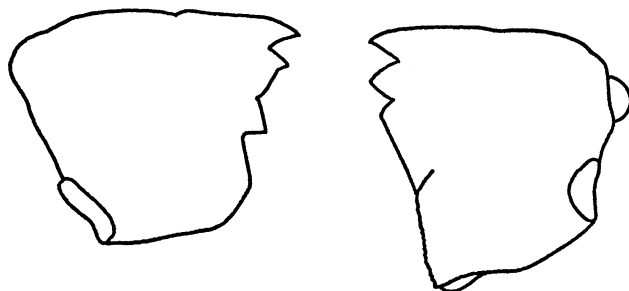


FIG. 12. Mandibles of imago of *Rugitermes nodulosus* (Hagen). Brazil.

simple; radial sector with seven to eight branches; media as heavily sclerotized as radial sector, coalescing with radial sector about one-fifth to one-tenth of length of wing from suture, close to radial sector, with an upward bend soon after suture; cubitus weak and unsclerotized; cross branches between radial sector and cubitus in distal end of wing (fig. 13). Hind wing with media absent, present in all other genera of the family Kalotermitidae. Tibial spurs 3:3:3. Arolium present in all species.

SOLDIER (FIG. 14): Head long and narrow, sides parallel; medially depressed, only faintly bilobed; continuation of dorsal anten-

nal ridge medially, forming a prominent ridge in front. Eyes unpigmented. Antenna with 12 to 18 articles; third article in all cases longer than second, clavate. Mandibles short and stout, outer margin evenly rounded, with or without basal hump. Pronotum either slightly narrower than, as broad as, or broader than head; anterior margin shallowly concave or angular. Legs not swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago can be distinguished from all other genera in having a short, sclerotized median vein in the forewing which joins the radial sector very close to the wing suture. The median vein in the hind wing is absent. The soldier closely resembles

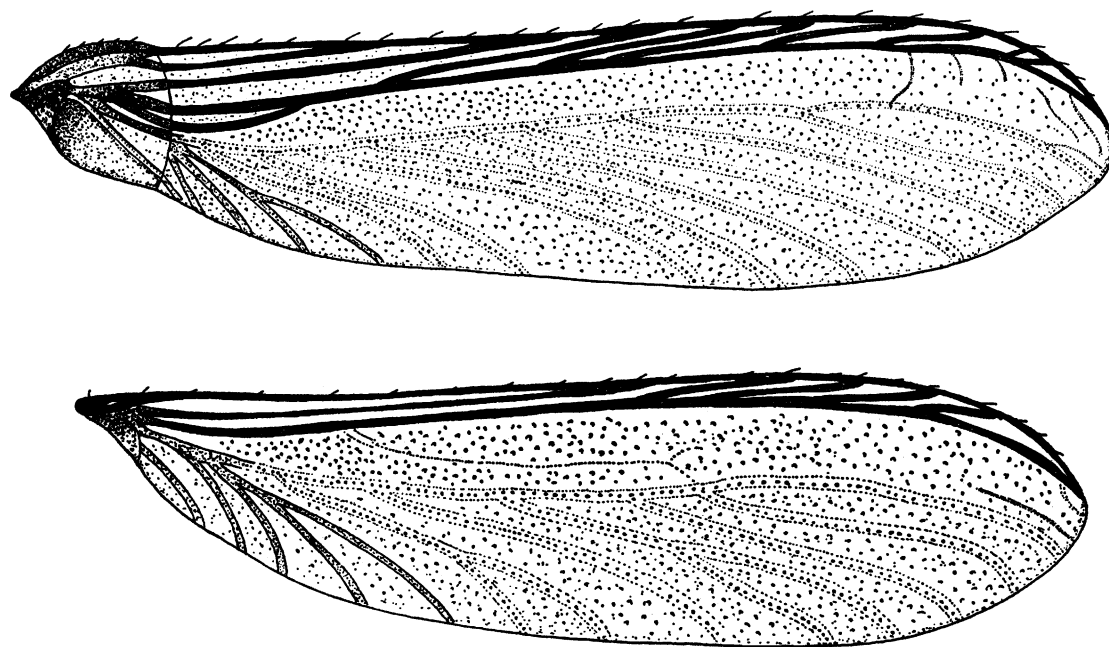


FIG. 13. Forewing and hind wing of *Rugitermes nodulosus* (Hagen). Brazil.

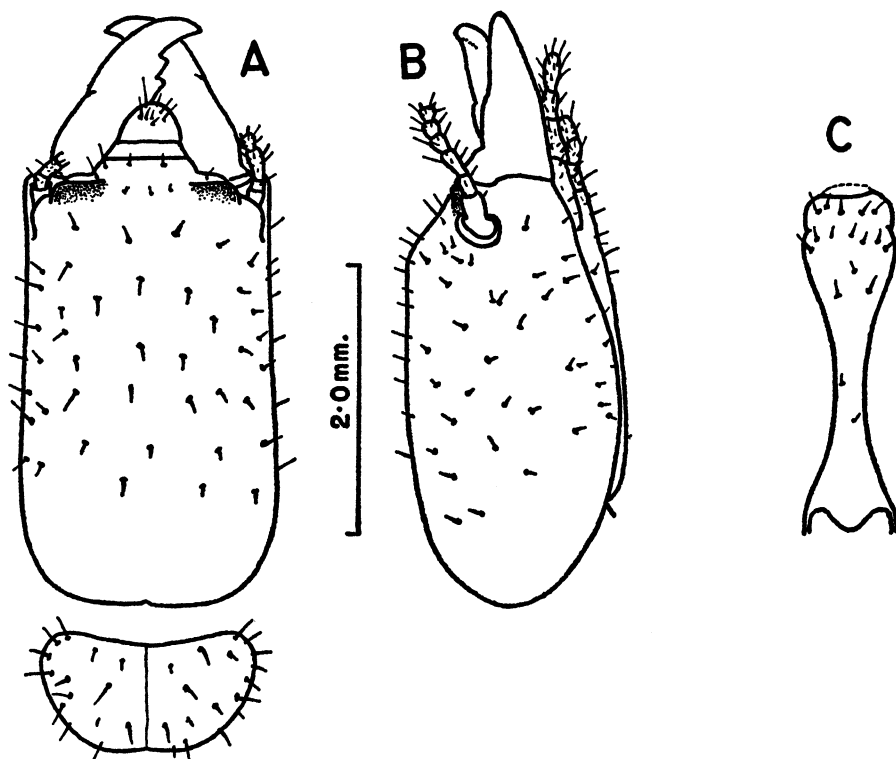


FIG. 14. Soldier of *Rugitermes nodulosus* (Hagen). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Brazil.

that of the genus *Neotermes*, but differs from it in having the third joint of the antenna clavate and in every case longer than the second; a prominent ridge is present in front of and medial to the antennal socket.

SPECIES INCLUDED

R. athertoni (Light), 1932
R. bicolor Emerson, 1925
R. costaricensis Snyder, 1926a
R. flavicinctus Emerson, 1925
R. kirbyi Snyder, 1926b
R. magninotus Emerson, 1925
R. nodulosus (Hagen), 1858a
R. occidentalis (Silvestri), 1901
R. panamae (Snyder), 1925a
R. rugosus (Hagen), 1858a
R. unicolor Snyder, 1952

GEOGRAPHICAL DISTRIBUTION: Papuan: Marquesas Islands. Neotropical: Central and South America.

GENUS **EUCRYPTOTERMES** HOLMGREN, 1911

= Subgenus *Eucryptotermes* HOLMGREN, 1911a, pp. 53, 55, 59-61.

= Subgenus *Eucryptotermes* EMERSON, 1928, p. 405.

= Genus *Eucryptotermes* SNYDER, 1949, p. 44.

= Genus *Eucryptotermes* GRASSÉ, 1949, p. 531.

= Genus *Eucryptotermes* AHMAD, 1950, pp. 44, 50.

= Genus *Eucryptotermes* WEIDNER, 1955a, pp. 48, 68.

= Genus *Eucryptotermes* EMERSON, 1955, pp. 469, 492, 508.

TYPE SPECIES: *Eucryptotermes wheeleri* Snyder and Emerson.

IMAGO (FIG. 15): Uniformly brownish yellow. Diameter of eye, 0.43 mm. Ocellus touching eye. Antenna with 14 to 16 articles. Mandibles as in the genus *Glyptotermes*, i.e., left mandible with first plus second marginal tooth equal to third marginal tooth (fig. 16). Right mandible with posterior margin of second marginal tooth slightly longer than molar plate (fig. 16). Pronotum narrower than head. Anterior margin of forewing scale almost straight or very slightly convex as in

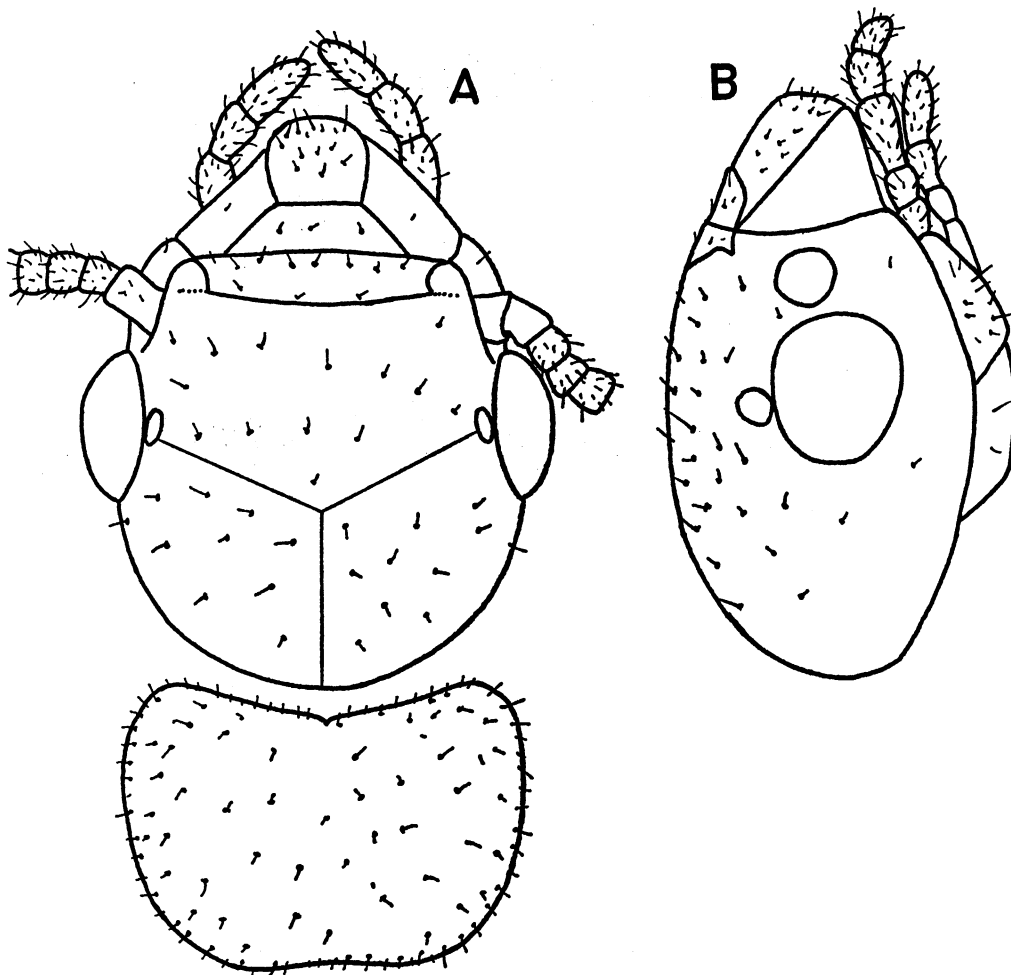


FIG. 15. Imago of *Eucryptotermes wheeleri* Snyder and Emerson. A. Head and pronotum from above. B. Head from side. Cotype from Blumenau, Brazil. Drawn by A. E. Emerson.

the genera *Glyptotermes* and *Calcaritermes* (fig. 17). Forewing with all major veins arising independently at wing suture; radius (R_1) simple; radial sector with five to six branches, first branch arising at one-half of length of the wing from suture; media as strongly sclerotized as radial sector and running very close and parallel to radial sector; cross veins between media and radial sector; cubitus weak and unsclerotized (fig. 17). Tibial spurs 3:3:3. Arolium present.

SOLDIER (FIG. 18): Head blackish and phragmotic, short and thick; sides fairly straight and parallel, somewhat constricted in region of antenna; frontal area smooth, hollowed out, with no sculpturing; a sharp circular ridge extending between frons and

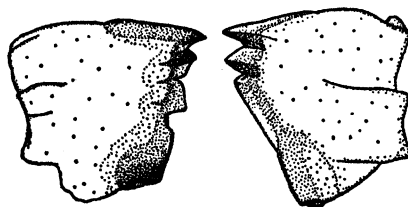


FIG. 16. Mandibles of imago of *Eucryptotermes wheeleri* Snyder and Emerson. Cotype from Blumenau, Brazil. Drawn by A. E. Emerson.

vertex and front and sides; frontal area extending out in front of base of mandibles; profile of front steep; antennal socket at about one-third or one-half of length of head from front sides. Eyes present, but indistinct

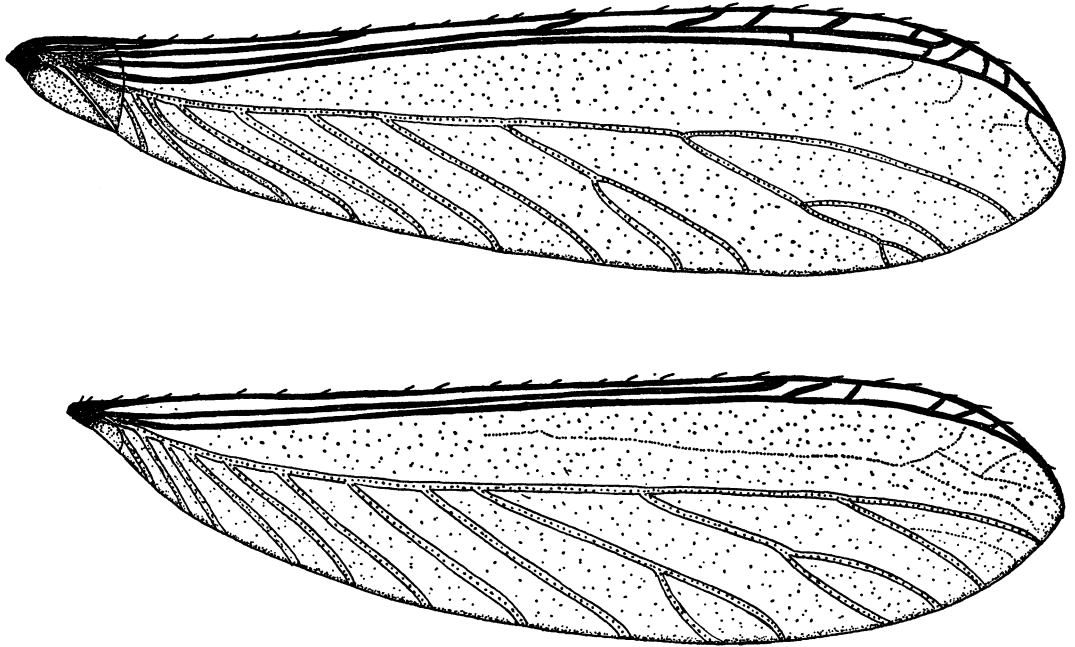


FIG. 17. Forewing and hind wing of *Eucryptotermes wheeleri* Emerson and Snyder.
Cotype from Blumenau, Brazil.

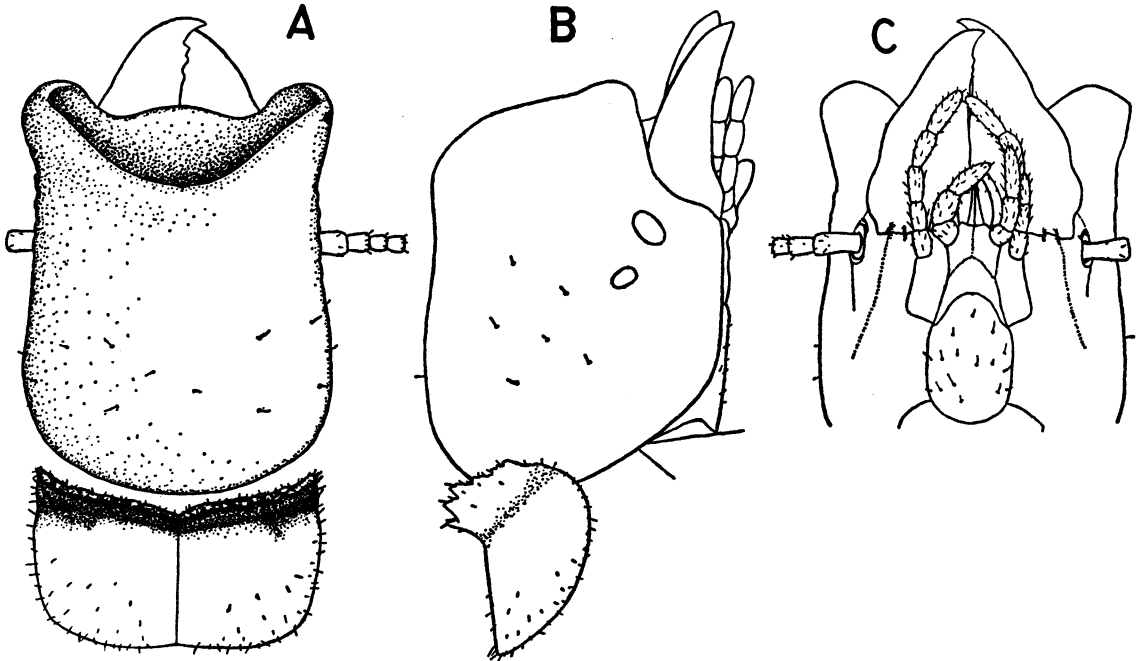


FIG. 18. Soldier of *Eucryptotermes wheeleri* Snyder and Emerson. A. Head and pronotum from above. B. Head and pronotum from side. C. Head from below. Cotype from Blumenau, Brazil. Drawn by A. E. Emerson.

and narrow. Antenna with 11 articles; third article shorter than second. Labrum not visible from above, black concave front of head extending beyond its normal position. Mandibles short, broad at base, and with a distinct basal hump. Postmentum short, oval. Pronotum with anterior margin rising abruptly from flatly arched posterior portion in profile; from above, anterior margin angularly emarginate and strikingly serrated. Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: The wing venation and imago mandible are similar to those of *Neotermes*. *Neotermes* differs, however, in having the anterior margin of the forewing scale more convex. Otherwise, it is difficult to distinguish the imago in the two genera. The soldier resembles that of the genus *Cryptotermes* because of convergent evolution of the phragmotic head.

SPECIES INCLUDED

Eucryptotermes wheeleri Snyder and Emerson, 1949

GEOGRAPHICAL DISTRIBUTION: Neotropical: South America.

? GENUS **PROKALOTERMES** EMERSON, 1933

<Genus *Parotermes* SCUDDER, 1890, p. 110.

= Genus *Prokalotermes* EMERSON, 1933, p. 189.

= Genus *Prokalotermes* EMERSON, 1942, pp. 9, 10.

= Genus *Prokalotermes* SNYDER, 1949, p. 357.

= Genus *Prokalotermes* GRASSÉ, 1949, p. 530.

= Genus *Prokalotermes* WEIDNER, 1955a, pp. 46, 68.

= Genus *Prokalotermes* EMERSON, 1955, p. 507.

TYPE SPECIES: *Prokalotermes hageni* (Scudder).

Emerson (1933) erected the genus *Prokalotermes* for *Parotermes hageni* Scudder on the basis of the following characters: cerci with four to five articles; ocellus present, imago mandible *Kalotermes*-like; pronotum broader than head.

I have very carefully examined a specimen of *Prokalotermes hageni* determined by A. E. Emerson. The fossil specimen is very poor, and the number of articles of the cercus is highly questionable. In the forewing the costal area is very broad, as in the genus *Kalotermes*. The radius (R_1) has three to four

branches at the suture, and the radial sector has seven to eight branches. The media runs midway between the radial sector and the cubitus. There are no other distinguishing characters for this genus, with the exception of the three to four branches of the radius (R_1). However, this character may be variable. From the known characters of the species, this genus could be synonymous with *Kalotermes*. Until more specimens can be examined, it is thought best to retain the present name with a question mark.

GEOGRAPHICAL DISTRIBUTION: Florissant beds of Colorado.

GEOLOGICAL DISTRIBUTION: Oligocene.

GENUS **KALOTERMES** HAGEN, 1853

= Genus *Kalotermes* HAGEN, 1853, p. 479 (no type mentioned).

<Genus *Kalotermes* HAGEN, 1854, p. 222 (only two fossil species mentioned).

<Gruppe *Kalotermes* HAGEN, 1856, p. 49.

<Genus *Calotermes* HAGEN, 1858a, pp. 31–38.

<Genus *Calotermes* HAGEN, 1858b, p. 1.

<Genus *Kalotermes* HAGEN, 1862, p. 58.

<Genus *Calotermes* GIRARD, 1879, p. 267.

<Genus *Calotermes* FROGGATT, 1896, pp. 517, 521.

<Genus *Calotermes* WASMANN, 1897, pp. 150, 172.

<Subgenus *Calotermes*, *sensu stricto*, WASMANN, 1897, pp. 150, 172.

<Genus *Calotermes* HAVILAND, 1898, pp. 371, 373.

<Genus *Calotermes* SJÖSTEDT, 1900b, pp. 19, 20, 21, 35.

<Genus *Calotermes* SILVESTRI, 1901, pp. 1–3.

<Genus *Calotermes* SILVESTRI, 1903, pp. 20, 104.

<Genus *Calotermes* DESNEUX, 1904b, p. 283.

<Genus *Calotermes* DESNEUX, 1904d, pp. 20–24

<Genus *Calotermes* FROGGATT, 1905, p. 19.

<Genus *Calotermes* SJÖSTEDT, 1907b, pp. 8, 9.

<Genus *Calotermes* WASMANN, 1909, p. 172.

<Genus *Calotermes*, BUGNION AND POPOFF, 1910, pp. 124, 125.

<Subgenus *Calotermes* HOLMGREN, 1910a, p. 137.

<Subgenus *Calotermes*, *sensu stricto*, HOLMGREN, 1911a, pp. 53, 56, 57, 58, 60, 61.

<Subgenus *Cryptotermes* HOLMGREN, 1911a, pp. 53, 55.

<Subgenus *Calotermes*, *sensu stricto*, HOLMGREN, 1913a, p. 37.

<Genus *Kalotermes* BUGNION, 1914, p. 175.

<Genus *Calotermes* PONGRÁČZ, 1917, pp. 33, 35.

<Genus *Kaloterme*s BANKS AND SNYDER, 1920, pp. 16, 17.

<Genus *Caloterme*s FULLER, 1921, pp. 16, 19, 22, 23, 28.

<Genus *Kaloterme*s SNYDER, 1925d, p. 156.

<Genus *Caloterme*s SJÖSTEDT, 1926, pp. 22, 23.

<Genus *Neoterme*s SJÖSTEDT, 1926, pp. 22, 23, 33.

<Genus *Glyptoterme*s SJÖSTEDT, 1926, pp. 22, 23, 42.

<Subgenus *Kaloterme*s, *sensu stricto*, EMERSON, 1928, pp. 405, 412.

Genus *Caloterme*s SILVESTRI, 1934, p. 33.

Subgenus *Kaloterme*s, *sensu stricto*, HARE, 1937, pp. 461, 474, 475.

<Subgenus *Cryptoterme*s HILL, 1942, p. 65.

> <Subgenus (?) HILL, 1942, p. 37.

<Genus *Kaloterme*s EMERSON, 1942, pp. 7, 8, 9, 10.

<Subgenus *Kaloterme*s SNYDER, 1948, pp. 232, 234.

Genus *Caloterme*s CACHAN, 1949, p. 180.

> <Genus *Proglyptoterme*s EMERSON, 1949, p. 320.

<Genus *Kaloterme*s COATON, 1949, pp. 14, 15.

<Genus *Kaloterme*s SNYDER, 1949, pp. 11–21, 358.

<Genus *Caloterme*s GRASSÉ, 1949, p. 530.

> <Genus *Proglyptoterme*s COATON, 1950, pp. 3, 28.

<Genus *Kaloterme*s AHMAD, 1950, pp. 44, 48, 50.

<Genus *Kaloterme*s EMERSON, 1951, pp. 156, 157.

<Subgenus *Cryptoterme*s RATCLIFFE, GAY, AND GREAVES, 1952, pp. 54, 55, 66–68.

<Genus *Kaloterme*s STROUD, 1953, pp. 77, 78, 88, 91.

> <Genus *Proglyptoterme*s STROUD, 1953, pp. 77, 78, 88, 91.

<Genus *Kaloterme*s WEIDNER, 1955a, pp. 19, 46–48, 68.

<Genus *Kaloterme*s EMERSON, 1955, pp. 467, 472, 473, 478, 483, 490–492, 507.

<Genus *Kaloterme*s AHMAD, 1958, p. 36.

TYPE SPECIES: *Kaloterme flavicollis* (Fabricius).

Hagen (1853) named the genus *Kaloterme*s. In his description, he did not mention species, but instead mentioned soldiers, larvae, and nests. He thus had in mind a living termite. In 1854 he mentioned two fossil species only (*K. berendtii* Pictet and *K. affinis* Hagen) under the genus *Kaloterme*s. One living species, *Termes flavicollis* Fabricius, he considered a *Termes*. However, Hagen (1856) included *T.*

berendtii, *T. affinis*, and *T. flavicollis*, all with a generic abbreviation for *Termes*, in the genus *Kaloterme*s. He also stated that *T. flavicollis* and some undescribed species from Rio de Janeiro, Brazil, Colombia, and Cuba are the living forms belonging to the genus. Thus it seems clear that in the original description of the genus *Kaloterme*s, Hagen had the living species *K. flavicollis* in mind, which should therefore be the generitype.

There has been a diversity of opinion about the correct spelling of the name *Kaloterme*s. Hagen (1853), in his original description, used the spelling *Kaloterme*s. However, later (1858a) he revised the spelling to *Caloterme*s, and this spelling is used by Desneux, Silvestri, Holmgren, Fuller, Sjöstedt, Hill, Grassé, and others. Banks and Snyder (1920) have challenged this deviation from the rules of nomenclature and reinstated the original spelling; the latter is adopted by Light, Emerson, Ahmad, Coaton, and myself.

Hagen (1858a) included 18 living and two fossil species in "*Caloterme*s." He recognized three main groups within the genus: (1) *C. castaneus* and its relatives, (2) *C. flavicollis* and its relatives, and (3) *C. brevis* and its relatives. These groups were later described as the subgenera *Neoterme*s, *Kaloterme*s, *sensu stricto*, and *Cryptoterme*s, respectively. Thus Hagen (1858a) was treating the genus in a broad sense, including in it several groups.

Wasmann (1897) divided the genus *Caloterme*s Hagen, *sensu lato*, into two subgenera: *Caloterme*s, *sensu stricto*, with *C. flavicollis* as the generitype, and *Serriterme*s, now placed in the family Termitidae, subfamily Serritermitinae (Snyder, 1949).

The concept of the genus used by Froggatt (1896, 1905), Haviland (1898), Sjöstedt (1900b, 1907b), Silvestri (1901, 1903), Desneux (1904b, 1904d), and Wasmann (1909) was fundamentally the same as that of Hagen (1858a).

Holmgren (1910a, 1911a) divided the genus *Caloterme*s Hagen, *sensu lato*, into nine subgenera: *Caloterme*s, *sensu stricto*, *Proneoterme*s, *Neoterme*s, *Rugiterme*s, *Cryptoterme*s, *Procryptoterme*s, *Eucryptoterme*s, *Glyptoterme*s, and *Lobiterme*s. Emerson (1925, 1928), Hill (1942), and others retained the subgenera of Holmgren, while Banks and Snyder (1920), Fuller (1921), Sjöstedt (1926), Silvestri

(1934), Emerson (1942, 1955), Snyder (1949), Coaton (1949), and Weidner (1955a) have raised Holmgren's subgenera to generic rank. I am also treating these groups as genera.

Holmgren (1911a) described eight species in the subgenus *Calotermes* Hagen, *sensu stricto*, and assigned *C. flavicollis* as the generic type. Banks (1919), Banks and Snyder (1920), Fuller (1921), Light (1921, 1930, 1933), Sjöstedt (1926), Hill (1942), Coaton (1949), and others added a number of species from Africa, Australia, North America, South America, and other regions of the world.

Hill (1942) mentioned seven species of the genus *Kalotermes*, without assigning them to the subgenus. For this group, Emerson (1949) proposed a new genus, *Proglyptotermes*, with *Proglyptotermes hilli* Emerson, a new name for *K. obscurus*, as the generic type. The species included in this genus were *P. atratus* (Hill),

P. brouni (Froggatt), *P. banksiae* (Hill), *P. pallidinotum* (Hill), *P. rufinotum* (Hill), *P. spoliator* (Hill), *P. tillyardi* (Hill), and a new species from South Africa, described by Coaton (1949) as ? *Glyptotermes umtatae*. The genus *Proglyptotermes* was a preliminary grouping of species, which was published by Kirby (1949a) through a misunderstanding, and it was not adopted by Snyder (1949) or Emerson (1955).

Stroud (1953) for the first time applied the technique of multiple factor analysis, a quantitative analytical approach to the field of systematics. By this method he examined 48 species of the genus *Kalotermes*, in an attempt to elucidate its systematic structure. He thus tentatively separated a group of 15 species, many of which had been assigned to the genus *Proglyptotermes* by Emerson (1949).

Stroud (1953) treated the genus *Kalotermes*

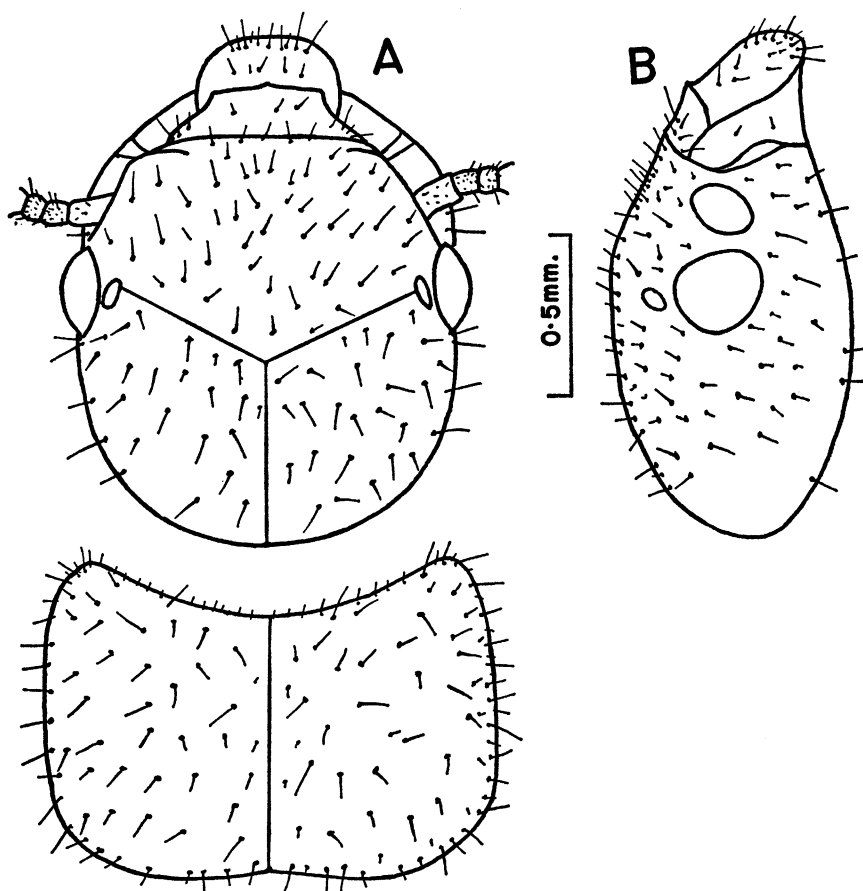


FIG. 19. Imago of *Kalotermes flavicollis* (Fabricius). A. Head and pronotum from above. B. Head from side. France.



FIG. 20. Mandibles of imago of *Kaloterмес flavicollis* (Fabricius). France.

as handled by Snyder (1949) and others and therefore was dealing with a large heterogeneous group. In the present study I am restricting the concept of the genus *Kaloterмес* to *K. flavicollis* and its relatives only (see list), and have reassigned most of the species to other genera, many of them new. Stroud was thus not evaluating the genus *Kaloterмес* as restricted in this paper (*K. flavicollis* and its relatives) but was instead examining a much larger group.

The present study has shown that the generitype species of *Proglyptoterмес* is congeneric with *K. flavicollis* and its relatives. The imagoes of the genus *Proglyptoterмес*, as are those of *K. flavicollis* and its relatives, are small, darkly pigmented, and in all cases have an arolium; the imago-nymph mandibles are

similar; the soldiers are alike. *Proglyptoterмес* should therefore be treated as a synonym of *Kaloterмес*, as *K. flavicollis* is the generitype of the genus, and also bears an older name.

The method of multiple factor analysis used by Stroud (1953) in defining taxonomic categories thus failed to show that *Kaloterмес flavicollis* was related to some of the species included tentatively in the genus *Proglyptoterмес*. The genus *Proglyptoterмес* as treated by Stroud (1953, p. 88) is a heterogeneous group; the statistical technique also failed to show this. In the present work I have reassigned some of its species to other genera.

IMAGO (FIG. 19): Size small. Darkly pigmented. Eyes small; diameter, 0.25–0.35 mm. Ocellus in contact with eye or approximately 0.02 mm. from eye. Antenna with 12 to 17 articles. Left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth (fig. 20). Right mandible with posterior margin of second marginal tooth subequal to molar plate (fig. 20). Pronotum broader than head; anterior margin concave. Anterior margin of forewing scale convex. Wing membrane densely covered with small, pimple-like, pigmented nodules. Region between costal margin and radial sector broad. Forewing with all major veins arising independ-

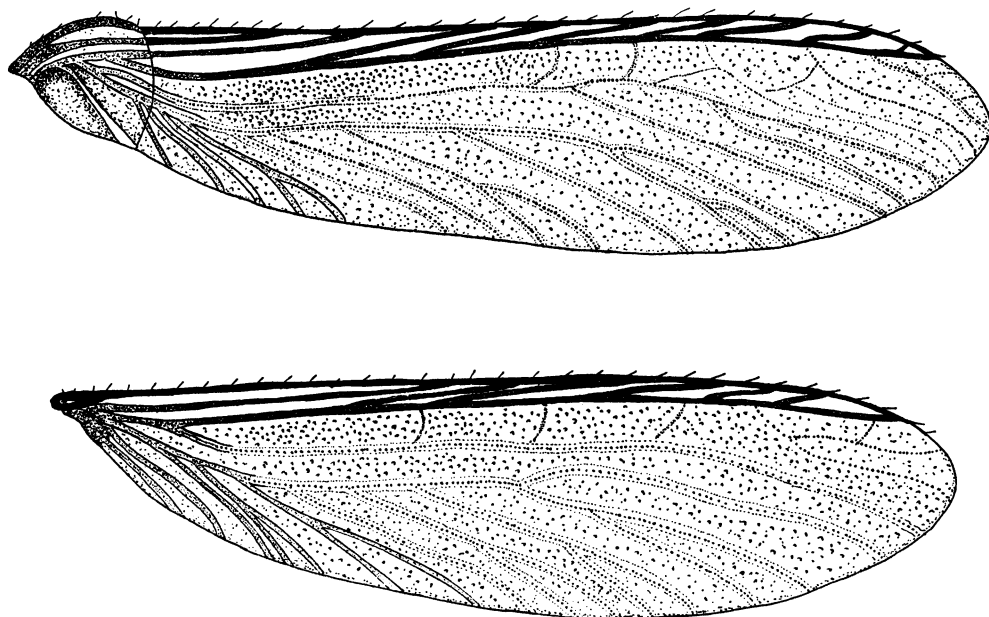


FIG. 21. Forewing and hind wing of *Kaloterмес flavicollis* (Fabricius). Megiddo, Israel.

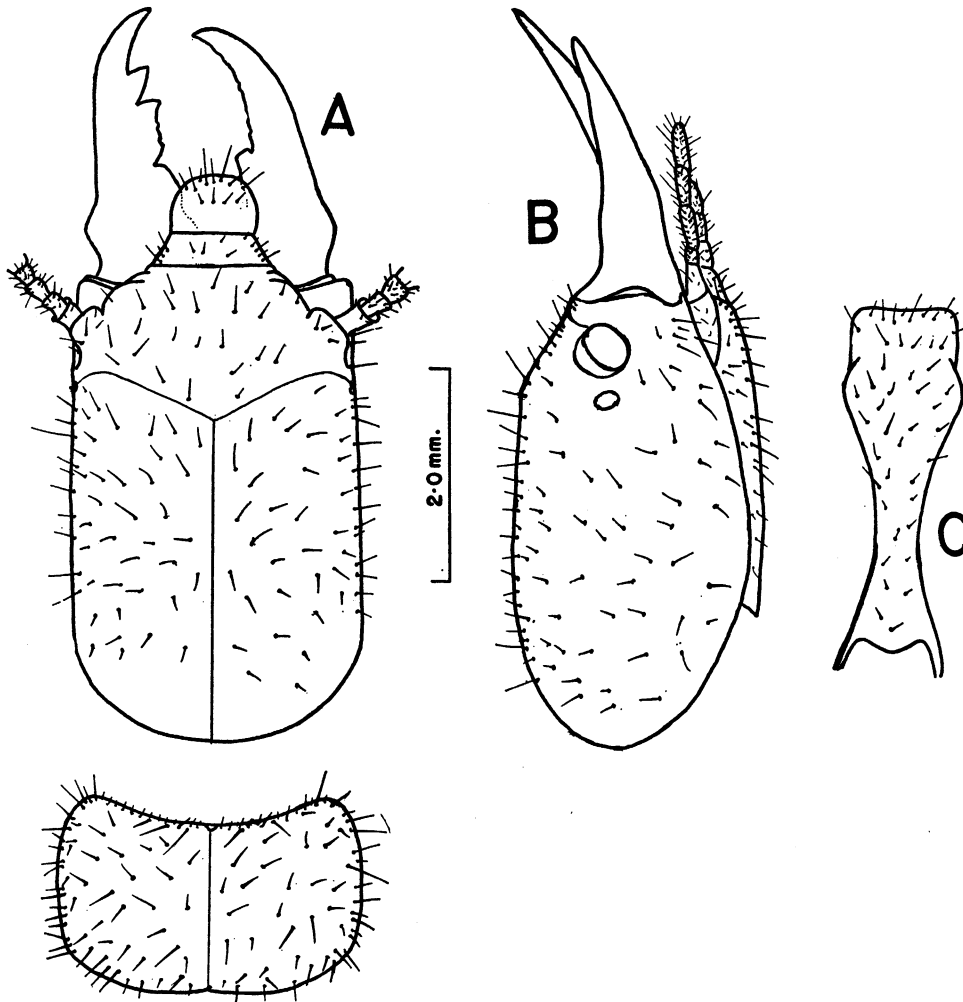


FIG. 22. Soldier of *Kaloterмес flavicollis* (Fabricius). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Homotype from Gennazano, Italy.

ently at wing suture; short subcosta present; radius (R_1) strong and simple; radial sector strongly sclerotized, with approximately eight to 12 branches; media weak, unsclerotized, running almost midway between radial sector and cubitus, in some species joining distal part of radial sector and emerging again to join wing tip; cubitus weak and unsclerotized, with variable number of branches to inner margin of wing (fig. 21). Tibial spurs 3:3:3. Arolium present in all species.

