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## A Revision of the Tertiary Fossil Species of the Kalotermitidae (Isoptera)

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### INTRODUCTION

The present article belongs in a series that attempts to redescribe named species, to describe new species, and to classify those species of fossil Tertiary termites that have been available for firsthand study.

Preceding the present article, one (Emerson, 1965) dealt with the Mastotermitidae, one (Emerson, 1968a) described a new genus of the Hodotermitidae from Cretaceous rocks of Labrador, and one (Emerson, 1968b) dealt with the genus *Ulmeriella* of the Hodotermitidae. Weidner (1967) also revised *Ulmeriella* and described a new species from the Pliocene of Germany. Earlier (Emerson, 1933), the fossil species of the subfamily Termopsinae, family Hodotermitidae, were revised.

All known termite fossils are found in Cretaceous and Tertiary deposits with the exception of some that are found in Pleistocene copal from tropical Africa and the New World, which have not been studied by the author.

Of the nine genera and 16 named species of Tertiary Kalotermitidae, including those described herein, the author has examined specimens of 12 species. The remaining four are mentioned for bibliographical completeness. Type specimens have been studied when available, and lectotypes or neotypes have been selected if the holotypes were not

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designated by the original or subsequent authors or have been lost or destroyed.

In numerous cases the redescrptions enable a more adequate classification of species and genera, the systematic status of which has been poorly understood. Zoogeographical, ecological, and phylogenetic interpretations of generic order are discussed.

To monograph the fossil termites from redescrptions of named specimens is impossible, because collections have been lost or destroyed during wars, or, if still in existence, are so scattered in institutions around the world as to be unavailable to a single investigator. Some institutions have a policy of not lending types, and some are not sufficiently staffed for the search and loan of specimens.

Fossils do not allow the same degree of taxonomic accuracy as the abundant living species represented by all castes in nest series, but comparisons of fossils with living relatives remove some of these handicaps, and add an indispensable time dimension to phylogenetic and zoogeographic interpretations. The specialist dealing with a small order, such as the Isoptera, cannot possibly make the geological collections or assemble the fossils. He is therefore in great debt to the paleontologist for field collections, information about geologic strata, their age, and the associated fossil fauna and flora.

#### ACKNOWLEDGMENTS

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Type specimens of fossil termites were lent by Dr. Frank M. Carpenter, Curator of Fossil Insects, Museum of Comparative Zoology, Harvard University; Drs. Jerome G. Rozen, Jr., and Kumar Krishna, Department of Entomology, the American Museum of Natural History; Drs. W.

Dwight Pierce, Charles L. Hogue, and Herbert Friedmann, Los Angeles County Museum of Natural History; Dr. Rupert L. Wenzel and Henry Dybas, Field Museum of Natural History, Chicago; and Drs. Joseph H. Peck, Paul Hurd, W. B. N. Berry, and J. Wyatt Durham of the Museum of Paleontology, University of California, Berkeley.

Unidentified fossil specimens, including some new or rare species, were lent by the above institutions, and also by Dr. Sv. G. Larsson, Universitetets Zoologiske Museum and Mineralogic Museum, Copenhagen.

Preserved living termites for comparative studies were lent or given by Drs. Kumar Krishna; T. E. Snyder; W. V. Harris; H. Bytinski-Salz, Department of Entomology, Division of Plant Protection, Jaffa, Israel; E. M. Miller, University of Miami, Coral Gables, Florida; and W. L. Nutting, Department of Entomology, University of Arizona, Tucson.

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#### FAMILY KALOTERMITIDAE FROGGATT

Krishna (1961, pp. 312-315) provided a complete synonymy of the family, revised the genera, and placed the two subfamilies, the Electrotermittinae and the Kalotermitinae, proposed by Emerson (1942) in the family Kalotermitidae without division into subfamilies. The author is in agreement with Krishna that groups of genera in the Kalotermitidae are not worthy of subfamily separation, although some of the genera may be grouped to indicate phylogenetic relationships.

In the present revision of the fossil genera and species, *Eotermes* is considered the most primitive of the genera included within the family; *Prokalotermes* is redescribed and its phylogenetic position reviewed; and two new fossil species representing the first known Tertiary records of two genera, *Calcaritermes* and *Incisitermes*, are added.

Froggatt (1896, p. 516) first named the subfamily Calotermitinae and is also the author of the higher taxon that includes *Kalotermes* (= *Calotermes*) and its related genera.

The Kalotermitidae are divided into 25 genera, four of which are

known only from Tertiary fossils. Of the 21 genera in the living fauna of the world, five have fossil species in the Tertiary.

The evidence indicates that the Kalotermitidae originated from a more primitive group of termites remotely related to the Mastotermitidae, because of a similarity in the dentition of the left imago mandible in the two families, the possession of two ocelli, and other characters found in *Eotermes*. Of the two families, the Mastotermitidae are much more primitive in wing venation, tibial spines, and numerous other characters (Emerson, 1965). The Hodotermitidae are more primitive than the Mastotermitidae or the Kalotermitidae in the dentition of the left imago mandible (Ahmad, 1950), but are derivative in the homologous regression of ocelli in every known genus, and in the wing venation (Emerson, 1933; 1968b). The Rhinotermitidae are similar to the Hodotermitidae in the dentition of the imago mandibles, but possess ocelli in the majority of all species and genera, including the most primitive genera. The possession of a primitive character is much more important for phylogenetic interpretation than the loss of the same character as the result of regressive evolution (Emerson, 1961, 1962, 1965). Also, there may be parallel reduction in two or more branches of the phylogenetic tree as is illustrated by the reduction of the compound eye in unrelated insects, or the occurrence of vestigial eyes in unrelated cave fishes and salamanders. The reduction and fusion of the second marginal tooth of the left imago mandible in the Mastotermitidae and the Kalotermitidae might be considered parallel analogous regression and not homologous regression, if it were not for several additional correlated characters, which are described and discussed in the redescription of *Eotermes* below.

Although the first and second marginal teeth of the left imago mandible are fused so that the originally separate teeth cannot be distinguished, there is no doubt that the fused teeth are homologous with the separated teeth in the Blattodea, the Hodotermitidae, the Rhinotermitidae, and the most primitive genus of the Termitidae, *Protohamitermes*. In this respect, the Mastotermitidae and the Kalotermitidae are more advanced than other primitive termites. In spite of the awkwardness of the term "first plus second marginal tooth," it is far better to use the term "third marginal tooth" for a structure that is homologous throughout the Isoptera and Blattodea than to use the term "second marginal tooth" for those genera in which the first and second marginal teeth are fused, thus obscuring the homologous relationships of the families (see Ahmad, 1950, pp. 46, 52, 76, 78; on p. 50 the nomenclature of the dentition is not consistent with the concepts of homology expressed on the other pages). Also, the sharp tip of the first

plus second marginal tooth of the Kalotermitidae is homologous with the first marginal tooth of the Hodotermitidae and the Rhinotermitidae, and the posterior portion of the cutting edge of the first plus second marginal tooth is mostly homologous with the cutting edge of the second marginal tooth of the Hodotermitidae and the Rhinotermitidae. The genetic theory underlying developmental and structural homology and regressive evolution of vestiges was discussed by Emerson (1961).

#### GENUS *EOTERMES* STATZ

= *Eotermes* STATZ, 1939, p. 13. EMERSON, 1942, pp. 9, 10. SNYDER, 1949, p. 356. EMERSON, 1955, p. 507. WEIDNER, 1955b, p. 45. KRISHNA, 1961, pp. 314, 315.

TYPE SPECIES: *Eotermes grandaeva* Statz.

Haupt (1956, p. 28, fig. 24) gave the name *Eotermes multivenosus* to wings from Eocene beds of Geiseltales, East Germany (latitude 51° 18' N., longitude 11° 52' E.), obviously without knowledge of *Eotermes* Statz (1939). The generic name *Eotermes* Haupt is preoccupied by *Eotermes* Statz, and the venation of the wing in the figure in Haupt (1956) appears to be cockroach-like rather than termite-like. The present author has removed *Eotermes multivenosus* Haupt from his catalogue of fossil termites.

Because the original description was inadequate and no subsequent examination of the type series was made, *Eotermes* Statz has confused all investigators. Statz (1939) placed *Eotermes* in the tribe Termopsinae, subfamily Calotermitinae, and family Termitidae. Later, Statz (1941, p. 8) recognized the families Mastotermitidae, Calotermitidae, and Termitidae. Emerson (1942, 1955), Snyder (1949), and Weidner (1955b) included the genus in the Electrotermitinae, which Krishna (1961, pp. 313, 314) placed in synonymy with the Kalotermitidae. Krishna (1961) placed *Eotermes* in the Hodotermitidae as a result of the poor description and figures by Statz (1939), but did not assign the genus to any known subfamily.

Although specimens of *Eotermes grandaeva* Statz are few and in some cases fragmentary, the present author believes that there is sufficient available evidence to place *Eotermes* as the most primitive genus in the Kalotermitidae. A number of characters suggest phylogenetic relationship with the Mastotermitidae. Ahmad (1950, pp. 49, 50) gave some evidence for the phylogenetic relationship of the Mastotermitidae and the Kalotermitidae, but more data are now available. The short third to sixth antennal articles are similar in *Eotermes* and *Mastotermes*. The dentition of the imago mandibles (fig. 1B, C) resembles that of *Mastotermes* and

*Neotermes* (Ahmad, 1950, fig. 5) with the fusion of the first and second marginal teeth of the left mandible. The presence of ocelli in *Eotermes* resembles the condition in the Mastotermitidae, the Kalotermitidae, and most other termites, except for the Hodotermitidae in which the ocelli have surely undergone regressive evolution. Numerous lateral spines in two rows on the middle tibia (fig. 2B) are close to, but probably somewhat more primitive than, those of *Proelectrotermes* (Krishna, 1961, fig. 2), although the spurs and spines of *Proelectrotermes* are proportionally longer. The tibial spurs and spines of *Mastotermes* are distinctly more primitive than those of any known kalotermitid in larger number and disposition, and indicate the origin of the termites from the still more primitive cockroaches. *Mastotermes* has three spurs and no spines on the front tibia; four spurs, three inner spines, and two outer spines on the middle tibia; and four spurs, two or three inner spines, and one or no outer spine on the hind tibia. Somewhat indistinct marks indicate that *Eotermes* (fig. 2A-C) has three to five tibial spurs on each tibia; no lateral spines on the front tibia; one outer and three inner lateral spines on the middle tibia; and one inner lateral spine on the hind tibia close to the spurs. The tarsus of *Mastotermes* has five articles, whereas that of all the Kalotermitidae including *Eotermes* has four articles. The forewing of *Eotermes* (fig. 1A) resembles that of the most primitive genera of the Kalotermitidae in the appearance of Sc, R<sub>1</sub>, R<sub>2</sub>, R<sub>3</sub>, Rs, M, and Cu at the humeral suture. M is weak, with the main stem close to, and parallel with, Rs and also close to Cu, a character somewhat similar to that in *Mastotermes*, with branching about one-third of the length of the wing from the suture. The branches of Cu in the forewing near the suture (fig. 1A) radiate in a fan-shaped group of veins more like the venation of *Mastotermes* than that of any other described genus of the Kalotermitidae. The Mastotermitidae have an anal lobe at the base of the hind wing, whereas *Eotermes* and all other genera of the Kalotermitidae have no anal lobe. A short anal vein is probably invariably present in the hind wing of each genus of the Kalotermitidae (Krishna, 1961, figures of hind wings).

Among the genera of the Kalotermitidae, *Eotermes* differs markedly in its dentition (fig. 1B, C) from *Incisitermes*, *Marginitermes*, *Allotermes*, *Tauritermes*, *Proneotermes*, *Bifiditermes*, *Bicornitermes*, *Epicalotermes*, *Procryptotermes*, and *Cryptotermes* (Krishna, 1961, figures of dentition). The position of M in relation to Rs in the forewing of *Eotermes* (fig. 1A) differs from that in *Proelectrotermes*, *Electrotermes*, *Prokalotermes*, *Rugitermes*, *Kalotermes*, *Glyptotermes*, *Calcaritermes*, and *Pterotermes* (Krishna, 1961, figures of forewings). R<sub>1</sub> apparently is proportionally longer in *Eotermes* than in most

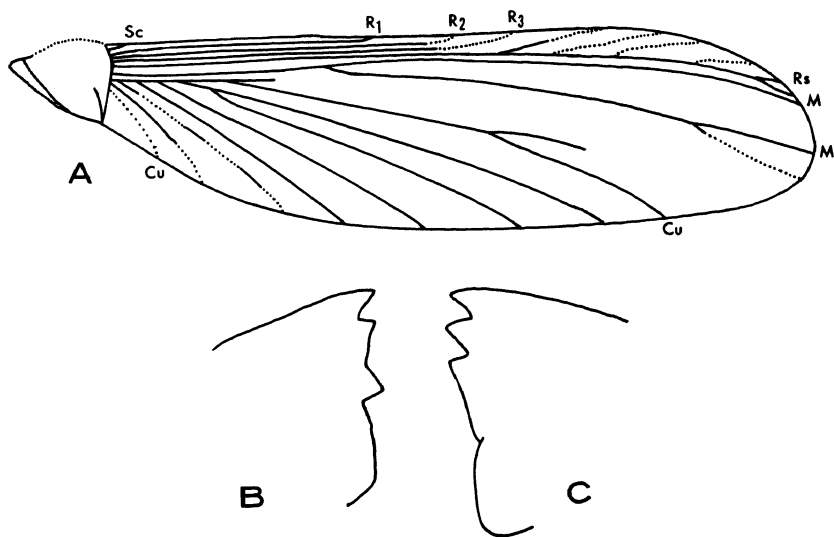


FIG. 1. *Eotermes grandaeva* Statz. A. Semi-diagrammatic construction of forewing from double impressions of same wing, paralectotype, IV-5. B. Left mandible constructed from double impressions of same mandible, paralectotype, IV-3. C. Right mandible constructed from double impressions of same mandible, paralectotype, IV-3.

genera, including *Electrotermes*, *Eucryptotermes*, *Ceratokalotermes*, and *Comatermes*. In general, *Eotermes* seems to be closest to *Proelectrotermes* in a number of primitive characters, but bridges some of the gaps between the Mastotermitidae and the Kalotermitidae. *Eotermes* is much larger in size than any other genus of the Kalotermitidae, and, generally speaking, comparatively large size is associated with other primitive characters in the more primitive genera on each phyletic branch of termites.

#### *Eotermes grandaeva* Statz

*Eotermes grandaeva* STATZ, 1939, pp. 13, 35, 39, table 4, pl. 6, figs. 23-25 (imago). SNYDER, 1949, p. 356 (systematics). WEIDNER, 1955b, pp. 45, 53, fig. 33 (wing), captions of figs. 30 and 33 erroneously transposed.

IMAGO: Y-suture visible with angle of branches in front close to, or a little wider than a right angle. Eye oval, moderately small compared with head width. Ocellus visible and apparently in contact with eye. Antennal fossa close to eye. Antenna with 17-20 counted articles in two specimens, but one antenna not entire and other not clear (Statz, 1939, described the antenna with 22 articles), third to sixth articles short. Postclypeus

TABLE 1

APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF LECTOTYPE, FOUR PARALECTOTYPES,  
AND ADDITIONAL HIND LEG OF IMAGOS OF *Eotermes grandaeva* STATZ

Length of head from front margin of postclypeus	4.15
Length of median arm of Y-suture	1.70
Width of head	4.80-4.88
Length of eye	0.97-1.16
Length of ocellus	0.11-0.12
Length of postclypeus	0.26
Tip of apical tooth to tip of first marginal tooth of left mandible	0.16
Tip of first marginal tooth to tip of third marginal tooth of left mandible	0.37
Length of pronotum	2.01-2.56
Width of pronotum	5.12
Length of front tibia	2.09-2.44
Width of front tibia	0.57
Length of middle tibia	2.37-2.93
Length of inner spur of middle tibia	0.32-0.46
Length of fourth article of tarsus of middle leg	0.81-0.84
Length of tarsal claw of middle leg	0.29
Width of middle tibia	0.60
Length of hind tibia	3.54-3.96
Length of inner spur of hind tibia	0.31
Length of inner spine of hind tibia	0.29
Base of inner spine to tip of inner spur of hind tibia	1.15
Length of costal margin of forewing scale	3.95
Length of forewing, including scale	33.18
Length of forewing from costal suture	31.40-31.58
Width of forewing	8.27
Space between costal margin and inside Rs in middle third of forewing	0.83-0.93
Space between costal margin and inside M in middle third of forewing	1.10-1.40
Space between inside Rs to outside M in middle third of forewing	0.12-0.35
Space between inside M to outside Cu in middle of forewing	1.50

short in proportion to width, resembling that of *Neotermes* (Krishna, 1961, fig. 7). Left mandible dentition (fig. 1B) clear and close to that of *Neotermes* (Krishna, 1961, fig. 8), notch between first plus second marginal tooth and third marginal tooth not quite midway between points of teeth, so that cutting edge of first plus second marginal tooth a little longer than anterior edge of third marginal tooth, angle of notch greater than a right angle. Right mandible (fig. 1C) similar to that of *Neotermes* and many other genera of the Kalotermitidae.

