

PHYLOGENY AND GENERIC
RECLASSIFICATION OF THE
CAPRITERMES COMPLEX
(ISOPTERA, TERMITIDAE,
TERMITINAE)

KUMAR KRISHNA

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 138 : ARTICLE 5 NEW YORK · 1968

PHYLOGENY AND GENERIC
RECLASSIFICATION OF THE
CAPRITERMES COMPLEX (ISOPTERA,
TERMITIDAE, TERMITINAE)

KUMAR KRISHNA

*Research Associate, Department of Entomology
The American Museum of Natural History
Assistant Professor, Department of Biology
City College, City University of New York*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 138 : ARTICLE 5
NEW YORK : 1968

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 138, article 5, pages 261–324, figures 1–46, table 1

Issued July 12, 1968

Price: \$1.50 a copy

CONTENTS

INTRODUCTION	265
Terminology	265
Phylogeny	265
SYSTEMATICS	270
Key to the Genera	270
<i>Paracaprithermes</i> Hill	271
<i>Protocaprithermes</i> Holmgren.	274
<i>Quasitermes</i> Emerson	278
<i>Capritermes</i> Wasmann.	280
<i>Homallotermes</i> John	284
<i>Dicuspiditermes</i> Krishna	286
<i>Pericaprithermes</i> Silvestri	290
<i>Procapritermes</i> Holmgren	294
<i>Labiocaprithermes</i> , New Genus	304
<i>Mirocapritermes</i> Holmgren	305
<i>Cornicaprithermes</i> Emerson	308
<i>Dihoplotermes</i> Araujo	310
<i>Neocaprithermes</i> Holmgren	312
<i>Planicaprithermes</i> Emerson	316
SUMMARY	320
BIBLIOGRAPHY	320

INTRODUCTION

THE PRESENT PAPER is the second in a series dealing with the taxonomy and phylogeny of the group of termite genera with soldiers having asymmetrical snapping mandibles, here referred to as the *Capritermes* complex.

The soldiers of this group are the most advanced and specialized in the subfamily Termitinae of the family Termitidae. Their asymmetrical snapping mandibles are distinctive. The left is twisted and arched in the middle, and the right is flat, straight, and bladeliike; in defense they are locked together and released with a loud click, flipping the soldier several inches through the air. It is most likely that the purpose of this action is to communicate alarm, although it has been suggested that it is to deliver a defensive blow or even to dodge the enemy.

The taxonomy and phylogeny of the genera of the *Capritermes* complex have been in a confused state, because some of the genera as hitherto treated have been composed of heterogeneous elements. The purpose of the present paper is to reclassify the species and to re-evaluate and clarify the phyletic relationships of the genera *Paracapritermes*, *Protocapritermes*, *Quasitermes*, *Capritermes*, *Homalotermes*, *Pericapritermes*, *Dicuspitermes*, *Procapritermes*, *Pseudocapritermes*, *Mirocapritermes*, *Cornicapritermes*, *Dihoplotermes*, *Neocapritermes*, and *Planicapritermes*.

Ninety-one described species and a number of new ones are included in this study. Some species are treated as synonyms for the first time here, although without full explanation. A detailed re-evaluation of the described species and descriptions of new species will be dealt with in a comprehensive species revision of these genera, to be undertaken by the author in the near future.

This study is based on specimens in the collection of the American Museum of Natural History. The research resulting in this paper has been supported by National Science Foundation Grants GB-388 and GB-5158.

I am indebted to Dr. Alfred E. Emerson for critical discussion and generous use of his systematic card catalogues; to my wife,

Mrs. Valerie Krishna, for editing the manuscript; and to Mr. Thomas Hayden for preparing most of the illustrations.

TERMINOLOGY

In this paper the top tooth of the left and right mandibles of the imago worker is referred to as the "apical tooth," the term used by all authors (fig. 3, ap). In the left mandible, the next tooth (referred to as the first marginal tooth by Ahmad, 1950; Mathur and Thapa, 1961, p. 5; Roonwal and Sen-Sarma, 1960, p. 32; and Roonwal and Chhotani, 1962, pls. 21, 23) is designated here as the fused first plus second marginal tooth (fig. 3, m_{1+2}). The next tooth, referred to as the second marginal tooth by the above authors, is here designated as the third marginal tooth (fig. 3, m_3).

On the under side of the left molar plate is a small, toothlike process not usually visible from above. In *Cornicapritermes* and *Dihoplotermes* it is partially visible, and Araujo (1961) and Ahmad have referred to it as the third marginal tooth. It is here designated as the molar tooth (fig. 37, mt).

In the right mandible the terms used here are those used by Ahmad (1950) and other authors, that is, "first marginal tooth" and "second marginal tooth" to designate the two teeth below the apical tooth (fig. 3, m_1 and m_2).

PHYLOGENY

In any discussion of the phylogeny of a taxon, it is essential to state (1) whether a given character is primitive or derivative (advanced), and (2) whether a character state has arisen once and is unique or whether it arose independently several times during its evolutionary history. It must be borne in mind, however, that terms such as "primitive" (plesiomorphic) and "derivative" (apomorphic) are, of course, relative and are significant primarily in discussing evolution within a particular lineage. For example, in termite soldiers, a head with a frontal projection is usually considered an advanced or derivative condition, whereas a head without a frontal projection is considered primitive. In the

genera under consideration here, however, the opposite is true: the evidence strongly indicates that the presence of a frontal projection in this case is primitive.¹ It should also be borne in mind that an animal can exhibit both primitive and derivative characters at the same time.

The termite genera belonging to the subfamily Termitinae fall into two main groups: the first with soldiers having biting mandibles, and the second with soldiers having snapping mandibles, the second group probably having evolved from the first (Ahmad, 1950). The second group has branched further into two main lines: one with relatively symmetrical snapping mandibles, and the other with mandibles of various degrees of asymmetry, the latter probably having evolved from the former (Ahmad, 1950).

In support of this contention (with which the present author agrees), that the genera with soldiers that have asymmetrical snapping mandibles (*Paracapritermes*, *Capritermes*, *Homallotermes*, and so on) have evolved from a group with soldiers that have symmetrical snapping mandibles (*Promirotermes*, *Angulitermes*, and *Termes*), Ahmad called attention to what he regards as a similarity between the imago-worker mandibles of *Paracapritermes* and those of *Promirotermes*. But, according to the studies of the present author, the imago mandible of *Paracapritermes* is not the most primitive in the *Capritermes* complex, as implied by Ahmad, because its second right marginal tooth is more reduced than that of *Homallotermes* and therefore more advanced. On the contrary, the imago mandible of *Homallotermes* is the most primitive of the *Capritermes* complex, and in fact its dentition is as primitive as that of *Promirotermes* and that of *Angulitermes*.²

¹ If the *absence* of a frontal projection were assumed to be primitive, then the frontal projection would have had to evolve independently in the different phyletic lines where it appears. It is more likely that a complex character will regress and be lost independently than that it will develop several times independently. Also, the genera with symmetrical snapping mandibles (*Promirotermes*, *Angulitermes*, and *Termes*), which presumably gave rise to the *Capritermes* complex, have a frontal projection.

² Ahmad (1950) stated that *Angulitermes* is more advanced than *Termes* and probably derived from it. The

Ahmad further stated that among the living genera with soldiers that have symmetrical mandibles, *Promirotermes* is most closely related to the *Capritermes* complex. To characterize the relationship between the two groups more specifically, the present author is of the opinion that some now-extinct form, which had *Promirotermes*-like or *Angulitermes*-like primitive mandibles in the imago and an advanced head with a tapering frontal projection in the soldier, more like the head of *Angulitermes* or *Termes*³ than like that of *Promirotermes*, gave rise to the genera with soldiers having asymmetrical mandibles. (The soldier of *Promirotermes* has a blunt frontal hump but does not have a pointed frontal projection, and therefore *Promirotermes* as such cannot be regarded as the direct ancestor.) Without the postulation of such an ancestor, the presence of a pointed frontal projection in both *Termes* and *Angulitermes*, on the one hand, and the *Capritermes* complex, on the other, would necessitate the independent development of this character in the two lines. But the development of a complex character so similar in morphological detail in the two lines is unlikely; therefore the hypothetical ancestral form must have already developed a prominent frontal projection like that of *Termes* or *Angulitermes*. This hypothetical ancestor (A) probably later developed asymmetrical mandibles in the soldier caste and gave rise to the living genera of the *Capritermes* complex. It presumably had all the primitive characters enumerated above.

A suggested phylogeny of the genera of the *Capritermes* complex is shown in figure 1.

One line (A₁) split early from the ancestral lineage (A) and gave rise to the two advanced genera, *Neocapritermes* and *Planicapritermes*. These two genera have unique features not

present author's studies, however, indicate that the imago mandible of *Angulitermes* is as primitive as that of *Promirotermes*, since the second right marginal tooth is equally well developed in both, and the dentitions are identical in other respects. Therefore, *Angulitermes* is closer to *Promirotermes* than it is to *Termes*, and *Termes* is more advanced than *Angulitermes*. Thus the order should be *Promirotermes*, *Angulitermes*, and *Termes*.

³ *Termes* as treated here presently contains many heterogeneous elements and needs revision. Many species presently placed in it must eventually be reassigned.

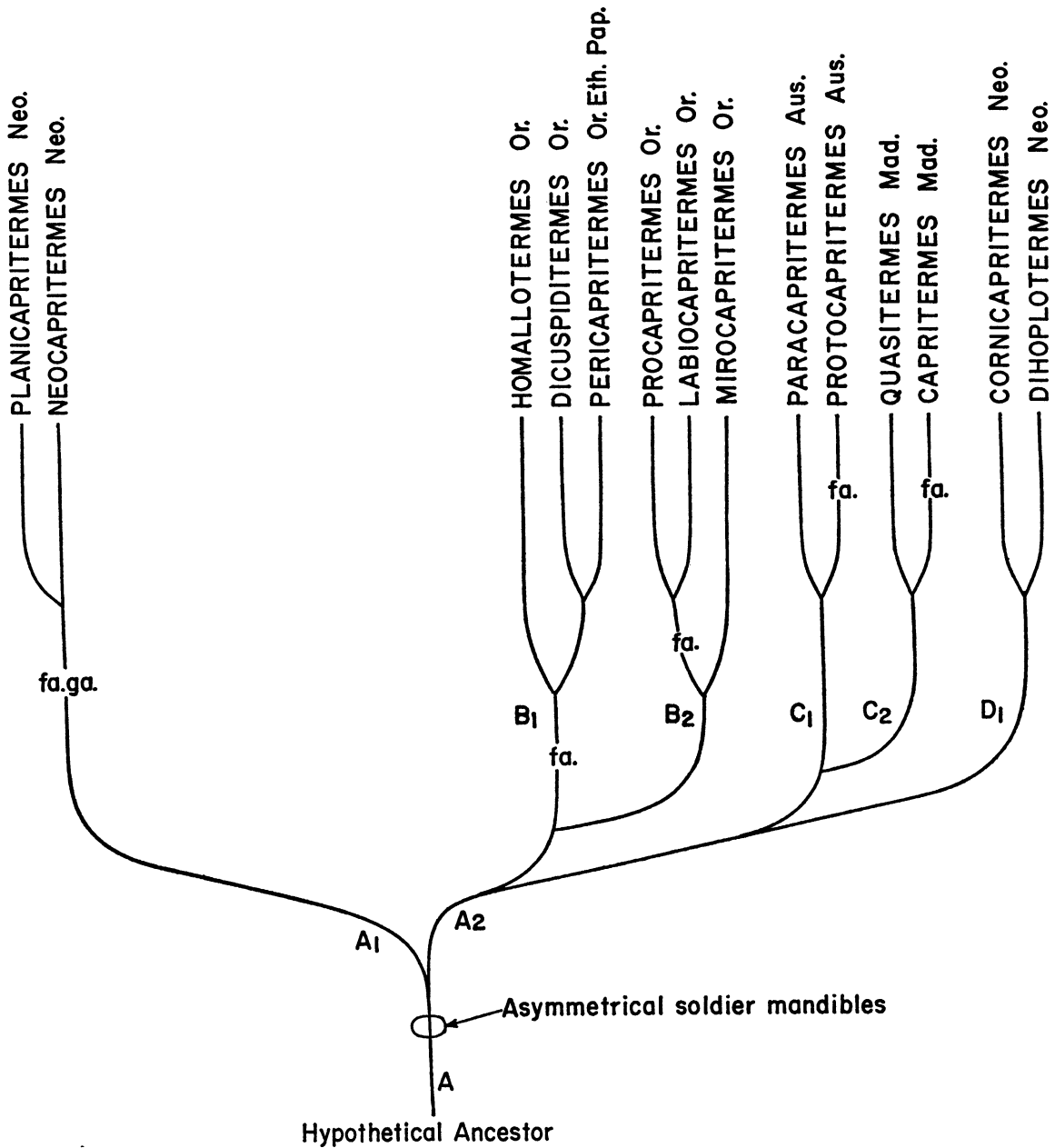


FIG. 1. Phylogenetic diagram of the *Capritermes* complex.