SOLDIER (FIG. 22): Head shape variable; usually long, narrow, sides parallel; sometimes dorsoventrally flat; frontal area depressed medially; sloping downward to mandibles at angle of approximately 40 to 45

degrees. *Kaloterмес atratus* (Hill) has a short, thick, truncated head, as in the genus *Cryptoterмес*. Eyes small, faceted, non-pigmented. Antenna with 11 to 18 articles; third article variable, longer or shorter than second; in *K. flavicollis* (Fabricius) third slightly longer than second. Mandibles strong, dentition variable. Left mandible with two to four marginal teeth. Right mandible with two marginal teeth. Pronotum as wide as or wider than head, anterior margin broadly emarginate. Femur in some species slightly swollen. Tibial spurs 3:3:3.

SPECIES INCLUDED

- K. approximatus* Snyder, 1920a
- K. atratus* (Hill), 1933

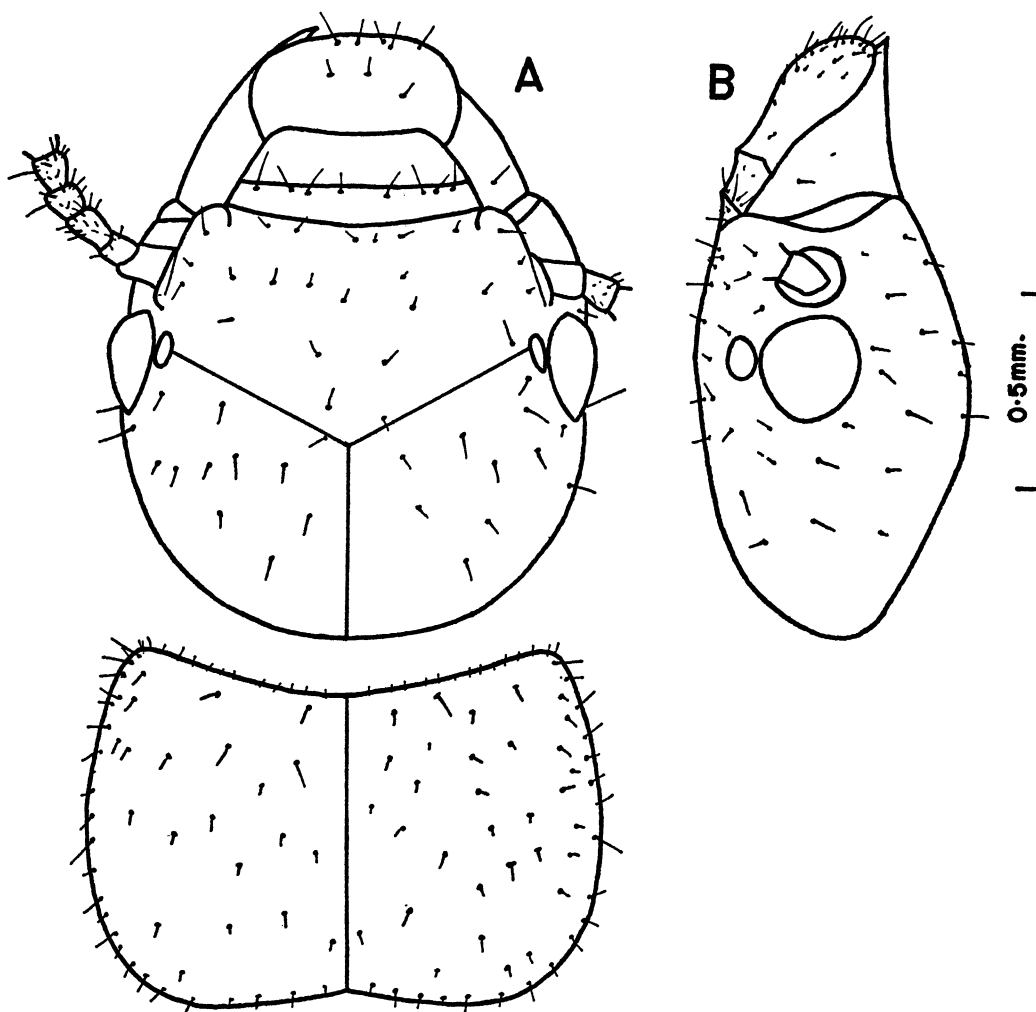


FIG. 23. Imago of *Paraneotermes simplicicornis* (Banks). A. Head and pronotum from above. B. Head from side. Thermal, California.

K. banksiae Hill, 1942
*K. bosniaskii*¹ Handlirsch, 1908
K. brouni Froggatt, 1896
K. capicola Coaton, 1949
K. convexus (Walker), 1853
K. dispar Grassé, 1938
K. flavicollis (Fabricius), 1793
K. gracilignathus (Emerson), new combination =
Neotermes gracilignathus Emerson 1923
K. hilli (Emerson), 1949
 ? *K. inamuræ* Oshima, 1912
K. isaloensis (Cachan), new combination = *Neotermes isaloensis* Cachan, 1949
K. jepsoni Kemner, 1932b
*K. oeningensis*¹ von Rosen, 1913
K. pallidinotum Hill, 1942

¹ Fossil species.

*K. piacentinii*¹ (Piton and Theobald), 1937
*K. rhenanus*¹ Hagen, 1863
K. rufinotum Hill, 1925a
K. sinaiticus Kemner, 1932a
K. tillyardi Hill, 1932b
K. umtatae (Coaton), new combination = ? *Glyptotermes umtatae* Coaton, 1949

GEOGRAPHICAL DISTRIBUTION: Australian: Australia and New Zealand. Papuan: Juan Fernandez Island. Indo-Malayan: Ceylon, Formosa. Ethiopian: Africa. Malagasy: Madagascar. Palearctic: Europe, Canary Islands. Nearctic: North America.

GENUS *PARANEOTERMES* LIGHT, 1934

<Genus *Kalotermes* BANKS AND SNYDER, 1920, p. 16.

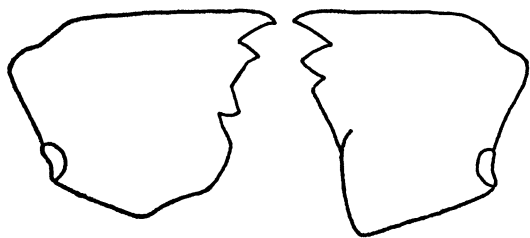


FIG. 24. Mandibles of imago of *Paraneotermes simplicicornis* (Banks). Thermal, California.

<Genus *Cryptotermes* BANKS AND SNYDER, 1920, p. 35.

=Subgenus ? LIGHT, 1933, pp. 82-84.

=Subgenus *Paraneotermes* LIGHT, 1934, pp. 208, 209, 215, 216, 311-313.

=Subgenus *Paraneotermes* LIGHT, 1937, p. 449.

=Subgenus *Paraneotermes* SNYDER, 1948, pp. 232, 234, 235.

=Genus *Paraneotermes* SNYDER, 1949, p. 33.

=Genus *Paraneotermes* GRASSÉ, 1949, p. 531.

=Genus *Paraneotermes* AHMAD, 1950, pp. 44, 48, 50.

=Genus *Paraneotermes* WEIDNER, 1955a, pp. 48, 68.

=Genus *Paraneotermes* EMERSON, 1955, pp. 490, 508.

TYPE SPECIES: *Paraneotermes simplicicornis* (Banks).

IMAGO (FIG. 23): Dark, smoky brown. Eyes small; diameter, 0.28 mm. Ocellus approximately 0.02 mm. from eye. Antenna with 14 to 15 articles. Left mandible with base of first plus second marginal tooth broader than third marginal tooth; posterior margin of first plus second marginal tooth slightly longer than anterior margin of third marginal tooth; posterior edge of first plus second marginal tooth not straight but bent at obtuse angle, at one-fourth of distance from tip of first plus second marginal tooth (fig. 24). Right mandible with molar plate subequal to posterior margin of second marginal tooth (fig. 24). Pronotum slightly broader than head; anterior margin broadly but shallowly concave. Forewing with all major veins arising independently at wing suture; radial sector with six to seven branches; media lighter and less heavily sclerotized than radial sector, running closer to radial sector than to cubitus, especially in distal part of wing; a few cross veins between radial sector and media; cubitus weak and unsclerotized (fig. 25). Tibial spurs 3:3:3. Arolium absent.

SOLDIER (FIG. 26): Head long and dorso-ventrally flat; frons faintly depressed in mid-longitudinal line, sloping down at angle of approximately 35 degrees towards anteclypeus. Eyes unpigmented. Antenna with 13 to

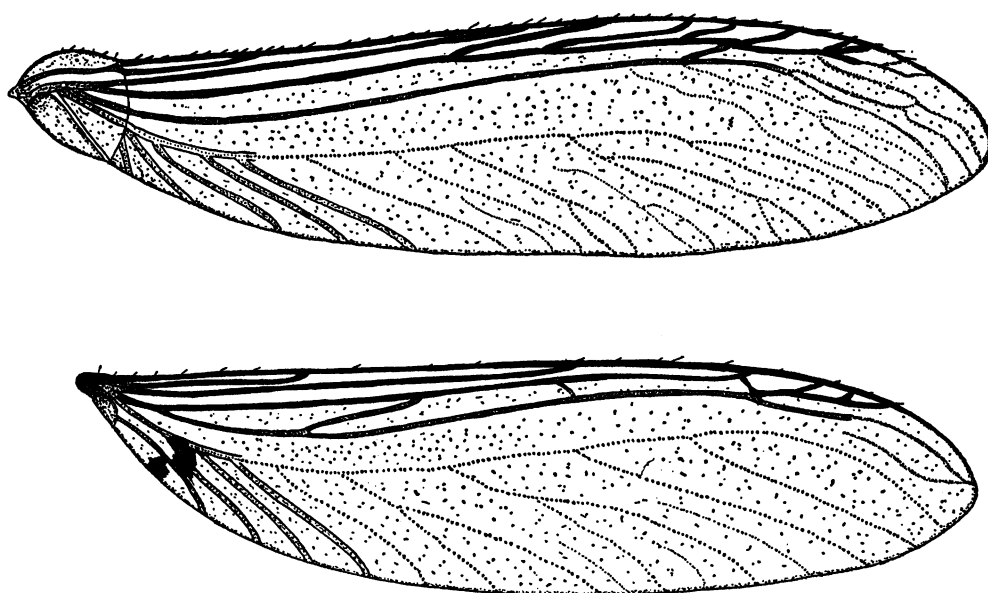


FIG. 25. Forewing and hind wing of *Paraneotermes simplicicornis* (Banks). Thermal, California.

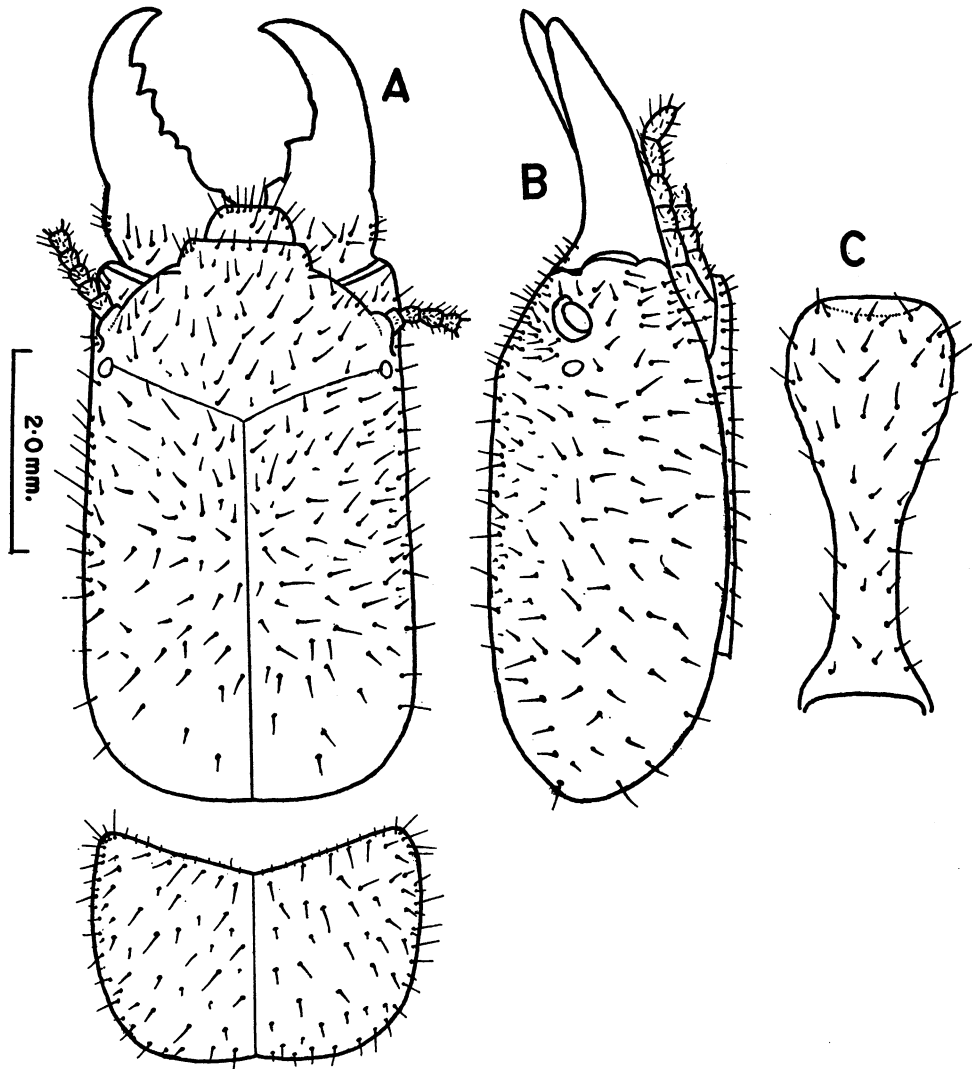


FIG. 26. Soldier of *Paraneotermes simplicicornis* (Banks). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Sabino Canyon, Santa Catalina Mountains, Arizona.

15 articles; third article equal to second. Mandibles short in proportion to head length; strong, with a hump in basal region. Postmentum very broad in front. Pronotum as broad as head; anterior margin broadly emarginate. Femur noticeably swollen. Tibial spurs 3:3:3.

COMPARISONS: See *Comatermes* and *Ceratokalotermes*.

SPECIES INCLUDED

Paraneotermes simplicicornis Light, 1934

GEOGRAPHICAL DISTRIBUTION: Nearctic: Southwestern United States and western Mexico.

CERATOKALOTERMES, NEW GENUS

<Subgenus (?) HILL, 1942, pp. 37, 111.

<Genus *Kalotermes* SNYDER, 1949, p. 21.

<Genus *Proglyptotermes* EMERSON, 1949, p. 321.

<Genus *Proglyptotermes* STROUD, 1953, p. 88.

TYPE SPECIES: *Ceratokalotermes spoliator* (Hill) [= *Calotermes* (?) *spoliator* Hill].

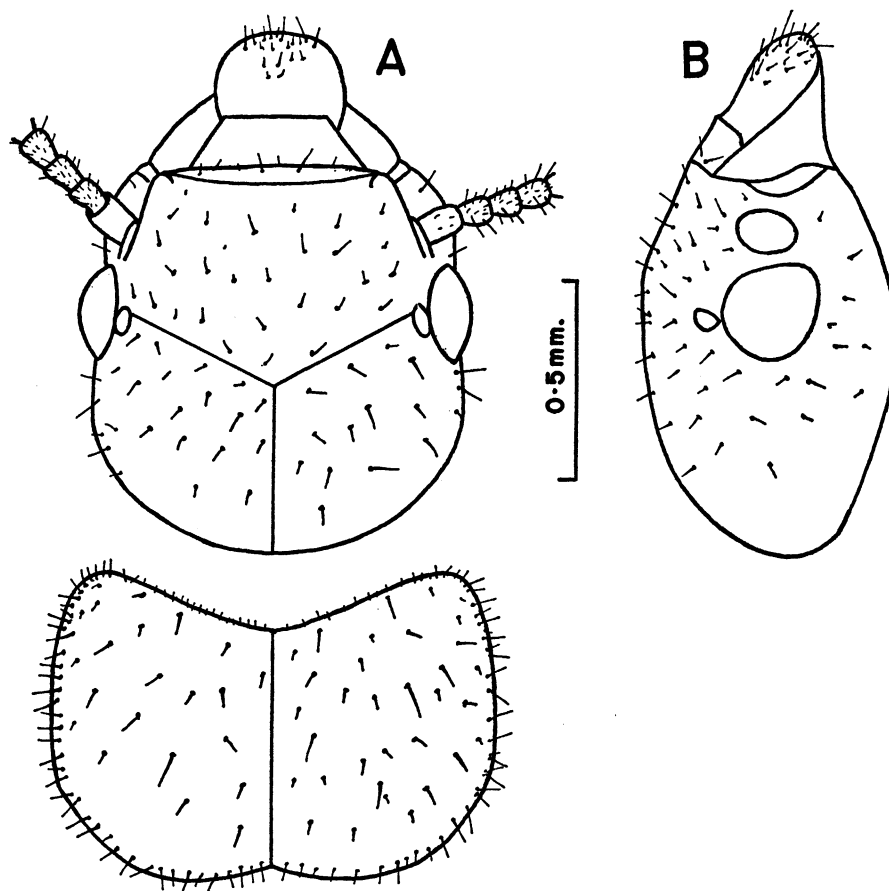


FIG. 27. Imago of *Ceratokalotermes spoliator* (Hill). A. Head and pronotum from above. B. Head from side. Morphotype colony from Federal Capital Territory, Australia.

I am erecting this genus for the single species *Ceratokalotermes spoliator*. Hill (1942) placed it in the genus *Kalotermes*, *sensu lato*, without assigning it to a subgenus. Emerson (1949) and Stroud (1953) included it in the genus *Proglyptotermes* (see discussion under the genus *Kalotermes*).

IMAGO (FIG. 27): Dark brown. Eyes small; diameter, 0.25 mm. Ocellus touching eye. Antenna with 13 to 14 articles. Mandibles as in the genus *Kalotermes*, i.e., left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth (fig. 28). Right mandible with molar plate subequal to posterior margin of second marginal tooth (fig. 28). Pronotum wider than head; anterior margin concave. Forewing with all major veins

arising independently at wing suture; radius (R_1) usually branched; radial sector with seven to eight branches, the first branch arising about one-sixth of length of wing from suture; media as in the genera *Paraneotermes* and *Comatermes*, less heavily sclerotized than

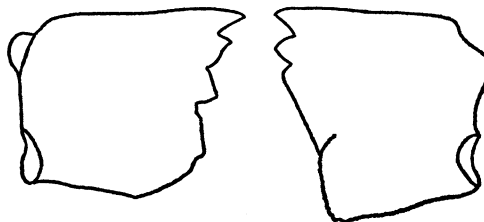


FIG. 28. Mandibles of imago of *Ceratokalotermes spoliator* (Hill). Morphotype colony from Federal Capital Territory, Australia.

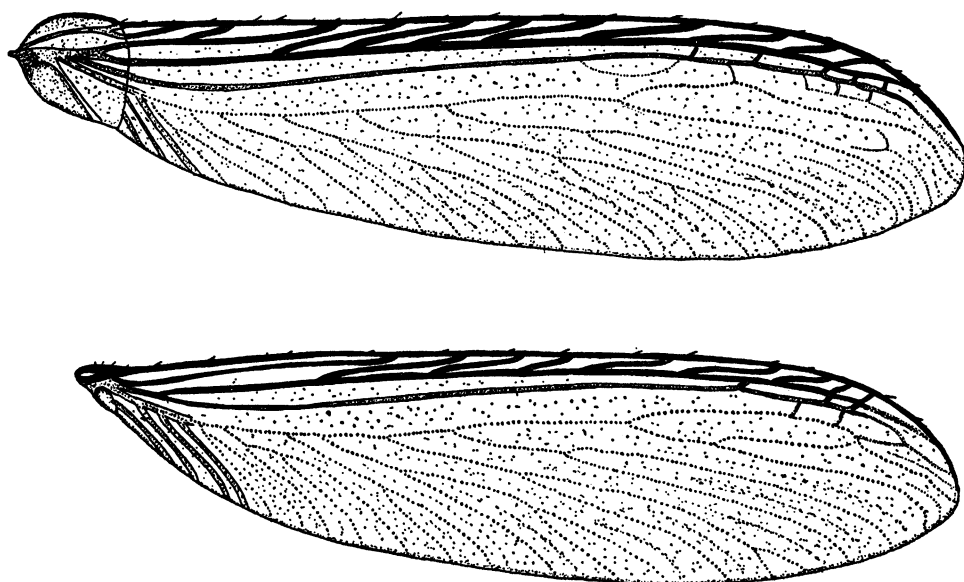


FIG. 29. Forewing and hind wing of *Ceratokalotermes spoliator* (Hill).
Autotype colony, Australia.

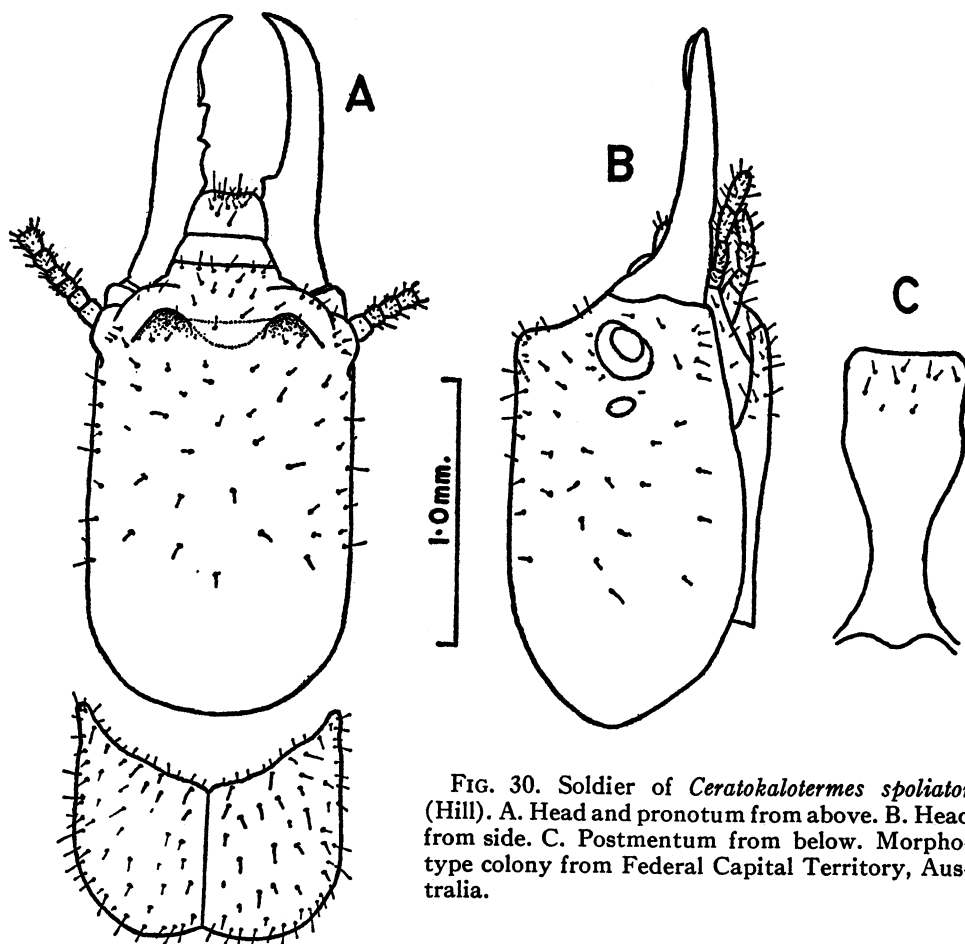


FIG. 30. Soldier of *Ceratokalotermes spoliator* (Hill). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Morpho-type colony from Federal Capital Territory, Australia.

radial sector, running closer to radial sector than to cubitus; a few cross branches between radial sector and media in distal third of wing; cubitus weak (fig. 29). Tibial spurs 3:3:3. Arolium present.

SOLDIER (FIG. 30): Head somewhat phragmotic, narrow, sides parallel; antennal carinae large and markedly projecting; frons concave and sloping down sharply to anteclypeus; anterodorsal surface with two large prominences or lobes, with an even curve between. Eyes unpigmented. Antenna with 11 to 14 articles; third article unmodified and subequal to second. Mandibles long and slender. Pronotum as wide as head, arched transversely; anterior margin raised, deeply and angularly emarginate, with a notch in the middle. Legs short and stout. Tibial spurs 3:3:3.

COMPARISONS: The imago most closely resembles that of *Paraneotermes* and that of *Comatermes*. *Ceratokalotermes* can be distinguished from *Comatermes* by the absence of long wavy hairs on the head and pronotum. *Paraneotermes* has an imago mandible with a distinct angle in the posterior margin of the first plus second marginal tooth, and the arolium is absent. The soldiers of *Paraneotermes* and *Comatermes* differ in having short and strong mandibles; the anterodorsal prominences in the head are very faint or absent; the anterior margin of the pronotum is not deeply emarginate.

SPECIES INCLUDED

Ceratokalotermes spoliator (Hill), new combination = *Calotermes* (?) *spoliator* Hill, 1932b

GEOGRAPHICAL DISTRIBUTION: Australian: Australia.

COMATERMES, NEW GENUS

<Genus *Calotermes* HAGEN, 1858a, pp. 31-38.

<Genus *Calotermes* HAGEN, 1858b, p. 1.

<Genus *Neotermes* SNYDER, 1949, p. 21.

TYPE SPECIES: *Comatermes perfectus* (Hagen) (= *Kalotermes perfectus* Hagen).

The single species *Comatermes perfectus* now constitutes this monotypic genus. *Comatermes perfectus* was described by Hagen (1858a) from the imago caste from an unknown locality and was placed by him in the genus *Kalotermes*. Snyder (1949) placed this

species in the genus *Neotermes*. Snyder (1926d) described *Neotermes manni*, based on the soldier caste alone, from Mapiri, Bolivia. In the collection of A. E. Emerson there is a homotype series with both imagoes and soldiers, collected by A. M. Adamson, from El Tucuche, Trinidad, the West Indies, determined and compared by Emerson as *Neotermes manni*. Emerson in 1957 studied the unique type of *Comatermes perfectus* at the British Museum (Natural History), London, and made a detailed description. A recent comparison by Emerson and myself of the associated homotype series of *Neotermes manni* with *Comatermes perfectus* shows that *Neotermes manni* is conspecific with *Comatermes perfectus* and therefore should be treated as a synonym.

IMAGO (FIG. 31): Dark brown. Head and pronotum with remarkably long hairs, which are not stiff, but thin and somewhat wavy. Eyes small; diameter, 0.29-0.31 mm. Ocellus in contact with eye. Antenna with 14 articles. Mandibles as in the genus *Kalotermes*, i.e., left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth. Pronotum broader than head. Wing venation closely resembling that of *Paraneotermes* and that of *Ceratokalotermes*. Forewing with all major veins arising independently at wing suture; radial sector with nine to 10 branches; media more weakly sclerotized than radial sector, running closer to radial sector than to cubitus; many cross branches between media and radial sector; cubitus weak (fig. 32). Tibial spurs 3:3:3. Arolium present.

SOLDIER (FIG. 33): Head usually long; sometimes two types of soldiers are found (a long-headed and a short-headed); head dorso-ventrally flattened; frons depressed medially, concave in front, with two faint anterodorsal prominences. Eyes unpigmented. Antenna with 13 to 14 articles; third article unmodified, equal to second. Mandibles strong and shorter in proportion to head length. Pronotum as wide as head; anterior margin shallowly and broadly concave. Femur swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago closely resembles that of *Paraneotermes* and that of *Ceratokalotermes* in wing venation and other characters, but differs in having long, thin, somewhat

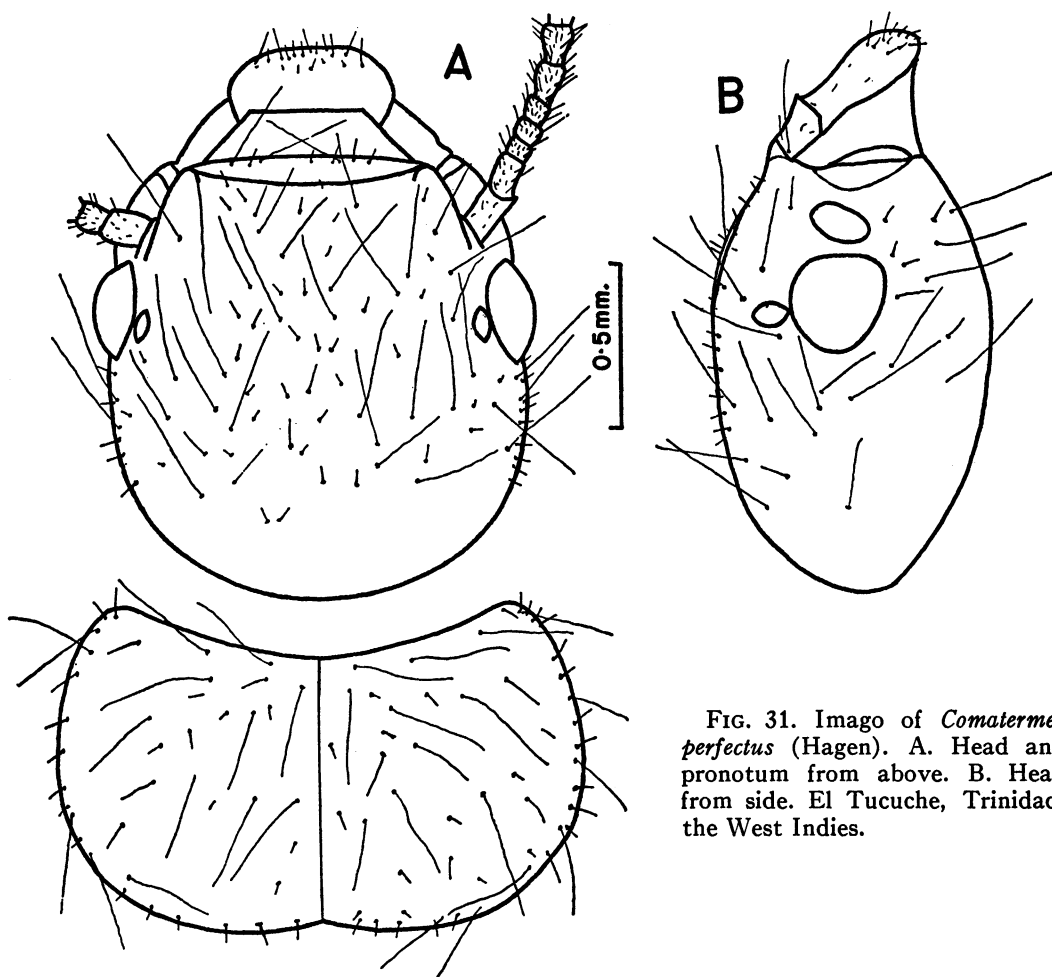


FIG. 31. Imago of *Comatermes perfectus* (Hagen). A. Head and pronotum from above. B. Head from side. El Tucuche, Trinidad, the West Indies.

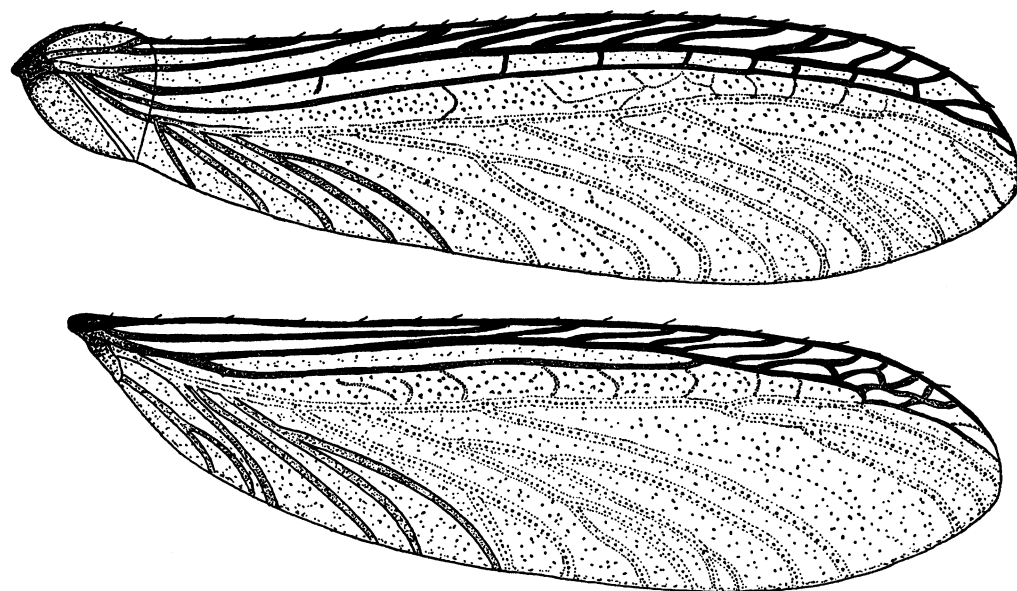


FIG. 32. Forewing and hind wing of *Comatermes perfectus* (Hagen). El Tucuche, Trinidad, the West Indies.

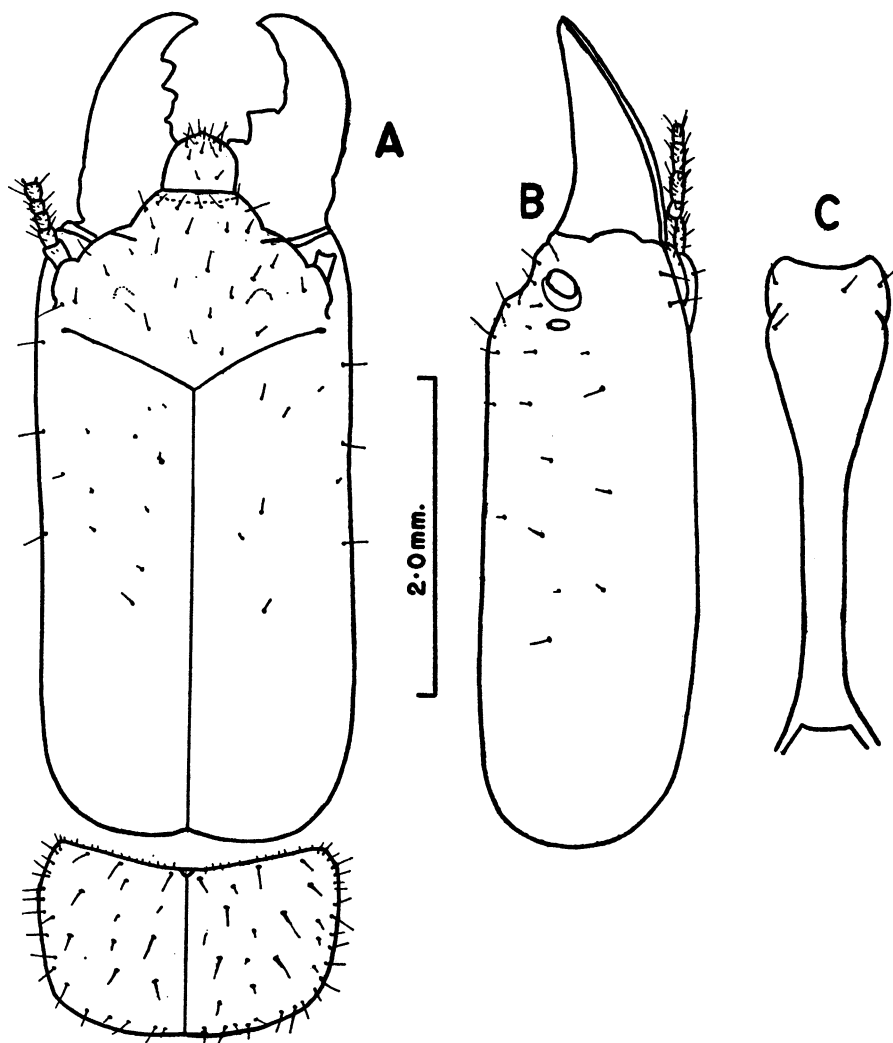


FIG. 33. Soldier of *Comatermes perfectus* (Hagen). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. El Tucuche, Trinidad, the West Indies.

wavy hairs in the head and pronotum. The imago mandible of *Paraneotermes* is different from that of *Comatermes*. The soldier of *Ceratokalotermes* has two prominent lobes on the anterodorsal surface of the head, and the anterior margin of the pronotum is raised and deeply emarginate.

SPECIES INCLUDED

Comatermes perfectus (Hagen), new combination = *Calotermes perfectus* Hagen, 1858a

GEOGRAPHICAL DISTRIBUTION: Neotropical: South America.

GENUS *GLYPTOTERMES* FROGGATT, 1896

<Genus *Calotermes* HAGEN, 1858a, pp. 31–38.

<Genus *Calotermes* HAGEN, 1858b, p. 1.

= Genus *Glyptotermes* FROGGATT, 1896, pp. 518, 543.

<Genus *Calotermes* HAVILAND, 1898, pp. 371, 373.

<Genus *Calotermes* DESNEUX, 1904d, pp. 20–24.

= Genus *Glyptotermes* FROGGATT, 1905, pp. 17, 23, 24.