Pronotum distorted and broken in specimens, possibly with a shallow notch in middle of hind margin. Front tibia wide, one outer and one inner spur visible in profile, and another outer spur possibly present but not clear (fig. 2A). Middle tibia (fig. 2B) with two distinct inner spurs



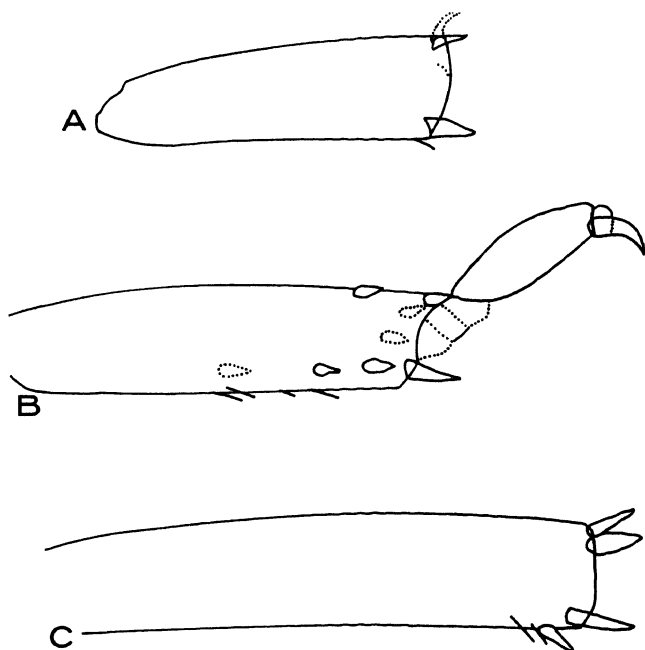


FIG. 2. *Eotermes grandaeva* Statz, lectotype, IV-1. A. Front tibia. B. Middle tibia and tarsus. C. Hind tibia.

and one fairly distinct outer spur; two indistinct spurs or spines occurring near end of tibia that do not seem aligned with outer and inner rows of spines and possibly indicating a total of four or five spurs; one outer lateral spine and three inner lateral spines apparently present, together with some stiff bristles; bases of some internal spines visible as oval marks similar to those in living termites. Hind tibia (fig. 2C) with three terminal spurs visible, one inside and two on outer end (normally the Kalotermitidae have two inner spurs and one outer spur, whereas *Eotermes* apparently has two outer spurs on the fore tibia and hind tibia, and two inner spurs, but the spurs are not sufficiently clear to allow identification of the number and position of all); one inner spine close to end of hind tibia; numerous coarse bristles on surface of tibia and femur of hind leg. Tarsus with four articles (indistinct), terminal article much longer than other three combined; one of tarsal claws visible in profile; arolium present, but not distinct because of position of leg.

Forewing (fig. 1A) large, much longer than that of any other genus of Kalotermitidae, three-fourths as long as longest termite wing (wing of

*Macrotermes goliath* 43.00 mm. from costal suture). Costal margin of scale strongly convex, although impression not completely clear. Scale resembling that of *Neotermes* (Krishna, 1961, fig. 9), with humeral suture strongly curved from Rs to costal margin and slightly less curved from Rs to inner margin. Costal margin of wing beyond suture nearly straight for two-thirds of length. Inner margin of wing slightly convex in middle and more convex near base and tip. Indistinct reticulations between Rs and M in outer portion of wing. Area between Rs and costal margin narrow in comparison to *Ulmeriella* (Emerson, 1968b). Veins at suture not wholly clear, but apparently a short Sc, a long  $R_1$  that reaches about one-third of length of wing from suture, and  $R_2$  and  $R_3$  separated and reaching half of length of wing or a little more. Rs with three to five visible superior branches from main stem that reaches almost to tip of wing; no inferior branches seen. M seems weaker than Rs and runs close to and parallel to Rs, slightly closer to Cu near base, with some branches too indistinct to describe. Outer branches of M apparently ending both at costal and inner margins and tip of wing. Cu with numerous radiating, fanlike branches near base, but number and extent of branches indistinct and some confusion in identification of M and Cu occurring in apical half of wing. Anal not seen and probably absent.

Hind wing venation faint, but visible portions apparently similar to those of forewing, with probable absence of Sc and presence of A. Fusion of M and Rs not seen, although typical of hind wing of *Kalotermitidae* (Krishna, 1961). M branching at least once about one-third of length of wing from suture. Anal lobe of *Mastotermitidae* certainly lacking.

**SPECIMENS:** Fragments of five individuals determined and collected by Statz in the Statz Collection deposited in the Los Angeles County Museum, from Upper Middle Oligocene beds at Rott (latitude  $50^{\circ} 44'$  N., longitude  $7^{\circ} 15'$  E.), Siebengebirge, West Germany. Statz (1939) made his original descriptions and figures from these specimens, which include the lectotype imago (IV-1, 1929) selected by Emerson, four paralectotypes (dealate, IV-2, March, 1933; dealate, IV-3; forewing and middle leg, IV-4; and a forewing with reverse impression, IV-5) selected by Emerson. One hind leg (V-26) not recognized by Statz and determined by Emerson was found on the same piece of rock with a wing of *Kalotermes* (labeled *Calotermes*) *rhenanus* Hagen determined and collected by Statz.

#### GENUS *PROKALOTERMES* EMERSON

**TYPE SPECIES:** *Parotermes Hagenii* Scudder.

Krishna (1961, pp. 314, 315, 331) provided the synonymy of the genus, first proposed by Emerson (1933, p. 189), and questioned its validity. Because the fossil specimens are fragmentary in the Florissant shales, their structures and relationships to other genera remain in doubt. Sufficient details are known, however, to indicate a separate genus with primitive structures related to, but not synonymous with, *Proelectrotermes*. Unfortunately, Emerson (1933, p. 189) confused three species of three genera in his original description, two of which belong to the Kalotermitidae and are here referred to as *Prokalotermes hageni* (Scudder) and *Proelectrotermes fodinae* (Scudder). The third species included in the original description of *Prokalotermes* is known from a single fossil imago in the United States National Museum (collected by Cockerell, No. 4925, Ao C14), from the Miocene shales of Florissant, Colorado, which has been examined by the author, but lacks sufficient detail for adequate taxonomic placement. From the wing venation, the author guesses that the specimen belongs to the Hodotermitinae, but generic assignment cannot be made with confidence.

So far as can be ascertained from the fragmentary specimens, *Prokalotermes* differs from other genera of the Kalotermitidae in a combination of characters. The head and the distance of the ocellus from the eye are apparently as in *Proelectrotermes*. The antenna has 24–26 articles, the most of any known genus in the family (*Proelectrotermes* has 19–20 antennal articles). The dentition of the left mandible of *Prokalotermes* (fig. 3A) is as close to that of *Kalotermes* as to that of any other genus, but apparently has no undulating posterior cutting edge of the first plus second marginal tooth (Krishna, 1961, fig. 20). The length of the first plus second marginal tooth is about equal to the anterior cutting edge of the third marginal tooth. The pronotum is about the same width as the head, whereas in *Proelectrotermes* the pronotum is wider than the head. The tibial spurs are probably 3:3:3, and in one case one inner and two outer lateral spines of the middle tibia apparently resemble those of *Proelectrotermes* although they are indistinct. The tarsus has four articles. The presence or absence of the arolium is unknown. The wing venation and the shape of the humeral suture (fig. 3B) of the forewing are close to those of *Proelectrotermes*, but the costal margin of the forewing scale is far less convex than that of *Proelectrotermes*. The position and strength of M in the forewing are roughly similar to those in *Proelectrotermes*. In one specimen, M apparently is closer to Cu than to Rs, resembling *Pterotermes* (Krishna, 1961, fig. 43). In some cases, Sc, R<sub>1</sub>, R<sub>2</sub>, R<sub>3</sub>, Rs, M, and Cu are separate at the humeral suture, but in other cases there is a fusion of R<sub>2</sub> and R<sub>3</sub> to form a single vein, R<sub>2+3</sub>.

Krishna (personal communication) has seen  $R_1$  and  $R_{2+3}$  beyond the suture in a specimen of *Kaloterme gracilignathus* (Emerson). He also has seen variation of the radial branches in specimens of *Postelectrotermes* (Krishna, 1961, fig. 5) and *Rugitermes*. Both Krishna and the present author (Emerson, 1965, pp. 5, 6) realize that the wing venation of primitive termites is variable, but is also of taxonomic value within defined limits and statistical averages [see variation of wings of *Bifiditermes* (= *Caloterme*) *durbanensis*, Fuller, 1919]. The number of articles in the cercus is unknown for *Prokaloterme*. The statement by Emerson (1933) that the cercus has four to five articles may be due to artifacts or may apply to the specimen that possibly belongs to the *Hodotermitinae*. Invisibility or inaccuracy of detail renders the classification of *Prokaloterme* tentative until more data are available. Because of the large number of antennal articles, *Prokaloterme* is placed in front of *Proelectrotermes* in the linear and phylogenetic arrangement, but the evidence is insufficient for a firm conclusion that either genus is more primitive. Both would seem to be derivative compared with *Eoterme* and primitive compared with *Electrotermes*.

The Florissant, Colorado, fauna indicates a warm temperate climate during the Miocene period. A species of *Sequoia* is known from stumps, logs, leaves, and cones in nearby deposits, and the associated species of *Reticulitermes*, *Paroterme*, and *?Zootermopsis* indicate temperate conditions at the time of fossilization, but the climate was warmer than the present temperatures on mountain elevations (8178 feet at Florissant).

*Prokaloterme hageni* (Scudder)

*Paroterme Hagenii* SCUDDER, 1883, p. 139 (imago).

*Paroterme hagenii*: SCUDDER, 1890, p. 110, pl. 12, fig. 2 (imago). SNYDER, 1925, p. 159 (remarks).

*Paroterme Hageni*: HANDLIRSCH, 1906-1908, p. 698. ROSEN, 1913, p. 327 (remarks).

*Kaloterme hageni*: SNYDER, 1925, chart.

*Prokaloterme hageni*: EMERSON, 1933, p. 189 (imago in part). SNYDER, 1949, p. 357 (synonymy); 1950, p. 191.

*Caloterme hageni*: STATZ, 1939, table 4.

*?Prokaloterme hageni*: KRISHNA, 1961, p. 331 (imago).

IMAGO: Head with rather rounded sides. Y-suture distinct, with angle between branches about 112-126 degrees. Eye relatively small and slightly prominent at sides. Ocellus small, slightly removed from eye (several marks can be confused with ocellus, but presence reasonably sure). Antenna having 24 or 26 articles, but number not exact (Scudder, 1890, p. 110, reported 26 articles). Postclypeus short in relation to width.

Dentition of left mandible (lectotype) indistinct, but apparently on *Kalotermes* branch; edge between tip of first marginal tooth and third marginal tooth evenly curved; left mandible of one paralectotype (No. 267) fairly distinct (fig. 3A), angle between apical and first marginal teeth rather deep, less than right angle; angle between first plus second marginal tooth and third marginal tooth greater than right angle, half-way between tips of teeth. Undulations in cutting edges of teeth of left mandible not apparent.

Pronotum fairly clear, with distinct median longitudinal line, front margin evenly concave as in *Kalotermes flavicollis* (Krishna, 1961, fig. 19), side margins probably somewhat flattened from normal convex arch, front angles sharply rounded as in *K. flavicollis*, but sides curved similar to shape of *Glyptotermes tuberculatus* (Krishna, 1961, fig. 34), hind angles not pronounced, hind margin with slight notch. One front tibia possibly having three spurs. One middle tibia with spurs and spines resembling those of *Proelectrotermes berendti* (Krishna, 1961, fig. 2), but arrangement unclear. Tarsi of a paralectotype with four articles each.

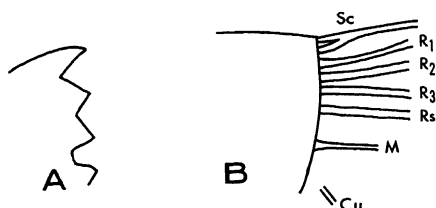


FIG. 3. *Prokalotermes hageni* (Scudder). A. Left mandible, paralectotype, No. 267. B. Sketch of reconstruction of base of right forewing, lectotype, No. 268.

Costal margin of forewing scale (fig. 3B) slightly convex but not so strongly curved as in *Proelectrotermes berendti* or *Electrotermes affinis* (Krishna, 1961, figs. 1, 3). Humeral suture of forewing (fig. 3B) evenly curved as in *Proelectrotermes*. Sc joining costal margin about 0.85 mm. from suture.  $R_1$ ,  $R_2$ ,  $R_3$ , and Rs apparently distinct near costal margin, separation of  $R_2$  and  $R_3$  at suture not certain in lectotype, but four branches of radius,  $R_1$ ,  $R_2$ ,  $R_3$ , and Rs, apparently separate at suture in one paralectotype (No. 267). Eight superior branches of Rs joining costal margin, and main stem ending near tip of wing. M closer to Cu than to Rs near base as in *Proelectrotermes*, but position of weak M in middle of wing not clear. Cu weak, not well defined.

In hind wing, M separating from Rs about 0.55 mm. from suture.

Abdomen fairly clear, with numerous tergites, but styli or cerci not seen.

SPECIMENS: Five specimens from Miocene shales (some authors place these deposits in the Oligocene) of Florissant (latitude  $38^{\circ} 56' N.$ , longitude  $105^{\circ} 19' W.$ , altitude 8178 feet), Colorado, in the type series of "*Parotermes hageni* Scudder," in the Museum of Comparative Zoology. One specimen (No. 268) has been selected by Emerson as lectotype, and perfectly matches the drawing in Scudder (1890, pl. 12, fig. 2; it is No. 8616 in Scudder, 1890, p. 112, caption of figure). The lectotype is

TABLE 2

APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF LECTOTYPE AND PARALECTOTYPES OF  
*Prokalotermes hageni* (SCUDDER)

Width of head	2.07-2.11
Length of eye	0.49-0.69
Length of ocellus	0.09-0.17
Width of ocellus	0.07
Ocellus from eye	0.02
Length of antenna	2.56
Length of postclypeus	0.17
Length of pronotum	0.94-1.28
Width of pronotum	2.09-2.32
Length of outside spur of middle tibia	0.08
Length of forewing scale at costal margin	1.10
Length of forewing from suture	12.50
Width of forewing	3.66-4.18
Rs to costal margin in outer half of forewing	0.67
Space between Rs and M in middle of forewing	0.55-0.61

rather well preserved for a shale impression, but some distortion and lack of definition occur, and the measurements should not be considered accurate. Also, one or more fragments of a small species (*?Reticulitermes*) on top obscure some delicate structures. Two other specimens (Nos. 267, 283) in the type series are selected as paralectotypes. Two more specimens in the type series (Nos. 266, 284) are too poorly preserved to be designated as paralectotypes.