Abbreviations: Aus., Australia; Eth., Ethiopian; fa., frontal projection absent; fa.ga., frontal projection and gland absent; Mad., Madagascar; Neo., Neotropical; Pap., Papuan; Or., Oriental.

found in any other genera of the *Capritermes* complex. The soldier has lost the frontal projection and also the frontal gland, although there is an opening in the gland area; its antenna is 14- to 16-segmented; and its

labrum is tongue-shaped or three-lobed. The imago has a sclerotized fontanelle plate with a visible opening; and in the right mandible the angle between the first and second marginal tooth is sharp, and the posterior mar-

TABLE 1

PRIMITIVE OR DERIVATIVE CHARACTERS IN THE *Capritermes* COMPLEX

Primitive Condition	Derivative Condition
IMAGO	IMAGO
Head densely covered with hairs and bristles	Head sparsely covered with hairs and bristles
Fontanelle small	Fontanelle large
Fontanelle flat, not bulging above surface of head	Fontanelle convex, bulging above surface of head
Left mandible with third marginal tooth well developed	Left mandible with third marginal tooth somewhat reduced, rudimentary, or absent
Right mandible with second marginal tooth well developed	Right mandible with second marginal tooth rudimentary or absent
Antenna 16- or 17-segmented	Antenna 14- or 15-segmented
Tibial spurs 3:2:2	Tibial spurs 2:2:2
Middle tibia with spinelike bristles	Middle tibia without spinelike bristles
SOLDIER	SOLDIER
Monomorphic	Dimorphic
Head thick, with vertex in front high and frontal slope steep	Head flat, with vertex in front not high and frontal slope not steep
Posterior margin of head evenly rounded	Posterior margin of head trilobed
Frontal gland large	Frontal gland reduced or absent
Frontal projection present	Frontal projection absent
Labrum relatively small and not swollen	Labrum large and swollen
Labrum with lateral margins even	Labrum with lateral margins serrated
Labrum with anterolateral corners with short points	Labrum with anterolateral corners with long points
Labrum with anterior margin straight or concave	Labrum tongue-shaped or trilobed anteriorly
Left mandible weakly bent in middle (weakly asymmetrical)	Left mandible strongly bent in middle (strongly asymmetrical)
Mandible with apex hooked	Mandible with apex blunt
Antennal segments elongated	Antennal segments short
Antenna 15- or 16-segmented	Antenna 13- or 14-segmented
Tibial spurs 3:2:2	Tibial spurs 2:2:2
Middle tibia with spinelike bristles present	Middle tibia with spinelike bristles absent

gin of the second marginal tooth is straight (figs. 43 and 46).

The other line (A_2), which was the main evolutionary line and has changed little, gave rise to all the other genera of the *Capritermes* complex. In this line, all the genera have a 13- or 14-segmented antenna in the soldier and a 14- or 15-segmented antenna in the imago. The imago-worker mandible is like the ancestral form (A) in that the angle between the first and second right marginal tooth is not sharp but wide, and the posterior margin of the second right marginal tooth is curved. This line (A_2) gave rise to three major offshoots, which in turn gave rise to groups B_1 and B_2 , C_1 and C_2 , and D_1 . In groups B_1 and B_2 the right imago-worker mandible is well developed.

In group B_1 (*Homallotermes*, *Discupiditermes*, and *Pericapritermes*) the dentition of the imago-worker mandible has changed little from the ancestral form: in the left mandible the apical tooth is shorter than the fused first plus second marginal tooth, and the third marginal tooth is well developed; in the right mandible the second marginal tooth is well developed. The soldier in this group has lost the frontal projection, although in some species of *Discupiditermes* the forehead is steep and the frons has a faint hump. *Homallotermes* is the most primitive genus in this group—in fact, the most primitive of all the genera of line A_2 , because the imago mandibles most closely resemble those of *Promirotermes* and *Angulitermes*. The soldier mandibles of *Homallotermes* are thin,

and the left is slightly bent in the middle. *Dicuspiditermes* is more advanced than *Homallotermes*, since the right imago mandible has the posterior margin of the first marginal tooth more elongated, and the soldier mandible is more bent in the middle. The imago mandible of *Pericapritermes* is almost identical with that of *Dicuspiditermes*. The soldier of *Pericapritermes* is the most advanced in this group in that the mandibles are robust and strong; the left mandible is strongly bent in the middle, with its apex blunt; the head is flat; the forehead is not steep; and the frontal gland is much reduced.

In group B₂ (*Procapritermes*, *Labiocapritermes*, and *Mirocapritermes*) the left imago-worker mandible has the apical tooth long and robust, the posterior margin of the fused first plus second marginal tooth gradually elongated, and the third marginal tooth gradually reduced. In the right imago mandible of this group the second marginal tooth is well developed, and the posterior margin of the first marginal tooth is long. With respect to this latter character B₂ is similar to *Dicuspiditermes* and *Pericapritermes* of group B₁. It is because of this similarity that I assume that B₁ and B₂ have branched from a common ancestor (B). The soldier of this group has a left mandible in which there is a distinct tooth in front of the prominent, basal, toothlike projection (in *Labiocapritermes* this tooth is rudimentary). The imago-worker mandibles of *Labiocapritermes* and *Mirocapritermes* are more advanced than those of *Procapritermes* because the third left marginal tooth is greatly reduced (figs. 25, 32, 35). *Mirocapritermes*,

however, still has a small frontal projection in the soldier, which is absent from *Procapritermes* and *Labiocapritermes* and thus presumably was lost independently again in this group.

In group C₁ (*Paracapritermes* and *Protocapritermes*) the imago-worker mandibles are almost identical: the left apical tooth is short, the third left marginal tooth is well developed, and the second right marginal tooth is slightly reduced. The soldier of *Paracapritermes* has a prominent frontal projection, but in *Protocapritermes* this projection is rudimentary and thus lost independently in this group.

In group C₂ (*Quasitermes* and *Capritermes*) the imago-worker mandible has the left apical tooth longer than the fused first plus second marginal tooth, the third left marginal tooth slightly reduced, and the second right marginal tooth more reduced, than in group C₁. The labrum of the soldier has the middle region between the pointed anterolateral corners bilobed. The soldier of *Quasitermes* has the frontal projection, whereas in *Capritermes* it is again lost.

In group D₁ (*Cornicapritermes* and *Dihoplotermes*) the imago-worker mandible is the most advanced, with the third left marginal tooth completely lost and the second right marginal tooth extremely rudimentary or completely lost. The soldiers of both these genera have prominent frontal projections. *Dihoplotermes* is more advanced than *Cornicapritermes*, as the soldiers of *Dihoplotermes* are dimorphic, and from the imago-worker mandible the second right marginal tooth is completely absent.

SYSTEMATICS

KEY TO THE GENERA OF THE *CAPRITERMES* COMPLEX

IMAGO¹

1. Second right marginal tooth extremely rudimentary or absent; third left marginal tooth absent (figs. 37, 39) 2
Second right marginal tooth present; third left marginal tooth present (prominent or reduced); Neotropical, Oriental, Ethiopian 3
2. Second right marginal tooth rudimentary; Neotropical (fig. 37) . . . **Cornicapritermes*
Second right marginal tooth completely absent; Neotropical (fig. 39) . . . **Dihoplotermes*
3. Antennae with 16-17 articles; angle between first and second right marginal tooth sharp; posterior margin of second right marginal tooth straight; Neotropical (fig. 43) *Neocapritermes*
Antennae with 14-15 articles; angle between first and second right marginal tooth wide; posterior margin of second right marginal tooth curved; Australian, Papuan, Oriental, Ethiopian, Madagascar 4
4. Second right marginal tooth somewhat reduced; Australian, Madagascar (figs. 3, 6, 10, 12) 5
Second right marginal tooth well developed; Oriental, Papuan, Ethiopian (figs. 15, 18, 21, 25, 32, 35) 8
5. Left apical tooth long, longer than fused first plus second marginal tooth; Madagascar (figs. 10, 12) 6
Left apical tooth short, equal to or shorter than fused first plus second marginal tooth; Australian (figs. 3, 6) 7
6. Second right marginal tooth much reduced; Madagascar (fig. 10) **Quasitermes*
Second right marginal tooth moderately reduced; Madagascar (fig. 12) . . . *Capritermes*
7. Head width, 0.83-0.98 mm.; mandible dentition as shown in figure 3; Australian *Paracapritermes*
Head width, 1.09 mm.; mandible dentition as shown in figure 6; Australian *Procapritermes*

8. Left apical tooth short (figs. 15, 18, 21) 9
Left apical tooth long (figs. 25, 26, 27, 32, 35) 11
9. Fontanelle large, oval, short diameter, 0.05-0.10 mm. (fig. 20) *Pericapritermes*
Fontanelle usually long, narrow, slit-shaped, in some cases circular with short diameter 0.05 mm. (figs. 14, 17) 10
10. Posterior margin of first right marginal tooth short (fig. 15) *Homallotermes*
Posterior margin of first right marginal tooth long (fig. 18) *Dicuspiditermes*
11. Postclypeus swollen, length/width index, 0.50; third marginal tooth greatly reduced (figs. 31, 32) *Labiocapritermes*
Postclypeus not swollen, length/width index, 0.27-0.33; third marginal tooth moderately reduced (figs. 23, 24, 25, 26, 27) *Procapritermes*

SOLDIER

1. Frontal projection present 2
Frontal projection absent 6
2. Dimorphic; frontal projection very long; labrum large, with anterior margin and anterolateral corners rounded; Neotropical (figs. 40, 41) *Dihoplotermes*
Monomorphic; frontal projection small or medium-sized; labrum small, with anterior margin straight, angular, or faintly bilobed and anterolateral corners pointed 3
3. Left mandible short, blunt at tip, broad in middle; in dorsal view, frontal projection covering entire labrum and part of mandibles; Neotropical (fig. 36) *Cornicapritermes*
Left mandible long, hooked at tip, narrow in middle; in dorsal view frontal projection not covering entire labrum and part of mandibles 4
4. Left mandible with a tooth in front of basal toothlike projection; frontal projection short, broadly rounded, and not sharply pointed at tip; labrum with anterior margin deeply concave; Oriental (fig. 34) *Mirocapritermes*
Left mandible without a tooth in front of basal toothlike projection; frontal projection more prominent, narrow, sharply pointed at tip; labrum with anterior margin straight or faintly convex; Australian, Madagascar (figs. 4, 9) 5
5. Labrum with anterior margin straight; Aus-

¹ The imago caste is unknown for the genera marked with an asterisk. In such cases the worker mandible is used to key out the genera. The imago of *Planicapritermes* is unknown, but the dentition of the worker mandible is the same as that of *Neocapritermes*. The imago of *Mirocapritermes* is also unknown; the worker mandible is almost identical with that of *Labiocapritermes*.