= Subgenus *Glyptotermes* HOLMGREN, 1910a, p. 285 (no description).

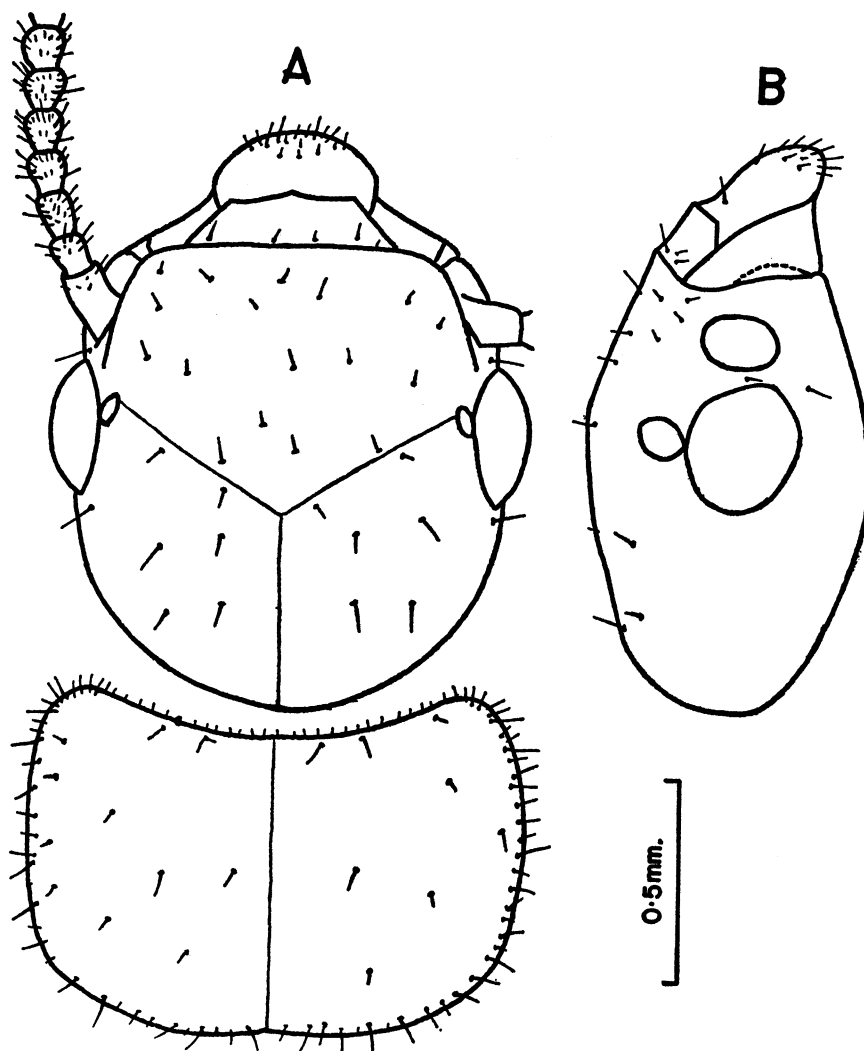


FIG. 34. Imago of *Glyptotermes tuberculatus* Froggatt. A. Head and pronotum from above. B. Head from side. Homotype colony from Galston, New South Wales, Australia.

= Subgenus *Glyptotermes* HOLMGREN, 1910b, p. 140.

> < Subgenus *Glyptotermes* HOLMGREN, 1911a, pp. 53, 55, 58–61.

> Subgenus *Lobitermes* HOLMGREN, 1911a, pp. 53, 56, 59–61.

> Subgenus *Glyptotermes* HOLMGREN, 1913a, pp. 37, 49.

> Subgenus *Lobitermes* HOLMGREN, 1913a, pp. 37, 59.

= Genus *Glyptotermes* FROGGATT, 1915, p. 25.

> Genus *Glyptotermes* SNYDER, 1924, pp. 1, 9, 10.

> Subgenus *Glyptotermes* SNYDER, 1925b, pp. 152, 157.

> Subgenus *Lobitermes* SNYDER, 1925b, p. 158.

> Subgenus *Glyptotermes* EMERSON, 1925, pp. 301, 313, 331.

> < Subgenus *Lobitermes* EMERSON, 1925, p. 337.

< Genus *Glyptotermes* SJÖSTEDT, 1926, pp. 22, 23, 42.

> Subgenus *Glyptotermes* EMERSON, 1928, pp. 405, 412, 418.

> < Subgenus *Lobitermes* EMERSON, 1928, p. 406.

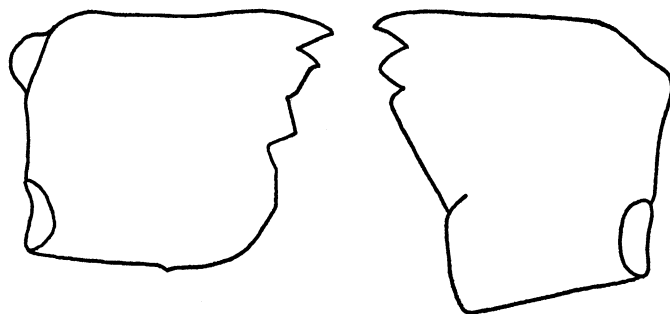


FIG. 35. Mandibles of imago of *Glyptotermes tuberculatus* Froggatt. Homotype colony from Galston, New South Wales, Australia.

=Genus *Glyptotermes* LIGHT, 1930, pp. 15, 16, 18.

> <Subgenus *Lobitermes* LIGHT, 1933, pp. 82, 101.

>Subgenus *Glyptotermes* SNYDER, 1933b, p. 67.

=Subgenus *Glyptotermes* SNYDER, 1934b, pp. 24, 27.

=Genus *Glyptotermes* KEMNER, 1934, pp. 30, 38.

Subgenus *Glyptotermes* HARE, 1937, pp. 461, 474, 475.

=Subgenus *Glyptotermes* HILL, 1942, pp. 7, 85.

=Genus *Glyptotermes* SNYDER, 1949, pp. 45, 359.

<Genus *Glyptotermes* CACHAN, 1949, pp. 180, 185, 190, 208.

=Genus *Glyptotermes* GRASSÉ, 1949, p. 531.

=Genus *Glyptotermes* AHMAD, 1950, pp. 44, 50.

=Genus *Glyptotermes* WEIDNER, 1955a, pp. 46, 48, 68.

=Genus *Glyptotermes* EMERSON, 1955, pp. 468, 473, 476-478, 492, 507, 508.

=Genus *Glyptotermes* HARRIS, 1957, p. 25.

=Genus *Glyptotermes* AHMAD, 1958, pp. 35, 36.

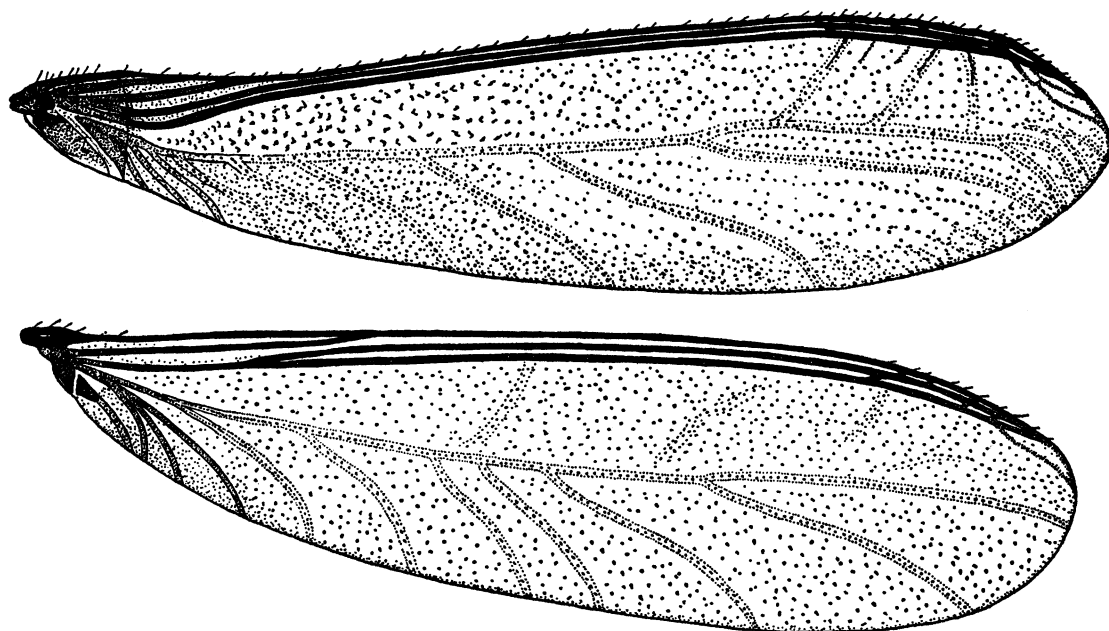


FIG. 36. Forewing and hind wing of *Glyptotermes canellae* (Fr. Müller). Cotype from Blumenau, Brazil. Drawn by A. E. Emerson.

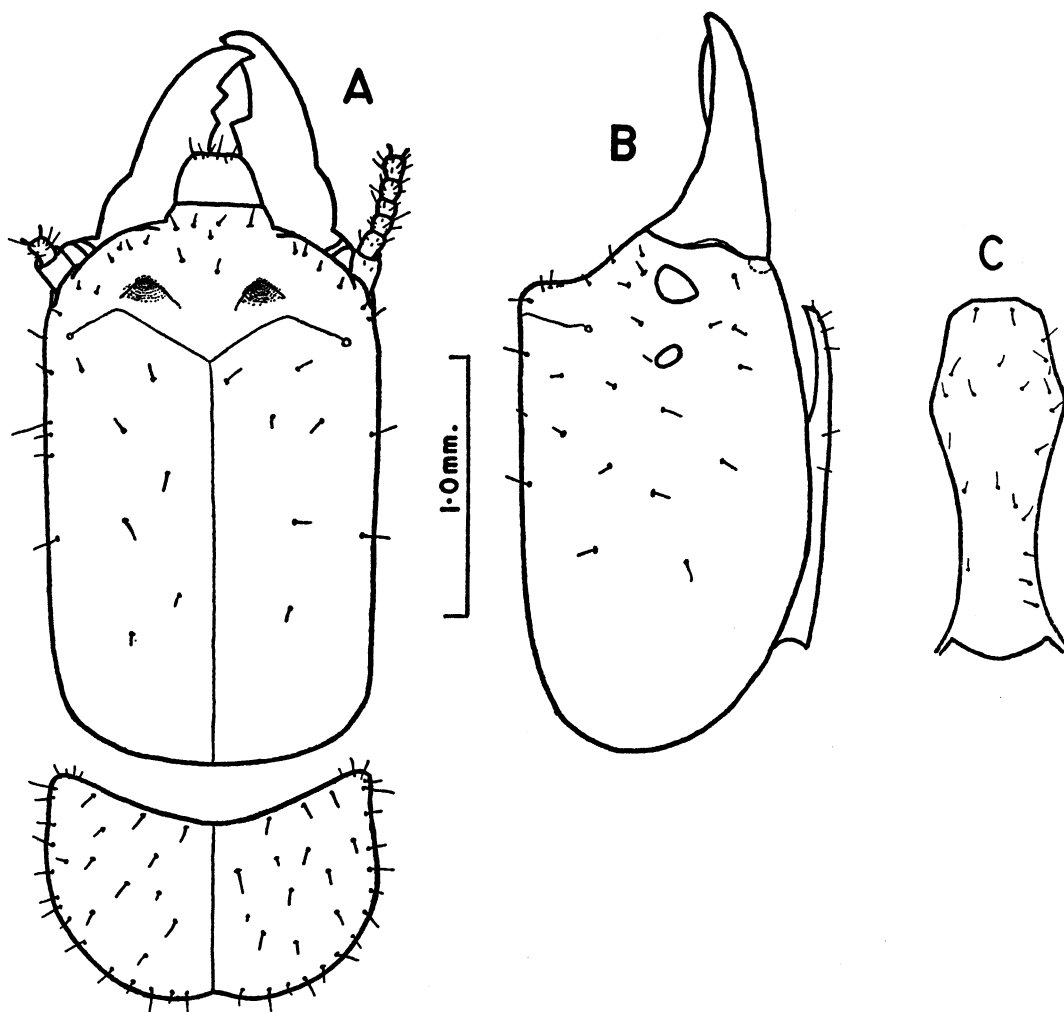


FIG. 37. Soldier of *Glyptotermes tuberculatus* Froggatt. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Homotype colony from Galston, New South Wales, Australia.

TYPE SPECIES: *Glyptotermes tuberculatus* Froggatt.

Holmgren (1911a) designated the species *Glyptotermes borneensis* (Haviland) as the generotype of the genus *Glyptotermes*. This species was not mentioned by Froggatt (1896) when he named the genus *Glyptotermes*. The species he mentioned were *G. tuberculatus*, *G. iridipennis*, *G. brevicornis*, and *G. eucalypti*. According to the Rules of Zoological Nomenclature (Article 30e), *G. borneensis* cannot be the generotype. Snyder (1949) selected *G. tuberculatus* as the generotype.

IMAGO (FIG. 34): Reddish brown to dark

brown. Diameter of eye, 0.29–0.48 mm. Ocellus in most species touching the eye. Antenna with 11 to 17 articles. Left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth; in some species no distinct notch between first plus second marginal tooth and third marginal tooth (fig. 35). Right mandible with posterior margin of second marginal tooth slightly longer than molar plate (fig. 35). Pronotum as wide as or slightly narrower than head. Anterior margin of forewing scale almost straight or slightly convex. Wing membrane smoky brown in

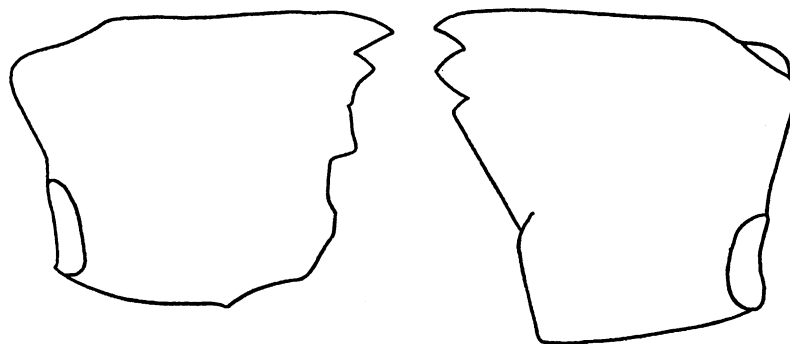


FIG. 38. Mandibles of nymph of *Calcaritermes imminens* Snyder. Cotype from type colony from Cincinnati, Colombia.

color, with small, pimple-like, pigmented nodules, as in the genera *Kaloterмес* and *Rugiterмес*. Forewing with all major veins arising independently at wing suture; radius (R_1) short; radial sector heavily sclerotized, running very close and parallel to costal border, without branches; media as heavily sclerotized as radial sector, running very close to and parallel to it; faint cross branches between radial sector and media, and between media and cubitus, in distal end of wing; cubitus weak (fig. 36). Tibial spurs 3:3:3. Arolium always present.

SOLDIER (FIG. 37): Head more or less elongated; some species (*G. asperatus*) having extremely phragmotic head, with frontal area sloping quite steeply to vertical, and in some species concave; either distinctly or faintly bilobed, with V- or U-shaped depression between lobes. Eyes unpigmented. Antenna with 10 to 15 articles; third article shorter than second and not modified. Mandibles short and broad, with or without basal hump. Pronotum slightly narrower, as broad as, or wider than, head; anterior margin either shallowly or deeply emarginate or concave. Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago can be distinguished from that of all other genera except *Calcariterмес* in having the radial sector with no branches and the media heavily sclerotized and running close to and parallel to the radial sector. The soldier resembles that of the genus *Cryptoterмес* because of convergent evolution of the phragmotic head. *Cryptoterмес* has an extremely phragmotic head, with the frontal area scooped or vertical and

with an anterior rim between the frons and the vertex and a horn-like projection in front, either above or below the antennal socket. The anterior margin of the pronotum is serrated.

SPECIES INCLUDED

G. almorensis Gardner, 1944
G. angustus Snyder, 1925a
G. asperatus (Snyder), 1926a
G. bilobatus Snyder, 1934a
G. borneensis (Haviland), 1898
G. brevicaudatus (Haviland), 1898
G. brevicornis Froggatt, 1896
G. buttel-reepeni Holmgren, 1914
G. canellae (Müller), 1873
G. caudomunitus Kemner, 1932b
G. ceylonicus Holmgren, 1911d
G. chapmani Light, 1930
G. contracticornis (Snyder), 1925b
G. coorgensis K. and N. Holmgren, 1917
G. dentatus (Haviland), 1898
G. dilatatus (Bugnion and Popoff), 1910
G. eucalypti Froggatt, 1896
G. franciae Snyder, 1958
G. fuscus Oshima, 1912
G. guianensis Emerson, 1925
G. hospitalis Emerson, 1925
G. ignotus Wilkinson, 1959
G. insulanus Silvestri, 1912
G. iridipennis Froggatt, 1896
G. kawandae Wilkinson, 1954
G. liberatus (Snyder), 1929
G. luteus Kemner, 1931
G. magsaysayi Snyder, 1958
G. marlatti, Snyder, 1926a
G. minutus Kemner, 1932b
G. montanus Kemner, 1934
G. neotuberculatus Hill, 1933
G. nevermani Snyder, 1926a

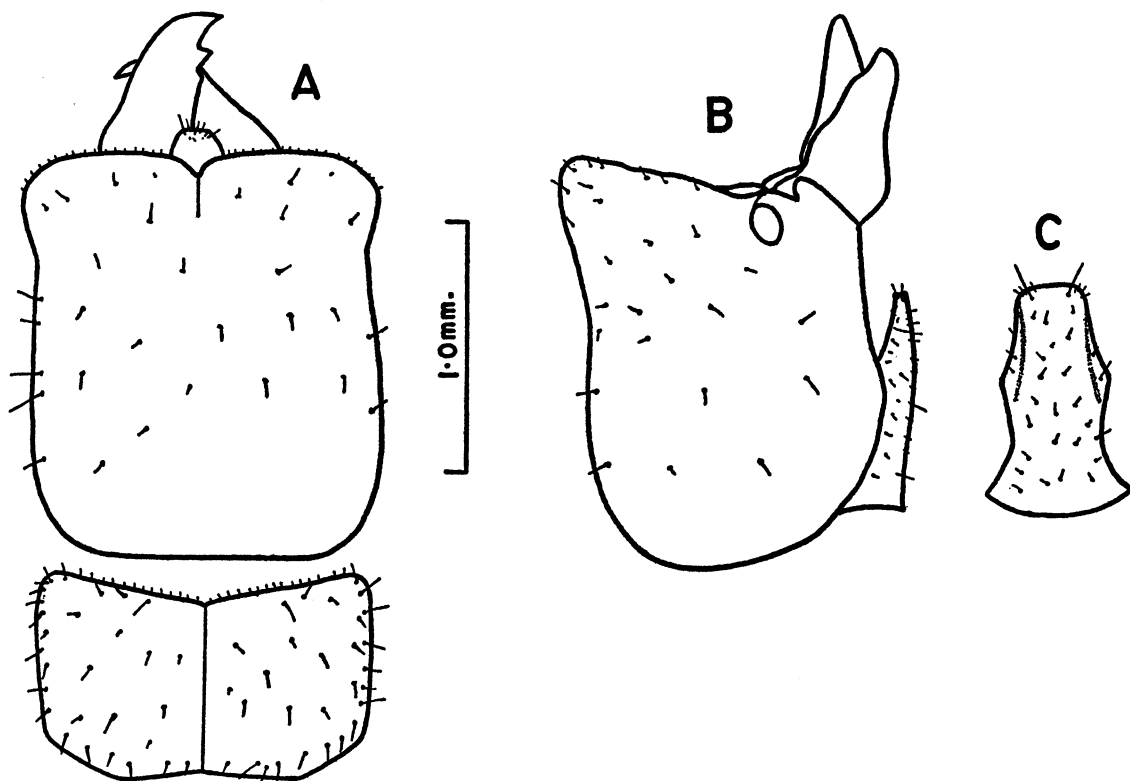


FIG. 39. Soldier of *Calcaritermes imminens* Snyder. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Cotype from type colony from Cincinnati, Colombia.

G. niger Kemner, 1934
G. parvulus (Sjöstedt), 1907a
G. pellucidus Emerson, 1925
G. perparvus Emerson, 1925
G. pinangae (Haviland), 1898
G. planus Snyder, 1925b
G. posticus (Hagen), 1858a
G. pubescens Snyder, 1924
*G. pusillus*¹ (Heer), 1849
G. reticulatus Wilkinson, 1954
G. satsumensis (Matsumura), 1907
G. scotti Holmgren, 1910b
G. suturis Snyder, 1925b
G. taveuniensis Hill 1926d
G. tuberculatus Froggatt, 1896
G. ueleensis Coaton, 1955
G. verrucosus (Hagen), 1858a
G. xantholabrum Hill, 1926e

GEOGRAPHICAL DISTRIBUTION: Australian: Australia, New Zealand. Papuan: Amboina, Fiji Islands, New Britain, Samoa. Indo-

Malayan: Borneo, Ceylon, Formosa, India, Japan, Java, Malacca, Philippines, Sumatra. Ethiopian: Africa. Malagasy: Seychelles. Neotropical: Central and South America, the West Indies, Puerto Rico.

GEOLOGICAL DISTRIBUTION: Oligocene, Recent.

GENUS *CALCARITERMES* SNYDER, 1925

<Genus *Calotermes* SILVESTRI, 1903, p. 20.

<Genus *Procryptotermes* HOLMGREN, 1911a, p. 55.

=Subgenus *Calcaritermes* SNYDER, 1925b, p. 155.

<Subgenus *Lobitermes* EMERSON, 1925, p. 337.

> <Subgenus *Lobitermes* EMERSON, 1928, p. 406.

=Subgenus *Calcaritermes* SNYDER, 1933b, p. 67.

=Subgenus *Calcaritermes* LIGHT, 1933, p. 82.

=Subgenus *Calcaritermes* HARE, 1937, pp. 461, 474.

=Subgenus *Calcaritermes* SNYDER, 1948, pp. 232, 234, 235.

¹ Fossil species.

= Genus *Calcaritermes* SNYDER, 1949, p. 52.

= Genus *Calcaritermes* GRASSÉ, 1949, p. 531.

= Genus *Calcaritermes* AHMAD, 1950, pp. 44, 50.

= Genus *Calcaritermes* WEIDNER, 1955a, pp. 48, 68.

= Genus *Calcaritermes* EMERSON, 1955, pp. 472, 490, 492, 498, 508.

TYPE SPECIES: *Calcaritermes imminens* Snyder.

IMAGO: Dark brown. Eyes small; diameter, 0.29–0.34 mm. Ocellus touching eye in most species. Antenna with 13 to 14 articles. Left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth; in most species, notch between first plus second and third marginal tooth absent; posterior margin of first plus second merging with anterior margin of third, forming a concave cutting edge (fig. 38). Right mandible with posterior margin of second marginal tooth slightly longer than molar plate (fig. 38). Pronotum slightly narrower than head. Wing venation similar to that of the genus *Glyptotermes*. Tibial spurs 3:3:3. Arolium present in all species.

SOLDIER (FIG. 39): Head dark, thick, and semicylindrical; distinctly bilobed, with V- or U-shaped depression between lobes; front profile steep, varying from greater than vertical to less than vertical, in some species with dorsal rim overhanging, or concave between upper rim and clypeus; in some species a horn-like projection of ventral genae between mandible base and below antennal socket. Eyes either distinct or indistinct and unpigmented. Antenna with 10 to 12 articles; third article short and unmodified. Mandibles usually short and broad, either with or without basal hump. Pronotum either narrower, as broad as, or broader than, head. Anterior margin shallowly angular or conspicuously concave. Tibial spurs 3:3:3; front tibia with a thick, conspicuous spur near apex of outer side, much larger than the other two apical spurs (fig. 40). Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago is similar in all respects to that of the genus *Glyptotermes*. The soldier can be distinguished by its front tibia, which has a large, thick outer spur near the apex, much larger than other apical spurs.

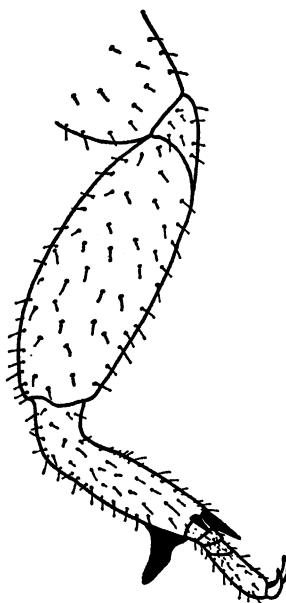


FIG. 40. Left foreleg of *Calcaritermes imminens* Snyder. Cotype from type colony from Cincinnati, Colombia.

SPECIES INCLUDED

- C. brevicollis* (Banks), 1918
- C. emarginicollis* (Snyder), 1925a
- C. fairchildi* Snyder, 1926a
- C. guatemalae* Snyder, 1926a
- C. imminens* Snyder, 1925b
- C. nearcticus* Snyder, 1933b
- C. nigriceps* (Emerson), 1925
- C. parvinotus* Light, 1933
- C. recessifrons* Snyder, 1925b
- C. temnocephalus* (Silvestri), 1901

GEOGRAPHICAL DISTRIBUTION: Nearctic: North America (Florida). Neotropical: Central and South America.

GENUS *PTEROTERMES* HOLMGREN, 1911

- <Genus *Termes* (part) WALKER, 1853, p. 529.
- <Genus *Termopsis* HAGEN, 1858a, pp. 74, 75, 77, 78.
- <Genus *Termopsis* HAGEN, 1858b, p. 12.
- <Genus *Termopsis* HAGEN, 1874, p. 572.
- <Genus *Termopsis* GIRARD, 1879, p. 270.
- <Genus *Termopsis* FROGGATT, 1896, pp. 517, 535.
- <Genus *Termopsis* WASMANN, 1897, p. 149.
- <Genus? *Termopsis* DESNEUX, 1904d, p. 14.
- = Genus *Pterotermes* HOLMGREN, 1911a, pp. 42, 43.

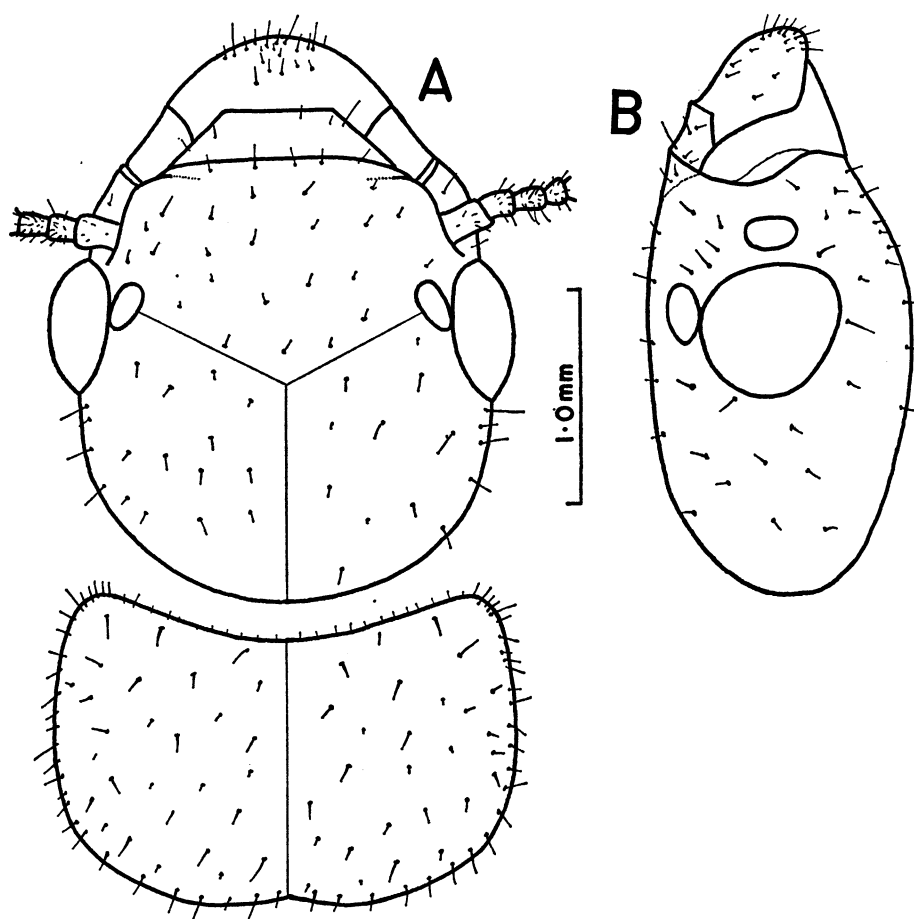


FIG. 41. Imago of *Pterotermes occidentis* (Walker). A. Head and pronotum from above. B. Head from side. St. Xavier Mission, Tucson, Arizona.

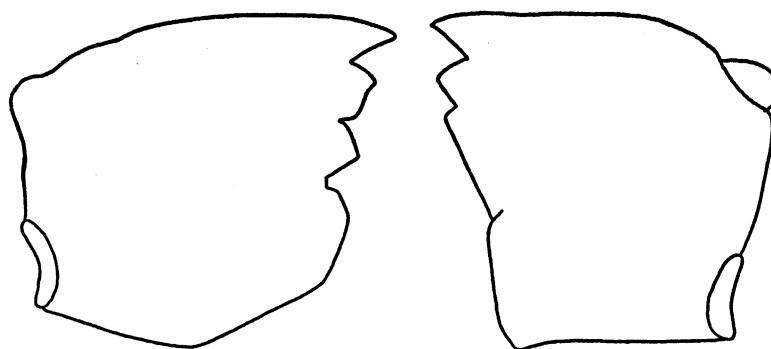


FIG. 42. Mandibles of imago of *Pterotermes occidentis* (Walker). St. Xavier Mission, Tucson, Arizona.

<Genus *Kaloterмес* BANKS AND SNYDER, 1920, pp. 16-20.

<Genus *Kaloterмес* SNYDER, 1922, p. 1.

<Genus *Kaloterмес* SNYDER, 1925d, pp. 156, 157.

<Genus *Kaloterмес* LIGHT, 1929, pp. 67-69.

<Genus *Kaloterмес*, *sensu stricto*, LIGHT, 1933, pp. 82, 83, 85, 86.

<Subgenus *Kaloterмес* SNYDER, 1948, pp. 228, 232, 234, 235.

<Genus *Kaloterмес* SNYDER, 1949, pp. 11, 19.

TYPE SPECIES: *Pterotermes occidentis* (Walker).

Walker in 1853 described *T. occidentis*, a large and primitive species, and placed it in the genus *Termes*. Later, Hagen (1858a), Froggatt (1896), and Wasmann (1897) placed *T. occidentis* in the genus *Termopsis*. Holmgren (1911a) described a monotypic genus *Pterotermes* for *T. occidentis* Walker and placed the genus in the subfamily Hodotermitinae. Banks and Snyder (1920), however, considered it to be a *Kaloterмес* in all essential characters and therefore treated *Pterotermes* as a synonym. Light (1933) and Snyder

(1949) followed Banks and Snyder (1920). I am resurrecting the genus *Pterotermes*, because I am of the opinion that *Pterotermes* is a specialized genus, distinct from *Kaloterмес*, as I am treating *Kaloterмес* in the present paper, and is closely related to *Incisiterмес* and *Marginiterмес*. The imago of *Kaloterмес* is dark and has small eyes; the wing membrane has small, pimple-like nodules; the arolium is absent. The soldier of *Kaloterмес* is small, with eyes unpigmented; the head slopes in front at an angle of approximately 40 to 45 degrees; a horn-like projection between the antenna and the side base of the mandible is absent. The anterior margin of the pronotum is broadly emarginate.

IMAGO (FIG. 41): Brownish. Eyes large; diameter, 0.68-0.71 mm. Ocellus touching eye. Antenna with 20 to 21 articles. Left mandible with first plus second marginal tooth at base equal to third marginal tooth; posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth (fig. 42); in left mandible of nymph, anterior margin of third marginal

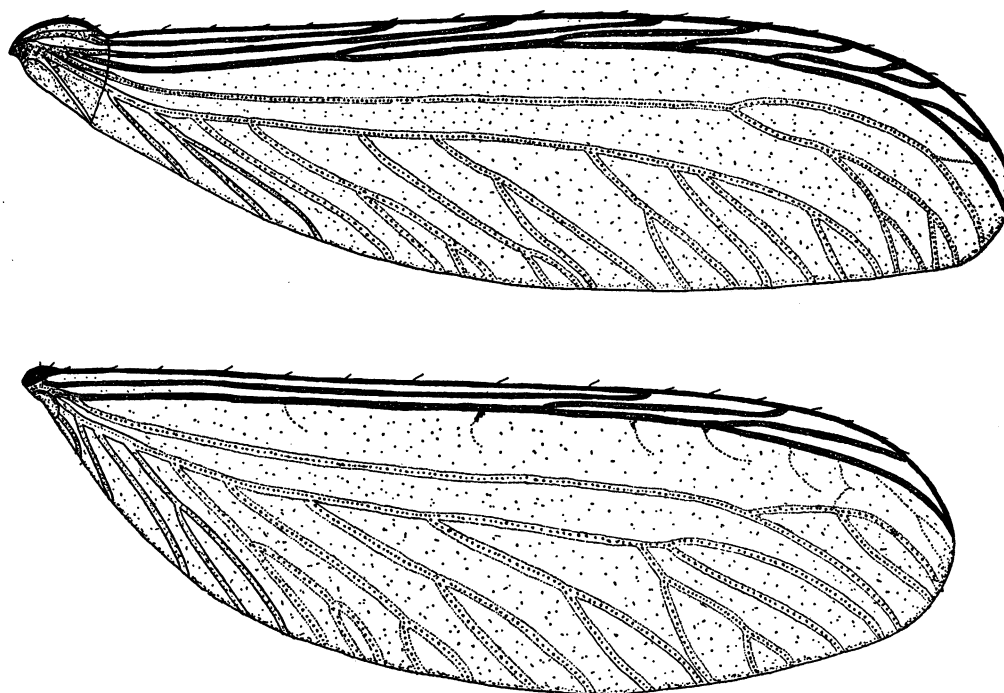


FIG. 43. Forewing and hind wing of *Pterotermes occidentis* (Walker).
St. Xavier Mission, Tucson, Arizona.

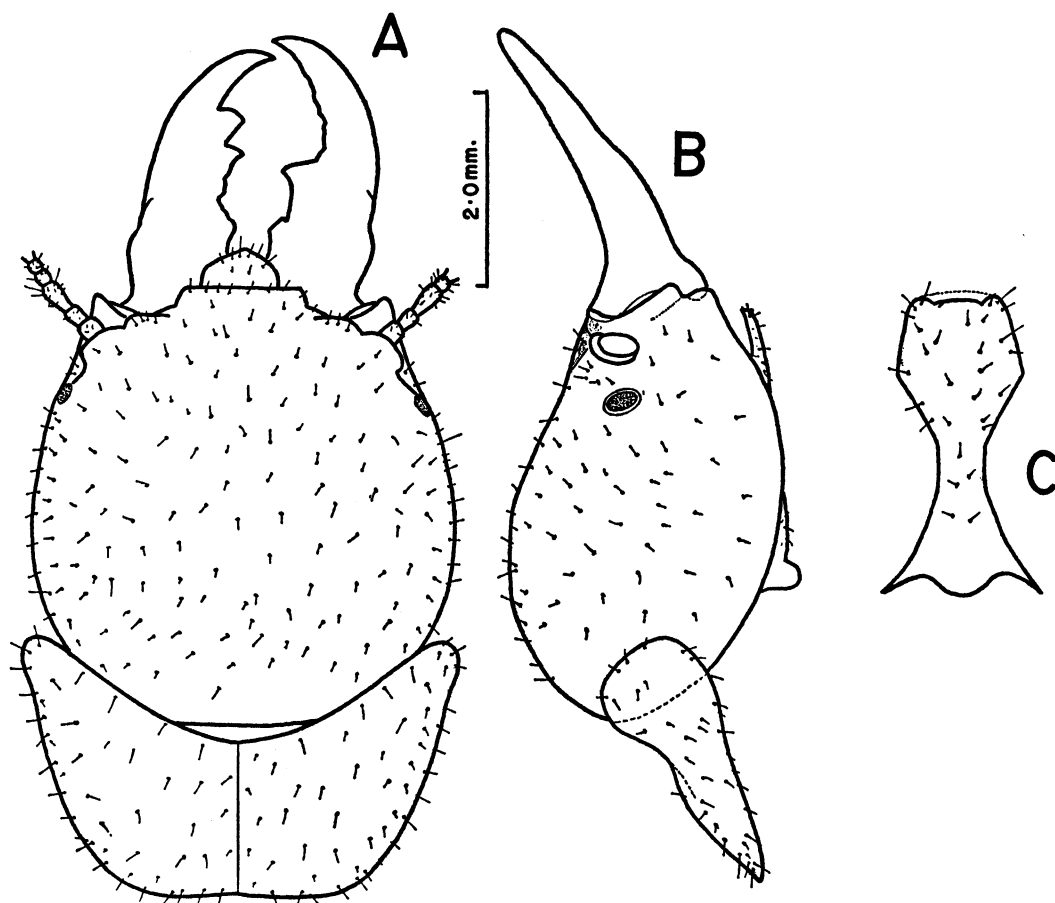


FIG. 44. Soldier of *Pterotermes occidentis* (Walker). A. Head and pronotum from above. B. Head and pronotum from side. C. Postmentum from below. San José Island, Baja California.

tooth plainly longer than posterior margin of first plus second marginal tooth. Right mandible with posterior margin of second marginal tooth equal to molar plate (fig. 42). Pronotum as broad as head. Forewing with all major veins arising independently at wing suture; subcosta long and unbranched; radial sector with five to six branches, first branch arising at one-fourth of length of wing from suture; media weak, unsclerotized, running midway between radial sector and cubitus, in some specimens branching in distal end of wing; cubitus weak and unsclerotized (fig. 43). Tibial spurs 3:3:3. Arolium always absent.