#### GENUS *PROELECTROTERMES* ROSEN

TYPE SPECIES: *Termes Berendtii* Pictet (1854, p. 370), designated by Rosen (1913, p. 331) for the subgenus *Proelectrotermes* of the genus *Calotermes*.

Bibliographical references to *Proelectrotermes* and its synonymy were given by Krishna (1961, pp. 314-318, 383, 385) to which is added Hagen (1856, pp. 48, 49) and Banks and Snyder (1920, p. 97). The

synonymy of *P. berendti* that follows gives bibliographic references to the genus.

The generic characters and the phylogenetic position of *Proelectrotermes* were discussed by Krishna (1961). The relatively large size, the proportionally large eye, the primitive condition of the single inner lateral spine and the two outer lateral spines on the middle tibia in addition to the three terminal spurs, the single lateral spine on the hind tibia, the presence of an arolium, the slightly curved humeral suture of the forewing, the short Sc in the forewing (fig. 4), the relatively long  $R_1$ , the presence of  $R_2$  and  $R_3$  or  $R_{2+3}$ , the numerous superior branches of Rs, and the weak M a little closer to Rs than to Cu in the middle of the forewing provide the morphological data for considering the extinct fossil *Proelectrotermes* only a little less primitive than the extinct fossil *Eotermes*. Of these characters, the position of the weak M possibly is slightly more advanced than the more median position in *Prokalotermes*, *Kalotermes*, *Pterotermes*, and *Marginitermes* (Krishna, 1961), but the difference is not great. Also the lack of the independent veins  $R_2$  or  $R_3$  at the humeral suture is derivative compared with their presence in some specimens of *Electrotermes affinis* (Hagen) and *Prokalotermes hageni* (Scudder), although the presence or absence of these veins may prove to be variable when more data are available (Emerson, 1965, p. 6). *Prokalotermes* resembles *Proelectrotermes* in size, curvature of the humeral suture of the forewing, and wing venation, but differs from *Proelectrotermes* in the less strongly convex costal margin of the forewing scale. The presence or absence of lateral tibial spines is not sufficiently distinct in *Prokalotermes* for significant comparison.

*Proelectrotermes berendti* (Pictet)

*Termes Berendtii* PICTET, 1854, p. 370 (stated the species was described by Pictet and Berendt, probably referring to subsequent publication in Berendt, 1856). PICTET AND HAGEN, 1856, pp. 48, 49, pl. 5, fig. 2 (imago), placed in Gruppe *Kalotermes* by Hagen.

*Kalotermes Berendtii*: HAGEN, 1854, pp. 222, 223, 224 (mentioned a few general characters of the imago and referred to Pictet as author of name).

*Calotermes Berendtii*: HAGEN, 1858a, pp. 32, 50 (imago); 1858b, p. 7 (imago); 1860, p. 100 (remarks).

(*Calotermes*) *Berendtii*: HANDLIRSCH, 1906–1908, p. 697 (synonymy).

*Calotermes (Proelectrotermes) Berendtii*: ROSEN, 1913, pp. 330, 331, pl. 29, fig. 15, pl. 30, fig. 19 (imago).

*Kalotermes berendtii*: BANKS AND SNYDER, 1920, p. 9 (type species of genus *Kalotermes*).

*Proelectrotermes berendtii*: SNYDER, 1925, chart. STATZ, 1939, table 4. SNYDER, 1949, p. 357 (synonymy). KRISHNA, 1961, pp. 317, 318 (systematics), figs. 1

(forewing), 2 (middle leg).

*Proelectrotermes berendti*: WEIDNER, 1955a, pp. 64, 65, 70 (imago), text fig. 6a (middle leg).

There is a question concerning the authorship of the species name according to the International Rules. Pictet (1854) only mentioned the species but did not describe it, although he stated that Pictet and Berendt had described *Termes Berendtii*. Hagen ascribed the species name to Pictet in all his references, and also referred to Pictet's types. It can be assumed that Hagen used a description or a figure by Pictet in the account of fossil termites that was obviously written by Hagen in Berendt (1856), and possibly by Hagen (1854), which seems to be the inference by subsequent authors. Of course the manuscripts awaiting publication had probably been completed before the publication of references to them, and the rules of priority in publication were not formulated until about 50 years later. Hagen (1858a, p. 53) indicated that Pictet drew the figure in Berendt (1856), the book that contains the article by Pictet and Hagen (1856). If the original published description was by Hagen alone, the author of the name should be Hagen, but Hagen collaborated with both Berendt and Pictet during this period, particularly with Berendt (1856).

IMAGO: Color of head, pronotum, wing scales, and tergites generally dark brown or almost black, but possibly modified by preservation.

Head sparsely covered with bristles or hairs. Margin of pronotum and area of forewing scale with bristles. Costal margin of forewing with few hairs. Inner margin of forewing, and wing membrane without hairs.

Head oval, sides rather straight in region of eyes. Arms and stem of Y-suture distinct. Postmentum rather long. Eye large, with fairly straight margin in front, and eyes not extending much, if any, beyond edge of head when viewed from below. Ocellus oval, fairly large, close to eye. Antenna with 19-20 articles, second equal to third, and fourth slightly longer than third. Postclypeus short. Labrum tongue-shaped. First plus second marginal tooth of left mandible partially visible from below in dealate determined by Emerson, and apparently with long (estimated, 0.09 mm.) and slightly sinuate cutting edge.

Pronotum wider than head, profile evenly arched except front margin with ridge on sides. Front margin from above apparently concave. Sides from above somewhat rounded but not converging toward rear. Hind margin slightly emarginate with somewhat rounded sides. Margins of mesonotum and metanotum invisible. Femora grooved to fit contracted tibiae, front femur swollen and longer than front tibia. Front tibia with three apical spurs and no lateral spines. Middle tibia with three apical



spurs and two distinct outer, and one inner, lateral spines (Rosen, 1913, fig. 15; Krishna, 1961, fig. 2). Hind tibia longer than femur, three apical spurs and one lateral spine near apex on inner side. Apical spurs of tibiae with minute serrations on edges. Tarsus with four articles and arolium.

Scale of forewing proportionally large, overlapping base of much smaller scale of hind wing; costal margin strongly convex (fig. 4; Krishna, 1961, fig. 1). Humeral suture of forewing (fig. 4) slightly curved at costal and inner ends, but nearly straight or slightly curved in middle (close to that shown in Krishna, 1961, fig. 1). Forewing membrane with reticulations between veins. Sc short (about 0.17 mm. long in neotype).  $R_1$  joining costal margin about one-third of length of wing from suture

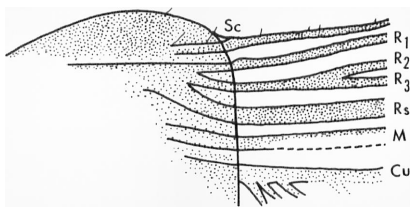


FIG. 4. *Proelectrotermes berendti* (Pictet), sketch of base of forewing, neotype.

(4.98 mm. in neotype).  $R_{2+3}$  proportionally long, unbranched at suture, occasionally branched into  $R_2$  and  $R_3$  beyond suture (branched in neotype about 0.41 mm. from suture), joining costal margin over three times length of scale from suture (Krishna, 1961, fig. 1).  $R_s$  extending to wing tip, seven branches reaching costal margin and tip.  $M$  branched at tip.

Other details of the wing venation were not seen by the present author, but Krishna (1961, fig. 1) showed a weak  $M$  slightly closer to  $R_s$  than to  $Cu$ , and  $Cu$  with about 12 branches in the basal two-thirds (?) of the forewing, some branched secondarily. The venation and its interpretation are based primarily on one specimen examined in Munich in 1927 and later destroyed, and also on the neotype. A drawing of the neotype (Krishna, 1961, fig. 1) did not show the short  $Sc$  beyond the suture, or the branched  $R_{2+3}$ , and one specimen in Munich had an unbranched  $R_{2+3}$ . These veins are difficult to observe in the arched wing base of the neotype but are visible at certain angles and in favorable light (fig. 4).

The abdomen of the Munich specimens was opaque owing to bubbles and clouds in the amber, but the dealate determined by Emerson had two articles in the cercus.

Aside from the slightly longer length with the wings (19–20 mm.),

the description and figure by Weidner (1955a, pp. 64, 65) conform to redescrptions and measurements given herein.

**SPECIMENS:** The present author examined two of the original series described by Hagen from Lower Oligocene Baltic amber collected at the type locality, Samland Peninsula (latitude 54° 55' N., longitude 20° 00' E.), U.S.S.R., borrowed by Kurt von Rosen from the Königsberg Museum, and studied in the Staatsammlung, Munich, in 1927. The Baltic amber collection on loan in Munich was destroyed in the bombing of the city in World War II. One of these specimens was

TABLE 3  
APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF FOUR IMAGOS OF  
*Proelectrotermes berendti* (Pictet)

Length with wings	17.26
Length without wings	9.79
Width of head	2.12-2.66
Width of postmentum	0.87
Diameter of eye	0.52
Length of ocellus	0.19
Width of ocellus	0.14
Ocellus from eye	0.03-0.09
Length of postclypeus in middle	0.29
Width of postclypeus	1.12
Width of labrum	1.00
Length of pronotum	1.23-1.53
Width of pronotum	2.68-2.82
Length of hind tibia	1.59-2.72
Length of forewing scale	1.53-1.91
Length of forewing from costal suture	12.85
Length of cercus	0.35

labeled "*Termes Berendti* Pict. *Phryganea fossilis* Pict. Phys. Oek. Ges. No. 14681. I 1. No. 61." It was a fairly well-preserved imago and is the one on which the present redescription of the species is based, supplemented by the second specimen labeled "Coll. Dr. Klebs K7808," in Munich in 1927; the neotype determined and selected by Krishna, in the Field Museum of Natural History; and the dealate determined tentatively by Emerson in the Universitetets Zoologiske Museum, Copenhagen. Neither of the two specimens determined by Hagen was the holotype referred to by Weidner (1955a, p. 65) and labeled "*(Termes gedanensis)* *Termes Berendtii* Pictet in Coll. Berendt, Danzig." Hagen (1856, pp. 48-49) mentioned three specimens, one of which he called the type of Pictet earlier known as "*T. Gedanensis*," so this latter specimen is the

same as the holotype referred to by Weidner and mentioned by Hagen (1858a, p. 51) "in der Sammlung des Rechtsanwalts Meier in Königsberg." Hagen (1860, p. 100) recorded a fourth specimen known to him. It is the opinion of Weidner (1955a, p. 65), Krishna (1961, p. 318), and the present author that all the specimens mentioned by Hagen have been lost or destroyed. A dealate labeled "Isoptera. C. V. Henningsen 1-7 1966" in Baltic amber from Denmark, and tentatively determined as *Proelectrotermes berendti* (Pictet) by Emerson, was lent by Sv. G. Larsen, Universitetes Zoologiske Museum, Copenhagen. Although its position and the flaws in the amber obscure important characters, the specimen is included in the redescription because of the relative rarity of this species.

*Proelectrotermes fodinae* (Scudder), new combination

*Parotermes fodinae* SCUDDER, 1883, p. 141 (imago); 1890, p. 112, pl. 12, figs. 3, 22 (imago). ROSEN, 1913, p. 327 (remarks). SNYDER, 1925, p. 159 (discussion).

*Parotermes Fodinae*: HANDLIRSCH, 1906-1908, p. 698 (synonymy).

*Kalotermes fodinae*: SNYDER, 1925, chart.

*Prokalotermes hageni*: EMERSON, 1933, p. 189 (imago in part). SNYDER, 1949, p. 357 (*fodinae* in synonymy).

*Calotermes fodinae*: STATZ, 1939, table 4.

Emerson (1933, p. 189) mistakenly placed this species in synonymy with *Prokalotermes hageni* (Scudder) from the same Florissant shales of Miocene age. He also misidentified a specimen collected by Cockerell. More careful examination indicates that three different species and genera were confused by Emerson. Two of these belong to the Kalo-termitidae; the other is not sufficiently distinct for precise classification, although inferior branches of Rs and more than two articles in the cercus suggest that it belongs to the Hodotermitinae near *Ulmeriella*.

IMAGO: Head with Y-suture. Shape of eye not clear. Ocellus reniform, very close to, or in contact with, eye. Antenna with about 20-21 articles. Left mandible (fig. 5A) with distance from point of first marginal to point of third marginal tooth 0.115 mm.; length of cutting edge of first plus second marginal tooth 0.057 mm.; length of cutting edge of third marginal tooth 0.067 mm.; angle between apical and first marginal tooth about 45-50 degrees; angle between first plus second marginal tooth and third marginal tooth about 110 degrees.

Pronotum (fig. 5B) sufficiently clear for estimate of its shape. Front margin somewhat angular in lectotype and two other specimens, but straighter in one paralectotype, possibly because of slight difference in position. Front lateral angles fairly sharp. Sides behind front lateral angles straight, with two blunt angles toward rear. Sides and hind mar-

gin fairly evenly joined. Hind margin with shallow notch in two specimens and nearly straight in one paralectotype.

Costal margin of forewing scale (fig. 5C) convex. Humeral suture evenly and slightly curved. Costal margin of forewing beyond suture fairly straight. Venation fairly clear in right wing, but some sections obscure. Costal margin in vicinity of Sc lacking. Sc short.  $R_1$  not clear, but apparently short and joining costal margin 1.56 mm. from suture.  $R_{2+3}$  fused near suture but branching into  $R_2$  and  $R_3$ ;  $R_2$  joining costal margin about 2.26 mm. from suture. Rs with three superior branches visible, but outer portion of wing obscure. M and Cu weak, visible only near suture, with position of M roughly estimated at about halfway between Rs and Cu.

Costal margin of hind-wing scale rather strongly convex. Humeral suture straight in middle, but proportionally more curved compared to forewing suture at both costal and inner margins.

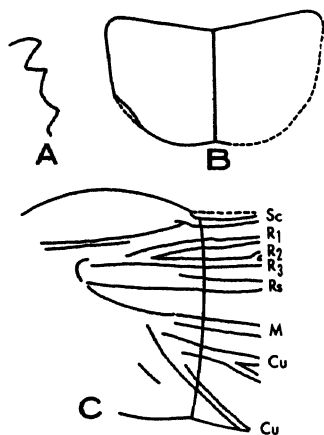


FIG. 5. *Proelectrotermes fodinae* (Scudder), lectotype. A. Dentition of left mandible. B. Pronotum. C. Base of forewing.

COMPARISONS: The dentition of the left mandible of *Proelectrotermes fodinae* (fig. 5A) is fairly distinct and not precisely similar to that of any other genus (see Krishna, 1961), although it is close to that of *Prokalotermes hageni* (fig. 3A). Apparently there is a slight concave outline of the cutting edge of the third marginal tooth in the lectotype of *Proelectrotermes fodinae*, but not in one paralectotype, and the cutting edge of the first plus second marginal tooth is straight in comparison with the slightly sigmoid edge in several genera, including *Eotermes* (fig. 1B), *Neotermes*, *Kalotermes* (Krishna, 1961, figs. 8, 20), and in the obscure left

TABLE 4  
APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF FOUR IMAGOS OF  
*Proelectrotermes fodinae* (SCUDDER)

Width of head	1.46-1.74
Length of eye	0.39-0.44
Length of ocellus	0.08
Width of ocellus	0.04
Ocellus from eye	0.00
Length of antennal fossa	0.29
Width of antennal fossa	0.21
Length of postclypeus	0.16
Width of postclypeus	0.46
Length of pronotum	0.52-0.61
Width of pronotum	1.22-1.26
Length of costal margin of forewing scale	1.10-1.22
Length of forewing from costal suture	9.40-11.18
Width of forewing	3.29
Length of costal margin of hind wing scale	0.61

mandible of *Proelectrotermes berendti*. *Proelectrotermes berendti* differs from *P. fodinae* in the following characters: much larger size, ocellus farther from eye, antenna with 19-20 articles, and pronotum wider than head. Because of its size and the separation of the ocellus from the eye, it is possible that *P. berendti* and *P. fodinae* do not belong to the same genus, although these characters are variable in some genera. The crucial characters of the dentition of the left mandible and the lateral spines on the middle tibia are not adequately compared because of preservation. The author hesitates to erect a new genus based on poorly preserved specimens, so he tentatively places *P. fodinae* in *Proelectrotermes*. The humeral suture of the forewing is only slightly curved in *Prokalotermes hageni*, *Proelectrotermes berendti*, and *P. fodinae*. The costal margin of the forewing scale is flat in *Prokalotermes hageni* (fig. 3B), whereas it is distinctly convex in *Proelectrotermes berendti* (fig. 4), *P. fodinae* (fig. 5C), *Postelectrotermes*, *Ceratokalotermes*, *Comatermes*, and *Pterotermes* (Krishna, 1961). The larger number of antennal articles (24-26) in *Prokalotermes hageni*, and the flat curvature of the costal margin of the forewing scale, indicate the improbability that it is congeneric with *Proelectrotermes fodinae*. *Electrotermes* has a much more strongly angular and curved humeral suture of the forewing (fig. 6) than *Proelectrotermes* (figs. 4, 5C).