- tralian (fig. 4). *Paracapritermes*
 Labrum with anterior margin faintly biconvex; Madagascar (fig. 9) . . . *Quasitermes*
6. Labrum tongue-shaped or trilobed, with anterolateral corners not pointed; frontal gland absent; antennae usually with 15 or 16 segments, rarely with 14 segments; Neotropical 7
 Labrum not tongue-shaped, with anterior margin straight, faintly biconvex, or faintly or deeply concave, its anterolateral corners with points; antennae with 13 or 14 segments; Ethiopian, Madagascar, Oriental, Australian 8
7. Head extremely flat, its posterior margin distinctly three-lobed; antennae with 14 segments (fig. 45) *Planicapritermes*
 Head not flat, its posterior margin even or faintly indented in middle; antennae with 15 or 16 segments (fig. 44)
 *Neocapritermes*
8. Head with anterolateral corners extended into distinct tubercle-like projections in front of and below antennal sockets; Oriental (fig. 19) *Dicuspidermes*
 Head with anterolateral corners rounded, without tubercle-like projections in front of and below antennal sockets 9
9. Labrum swollen and enlarged (fig. 33)
 *Labiocapritermes*
 Labrum not swollen and enlarged 10
10. Labrum with anterior margin straight, faintly biconvex, or faintly angular, its anterolateral points short (figs. 7, 13, 22) . . . 11
 Labrum with anterior margin concave, its anterolateral points long (figs. 16, 28, 29) 13
11. Head with a rudimentary projection on frons; gland opening below projection; left mandible hooked at tip; Australian, Madagascar 12
 Head without rudimentary projection on frons; frons sloping evenly; small, circular dorsal gland opening; left mandible blunt at tip; Ethiopian, Oriental, Papuan (fig. 22)
 *Pericapritermes*
12. Left mandible only faintly bent in middle; labrum with anterior margin very faintly angular; Australian (figs. 7, 8)
 *Protocapritermes*
 Left mandible moderately bent in middle; labrum with anterior margin biconvex in middle; Madagascar (fig. 13)
 *Capritermes*
13. Antennae with 13 segments; mandibles thin, slender, and moderately bent in middle; Oriental (fig. 16) *Homallotermes*
 Antennae with 14 segments; mandibles thick,

faintly to deeply bent in middle; Oriental (figs. 28, 29, 30) *Procapritermes*

GENUS PARACAPRITERMES HILL, 1942

<Genus *Mirotermes*: SILVESTRI, 1909, p. 298. HOLMGREN, 1912, p. 109. HILL, 1927, p. 92.

<Subgenus *Mirotermes*: HILL, 1942, pp. 379, 391-393.

>Subgenus *Paracapritermes* (of genus *Mirotermes*) HILL, 1942, pp. 10, 13, 379, 416.

>Genus *Paracapritermes*: SNYDER, 1949, p. 190.

<Genus *Termes*: SNYDER, 1949, pp. 178, 182.

= Genus *Paracapritermes*: AHMAD, 1950, pp. 45, 72, 74. EMERSON, 1950, pp. 13-15; 1955, pp. 469, 477, 503, 512. GAY, 1956, p. 210. WEIDNER, 1955, p. 73. CALABY AND GAY, 1959, p. 212. HARRIS, 1961, p. 64.

TYPE SPECIES: *Paracapritermes primus* (Hill).

Hill (1942) created the subgenus *Paracapritermes* of the genus *Mirotermes* (now = *Termes*) for the single species *Paracapritermes primus* (Froggatt). Snyder (1949) raised the subgenus *Paracapritermes* to generic rank, a course that I am adopting here.

The species *kraepelinii* was included by Silvestri (1909) in the genus *Mirotermes* (now = *Termes*), a genus that has symmetrical snapping soldier mandibles. Silvestri's description made no mention of asymmetry in the soldier mandibles, although his figures (pl. 19, figs. 133-135) distinctly show it. For this reason one might suspect that his material contained mixed series, with both types of soldiers. The holotype soldier present in the Zoologisches Museum, Hamburg, has asymmetrical mandibles of the type shown by Silvestri in his figures.

Hill (1927) mentioned five varieties of soldiers of *Mirotermes kraepelinii* but he failed to recognize that he also was dealing with mixed series (with soldiers having both asymmetrical and symmetrical mandibles) and therefore failed to establish that the soldier of *M. kraepelinii* had asymmetrical mandibles. Hill (1942) continued to include *kraepelinii* in *Mirotermes*. Snyder (1949) included it in *Termes*. Gay (1956) has recently examined the material studied by Hill and found that the soldiers of *kraepelinii*, with the asymmetrical type of mandible of *Paracapritermes*, were mixed in the same vials with soldiers of some other

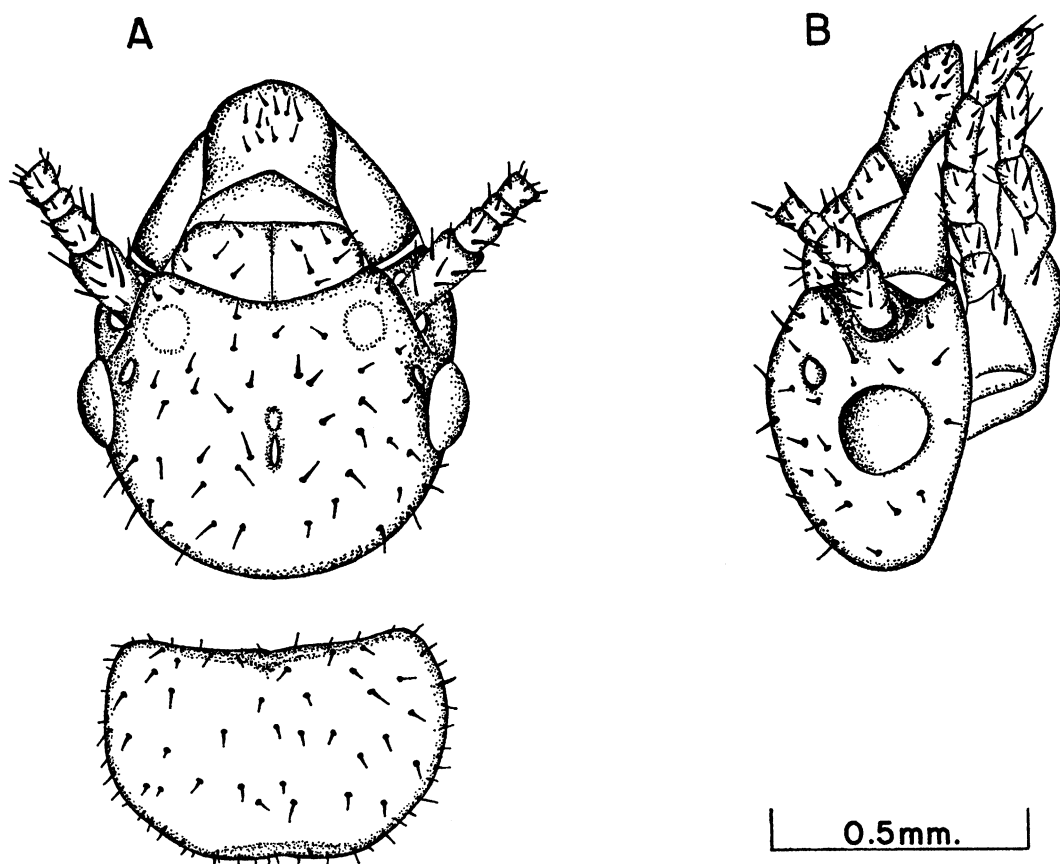


FIG. 2. Imago of *Paracapritermes primus* (Hill), type colony; Mount Molloy, north Queensland, Australia. A. Head and pronotum from above. B. Head from side.

species that had the symmetrical type of mandible of *Termes*. Gay has sent us many such vials, containing mixed series that were collected in Western Australia.

I am here transferring *Mirotermes kraepelinii* to the genus *Paracapritermes*, because it has asymmetrical soldier mandibles and because the imago mandibles are of the *Paracapritermes* type.

Gay (1956) included a second species, *hesperus*, in the genus *Paracapritermes*. Further studies by Emerson, Gay, and the present author have shown that *P. hesperus* is conspecific with *P. kraepelinii* (Silvestri).

IMAGO (FIG. 2): Small, dark brown. Head densely hairy, with numerous stiff bristles interspersed with short hairs. Fontanelle distinct, narrow, elliptical. Eyes small. Antennae with 15 articles; third article shortest. Imago-worker mandibles as shown in figure

3. Left mandible with apical tooth slightly shorter than fused first plus second marginal tooth, and third marginal tooth well developed. Right mandible with second marginal tooth slightly reduced. In *kraepelinii* left apical tooth shorter than in *primus*.

SOLDIER (FIG. 4): Head with frontal projection well developed, pointed, and bent upward at tip (most developed in *kraepelinii*) and fontanelle opening below frontal projection. Labrum with anterior margin almost straight or faintly angular, in some individuals faintly indented in middle, and anterolateral corners slightly pointed. Mandibles asymmetrical, with tips pointed and hooked. Left mandible with prominent toothlike projection in basal region; in *primus* moderately bent in middle, with outer margin strongly curved; in *kraepelinii*

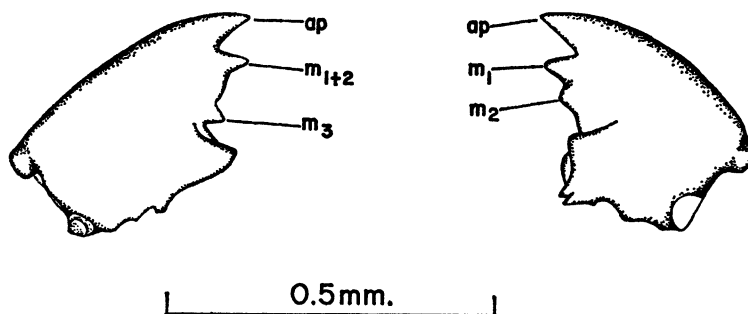


FIG. 3. Mandibles of worker of *Paracapritermes primus* (Hill), type colony, Mount Molloy, north Queensland, Australia.

Abbreviations: ap, apical tooth; m_{1+2} , fused first plus second left marginal tooth; m_3 , third left marginal tooth; m_1 , first right marginal tooth; m_2 , second right marginal tooth.