SOLDIER (FIG. 44): Largest in the family Kalotermitidae. Head very large; sides rounded; frons sloping in front gradually from almost middle of head; mesial ridge present

on each side of postclypeus, as in *Rugitermes*. A horn-like projection present, in front of and below antennal socket, near side base of mandibles. Eyes pigmented. Antenna with 17 articles; third article longer than second or fourth. Mandibles long and stout, toothed, with a distinct basal hump. Postmentum with a sclerotized swelling in basal region. Pronotum broader than head, somewhat saddle shaped; anterior margin covering posterior region of head, deeply concave; anterolateral corners raised; mesonotum and metanotum with distinct wing pads. Femur swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago closely resembles that of *Incisitermes* and that of *Marginitermes* in wing venation and other characters. It can be distinguished from the imagoes of

these genera by the large eye size, and the antennae, each of which has 20 to 21 articles. The imago mandible is as in the genus *Kalotermit*, i.e., the first plus second marginal tooth is equal to the third marginal tooth. The soldier can be distinguished by large pigmented eyes, a somewhat saddle-shaped pronotum, and a sclerotized swelling at the basal region of the postmentum.

SPECIES INCLUDED

Pterotermes occidentis (Walker), 1853

GEOGRAPHICAL DISTRIBUTION: Nearctic: Western North America and western Mexico.

INCISITERMES, NEW GENUS

- <Genus *Calotermit* HAGEN, 1858a, pp. 31-38.
- <Genus *Calotermit* HAGEN, 1858b, p. 1.

- <Genus *Calotermit* SILVESTRI, 1903, p. 20.
- <Genus *Calotermit* DESNEUX, 1904d, pp. 20-24.
- <Subgenus *Calotermit*, *sensu stricto*, HOLMGREN, 1911a, pp. 53, 56-58, 60, 61.
- <Genus *Kalotermit* BANKS, 1919, pp. 476, 477.
- <Genus *Kalotermit* BANKS AND SNYDER, 1920, pp. 16, 17.
- <Genus *Kalotermit*, *sensu stricto*, LIGHT, 1921, pp. 23, 29.
- <Genus *Kalotermit* SNYDER, 1922, pp. 8, 9.
- <Genus *Kalotermit* LIGHT, 1924, p. 52.
- <Genus *Kalotermit* SNYDER, 1925d, p. 156.
- <Subgenus *Kalotermit*, *sensu stricto*, EMERSON, 1928, p. 405.
- <Genus *Kalotermit*, *sensu stricto*, LIGHT, 1930, pp. 15, 16, 18, 21.
- <Genus *Kalotermit*, *sensu stricto*, LIGHT, 1933, pp. 82, 83.
- <Subgenus *Kalotermit*, *sensu stricto*, HARE, 1937, pp. 461, 474, 475.

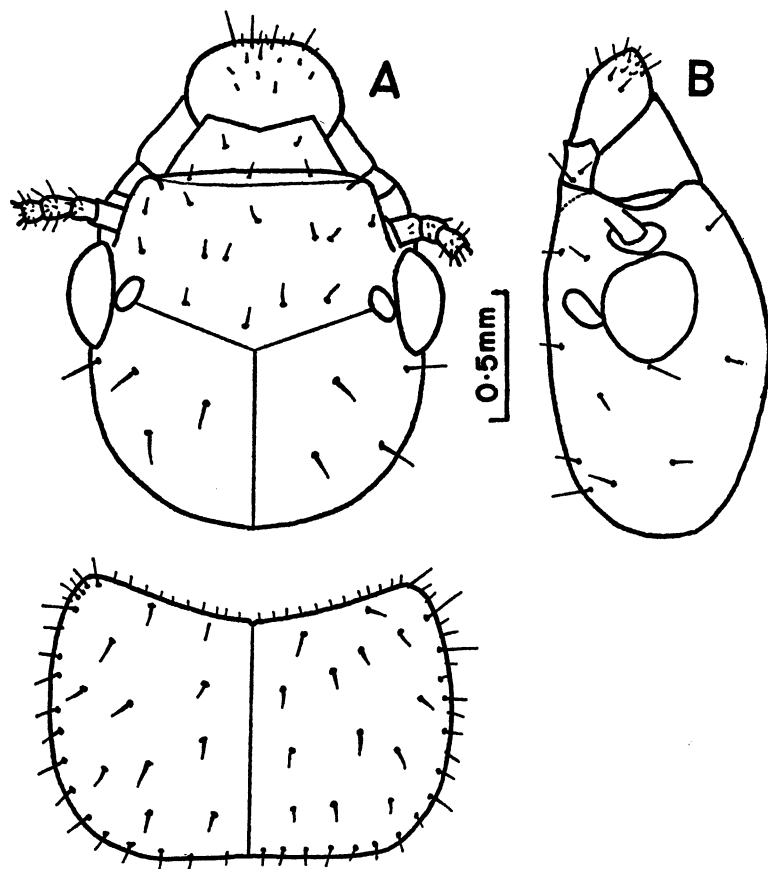


FIG. 45. Imago of *Incisitermes schwarzi* (Banks). A. Head and pronotum from above. B. Head from side. Cotype from Paradise Key, Florida.

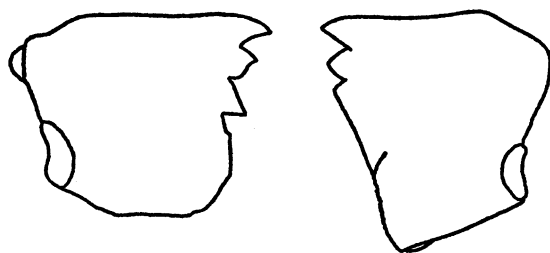


FIG. 46. Mandibles of imago of *Incisitermes schwarzi* (Banks). Homotype colony from Coral Gables, Florida.

<Subgenus *Calotermes*, *sensu stricto*, HILL, 1942, p. 38.

<Subgenus *Kalotermes* SNYDER, 1948, pp. 232, 234, 235.

> <Genus *Kalotermes* SNYDER, 1949, pp. 11, 12.

<Genus *Calotermes* GRASSÉ, 1949, p. 530.

<Genus *Kalotermes* AHMAD, 1950, pp. 44, 48, 50.

<Genus *Kalotermes* STROUD, 1953, pp. 77, 78, 88, 91.

<Genus *Kalotermes* WEIDNER, 1955a, pp. 19, 46, 47, 48, 68.

<Genus *Kalotermes* EMERSON, 1955, pp. 467, 472, 473, 478, 483, 490-492, 507, 508.

<Genus *Kalotermes* AHMAD, 1958, p. 36.

■ TYPE SPECIES: *Incisitermes schwarzi* (Banks) (= *Kalotermes schwarzi* Banks).

I am proposing this genus for species that were previously placed by Snyder (1949) and others in the genus *Kalotermes*. This group is distinct from the genus *Kalotermes* and belongs to the *Procryptotermes*-*Cryptotermes* branch, as is indicated by the imago mandible. The genus *Incisitermes* differs from the genus *Kalotermes* in the following ways: (1) the left imago mandible has the anterior margin of the third marginal tooth longer than the posterior margin of the first plus second marginal tooth; (2) the imago is larger, not so darkly pigmented, and has larger eyes; (3) the wings are hyaline, without pimple-like nodules; (4) the costal region of the forewing is narrower; (5) the arolium is usually present, but in a few species it is absent; (6) the soldier is, in general, larger, the anterior margin of the pronotum deeply cut, the femur usually swollen, and the third antennal joint enlarged, club-shaped, and highly sclerotized.

IMAGO (FIG. 45): Usually light brown, a few species dark brown. Diameter of eye, 0.25-0.50 mm. Ocellus usually touching eye; in *I. minor* it is about 0.07 mm. from eye. Antenna with 13 to 20 articles. Left mandible with anterior margin of third marginal tooth slightly longer than posterior margin of first

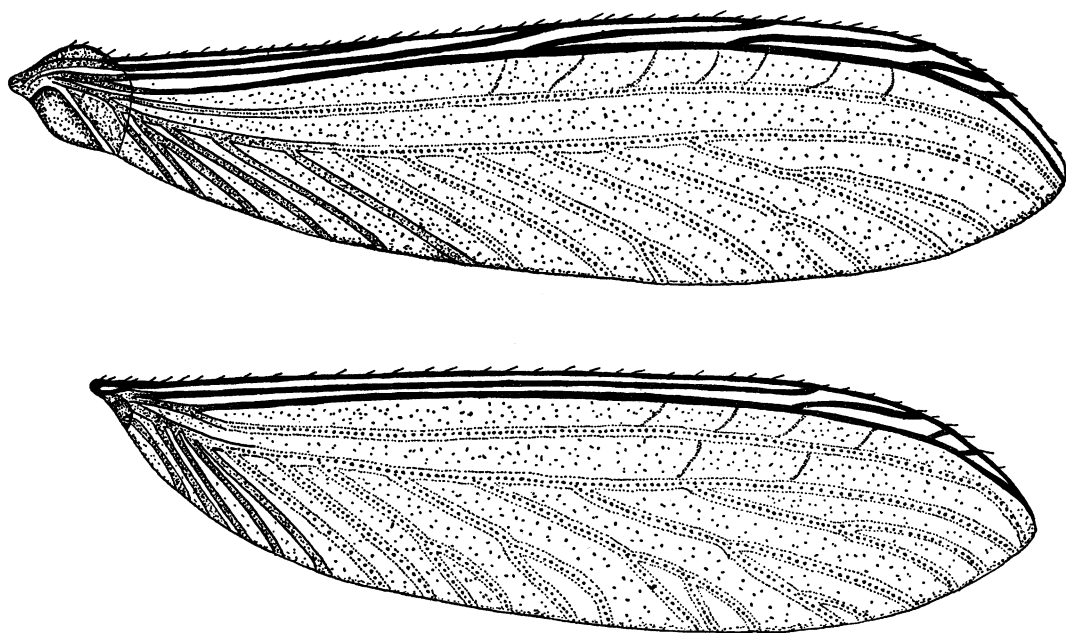


FIG. 47. Forewing and hind wing of *Incisitermes schwarzi* (Banks). Homotype colony from Coral Gables, Florida.

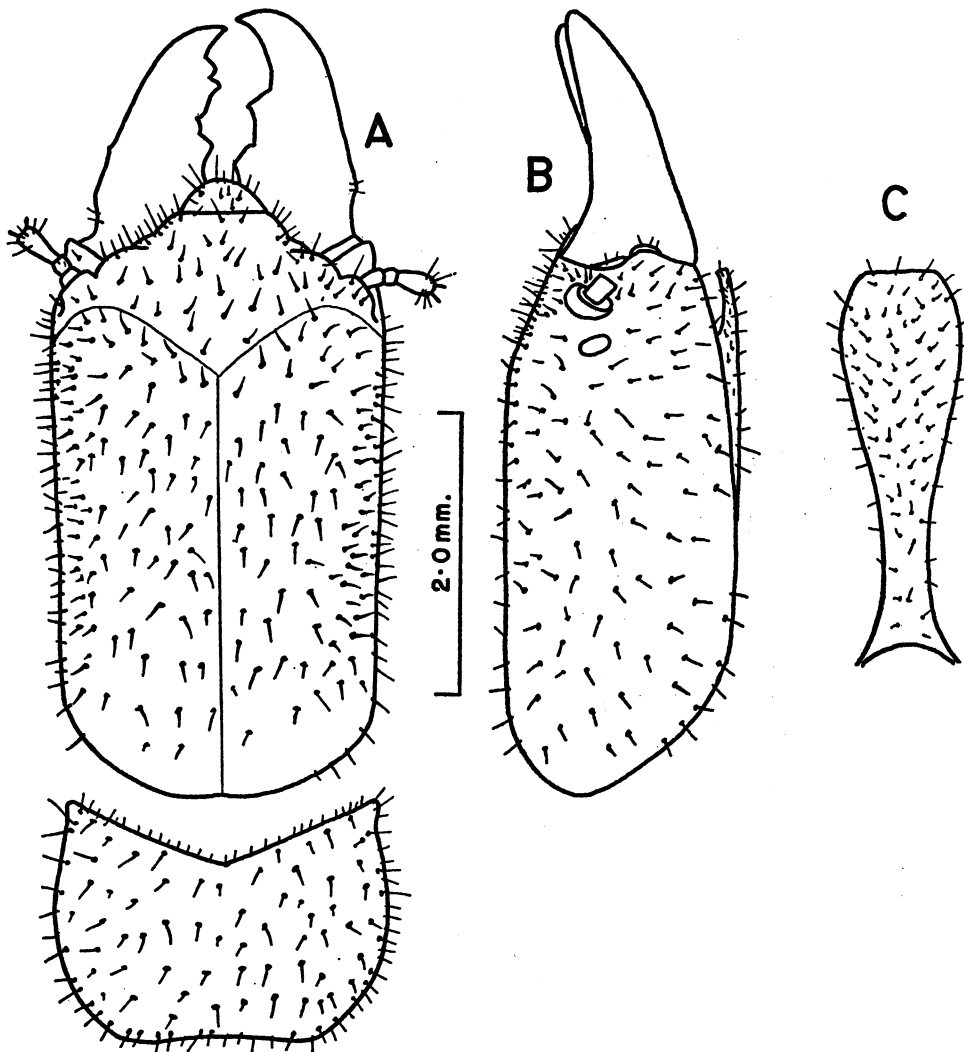


FIG. 48. Large soldier of *Incisitermes schwarzi* (Banks). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Cotype from Paradise Key, Florida.

plus second marginal tooth (fig. 46). Right mandible with molar plate subequal to posterior margin of second marginal tooth (fig. 46). Pronotum as broad as or broader than head. Wing transparent and lacking pimple-like nodules present in the genus *Kaloterмес*. Forewing with all major veins arising independently at wing suture; costal area much narrower than *Kaloterмес*; radius with three to eight branches; media weak, unsclerotized, running midway between radial sector and cubitus; cross branches between radial sector and media; cubitus weak and unsclerotized

(fig. 47). Tibial spurs 3:3:3. Arolium present in all species except *I. minor*, *I. galapagoensis*, and *I. marginipennis*.

SOLDIER (FIGS. 48 AND 49): Head long, dorsoventrally flat, sides parallel, head sloping very slightly in front, at angle of approximately 20 degrees; some species having, in addition, a short-headed soldier. Eyes mostly unpigmented; slightly pigmented in *I. schwarzi*, *I. minor*, *I. marginipennis*, *I. snyderi*, and *I. taylori*. Mandibles massive and short, compared to rest of head capsule; with or without basal hump. Antenna with 10 to 17

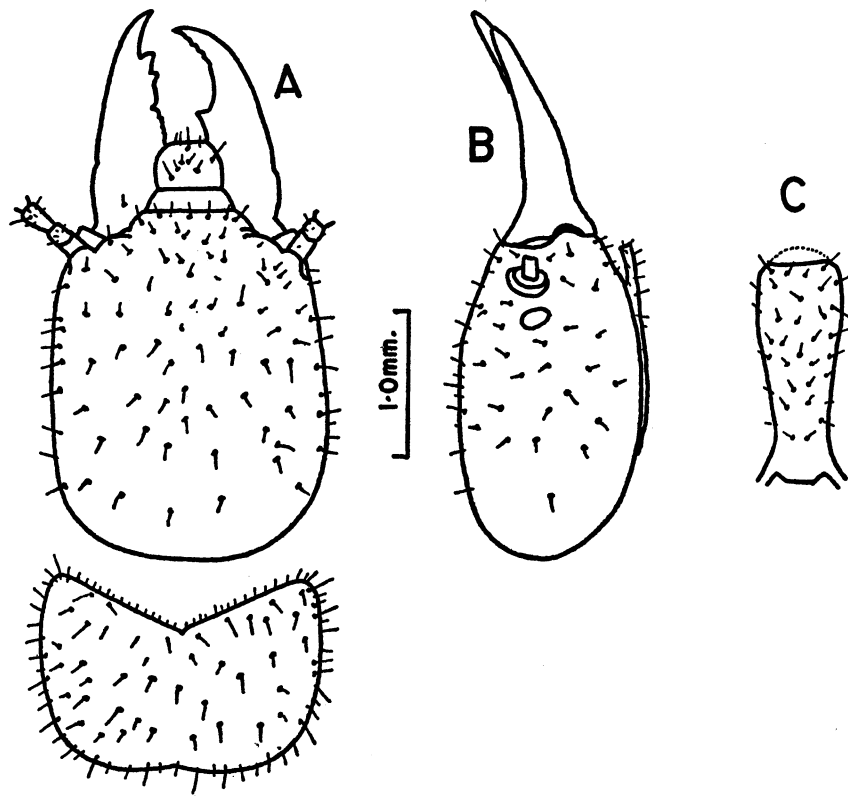


FIG. 49. Small soldier of *Incisitermes schwarzi* (Banks). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Homotype from Coral Gables, Florida.

articles; third article longest, sclerotized, darker, and often club-shaped, attaining its maximum size in *I. marginipennis*. Pronotum as broad as or broader than head; anterior margin deeply angular, sides evenly rounded. Femur usually swollen. Tibial spurs 3:3:3.

SPECIES INCLUDED

- I. arizonensis* (Snyder), new combination = *Kaloterms arizonensis* Snyder, 1926c
- I. banksi* (Snyder), new combination = *Kaloterms banksi* Snyder, 1920b
- I. bequaerti* (Snyder), new combination = *Kaloterms bequaerti* Snyder, 1929
- I. emersoni* (Light), new combination = *Kaloterms emersoni* Light, 1933
- I. galapagoensis* (Banks), new combination = *Kaloterms galapagoensis* Banks, 1901
- I. immigrans* (Snyder), new combination = *Kaloterms immigrans* Snyder, 1922
- I. incisus* (Silvestri), new combination = *Kaloterms incisus* Silvestri, 1901
- I. marginipennis* (Latreille), new combination = *Termes marginipenne* Latreille, 1811-1832
- ? *I. marianus* (Holmgren), new combination = *Caloterms marianus* Holmgren, 1912
- I. marjoriae* (Snyder), new combination = *Kaloterms marjoriae* Snyder, 1924
- I. mcgregori* (Light), new combination = *Kaloterms mcgregori* Light, 1921
- I. milleri* (Emerson), new combination = *Kaloterms milleri* Emerson, 1943
- I. minor* (Hagen), new combination = *Caloterms minor* Hagen, 1858a
- I. nigrinus* (Snyder), new combination = *Kaloterms nigrinus* Snyder, 1946
- I. pacificus* (Banks), new combination = *Kaloterms pacificus* Banks, 1901
- I. platycephalus* (Light), new combination = *Kaloterms platycephalus* Light, 1933
- I. repandus* (Hill), new combination = *Caloterms repandus* Hill, 1926d
- I. schwarzi* (Banks), new combination = *Kaloterms schwarzi* Banks, 1920
- I. seeversi* (Snyder and Emerson), new combination = *Kaloterms seeversi* Snyder and Emerson, 1949
- I. semilunaris* (N. and K. Holmgren), new com-

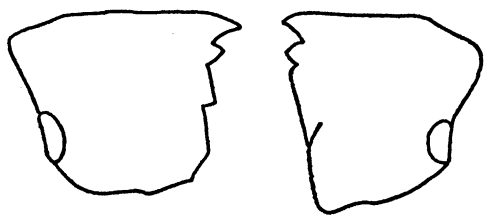


FIG. 50. Mandibles of nymph of *Allotermes paradoxus* Wasmann. Homotype colony from 6 kilometers southeast of Tulear, Madagascar.

ination = *Neotermes semilunaris* N. and K. Holmgren, 1915

I. snyderi (Light), new combination = *Kalotermes snyderi* Light, 1933

I. tabogae (Snyder), new combination = *Kalotermes tabogae* Snyder, 1924

I. taylori (Light), new combination = *Kalotermes taylori* Light, 1930

I., new species, from Gibson Island

I., new species, from Nissan Island

GEOGRAPHICAL DISTRIBUTION: Papuan:

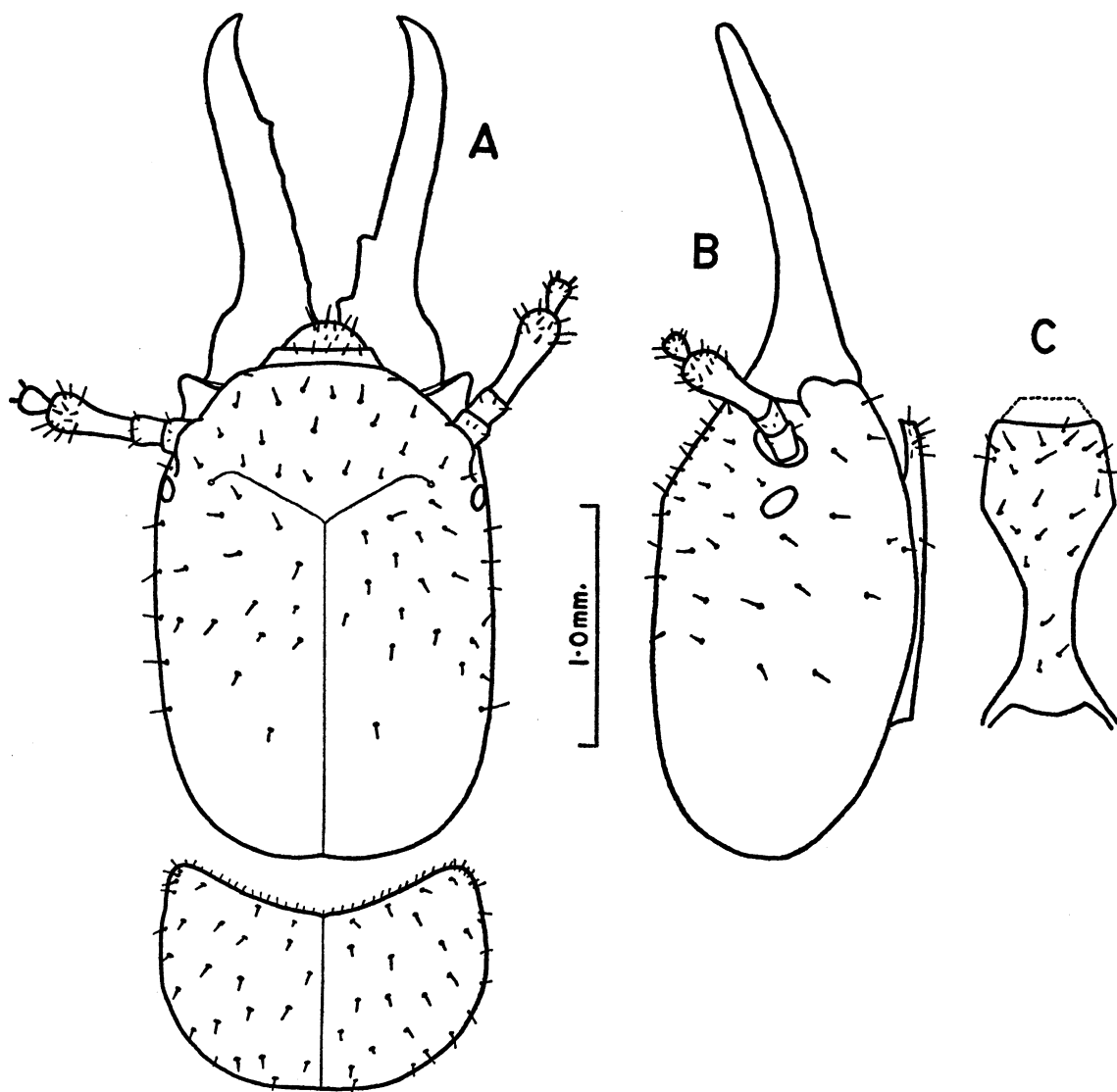


FIG. 51. Soldier of *Allotermes paradoxus* Wasmann. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Homotype from 6 kilometers southeast of Tulear, Madagascar.

Fiji, Guam, Hawaii, Loyalty Islands, Samoa, Nissan Island. Indo-Malayan: Philippine Islands. Nearctic: North America. Neotropical: Central and South America, Galapagos Islands, the West Indies, western Mexico.

GENUS *ALLOTERMES* WASMANN, 1910

= Genus *Allotermes* WASMANN, 1910, p. 121.

< Genus *Procryptotermes* HOLMGREN, 1911a, p. 55.

< Genus *Procryptotermes* SJÖSTEDT, 1926, p. 31, 32.

< Genus *Procryptotermes* CACHAN, 1949, pp. 185, 187, 211.

< Genus *Procryptotermes* SNYDER, 1949, pp. 36, 37.

TYPE SPECIES: *Allotermes paradoxus* Wasmann.

The genus *Allotermes* was named by Wasmann (1910) for *Allotermes paradoxus*, based on the soldier caste alone. Holmgren (1911a) treated *Allotermes* as a synonym of *Procryptotermes*, because the third joint of the soldier antenna was highly enlarged and club-shaped, as in the genus *Procryptotermes*. Sjöstedt (1926) and Snyder (1949) followed Holmgren. In this paper I am resurrecting this genus, as I am of the opinion that it is distinct from *Procryptotermes*. The forewing pad of the nymph of *Allotermes* has a weak median vein which runs midway between the radial sector and the cubitus to the tip of the wing; the arolium is absent. The soldier also differs from *Procryptotermes* in lacking the ridge between the vertex and the frons. I am also including two new species in this genus; they will be described at a later date.

IMAGO: Diameter of eye, 0.35–0.36 mm. Ocellus in contact with eye. Antennal joints unknown. Mandibles as in the genus *Cryptotermes*, i.e., left mandible with first plus second marginal tooth much smaller at base than third marginal tooth; posterior margin of first plus second marginal tooth half of length of anterior margin of third marginal tooth (fig. 50). Right mandible with posterior margin of second marginal longer than molar plate (fig. 50). Pronotum slightly narrower than or as broad as head. Forewing pad of nymph with media weak, running midway between radial sector and cubitus to tip of wing. Tibial spurs 3:3:3. Arolium absent.

SOLDIER (FIG. 51): Head long, narrow; sides parallel, sloping in front at angle of approximately 45 degrees; ridge absent between frons and vertex; faint horn-like projection formed by prolongation of ventral genae, below and in front of antennal socket. Eyes distinct, in some species pigmented. Antenna with 10 to 12 articles, third article darker and heavily sclerotized, long, and club-shaped. Mandibles long, with a prominent basal hump; teeth rudimentary. Pronotum as broad as head; anterior margin broadly and deeply concave; sides evenly rounded. Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago resembles that of *Incisitermes* in wing venation, but differs from it in having the arolium always absent and the first plus second marginal tooth in the left mandible much smaller than the third. The soldier can also be distinguished from that of *Incisitermes* in having a faint horn-like projection below and in front of the antennal socket, the head not dorsoventrally flattened, the mandible long and slender, and the femur not swollen.

SPECIES INCLUDED

A. paradoxus Wasmann, 1910

A., new species, from 8 kilometers south of Mahabo, Madagascar

A., new species, from 39 kilometers east of Tsihombe, Madagascar

GEOGRAPHICAL DISTRIBUTION: Malagasy: Madagascar.

MARGINITERMES, NEW GENUS

< Genus *Kalotermes* BANKS AND SNYDER, 1920, pp. 16, 17.

< Genus *Kalotermes*, *sensu stricto*, LIGHT, 1933, pp. 82–84.

< Subgenus *Kalotermes* SNYDER, 1948, pp. 228, 232, 234.

< Genus *Procryptotermes* SNYDER, 1949, p. 36.

TYPE SPECIES: *Marginitermes hubbardi* (Banks) (= *Kalotermes hubbardi* Banks).

This new monotypic genus is proposed for the species described by Snyder (1920) under the name "*Kalotermes hubbardi*." This species was later included by Snyder (1949) in the genus *Procryptotermes*. The present study has shown that it is distinct from the genus *Procryptotermes* and is closely related to

Incisitermes. The imago of *Marginitermes* has a weak median vein in the forewing which runs midway between the radial sector and the cubitus to the tip of the wing. The imago of *Procryptotermes* has a forewing with the median vein joining the radial sector. The arolium is absent in the imago of *Marginitermes*; it is present in *Procryptotermes*. In the left imago mandible of *Marginitermes* the first plus second marginal tooth is slightly smaller at the base than the third marginal tooth; in *Procryptotermes* the first marginal tooth is much smaller at the base than the second marginal tooth. The soldier of *Marginitermes*

resembles that of *Procryptotermes*, but differs from it in not having a horn-like projection below and in front of the antennal socket; the anterior margin of the pronotum is deeply concave, and the anterolateral corners are serrated.

IMAGO (FIG. 52): Light yellowish. Diameter of eye, 0.46–0.48 mm. Ocellus approximately 0.01 mm. from eye. Antenna with 16 articles. Left mandible with posterior margin of first plus second marginal tooth slightly shorter than anterior margin of third marginal tooth (fig. 53). Right mandible with posterior margin of second marginal tooth slightly longer

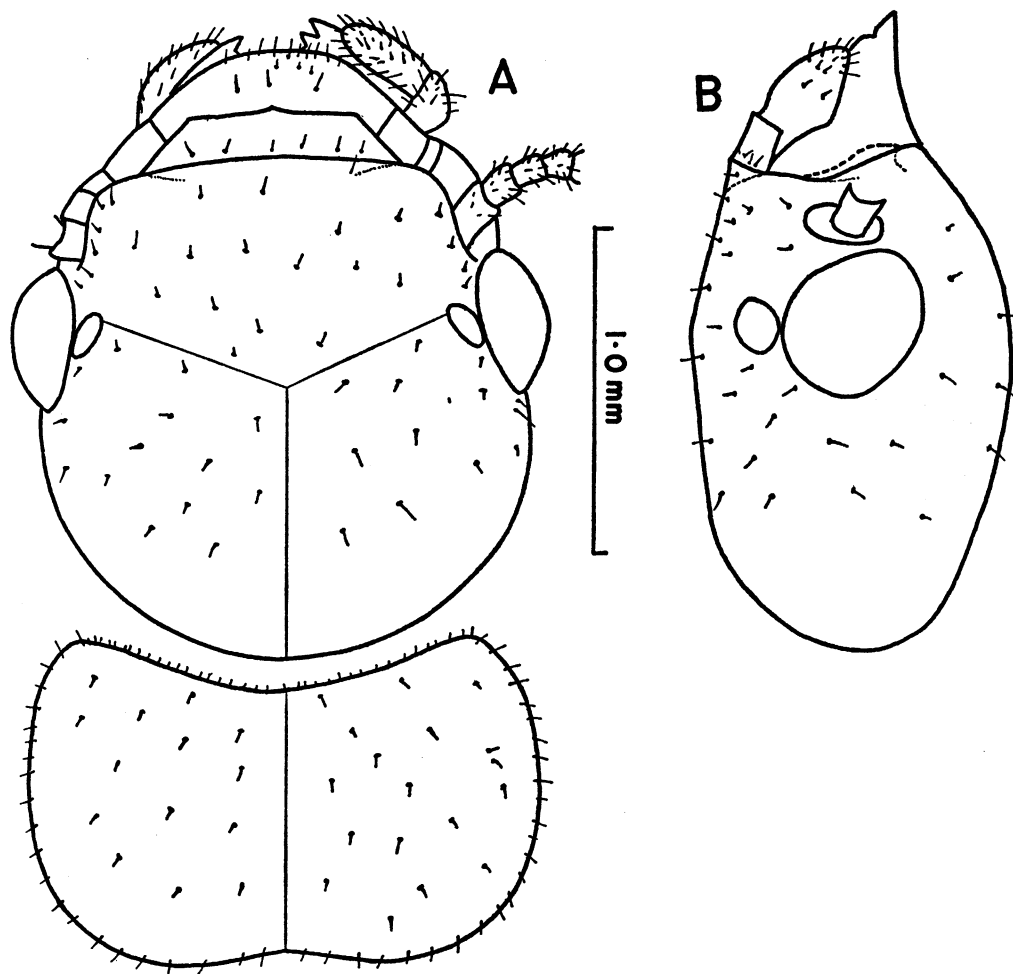


FIG. 52. Imago of *Marginitermes hubbardi* (Banks). A. Head and pronotum from above. B. Head from side. Homotype from Sabino Canyon, Santa Catalina Mountains, Arizona.

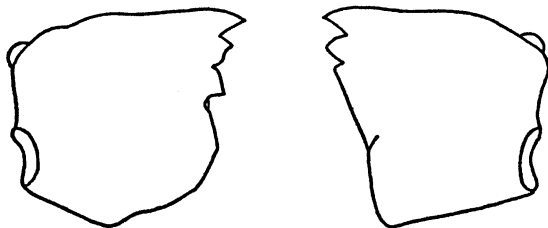


FIG. 53. Mandibles of imago of *Marginitermes hubbardi* (Banks). Homotype from Sabino Canyon, Santa Catalina Mountains, Arizona.

than molar plate (fig. 53). Pronotum slightly narrower than head. Wings hyaline. Forewing with all major veins arising independently at wing suture; radial sector with eight to nine branches, first branch arising at approximately one-third of length of wing from suture; media weak and unsclerotized, running midway between radial sector and cubitus, to tip of wing; cubitus weak and unsclerotized (fig. 54). Tibial spurs 3:3:3. Arolium always absent.

SOLDIER (FIG. 55): Head long, sloping in front at angle of approximately 40 degrees; raised ridge between frons and vertex which is thicker and more raised just above antennal

base. Eyes distinct, slightly pigmented. Antenna with 10 to 11 articles; first and second segments dark brownish and heavily sclerotized; third segment greatly elongated, clavate, dark-colored, and as long as next five to seven segments together. Mandibles long, slender, toothed, with a prominent basal hump. Pronotum as broad as head; anterior margin deeply concave, with anterolateral corners irregularly serrated; sides evenly rounded, with no median incision. Femur slightly swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago so closely resembles that of the genus *Incisitermes* that it is difficult to separate them. The soldier differs

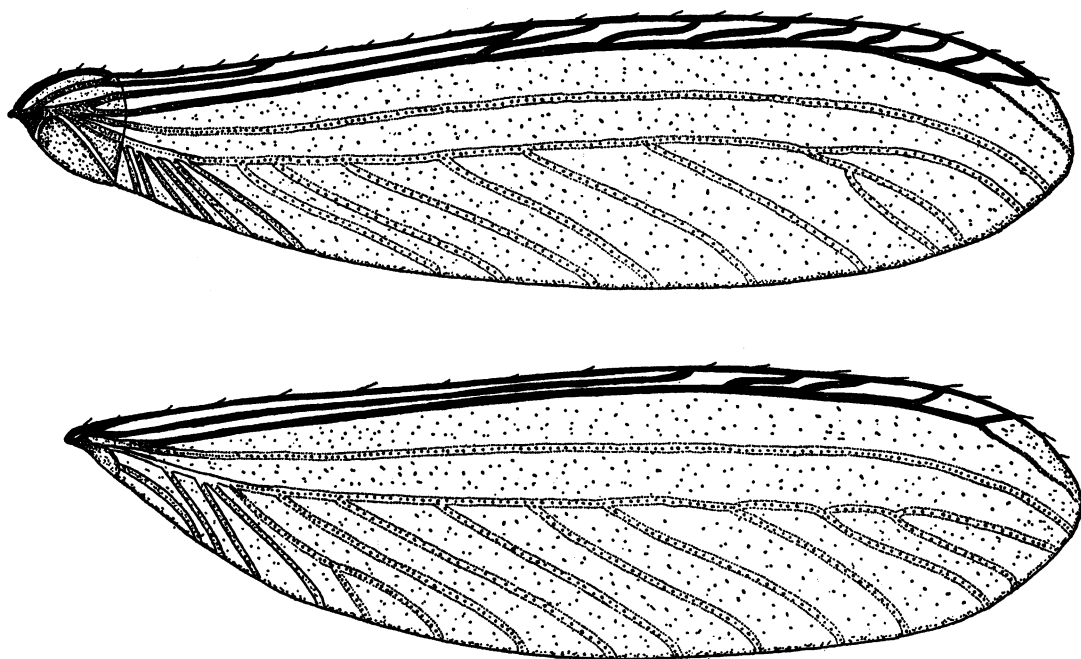


FIG. 54. Forewing and hind wing of *Marginitermes hubbardi* (Banks). Homotype from Sabino Canyon, Santa Catalina Mountains, Arizona.

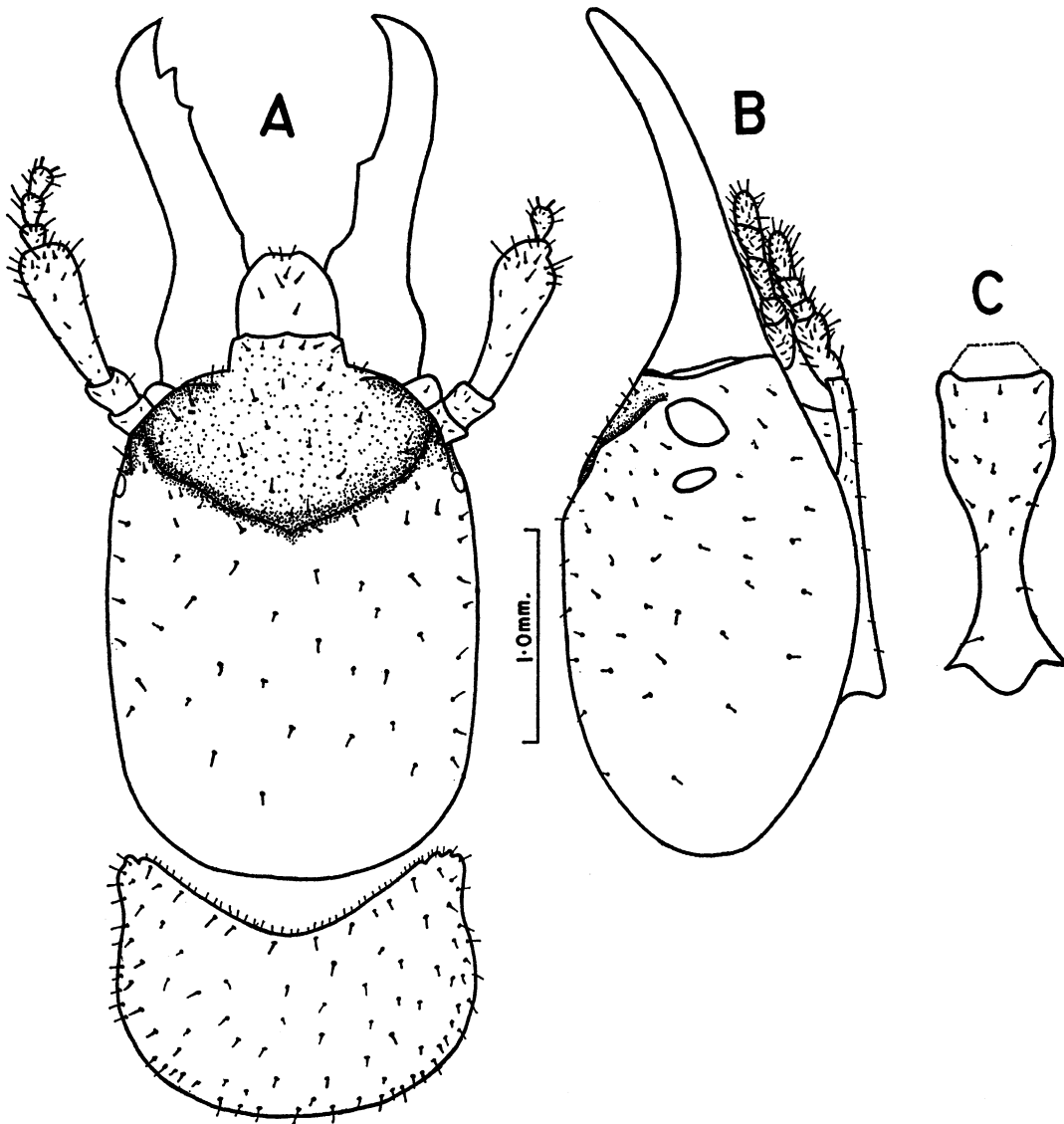


FIG. 55. Soldier of *Marginitermes hubbardi* (Banks). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Homotype from Sabino Canyon, Santa Catalina Mountains, Arizona.

from that of *Incisitermes* in having a ridge between the frons and the vertex and the third antennal segment greatly enlarged. Also, the anterolateral corners of the pronotum are serrated.