SPECIMENS: Four imagos from Miocene shales at the type locality, Florissant (latitude 38° 56' N., longitude 105° 19' W., altitude 8178 feet), Colorado; all in the original series determined by Scudder in the

Museum of Comparative Zoology, and kindly lent by the Curator of Fossil Insects, Dr. Frank M. Carpenter. The best-preserved specimen, M.C.Z. No. 4110 (No. 1247, Scudder, 1890, pl. 12, fig. 3), is selected by the present author as lectotype. M.C.Z. No. 277 is selected as a paralectotype. M.C.Z. No. 278 (No. 1253 or 7608, Scudder, 1890, p. 113) is selected as a paralectotype. M.C.Z. No. 270 (No. 14391, Scudder, 1890, p. 113) is not sufficiently well preserved for designation as a paralectotype, although it belongs to the original series.

#### GENUS *ELECTROTREMES* ROSEN

TYPE SPECIES: *Termes* (*Kalotermes*) *affinis* Hagen.

There is little to add to the synonymy and description of *Electrotermes* provided by Krishna (1961, pp. 314–316, 318–319, 383, 385, fig. 3, forewing, fig. 4, middle leg), who placed the two fossil genera *Proelectrotermes* and *Electrotermes* together on a branch of the Kalotermitidae with the closely related living genus *Postelectrotermes*. All genera on this branch have lateral tibial spines that show a gradation of reduction to a single lateral spine on the middle tibia of *Postelectrotermes*. With the exceptions of *Eotermes*, and probably *Prokalotermes*, all other genera of the Kalotermitidae have lost lateral spines on the tibiae.

*Electrotermes* is distinguished from *Proelectrotermes* by the loss of the inner lateral spine on the middle tibia and hind tibia. The presence of Sc, R<sub>1</sub>, and R<sub>2+3</sub> beyond the humeral suture of the forewing (fig. 6) in some but not all specimens indicates a more primitive venation than that of other described genera of the Kalotermitidae except *Eotermes*, *Prokalotermes*, and *Proelectrotermes*. Although doubtless variable (see figures of wings of *Bifiditermes* [= *Calotermes*] *durbanensis*, Fuller, 1919), the relatively long Sc and R<sub>1</sub> indicate a primitive condition. The relative position and strength of M, and the presence of an arolium, are similar in *Proelectrotermes* and *Electrotermes*. The strength and position of M close to Rs in *Postelectrotermes* approach the condition in *Neotermes* (Krishna, 1961).

#### *Electrotermes affinis* (Hagen)

*Termes obscurus* PICTET, 1854, p. 370 (not described). PICTET AND HAGEN, 1856, pl. 5, fig. 5 (imago).

*Kalotermes affinis* HAGEN, 1854, p. 222 (imago mentioned but not described).

*Termes* (*Kalotermes*) *affinis*: HAGEN, 1856, pp. 49, 50 (synonymy, imago).

*Calotermes affinis*: HAGEN, 1858a, p. 53 (synonymy, imago); 1858b, p. 8 (imago); 1860, p. 100 (imago comparisons).

(*Calotermes*) *affinis*: HANDLIRSCH, 1906–1908, p. 697 (synonymy).

*Calotermes* (*Electrotermes*) *affinis*: ROSEN, 1913, p. 331 (remarks), pl. 28, fig. 12 (forewing).

*Electrotermes affinis*: SNYDER, 1925, chart. STATZ, 1939, table 4. SNYDER, 1949, p. 357 (synonymy). WEIDNER, 1955a, pp. 58, 65, pl. 1, figs. 2, 3 (imago). KRISHNA, 1961, p. 319 (systematics), fig. 3 (forewing), fig. 4 (middle leg).

Hagen (1856, p. 50) wrote: "Die Beschreibung ist fast nur nach Pictets Type entworfen." He based his description of *Termes* (*Kalotermes*) *affinis* on the type specimen of *Termes obscurus* Pictet (Pictet and Hagen, 1856, pl. 5, fig. 5) which is thus the holotype of *Electrotermes affinis* (Hagen). Hagen placed *Termes obscurus* Pictet in synonymy because of the prior names *Termes obscurum* Blanchard [= *Syntermes dirus* (Burmeister)], and *Termes obscurus* Heer (1849, p. 33, pl. 3, fig. 4), a fossil of doubtful genus. Walker (1853, p. 527) also described *Termes obscurus* Walker, which was renamed *Proglyptotermes hilli* by Emerson (in Kirby, 1949) and later classified as *Kalotermes hilli* (Emerson) by Snyder (1949, p. 15), and Krishna (1961, pp. 336, 396, 399).

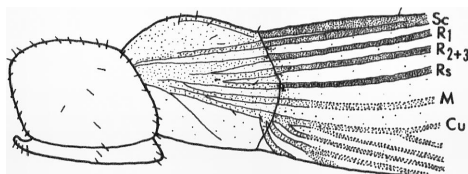


FIG. 6. *Electrotermes affinis* (Hagen), autotype, neotype. Pronotum and base of right wing. Top of drawing close to normal proportions, but lower part in depressed position in amber piece.

IMAGO: Numerous hairs and bristles present on head (longest 0.17 mm.), pronotum (longest 0.16 mm.), and wing scales (longest 0.14 mm.). Many short hairs on outer portion of costal margin of forewing (longest 0.06 mm.) and rarely a hair near humeral suture. A few or no hairs on veins, membrane, or inner margin of forewing. A few hairs on costal margin of hind wing, but none on veins, membrane, or inner margin.

Branches of Y-suture forming angle slightly wider than right angle. Eye relatively small, front margin somewhat straight or slightly convex. Ocellus large, about one-third of diameter of eye, slightly separated from or in contact with ocular suture. Antenna with 15–18 visible articles (possibly incomplete), length of third equal to second, fourth and fifth about equal.

Pronotum (fig. 6) flatly arched, as wide as or slightly wider than head. Front margin evenly concave. Front lateral sides rounded. Sides somewhat angular. Hind margin slightly emarginate, somewhat angular at junction with sides. Tibial spurs 3:3:3. Front tibia with outer bristles

TABLE 5  
APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF 14 MALE AND FEMALE IMAGOS OF  
*Electrotermes affinis* (HAGEN)

	No.	Range
Width of head	2	1.05-1.27
Diameter of eye	6	0.23-0.35
Eye from lower margin of head	1	0.17
Length of ocellus	1	0.15
Width of ocellus	1	0.09
Length of pronotum in middle	3	0.59-0.69
Width of pronotum	3	1.10-1.27
Width of hind femur	1	0.35
Length of hind tibia	4	0.87-1.04
Width of hind tibia	1	0.17
Maximum length of forewing scale	3	0.88-1.04
Length of forewing with scale	1	8.84
Length of forewing from costal suture	5	7.90-8.46
Length of Sc from forewing suture	3	0.46-0.85
Length of R <sub>1</sub> from forewing suture	3	1.22-1.62
Length of R <sub>2+3</sub> from forewing suture	4	1.58-2.80
Width of forewing	2	2.32-2.49
Length of hind wing with scale	2	7.52-8.08
Length of hind wing from costal suture	1	7.24
Width of hind wing	1	2.63
Length of male stylus	1	0.14
Length of cercus	1	0.15

nearly as thick as lateral spines on middle tibia. Middle tibia with two outer lateral spines in longitudinal row, each about same size as outer spur. Hind tibia with no visible lateral spines. Hind femur about twice as wide as hind tibia. Tarsus with four articles. Arolium present.

Forewing with costal margin of scale (fig. 6) moderately to strongly convex (see Krishna, 1961, fig. 3). Humeral suture fairly straight from Rs to inner margin, more strongly curved toward base between Rs and costal margin than in figure by Krishna (1961, fig. 3), more curved and angular than *Proelectrotermes* (present paper, figs. 4, 5C). Costal margin of forewing fairly straight in middle. Membrane with numerous accessory thickenings or reticulations in outer portion of wing between veins and branches of Rs, M, and Cu. Veins at humeral suture (fig. 6) including short Sc, R<sub>1</sub>, unbranched R<sub>2+3</sub>, M, and Cu. Rs with five to eight branches that join costal margin before reaching tip of wing (in one specimen, first superior branch of Rs joining R<sub>2+3</sub> 1.73 mm. from suture). M weak and slightly closer to Rs than to Cu in middle of wing,



few branches in outer fourth of wing and near tip, occasionally with secondary branches or branch ending in membrane. Cu with nine to 10 primary and several secondary branches, 13-16 branches reaching inner margin.

Hind wing scale relatively small compared with forewing scale. Humeral suture barely discernible. Veins at humeral suture including  $R_1$ ,  $R_{2+3}$ ,  $Rs+M$ , Cu, and short, heavily sclerotized, unbranched A.  $Rs$  having few superior branches. M joined to  $Rs$  near suture, otherwise similar to forewing. Cu having at least five primary inferior branches and occasional secondary branch joining inner margin (in one specimen, an inferior branch of Cu joining anal vein).

Male with two styli reaching tip of abdomen. In some specimens, cercus apparently having three or four articles, but number probably artifact due to preservation.

All known genera of the Kalotermitidae have two articles in the cercus (Krishna, 1961, p. 315).

COMPARISONS: Krishna (1961, fig. 3) did not show  $R_{2+3}$  in his figure, but in the text (p. 319) he stated, "occasionally a second branch of the radius present." All the forewings examined by the present author had an unbranched  $R_{2+3}$ . The variation in the presence of  $R_2$ ,  $R_3$ , or  $R_{2+3}$  is known to be great in a few genera of the Kalotermitidae and the Hodotermitidae, although  $R_2$ ,  $R_3$ , or the fusion in  $R_{2+3}$  that may be branched or unbranched, is a primitive character compared with the absence of  $R_{2+3}$  in the more advanced genera of the Kalotermitidae (figs. 8, 10B, 12B, 12D; Krishna, 1961, figs. 9, 13, 17, 21, 25, 32, 36, 43, 47, 54, 60, 64, 68, 71, 75, 79).

SPECIMENS: All recorded specimens are from Lower Oligocene deposits of Baltic amber. Amber is doubtless redeposited from older terrestrial sites, but the gap in time between fossilization and inclusion in geological strata is not known. The type locality is most probably the Samland Peninsula (latitude  $54^\circ 55' N.$ , longitude  $20^\circ 00' E.$ , near sea level), U.S.S.R. (formerly East Prussia), but Baltic amber occurs naturally at various localities on the southern shores of the Baltic Sea. No evidence from the termite fauna suggests that an evolutionary change in species occurs between possibly early and late fossilization, although there is no question that some species are common and some rare, and the rare species are known from too few specimens for general distribution in time or space to be indicated. The amber fauna lived in a warm temperate climate.

The holotype of *Termes obscurus* Pictet (= *Electrotermes affinis*) was in the Berendt collection in Danzig (Weidner, 1955a, p. 65), but Weidner

(personal communication) doubts that this collection survived World War II. Hagen (1858a) examined 38 specimens, and Rosen saw 150 specimens of the genus. The present author has drawn his redescription from 14 specimens listed below.

One specimen in the Museum of Comparative Zoology is labeled "*Calotermes affinis* Hagen. Linn. X. 53\* Hagen. Type 190. Succinum. Prussia. Coll. Menge." This specimen (fig. 6) and others collected by Menge were probably those referred to by Hagen (1860, p. 100) and should be considered as autotypes rather than the original series described in 1856. If the holotype and all the original type series have been lost or destroyed, the specimen (fig. 6) determined by Hagen is selected by the present author as the neotype. An autotype specimen has the same original label as the neotype, but is not so well preserved. A male (Menge collection No. 3897) and other specimens (Nos. 9740, 9776, 9780, 9781, 9788) are in the Museum of Comparative Zoology. Two male imagoes determined by Rosen and redetermined by Krishna and Emerson are in the American Museum of Natural History, one of which is a homoautotype compared by both Rosen and Emerson. Four specimens lent by Sv. G. Larsson, Universitetets Zoologiske Museum, Copenhagen, determined by Emerson in 1967, include one imago (coll. Dr. J. Ipsen, 1.VI.1952); a headless imago (Valby Bakke, Denmark, "1897-367," Mineralogic Museum, Copenhagen); one imago (Valby, Denmark, coll. Urejer Madsen, 1900, Mineralogic Museum, Copenhagen); and one imago (Denmark, coll. C. V. Hennigsen, 3.V.1960, Universitetets Zoologiske Museum, Copenhagen).

*Electrotermes girardi* (Giebel)

*Termes* (*Termopsis*) *Girardi* GIEBEL, 1856, p. 294 (imago).

*Termes Girardi*: SCHLECHTENDAL, 1888, p. 491 (synonymy).

(*Termopsis*) *Girardi*: HANDLIRSCH, 1906-1908, p. 697 (synonymy).

*Calotermes* (*Electrotermes*) *Girardi*: ROSEN, 1913, pl. 29, fig. 16 (middle tibia), pl. 30, figs. 20(?), 21 (imago).

*Electrotermes girardi*: SNYDER, 1925, chart. EMERSON, 1933, p. 191 (remarks). SNYDER, 1949, p. 358 (synonymy). WEIDNER, 1955a, pp. 57, 64, 66, 70 (imago), text fig. 6b (middle leg), [*Electrotermes* sp., pl. 2, fig. 5 (hind wing)]. KRISHNA, 1961, p. 319 (systematics).

Hagen (1858a, pp. 53, 54) placed this name in synonymy with "*Calotermes affinis*," and it is not yet clear whether more than one distinct species in Baltic amber should be included in *Electrotermes*. Rosen (1913, p. 331) discussed the variation in 150 specimens and suggested the possibility that five species might be recognized, but he referred to *E. affinis* and *E. girardi* only.

IMAGO: Antenna with 15 articles. Pronotum about the same width as head. Front tibia with at least two spurs (probably three), no inner or outer lateral spines. Middle tibia with three apical spurs and two outer spines, not solid but thin at base as in *E. affinis*, resembling figure in Rosen (1913, pl. 29, fig. 16, which incorporates clouded portions of the amber). Tarsus of middle leg with four articles. Portions of wing venation indistinct, but apparently similar to that of *E. affinis*, particularly veins Rs, M, and Cu of forewing.

APPROXIMATE MEASUREMENTS: Length of forewing with scale (earlier descriptions), 6.00 mm.; width of forewing (Emerson), 1.77 mm.

COMPARISONS: The only distinction between *Electrotermes girardi* and *E. affinis* so far recorded is the size of the forewing. Weidner (1955a, p. 65) separates *E. affinis*, with a total wing length of 8 mm. (8.84 mm. in male imago in the American Museum of Natural History), from *E. girardi*, with a total wing length of 6 mm., on the basis of earlier descriptions rather than personal examination. Size alone is unreliable because of the variation between the sexes and the rather large range found within species of primitive termites, but the present author considers it is best to retain these species names, following recent authors.