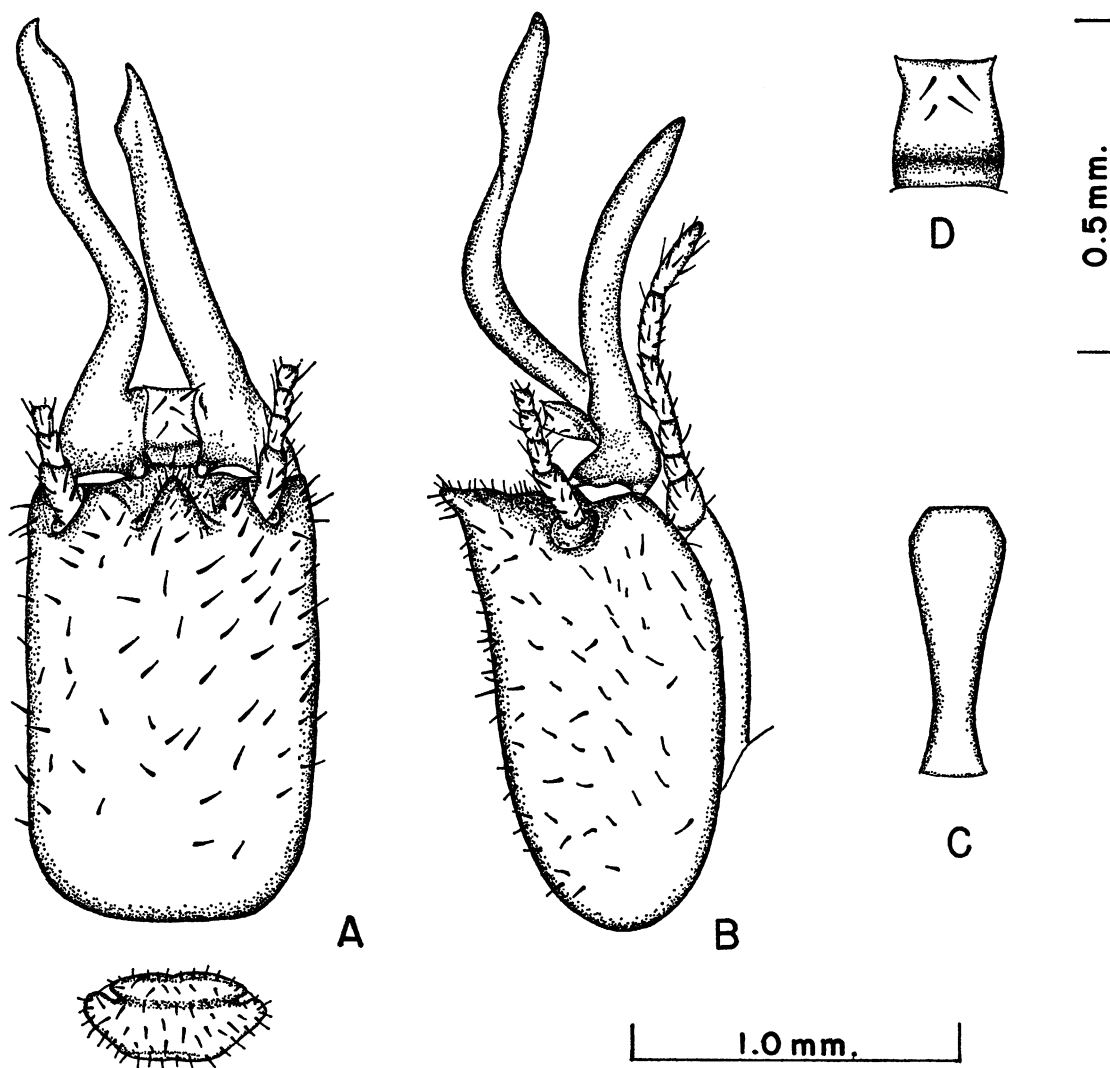


FIG. 4. Soldier of *Paracapritermes primus* (Hill), paratype from type colony; Mount Molloy, north Queensland, Australia. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

faintly bent in middle. Right mandible shorter than left mandible, with distinct indentation in basal region. Antennae with 14 articles; fourth article shortest, third subequal to second. Tibial spurs 3:2:2. Middle tibia with one spine in *primus*, two in *kraepelinii*.

RELATIONSHIPS AND COMPARISONS: Ahmad (1950) stated that *Paracapritermes* is the most primitive genus of this complex and part of a natural grouping of genera with frontal projections in the soldiers, namely, *Quasitermes*, *Mirocapritermes*, and *Cornicapritermes*. The dentition of the imago-worker mandible indicates, however, that *Paracapritermes* is not the most primitive genus of the *Capritermes* complex, but is most closely related to *Protocapritermes*. In the imago of *Paracapritermes* and of *Protocapritermes* the third marginal tooth of the left mandible is well developed; the apical and fused first plus second marginal teeth of the left mandible are approximately the same size; and the second marginal tooth of the right mandible is reduced. In the soldiers of both genera the anterior margin of the labrum is almost straight or only slightly indented. The asymmetry of the soldier mandibles of *Paracapritermes* is variable. The left soldier mandible of *Paracapritermes primus* is much more bent in the middle and twisted than that of *Protocapritermes krisiformis*. However, the soldier mandibles of *Paracapritermes kraepelinii* have the same degree of asymmetry as those of *Protocapritermes krisiformis*.

Protocapritermes differs from *Paracapritermes* in that the frontal projection of the soldier is greatly reduced and appears only as a faint bump.

Although the soldiers of *Quasitermes*, *Mirocapritermes*, and *Cornicapritermes* all have frontal projections, these genera are not so closely related to *Paracapritermes* as suggested by Ahmad. In *Quasitermes* the anterior margin of the soldier labrum is biconvex, with its anterolateral points more developed; the apical tooth of the left imago-worker mandible is proportionally longer than the fused first plus second marginal tooth; and the second marginal tooth of the right imago-worker mandible is more reduced. In *Mirocapritermes* and *Cornicap-*

ritermes the anterior margin of the soldier labrum is deeply indented or concave, and in the left imago-worker mandible the posterior margin of the fused first plus second marginal tooth is longer, and the third marginal tooth is reduced or absent. Further, the soldier of *Mirocapritermes* has a small, blunt frontal projection, whereas the frontal projection is much more prominent and pointed in *Cornicapritermes*.

SPECIES INCLUDED

P. kraepelinii (Silvestri), new combination = *Mirotermes kraepelinii* Silvestri, 1909

[New synonymy: *Paracapritermes hesperus* Gay, 1956]

P. primus (Hill), 1942

GEOGRAPHICAL DISTRIBUTION: Australia.

GENUS *PROTOCAPRITERMES* HOLMGREN, 1912

<Genus *Termes*: subgenus *Eulermes*: DESNEUX, 1904, pp. 26, 28, 29, 39, 40.

=Subgenus *Protocapritermes* (of genus *Mirotermes*) HOLMGREN, 1912, pp. 107-108. EMERSON, 1925, p. 432; 1928, p. 408. HARE, 1937, p. 478. HILL, 1942, pp. 10, 13, 319, 414.

=Genus *Protocapritermes*: SNYDER, 1949, p. 187. AHMAD, 1950, pp. 45, 72, 74, 75. EMERSON, 1955, p. 512. WEIDNER, 1955, p. 73. CALABY AND GAY, 1959, p. 212. HARRIS, 1961, p. 64.

TYPE SPECIES: *Protocapritermes krisiformis* (Froggatt).

Holmgren (1912) named *Protocapritermes* as a subgenus and placed it, along with the subgenera *Cubitermes*, *Basidentitermes*, *Mirotermes*, *sensu stricto*, *Spinitermes*, and *Tuberculitermes*, in the genus *Mirotermes*. Hill (1942) treated *Protocapritermes* as a subgenus, and, along with *Mirotermes*, *sensu stricto*, and *Paracapritermes*, placed it in the genus *Mirotermes*. Snyder (1949) raised it to generic rank, a course that I am adopting here.

IMAGO (FIG. 5): Head and pronotum dark rusty brown, wings smoky. Head and pronotum with numerous bristles and hairs. Fontanelle small, elongate, oval. Eyes small. Ocellus oval, not touching eye. Antennae with 15 articles; third article shortest. Imago-worker mandibles as shown in figure 6. Left mandible with apical tooth shorter than fused first plus second marginal tooth,

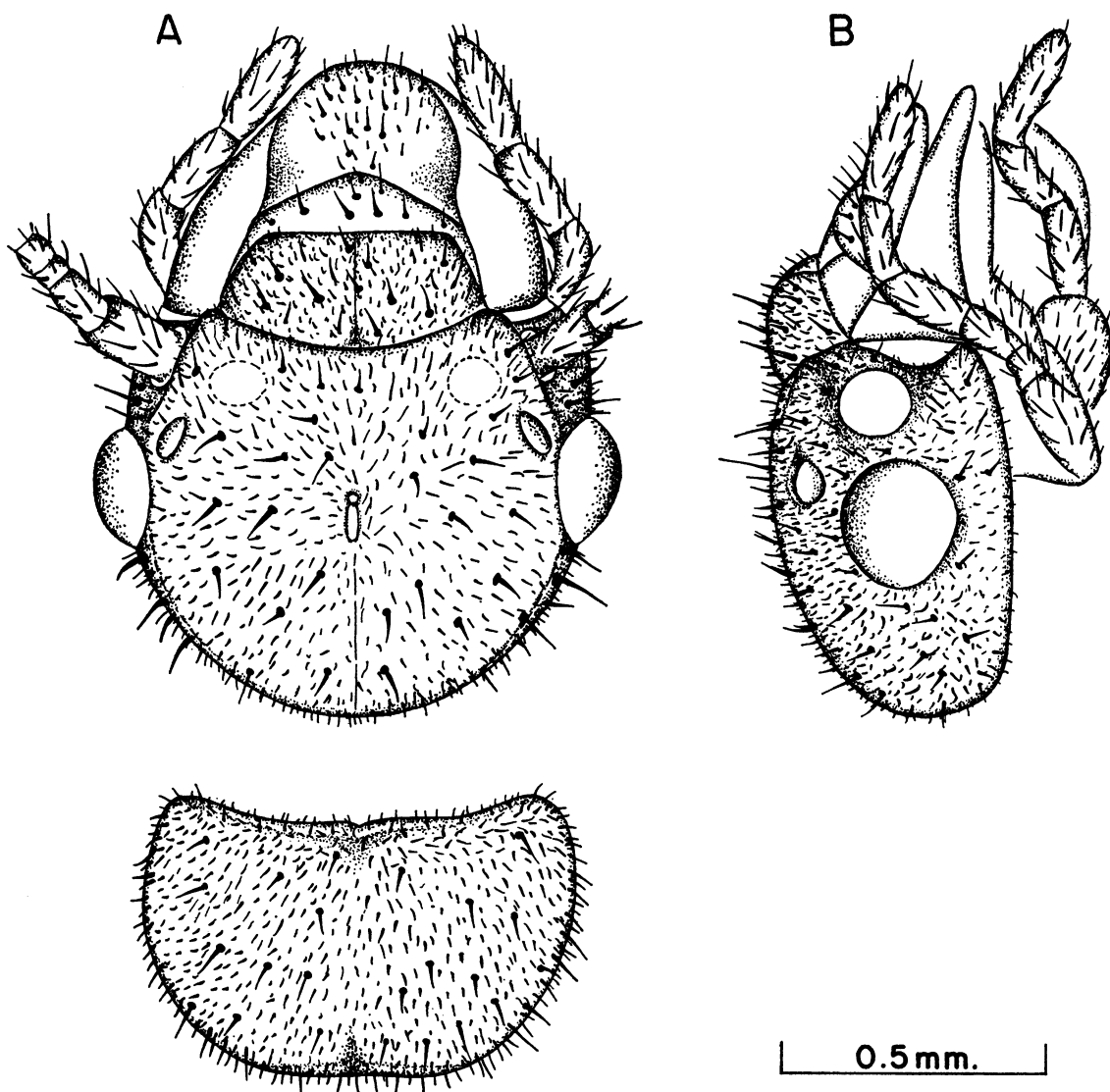


FIG. 5. Imago of *Protocapritermes krisiformis* (Froggatt), morphotype colony; Noundoc, New South Wales, Australia. A. Head and pronotum from above. B. Head from side.