SPECIES INCLUDED

M. hubbardi (Banks), new combination = *Kalotermites hubbardi* Banks, 1920

GEOGRAPHICAL DISTRIBUTION: Nearctic: Western United States and western Mexico.

TAURITERMES, NEW GENUS

<Genus *Calotermites* SILVESTRI, 1901, p. 3.

<Genus *Calotermites* SILVESTRI, 1903, p. 20.

<Subgenus *Procryptotermites* HOLMGREN, 1911a, p. 55.

<Subgenus *Glyptotermes* EMERSON, 1925, p. 331.

<Genus *Procryptotermes* SNYDER, 1949, pp. 36, 38.

TYPE SPECIES: *Tauritermes taurocephalus* (Silvestri) (= *Calotermes taurocephalus* Silvestri).

This new genus is proposed for two species described by Silvestri (1901) under the names "*Calotermes taurocephalus*" and "*Calotermes triceromegas*." These were later included by Holmgren (1911a) and Snyder (1949) in the subgenus *Procryptotermes*. The present study has shown that they do not belong to the genus *Procryptotermes*. The imago of *Procryptotermes* has a forewing with a weak median vein running midway between the radial sector and the cubitus in the proximal end of

the wing, bending up near the middle or beyond the middle to unite with the radial sector. The soldier of *Tauritermes* resembles that of *Procryptotermes* because of convergent evolution of the phragmotic head. The soldier of *Procryptotermes* differs in having the head with two pairs of horn-like projections: one situated near each side of the postclypeus, in front and above the antennal socket, the other formed by a prolongation of the ventral genae in front of and below the antennal socket. Also, the anterior margin of the soldier pronotum is not serrated.

IMAGO: Unknown.

SOLDIER (FIG. 56): Head phragmotic; anterior region dark and sculptured; profile of front steep; frons with two well-developed prominences, widely concave between promi-

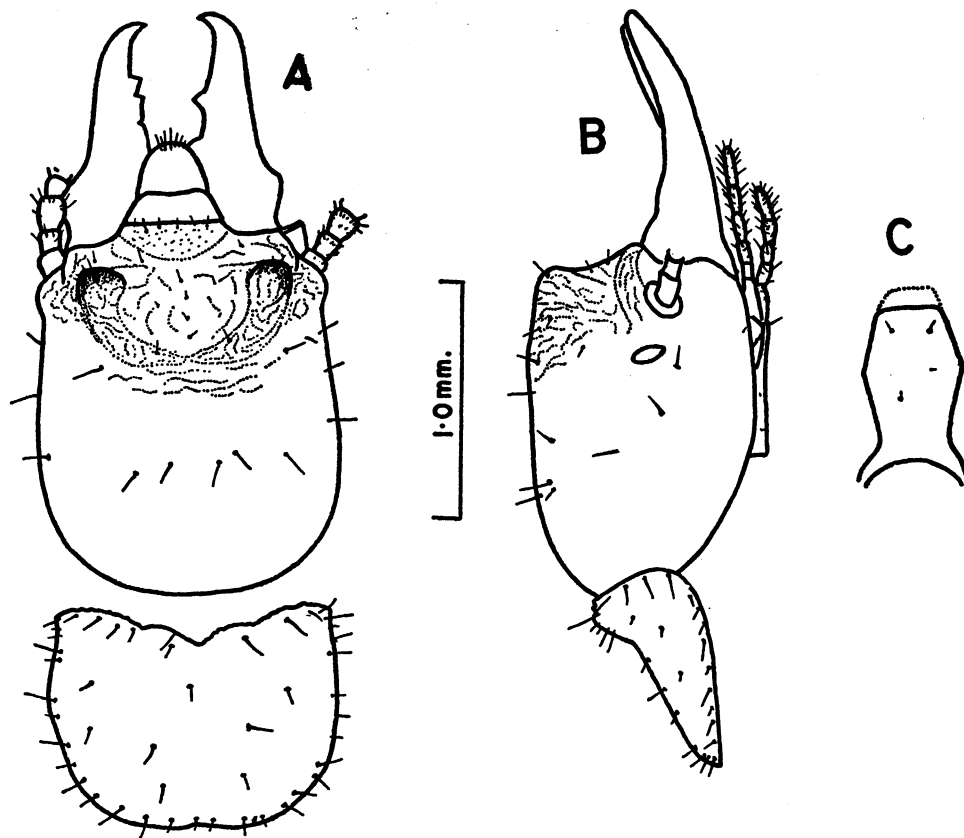


FIG. 56. Soldier of *Tauritermes taurocephalus* (Silvestri). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Cotype from Corumba, Mato Grasso, Brazil.

nences; horn-like projections absent in front of and above or below antennal socket; antennal carinae slightly prominent and rounded; a very faint ridge between frons and vertex, not so sharp as in the genus *Procryptotermes*. Eyes distinct and unpigmented. Antenna with 10 to 11 articles; third article wider and longer than second. Mandibles slender, with marked basal hump. Pronotum as broad as head; anterior margin raised and covering posterior region of head, deeply emarginate, sinuate, and serrated. Femur not swollen. Tibial spurs 3:3:3.

NYMPH: Mandibles as in the genus *Cryptotermes*. Left mandible with first plus second marginal tooth at the base smaller than third marginal tooth (fig. 57). Right mandible with posterior margin of second marginal tooth distinctly longer than molar plate (fig. 57). Forewing pad with media weak and unsclerotized, running midway between radial sector and cubitus, to tip of wing.

COMPARISONS: The imago of this genus is unknown, but the wing-pad venation and mandible of the nymph show that it is related to *Incisitermes*, *Marginitermes*, and *Alloptermes*. The soldier differs from that of either of these genera in having the frons of the head with two distinct prominences, the region between them concave, and the anterior margin of the pronotum serrated.

SPECIES INCLUDED

T. taurocephalus (Silvestri), new combination = *Calotermes taurocephalus* Silvestri, 1901

T. triceromegas (Silvestri), new combination = *Calotermes triceromegas* Silvestri, 1901

GEOGRAPHICAL DISTRIBUTION: Neotropical: South America.

GENUS PRONEOTERMES HOLMGREN, 1911

<Genus *Calotermes* SILVESTRI, 1903, pp. 20, 26.

> <Subgenus *Proneotermes* HOLMGREN, 1911a, pp. 53, 54, 57, 58, 61.

<Subgenus *Neotermes* HOLMGREN, 1911a, p. 54.

<Genus *Proneotermes* SJÖSTEDT, 1926, pp. 22, 23, 32.

<Subgenus *Proneotermes* EMERSON, 1928, p. 405 (no description).

<Subgenus *Kalotermes*, *sensu stricto*, HARE, 1937, pp. 461, 474.

<Genus *Proneotermes* CACHAN, 1949, pp. 180, 185, 190, 193.

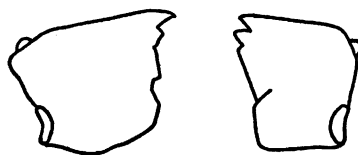


FIG. 57. Mandibles of nymph of *Tauritermes taurocephalus* (Silvestri). Cotype from Corumba, Mato Grosso, Brazil.

<Genus *Proneotermes* GRASSÉ, 1949, p. 530.

<Genus *Procryptotermes* SNYDER, 1949, p. 37.

<Genus *Glyptotermes* SNYDER, 1949, p. 49.

<Genus *Proneotermes* CACHAN, 1951, p. 1.

TYPE SPECIES: *Proneotermes perezii* Holmgren.

Holmgren (1911a) created the subgenus *Proneotermes*, with *Calotermes* (P.) *perezii* as the generitype, and including *Calotermes* (P.) *madagascariensis*. He described the species *Calotermes* (P.) *perezii* incompletely, giving only descriptions of wings and a poor photograph of the soldier. Sjöstedt (1926) treated the name *Calotermes* (P.) *perezii* as a *nomen nudum*, considering the description to be inadequate, and therefore selected *Calotermes* (P.) *madagascariensis* as the generitype. The name *Calotermes* (P.) *perezii* is valid according to the Rules of Nomenclature (Article 25). Snyder (1949) placed *P. perezii* in the genus *Procryptotermes* and *C. madagascariensis* in the genus *Kalotermes*. The present study has shown that *Proneotermes* is a valid genus, distinct from *Procryptotermes*. I am therefore resurrecting the genus *Proneotermes*, with *P. perezii* as the generitype, and am including *Calotermes latifrons*, which was previously included by Snyder (1949) in the genus *Glyptotermes*. The species *C. madagascariensis* is included in a new genus, *Bifiditermes*.

IMAGO (FIG. 58): Yellowish. Eyes fairly small; diameter, 0.39–0.43 mm. Ocellus touching eye. Antenna with 17 to 18 articles. Left mandible with first plus second marginal tooth slightly shorter at base than third marginal tooth (fig. 59). Right mandible with posterior margin of second marginal tooth slightly longer than molar plate (fig. 59). Pronotum slightly broader than head. Wing membrane hyaline. Forewing with all major veins arising independently at wing suture;

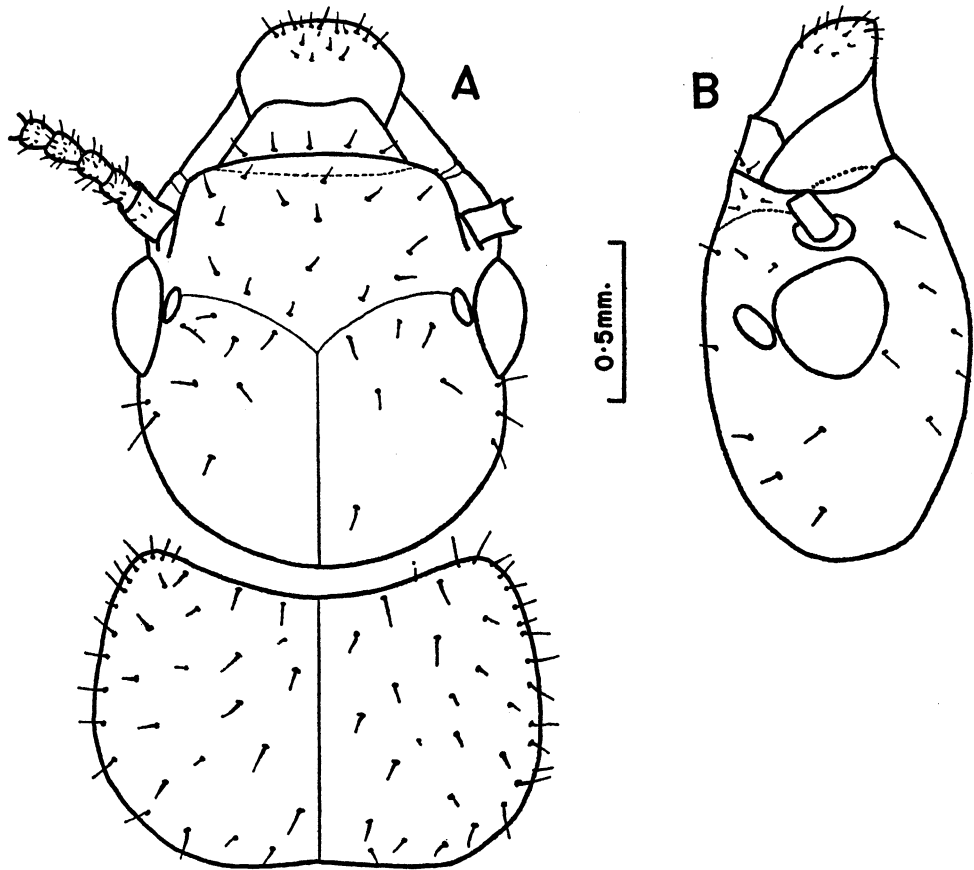


FIG. 58. Imago of *Proneotermes perezii* Holmgren. A. Head and pronotum from above. B. Head from side. Homotype from near La Gloria, 7 miles south of San José, Costa Rica.

radius (R_1) simple, extending about half of length of wing from suture; radial sector with about four to six branches, first branch arising at about half of length of wing from suture; media more weakly sclerotized than radial sector, running parallel and closer to radial sector than to cubitus; a few cross veins between radial sector and media. Cubitus weak and unsclerotized (fig. 60). Tibial spurs 3:3:3. Arolium present.

SOLDIER (FIG. 61): Color nearly black in front of head, grading to yellowish in back. Head with parallel sides; front somewhat truncate, sloping at angle of approximately 45 degrees to clypeus; dorsolateral corners of frons slightly raised; a very faint ridge between vertex and frons; sides above antennal socket roughened; horn-like projections

above and below antennal socket absent. Eye spots distinct, unpigmented. Antenna with 13 to 14 articles; third article longer than either fourth or second, club-shaped. Mandibles strong, with a distinct basal hump. Pronotum as broad as head; anterior margin slightly raised, deeply emarginate; sides and hind

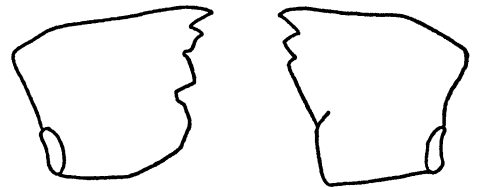


FIG. 59. Mandibles of imago of *Proneotermes perezii* Holmgren. Homotype from near La Gloria, 7 miles south of San José, Costa Rica.

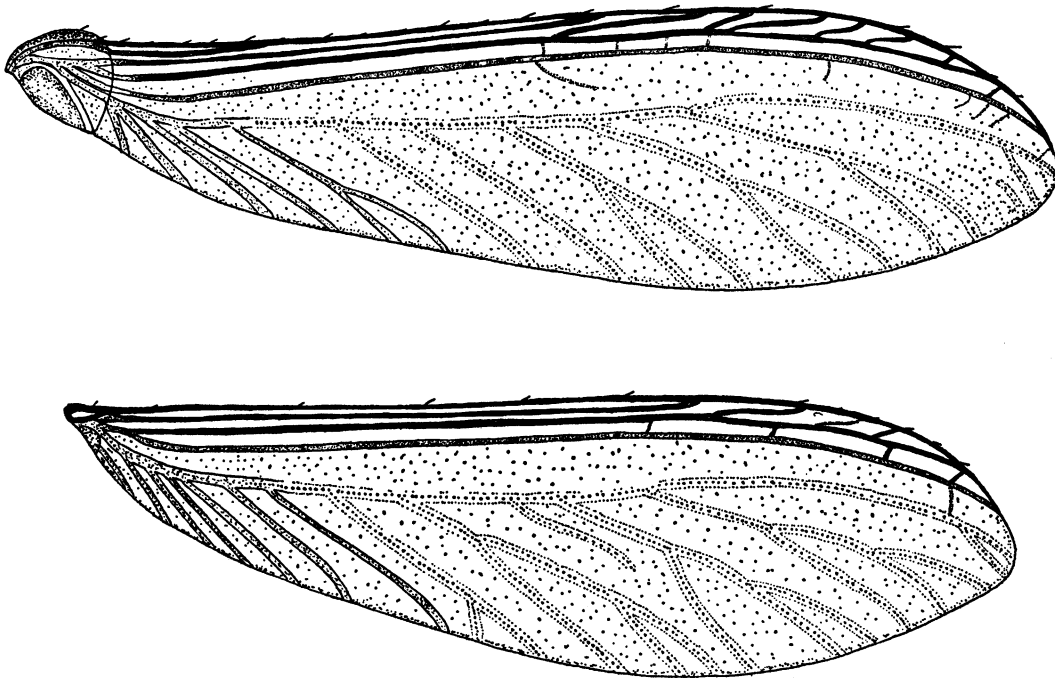


FIG. 60. Forewing and hind wing of *Proneotermes perezii* Holmgren. Homotype from near La Gloria, 7 miles south of San José, Costa Rica.

margin fairly rounded. Tibial spurs 3:3:3. Femur thick and short.

COMPARISONS: The imago differs from that of *Incisitermes* and that of *Marginitermes* in having the forewing with the median vein weakly sclerotized and running closer to the radial sector than to the cubitus. This wing venation resembles that of *Paraneotermes* and that of *Comatermes* because of convergent evolution. The imago of *Procryptotermes* has the forewing with a weak and unsclerotized median vein which runs midway between the radial sector and the cubitus in the proximal half of the wing and then bends up near the middle or beyond the middle of the wing to meet the radial sector. In the soldier of *Marginitermes*, the third antennal segment is much longer than that of *Proneotermes*, the ridge between the frons and the vertex is more prominent, the mandibles are long, and the anterolateral corners of the pronotum are serrated. In *Incisitermes* the soldier head is dorsoventrally flat and not so phragmotic as in *Proneotermes*; the frons slopes slightly in

front, at an angle of approximately 20 degrees; the faint ridge between the frons and the vertex is absent.

SPECIES INCLUDED

- P. perezii* Holmgren, 1911a
P. latifrons (Silvestri), new combination = *C. latifrons* Silvestri, 1901

GEOGRAPHICAL DISTRIBUTION: Neotropical: Central and South America.

BIFIDITERMES, NEW GENUS

- <Subgenus *Calotermes* WASMANN, 1897, p. 150.
 <Genus *Calotermes* HAVILAND, 1898, pp. 371, 373.
 <Genus *Calotermes* SJÖSTEDT, 1900b, pp. 19–21, 35.
 <Genus *Calotermes* DESNEUX, 1904d, pp. 20–24.
 <Subgenus *Proneotermes* HOLMGREN, 1911a, pp. 53, 54.
 <Subgenus *Calotermes* HOLMGREN, 1913a, p. 37.
 <Genus *Calotermes* FULLER, 1921, pp. 16, 19, 22, 23, 28.

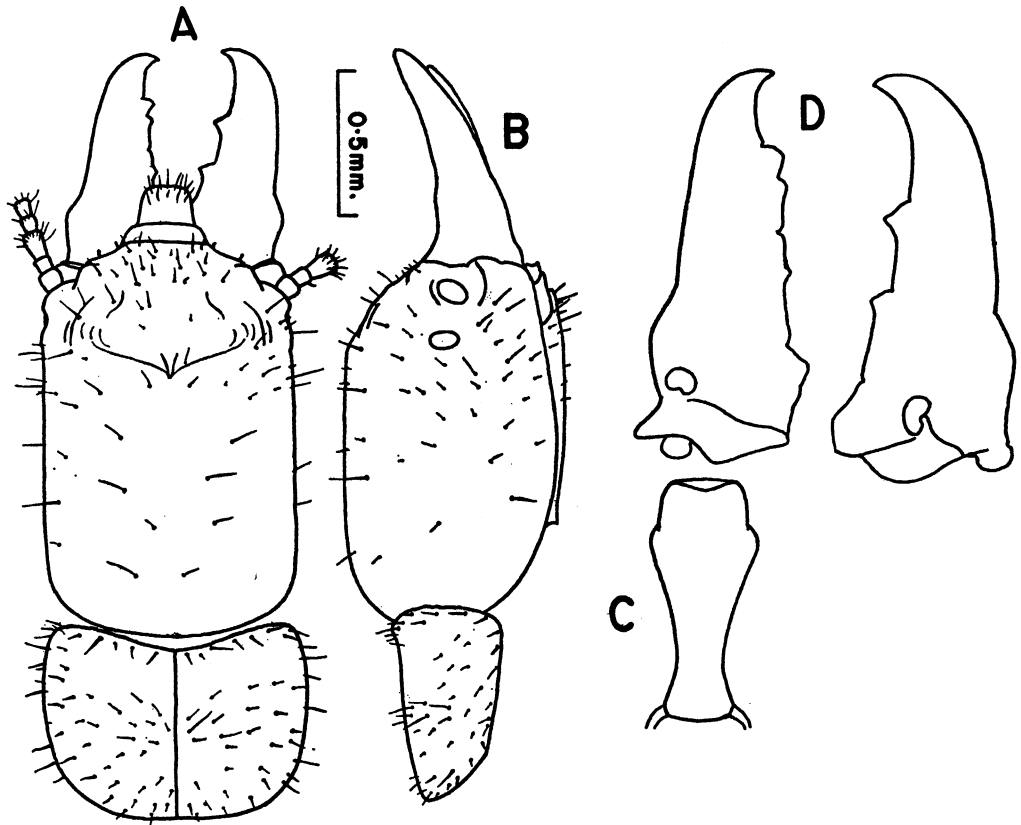


FIG. 61. Soldier of *Proneotermes perezii* Holmgren. A. Head and pronotum from above. B. Head and pronotum from side. C. Postmentum from below. D. Mandibles. Homotype from near La Gloria, 7 miles south of San José, Costa Rica. Drawn by A. E. Emerson.

<Genus *Calotermes* SJÖSTEDT, 1926, pp. 22, 23, 27.

<Genus *Proneotermes* SJÖSTEDT, 1926, pp. 22, 23, 32.

<Genus *Calotermes*, *sensu stricto*, KEMNER, 1934, pp. 29, 30.

<Subgenus *Calotermes* HILL, 1942, p. 38.

<Genus *Proneotermes* CACHAN, 1949, pp. 180, 185, 186, 190, 195.

<Genus *Kalotermes* SNYDER, 1949, p. 11.

<Genus *Procryptotermes* SNYDER, 1949, p. 36.

<Genus *Kalotermes* COATON, 1949, pp. 14, 15, 16.

<Genus *Procryptotermes* COATON, 1950, p. 28.

<Genus *Kalotermes* AHMAD, 1958, p. 36.

TYPE SPECIES: *Bifiditermes madagascariensis* (Wasmann) (= *Calotermes madagascariensis* Wasmann).

The species that now constitute this new

genus were previously placed by Snyder (1949), Emerson (1955), and others in the genera *Kalotermes* and *Procryptotermes*. This genus is distinct from the genera *Kalotermes* and *Procryptotermes* and is closely related to the genera *Epicalotermes* and *Bicornitermes*, as indicated by the wing venation and the imago mandible. The left imago mandible of *Kalotermes* has the anterior margin of the third marginal tooth equal to the posterior margin of the first plus second marginal tooth; in *Bifiditermes* the anterior margin is longer than the posterior margin of the first plus second marginal tooth. The imago of *Kalotermes* is smaller than that of *Bifiditermes* and darkly pigmented; the wing membrane has pimple-like nodules, which are lacking in most species of *Bifiditermes*. The arolium is

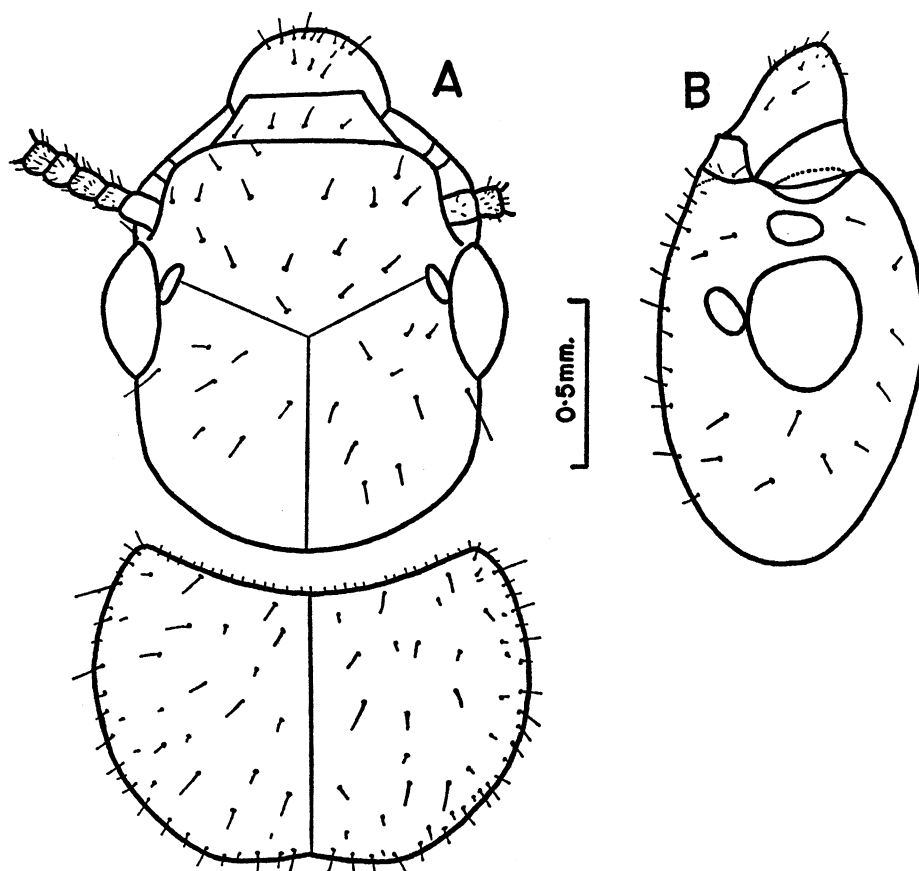


FIG. 62. Imago of *Bifiditermes madagascariensis* (Wasmann). A. Head and pronotum from above. B. Head from side. Homotype from Marohogo, 20 kilometers east of Majunga, Madagascar.

present in *Kaloterмес*, absent in *Bifiditermes*. In *Kaloterмес* the forewing has all the major veins arising independently at the wing suture; in *Bifiditermes* the media and cubitus arise from a common stem beyond the wing suture. The soldier of *Kaloterмес* is much smaller, and the mandibles are not so long and robust, as in the genus *Bifiditermes*. The genus *Procryptotermes* differs in wing venation and several soldier characters.

IMAGO (FIG. 62): Light brown to dark brown. Diameter of eye, 0.37–0.64 mm. Ocellus usually touching eye, but in a few species 0.01–0.03 mm. from eye. Antenna with 15 to 20 articles. Left mandible with anterior margin of third marginal tooth clearly longer (but not more than 1.5 times

longer) than posterior margin of first plus second marginal tooth (fig. 63). Right mandible with molar plate clearly smaller than posterior margin of second marginal tooth

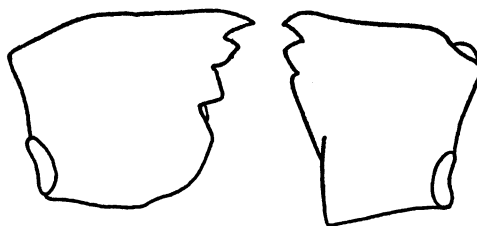


FIG. 63. Mandibles of imago of *Bifiditermes madagascariensis* (Wasmann). Type from Nossi-bé, Madagascar.

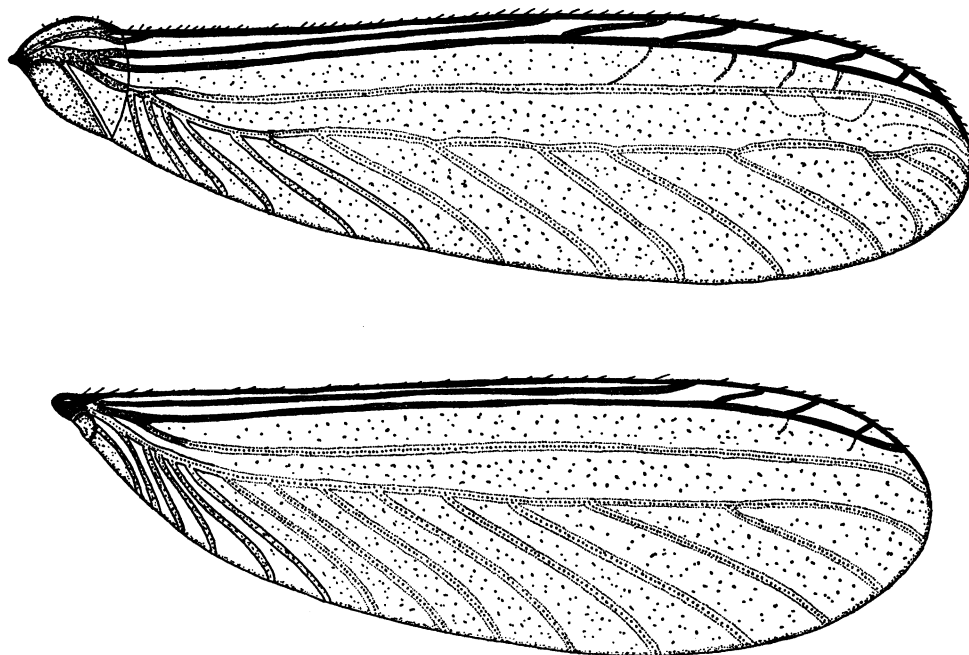


FIG. 64. Forewing and hind wing of *Bifiditermes madagascariensis* (Wasmann).
Type from Nossi-bé, Madagascar.

(fig. 63). Pronotum as broad as or slightly broader than head. Wings hyaline, slightly iridescent, usually covered with deposits of unpigmented papillae, in some species covered with pigmented papillae, as in *B. sibayensis*. Forewing with costal border, subcosta, radius, and radial sector strongly and heavily sclerotized, arising independently at wing suture; radial sector with five to seven branches; media and cubitus weak and unsclerotized, forking from a common stem beyond wing suture; media running midway between radial sector and cubitus; cross branches between radial sector and media (fig. 64). Tibial spurs 3:3:3. Arolium absent.

SOLDIER (FIG. 65): Head long and thick; sides straight and parallel; frontal area rough, depressed medially, moderately steep, sloping downward towards anteclypeus at angle of approximately 45 degrees; in some species lateral-dorsal corners of frons above antennal base slightly prominent and elevated. Eyes large, either pigmented or unpigmented. Antenna with 10 to 18 articles; third article longest and clavate. Mandibles long, outer

sides almost straight, curved near apex; basal hump present; dentition variable. Pronotum arched transversely; anterior margin deeply or broadly concave; sides evenly rounded. Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: This genus is related to the genera *Epicalotermes* and *Bicornitermes*. *Bifiditermes* differs in having the anterior margin of the third marginal tooth shorter than that of the genus *Epicalotermes*; otherwise the imago is similar in wing venation and other respects. The imago of the genus *Bifiditermes* is indistinguishable from that of the genus *Bicornitermes*. The soldier of *Bifiditermes* differs from that of *Epicalotermes* in having a thicker head; also, the mandibles are not so curved as in the genus *Epicalotermes*. *Bicornitermes* has a short and much more truncated head, the mandibles are short, and the anterior margin of the pronotum is distinctly serrated.

SPECIES INCLUDED

B. angulatus (Wilkinson), new combination
= *Kalotermes angulatus* Wilkinson, 1959

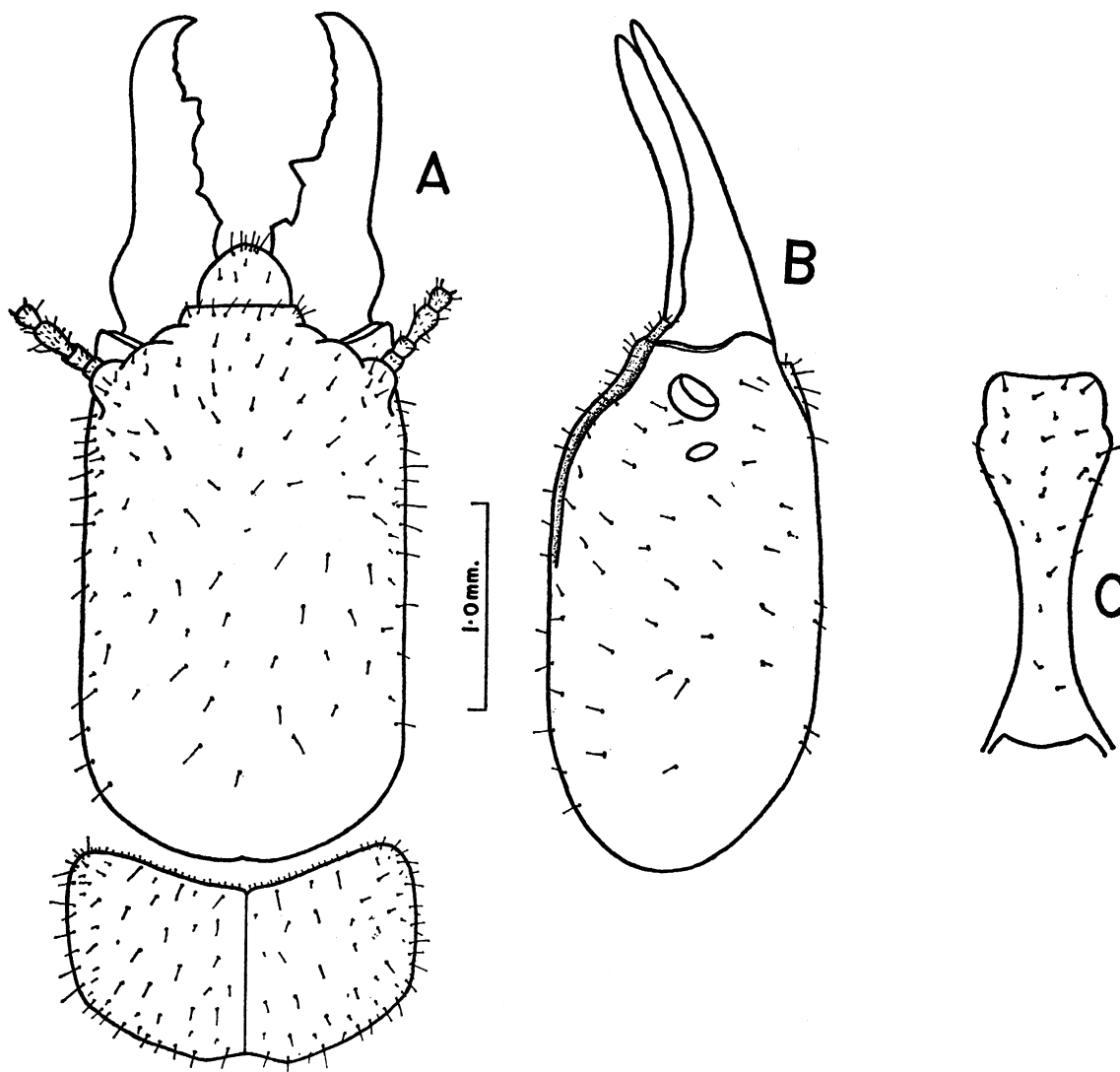


FIG. 65. Soldier of *Bifiditermes madagascariensis* (Wasmann). A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Homotype from Marohogo, 20 kilometers east of Majunga, Madagascar

B. beelsoni (Gardner), new combination = *Kaloterms beelsoni* Gardner, 1944

B. condonensis (Hill), new combination = *Caloterms* (C.) *condonensis* Hill, 1922

B. durbanensis (Haviland), new combination = *Caloterms durbanensis* Haviland, 1898

B. indicus (Holmgren), new combination = *Caloterms* (C.) *indicus* Holmgren, 1913a

? *B. improbus* (Hagen), new combination = *Caloterms improbus* Hagen, 1858a

B. jeannelanus (Sjöstedt), new combination = *Caloterms jeannelanus* Sjöstedt, 1915

B. madagascariensis (Wasmann), new combination = *Caloterms madagascariensis* Wasmann, 1897

B. mutabae (Harris), new combination = *Caloterms mutabae* Harris, 1948

B. pinto (Kemner), new combination = *Kaloterms pinto* Kemner, 1932b

B. sibayensis (Coaton), new combination = *Kaloterms sibayensis* Coaton, 1949

B. sylvaticus (Wilkinson), new combination = *Kaloterms sylvaticus* Wilkinson, 1959

B., new species, from Transvaal, South Africa

B., new species, from India

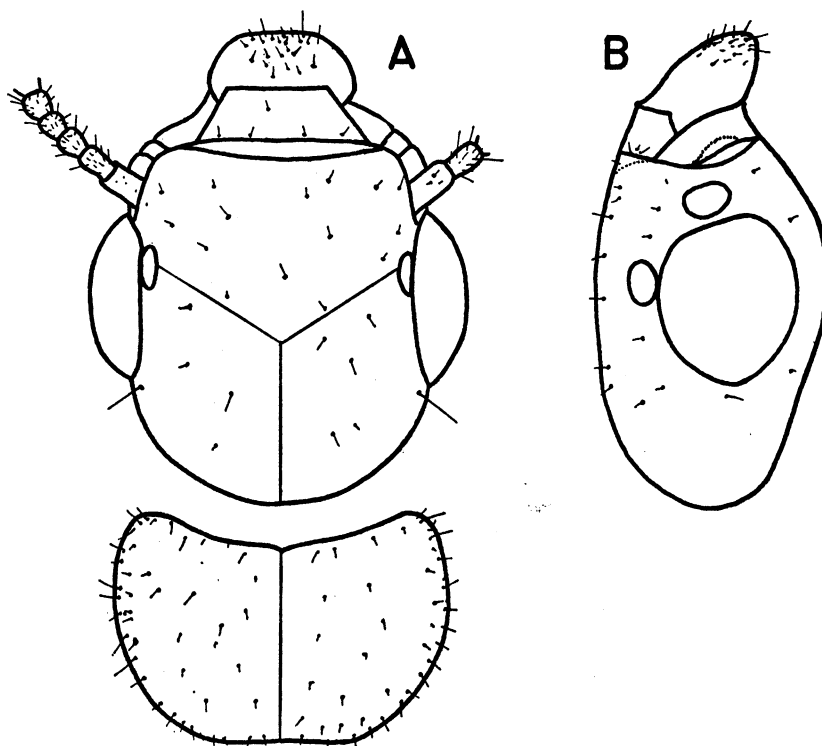


FIG. 66. Imago of *Bicornitermes bicornis*, new species. A. Head and pronotum from above. B. Head from side. Paratype from type colony.