SPECIMENS: All records are from Lower Oligocene Baltic amber from the type locality, Samland Peninsula (latitude 54° 55' N., longitude 20° 00' E.), U.S.S.R. (formerly East Prussia). Specimens from Königsberg lent Rosen were destroyed during World War II. The present re-description was made in 1927 in the Staatsammlung, Munich, from a specimen labeled "*Termes (Kalotermes) Girardi* Giebel = *affinis* Hagen = *obscurus* Pictet. Bernstein. det. von Hagen als *T. affinis* Hag. revd 1888, v. Schl." Rosen regarded this specimen as the type, but the label does not establish it as Giebel's type. Weidner (personal communication) believes that the holotype is in the Geological Collection, Halle, East Germany, and might still be found.

#### GENUS *NEOTERMES* HOLMGREN

TYPES SPECIES: *Termes castaneus* Burmeister.

*Neotermes* is probably derived from *Postelectrotermes*. It is a successful tropicopolitan genus with 76 named species, two of which overlap into the Nearctic from the Neotropical Region, one of which overlaps into the Palearctic from the Oriental Region, and one of which is a fossil from the Eocene of France. Numerous unnamed species are in the collection of the American Museum of Natural History, but the number of species in each zoogeographical region remains close to those listed by Emerson (1955, p. 508) before the revision of the family by Krishna

(1961). The time and place of origin are not clear from the present distribution, but the wide tropical range without marked concentration of species in any one region suggests a mid-Mesozoic origin and later extinctions of species characteristic of semi-relict genera (Emerson, 1955, p. 468). The species are adapted to damp dead wood, sometimes in living trees, mostly in humid habitats, but some species are also found in somewhat dry climates. The single species known from Australia, and the numerous species, named and unnamed, from New Guinea, probably reflect the lack of adjustment to dry climates rather than a relatively late dispersion.

*Neotermes grassei* Piton

*Neotermes grassei* PITON, 1940, p. 144, fig. 21 (wing). SNYDER, 1949, p. 359 (synonymy). KRISHNA, 1961, p. 325 (list).

No specimen of this species has been examined by the present author, and no new information is available. Several genera have a wing venation that is close to that of *Neotermes*, including *Postelectrotermes*, *Comatermes*, and *Proneotermes*, so that generic identification on the basis of a fossil wing is tentative. Although some species of *Neotermes* are native in warm temperate climates near the borders of the tropics, this Eocene species from Menat (latitude 46° 06' N., longitude 2° 56' E.), Puy-de-Dôme, France, if it is substantiated, is an interesting Tertiary extension of the present range of the genus. The existence of *Neotermes* in the Eocene is expected, and more fossil species probably have not been discovered because of the rarity of tropical fossils.

SPECIMEN: The holotype is probably in the private collection of Piton, the whereabouts of which is unknown to the present author.

GENUS *KALOTERMES* HAGEN

TYPE SPECIES: *Termes flavicollis* Fabricius.

Krishna (1961, pp. 331-336) has revised the genus and given the synonymy accepted by the author.

There has been confusion with regard to the type species and also disagreement on the spelling of the generic name. Krishna (1961, p. 332) discussed the reasons for the earlier spelling of *Kalotermes*, which should be used in conformity to the International Rules, and also gave the reasons why *Kalotermes flavicollis* (Fabricius) should be considered the type species. The present author agrees wholly with Krishna and disagrees with the numerous authors who still use the later spelling *Calotermes* (Hagen, 1858a, pp. 31-38). Both Krishna and the present author are convinced that "*Kalotermes Berendtii*" cannot be made the type species

of the genus *Kalotermes* as Banks (Banks and Snyder, 1920, p. 9) did, in spite of the fact that Hagen (1853, p. 479) did not name the living species incorporated in his original description. It is quite obvious that Hagen described *Kalotermes* with the living *K. flavicollis* (Fabricius) in mind, because he mentioned soldiers, larvae, and the nest excavations. He subsequently included fossil species in *Kalotermes* that are now classified as *Proelectrotermes berendti* (Pictet) and *Electrotermes affinis* (Hagen), known only from the imago caste. Hagen's failure to name a type species of *Kalotermes* and his subsequent change of the initial letter of *Calotermes* were actions taken many decades before the formulation of the International Code.

We do not know whether the Greek root used by Hagen was *kalon*, meaning wood, or *kalos*, meaning beauty. The present author is inclined to think the root is *kalos* because of the striking color differences between the head, pronotum, and wings of *Kalotermes flavicollis*. *Termes* or *tarmes* is a Latin derivative of a Greek word for wood-worm, so that it is appropriate to use either Greek or Latin roots in the construction of compound generic names with *termes*. The letter K is often used interchangeably with the letter C, and both are considered good usage. It is, however, bad practice to use different initial letters for the name of the same taxon because of the consequent confusion in indexes. The present author hopes that the discussion by Krishna (1961) and the above remarks will result in a uniform usage of *Kalotermes* for the genus, with *K. flavicollis* (Fabricius) as the type species. When the letter C is used for the root spelling as in *Epicalotermes* Silvestri, or when the letter K is used as in *Prokalotermes* Emerson or *Ceratokalotermes* Krishna, the original spelling for the generic name should have priority according to the International Code.

With the exception of the proportional sizes of the marginal teeth of the left mandible of the imago, *Kalotermes* and *Incisitermes* are very closely related in a large number of generic characters (Krishna, 1961, pp. 331, 353, 385, figs. 20, 46). *Kalotermes* has the posterior cutting edge of the fused first plus second marginal tooth of the left mandible slightly longer or about equal to the anterior cutting edge of the third marginal tooth (Krishna, 1961, fig. 20), whereas *Incisitermes* and its derivative genera have the anterior margin of the third marginal tooth longer than the posterior cutting edge of the fused first plus second marginal tooth. This difference in dentition is more primitive in *Kalotermes* and more derivative in *Incisitermes*, but the dentition is unknown for most of the fossil species assigned to *Kalotermes*, and it is possible that some belong to *Incisitermes*. The known geographical distribution is more in con-

formity with the contemporary distribution of *Kaloterms* (fig. 7). Both genera are primitive in wing venation and the presence of an arolium (in most species), although both lack the primitive inner and outer lateral spines on the middle tibiae.

The wider distribution of *Kaloterms* (fig. 7) possibly indicates an earlier origin in the Mesozoic than that of *Incisiterms* (fig. 11). Much extinction of species is postulated, with only scattered relicts surviving at present in peripheral ecological habitats removed from competition with more advanced derivative genera including complementary incompatibility of *Kaloterms* and *Incisiterms*.

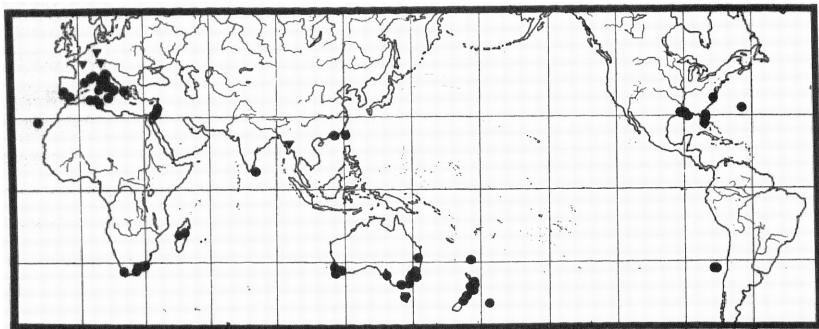


FIG. 7. Distribution of genus *Kaloterms*. Black circles indicate localities for 18 living species. Black triangles indicate localities for five fossil species. *Kaloterms bosniaskii*, Upper Miocene, Gabbro (latitude  $43^{\circ} 29' N.$ , longitude  $10^{\circ} 26' E.$ ), Italy, is not included.

*Kaloterms*, as revised by Krishna (1961) with a few additions and subtractions, includes 18 living species and six fossil species from the Eocene, Oligocene, and Miocene of Europe and Upper Burma. *Kaloterms piacentinii* (Piton and Théobald) is included in the genus with considerable doubt. *Kaloterms bosniaskii* Handlirsch, Miocene, Gabbro (latitude  $43^{\circ} 29' N.$ , longitude  $10^{\circ} 26' E.$ ), and *K. oeningensis* Rosen have not been seen by the present author, and the generic assignments should be checked. The fossil species *K. rhenanus* Hagen and *K. swinhoei* (Cockerell) apparently are accurately placed in *Kaloterms*, and *K. tristis* (Cockerell) possibly belongs to this genus. The living species need a thorough monographic treatment. When this is done, a few other species may be placed in synonymy and a few new species may be added, but the general distribution of *Kaloterms* will probably not be greatly altered. Figure 7 shows the worldwide distribution of the genus. Occur-

rences tend to be more common in temperate regions of both the Northern and Southern Hemispheres, and fairly close to salt-water shorelines on continents and islands, in both the tropics and the temperate regions. One species is found in New Zealand (introductions by man not included), six species are Australian, two species are Oriental, four species are Palearctic, two species are Ethiopian in South Africa, one species is found in the Malagasy subregion, one species is Nearctic, and one species is endemic on the Juan Fernandez Islands, which probably belong to the Neotropical Region.

The concentration of species numbers is only one indication of origin in any particular zoogeographical region, and is not reliable for a semi-relict genus such as *Kaloterмес* (Emerson, 1955, p. 468). The numbers are so large, however, in the Old World and so few in the New World that one might guess an Old World origin. The relative scarcity of species in the tropics is evidently due to elimination, possibly by competition with more advanced termites living in similar habitats. The worldwide distribution indicates an origin in the middle or early Mesozoic, with subsequent extinction of many species, leaving a spotty pattern at present. The endemic occurrence of one species in New Zealand, where it is found with only one other endemic species of archaic termite (*Stoloterмес*, Hodotermitidae), may indicate an origin as early as Triassic times, although the evidence is insufficient for more than speculation.

Of the six fossil species, four [*K. bosniaskii* Handlirsch from Upper Miocene, Gabbro, Italy; *K. oeningensis* Rosen from Upper Miocene, Oeningen, Germany; *K. rhenanus* Hagen from Upper or Middle Oligocene, Rott, Germany; and ?*K. piacentinii* (Piton and Théobald) from Eocene, Menat, France] are from temperate Europe, mostly a little north of the distribution of the living species, *K. flavicollis*. This pattern suggests a warmer climate at the same latitude during early to middle Tertiary than is found at present, a conclusion that is amply verified by the fossils of warm temperate plants and animals in associated deposits. The two fossil species [*K. swinhoei* (Cockerell) and *K. tristis* (Cockerell)], from Miocene amber of Upper Burma, probably lived in a tropical climate. If abundant fossils of the Mesozoic from the tropics are found in the future, *Kaloterмес* may be expected to occur among them. No evidence of marked evolution of nesting behavior or ecological adaptation of the genus through the ages is evident.

#### *Kaloterмес rhenanus* Hagen

*Caloterмес rhenanus* HAGEN, 1863, p. 250, pl. 44, figs. 1, 2 (imago). ROSEN, 1913, p. 323 (remarks). STATZ, 1939, pp. 3, 4, 17, 35, 40, table 4, pl. 8, figs. 34,

35 (imago, placed in tribe Calotermitini).

(*Calotermes*) *rhenanus*: HANDLIRSCH, 1906-1908, p. 698 (systematics).

*Kalotermes rhenanus*: SNYDER, 1925, chart (?two species). SNYDER, 1949, p. 358 (synonymy). KRISHNA, 1961, p. 336 (systematics).

IMAGO (FIG. 8): Y-suture close to that of *K. flavicollis* (Krishna, 1961, fig. 19), angle of arms greater than right angle. Eye rather flat in outline, not prominent; front margin somewhat straight. Ocellus close to, or in contact with, eye. Antenna with 17 indistinct articles in one specimen. Dentition fairly distinct in some specimens and resembles that of *K. flavicollis* (Krishna, 1961, fig. 20). Left mandible (fig. 8) with apical and first marginal teeth distinct, angle between less than a right angle;

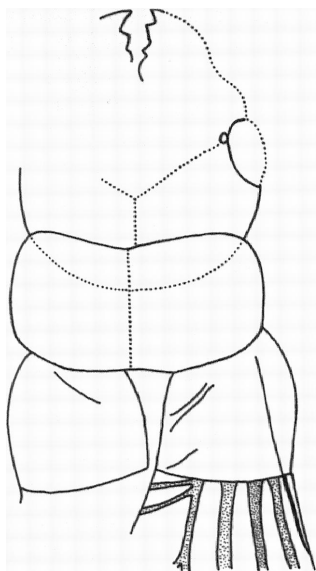


FIG. 8. *Kalotermes rhenanus* Hagen, imago, determined and collected by Statz, V-12. Mandibles viewed from below, so that left mandible appears on right side of drawing.

length from tip of apical tooth to tip of first marginal tooth 0.06 mm.; cutting edge of first plus second marginal tooth slightly sinuate, a little longer (0.08 mm.) than length of anterior edge of third marginal tooth (0.06 mm.); angle of notch between first plus second and third marginal teeth about 110 degrees; length from tip of apical tooth to tip of third marginal tooth 0.12 mm.; six to eight ridges of molar plate visible in some specimens. Right mandible with apical and first marginal teeth sharp, first marginal tooth sharper than that of *K. flavicollis* (Krishna, 1961, fig. 20). Length from tip of apical tooth to tip of first marginal tooth 0.08 mm., second marginal tooth somewhat small as in *K. flavi-*



TABLE 6  
APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF IMAGOS OF  
*Kalotermes rhenanus* HAGEN

	No.	Range	Average
Width of head	9	1.26-1.45	1.36
Length of eye	11	0.32-0.45	0.37
Width of eye	1	0.23	0.23
Length of ocellus	5	0.08-0.09	0.08
Width of ocellus	5	0.04-0.06	0.05
Ocellus from eye	7	0.00-0.03	0.004
Length of postclypeus	1	0.14	0.14
Width of postclypeus	1	0.49	0.49
Length of pronotum	15	0.64-0.80	0.69
Width of pronotum	13	1.43-1.68	1.51
Length of hind tibia	2	1.16-1.22	1.19
Length of costal margin of forewing scale	5	0.81-1.10	0.97
Length of forewing from costal suture	15	6.48-8.65	7.47
Width of forewing	10	1.95-2.44	2.19
Length of costal margin of hind wing scale	2	0.49-0.52	0.50
Length of hind wing from costal suture	2	6.77-6.96	6.86
Width of hind wing	2	2.03-2.32	2.17

*collis*; length from tip of first marginal tooth to tip of second marginal tooth 0.07 mm.; five ridges of molar plate visible in one specimen.

Pronotum (fig. 8) wider than head and proportionally shorter than in *K. flavicollis* (Krishna, 1961, fig. 19). Front margin with wide angle of about 150-162 degrees and slight median notch. Sides moderately convex and not converging much toward rear. Angles between sides and hind margin bluntly rounded. Hind margin with shallow notch in middle. Front tibia with three visible spurs. Middle tibia with three spurs. Hind femur with thick, strongly convex outer edge. Hind tibia with two visible spurs (probably three present). Tarsi of front and middle legs with four articles each, probably four articles in hind leg.

Forewing scale large (fig. 8), overlapping base of hind wing scale. Costal margin of forewing scale rather strongly convex, more so in one specimen than in *K. flavicollis* and less so in two other specimens, probably because of preserved position. Humeral suture of forewing evenly and moderately curved, or with slightly greater curvature between costal margin and Rs. Forewing similar in proportions and venation to that of *K. flavicollis* (Krishna, 1961, fig. 21), with distinct notch at junction of suture and costal margin. Sc short, 0.61-1.22 mm. R<sub>1</sub> single, about twice length of Sc, joining costal margin about as far from suture as

emergence of first branch of Rs. Rs with five to eight superior branches, first branch in one specimen 1.37–1.50 mm. from suture. M weak except near suture, running roughly about halfway between Rs and Cu or slightly closer to Rs in middle of wing, outer portion branched. Cu with as many as 11 branches, main stem reaching tip of wing.

Hind wing with costal margin of scale nearly straight or very slightly convex. Humeral suture moderately and evenly curved. Sc very short and visible only as a thickening in costal margin.  $R_1$  about twice as long as Sc. Rs with about three or four superior branches. M joined to Rs for short distance beyond suture, slightly closer to Rs than to Cu in middle of wing.