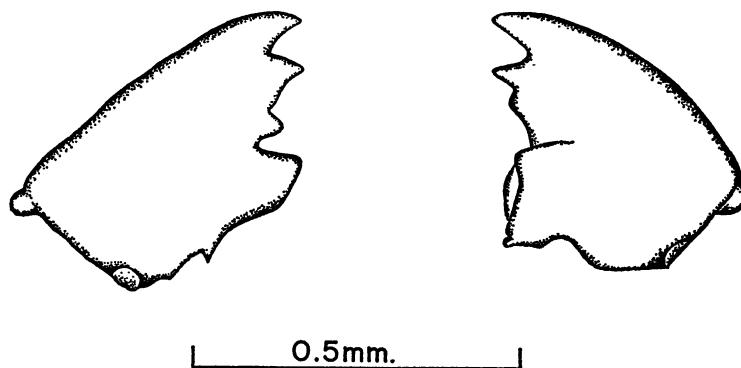


FIG. 6. Mandibles of worker of *Protocapritermes krisiformis* (Froggatt), cotype colony; Sydney, Australia.

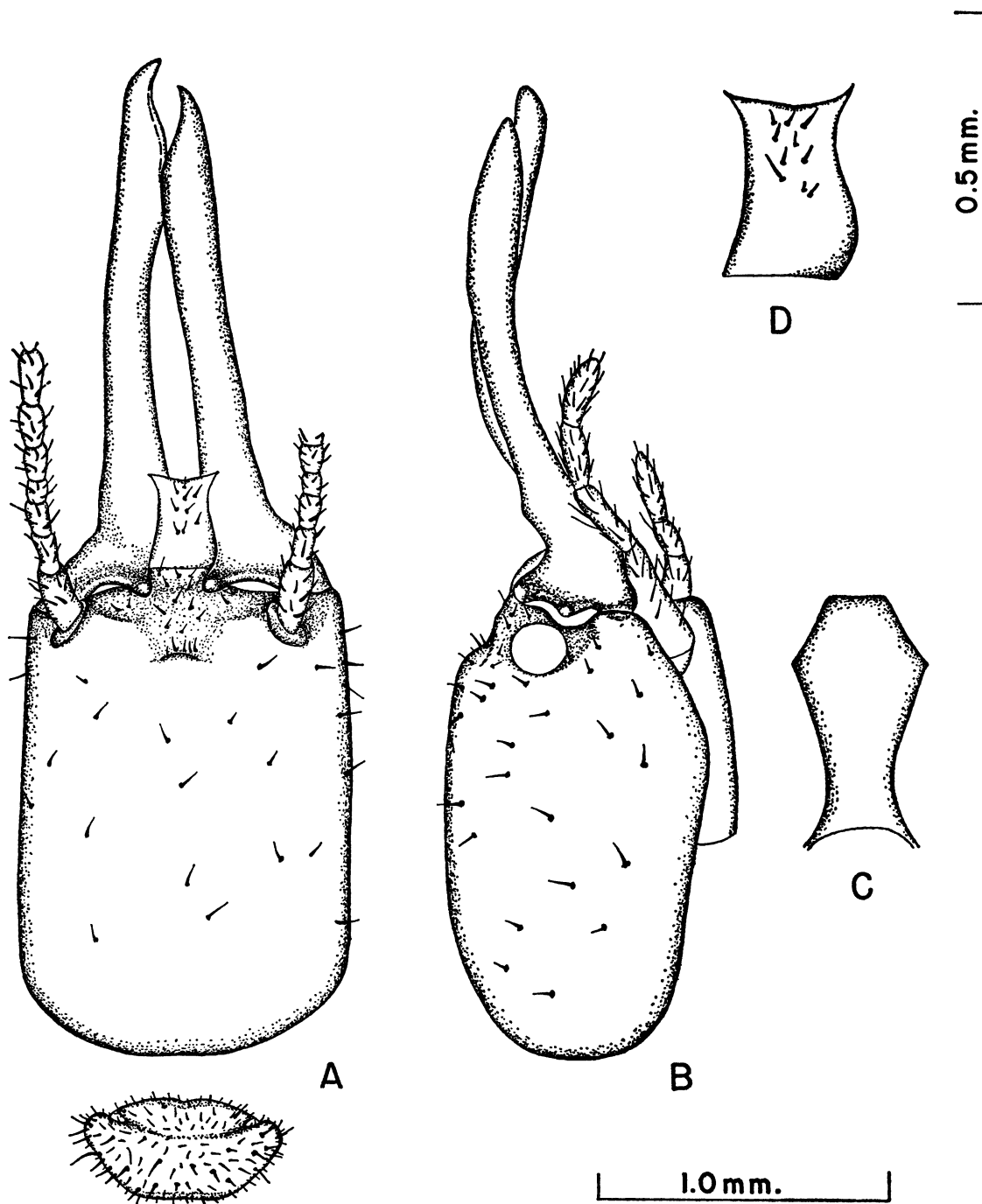


FIG. 7. Soldier of *Protocapritermes krisiformis* (Froggatt), cotype; Sydney, Australia. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

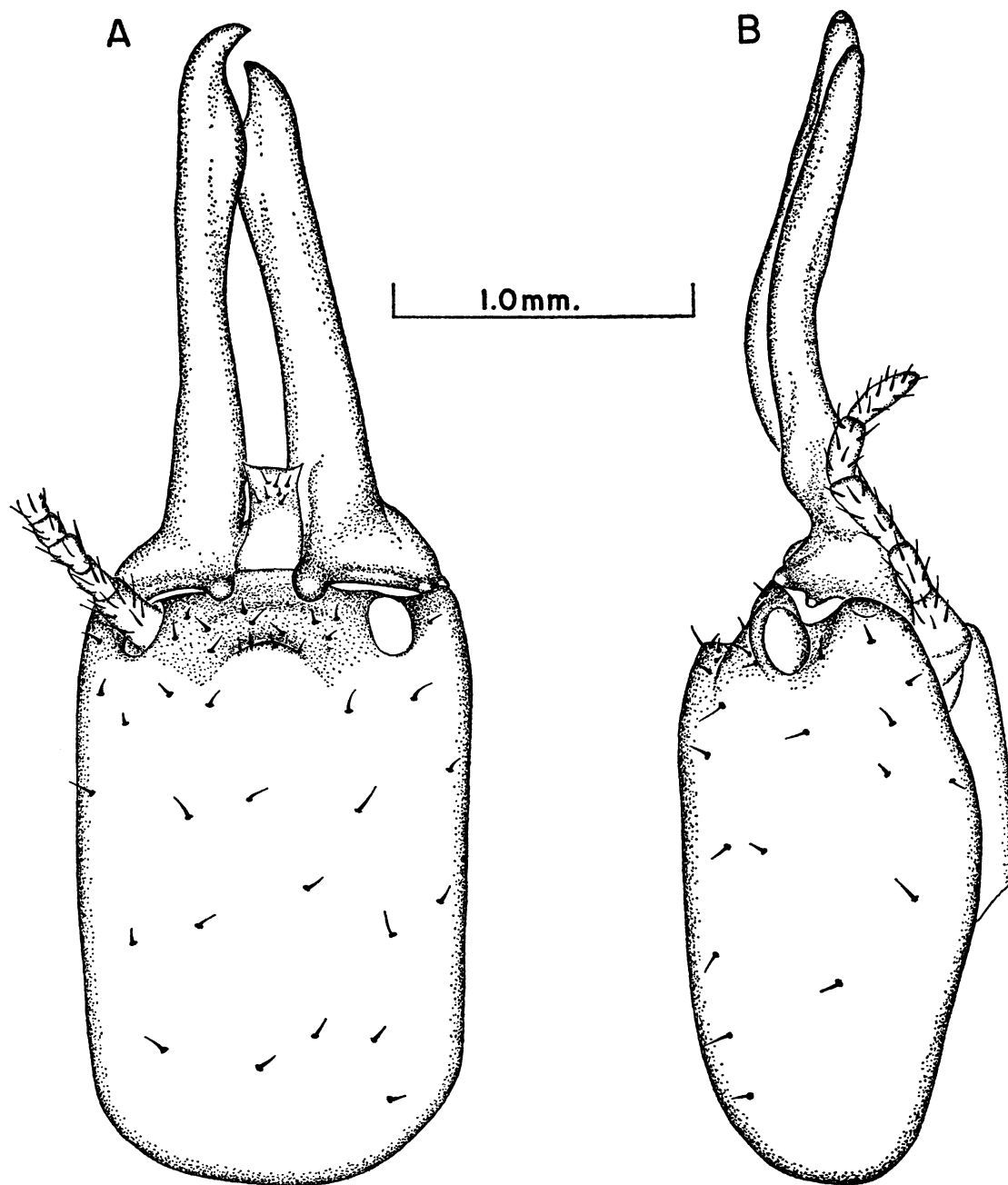


FIG. 8. Soldier of *Protocapritermes krisiformis* (Froggatt), morphotype colony; Noundac, New South Wales, Australia. A. Head from above. B. Head from side.

and third marginal tooth well developed. Right mandible with second marginal tooth somewhat reduced.

SOLDIER (FIGS. 7 AND 8): Head yellow-brown, with a few scattered bristles and

fringe of bristles surrounding frontal gland opening. Head wide, somewhat flat, its frontal projection greatly reduced, with remnant faintly seen in side view. Labrum with anterior margin faintly angular and

anterolateral corners pointed. Mandibles stout, faintly asymmetrical, hooked at tips, as long as or longer than head capsule. Left mandible only slightly bent, with prominent projection in basal region. Antennae with 14 articles; second article equal to third, fourth shortest. Tibial spurs 3:2:2. Middle tibia with one spine.

RELATIONSHIPS AND COMPARISONS: Holmgren (1912) stated that *Protocapritermes* is ancestral to the genus *Procapritermes*. Ahmad (1950) grouped *Protocapritermes* with genera that have lost the frontal projection and placed them in the following order: *Homallotermes*, *Pericapritermes*, *Protocapritermes*, *Capritermes*, *Procapritermes*, and *Pseudocapritermes*. The present study indicates that *Protocapritermes* is more closely related to *Paracapritermes* than to the genera with no frontal projection. The frontal projection is greatly reduced in *Protocapritermes*, but a faintly visible remnant of it still remains. The dentitions of the imago mandible in *Paracapritermes* and *Protocapritermes* are almost identical.

There are significant differences between the genus *Protocapritermes* and the genera *Pericapritermes*, *Procapritermes*, *Capritermes*, and *Homallotermes*.

In the soldier of *Pericapritermes* the left mandible is extremely bent and twisted, the frontal projection is absent, and the fontanelle is present on the dorsal side as a small circular opening. In the imago of *Pericapritermes* the fontanelle is larger, and, in the imago-worker mandible, the fused first plus second marginal tooth has a longer cutting edge, and the second right marginal tooth is much more developed.

In the soldier of *Procapritermes* the labrum is more deeply concave, and the frontal projection is completely absent. In the imago-worker mandible of *Procapritermes* the fused first plus second left marginal tooth has a longer cutting edge, the third left marginal tooth is reduced, and the second right marginal tooth is much more developed.

The soldiers of both *Capritermes* and *Protocapritermes* have a rudimentary frontal projection, but *Capritermes* differs from *Protocapritermes* in the following respects: in the left imago-worker mandible the apical tooth is longer than the fused first plus sec-

ond marginal tooth, and the third marginal tooth is not so prominent; in the right imago-worker mandible the second marginal tooth is more reduced; and in the soldier the anterior margin of the labrum is biconvex, and the left mandible is more bent in the middle (fig. 13).