B., new species, from 10 kilometers south of Besangoa, Madagascar

GEOGRAPHICAL DISTRIBUTION: Australian: Australia, New Zealand. Indo-Malayan: Ceylon, India, Thailand. Ethiopian: Africa. Madagascar: Madagascar.

BICORNITERMES, NEW GENUS

TYPE SPECIES: *Bicornitermes bicornis*, new species.

IMAGO (FIG. 66): Light yellowish brown. Eyes large; diameter, 0.41–0.46 mm. Ocellus touching eye. Antenna with 12 to 15 articles. Mandibles as in the genus *Bifiditermes*, i.e., left mandible with anterior margin of third marginal tooth clearly longer (but not more than 1.5 times longer) than posterior margin of first plus second marginal tooth (fig. 67). Right mandible with molar plate distinctly shorter than posterior margin of second marginal tooth (fig. 67). Pronotum narrower

than head. Wing membrane hyaline, with unpigmented, indistinct papillae. Wing venation as in the genera *Epicalotermes* and *Bifiditermes*. Forewing with costal border, subcosta, radius, and radial sector heavily sclerotized and arising independently at wing suture; radial sector with six or seven branches; media and cubitus weak and forking from a common stem beyond wing suture; media running midway between radial sector

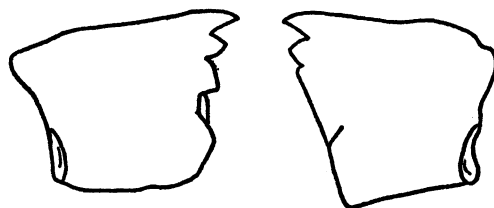


FIG. 67. Mandibles of imago of *Bicornitermes bicornis*, new species. Paratype from type colony.

and cubitus (fig. 68). Tibial spurs 3:3:3. Arolium absent.

SOLDIER (FIG. 69): Head dark, short, and truncate, sloping steeply in front; latero-frontal area raised into prominent and rounded lobes; region between lobes depressed; lateral corners of frons near postclypeus drawn forward into a horizontal projection or ridge, linked to dorsal margin of antennal socket; another prominent, horn-like projection in front of and below antennal socket. Eyes unpigmented. Antenna with 11 to 15 articles; third article subequal to second or fourth. Mandibles short, with a prominent basal hump. Pronotum narrower than, or as broad as, head; anterior margin raised, serrated, and deeply emarginate.

COMPARISONS: The imago closely resembles that of the genus *Bifiditermes*. It can be distinguished from that of *Epicalotermes* in having a shorter anterior margin in the third left marginal tooth. The soldier head is highly phragmotic and analogously resembles that of the genus *Cryptotermes* in the strong, sharp serration of the anterior margin of the pronotum.

The ridge between the vertex and frons is absent.

SPECIES INCLUDED

- B. bicornis*, new species
- B. exsertifrons* (Wilkinson), new combination
= *Kalotermes exsertifrons* Wilkinson, 1958
- B. spinicollis* (Wilkinson), new combination
= *Kalotermes spinicollis* Wilkinson, 1958
- B.*, new species, from Leopoldville, the Congo

GEOGRAPHICAL DISTRIBUTION: Ethiopian: Africa.

Bicornitermes bicornis, new species

IMAGO (FIG. 66): Head yellowish brown, lighter behind eyes; ocellus white; eyes black; postclypeus smoky brown and darker than head; anteclypeus whitish; labrum yellow; pronotum yellowish, almost same color as labrum or slightly darker; tibia pale yellow; antenna and femur brownish yellow; wing scale yellowish brown; wing membrane clear and transparent, with a slight brownish tinge; costal region yellowish brown, five or six branches of cubitus near wing scale with a

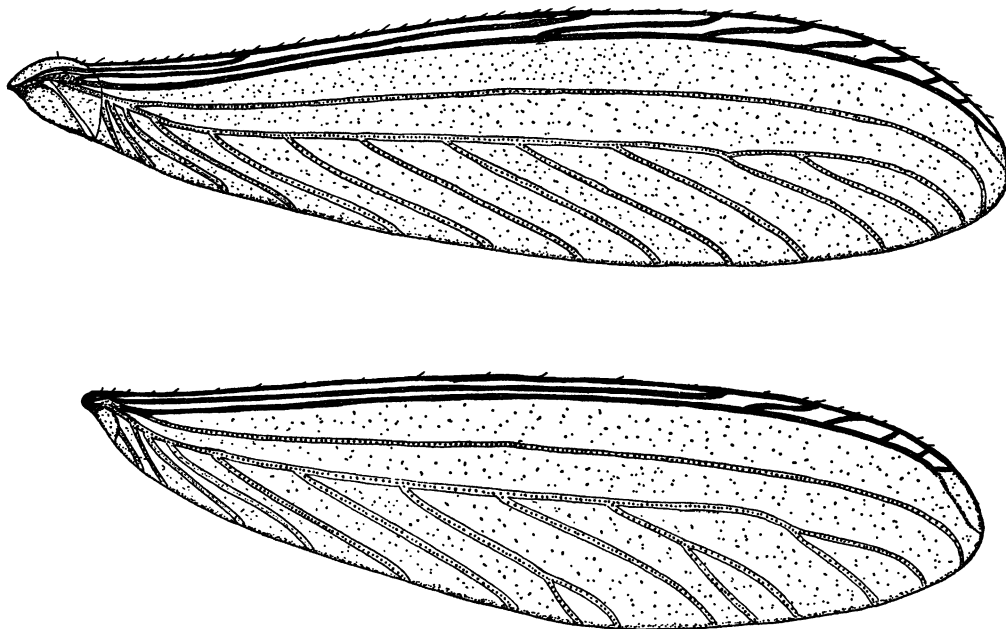


FIG. 68. Forewing and hind wing of *Bicornitermes bicornis*, new species. Paratype from type colony.

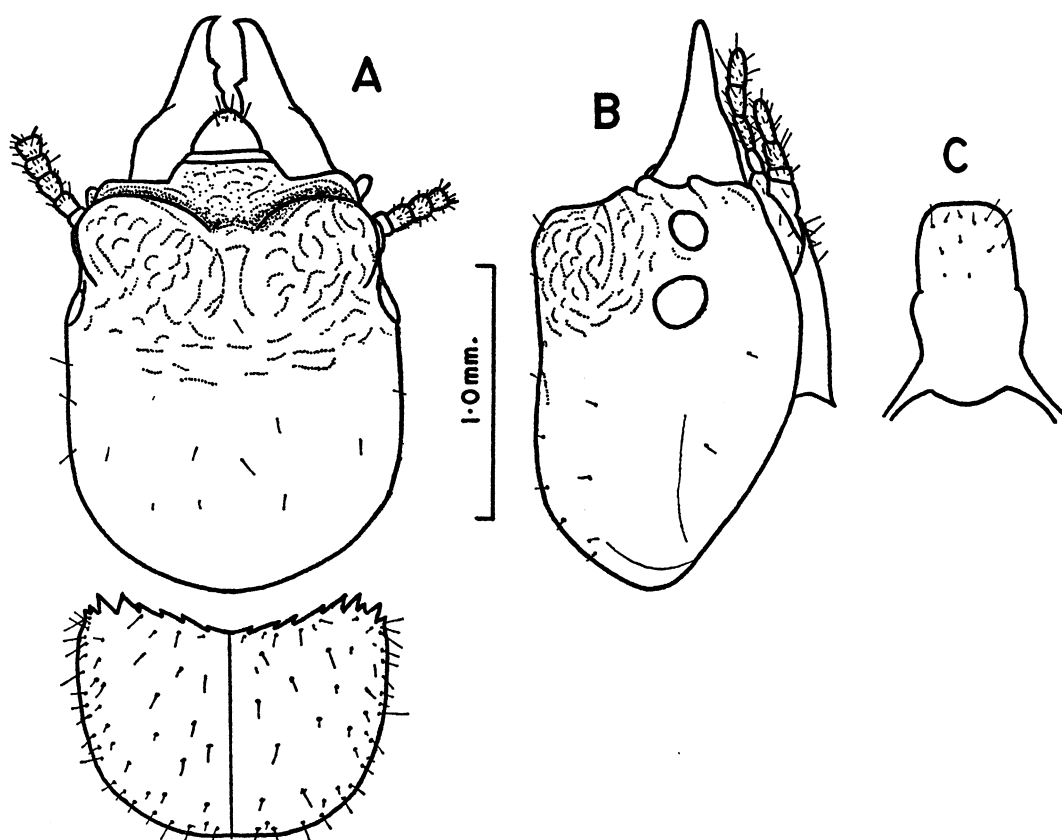


FIG. 69. Soldier of *Bicornitermes bicornis*, new species. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Paratype from type colony.

brownish tinge; sternites brownish yellow; tergites pale yellow. Head with a few scattered, short bristles; pronotum with either long or short stiff bristles on the margin and lobe; costal margin of forewing and hind wing with short hairs. Frons sloping slightly towards postclypeus. Anteclypeus with sides straight, converging anteriorly; anterior margin straight or slightly emarginate. Eyes large, moderately convex; lower margin not far removed from lower margin of head; anterior margin straight. Ocellus suboval, touching eye. Antenna with 14 to 15 articles; second article longer than third or fourth; third subequal to fourth. Pronotum transversely arched, narrower than head; anterior margin concave, with an incision in middle; sides rounded, converging posteriorly; posterolateral corners broadly rounded; pos-

terior margin slightly concave in middle. Wing membrane reticulated with indistinct papillae. Forewing with subcosta simple; radius long and unbranched; radial sector with six to seven branches; cubitus with 13 to 14 branches (fig. 68). In hind wing radial sector with five to six branches. Tibial spurs 3:3:3. Arolium absent.

SOLDIER (FIG. 69): Head brown posteriorly, grading forward to reddish brown, with anterior part almost black; mandible dark reddish brown; labrum reddish brown; pronotum yellow, anterior raised portion brown; legs and antenna light brownish yellow. Head sparsely covered with minute bristles. Pronotum moderately clothed with various-sized bristles. Head short and truncate; sides straight up to eyes, converging anteriorly up to side base of mandibles; frontal region

rough and wrinkled; laterofrontal area raised into prominent and rounded lobes, region between lobes depressed and sloping down to postclypeus; lateral corners of frons drawn forward into a horizontal projection, linked to dorsal margins of antennal socket; another prominent horn-like process in front and below antennal socket. Eyes large and unpigmented. Antenna with 12 to 13 articles; third article subequal to second or fourth. Mandibles short, broad at base, curved towards tip, with a prominent basal hump. Left mandible with three not very prominent marginal teeth, posterior margin of first marginal tooth merging with anterior margin of second marginal tooth, forming a concave cutting edge; concave cutting edge between second and third marginal teeth not so broad as between first and second marginal teeth. Right mandible with two marginal teeth; posterior margin of first marginal tooth longer than anterior margin. Labrum with sides converging anteriorly into a blunt point. Postmentum as in figure 69C. Pronotum narrower than head, transversely arched; anterior margin raised and distinctly serrated; posterolateral corners broadly rounded, in some specimens flattened. Femur not swollen.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF EIGHT
IMAGOS OF *Bicornitermes bicornis*,
NEW SPECIES

	Range	Mean
Length of head to tip of labrum	1.52-1.68	1.58
Length of head to side base of mandibles	1.10-1.22	1.16
Width of head	1.25-1.28	1.27
Diameter of eye	0.47-0.59	0.53
Eye from lower margin	0.06-0.12	0.09
Length of ocellus	0.10-0.13	0.12
Median length of pronotum	0.61-0.70	0.65
Maximum length of pronotum	0.70-0.79	0.73
Width of pronotum	1.04-1.10	1.08
Length of hind tibia	0.98-1.10	1.05
Length of forewing from suture	10.15-10.72	10.37
Width of forewing	2.82- 2.91	2.84
Length of forewing scale	0.98- 1.07	1.05

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF EIGHT
SOLDIERS OF *Bicornitermes bicornis*,
NEW SPECIES

	Range	Mean	Holo- type
Length of head to side base of mandible	1.62-1.71	1.67	1.71
Maximum width of head	1.37-1.43	1.40	1.40
Maximum height of head	1.22	1.22	1.22
Length of left mandible	0.70-0.73	0.73	0.73
Maximum width of postmentum	0.46-0.49	0.49	0.49
Minimum width of postmentum	0.40-0.46	0.43	0.43
Length of postmentum	0.79-0.85	0.81	0.79
Median length of pronotum	0.67-0.85	0.78	0.85
Maximum length of pronotum	0.85-1.00	0.96	0.98
Maximum width of pronotum	1.28-1.37	1.33	1.28
Length of hind tibia	0.98-1.10	1.05	1.10

COMPARISONS: The imago of *Bicornitermes bicornis*, new species, is larger in all respects than that of *B. spinicollis* (Wilkinson) and that of *B. exsertifrons* (Wilkinson). The soldier of *B. spinicollis* is smaller; the mandibles are shorter; the laterofrontal lobes are not so prominent; the frontal area is not so depressed medially; the eyes are smaller; the postmentum shape is different; and the pronotum has the posterolateral corners more broadly rounded. The soldier of *B. exsertifrons* is smaller; the head anteriorly is reddish brown; the medial depression between the frontal lobes is deeper and narrower; and the anterior margin of the pronotum is more deeply emarginate and has fewer serrations, which are not so prominent.

TYPE LOCALITY AND DISTRIBUTION: Camp Putnam (latitude 1° 24' N., longitude 28° 36' E.) on the Epulu River, the Congo (type locality), soldiers (holotype and paratype) and imagos (morphotype and paratype),

collected by A. E. Emerson, April 14, 1948, in hard dry wood of standing dead tree on the edge of Epulu River.

GENUS *EPICALOTERMES* SILVESTRI, 1918

= Genus *Epicalotermes* SILVESTRI, 1918, p. 347.

= Genus *Epicalotermes* SJÖSTEDT, 1926, pp. 23, 44.

= Subgenus *Epicalotermes* EMERSON, 1928, p. 405 (no description).

< Genus *Kalotermes* COATON, 1949, pp. 14–16.

< Genus *Kalotermes* SNYDER, 1949, p. 12.

= Genus *Epicalotermes* GRASSÉ, 1949, p. 531.

< Genus *Kalotermes* COATON, 1950, pp. 3, 4, 31, 32.

= Subgenus *Epicalotermes* WILKINSON, 1954, p. 77.

TYPE SPECIES: *Epicalotermes aethiopicus* Silvestri.

Silvestri (1918) proposed this genus for the species *Epicalotermes aethiopicus*. Snyder (1949) regarded it as a synonym of the genus *Kalotermes*, but I am resurrecting it, as it is distinct from the genus *Kalotermes* and belongs to the *Procryptotermes*-*Cryptotermes* branch, as is indicated by the imago mandible. It differs from *Kalotermes* in having the left imago mandible with the anterior margin

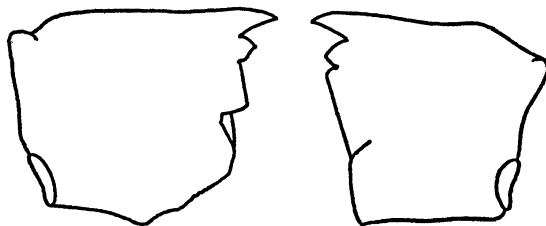


FIG. 70. Mandibles of nymph of *Epicalotermes aethiopicus* Silvestri. Cotype from Mayabal, Eritrea.

of the third marginal tooth longer than the posterior margin of the first plus second marginal tooth; the imago larger than *Kalotermes* and the eyes much smaller; the media and cubitus vein in the forewing arising from a common stem beyond the wing suture; the arolium absent; and the soldier head larger and dorsoventrally flat, the eyes pigmented, and the mandibles long, robust, and strongly curved towards the apex.

IMAGO: Yellowish brown. Diameter of eye, 0.35–0.55 mm. Ocellus always touching eye. Antenna with 14 to 19 articles. Left mandible with anterior margin of third marginal tooth more than one and one-half times length of

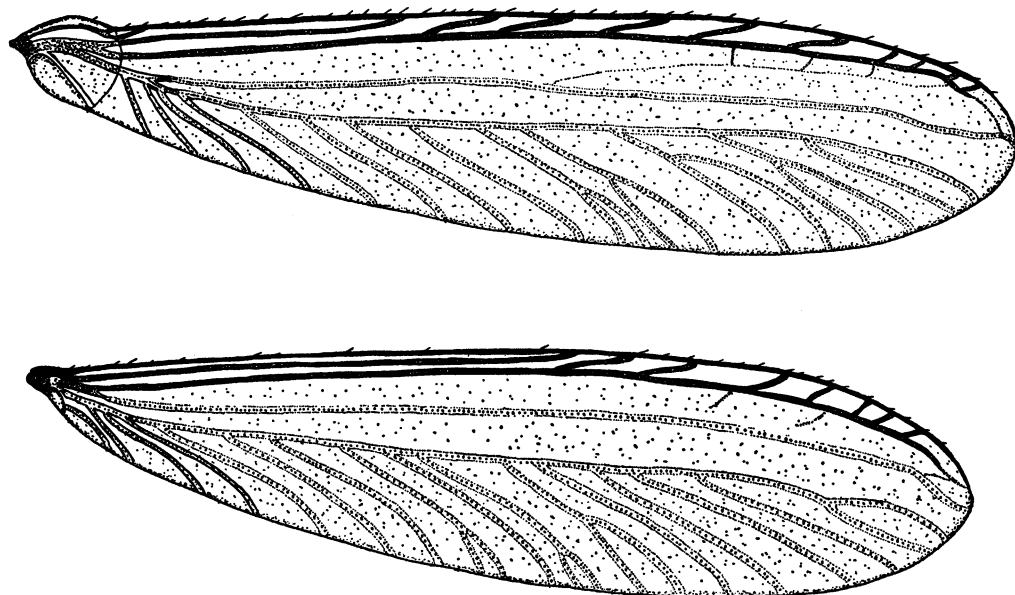


FIG. 71. Forewing and hind wing of *Epicalotermes kempae* (Wilkinson). Lake Chala, near Taveta, Kenya.

posterior margin of first plus second marginal tooth; first plus second marginal tooth shorter at base than third marginal tooth (fig. 70). Right mandible with molar plate shorter than posterior margin of second marginal tooth (fig. 70). Pronotum slightly narrower than or nearly as broad as head; anterior margin concave. Wing membrane clear, covered with hyaline papillae. Forewing with costal margin, subcosta, radius, and radial sector strongly developed and sclerotized and arising independently at wing suture; radial sector with five to nine branches to costal margin; media and cubitus weak and un-

sclerotized, arising from a common stem beyond wing suture; media may be simple or forked, running midway between radial sector and cubitus (fig. 71). Tibial spurs 3:3:3. Arolium absent.

SOLDIER (FIG. 72): Head long and broad; dorsoventrally flat; sides converging anteriorly; genal region below the antennal fossa depressed; frons sloping in front, the slope gradual and beginning at about half of length of head; frons depressed medially, concave; dorsal rim of antennal foveolae very prominent and dorsally appearing in form of small tube. Eyes large, pigmented. Labrum sub-

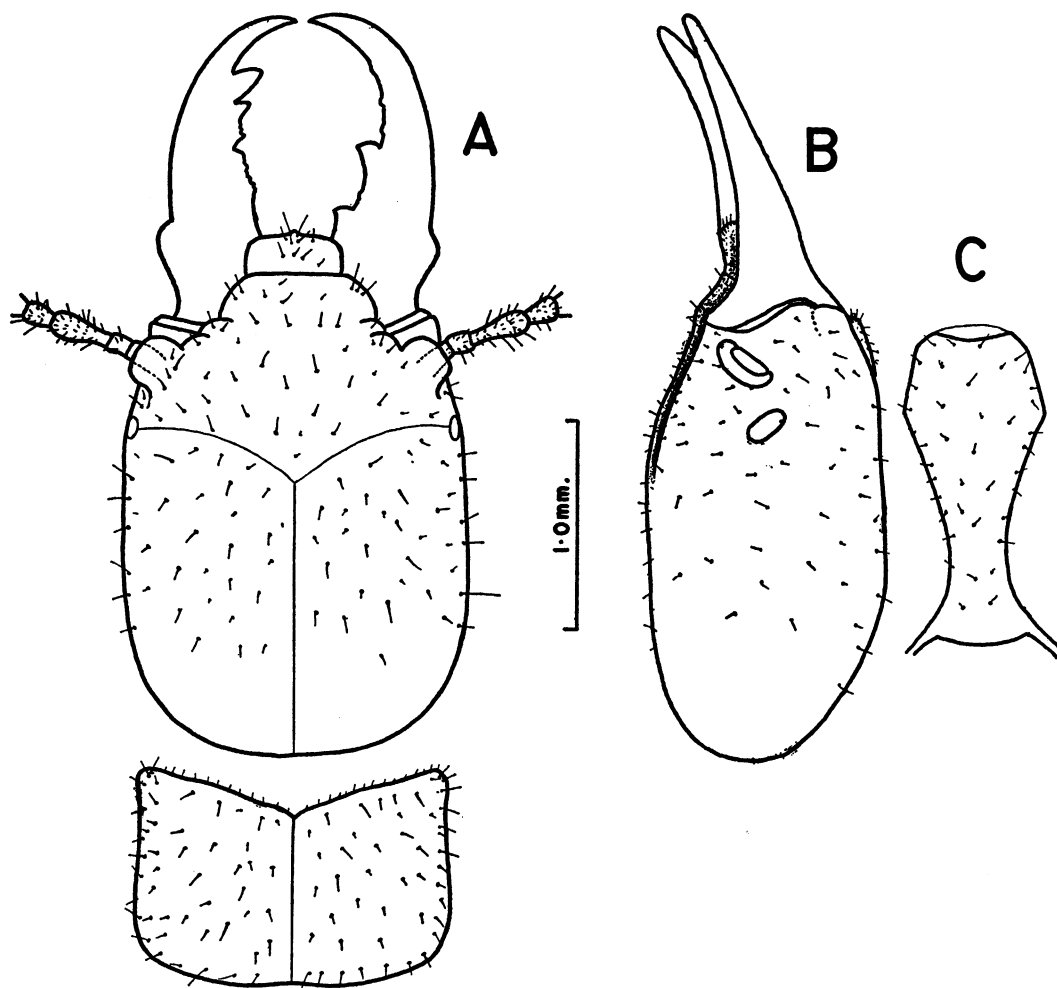


FIG. 72. Soldier of *Epicalotermes aethiopicus* Silvestri. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Cotype from Mayabal, Eritrea.

rectangular, broader than long, anterior margin convex, with a small, median, anterior projection. Antenna with 10 to 13 articles; third article dark, club-shaped, longest. Mandibles long and robust, strongly curved from near basal hump towards apex, with a prominent hump at outer bases. Pronotum as broad as or slightly narrower than head, transversely arched, subrectangular; anterior margin slightly raised, deeply and angularly indented; sides fairly straight. Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago is similar to that of *Bifiditermes* and that of *Bicornitermes* in wing venation and other respects. In the left imago mandible of *Epicalotermes* the anterior margin of the third marginal tooth is more than one and one-half times longer than the posterior margin of the first plus second marginal tooth; in *Bifiditermes* and *Bicornitermes* such is not the case. The soldier head of *Epicalotermes* is more dorsoventrally flattened than that of *Bifiditermes*, and the mandibles are more strongly curved from near the basal hump towards the apex.

SPECIES INCLUDED

- E. aethiopicus* Silvestri, 1918
E. kempae (Wilkinson), new combination = *Kalotermes kempae* Wilkinson, 1954
E. munroi (Coaton), new combination = *Kalotermes munroi* Coaton, 1949
E. mkuzii (Coaton), new combination = *Kalotermes mkuzii* Coaton, 1949
E., new species, from Tulear, Madagascar

GEOGRAPHICAL DISTRIBUTION: Ethiopian: Africa. Malagasy: Madagascar.

GENUS *PROCRIPTOTERMES* HOLMGREN, 1910

- = Subgenus *Procryptotermes* HOLMGREN, 1910a, p. 285 (no description).
 = Subgenus *Procryptotermes* HOLMGREN, 1910b, p. 139.
 < Subgenus *Procryptotermes* HOLMGREN, 1911a, pp. 53, 55, 58, 61.
 < Subgenus *Procryptotermes* HOLMGREN, 1911c, p. 550.
 < Genus *Procryptotermes* SJÖSTEDT, 1926, pp. 22, 23, 31.
 < Subgenus *Procryptotermes* EMERSON, 1928, p. 405.
 < Subgenus *Cryptotermes* HILL, 1942, pp. 7, 65.
 < Genus *Procryptotermes* CACHAN, 1949, pp. 185, 187, 190, 211.

Genus *Procryptotermes* GRASSÉ, 1949, p. 530.

< Genus *Procryptotermes* SNYDER, 1949, p. 36.

< Genus *Procryptotermes* AHMAD, 1950, pp. 44, 50.

< Genus *Procryptotermes* WEIDNER, 1955a, pp. 48, 68.

< Genus *Procryptotermes* EMERSON, 1955, pp. 472, 473, 478, 490, 492, 498, 508.

TYPE SPECIES: *Procryptotermes fryeri* Holmgren.

The genus *Procryptotermes*, as treated in this paper, is used in a more restricted sense than it was by Snyder (1949) and Emerson (1955). I have excluded the following species, which were included by Snyder (1949) in the genus: *P. canalensis*, *P. hubbardi*, *P. jeannelanus*, *P. paradoxus*, *P. perezi*, *P. queenslandis*, *P. taurocephalus*, and *P. triceromegas*.

The species *P. canalensis* was described by N. and K. Holmgren (1915) from the winged adult alone from Canala, New Caledonia. Hill (1942, p. 73) described the soldier from a series comprising six soldiers and many nymphs, which were collected from Noumea, New Caledonia, about 60 miles from the type locality of the imago; he therefore assumed that these soldiers belonged to the species *P. canalensis*. In the collection of A. E. Emerson there is an associated series with imagoes and soldiers, collected by L. J. Dumbleton from Noumea, New Caledonia. A recent study by Emerson has shown that the imago of this series differs from the type imago of *P. canalensis*; the soldier, however, is conspecific with the morphotype soldier described by Hill (1942, p. 73). In view of the above facts, the soldier described by Hill (1942, p. 73) from Noumea, New Caledonia, does not belong to the species *P. canalensis* but constitutes a distinct species to which Emerson has given the new name *Procryptotermes krishnai*. A study by Emerson has also shown that *P. canalensis* belongs to the genus *Cryptotermes*. In the present paper I also transfer *P. queenslandis* to the genus *Cryptotermes*. Its soldier has a much shorter mandible, and the soldier head is more like that of the genus *Cryptotermes* than that of the genus *Procryptotermes*. Also, the anterior margin of the pronotum is serrated, as in some species of the genus *Cryptotermes*.

IMAGO (FIG. 73): Color reddish brown to

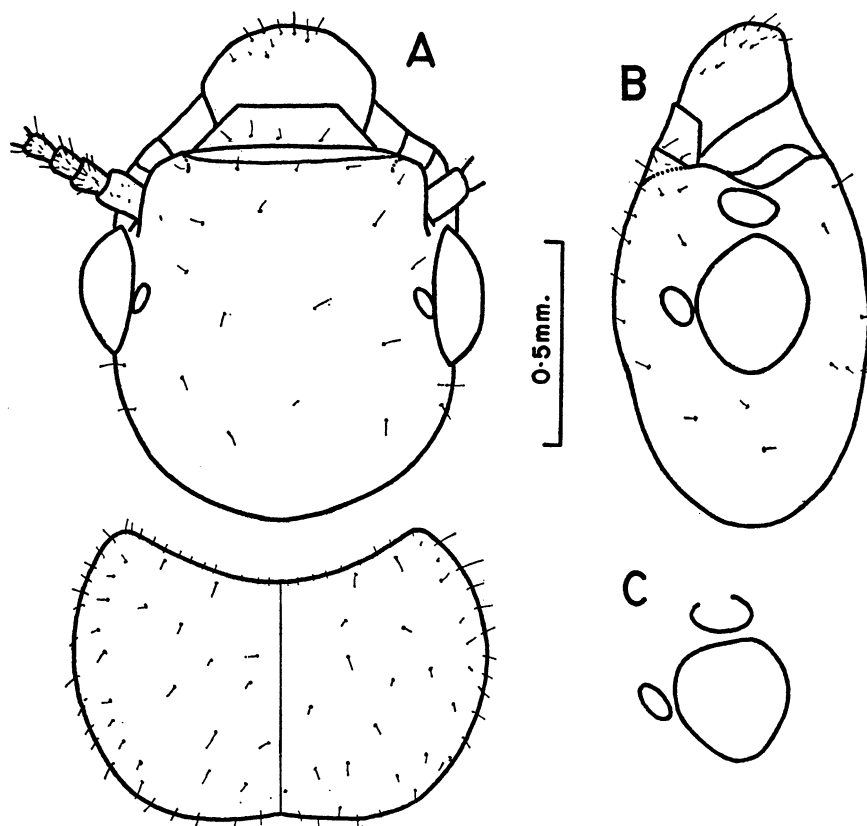


FIG. 73. Imago of *Procryptotermes fryeri* Holmgren. A. Head and pronotum from above. B. Head from side. C. Left eye. Cotype from type colony from Takamaka, Aldabra Islands.

brown. Eyes small; diameter, 0.34–0.39 mm. Ocellus touching eye. Antenna with 16 to 18 articles. Left mandible with first plus second marginal tooth much smaller at base than third marginal tooth; anterior margin of third marginal tooth about one and one-half times longer than posterior margin of first plus second marginal tooth (fig. 74). Right mandible with molar plate distinctly shorter than posterior margin of second marginal tooth (fig. 74). Pronotum as broad as or broader than head. Forewing with all major veins arising independently at wing suture; radius (R_1) simple; radial sector with four to five branches, first branch arising at one-third of length of wing from suture; media weak and unsclerotized, running midway between radial sector and cubitus in proximal half of

wing, bending up near middle or beyond middle of wing to meet radial sector. Cubitus weak and unsclerotized (fig. 75). Tibial spurs 3:3:3. Arolium present.

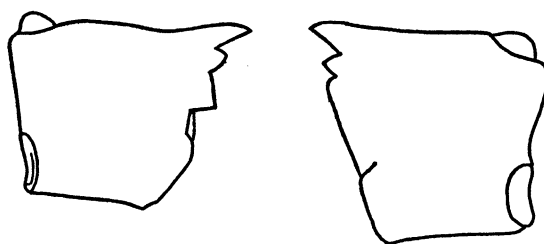


FIG. 74. Mandibles of imago of *Procryptotermes fryeri* Holmgren. Cotype from type colony from Takamaka, Aldabra Islands.

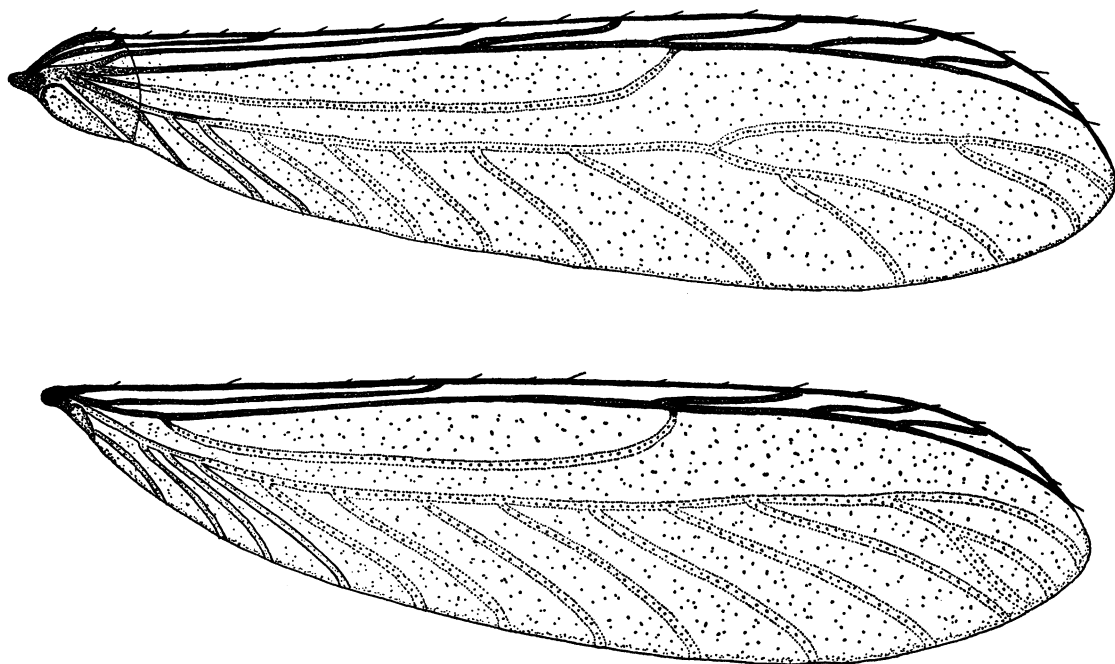


FIG. 75. Forewing and hind wing of *Procryptotermes fryeri* Holmgren.
Cotype from Takamaka, Aldabra Islands.

SOLDIER (FIG. 76): Head long, sides almost parallel; front sloping at angle of approximately 45 degrees to clypeus; prominent ridge (frontal flange of Hill, 1942) present between frons and vertex, with a shallow, median, U-shaped incision in *P. fryeri* and a few other species; in some species ridge less prominent or absent; anterolateral region of head with two pairs of horn-like projections: one situated near lateral margin of postclypeus, in front of antennal socket; the other formed by a prolongation of ventral genae in front and below antennal socket; in some the upper or lower projection absent or not so prominent. Eyes unpigmented. Antenna with 11 to 16 articles; third article usually long and club-shaped, longer than second; in *P. rapae*, third article shorter than second. Mandible length ranging from 1.28 to 1.58 mm.; basal region thick and with a hump. Teeth present in most species; in some, as *P. fryeri*, absent. Pronotum as broad as head; markedly arched transversely; anterior margin shallowly or deeply emarginate. Femur not swollen. Tibial spurs 3:3:3.

COMPARISONS: The imago is similar in all respects to that of the genus *Cryptotermes*. The soldier differs from that of *Cryptotermes* in having longer mandibles and a less phragmotic head; also the anterior margin of the pronotum is even, rather than serrated.

SPECIES INCLUDED

- P. fryeri* Holmgren, 1910b
- P. corniceps* (Snyder), 1923
- P. dioscurae* Harris, 1954
- P. krishnai* Emerson (new name for the soldier described by Hill, 1942, p. 73, under the name *Procryptotermes canalensis*)
- P. rapae* Light and Zimmermann, 1936
- P. speiseri* N. and K. Holmgren, 1915
- P.*, new species, from west of Plumb Point Lighthouse, Jamaica
- P.*, new species, from Port de Galles, Réunion Island

GEOGRAPHICAL DISTRIBUTION: Papuan: New Caledonia, New Hebrides, Rapa Island. Ethiopian: Socotra Island. Malagasy: Aldabara Island, Réunion Island. Neotropical: Jamaica, Mona Island, Puerto Rico.

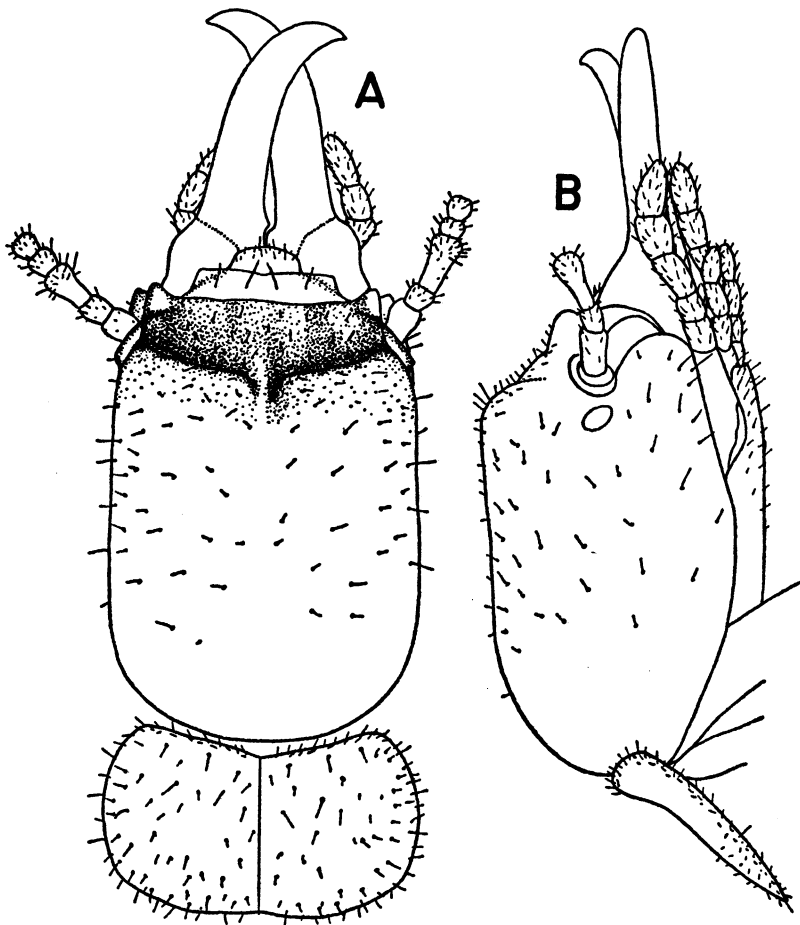


FIG. 76. Soldier of *Procryptotermes fryeri* Holmgren. A. Head and pronotum from above. B. Head and pronotum from side. Cotype from type colony, Takamaka, Aldabra Islands. Drawn by A. E. Emerson.

GENUS **CRYPTOTERMES** BANKS, 1906

- <Genus *Calotermes* HAGEN, 1858a, pp. 31-38.
- <Genus *Calotermes* HAGEN, 1858b, p. 1.
- <Genus *Calotermes* HAVILAND, 1898, pp. 371, 373.
- <Genus *Calotermes* DESNEUX, 1904d, pp. 20-24.
- = Genus *Cryptotermes* BANKS, 1906, p. 336.
- = Subgenus *Cryptotermes* HOLMGREN, 1910a, p. 285 (no description).
- <Subgenus *Cryptotermes* HOLMGREN, 1911a, pp. 53, 55, 58, 60, 61.
- <Subgenus *Cryptotermes* HOLMGREN, 1911c, p. 549 (no description).
- Subgenus *Cryptotermes* HOLMGREN, 1913a, p. 37.
- = Genus *Cryptotermes* BANKS, 1919, p. 476.