Cercus with two articles. Two styli present in some specimens presumed to be males.

**SPECIMENS:** All known specimens are from the type locality, upper Middle Oligocene "Braunkole," Rott (latitude 50° 44' N., longitude 7° 15' E.), Siebengebirge, Germany. The type specimen (Rosen, 1913) is in the British Museum (Natural History). The present author has not examined the type. The geological horizon is reported as Upper Oligocene by Rosen, Handlirsch, and Snyder (1925), and as upper Middle Oligocene by Statz, and by Snyder (1949).

Thirty-one specimens were collected and 30 were identified by Statz and are now deposited in the Statz collection, Los Angeles County Museum. These specimens are incorporated in the redescription by the present author. The dates of the collections are not on the specimens, but other species from the same stratum were collected from 1930 to 1935. Two of the specimens were figured by Statz (1939). The Statz collection includes 15 imagoes (V-2, V-4, V-5, V-6, V-7, V-8, V-9 male, V-10, V-11, V-12 (fig. 8), V-13, V-14, V-15, V-18, and V-31 det. Emerson and not labeled by Statz); two dealates (V-1, V-3); nine forewings (V-16, V-21, V-22, V-23, V-24, V-25, V-26 with hind leg of *Eotermes grandaevus* Statz on same piece, V-29, V-30); two questionable forewings (V-20, V-27); two hind wings (V-17, V-19); and one wing fragment (V-28).

*Kalotermes swinhoi* (Cockerell)

*Termopsis swinhoi* COCKERELL, 1916, p. 138, fig. 4 (imago). SNYDER, 1925, p. 157 (remarks), chart. EMERSON, 1933, p. 190 (remarks).

*Termopsis?* *swinhoi*: SNYDER, 1949, p. 370 (systematics).

*Kalotermes swinhoi*: WILLIAMS, 1968, pp. 547–550 (redescription, discussion, relationship to *K. tristis*), figs. 1–3.

The present author and Krishna were of the opinion that *Kalotermes*

*tristis* (Cockerell), from the same locality and deposit, was probably a synonym of *K. swinhoei*, but Williams (1968) concluded from additional evidence that the two species are separate. The author, Krishna, and Williams agree in tentatively placing the species in the genus *Kalotermitis* as revised by Krishna (1961), but acknowledge the difficulties of making accurate generic or species assignments from rather fragmentary specimens, many of which indicate deterioration when embedded in the resin that later turned into fossil amber.

IMAGO: Eyes relatively small. Wings with small pigmented nodules on membrane. Forewing with Rs showing four to seven superior branches on main stem. M weak and in general about midway between Rs and Cu.

MEASUREMENTS OF HOLOTYPE IMAGO: Diameter of eye, 0.25 mm.; length of forewing, 4.49 mm.

SPECIMENS: The author briefly examined the holotype in the British Museum (Natural History) in 1957. Later Krishna also examined the holotype, and most of the description and measurements herein are based on his notes. Williams (1968) recently described and measured the holotype and associated specimens and included figures of the pronotum and portions of the forewing and hind wing.

The type locality of the Lower Miocene amber strata, Upper Burma, is not known to the present author. Cockerell (1920, 1922) discussed the age and location of the Burmese amber deposits. Amber is redeposited from older strata, but Cockerell (1922) and Snyder (1925) speculated with little evidence when they assigned *K. swinhoei* to an early Tertiary or Mesozoic age.

### *Kalotermitis tristis* (Cockerell)

*Hodotermitis tristis* COCKERELL, 1917, p. 329, fig. 10 (hind wing). EMERSON, 1933, p. 190 (remarks). SNYDER, 1949, p. 370 (systematics).

*Kalotermitis tristis*: WILLIAMS, 1968, pp. 549-550 (redescription, discussion, relationship to *K. swinhoei*), fig. 4 (holotype hind wing and associated imagoes).

IMAGO: According to Williams (1968), *K. tristis* differs from *K. swinhoei* in the shape of the head and eye (distorted), the absence of an arolium in contrast to its presence in *K. swinhoei*, the shorter and relatively narrower wings, and the larger measurements of most structures.

APPROXIMATE MEASUREMENTS OF IMAGO: Diameter of eye, 0.20 mm.; length of forewing, 3.96-4.32 mm.; width of forewing, 1.12 mm.

COMPARISONS: Much of the discussion under *K. swinhoei* also applies to *K. tristis*. Inasmuch as the holotype is a hind wing, possibly some of the measurements taken from Krishna's notes apply to associated imagoes

determined by Williams as *K. swinhoi*, but such a surmise has not been verified. The present author now separates *K. tristis* from *K. swinhoi*, following Williams (1968), contrary to an earlier agreement with Krishna that the two names were probably synonymous. The absence of the arolium from associated specimens of *K. tristis* determined by Williams differs from the description of *Kaloterme*s by Krishna (1961, p. 335). All formerly known species of the genus possess this relatively primitive character. The arolium is usually, but not always, of generic importance in the Kalotermitidae. Some species of *Cryptoterme*s and *Neoterme*s have an arolium, but others do not. Although the misidentification of the genus by Cockerell, who placed the two species in two genera presently included in the Hodotermitidae, is corrected, the generic and species classification remains somewhat tentative.

**SPECIMENS:** The holotype hind wing and associated imagoes, determined by Cockerell and later redetermined by Williams, came from Lower Miocene amber, Upper Burma, and are in the British Museum (Natural History). Cockerell (1920, 1922) discussed the age and location of the amber deposits. The exact type locality is unknown to the present author.

#### GENUS *Calcaritermes* SNYDER

**TYPE SPECIES:** *Calcaritermes imminens* Snyder.

The genus was described, and its complete synonymy was given by Krishna (1961, 1962).

*Calcaritermes* is distinguished from its close ally, *Glyptoterme*s, primarily by the very thick outer spur on the front tibia of the soldier. Unfortunately, the imago castes of *Calcaritermes* and *Glyptoterme*s have no distinguishing generic characters.

Krishna (1961, p. 385) placed *Calcaritermes* in the most advanced position on the branch of the Kalotermitidae that includes *Proelectrotermes*, *Pteroterme*s, *Kaloterme*s, and *Glyptoterme*s. In his description and discussion, Krishna (1961, pp. 314–316, 348, 384–386, 389; 1962, pp. 1, 2) postulated the emergence of *Calcaritermes* directly from its ancestral genus *Glyptoterme*s in the Neotropical Region during Tertiary times, a conclusion with which the present author is in entire agreement.

*Calcaritermes* is known from 13 living and one fossil species (fig. 9), 13 of which are Neotropical and one of which is Nearctic in warm temperate Florida. The species are concentrated in the Central American and Caribbean areas, but one is found as far south as the state of Rio de Janeiro, Brazil. If the genus originated before the Tertiary, one would expect a worldwide distribution, like that of *Glyptoterme*s, which

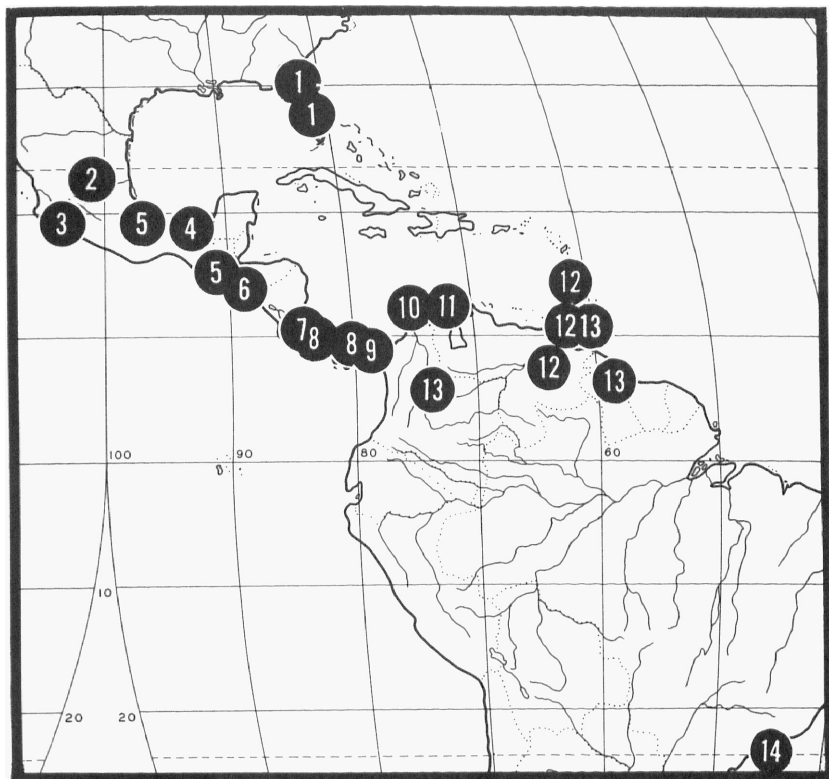


FIG. 9. Distribution of fossil and recent species of *Calcaritermes* Snyder. 1. *C. nearcticus* Snyder. 2. *C. colei* Krishna. 3. *C. parvinotus* Light. 4. *C. vetus* Emerson, fossil from Oligocene-Miocene, Mexico. 5. *C. guatemalae* Snyder. 6. *C. snyderi* Krishna. 7. *C. fairchildi* Snyder. 8. *C. emarginicollis* (Snyder). 9. *C. brevicollis* (Snyder). 10. *C. imminens* Snyder, latitude 11° 07' N., longitude 74° 02' W. 11. *C. recessifrons* Snyder, latitude 11° 07' N., longitude 74° 02' W. 12. *C. temnocephalus* (Silvestri). 13. *C. nigriceps* (Emerson). 14. *C. rioensis* Krishna.

probably dispersed over tropical land connections in the Bering Region to the Orient, Australia, and Africa during the Mesozoic. If *Calcaritermes* had originated by Eocene times, one would expect a more general distribution in tropical South America. The distributions of *Calcaritermes* and *Glyptotermes* are not complementary, so there is no evidence of competitive elimination of one genus by the other.

The description and synonymy of *Glyptotermes*, with a list of included species, were given by Krishna (1961, pp. 313-317, 343, 384-386, 389) and by Krishna and Emerson (1962, pp. 1, 2). A few additional species have

been added more recently, particularly from the Oriental Region. Seventy-five named species of *Glyptotermes* are presently included in the genus, distributed in the Australian and Papuan regions (13), the Oriental Region (24), the Ethiopian and Malagasy regions (13 including one Pleistocene or recent fossil from African copal, one living species from the Seychelles, and an unnamed species from Madagascar), and the Neotropical Region, including Central America and the West Indies (24). One named species is from an unknown locality. Probably there are a few synonyms among these species, and several new species in collections await descriptions.

Emerson (1955, pp. 468, 473, 476-478, 490, 492, 498, 507, 508) and Krishna and Emerson (1962, p. 2) discussed the indicated time and place of origin of *Glyptotermes* in the Neotropical Region during Jurassic or Cretaceous times. The time of origin is indicated by the concentration of species, the geographical order of species, and the methods of dispersal in relation to climate and ancient barriers. *Glyptotermes* has always been a tropical genus unable to disperse over wide oceanic barriers, so one must assume its origin and dispersion at the time of tropical land connections or approximations between the Neotropical and Oriental regions, and between the Oriental and Australian regions during the Mesozoic. The present author is unable to construct a plausible alternative to this hypothesis. Of the 89 named species in *Glyptotermes* and *Calcaritermes* combined, only a single Florida species, *Calcaritermes nearcticus* Snyder, has invaded the temperate zone, possibly during tropical interglacial climates during the Pleistocene. Neither genus indicates a distribution in peripheral ecological or geographical regions, and neither can be placed in the semi-relict category to which some genera of the Kalotermitidae are assigned (figs. 7, 11). Each genus is found in interior tropical continental environments where it is assumed to compete effectively with an advanced termite fauna. Both genera are found in tropical forests, and also in some arid habitats, so that no ecological barrier to their dispersal within continuous tropical land masses is apparent. Both are dry-wood termites with advanced phragmotic soldier heads that plug their narrow galleries and prevent invasion of their nest burrows by predators.

Because of the lack of distinguishing generic characters in the imago caste, the assignment of fossil imagoes in amber from Chiapas, Mexico, to *Calcaritermes* must be considered tentative. Both *Calcaritermes* and *Glyptotermes* are known from living species in Mexico and Central America, although *Calcaritermes* has more species in the general area. In some localities, species of both genera are found in similar habitats. From

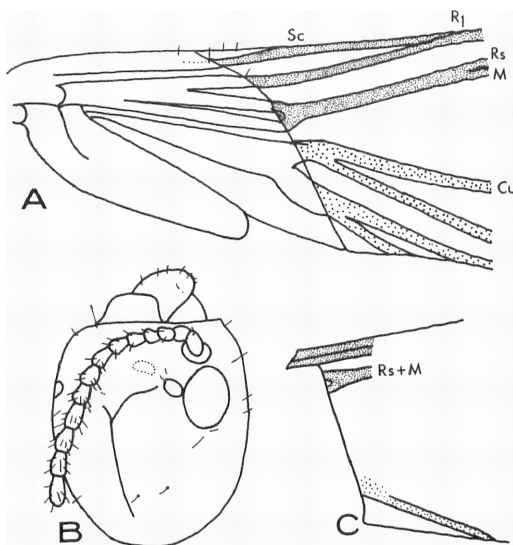


FIG. 10. *Calcaritermes vetus*, new species. A. Base of right forewing, holotype. Central portion arched and costal and inner margins depressed, with consequent foreshortening. Humeral suture accurate except that short curvature near inner margin is obscured by position. B. Head of female, holotype. C. Humeral suture and base of left forewing from below, paratype male;  $R_1$  and Sc curved under in specimen.

the discussion above, it is expected that both genera inhabited tropical Mexico during the Oligocene-Miocene period when the termites were fossilized in amber.

#### ***Calcaritermes vetus*, new species**

**HOLOTYPE FEMALE AND PARATYPE MALE IMAGOS:** Head (fig. 10B) and pronotum with a few scattered bristles, longest on head 0.10 mm., longest on pronotum 0.12 mm. Forewing scale (fig. 10A) with numerous very short hairs. Costal margin of forewing with short hairs numerous from near humeral suture to end of Rs near tip, but more on apical half of wing, longest 0.07 mm. No hairs on membrane, veins, or inner margin. Numerous scattered bristles on abdominal tergites, longest 0.14 mm.

Color of head medium dark brown. Pronotum about same color as head. Wings hyaline, with membrane about same color as or a little darker than surrounding clear amber. Veins near costal margin, including branches of R and M, dark brown. Cu light. Abdominal tergites

same color as head. Sternites lighter brown. To what extent color of amber fossils is similar to color in life is not known, but differences in various parts of body are similar to those in some living species.

Surface texture of top and sides of head minutely roughened or

TABLE 7  
APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF HOLOTYPE FEMALE AND PARATYPE  
MALE IMAGO OF *Calcaritermes vetus*, NEW SPECIES

	Male	Female
Length of head to base of postclypeus	—	0.85
Width of head	0.69	0.75
Thickness of head capsule	0.51	0.41
Length of eye including ocular sclerite	—	0.28
Width of eye including ocular sclerite	0.21	0.23
Length of ocellus	—	0.11
Width of ocellus	—	0.07
Length of antennal fossa	—	0.14
Width of antennal fossa	—	0.09
Length of pronotum in middle	0.49	0.51
Width of flattened pronotum	—	0.86
Length of costal margin of forewing scale	—	0.57
Length of inner margin of forewing scale	—	0.86
Length of forewing with scale	—	5.73
Length of forewing from costal suture	4.98	5.18
Width of forewing	1.22	1.25
Length of Sc from suture	0.20	0.15
Length of R <sub>1</sub> from suture	0.77	0.55
Length of fused Rs and M in forewing	0.66-0.71	—
Length of costal margin of hind wing scale	—	0.37
Length of inner margin of hind wing scale	—	0.52
Length of anal vein in hind wing	0.57	—

shagreened, as in many species of *Calcaritermes* and *Glyptotermes*. Head (fig. 10B) proportionally evenly arched and thick. Y-suture visible as thin lines in middle of head. Eye relatively far removed from lower margin of head, oval or slightly pear-shaped, with long axis parallel to long axis of head, proportionally small as in *Calcaritermes* and *Glyptotermes*. Ocellus oval, touching ocular sclerite, long axis slanting in relation to long axis of eye. Antenna with 13 articles, third slightly longer than second or fourth, second about equal to fourth. Edge of white membranous antennal fossa or depression extremely close (0.01 mm.) to front part of ocular sclerite, dark rim of antennal fossa actually in touch with ocular sclerite, a character that may distinguish this species.