In the *Homallotermes* soldier the frontal projection is completely absent, the labrum is broadly concave, the antennae are 13-segmented, the mandibles are slender, and the inner margin of the left mandible at the apex is faintly serrated. In the imago-worker mandible of *Homallotermes* the second right marginal tooth is more developed and prominent.

SPECIES INCLUDED

P. krisiformis (Froggatt), 1897

GEOGRAPHICAL DISTRIBUTION: Australia.

GENUS QUASITERMES EMERSON, 1950

<Genus *Mirotermes*: CACHAN, 1949, pp. 186, 241; 1951, p. 15.

= Genus *Quasitermes* EMERSON, 1950, pp. 10-13; 1955, pp. 469, 488, 512. AHMAD, 1950, pp. 72, 74, 84. WEIDNER, 1955, p. 73.

TYPE SPECIES: *Quasitermes incisus* (Cachan).

Emerson (1950) described this monotypic genus for *Quasitermes caprinus*. Cachan (1949) described *Mirotermes incisus*. The studies of Cachan (1951) and Emerson have shown that *caprinus* is conspecific with *incisus*.

SOLDIER (FIG. 9): Head elongated and quadrangular, with sides parallel and frontal projection pointing forward and reaching level of front margin of antennal sockets, with gland opening below. Labrum with anterolateral corners pointed and anterior margin between lateral points faintly bilobed (fig. 9D). Mandibles asymmetrical, with tips hooked. Left mandible slightly bent, with outer margin sinuate. Antennae with 14 articles; fourth article shortest. Tibial spurs 3:2:2. Middle tibia with two spines.

WORKER (FIG. 10): Left mandible with apical tooth longer than fused first plus second marginal tooth. Right mandible with second marginal tooth reduced.

RELATIONSHIPS AND COMPARISONS: Emerson (1950) and Ahmad (1950) stated that

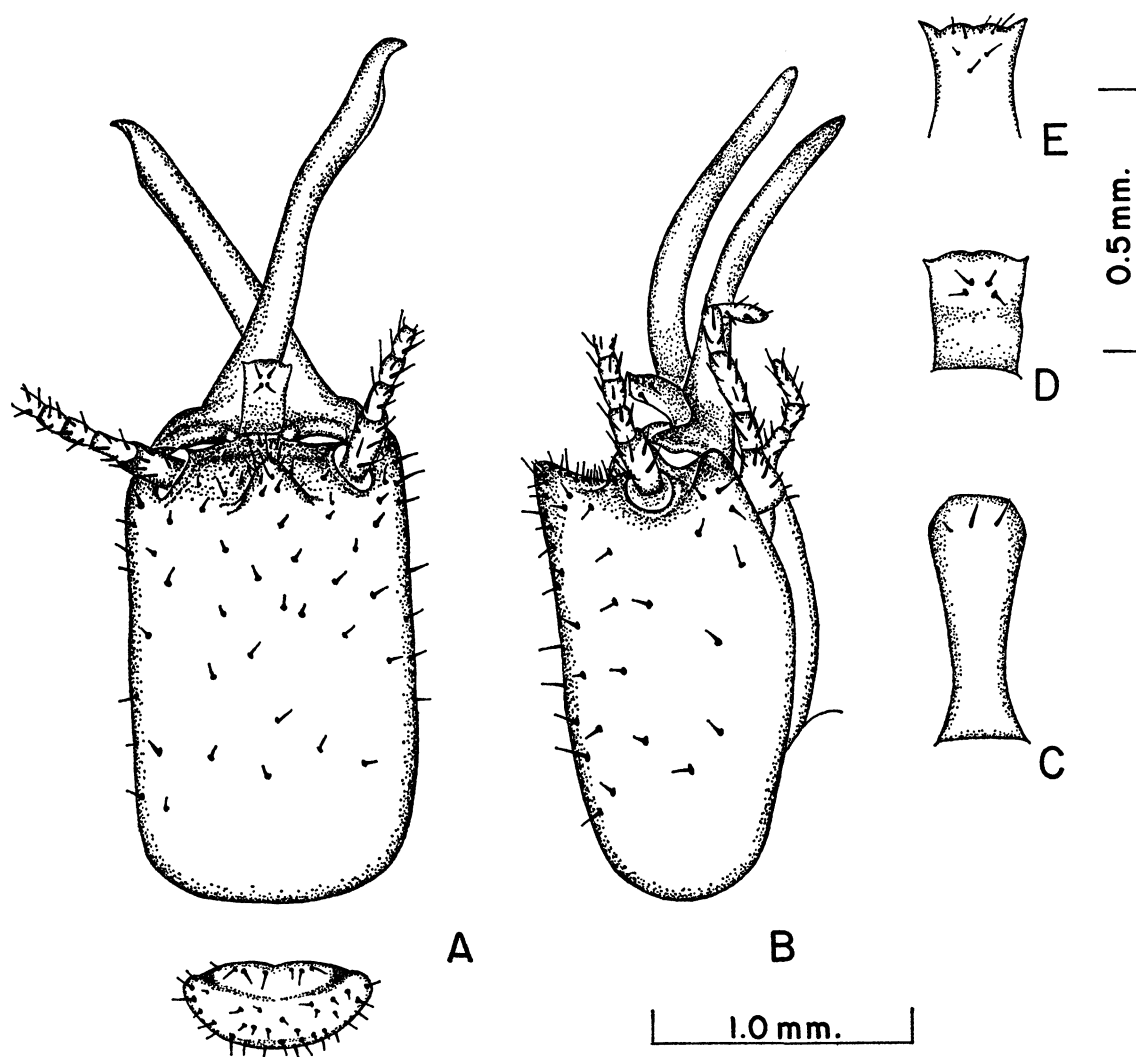


FIG. 9. Soldier of *Quasitermes incisus* (Cachan); Manantantely, near Fort Dauphin, Madagascar. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D, E. Labrum from above.

Quasitermes is most closely related to *Paracapritermes*, *Mirocapritermes*, and *Cornicapritermes* and that all together they form a natural grouping. The present study, however, shows that *Quasitermes* is most closely related to *Capritermes* (as treated in this paper in the more restricted sense).

This close relationship is indicated by the imago-worker mandibles: in both *Quasitermes* and *Capritermes* the second marginal tooth of the right mandible is relatively reduced, and the apical tooth is proportionally longer

than the fused first plus second marginal tooth of the left mandible. The soldier of *Quasitermes* and of *Capritermes* has a frontal projection, although this structure is greatly reduced in *Capritermes*, and the anterior margin of the soldier labrum in both genera is biconvex.

Cornicapritermes, *Mirocapritermes*, and *Paracapritermes* differ from *Quasitermes* in the following respects:

In the soldier of *Cornicapritermes* the anterior margin of the labrum is more deeply

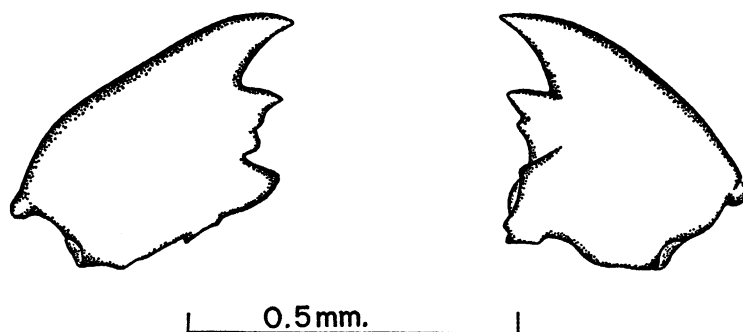


FIG. 10. Mandibles of worker of *Quasitermes incisus* (Cachan); Manantantely, Madagascar.

indented; the mandibles are more asymmetrical, the left mandible being more twisted and curved; and the tips of the mandibles are not hooked. In the imago-worker mandible of *Cornicapritermes* the cutting edge of the fused first plus second left marginal tooth is longer; the third left marginal tooth is absent; and the second right marginal tooth is greatly reduced.

In the soldier of *Mirocapritermes* the mandibles are more asymmetrical; the left mandible is more curved near the base; and the anterior margin of the labrum is more deeply curved, with its lateral points sharper and more prominent. In the imago-worker mandible of *Mirocapritermes* the cutting edge of the fused first plus second left marginal tooth is longer; the third left marginal tooth is greatly reduced; and the second right marginal tooth is more prominent.

In the *Paracapritermes* soldier the left mandible is somewhat more curved, the anterior margin of the labrum is not biconvex, and the lateral points of the labrum are not so prominent. In the imago-worker mandible of *Paracapritermes* the cutting edge of the fused first plus second left marginal tooth is longer, the apical tooth is proportionally shorter, and the second right marginal tooth is more prominent.

SPECIES INCLUDED

Q. incisus (Cachan), new combination = *Mirotermes incisus* Cachan, 1949

[New synonymy: *Q. caprinus* Emerson, 1949]

GEOGRAPHICAL DISTRIBUTION: Madagascar.

GENUS *CAPRITERMES* WASMANN, 1897

<Subgenus *Capritermes* (of genus *Termes*) WASMANN, 1897, pp. 150, 151.

<Genus *Eutermes*: SJÖSTEDT, 1900, pp. 20, 21, 139, 194.

<Genus *Termes*: subgenus *Eutermes*: DESNEUX, 1904, pp. 26, 28, 39, 40.

<Subgenus *Capritermes* (of genus *Capritermes*): HOLMGREN, 1912, pp. 114–118. EMERSON, 1925, p. 445; 1928, pp. 409, 412, 542.

<Genus *Capritermes*: SILVESTRI, 1901, pp. 4–5; 1903, p. 62. WASMANN, 1902, p. 125; 1911, p. 150. DESNEUX, 1904, p. 29. ESCHERICH, 1911, pp. 53, 55, 56, 145, 148. HOLMGREN, 1906, p. 37; 1911, p. 209; 1913, p. 242; 1914, p. 278. GREEN, 1913, p. 12. BUGNION, 1914, p. 184. EMERSON, 1929, p. 725; 1955, pp. 469, 478, 480, 486, 488, 489, 501, 502, 512. JOHN, 1925, p. 414. SJÖSTEDT, 1926, pp. 281, 282. SNYDER, 1926b, p. 64; 1934, pp. 26, 28; 1949, p. 192. LIGHT, 1930, pp. 16–18; 1931, p. 598. KEMNER, 1934, p. 171. WU, 1935, p. 221. HARE, 1937, pp. 459, 462, 463, 478. HILL, 1942, p. 419. CACHAN, 1949, pp. 180, 186, 188. AHMAD, 1950, pp. 47, 72, 74; 1955, pp. 2, 62; 1958, pp. 87, 88, 91, 183. TU, 1955, pp. 3, 6. WEIDNER, 1955, p. 73. HARRIS, 1957, pp. 25–27; 1961, pp. 14, 32, 61, 64. NOIROT AND KAVOOR, 1958, pp. 440, 452, 462, 466–468, 470. CALABY AND GAY, 1959, p. 213.

TYPE SPECIES: *Capritermes capricornis* (Wasmann).