- <Genus *Cryptotermes* BANKS AND SNYDER, 1920, pp. 7, 16, 35.
- = Genus *Cryptotermes* FULLER, 1921, pp. 19, 22-24, 29.
- >Genus *Cryptotermes* LIGHT, 1921, p. 36.
- >Genus *Planocryptotermes* LIGHT, 1921, p. 41.
- <Genus *Cryptotermes* SNYDER, 1922, pp. 12, 13.
- >Genus *Cryptotermes* LIGHT, 1924, p. 52.
- Subgenus *Cryptotermes* EMERSON, 1925, p. 326.
- = Genus *Cryptotermes* SJÖSTEDT, 1926, pp. 22, 23, 28.
- Subgenus *Cryptotermes* BATHELLIER, 1927, p. 127.
- >Subgenus *Cryptotermes* EMERSON, 1928, pp. 405, 412, 418.

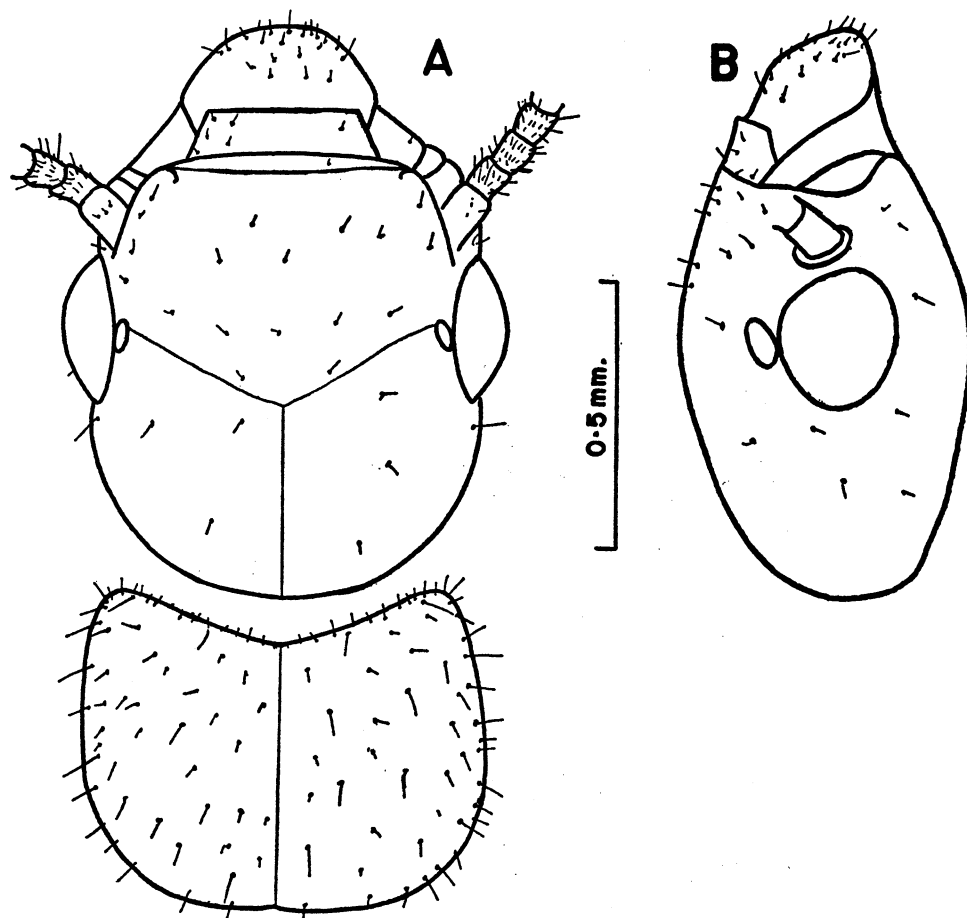


FIG. 77. Imago of *Cryptotermes cavifrons* Banks. A. Head and pronotum from above. B. Head from side. Near Strickland, Hammock, Florida.

>Subgenus *Planocryptotermes* EMERSON, 1928, p. 405.

=Genus *Cryptotermes* LIGHT, 1930, pp. 15, 16, 18.

>Subgenus *Planocryptotermes* LIGHT, 1930, pp. 15, 16, 18.

Genus *Cryptotermes* LIGHT, 1931, p. 586.

<Subgenus *Lobitermes* LIGHT, 1933, p. 101.

Subgenus *Cryptotermes* LIGHT, 1933, p. 82.

=Subgenus *Cryptotermes* SNYDER, 1934b, pp. 24, 27.

=Genus *Cryptotermes* KEMNER, 1934, pp. 30, 44.

>Subgenus *Cryptotermes*, *sensu stricto*, KEMNER, 1934, p. 45.

>Subgenus *Planocryptotermes* KEMNER, 1934, pp. 30, 47.

=Genus *Cryptotermes* WU, 1935, p. 217.

Subgenus *Cryptotermes* HARE, 1937, pp. 461, 474, 475.

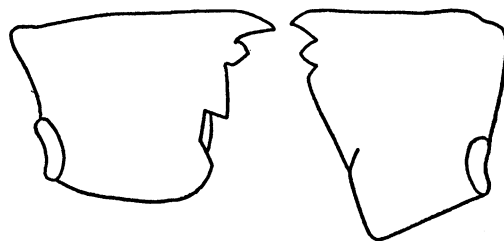


FIG. 78. Mandibles of imago of *Cryptotermes cavifrons* Banks. Near Strickland, Hammock, Florida.

<Subgenus *Cryptotermes* HILL, 1942, pp. 7, 65.
 =Subgenus *Cryptotermes* SNYDER, 1948, pp. 232, 234, 235.

=Genus *Cryptotermes* CACHAN, 1949, pp. 180, 185, 187, 190, 213.

>Genus *Cryptotermes* SNYDER, 1949, pp. 38, 359.

<Genus *Procryptotermes* SNYDER, 1949, p. 36.

Genus *Cryptotermes* GRASSÉ, 1949, p. 531.

=Genus *Cryptotermes* AHMAD, 1950, pp. 44, 50.

=Genus *Cryptotermes* COATON, 1950, pp. 4, 28.

=Genus *Cryptotermes* EMERSON, 1951, pp. 156, 157.

Genus *Cryptotermes* WEIDNER, 1955a, pp. 46, 48, 68.

>Genus *Cryptotermes* EMERSON, 1955, pp. 472, 478, 487, 490, 492, 508.

=Genus *Cryptotermes* HARRIS, 1957, pp. 25, 27.

=Genus *Cryptotermes* AHMAD, 1958, pp. 35, 36.

TYPE SPECIES: *Cryptotermes cavifrons* Banks.

IMAGO (FIG. 77): Yellowish brown to dark and smoky brown. Diameter of eye, 0.29–0.36 mm. Ocellus usually touching eye (in *C. kirbyi*, ocellus 0.01–0.02 mm. from eye). Antenna with 13 to 18 articles. Left mandible with first plus second marginal tooth half as large at base as third marginal tooth; anterior

margin of third marginal tooth twice as long as posterior margin of first plus second marginal tooth (fig. 78). Right mandible with posterior margin of second marginal tooth distinctly longer (one and one-half times) than molar plate (fig. 78). Pronotum slightly narrower, as broad as or broader than head. Forewing with all major veins arising independently at wing suture; radius (R_1) simple; radial sector with three to four branches; media weak and unsclerotized, running midway between radial sector and cubitus in proximal half of wing, near middle or beyond middle of wing to meet radial sector. Cubitus weak and unsclerotized (fig. 79). Tibial spurs 3:3:3. Arolium present in majority of species.

SOLDIER (FIG. 80): Head dark, phragmotic; short, thick, and in some rough on anterior portion of front and sides of head; profile of front vertical, near vertical, or overhanging; a thick ridge between frons and vertex, with or without a median, V-shaped notch. Two pairs of prominent, horn-like projections: one in lateral margin of postclypeus in front of antennal socket, the other formed by a prolongation of ventral genae, in front of and below antennal socket; upper, lower, or both

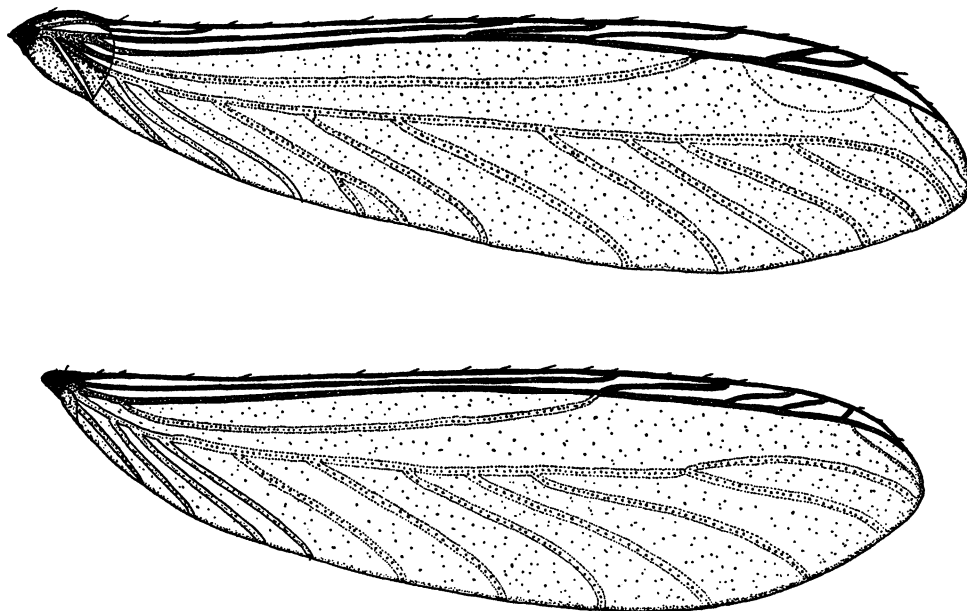


FIG. 79. Forewing and hind wing of *Cryptotermes cavifrons* Banks. Near Strickland, Hammock, Florida.

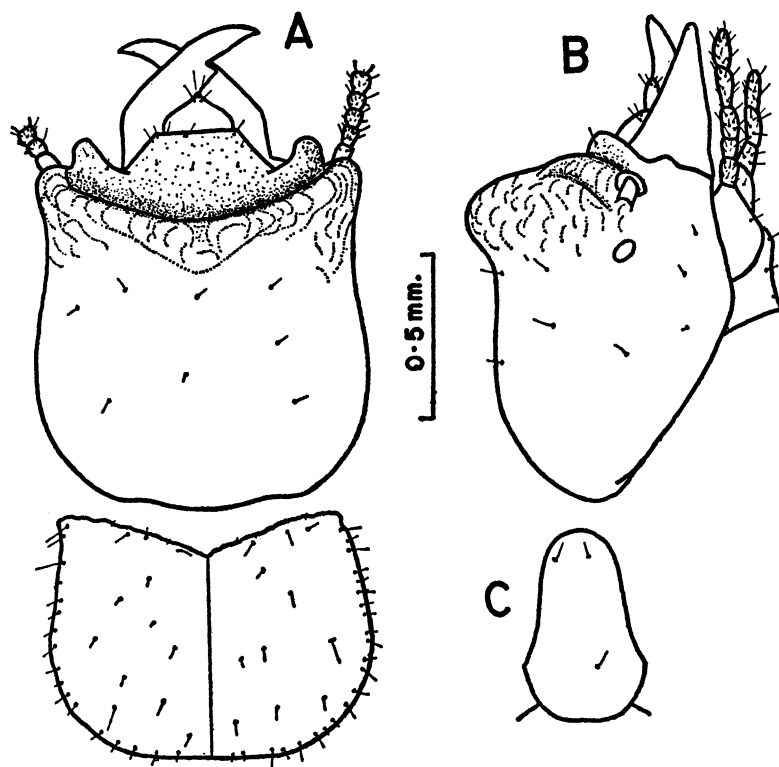


FIG. 80. Soldier of *Cryptotermes cavifrons* Banks. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. Near Strickland, Hammock, Florida.

projections lacking in some species. Eyes distinct, unpigmented. Mandibles short, 0.38–0.95 mm. in length, humped basally, bent sharply near middle, weakly toothed or not toothed. Antenna with 11 to 15 articles; third article not especially long. Labrum pointed at tip. Pronotum either slightly narrower than or as broad as head; anterior margin strongly concave, emarginate, usually irregularly wavy or serrated; anterolateral corners sharp; sides and hind margin evenly rounded.

SPECIES INCLUDED

C. albipes N. and K. Holmgren, 1915
C. brevis (Walker), 1853
C. canalensis (N. and K. Holmgren), 1915
C. cavifrons Banks, 1906
C. cubicoceps Emerson, 1925
C. cynocephalus Light, 1921
C. dolei Light, 1932
C. domesticus (Haviland), 1898
C. dudleyi Banks, 1918
C. fatulus Light, 1933

C. gearyi Hill, 1942
C. havilandi (Sjöstedt), 1900b
C. kirbyi Moszkowski, 1955
C. longicollis Banks, 1918
C. merwei Fuller, 1921
C. pallidus (Rambur), 1842
C. perforans Kemner, 1932b
C. primus Hill, 1921
C. queenslandis Hill, 1933
C. senegalensis Silvestri, 1914
C. solidus (Hagen), 1858a
C. sumatrensis Kemner, 1930
C. verruculosus Emerson, 1925

GEOGRAPHICAL DISTRIBUTION: Australian: Australia. Papuan: Hawaii, Loyalty Islands, Marquesas Islands, New Guinea, New Britain, Society Islands, Solomon Islands. Indo-Malayan: Ceylon, Formosa, India, Java, Philippines, Thailand, Singapore, Sumatra. Ethiopian: Africa. Malagasy: Madagascar, Mauritius. Nearctic: North America. Neotropical: Central and South America, Galapagos Islands, the West Indies.

PHYLOGENY

THERE ARE VARIOUS APPROACHES to the study of phylogeny, namely, comparative morphology, ecology, embryology, physiology, genetics, zoogeography, and paleontology. In the following pages I present the phylogeny of the genera of the family Kalotermitidae, based mainly on the comparative morphology of living forms, with some supplemental knowledge from Tertiary fossils. From a study of present-day geographical distribution and ecological limitations, and a knowledge of ancient land masses, land bridges, climate, and the geological possibilities of dispersal and isolation, correlated with clear phylogenetic stages and direction of evolution, one may find some indications of the place of origin, the time of origin, and the direction of ancient dispersion. Emerson (1952a, 1955) studied the biogeography of termites, using such an analysis. In the present study I also include the biogeography of the genera as used by Emerson, and some of the conclusions are also taken from his study. Because the conclusions presented here are based on circumstantial evidence, with many gaps, they are therefore tentative (fig. 81 and table 3).

The family Kalotermitidae probably arose in the remote past from a *Mastotermes*-like ancestor (Ahmad, 1950). The ancestral kalotermitid may be presumed to have had the following characteristics: (1) the imago mandible *Mastotermes*-like, i.e., the marginal teeth in the left mandible reduced from three to two by means of the reduction and fusion of the second marginal tooth with the first; the posterior margin of the first plus second marginal tooth equal to the anterior margin of the third marginal tooth; (2) the arolium present; (3) the median vein in the forewing weak, unsclerotized, and running midway between the radial sector and the cubitus to the tip of the wing; and (4) the middle tibia with extra spines in addition to the apical spurs.

From such an ancestor two major lines diverged. The first line is represented by the *Proelectrotermes-Calcaritermes* complex in which the imago mandible is like that of the ancestor, i.e., the posterior margin of the first plus second marginal tooth of the left mandible

is equal to the anterior margin of the third marginal tooth. The second line is represented by the *Incisitermes-Cryptotermes* complex and is characterized by the elongation of the anterior margin of the third marginal tooth and the shortening of the posterior margin of the first plus second tooth of the left mandible.

In the first line, *Proelectrotermes*, a fossil genus from Baltic amber of East Prussia, is the most primitive, as is indicated by the presence of extra spines in the middle tibia—two spines on the outer edge and one spine on the inner edge. The wing venation is more advanced; the median vein in the forewing, though weak and unsclerotized, is closer to the radial sector than to the cubitus. The arolium is present. The antenna has 19 to 20 articles.

The fossil genus *Electrotermes* from Baltic amber of East Prussia probably arose directly from the genus *Proelectrotermes*, having lost the outer spine from the middle tibia. The wing venation is similar to that of *Proelectrotermes*. The arolium is present. The antenna has 15 to 18 articles.

Postelectrotermes was probably derived directly from *Electrotermes*. In the middle tibia only one inner spine remains, one having been lost. The wing venation is more advanced than that of *Proelectrotermes* and *Electrotermes*: the media in the forewing is weakly sclerotized and has advanced closer to the radial sector than in the other two genera. The genus lives in damp wood and survives only in islands or on continental edges. The distribution of the species is: Indo-Malayan (two), Ethiopian (one), Malagasy (seven, including two new species), and Palearctic (two). Because of the presence of the ancestral genus *Electrotermes* in the Baltic amber of East Prussia and its present-day distribution, it is suspected that the genus originated in the Old World in Mesozoic times. The presence of a large number of species in Madagascar is probably due to reduced competition.

Neotermes probably descended directly from *Postelectrotermes*, as is indicated by the morphology and ecology. *Neotermes*, as is *Postelectrotermes*, is a damp-wood dweller. It shows an advance over *Postelectrotermes* in

having lost all the spines in the middle tibia, and in having the median vein in the forewing more strongly sclerotized and closer to the radial sector. The distribution of species is: Australian (one), Papuan (20, including one new species), Indo-Malayan (21, including one new species), Nearctic (one), and Neotropical (24, including seven new species). The genus is essentially tropical, except for one species, *Neotermes castaneus*, which is found in subtropical regions of Florida. Its wide distribution indicates an origin in either the Neotropical or Indo-Malayan region in Mesozoic times.

Rugitermes probably arose from a *Neotermes*-like stock and is more advanced than *Neotermes*. The sclerotized median vein in the forewing, instead of running parallel to the radial sector to the tip of the wing, joins the

radial sector close to the wing suture. The distribution of species is: Papuan (two, including one new species) and Neotropical (19, including eight new species). The distribution of species indicates that the genus originated in the Neotropical region in early Tertiary times. Emerson (1955) states that the presence of two endemic species in the eastern oceanic islands (Marquesas, Society, and Cook) of the Papuan Region indicates a western dispersal from America, and he thinks that they could probably have been carried in branches of floating trees.

Eucryptotermes is a highly specialized monotypic genus endemic to South America. It probably arose from *Neotermes*-like stock in South America. The wing venation is *Neotermes*-like; the soldier, however, is derivative and has developed a highly phragmotic head,

TABLE 3

THE NUMBER OF LIVING SPECIES IN EACH GENUS ARRANGED BY ZOOGEOGRAPHICAL REGIONS

	Australian	Papuan	Indo-Malayan	Ethiopian	Malagasy	Palaearctic	Nearctic	Neotropical	Unknown Region	Total	Named Species	New Species
<i>Postelectrotermes</i>	—	—	2	1	7	2	—	—	—	12	10	2
<i>Neotermes</i>	1	20	21	17	6	—	1	24	—	90	73	17
<i>Rugitermes</i>	—	2	—	—	—	—	—	19	—	21	12	9
<i>Eucryptotermes</i>	—	—	—	—	—	—	—	1	—	1	1	0
<i>Kalotermes</i>	7	1	1	2	1	3	1	—	—	16	16	0
<i>Paraneotermes</i>	—	—	—	—	—	—	1	—	—	1	1	0
<i>Ceratokalotermes</i>	1	—	—	—	—	—	—	—	—	1	1	0
<i>Comatermes</i>	—	—	—	—	—	—	—	1	—	1	1	0
<i>Glyptotermes</i>	5	8	21	12	2	—	—	25	1	74	51	23
<i>Calcaritermes</i>	—	—	—	—	—	—	1	13	—	14	10	4
<i>Pterotermes</i>	—	—	—	—	—	—	1	—	—	1	1	0
<i>Incisitermes</i>	—	8	2	—	1	—	7	16	—	34	23	11
<i>Allotermes</i>	—	—	—	—	3	—	—	—	—	3	1	2
<i>Marginitermes</i>	—	—	—	—	—	—	1	—	—	1	1	0
<i>Tauritermes</i>	—	—	—	—	—	—	—	2	—	2	2	0
<i>Proneotermes</i>	—	—	—	—	—	—	—	2	—	2	2	0
<i>Bifiditermes</i>	2	—	4	7	2	—	—	—	—	15	12	3
<i>Bicornitermes</i>	—	—	—	4	—	—	—	—	—	4	3	1
<i>Epicalotermes</i>	—	—	—	4	1	—	—	—	—	5	4	1
<i>Procryptotermes</i>	—	3	—	1	2	—	—	3	—	9	5	4
<i>Cryptotermes</i>	6	8	5	4	2	—	1	9	1	36	24	12
Total	22	50	56	52	27	5	14	115	2	343	254	89

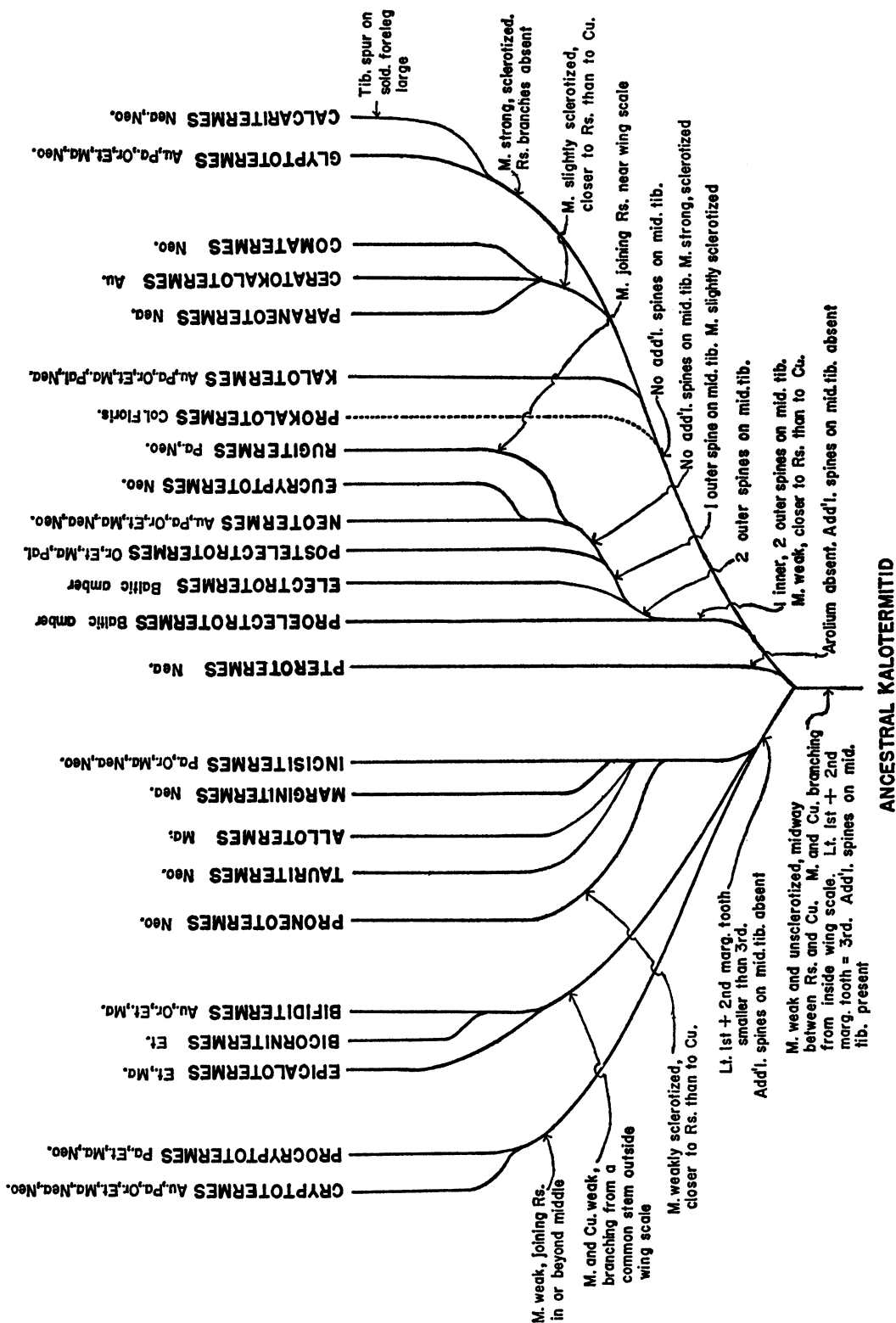


FIG. 81. Phylogenetic tree of the family Kalotermitidae. *Abbreviations:* Au., Australia; Cu., cubitus; Col. Floris., Colorado Florissant; Et., Ethiopian; M., media; Ma., Malagasy; marg., marginal; Nea., Nearctic; Neo., Neotropical; Or., Oriental; Pa., Papuan; Pal., Palearctic; Rs., radial sector; sold., soldier; tib., tibia.

which is convergent with that of *Cryptotermes*, *Glyptotermes*, *Calcaritermes*, and *Bicornitermes*.

The validity of the fossil genus *Prokalotermes* is questionable, and its relationship is obscure. From its known characters it could be synonymous with *Kalotermes*. Until more specimens can be examined, it is thought best to retain the present name.

The genus *Kalotermes* probably arose directly from the ancestral kalotermitid stock after losing all the additional spines. It has retained the primitive wing venation, imago mandible, and arolium. The distribution of the species is: Australian (seven), Papuan (one), Indo-Malayan (one), Ethiopian (two), Malagasy (one), Palearctic (seven, with four fossil species), and Nearctic (one). The genus is found mainly on islands and continental edges in tropical regions of Australia and Africa, and in the central continental area in temperate regions of Europe. The place of origin is obscure; the world-wide distribution of species probably indicates an early or mid-Mesozoic origin. The large number of species in Australia may be due to a somewhat reduced competition within its hardwood ecological niche.

From the *Kalotermes*-like stock probably arose three endemic genera, *Paraneotermes*, *Comatermes*, and *Ceratokalotermes*, in the Nearctic, Neotropical, and Australian regions.

Paraneotermes is a monotypic endemic genus of temperate Mexico and southwestern United States. The median vein in the forewing is weakly sclerotized and has shifted slightly closer to the radial sector, as compared to the position midway between the radial sector and the cubitus in *Kalotermes*. The arolium is absent.

Comatermes is a specialized, monotypic, endemic genus of the Neotropical Region. The wing venation is like that of *Paraneotermes*, i.e., the media is weakly sclerotized and is closer to the radial sector than to the cubitus. The imago head and pronotum have unique, very long, and wavy hairs. There are no living species of *Kalotermes* in the Neotropical Region, but the *Kalotermes*-like stock, from which *Comatermes* was derived, was probably present in ancient times.

Ceratokalotermes is an endemic genus of Australia. The wing venation is similar to

that of *Paraneotermes* and *Comatermes*. The soldier head is specialized, has two antero-lateral prominences on the head, and closely resembles that of *Glyptotermes* because of convergent evolution.

Glyptotermes shows an advance over *Comatermes*, *Paraneotermes*, and *Ceratokalotermes*. It probably arose from a *Kalotermes*-like ancestor near the base of the *Comatermes* complex. The costal area is more consolidated. The median vein in the forewing is as heavily sclerotized as the radial sector and runs very close and parallel to the radial sector; the radial sector has lost its branches to the costal margin. The soldier has a phragmotic head and is somewhat convergent with the specialized head of *Cryptotermes* soldiers. The distribution of the species is: Australian (five), Papuan (eight, including five new species), Indo-Malayan (21, including three new species), Ethiopian (12, including six new species), Malagasy (two, including one new species), and Neotropical (25, including eight new species). The genus is strictly tropical. Because of its abundance in the Neotropical Region, and the decline in numbers in a regular order in the Indo-Malayan, Ethiopian, Papuan, and Australian regions along the lines of dispersion, Emerson (1955) postulates an origin probably in the Neotropical Region, with late Jurassic or early Cretaceous dispersal.

Calcaritermes probably was derived directly from *Glyptotermes*. It is closely related in morphology and ecology to the genus *Glyptotermes*. The imago is similar to that of the genus *Glyptotermes*. The soldier has a prominent spur on the fore tibia. The head is phragmotic, as in the genus *Glyptotermes*. The distribution of species is: Nearctic (one) and Neotropical (13, including four new species). Because of its abundance and the limited distribution of the species, it may be postulated that the genus originated in the Neotropical Region. Emerson (1955) states that it originated in Central America during post-Eocene times, but the presence of a species in Ilha Grande, near Rio de Janeiro, Brazil, casts some doubt on this hypothesis.

Pterotermes probably also arose directly from the kalotermitid ancestor. It has retained the ancestral imago mandible and wing venation. The posterior margin of the

first plus second marginal tooth of the left mandible is equal to the anterior margin of the third marginal tooth. The median vein in the forewing is weak and unsclerotized and runs midway between the radial sector and the cubitus. The antenna has 20 to 21 articles. The arolium is absent. The soldier is large and highly specialized in some respects. The eyes are pigmented. The third article of the antenna is dark, large, and club-shaped. The posterior margin of the postmentum has a distinct, sclerotized swelling. Its large size and multi-segmented antenna suggest a primitive structure, in spite of the loss of the arolium.

The second line is represented by the *Incisitermes*-*Cryptotermes* complex. From the second line there developed three branches: the first branch developing into *Incisitermes* and its relatives, i.e., *Allotermes*, *Marginitermes*, *Tauritermes*, and *Proneotermes*; the second branch developing into *Bifiditermes*, *Bicornitermes*, and *Epicalotermes*; and the third branch developing into *Procryptotermes* and *Cryptotermes*. The trend of the dentition of the left mandible of the imago in this line has been towards further proportional elongation of the anterior margin of the third marginal tooth compared to the posterior margin of the fused first plus second marginal tooth. The maximum length of the anterior margin of the third marginal tooth is more than one and one-half times as long as the posterior margin of the first plus second marginal tooth. This extreme type of dentition is found in *Tauritermes*, *Allotermes*, *Epicalotermes*, *Procryptotermes*, and *Cryptotermes*, and has probably evolved independently in several of these genera of the three branches.

Incisitermes has retained the ancestral wing venation. The imago mandible, however, has advanced, i.e., the anterior margin of the third marginal tooth in the left mandible is plainly longer, but not more than one and one-half times longer, than the posterior margin of the first plus second marginal tooth. The arolium may be present or absent, because of convergent reduction. The soldier head is dorsoventrally flat; the anterior margin of the pronotum is deeply incised; the third article of the antenna is dark, long, and club-shaped. The distribution of the species is: Papuan (eight, including three new spe-

cies), Indo-Malayan (two), Malagasy (one new species), Nearctic (seven, including one new species), and Neotropical (16, including six new species). The distribution of species suggests a New World origin.

Marginitermes is an endemic genus of western United States and western Mexico. It probably arose from an *Incisitermes*-like stock. The imago mandible and wing venation are similar to those of *Incisitermes*. The arolium is always absent. The soldier is specialized and has a somewhat phragmotic head, with a raised margin between the vertex and the frons. The third antennal segment is enlarged and as long as the next five to seven segments together.

Allotermes is an endemic genus of Madagascar which probably arose from an *Incisitermes*-like stock. The wing venation resembles that of the genus *Incisitermes*. The imago mandible is slightly more advanced, i.e., the length of the anterior margin of the third marginal tooth of the left mandible is more than one and one-half times the length of the posterior margin of the first plus second marginal tooth.

Tauritermes also was probably derived from an *Incisitermes*-like stock. It is endemic to South America. The imago is unknown, but the nymph mandible is *Allotermes*-like. The soldier is specialized and has a phragmotic head.

Proneotermes probably arose from an *Incisitermes*-like base. The imago mandible is like that of *Incisitermes*. The wing venation is more advanced than that of *Incisitermes*. The median vein in the forewing is weakly sclerotized, running closer to the radial sector than to the cubitus. The wing venation resembles that of the genera *Paraneotermes*, *Ceratokalotermes*, and *Comatermes* of the first main line, because of convergent evolution. The genus is endemic to Central and South America.

The second branch is represented by *Bifiditermes*, *Bicornitermes*, and *Epicalotermes*, and arose from a common ancestor. The wing venation is similar in the three genera, i.e., the media and cubitus in the forewing branch from a common stem outside the wing scale. An arolium is lacking.

Bifiditermes is the most primitive genus of this branch. The imago mandible is similar to

that of the genus *Incisitermes*, i.e., the anterior margin of the third marginal tooth in the left mandible is plainly longer, but not more than one and one-half times longer, than the posterior margin of the first plus second marginal tooth. The distribution of the species is: Australian (two), Indo-Malayan (four, including one new species), Ethiopian (seven, including one new species), and Malagasy (two, including one new species). The genus is confined to the tropics of the Old World. The distribution pattern suggests a probable origin in the Ethiopian Region in Cretaceous times.

Bicornitermes probably descended directly from *Bifiditermes*. The imagoes of the two genera are similar. The soldier is specialized and has developed a highly phragmotic head. The distribution of species is Ethiopian (four, including one new species). The genus probably originated in Tertiary times in the Ethiopian Region.

Epicalotermes is more advanced than *Bifiditermes* and *Bicornitermes*, as is indicated by the imago mandible. The anterior margin of the third marginal tooth of the left mandible is more than one and one-half times longer than the posterior margin of the first plus second marginal tooth. The soldier has a flat head, and the mandibles are strongly curved. The distribution of species is: Ethiopian (four) and Malagasy (one new species). The genus probably originated in the Ethiopian Region and dispersed to Madagascar in the late Cretaceous or early Eocene before it became isolated from the mainland.

The third branch is represented by *Procryptotermes* and *Cryptotermes*. The imago mandible and wing venation are similar in the two genera. The anterior margin of the third

marginal tooth of the left mandible is more than one and one-half times longer than the posterior margin of the first plus second marginal tooth. The median vein in the forewing is weak and unsclerotized, running midway between the radial sector and the cubitus in the proximal half of the wing, bending up near the middle or beyond the middle to meet the radial sector.

Procryptotermes is more primitive than *Cryptotermes*, as is indicated by the soldier, which does not have such a highly developed, phragmotic head, or other adaptations that are associated with the phragmotic head. The distribution of species is: Papuan (three, including one new species), Ethiopian (one), Malagasy (two, including one new species), and Neotropical (three, including two new species). It is strictly a tropical genus and is found only on islands, an indication that it is an ecological relict. The place of origin is obscure.

Cryptotermes probably arose directly from *Procryptotermes*, which is indicated by a transition in the development of the phragmotic head from *Procryptotermes* to *Cryptotermes*. The distribution of species is: Australian (six, including two new species), Papuan (eight, including five new species), Indo-Malayan (five), Ethiopian (four), Malagasy (two, including one new species), Nearctic (one), and Neotropical (nine, including five new species). The genus is primarily tropical, with the exception of a single species in the warm temperate region of Florida, and capable of living under dry conditions; therefore it has often been introduced into other continents. The world-wide distribution indicates a very ancient origin. The place of origin is obscure.

DISCUSSION

CONSERVATIVE CHARACTERS

ALTHOUGH IT IS DIFFICULT to prove that a given structure has no adaptive value, the evidence sometimes points strongly in that direction. In termites, the imago-worker mandibles are adaptive in their biting and chewing functions, but the morphological differences in the dentition of various genera and higher categories are very conservative, non-adaptive, or weakly adaptive, slowly evolving characters, compared to the more rapidly evolving and highly adaptive characters of the soldier, which are presumably under high selection pressure. The dentition of the imago mandible does not change with change of food habits. Termites that eat the same food have entirely different dentitions according to their systematic relationships; conversely, closely related termites that occupy different niches and utilize different food have similar mandibles. Emerson (*in* Allee *et al.*, 1949) and Ahmad (1950) postulate that multiple genes that influence the development of the imago-worker mandible have pleiotropic effects, some of them affecting the development of vital adaptations in other bodily activities. Selection for these multiple effects gradually produces evolutionary changes in the imago-worker mandible. Circumstantial evidence indicates that these gene complexes have been stable for long geological periods. Therefore this highly conservative pattern gives us a clue to basic phylogenetic relationships.

CONVERGENCE

The present study reveals many cases of convergence in the phylogeny of the kalotermitid genera. Serious mistakes have been made in the use of such analogous characters for phylogenetic interpretations.

The phragmotic or truncate head is a defensive adaptation for a plugging of the passageways in the wood. The evolution of the extremely phragmotic head has taken place seven times in both major branches of the phylogenetic tree of the family Kalotermitidae. The genera that show this adaptation are: *Kalotermites*, *Eucryptotermites*, *Glyptotermites*, *Calcaritermites*, *Tauritermites*, *Bicornitermites*, and *Cryptotermites*.

On the basis of this adaptive character, some species were erroneously placed in *Cryptotermites* or *Procryptotermites*. The imago mandible, wing venation, and other associated characters show that this adaptation has evolved independently many times.

The third segment of the soldier antenna is greatly enlarged, dark, and highly sclerotized. The adaptive function of this enlarged segment is unknown; it is probably sensory. Such an adaptation has evolved independently in almost all the genera of the *Incisitermites-Cryptotermites* complex (except *Cryptotermites*), and in *Pterotermites*, *Rugitermites*, and a few species of *Neotermites*.

In *Proneotermites*, *Paraneotermites*, *Ceratokalotermites*, and *Comatermites*, the median vein in the forewing is slightly sclerotized, running midway between the radial sector and the cubitus. This wing venation has evolved independently in the two major branches of the phylogenetic tree.

The arolium has convergently regressed in some or all of the species of the following genera: *Pterotermites*, *Paraneotermites*, *Neotermites*, *Incisitermites*, *Marginitermites*, *Allostermites*, *Bifiditermites*, *Epicalotermites*, *Bicornitermites*, and *Cryptotermites*.

REGRESSION

The modern theory of regressive evolution formulated by Emerson (*in* Allee *et al.*, 1949) is based on the following factors: most genes (pleiotropic) affect more than one character; most characters (polygenic) are affected by more than one gene; each gene mutates at a specific statistical rate; most mutations are deleterious; and entire organisms or unitary populations are selected as whole entities as well as the parts of each.