Pronotum longitudinal axis arched, sides depressed, approximately same width as head, but angle of vision does not allow accurate measurements. Front margin evenly and moderately concave. Sides somewhat convex and angular as in *Calcaritermes temnocephalus* (Krishna, 1962, fig. 5), converging somewhat toward rear. Hind margin nearly straight in middle, without conspicuous notch. Front, middle, and hind tibiae with no lateral spines and at least two visible spurs (spurs probably 3:3:3). Each tarsus with four articles, terminal article of hind leg 0.26 mm. long. Arolium present but barely discernible in paratype.

Membranes and Cu in both forewing and hind wing covered with conspicuous nodules characteristic of *Calcaritermes* and *Glyptotermes*, base of each nodule in virtual contact with adjoining one, texture as a whole giving impression of coarse punctation. Extreme tip of forewing rather sharply convex. Costal margin of forewing scale almost straight, barely convex in middle, with only slightly concave outline at junction of humeral suture (fig. 10A). Humeral suture (fig. 10A, C) sharply slanted toward apex and inner margin, more sharply slanted from costal margin to  $R_1$  than from  $R_s$  to inner margin, foreshortened in holotype, but shape from M to basal branch of Cu of paratype showing short curve forward near inner margin, angle at junction of suture and inner margin close to right angle (fig. 10C). Shape and angle of humeral suture apparently a useful distinction between many species of *Calcaritermes* and *Glyptotermes*. Venation beyond humeral suture (fig. 10A) with short Sc.  $R_1$  joining costal margin slightly more than length of forewing scale.  $R_s$  and M separated for very short distance near humeral suture, fused into single vein for a distance about length of  $R_1$ , where  $R_s$  and M again separate into closely parallel veins of equal strength.  $R_s$  joining costal margin before reaching tip of wing. M ending at tip of wing. Cu weak and tuberculated in contrast to M, numerous (about 10) inferior branches, main stem reaching tip of wing or inner margin near tip. Numerous accessory veinlets between branches of Cu make it difficult to determine exact number of inferior branches.

In hind wing, M and  $R_s$  fused beyond suture for about 1 mm. Short A present.

Styli present in male. Cercus with two articles.

COMPARISONS: The separation of  $R_s$  and M at the humeral suture, their fusion for a short distance, and their separation again into parallel veins close to the costal margin occur in the four forewings of the holotype and paratype. The author has not seen this fusion of veins in the forewings of any other species of *Calcaritermes* or *Glyptotermes*, and it may be a species distinction, although it is also possible that this fusion is in-

dividual variation from the normally closely parallel costal margin, Rs, and M in other species of the two genera.

Except for the size of *Calcaritermes vetus*, the closest living species in structure and proportion apparently is *C. temnocephalus* (Silvestri), particularly in pilosity, proportions of the head and pronotum, and the shape of the pronotum. The ocular sclerite is slightly farther from the inside edge of the antennal fossa than that of *C. vetus*, and the long axis of the ocellus is at right angles to the long axis of the eye (Krishna, 1962, fig. 5). *Glyptotermes taveuniensis* Hill is close to *Calcaritermes vetus*, but the antennal fossa is farther from the ocular suture (0.02 mm.). The sharp slant of the humeral suture from the costal margin to  $R_1$  of the forewing, and the slight curve from M to the inner margin, are similar.

Those imagoes that have been described have not all been measured for some characters, particularly the distance of the ocular suture from the edge of the white membrane of the antennal fossa. The present author has measured all known imagoes of species of *Calcaritermes* and finds that the range of the distance of the antennal fossae from the ocular sclerites is 0.02–0.04 mm., with the majority measuring 0.03 mm., whereas species of *Glyptotermes* range from 0.02 to 0.06 mm. with a tendency to average larger than in *Calcaritermes*. Only *Calcaritermes vetus* measures 0.01 mm. for this character.

The antenna of all known imagoes of *Calcaritermes* has 13 articles, with an occasional individual having 14 articles, whereas *Glyptotermes* imagoes range from 11 to 17 antennal articles, with less than the majority of species having 13 articles.

The exact shape and angles of the humeral suture of the forewing seldom have been drawn or described (see Hill, 1942, fig. 2). From published figures and direct examination, the present author finds, however, that *Calcaritermes vetus* resembles some species of both *Calcaritermes* and *Glyptotermes* in the humeral suture of the forewing, whereas other species of both genera have a less sharp angle near Rs and a more curved suture from M to near the inner margin.

In view of the above comparisons, the generic assignment of *Calcaritermes vetus* is not assured, but when the characters and the geographical locality are both taken into account, it is probable that the fossil species belongs to *Calcaritermes* and is the first record of this genus from Tertiary deposits.

**SPECIMENS:** The holotype is a well-preserved female imago with spread wings in Oligocene-Miocene amber from Vega de la Campam on the San Pedro River west of the Simojovel River, Simojovel region (lati-

tude 18° 14' N., longitude 92° 40' W.), Chiapas, Mexico, on a slide (B-7051-8) in the Museum of Paleontology (Acc. No. 2072), University of California, Berkeley. It was purchased by Frans Blom in May, 1958. The paratype is a moderately well-preserved male imago with separated wings from Ixhuatan (latitude 17° 02' N., longitude 92° 01' W.), on Rio Tapilula (=Rio Teapa), collected by Frans Blom, 1960 (B-8413-128a), in a small plastic box (Acc. No. 2063), in the same museum. Fragments of apical portions of a forewing and hind wing, which probably belong to a new species of *Coptotermes* (B-8413-128b), are in the same piece of amber. In general, the paratype is not in such good condition as the holotype, but some characters can be better seen. Some bubbles and cracks in the amber in the immediate vicinity of the body of the paratype obscure a number of structures that are clearly seen in the holotype.

#### GENUS *INCISITERMES* KRISHNA

TYPE SPECIES: *Kalotermes schwarzi* Banks.

The genus was described and its synonymy was given by Krishna (1961, pp. 315-317, 353-358, 384, 385, 387-389).

Although closely related to, and derived from, *Kalotermes*, *Incisitermes* and *Kalotermes* are the basic stocks that gave rise to groups of genera on two branches of the phylogenetic tree of the family. The relatively small size of the fused first plus second marginal tooth compared with the third marginal tooth on the left imago mandible readily distinguishes the *Incisitermes* branch, but unfortunately the dentition of the mandibles is usually obscured in fossils, particularly amber fossils. The present author is of the opinion that, in the texture of the wing, there is no generic distinction between *Incisitermes* and *Kalotermes*. The generic characters of the new fossil species, *Incisitermes krishnai*, include the absence of lateral spines from the tibiae, the presence of an arolium, and the venation of the forewing, together eliminating all known genera of the Kalotermitidae except *Incisitermes*, *Kalotermes*, and possibly *Tauritermes* for which the imago is unknown (see Krishna, 1961).

Krishna (1961, pp. 356, 357) assigned 25 species to *Incisitermes*, one of which is doubtful, and two of which are undescribed. Earlier synonymies of species listed by Krishna were given by Snyder (1949). Krishna (1961, pp. 391, 397) referred to *I. lighti*, which he neglected to include in his list of species, probably because Snyder (1949, p. 12) had placed this species in synonymy with *Kalotermes* (= *Incisitermes*) *banksi*. *Kalotermes arizonensis* Snyder (1926, p. 393, figs. 5, 6) is regarded here as

a synonym of *Incisitermes minor* (Hagen). *Calotermes solidus* Hagen (1858a, p. 70, imago) from an unknown locality has been examined in the British Museum (Natural History) by Emerson, and later by Krishna, and is classified as *Incisitermes solidus* (Hagen), but it is doubtful whether it will be possible to identify this shrivelled and unique type imago positively without a type locality.

The present author includes 23 named species in the genus *Incisitermes*, one with doubt, and one new fossil species described here. Fossil

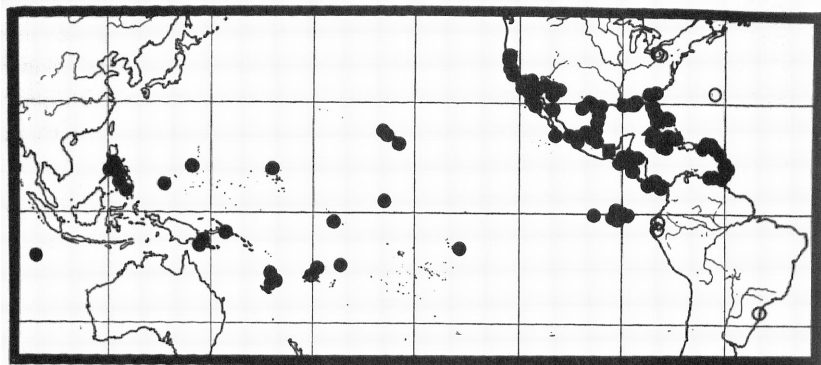


FIG. 11. Distribution of genus *Incisitermes*. Black circles indicate localities for 22 living described, and several undescribed or undetermined species. Open circles indicate localities presumed to be modern introductions through the agency of man. Black square is the locality of *I. krishnai*, new species, Oligocene-Miocene amber, tropical Mexico.

pellets, from the Pleistocene near St. Petersburg, Florida, were considered by Light (1930) to be excrement of *Kalotermes* (= *Incisitermes*) *schwarzi* Banks, or a closely related species. Some presently recognized species may prove to be synonyms. A few undescribed species from Cocos Keeling Islands in the Indian Ocean, Palau Islands in the western Pacific, Papua and New Guinea, and from Central America, are in the collection of the American Museum of Natural History and are included in the map (fig. 11). There is ample evidence that a few distinct species are sympatric. Some species have been carried by man to localities far removed from their natural ranges and places of origin. The genus is distributed in the Papuan Region, including New Guinea and both eastern and western South Sea islands (four named species), in the Oriental Region, including the Philippines and Cocos Keeling Islands (four named species), in the Neotropical Region, including northern South America, Central America, West Indies, and Bermuda

(12 named species), and the Nearctic Region, including southeastern, central, southwestern United States, and temperate Mexico (three named species). No named or unnamed species are known from continental Australia, Asia, Africa, or Madagascar. Apparently there is a concentration of species in the New World, but the numbers are not considered significant in a statistical sense. When the genus is revised and monographed, and new species are described, the numbers of species in the major geographical regions may indicate some probability of a particular time and place of origin in one region. Most species occur in the Neotropical Region, a few species have become adjusted to temperate climates in the Nearctic Region, and the genus as a whole (fig. 11) occupies warm temperate regions or ecologically peripheral areas in the tropics on or near coasts. All interior continental localities are temperate either at higher altitudes or latitudes. The new fossil species from mid-Tertiary Mexico is found in a region where living species occur, and the associated termite fauna (some new species will be described in subsequent articles) provides evidence that the climate was tropical at the time of fossilization as it is at present. Both the geographical and ecological distribution indicates that *Incisitermes* is a semi-relict genus (Emerson, 1955). The relatively primitive morphology compared with that of some more advanced genera, and the geographical pattern of distribution, probably indicate a Mesozoic origin, with the extinction of species in central continental areas now occupied by more advanced genera and families.

The distribution of *Incisitermes* (fig. 11) is complementary to that of its more primitive relative, *Kalotermes* (fig. 7). The only overlap is in southeastern United States where the two genera usually occupy slightly different ecological habitats. *Incisitermes* is more often found in damp logs or stumps, although both genera are "hardwood termites." It is surmised that *Incisitermes* is often dispersed in floating logs. The same species, *I. immigrans* (Snyder), is found on many isolated oceanic islands in the Pacific Ocean, and also on the coasts of Ecuador and Peru. Possibly modern man or the earlier Polynesians have been responsible for some of this dispersion, but endemism on some oceanic islands and differentiation of species in the Caribbean region suggest a dispersal by means of floating logs during Tertiary or earlier times when the Isthmus of Panama did not create a land barrier between the Pacific and Atlantic oceans.

The hypothesis is suggested that the genus is fairly primitive and only slightly advanced from its ancestral genus, *Kalotermes*, that *Incisitermes* is unable to compete effectively against more advanced genera of

the Kalotermitidae or the advanced genera of the families Rhinotermitidae and Termitidae that dominate the tropical interior continental regions, and that biotic barriers limit its present occurrence to islands, shores, and warm temperate interior continental areas (fig. 11). The absence of *Incisitermes* from continental Australia, Africa, Europe, and Madagascar possibly is explained by the presence of its competitor, *Kalotermes* (fig. 7), near the shores of these regions, together with a possible origin and dispersion at a later date in the Mesozoic. The absence of *Kalotermes* from the Philippines, New Guinea, and the equatorial Pacific islands possibly is due to competition with *Incisitermes*. Both genera are semi-relict (Emerson, 1955) and largely mutually exclusive. *Kalotermes* shows no indication of dispersion by floating logs in contrast to *Incisitermes* and, possibly for this reason, *Kalotermes* species are more restricted to smaller ranges than those of *Incisitermes*. Species of *Kalotermes* are rarely sympatric, whereas species of *Incisitermes* often are. These possible explanations of distribution in time and space are speculative, but are offered for future tests through the accumulation of facts from the fields of taxonomy, zoogeography, paleontology, and ecology.

### ***Incisitermes krishnai*, new species**

*Kalotermes nigrinus*: SNYDER, 1960, p. 493 (fossil from Tertiary amber only), pl. 70, fig. 3 (photograph of imago). HURD, SMITH, AND DURHAM, 1962, pp. 111, 116 (locality, geology, fauna, flora).

Snyder (1960) identified a well-preserved fossil imago from Mexican amber as the living species, *Kalotermes* (= *Incisitermes*) *nigrinus* Snyder, known from imagoes in an intercepted log transported from Guatemala to San Francisco, California, and soldiers intercepted from San José, Guatemala (Snyder, 1946, pp. 158–159). Dealates of *I. nigrinus*, determined by Emerson from Cuesta de los Cedros (latitude 22° 30' N., longitude 99° 20' W.), 36 kilometers east of Ciudad del Maiz, San Luis Potosí, Mexico, on Route 170, altitude 2250 feet, collected by W. L. Nutting in a mesophytic oak area in 1949, are in the American Museum of Natural History.

It is doubtful that a fossil from amber of Oligocene or Miocene age could belong to a contemporary species, although a few cases of such ancient species in other groups of animals are recorded. So far, no case of species identity of a Tertiary fossil termite with a living species is reliable. Pierce (1958) classified two Miocene fossils as subspecies of living species, but data from fragments of wings are not adequate for such an interpretation.

TABLE 8  
APPROXIMATE MEASUREMENTS (IN MILLIMETERS) OF HOLOTYPE AND PARATYPE IMAGOS  
OF *Incisitermes krishnai*, NEW SPECIES

	Holotype	Paratype
Length of head to front of anteclypeus	1.27	—
Length of head to front of postclypeus	1.22	—
Width of head	1.04	1.16
Maximum diameter of eye, including ocular sclerite	0.29	0.33
Length of ocellus	0.12	—
Ocellus from eye	0.00	—
Length of postclypeus	0.06	—
Width of postclypeus	0.52	—
Length of pronotum in middle	0.66	0.67
Width of pronotum	1.22	1.16
Length of middle tibia	0.69	—
Length of hind tibia	0.87	—
Maximum length of forewing scale	0.72	—
Length of forewing scale to costal suture	0.69	—
Length of forewing, including scale	6.54	—
Length of forewing from costal suture	5.85	5.60
Width of forewing	1.80	2.19
Width of space between costal margin and main stem of Rs in middle of wing	0.12	—

A careful examination of the amber specimen determined by Snyder provides numerous characters that differentiate it from any living species, and it is here described as new. The author takes pleasure in naming the new species in honor of his colleague and co-investigator, Dr. Kumar Krishna, for his numerous excellent contributions to termite taxonomy including the recognition of the genus *Incisitermes*.