Wasmann (1897) described the subgenus *Capritermes* (of the genus *Termes*), designating *C. capricornis* from Madagascar as the type species. Since then, additional species from the Oriental and Papuan regions have been added (Snyder, 1949). The present study has shown that the genus *Capritermes* as treated by Snyder (1949) and others is

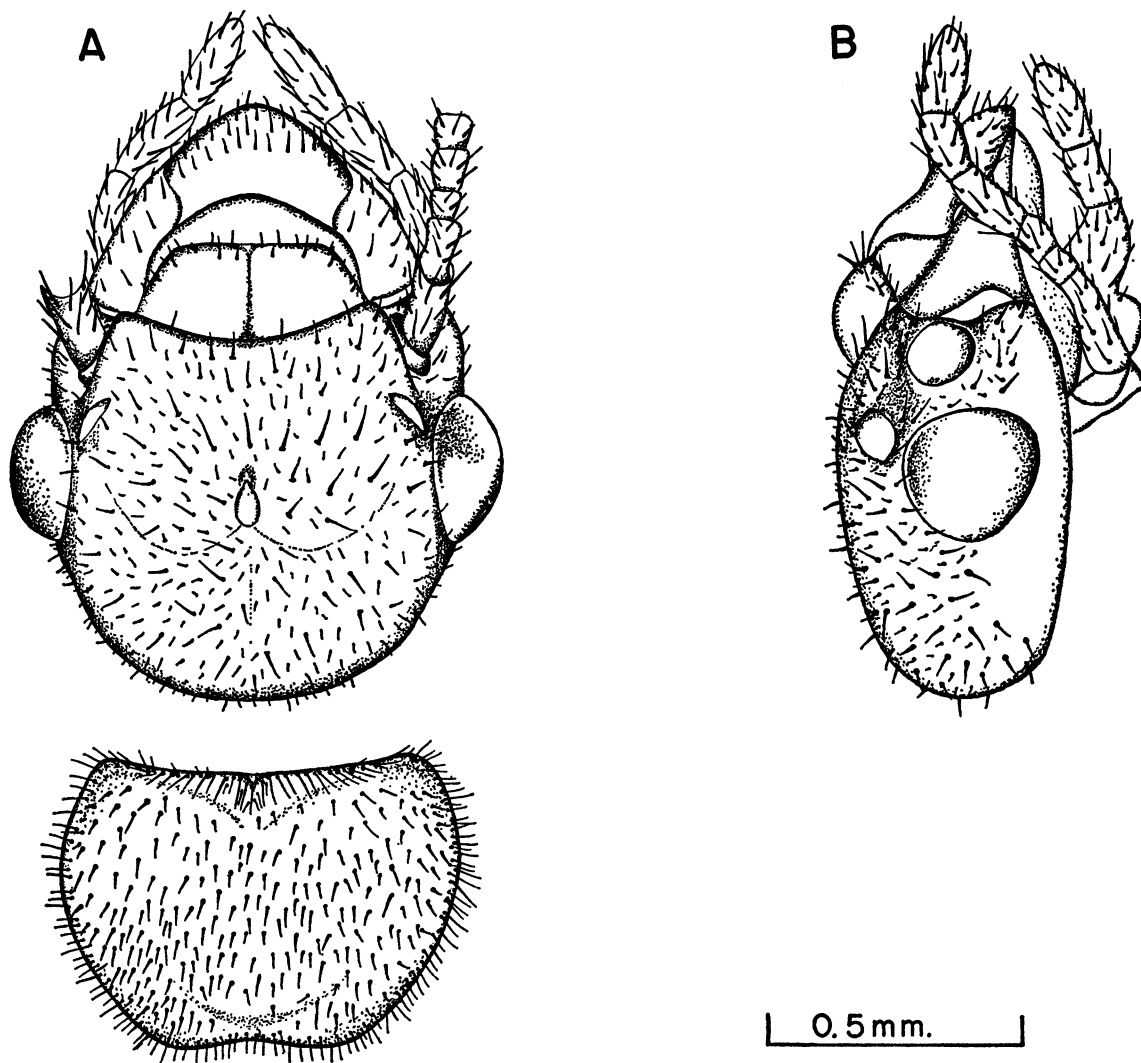


FIG. 11. Imago of *Capritermes capricornis* (Wasmann), cotype colony; Andrangoloaka, Madagascar.
A. Head and pronotum from above. B. Head from side.

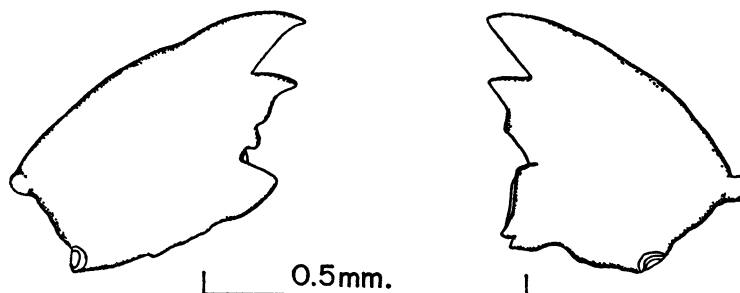


FIG. 12. Mandibles of worker of *Capritermes capricornis* (Wasmann), cotype colony; Andrangoloaka, Madagascar.

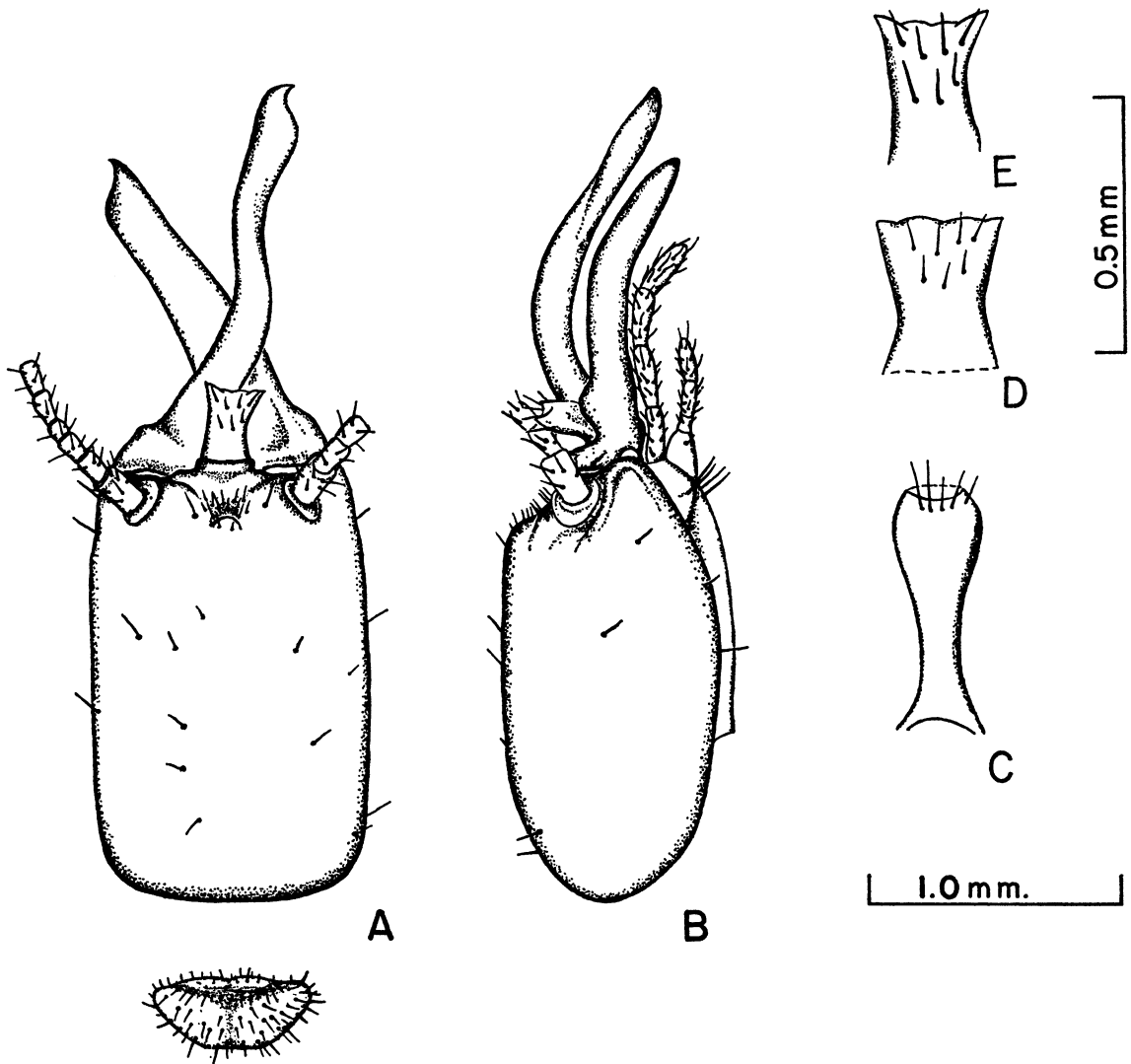


FIG. 13. Soldier of *Capritermes capricornis* (Wasmann), cotype; Andragoloaka, Madagascar. A. Head and pronotum from above. B. Head and sides. C. Postmentum from below. D, E. Labrum from above.

composed of heterogeneous elements, and that the species included from the Oriental and Papuan regions do not belong to this genus. These species are placed in other genera in this paper, and the genus *Capritermes* is restricted to the species *C. capricornis* (Wasmann).

IMAGO (FIG. 11): Dark-colored. Head and pronotum densely covered with hairs and bristles. Fontanelle wide, pear-shaped. Ocellus oval, not touching eye. Antennae with 15 articles; third article smaller than

second or fourth, fourth shorter than second. Imago-worker dentition as shown in figure 12. Left mandible with apical tooth longer than fused first plus second marginal tooth. Right mandible with second marginal tooth somewhat reduced.

SOLDIER (FIG. 13): Head sparsely covered with a few bristles, more numerous in frontal gland region. Head rectangular, with frontal projection present but greatly reduced, only remnant visible in side view. Labrum slightly asymmetrical, longer than

wide, with anterior margin bilobed and lateral points prominent (fig. 13). Mandibles asymmetrical, with tips hooked. Left mandible curved and twisted, with prominent basal projection. Antennae with 14 articles; fourth article shortest. Tibial spurs 3:2:2. Middle tibia with two spines.

RELATIONSHIPS AND COMPARISONS: Ahmad (1950), following Snyder (1949), treated *Capritermes* in the larger sense and placed this genus in the same phylogenetic branch as the genera without a frontal projection, namely, *Homallotermes*, *Protocapritermes*, *Pericapritermes*, *Procapritermes*, and *Pseudocapritermes*. I am of the opinion, however, that *Capritermes* as treated in the present

paper in the more restricted sense is most closely related to *Quasitermes*, a genus also confined to Madagascar.

For the similarities between *Capritermes* and *Quasitermes*, see the discussion under *Quasitermes*.

Protocapritermes differs from *Capritermes* in the following respects: In the imago-worker mandible the apical teeth are proportionally shorter; the cutting edge of the fused first plus second marginal tooth is longer; and the second right marginal tooth is not reduced. In the soldier the mandibles are less asymmetrical, the anterior margin of the labrum is not biconvex, and the lateral points are not so prominent.