A character would be expected to remain functional as long as it is maintained by a positive selection pressure. Decrease or loss of this selection pressure will not prevent the gradual regression of the structure. Regression may also take place in the absence of negative selection pressure. If one character decreases in importance relative to others, there will be a shift in the allelic frequency in many gene systems, with consequent degen-

TABLE 4

CHARACTERS THAT SHOW PHYLOGENETIC ADVANCE IN THE FAMILY KALOTERMITIDAE

Primitive Condition	Derivative Condition
IMAGO	
Left imago-nymph mandible with anterior margin of third marginal tooth equal to posterior margin of first plus second marginal tooth	Left imago-nymph mandible with anterior margin of third marginal tooth longer than posterior margin of first plus second marginal tooth
Right mandible with posterior margin of second marginal tooth equal to molar plate	Right mandible with posterior margin of second marginal tooth longer than molar plate
Median vein weak and unsclerotized, running midway between radial sector and cubitus, to tip of wing	Media strongly sclerotized, running closer to radial sector than to cubitus, to tip of wing or joining radial sector
Damp-wood dwellers	Dry-wood dwellers
SOLDIER	
Head long, thick, or flat	Head short, truncate, or phragmotic
Third segment of antennae short, and not strongly sclerotized	Third segment of antennae long, club-shaped, and highly sclerotized
Anterior margin of pronotum slightly emarginate	Anterior margin of pronotum deeply incised
Anterior margin of pronotum smooth	Anterior margin of pronotum serrated

eration of this less important character and an increased development of the others. Thus a positive selection pressure for other characters which are genetically and epigenetically interconnected with the regressed characters would secondarily produce a more rapid regression of the neutral or less valuable character.

HOST-PROTOZOA RELATIONSHIP

The Protozoa have accompanied the termites during their phylogenetic development, so are particularly related to the limited group of hosts in which they occur. For these reasons, the Protozoa have been used as indicators of relationship of the hosts (Kirby, 1937a, 1944, 1947, 1949b). Concomi-

TABLE 5

CHARACTERS THAT SHOW PHYLOGENETIC REGRESSION IN THE FAMILY KALOTERMITIDAE

Primitive Condition	Derivative Condition
IMAGO	
Median vein in hind wing present	Median vein in hind wing absent
Anal vein present	Anal vein absent
Subcosta present	Subcosta absent
Tibial spines in middle tibia present	Tibial spines in middle tibia absent
Arolium present	Arolium absent
Antennal segments numerous (21 in <i>Pterotermes</i>)	Antennal segments fewer (11 in <i>Glyptotermes</i>)
Branches of radial sector present	Branches of radial sector absent
SOLDIER	
Mandibles long	Mandibles reduced
Left mandible with three prominent marginal teeth	Left mandible with reduced number of or no marginal teeth
Right mandible with two marginal teeth	Right mandible with reduced number of or no marginal teeth
Eyes pigmented	Eyes unpigmented
Wing pads present	Wing pads absent
Antenna with numerous segments (maximum number 19)	Antenna with fewer segments (minimum number 10)
Spines in middle tibia present	Spines in middle tibia absent

tant studies of Protozoa and their hosts have been made a basis for conclusions about their phylogeny and biogeographical and evolutionary history. I compiled a Protozoa and host list (table 6) to find corroborative evidence for my present generic classification.

It is evident from the Protozoa-host data that evolution of the genera of Protozoa did

not occur in conjunction with the evolution of the kalotermitid genera. Because certain genera of Protozoa are characteristic of the family Kalotermitidae rather than of the genus of the host, it seems that the generic differentiation of the Protozoa took place before the differentiation of the kalotermitid genera.

TABLE 6

SYSTEMATIC LIST OF THE PROTOZOA SYMBIOTIC OF THE FAMILY KALOTERMITIDAE

Protozoa	Hosts
POLYMASTIGIDA	
FAMILY CALONYMPHIDAE	
<i>Calonympha grassii</i> Foà	<i>Cryptotermes brevis</i> (Walker)
<i>Coronympha clevelandi</i> Kirby	<i>Incisitermes immigrans</i> (Snyder)
<i>Coronympha octonaria</i> Kirby	<i>Incisitermes emersoni</i> (Light)
	<i>Incisitermes pacificus</i> (Banks)
	<i>Incisitermes tabogae</i> (Banks)
	<i>Incisitermes platycephalus</i> (Light)
	<i>Incisitermes lighti</i> (Snyder)
<i>Diplonympha foae</i> Grassi	<i>Glyptotermes parvulus</i> (Sjöstedt)
<i>Metacoronympha senta</i> Kirby	<i>Incisitermes tabogae</i> (Banks)
	<i>Incisitermes lighti</i> (Snyder)
	<i>Incisitermes emersoni</i> (Light)
	<i>Incisitermes platycephalus</i> (Light)
<i>Snyderella bandeirantium</i> de Mello	<i>Cryptotermes brevis</i> (Walker)
<i>Snyderella tabogae</i> Kirby	<i>Cryptotermes longicollis</i> Banks
<i>Snyderella ypiranga</i> de Mello	<i>Rugitermes rugosus</i> (Hagen)
<i>Stephanonympha campinae</i> de Mello	<i>Neotermes hirtellus</i> (Silvestri)
<i>Stephanonympha erythrei</i> Grassi	<i>Neotermes erythraeus</i> Silvestri
<i>Stephanonympha havilandi</i> Grassi	<i>Cryptotermes havilandi</i> (Sjöstedt)
<i>Stephanonympha nelumbium</i> Kirby	<i>Cryptotermes domesticus</i> (Haviland)
<i>Stephanonympha reenstierna</i> de Mello	<i>Cryptotermes</i> sp.
<i>Stephanonympha silvestrii</i> Janicki	<i>Neotermes connexus</i> Snyder
FAMILY DEVESCOVINIDAE	
<i>Achemon platycaryon</i> Grassé and Hollande	<i>Cryptotermes havilandi</i> (Sjöstedt)
<i>Bullonympha silvestrii</i> Kirby	<i>Neotermes erythraeus</i> Silvestri
<i>Caduceia bugnioni</i> Kirby	<i>Neotermes greeni</i> (Desneux)
<i>Caduceia kalshoveni</i> Kirby	<i>Neotermes dalbergiae</i> (Kalshoven)
<i>Caduceia kofoidi</i> Kirby	<i>Glyptotermes guianensis</i> Emerson
	<i>Glyptotermes perparvus</i> Emerson
<i>Caduceia monile</i> Kirby	<i>Neotermes tectonae</i> (Dammermann)
<i>Caduceia nova</i> (Grassi)	<i>Neotermes</i> , new species, from Tanganyika
	<i>Neotermes erythraeus</i> Silvestri
<i>Caduceia pruvoti</i> (Duboscq and Grassé)	? <i>Kalotermes</i> sp. from Lifou, Loyalty Islands
<i>Caduceia theobromae</i> Franca	<i>Neotermes gestri</i> Silvestri
	<i>Neotermes aburiensis</i> Sjöstedt
<i>Devescovina arta</i> Kirby	<i>Bifiditermes mutabae</i> (Harris)
	<i>Bifiditermes</i> , new species, from Transvaal
	<i>Glyptotermes angustus</i> Snyder
	<i>Glyptotermes minutus</i> Kemner
	<i>Neotermes castaneus</i> (Burmeister)

TABLE 6—(Continued)

Protozoa	Hosts
<i>Devescovina coghilli</i> Kirby	<i>Cryptotermes merwei</i> Fuller
<i>Devescovina cometoides</i> de Mello and de Britto	? <i>Kalotermes</i> sp. from Damann, India
	<i>Cryptotermes dudleyi</i> Banks
	<i>Glyptotermes dilatatus</i> (Bugnion and Popoff)
	<i>Glyptotermes</i> , new species, from Java
	<i>Incisitermes repandus</i> (Hill)
<i>Devescovina cuneata</i> Kirby	<i>Neotermes</i> , new species, from El Salvador
<i>Devescovina exilis</i> Kirby	<i>Neotermes connexus</i> Snyder
<i>Devescovina fissa</i> Kirby	<i>Procryptotermes</i> , new species, from Réunion
<i>Devescovina glabra</i> Grassi	<i>Cryptotermes havilandi</i> (Sjöstedt)
	<i>Cryptotermes kirbyi</i> Moszkowski
	<i>Cryptotermes dudleyi</i> Banks
	<i>Glyptotermes caudomunitus</i> Kemner
	<i>Glyptotermes</i> , new species, from Sumatra
	<i>Bifiditermes madagascariensis</i> (Wasmann)
	<i>Neotermes zuluensis</i> Holmgren
	<i>Neotermes meruensis</i> (Sjöstedt)
	<i>Neotermes europae</i> (Wasmann)
<i>Devescovina hawaiiensis</i> Janicki	<i>Neotermes connexus</i> Snyder
<i>Devescovina insolita</i> Kirby	<i>Neotermes</i> , new species, from Tanganyika
	<i>Bifiditermes</i> , new species, from Transvaal
<i>Devescovina lemniscata</i> Kirby	<i>Cryptotermes domesticus</i> (Haviland)
	<i>Cryptotermes dudleyi</i> Banks
	<i>Cryptotermes fatulus</i> Light
	<i>Cryptotermes havilandi</i> (Sjöstedt)
	<i>Cryptotermes cynocephalus</i> Light
	<i>Cryptotermes queenslandis</i> Hill
	? <i>Kalotermes</i> sp. from Damann, India
	<i>Glyptotermes tuberculatus</i> Froggatt
	? <i>Glyptotermes caudomunitus</i> Kemner
	<i>Neotermes insularis</i> (White)
	<i>Neotermes larseni</i> Light
	<i>Postelectrotermes castaneiceps</i> (Sjöstedt)
	<i>Postelectrotermes</i> , new species, from near Ihosy, Madagascar
	<i>Postelectrotermes longiceps</i> (Cachan)
	<i>Postelectrotermes longus</i> (Holmgren)
<i>Devescovina lepida</i> Kirby	<i>Calcaritermes brevicollis</i> (Banks)
	<i>Calcaritermes emarginicollis</i> (Snyder)
	<i>Calcaritermes nearcticus</i> Snyder
	<i>Calcaritermes parvinotus</i> Light
	<i>Calcaritermes nigriceps</i> Emerson
	<i>Calcaritermes</i> , new species, from El Salvador
	<i>Cryptotermes longicollis</i> Banks
	<i>Neotermes castaneus</i> (Burmeister)
	<i>Neotermes holmgreni</i> Banks
<i>Devescovina minor</i> Kirby	<i>Glyptotermes perparvus</i> Emerson
	<i>Glyptotermes guianensis</i> Emerson
<i>Devescovina parasoma</i> Kirby	<i>Neotermes tectonae</i> (Dammermann)
	<i>Neotermes dalbergiae</i> (Kalshoven)
	<i>Neotermes sonneratae</i> Kemner
	<i>Cryptotermes cynocephalus</i> Light
	<i>Cryptotermes havilandi</i> (Sjöstedt)

TABLE 6—(Continued)

Protozoa	Hosts
<i>Devescovina robusta</i> Kirby	<i>Neotermes erythraeus</i> Silvestri
<i>Devescovina similis</i> Kirby	<i>Cryptotermes havilandi</i> (Sjöstedt)
<i>Devescovina striata</i> Foà	<i>Cryptotermes brevis</i> (Walker)
<i>Devescovina tendicula</i> Kirby	<i>Bifiditermes mutabae</i> (Harris)
<i>Devescovina transita</i> Kirby	<i>Cryptotermes cynocephalus</i> Light
	<i>Glyptotermes</i> , new species, from Java
	<i>Glyptotermes dilatatus</i> (Bugnion and Popoff)
	<i>Incisitermes repandus</i> (Hill)
<i>Devescovina uniflexa</i> Kirby	<i>Proneotermes perezi</i> Holmgren
<i>Devescovina vestita</i> Kirby	<i>Glyptotermes niger</i> Kemner
<i>Devescovina vittata</i> Kirby	<i>Bifiditermes jeannelanus</i> (Sjöstedt)
<i>Evemonia punctata</i> Grassé	<i>Neotermes aburiensis</i> Sjöstedt
<i>Evemonia ramosa</i> Kirby	<i>Neotermes aburiensis</i> Sjöstedt
<i>Foaina ? acontophora</i> Kirby	<i>Glyptotermes guianensis</i> Emerson
<i>Foaina acontophora</i> Kirby	<i>Glyptotermes perparvus</i> Emerson
	<i>Cryptotermes havilandi</i> (Sjöstedt)
	<i>Postelectrotermes castaneiceps</i> (Sjöstedt)
	<i>Postelectrotermes longiceps</i> (Cachan)
	<i>Postelectrotermes longus</i> (Holmgren)
<i>Foaina appendicula</i> Kirby	<i>Glyptotermes minutus</i> Kemner
<i>Foaina calmoni</i> de Mello	<i>Cryptotermes havilandi</i> (Sjöstedt)
<i>Foaina costata</i> Kirby	<i>Neotermes insularis</i> (White)
<i>Foaina decipiens</i> (Grassé)	<i>Neotermes aburiensis</i> Sjöstedt
<i>Foaina delicata</i> Kirby	<i>Glyptotermes iridipennis</i> Froggatt
	<i>Glyptotermes brevicornis</i> Froggatt
<i>Foaina dogieli</i> (Duboscq and Grassé)	<i>Glyptotermes neotuberculatus</i> Hill
<i>Foaina duo</i> Kirby	<i>Kalotermes flavicollis</i> (Fabricius)
<i>Foaina exempta</i> Kirby	<i>Glyptotermes niger</i> Kemner
<i>Foaina falcifera</i> Kirby	<i>Neotermes insularis</i> (White)
	<i>Glyptotermes contracticornis</i> (Snyder)
<i>Foaina fontesi</i> de Mello	<i>Glyptotermes montanus</i> Kemner
<i>Foaina funifera</i> Kirby	<i>Cryptotermes havilandi</i> (Sjöstedt)
	<i>Cryptotermes queenslandis</i> Hill
<i>Foaina gracilis</i> Janicki	<i>Glyptotermes tuberculatus</i> Froggatt
<i>Foaina grassii</i> (Duboscq and Grassé)	<i>Neotermes connexus</i> Snyder
	<i>Neotermes</i> , new species, from El Salvador
	<i>Kalotermes flavicollis</i> (Fabricius)
<i>Foaina hamata</i> Kirby	<i>Kalotermes dispar</i> Grassé
	<i>Glyptotermes hospitalis</i> Emerson
	<i>Glyptotermes ueleensis</i> Coaton
	<i>Glyptotermes parvulus</i> (Sjöstedt)
	<i>Glyptotermes caudomunitus</i> Kemner
	<i>Glyptotermes</i> sp. from Java
	<i>Cryptotermes kirbyi</i> Moszkowski
<i>Foaina hilli</i> (Duboscq and Grassé)	<i>Neotermes</i> , new species, from El Salvador
	<i>Glyptotermes iridipennis</i> Froggatt
<i>Foaina humilis</i> Kirby	<i>Glyptotermes brevicornis</i> Froggatt
<i>Foaina inflata</i> Kirby	<i>Cryptotermes brevis</i> (Walker)
<i>Foaina minuscula</i> Kirby	<i>Neotermes</i> , new species, from El Salvador
	<i>Allotermes</i> , new species, from near Mahabo, Madagascar
<i>Foaina nana</i> (Kirby)	<i>Calcaritermes</i> , new species, from El Salvador
	<i>Calcaritermes brevicollis</i> (Banks)

TABLE 6—(Continued)

Protozoa	Hosts
<i>Foaina nana</i> (Kirby)	<i>Calcaritermes emarginicollis</i> (Banks) <i>Calcaritermes nearcticus</i> Snyder <i>Calcaritermes nigriceps</i> (Emerson) <i>Cryptotermes cubicocephus</i> Emerson <i>Cryptotermes domesticus</i> (Haviland) <i>Cryptotermes cynocephalus</i> Light <i>Cryptotermes brevis</i> (Walker) <i>Cryptotermes dudleyi</i> Banks <i>Cryptotermes fatulus</i> Light <i>Cryptotermes havilandi</i> (Sjöstedt) <i>Glyptotermes dilatatus</i> (Bugnion and Popoff) <i>Glyptotermes taveuniensis</i> Hill <i>Glyptotermes</i> , new species, from Java <i>Glyptotermes</i> , new species, from Sumatra <i>?Kalotermes</i> sp. from Damann, India <i>Bifiditermes condonensis</i> (Hill) <i>Bifiditermes madagascariensis</i> (Wasmann) <i>Incisitermes repandus</i> (Hill) <i>Neotermes connexus</i> Snyder <i>Neotermes dalbergiae</i> (Kalshoven) <i>Neotermes greeni</i> (Desneux) <i>Neotermes larseni</i> Light <i>Neotermes sonneratae</i> Kemner <i>Neotermes tectonae</i> (Dammermann) <i>Allotermes</i> , new species, from near Mahabo, ² Madagascar <i>Rugitermes magninotus</i> Emerson <i>Rugitermes kirbyi</i> Snyder <i>Rugitermes panamae</i> (Snyder)
<i>Foaina ovata</i> Kirby	<i>Postelectrotermes howa</i> (Wasmann) <i>Neotermes desneuxi</i> (Sjöstedt) <i>Neotermes gracilidens</i> Sjöstedt
<i>Foaina parvula</i> Kirby	<i>Glyptotermes contracticornis</i> (Snyder) <i>Glyptotermes montanus</i> Kemner <i>Glyptotermes neotuberculatus</i> Hill <i>Glyptotermes taveuniensis</i> Hill <i>Bifiditermes jeannelanus</i> (Sjöstedt) <i>Bifiditermes</i> , new species, from Transvaal <i>Neotermes erythraeus</i> Silvestri <i>Postelectrotermes castaneiceps</i> (Sjöstedt) <i>Postelectrotermes longus</i> (Holmgren) <i>Postelectrotermes longiceps</i> (Cachan) <i>Neotermes</i> , new species, from Tanganyika
<i>Foaina ramulosa</i> Kirby	<i>Cryptotermes kirbyi</i> Moszkowski
<i>Foaina reflexa</i> Kirby	<i>Calcaritermes nigriceps</i> (Emerson) <i>Calcaritermes brevicollis</i> (Banks) <i>Calcaritermes emarginicollis</i> (Banks) <i>Calcaritermes nearcticus</i> Snyder <i>Calcaritermes parvinotus</i> Light <i>Proneotermes perezii</i> Holmgren <i>Cryptotermes brevis</i> (Walker) <i>Cryptotermes cavifrons</i> Banks <i>Cryptotermes longicollis</i> Banks

TABLE 6—(Continued)

Protozoa	Hosts
<i>Foaina reflexa</i> Kirby	<i>Cryptotermes havilandi</i> (Sjöstedt) <i>Bifiditermes jeannelanus</i> (Sjöstedt) <i>Bifiditermes mutabae</i> (Harris) <i>Epicalotermes mkuzii</i> (Coaton) <i>Neotermes castaneus</i> (Burmeister) <i>Neotermes erythraeus</i> Silvestri <i>Neotermes holmgreni</i> Banks <i>Neotermes meruensis</i> (Sjöstedt) <i>Neotermes zuluensis</i> Holmgren <i>Neotermes europae</i> (Wasmann) <i>Neotermes</i> , new species, from Tanganyika <i>Epicalotermes kempae</i> (Wilkinson) <i>Bifiditermes</i> , new species, from Transvaal <i>Neotermes</i> , new species, from El Salvador
<i>Foaina serrata</i> Kirby	<i>Bifiditermes jeannelanus</i> (Sjöstedt)
<i>Foaina signata</i> Kirby	<i>Neotermes meruensis</i> (Sjöstedt) <i>Neotermes zuluensis</i> Holmgren <i>Neotermes europae</i> (Wasmann)
<i>Foaina solita</i> Kirby	<i>Cryptotermes dudleyi</i> Banks <i>Cryptotermes longicollis</i> Banks <i>Cryptotermes havilandi</i> (Sjöstedt) <i>Glyptotermes angustus</i> Snyder <i>Glyptotermes dilatatus</i> (Bugnion and Popoff) <i>Glyptotermes parvulus</i> (Sjöstedt) <i>Glyptotermes tuberculatus</i> Froggatt <i>Glyptotermes ueleensis</i> Coaton <i>Glyptotermes</i> , new species, from near Rutchuru, the Congo <i>Glyptotermes</i> , new species, from Ruanda-Urundi, the Congo <i>Bifiditermes mutabae</i> (Harris) ? <i>Kalotermes</i> sp. from Damann, India <i>Bifiditermes madagascariensis</i> (Wasmann) <i>Incisitermes repandus</i> (Hill) <i>Cryptotermes queenslandis</i> Hill <i>Neotermes castaneus</i> (Burmeister) <i>Neotermes connexus</i> Snyder <i>Neotermes greeni</i> Holmgren <i>Neotermes holmgreni</i> Banks <i>Neotermes sonneratae</i> Kemner <i>Neotermes tectonae</i> (Dammermann) <i>Procryptotermes</i> , new species, from Réunion <i>Rugitermes kirbyi</i> Snyder <i>Rugitermes panamae</i> (Snyder) <i>Rugitermes magninotus</i> Emerson <i>Paraneotermes simplicicornis</i> (Banks) <i>Ceratokalotermes spoliator</i> (Hill) <i>Kalotermes umtatae</i> (Coaton) <i>Kalotermes brouni</i> Froggatt <i>Kalotermes rufinotum</i> Hill <i>Kalotermes banksiae</i> Hill <i>Postelectrotermes militaris</i> (Desneux) <i>Kalotermes pallidinotum</i> Hill <i>Kalotermes tillyardi</i> Hill
<i>Foaina taenicola</i> Kirby	
<i>Hyperdevescovina balteata</i> Kirby	
<i>Hyperdevescovina caudata</i> Kirby	
<i>Hyperdevescovina calotermitis</i> (Nurse)	
<i>Hyperdevescovina falcifera</i> Kirby	
<i>Hyperdevescovina insignita</i> Kirby	
<i>Hyperdevescovina mitrata</i> Kirby	

TABLE 6—(Continued)

Protozoa	Hosts
<i>Hyperdevescovina riciniata</i> Kirby	<i>Kaloterme atratus</i> (Hill)
<i>Hyperdevescovina torquata</i> Kirby	<i>Kaloterme hilli</i> (Emerson)
<i>Macrotrichomonas directa</i> Kirby	<i>Incisitermes</i> , new species, from El Salvador
<i>Macrotrichomonas emersoni</i> Kirby	<i>Glyptoterme hospitalis</i> Emerson
<i>Macrotrichomonas hirsuta</i> Grassé and Hollande	<i>Postelectrotermes barreto</i> (Grassé)
	<i>Postelectrotermes praecox</i> (Grassé)
<i>Macrotrichomonas lighti</i> (Connell)	<i>Paraneoterme simplicicornis</i> (Banks)
<i>Macrotrichomonas procera</i> Kirby	<i>Calcaritermes brevicollis</i> (Banks)
	<i>Calcaritermes emarginicollis</i> (Banks)
	<i>Calcaritermes nearcticus</i> Snyder
	<i>Calcaritermes parvinotus</i> Light
	<i>Calcaritermes</i> , new species, from El Salvador
<i>Macrotrichomonas pulchra</i> Grassi	<i>Glyptoterme parvulus</i> (Sjöstedt)
	<i>Glyptoterme ceylonicus</i> Holmgren
	<i>Glyptoterme contracticornis</i> (Snyder)
	<i>Glyptoterme brevicornis</i> Froggatt
	<i>Glyptoterme iridipennis</i> Froggatt
	<i>Glyptoterme montanus</i> Kemner
	<i>Glyptoterme neotuberculatus</i> Hill
	<i>Glyptoterme taveuniensis</i> Hill
	<i>Glyptoterme ueleensis</i> Coaton
	<i>Glyptoterme</i> , new species, from the Congo
	<i>Glyptoterme</i> , new species, from Ruanda-Urundi, the Congo
	<i>Glyptoterme magsaysayi</i> Snyder
<i>Macrotrichomonas ramosa</i> Kirby	<i>Glyptoterme brevicaudatus</i> (Haviland)
<i>Macrotrichomonas restis</i> Kirby	<i>Neoterme jouteli</i> (Banks)
<i>Macrotrichomonas unguis</i> Kirby	<i>Glyptoterme caudomunitus</i> Kemner
	<i>Glyptoterme</i> sp. from Java
	<i>Glyptoterme minutus</i> Kemner
<i>Macrotrichomonas virgosa</i> Kirby	<i>Alloterme</i> , new species, from Mahabo, Madagascar
<i>Metadevescovina carina</i> Kirby	<i>Bifiditerme madagascariensis</i> (Wasmann)
<i>Metadevescovina cristata</i> Kirby	<i>Bifiditerme angulatus</i> (Wilkinson)
<i>Metadevescovina cuspidata</i> Kirby	<i>Incisiterme minor</i> (Hagen)
<i>Metadevescovina debilis</i> Light	<i>Marginiterme hubbardi</i> (Banks)
<i>Metadevescovina fulleri</i> Kirby	<i>Bifiditerme madagascariensis</i> (Wasmann)
	<i>Bifiditerme durbanensis</i> (Haviland)
	<i>Epicaloterme munroi</i> (Coaton)
	<i>Epicaloterme mkuzii</i> (Coaton)
<i>Metadevescovina magna</i> Kirby	<i>Epicaloterme</i> , new species, from Tulear, Madagascar
<i>Metadevescovina mediocris</i> Kirby	<i>Incisiterme marginipennis</i> (Latreille)
	<i>Glyptoterme</i> , new species, from near Rutchuru, the Congo
	<i>Glyptoterme</i> , new species, from Ruanda-Urundi, the Congo
<i>Metadevescovina modesta</i> Kirby	<i>Glyptoterme angustus</i> Snyder
<i>Metadevescovina modica</i> Kirby	<i>Incisiterme marginipennis</i> (Latreille)
<i>Metadevescovina nitida</i> Kirby	<i>Alloterme paradoxus</i> Wasmann
	<i>Alloterme</i> , new species, from Tsihombe, Madagascar
<i>Metadevescovina nudula</i> Kirby	<i>Neoterme jouteli</i> (Banks)
<i>Metadevescovina patula</i> Kirby	<i>Bifiditerme condonensis</i> (Hill)
<i>Metadevescovina polyspira</i> (Lewis)	<i>Pteroterme occidentis</i> (Walker)
<i>Metadevescovina stereociliata</i> (Grassi)	<i>Glyptoterme parvulus</i> (Sjöstedt)
	<i>Glyptoterme ueleensis</i> Coaton

TABLE 6—(Continued)

Protozoa	Hosts
<i>Metadevescovina turbula</i> Kirby	<i>Neotermes jouteli</i> (Banks)
<i>Parajoenia grassii</i> Janicki	<i>Neotermes connexus</i> Snyder
<i>Pseudodevescovina brevirostris</i> Grassé	<i>Neotermes aburiensis</i> Sjöstedt
<i>Pseudodevescovina uniflagellata</i> Sutherland	<i>Neotermes insularis</i> (White)
<i>Stellaria nucleoflexa</i> (Kirby)	<i>Cryptotermes merwei</i> Fuller
	<i>Cryptotermes havilandi</i> (Sjöstedt)
	<i>Cryptotermes kirbyi</i> Moszkowski
FAMILY MONOCERCOMONADIDAE	
<i>Hexamastix claviger</i> Kirby	<i>Incisitermes marginipennis</i> (Latreille)
	<i>Cryptotermes dudleyi</i> Banks
	<i>Calcaritermes brevicollis</i> (Banks)
<i>Hexamastix conclaviger</i> Kirby	<i>Cryptotermes brevis</i> (Walker)
<i>Hexamastix disclaviger</i> Kirby	<i>Cryptotermes brevis</i> (Walker)
	<i>Cryptotermes longicollis</i> Banks
<i>Tricercomitus cunhai</i> de Mello	<i>Cryptotermes havilandi</i> (Sjöstedt)
<i>Tricercomitus damasmorai</i> de Mello	<i>Cryptotermes</i> sp.
<i>Tricercomitus divergens</i> Kirby	<i>Marginitermes hubbardi</i> (Banks)
	<i>Incisitermes minor</i> (Hagen)
	<i>Kalotermes flavicollis</i> (Fabricius)
	<i>Incisitermes immigrans</i> (Snyder)
	<i>Incisitermes lighti</i> (Snyder)
	<i>Incisitermes marginipennis</i> (Latreille)
	<i>Incisitermes tabogae</i> (Snyder)
	<i>Incisitermes</i> sp. from Galapagos Island
	<i>Incisitermes</i> sp. from Costa Rica
	<i>Calcaritermes brevicollis</i> (Banks)
	<i>Calcaritermes emarginicollis</i> (Snyder)
	<i>Glyptotermes angustus</i> Snyder
	<i>Glyptotermes contracticornis</i> (Snyder)
	<i>Cryptotermes longicollis</i> Banks
	<i>Neotermes connexus</i> Snyder
	<i>Neotermes holmgreni</i> Banks
	<i>Rugitermes kirbyi</i> Snyder
	<i>Rugitermes panamae</i> (Snyder)
	<i>Cryptotermes domesticus</i> Haviland
	<i>Cryptotermes brevis</i> (Walker)
	<i>Cryptotermes dudleyi</i> Banks
	<i>Cryptotermes domesticus</i> (Haviland)
	<i>Cryptotermes</i> sp. from Galapagos Island
FAMILY OXYMONADIDAE	
<i>Barroella coronaria</i> Cross	<i>Postelectrotermes howa</i> (Wasmann)
<i>Barroella zeteki</i> Zeliff	<i>Calcaritermes brevicollis</i> (Banks)
<i>Microrhopalodina hofmanni</i> (de Mello and de Mello)	<i>Cryptotermes</i> sp.
<i>Microrhopalodina inflata</i> Grassi and Foà	<i>Kalotermes flavicollis</i> (Fabricius)
<i>Microrhopalodina multinucleata</i> (Kofoid et al.)	<i>Cryptotermes dudleyi</i> Banks
<i>Microrhopalodina occidentis</i> (Lewis)	<i>Pterotermes occidentis</i> (Walker)
<i>Oxymonas barbouri</i> Zeliff	<i>Glyptotermes angustus</i> Snyder
<i>Oxymonas brevis</i> Zeliff	<i>Cryptotermes brevis</i> (Walker)
<i>Oxymonas caudata</i> Cross	<i>Proneotermes perezii</i> Holmgren
<i>Oxymonas clevelandi</i> Zeliff	<i>Incisitermes immigrans</i> (Snyder)
<i>Oxymonas dimorpha</i> Connell	<i>Paraneotermes simplicicornis</i> (Banks)
<i>Oxymonas di-undulata</i> Nurse	<i>Kalotermes brouni</i> Froggatt

TABLE 6—(Continued)

Protozoa	Hosts
<i>Oxymonas gracilis</i> Kofoid and Swezy	<i>Rugitermes magninotus</i> Emerson
<i>Oxymonas grandis</i> Cleveland	<i>Neotermes dalbergiae</i> (Kalshoven)
	<i>Neotermes tectonae</i> (Dammermann)
<i>Oxymonas granulosa</i> Janicki	<i>Neotermes connexus</i> Snyder
<i>Oxymonas hubbardi</i> Zelif	<i>Marginitermes hubbardi</i> (Banks)
<i>Oxymonas jouteli</i> Zelif	<i>Neotermes jouteli</i> (Banks)
<i>Oxymonas kirbyi</i> Zelif	<i>Rugitermes kirbyi</i> Snyder
<i>Oxymonas lutzi</i> de Mello	<i>Cryptotermes havilandi</i> (Sjöstedt)
<i>Oxymonas megakaryosoma</i> Cross	<i>Glyptotermes</i> , new species, from Uganda
<i>Oxymonas minor</i> Zelif	<i>Incisitermes minor</i> (Hagen)
<i>Oxymonas ovata</i> Zelif	<i>Calcaritermes brevicollis</i> (Banks)
<i>Oxymonas parvula</i> Kirby	<i>Cryptotermes domesticus</i> (Haviland)
<i>Oxymonas pediculosa</i> Kofoid and Swezy	<i>Calcaritermes nigriceps</i> (Emerson)
<i>Oxymonas projector</i> Kofoid and Swezy	<i>Glyptotermes perparvus</i> Emerson
<i>Oxymonas rotunda</i> Cross	<i>Calcaritermes emarginicollis</i> (Banks)
<i>Oxymonas snyderi</i> Zelif	<i>Cryptotermes domesticus</i> Haviland
FAMILY TRICHOMONADIDAE	
<i>Pentatrichomonoides scroa</i> Kirby	<i>Cryptotermes dudleyi</i> Banks
	<i>Cryptotermes longicollis</i> Banks
<i>Trichomonas barbouri</i> Kirby	<i>Glyptotermes angustus</i> Snyder
<i>Trichomonas brevicollis</i> Kirby	<i>Calcaritermes brevicollis</i> (Banks)
<i>Trichomonas cartagoensis</i> Kirby	<i>Glyptotermes contracticornis</i> (Snyder)
<i>Trichomonas holmgreni</i> Kirby	<i>Neotermes holmgreni</i> Banks
<i>Trichomonas</i> sp. (Duboscq and Grassé)	? <i>Kalotermes</i> sp. from Lifou, Loyalty Islands
HYPERMASTIGIDA	
FAMILY TRICHONYMPHIDAE	
<i>Eulophomonas calotermitis</i> Grassi	<i>Kalotermes flavicollis</i> (Fabricius)
<i>Hoplonympha natator</i> Light	<i>Paraneotermes simplicicornis</i> (Banks)
<i>Joenia annectens</i> Grassi	<i>Kalotermes flavicollis</i> (Fabricius)
<i>Kofoidia loriculata</i> Light	<i>Paraneotermes simplicicornis</i> (Banks)
<i>Mesojoenia decipiens</i> Grassi	<i>Kalotermes flavicollis</i> (Fabricius)
<i>Pseudotrichonympha sertaneja</i> de Mello	<i>Neotermes</i> , new species, from São Paulo, Brazil
<i>Spirotrichonympha polygyra</i> Cupp	<i>Paraneotermes simplicicornis</i> (Banks)
<i>Staurojoenina assimilis</i> Kirby	<i>Incisitermes minor</i> (Hagen)
<i>Staurojoenina</i> sp.	<i>Marginitermes hubbardi</i> (Banks)
<i>Staurojoenina mirabilis</i> Grassi	<i>Epicalotermes aethiopicus</i> Silvestri
<i>Trichonympha ampula</i> Kirby	<i>Pterotermes occidentis</i> (Walker)
<i>Trichonympha chattoni</i> Duboscq and Grassé	<i>Glyptotermes iridipennis</i> (Froggatt)
	<i>Glyptotermes brevicaudatus</i> (Haviland)
	<i>Glyptotermes brevicornis</i> Froggatt
	<i>Glyptotermes ceylonicus</i> Holmgren
	<i>Glyptotermes contracticornis</i> (Snyder)
	<i>Glyptotermes montanus</i> Kemner
	<i>Glyptotermes neotuberculatus</i> Hill
	<i>Glyptotermes parvulus</i> (Sjöstedt)
	<i>Glyptotermes taveuniensis</i> Hill
	<i>Glyptotermes ueleensis</i> Coaton
	<i>Glyptotermes</i> , new species, from Ruanda-Urundi, the Congo
	<i>Glyptotermes</i> , new species, from the Philippines
	<i>Incisitermes milleri</i> (Emerson)
	<i>Incisitermes schwarzi</i> (Banks)

TABLE 6—(Continued)

Protozoa	Hosts
<i>Trichonympha corbula</i> Kirby	<i>Allotermes</i> , new species, from near Mahabo, Madagascar
	<i>Postelectrotermes castaneiceps</i> (Sjöstedt)
	<i>Postelectrotermes longus</i> (Holmgren)
	<i>Postelectrotermes longiceps</i> (Cachan)
<i>Trichonympha divexa</i> Kirby	<i>Kalotermes umtatae</i> (Coaton)
<i>Trichonympha lighti</i> Kirby	<i>Incisitermes emersoni</i> (Light)
<i>Trichonympha peplophora</i> Kirby	<i>Postelectrotermes howa</i> (Wasmann)
	<i>Neotermes desneuxi</i> (Sjöstedt)
	<i>Neotermes gracilidens</i> Sjöstedt
	<i>Postelectrotermes amplius</i> (Sjöstedt)
<i>Trichonympha quasilla</i> Kirby	<i>Proneotermes perezii</i> Holmgren
<i>Trichonympha saepicula</i> Kirby	<i>Rugitermes kirbyi</i> Snyder
	<i>Rugitermes panamae</i> (Snyder)
<i>Trichonympha subquasilla</i> Kirby	<i>Incisitermes immigrans</i> (Snyder)
<i>Trichonympha tabogae</i> Kirby	<i>Incisitermes tabogae</i> (Snyder)
<i>Trichonympha teres</i> Kirby	<i>Neotermes meruensis</i> (Sjöstedt)
<i>Trichonympha zeylanica</i> (Dobell)	<i>Postelectrotermes militaris</i> (Desneux)
	<i>Kalotermes hilli</i> (Emerson)

SUMMARY

1. THE FAMILY Kalotermitidae is redescribed. The subfamily names "Electrotermitinae" and "Kalotermitinae" are placed in synonymy. The fossil genus *Eotermes* is removed from the family Kalotermitidae and placed in the family Hodotermitidae.

2. Three hundred and fifty-three species, fossil and living, are classified into 24 genera. Of these 24 genera, the following eight are new: *Postelectrotermes*, *Ceratokalotermes*, *Comatermes*, *Incisitermes*, *Marginitermes*, *Tauritermes*, *Bifiditermes*, and *Bicornitermes*. The genera *Pterotermes*, *Proneotermes*, *Allotermes*, and *Epicalotermes* are resurrected. The genus name "*Proglyptotermes*" is relegated to synonymy. All the genera are described, and the generitype species are illustrated.

3. The generic classification is based on a constellation of conservative, adaptive, and regressed characters of both the imago and the soldier castes.

4. The phylogeny of the genera is discussed. The imago-nymph mandible indicates

two main evolutionary lines. The first line is represented by the *Proelectrotermes-Calcaritermes* complex, and the second line by the *Incisitermes-Cryptotermes* complex.

5. Several cases of convergence are illustrated. In both the main lines of the family Kalotermitidae, the phragmotic head, the enlarged third antennal segment, and the slightly sclerotized median vein have all evolved independently many times. Also, the arolium has been convergently lost in many genera.

6. A discussion on conservative and regressed characters is included. Characters that show phylogenetic advancement or regression are also listed.

7. It is evident from the data on the hosts and Protozoa that the evolution of the genera of the Protozoa did not occur in conjunction with the evolution of the host genera and that the differentiation of the Protozoa genera took place before the differentiation of the host genera.

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