IMAGO HOLOTYPE AND PARATYPE (FIG. 12A-D): Head with numerous bristles scattered over front and vertex, longest 0.16 mm. Pronotum with a few moderately long bristles on disc and margins, longest 0.16 mm. Femora and tibiae covered with many hairs, some quite coarse and bristle-like. Forewing and hind wing with numerous short hairs of varying length on costal margin of scale and extending near tip of wing, longest hair on scale 0.05 mm., longest on costal margin 0.05 mm. Hairs lacking on inner margin, extreme tip of wing, and on veins and membranes. Longest bristle near tip of abdomen 0.17 mm.

Sides of head fairly straight and parallel. Y-suture with branches. Eye relatively small. Ocellus touching ocular sclerite. One entire antenna with 17 articles, second, third, and fourth about equal in length. Postclypeus short and wide. Dentition of left mandible barely visible in

paratype, but angle of vision insufficient for accurate description, although first plus second marginal tooth apparently slightly shorter than third marginal tooth, resembling *Incisitermes schwarzi* in proportions (Krishna, 1961, fig. 46); cutting edge of first plus second marginal tooth slightly concave as in *Incisitermes*, *Kaloterms*, and several other genera.

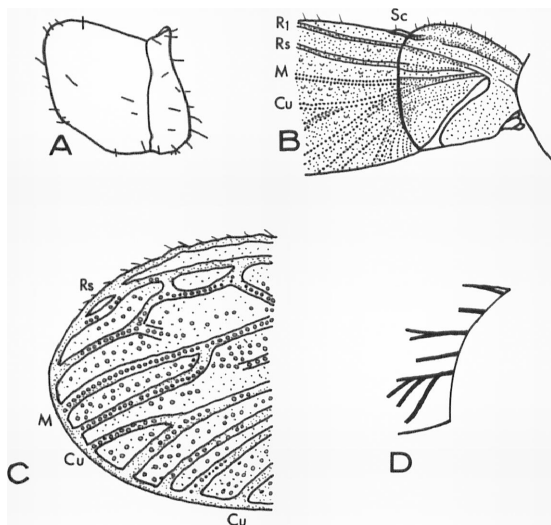


FIG. 12. *Incisitermes krishnai*, new species. A. Pronotum of holotype tilted at an angle of about 45 degrees. B. Scale and base of left forewing, holotype, distorted by arching, with peak between  $R_1$  and  $R_s$ , and inner margin depressed. C. Tip of left forewing, holotype. D. Sketch of base of left forewing, paratype, showing more normal shape of humeral suture than in distorted holotype.

Pronotum (fig. 12A) with wide angular notch in middle of front margin of holotype, but angle possibly exaggerated by perspective and some shriveling; pronotum of paratype with slightly notched but otherwise concave front margin. Sides straight toward front and probably fairly parallel. Sides somewhat angular and merging with hind margin that is emarginate with slightly concave margin in middle. Hind margin of mesonotum wide and nearly straight. Femur of front leg swollen from side, 0.27 mm. wide. Tibiae without lateral spines, and tibial spurs 3:3:3. Front tibia short and swollen at tip, length 0.52 mm., width 0.14 mm.; each spur with slightly serrated edges, length of one inner spur 0.12 mm. Length of one inner spur on hind tibia 0.09 mm. Each tarsus with four articles; arolium present.



Forewing scale (fig. 12B) with strongly convex costal margin; angular notch at costal end of humeral suture. Humeral suture strongly arched from costal margin to Rs, and fairly straight from Rs to inner margin (fig. 12B, D). Tip of wing comparatively rounded (fig. 12C). Wing membrane (fig. 12C) covered with many comparatively large tubercles, some series giving appearance of accessory veins, tubercles very clear in amber specimen and similar to those on dried wings of living species of *Incisitermes* and *Kaloterмес*, but wings under alcohol showing tubercles not so large as those in dried or fossil wings. Membrane with a few variable light and steeply slanting or vertical thickenings or veinlets that connect Rs and M in outer half of wing and become somewhat reticulate in pattern. Independent veins beyond suture include short Sc.  $R_1$  fairly long and joins costal margin about 2.3 mm. from suture.  $R_1$  and Rs somewhat farther apart just beyond suture than at suture, and space between them narrows as it extends toward end of  $R_1$ . Rs ends near tip of wing (fig. 12C), with four or five superior branches. M rather weak and not strongly sclerotized, about midway between Rs and Cu in middle of wing, ends near tip (fig. 12C). Cu has 10-11 primary branches that join inner margin, few if any showing secondary branches.

Hind wings not clearly seen largely because they are partially covered by the forewings in the specimens. Venation and texture similar to forewings except for family characters of hind wing.

COMPARISONS: Unfortunately, the dentition of the left mandible is only rarely visible in amber fossils, and, in the case of the holotype imago of *Incisitermes krishnai*, cannot be seen. The paratype imago apparently has dentition similar to that of the left mandible of *Incisitermes*, but the angle of vision makes it difficult to be sure of the proportions of the marginal teeth. Because of the variation and overlap of other characters, one cannot be completely sure whether the species belongs to *Kaloterмес* or to *Incisitermes*. The resemblances of various features of the forewing seem, however, to indicate a greater probability that the species belongs to *Incisitermes*. Although there is some overlap between temperate and tropical climates in the distribution of *Kaloterмес* and *Incisitermes* (figs. 7, 11), *Incisitermes* is more characteristic of tropical climates, whereas most species of *Kaloterмес* now live in temperate climates either in the Northern Hemisphere or in the Southern Hemisphere.

A paratype imago of *Incisitermes nigrinus* (Snyder) is similar to the imago of *I. krishnai* in pilosity and relative length of hairs on the head, pilosity of the pronotum, pilosity of the forewing and forewing scale,

including the length of the hairs, shape of head, relative size of the eye, and the presence of an arolium. *Incisitermes nigrinus* has a shorter, narrower, and more pointed forewing; the forewing scale has a slightly less convex costal margin;  $R_1$  is shorter and joins the costal margin about 0.58 mm. from the suture;  $R_s$  has seven to eight superior branches; and the pronotum has less angular sides and is more evenly curved to middle of hind margin. In general, *I. nigrinus* is smaller; some comparative measurements follow: longest diameter of eye, 0.28 mm.; length of pronotum, 0.58 mm.; width of pronotum, 0.93 mm.; length of hind tibia, 0.73 mm.; length of forewing from humeral suture, 5.20 mm.; width of forewing, 1.36 mm.; width of space between the costal marginal thickening and  $R_s$  in middle of wing, 0.09 mm.

In general, *I. milleri* (Emerson) is smaller than *I. krishnai*, but some measurements overlap.

One paratype female imago of *Incisitermes seeversi* (Snyder and Emerson) from Maria Madre Island, Tres Marias Islands, Mexico, is close to *I. krishnai* in pilosity; is slightly larger; and the shape of pronotum is fairly close; *I. seeversi* has slightly less angular sides of pronotum; both species have veinlets between  $R_s$  and  $M$  in the outer half of the wing; the shape of the humeral suture of the forewing is similar;  $Sc$  and  $R_1$  are similar; and the space between the costal margin and  $R_s$  in the middle of the wing is similar in proportion (0.17–0.23 mm. in *I. seeversi*). The eye of *I. seeversi* is proportionally larger; all four wings have a slightly concave notch near the apical junction of  $R_s$  and the costal margin; and the number of superior branches of  $R_s$  is eight in the two forewings. Measurements of some structures of *I. seeversi* are: width of head, 1.10 mm.; diameter of eye, about 0.34 mm.; length of pronotum, 0.75 mm.; length of hind tibia, 0.98 mm.; length of forewing from costal end of humeral suture, 7.96 mm.; width of forewing, 2.26 mm.

A cotype imago of *Incisitermes schwarzi* (Banks) from Paradise Key (Royal Palm Park), Florida, agrees with the imago of *I. krishnai* in the following characters: the relative abundance and length of the bristles and hairs on various parts (Krishna, 1961, fig. 45), longest on the head 0.12 mm.; the veinlets between  $R_s$  and  $M$ ; a few reticulations between  $M$  and  $Cu$  not shown in Krishna (1961, fig. 47); the relatively narrow space between the costal margin and  $R_s$  in the middle of the wing 0.23 mm. in *I. schwarzi*; and few (four) superior branches of  $R_s$ . *Incisitermes schwarzi* differs from *I. krishnai* in its larger size; proportionally larger eye; proportionally wider pronotum, and with less angulate sides; and more pointed tip of the wing.

Imagoes of *Kalotermes flavicollis* (Fabricius) (determined by Emerson, Birwah, Israel, collected by Bytinski-Salz, March 25, 1953) resemble those of *I. krishnai* in the proportions of the head, eye, and ocelli; the texture of the wing membrane; the convex costal margin of the forewing scale; and in veins Sc and Cu. In the forewing under examination, M joins Rs in the middle of the wing, and then emerges free at the tip, thus showing some individual variation compared with the wing of *Kalotermes flavicollis* figured by Krishna (1961, fig. 21). The thickenings or veinlets between Rs and M are less regular than in *I. krishnai* and other species of *Incisitermes* examined. Numerous species differences in pilosity, proportional width of the pronotum compared with that of the head, size, and the shape of the tip of the wing separate these species, but the genera are close in the visible characters of the amber fossil *I. krishnai*. Possibly the space between the costal margin and Rs in the middle of the forewing is most significant, 0.20 mm. in *K. flavicollis* compared with 0.12 mm. in *I. krishnai*.

Imagoes of *Kalotermes approximatus* Snyder [determined by Emerson, Bartow (latitude 27° 54' N., longitude 81° 51' W.), Florida, collected by Miller, November 24, 1940] are the closest living geographical representative of *Kalotermes* to the fossil *Incisitermes krishnai*. The pilosity of the costal margins of the forewings of both species is similar. The size of the eye and the proportion of the eye in relation to the head are similar in both species and in *Kalotermes flavicollis*. The pronotum is proportionally wider than the head in *Incisitermes krishnai*. The tip of the forewing is more pointed in *Kalotermes approximatus*, the scale of the forewing is similar in shape, the short Sc is similar, the space between the costal margin and Rs is similar, and the veins, curvature of veins, and proportional distances between veins are similar in general. M is divided with two main branches in the middle of one wing of *K. approximatus* (probably individual variation).

**SPECIMENS:** Holotype, female imago (No. 12613 in the Museum of Paleontology, University of California, Berkeley), earlier determined as *Kalotermes nigrinus* by Snyder; and paratype imago (No. 12945 in the same museum), Oligocene-Miocene amber, Simojovel area (latitude 18° 14' N., longitude 92° 40' W.), Chiapas, Mexico, are redescribed. The less well-preserved paratype from the same deposit as the holotype is probably from locality B-5103 in amber in sandstone from near the base of the western edge of Las Cruces landslide on the south slope near the southeast end of the major ridge locally known as Nichcalan or Cerro Balumtum. The characters that are visible are sufficiently close to those of the holotype for its assignment to the same species. The

paratype specimen is much distorted, the angles of vision are in some aspects rather awkward, and the wings are wrinkled, obscuring much of the venation. In a few particulars, such as the dentition of the mandibles, the specimen shows characters that cannot be seen so well in the holotype. The two specimens were lent through the courtesy of Drs. J. Wyatt Durham and Joseph H. Peck.

#### GENUS *CRYPTOTERMES* BANKS

TYPE SPECIES: *Cryptotermes cavifrons* Banks.

The description, phylogeny, synonymy of the genus, and a list of species were provided by Krishna (1961, pp. 379-382).

The junction of M with Rs in the outer half of each wing, both forewing and hind wing, is fairly characteristic of two related genera, *Procryptotermes* and *Cryptotermes* (Krishna, 1961, pp. 316, 376, 379). The assignment of *Cryptotermes ryshkoffi* Pierce, known only from a Miocene wing from California, to the genus *Cryptotermes* is somewhat tentative, although probably correct and in conformity with the geographical and climatic distribution of the genus. There is some variation in the venation of *Procryptotermes*, *Cryptotermes*, and other genera and species, but the venation has statistical significance and taxonomic value and is reliable when the sample is adequate. The occurrence of *Reticulitermes* (Rhinoitermitidae) in the same geological deposit is a strong indication of a temperate climate. All known species of *Procryptotermes* live in the tropics, whereas one species of *Cryptotermes* (*C. cavifrons* Banks) is native in warm temperate Florida in dry wood. Several species of *Cryptotermes* have been introduced by man into temperate localities and are well established in man-modified habitats.

#### *Cryptotermes ryshkoffi* Pierce

*Cryptotermes ryshkoffi* PIERCE, 1958, p. 19, pl. 5, fig. 1 (wings), pl. 6, fig. 6 (photograph of nodule).

WINGS: Wings large for *Cryptotermes*, but size alone not reliable for generic distinction. Aside from size, it is virtually impossible to distinguish wings of this species from those of most living species of the genus, but it is safe to assume that a Miocene species, particularly from a temperate climate, is different from any living species.

MEASUREMENTS OF HOLOTYPE: Length of forewing (Pierce), 10.50 mm.; width of forewing (Emerson), 0.71 mm.

SPECIMENS: Holotype wings from same individual, Miocene, Calico Mountains (latitude 34° 49' N., longitude 116° 57' W.), California, in

a calcareous nodule (Los Angeles County Museum No. S9097), examined by the present author in 1966 through the courtesy of Dr. W. D. Pierce.

## SUMMARY

Eight genera and 12 species of Tertiary fossil imago castes of termites of Kalotermitidae Froggatt of the order Isoptera are redescribed, or described from direct examination of specimens. The genera known from Tertiary fossils only are *Eotermes* Statz, *Prokalotermes* Emerson, *Proelectrotermes* Rosen, and *Electrotermes* Rosen. Genera that contain both living and fossil species are *Neotermes* Holmgren, *Kalotermes* Hagen, *Calcaritermes* Snyder, *Incisitermes* Krishna, and *Cryptotermes* Banks, of which fossil species are described for the first time in *Calcaritermes* and *Incisitermes*. The descriptions include *Eotermes grandaeva* Statz, Oligocene shales, West Germany; *Prokalotermes hageni* (Scudder), Miocene shales, Colorado; *Proelectrotermes berendti* (Pictet), Oligocene amber, Baltic Sea coasts, U.S.S.R. and Denmark; *Proelectrotermes fodinae* (Scudder), new combination for *Parotermes fodinae* Scudder, Miocene shales, Colorado; *Electrotermes affinis* (Hagen), Oligocene amber, Baltic Sea coasts, U.S.S.R. and Denmark; *Electrotermes girardi* (Giebel), Oligocene amber, Baltic Sea coasts, U.S.S.R.; *Kalotermes rhenanus* Hagen, Oligocene shales, West Germany; *Kalotermes swinhoei* (Cockerell), Miocene amber, Burma; *Kalotermes tristis* (Cockerell), Miocene amber, Burma; *Calcaritermes vetus*, new species, Oligocene-Miocene amber, Mexico; *Incisitermes krishnai*, new species, Oligocene-Miocene amber, Mexico; and *Cryptotermes ryshkoffi* Pierce, Miocene nodules in shale, California.

Numerous new characters of both genera and species are described, and the nomenclature, synonymies, systematics, comparisons, phylogenies, geographical distributions, ecology, and evolution of the fossil genera and species are discussed. Figures of fossil species and maps of distribution of the genera *Kalotermes*, *Calcaritermes*, and *Incisitermes* are included. Four previously described fossil species of *Neotermes* and *Kalotermes* that were not available for direct examination are discussed.

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