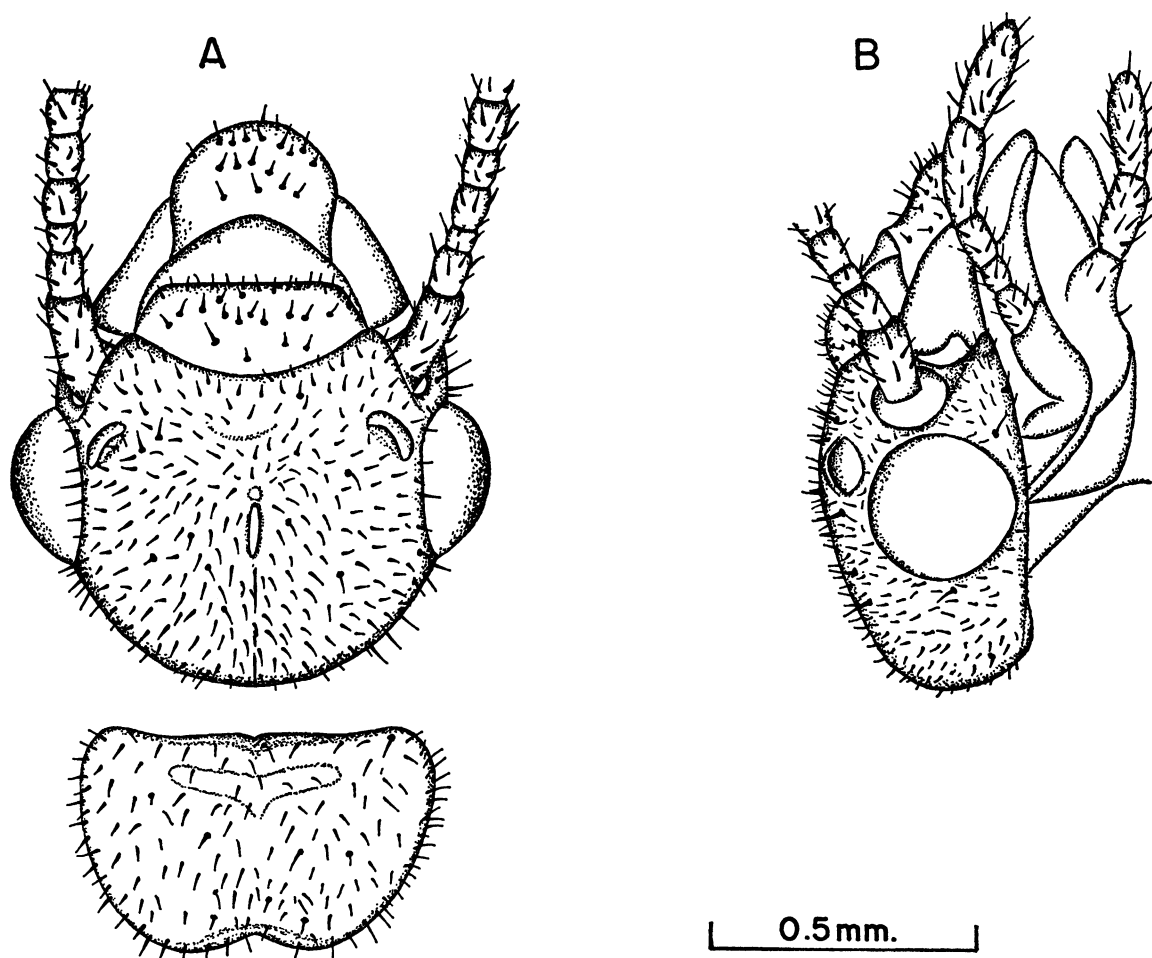


FIG. 14. Imago of *Homallotermes foraminifer* (Haviland); Bulkit Belata Forest Reserve, Malaya.
A. Head and pronotum from above. B. Head from side.

In *Homallotermes*, *Pericapritermes*, and *Procapritermes* the second marginal tooth of the right imago-worker mandible is well developed (reduced in *Capritermes*); the posterior margin of the fused first plus second marginal tooth of the left imago-worker mandible is long (shorter in *Capritermes*); and in the soldier the frontal projection is completely absent, and the anterior margin of the labrum is concave or straight (in *Capritermes* the frontal projection is rudimentary and the anterior margin of the labrum is biconvex).

SPECIES INCLUDED

C. capricornis (Wasmann), 1893

GEOGRAPHICAL DISTRIBUTION: Madagascar.

GENUS HOMALLOTERMES JOHN, 1925

= Genus *Termes* (section with *T. foraminifer* for type): HAVILAND, 1898, pp. 378, 419.

< Genus *Termes*: subgenus *Eutermes*: DESNEUX, 1904, pp. 26, 28, 39, 42.

< Genus and subgenus *Capritermes*: HOLMGREN, 1912, pp. 97, 114; 1914, p. 278.

= Genus *Homallotermes* JOHN, 1925, pp. 412-413. EMERSON, 1928, p. 409; 1955, pp. 469, 512. KEMNER, 1934, p. 168. SNYDER, 1949, p. 191. AHMAD, 1950, pp. 47, 72, 74, 75, 84; 1958, pp. 58, 88, 91, 183. WEIDNER, 1955, p. 73. HARRIS, 1961, p. 64. YU AND PING, 1964, p. 13.

= Genus *Microcapritermes* MATHUR AND THAPA, 1962, pp. 370-375. New synonymy.

TYPE SPECIES: *Homallotermes foraminifer* (Haviland).

John (1925) created the genus *Homallotermes* for the "section with *Termes foraminifer* for type" mentioned by Haviland (1898). Mathur and Thapa (1962) described a new genus, *Microcapritermes*, for a new species, *M. pilosus*. A comparison of *Microcapritermes* and *Homallotermes* indicates that the two are congeneric.

In the imago mandible of *Microcapritermes pilosus* (fig. 14B) the apical tooth is shorter in proportion to the fused first plus second marginal tooth than is that of *Homallotermes foraminifer*, the type species. However, this difference falls within the range of variation for the genus *Homallotermes* (fig. 15A, B, C). In addition, although the soldiers of *Microcapritermes* are very small, they resemble other soldiers of species included in *Homallo-*

termes in most respects (fontanelle, mandibles, labrum, antennal joints, and so on). The only distinction between *Microcapritermes* and *Homallotermes* is that the left soldier mandible has an additional small tooth in front of the basal tooth. This single distinction, however, does not warrant the inclusion of the species *pilosus* in a separate genus. I am therefore treating *Microcapritermes* as a synonym of *Homallotermes*.

IMAGO (FIG. 14): Head and pronotum moderately covered with hairs and bristles. Fontanelle long, narrow, slitlike. Ocellus not touching eye. Antennae with 15 articles; third article shorter than second or fourth, fourth shorter than third. Mandible dentition variable (fig. 15): in type species, *Homallotermes foraminifer*, left mandible with posterior margin of fused first plus second marginal tooth longer than apical tooth, third marginal tooth prominent and well developed (fig. 15A); in other species, apical tooth shorter and fused first plus second marginal tooth longer (figs. 15B, C); in right mandible second marginal tooth prominent and well developed in all species.

SOLDIER (FIG. 16): Head covered with a few scattered bristles. Head small, flattened, gradually declining anteriorly, without a frontal projection. Fontanelle opening circular, situated on frontal slope. Frontal gland large, extending to posterior region of head. Labrum almost symmetrical, with anterior margin either broadly or deeply concave. Mandibles asymmetrical, thin, slender, hooked at tips. Left mandible bent in middle, with prominent basal projection and in some cases an additional tooth. Antennae with 13 articles; third article shortest, fourth longer than third. Tibial spurs 3:2:2. Middle tibia with two spines.

RELATIONSHIPS AND COMPARISONS: John (1925) stated that the genus *Homallotermes* occupies an intermediate position between *Mirotermes* (= *Termes*) and *Capritermes*, and that it is more closely related to *Capritermes* than to *Mirotermes*. Ahmad (1950) placed *Homallotermes* with genera without a frontal projection in the soldier, namely, *Pericapritermes*, *Capritermes*, *Procapritermes*, *Protocapritermes*, and *Pseudocapritermes*. Ahmad also implied that *Homallotermes* is most closely related to *Pericapritermes*, as he

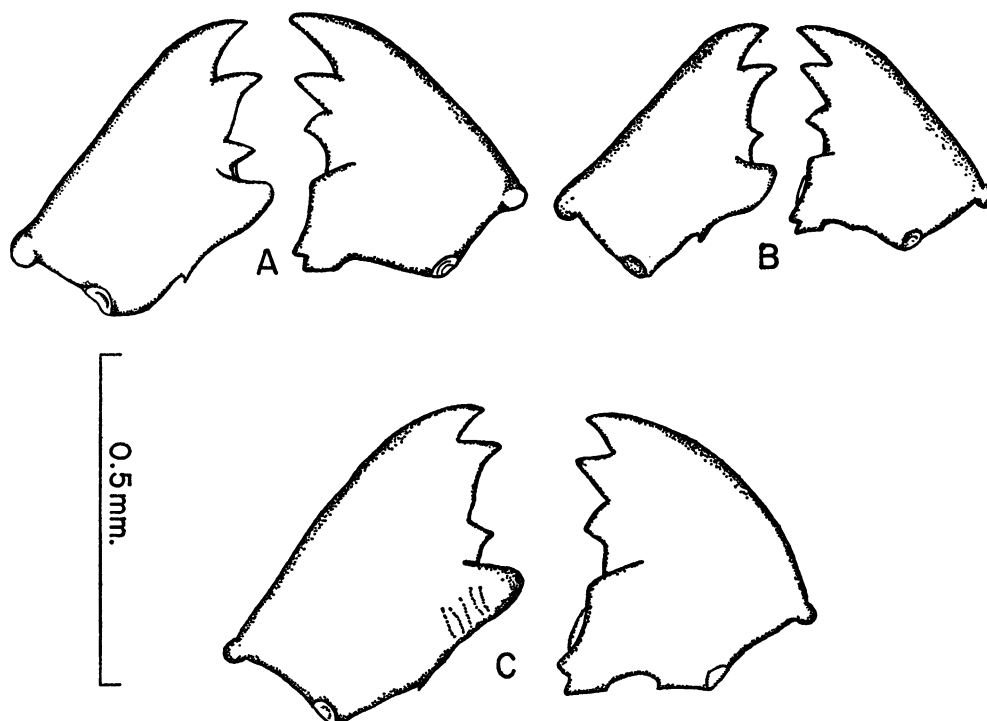


FIG. 15. Mandibles of workers. A. *Homallotermes foraminifer* (Haviland). B. *Homallotermes pilosus* (Mathur and Thapa). C. *Homallotermes*, new species, from Sarawak, Borneo.

stated that the latter has probably been derived from the former. This close relationship is indicated by the resemblance of the imago mandibles of the two genera (figs. 15 and 21). In both genera the third left marginal tooth and the second right marginal tooth are well developed, and the cutting edge of the fused first plus second marginal tooth in the left mandible is longer than the apical tooth. The soldier of *Pericapritermes* is very distinct from that of *Homallotermes*. In the *Pericapritermes* soldier the mandibles are more robust and thick, with their tips not hooked and the left strongly bent in the middle; the anterior margin of the labrum is almost straight, and the fontanelle is minute and dotlike; the antennae are usually 14-segmented, except for one species, *P. minimus* Weidner, which has a 13-segmented antenna.

Procapritermes differs from *Homallotermes* in the following respects: in the imago-worker mandible the third left marginal tooth is much reduced, and in the soldier the frontal gland is reduced, the fontanelle is

smaller and in some cases is in a depression, the antennae are 14-jointed, and the mandibles are thicker.

Capritermes as treated in this paper also differs from *Homallotermes* in that in the imago-worker mandible the right second marginal tooth is reduced, and the left apical tooth is proportionally longer than the cutting edge of the fused first plus second marginal tooth. The soldier of *Capritermes* has a rudimentary frontal projection, its mandibles are much thicker and more robust, and the anterior margin of its labrum is bilobed.

SPECIES INCLUDED

- H. foraminifer* (Haviland), 1898
 [New synonymy: *H. penangi* (Holmgren), 1914]
H. pilosus (Mathur and Thapa), new combination
 = *Microcapritermes pilosus* Mathur and Thapa, 1962
H., new species, from Sarawak

GEOGRAPHICAL DISTRIBUTION: Oriental Region: Borneo, India.

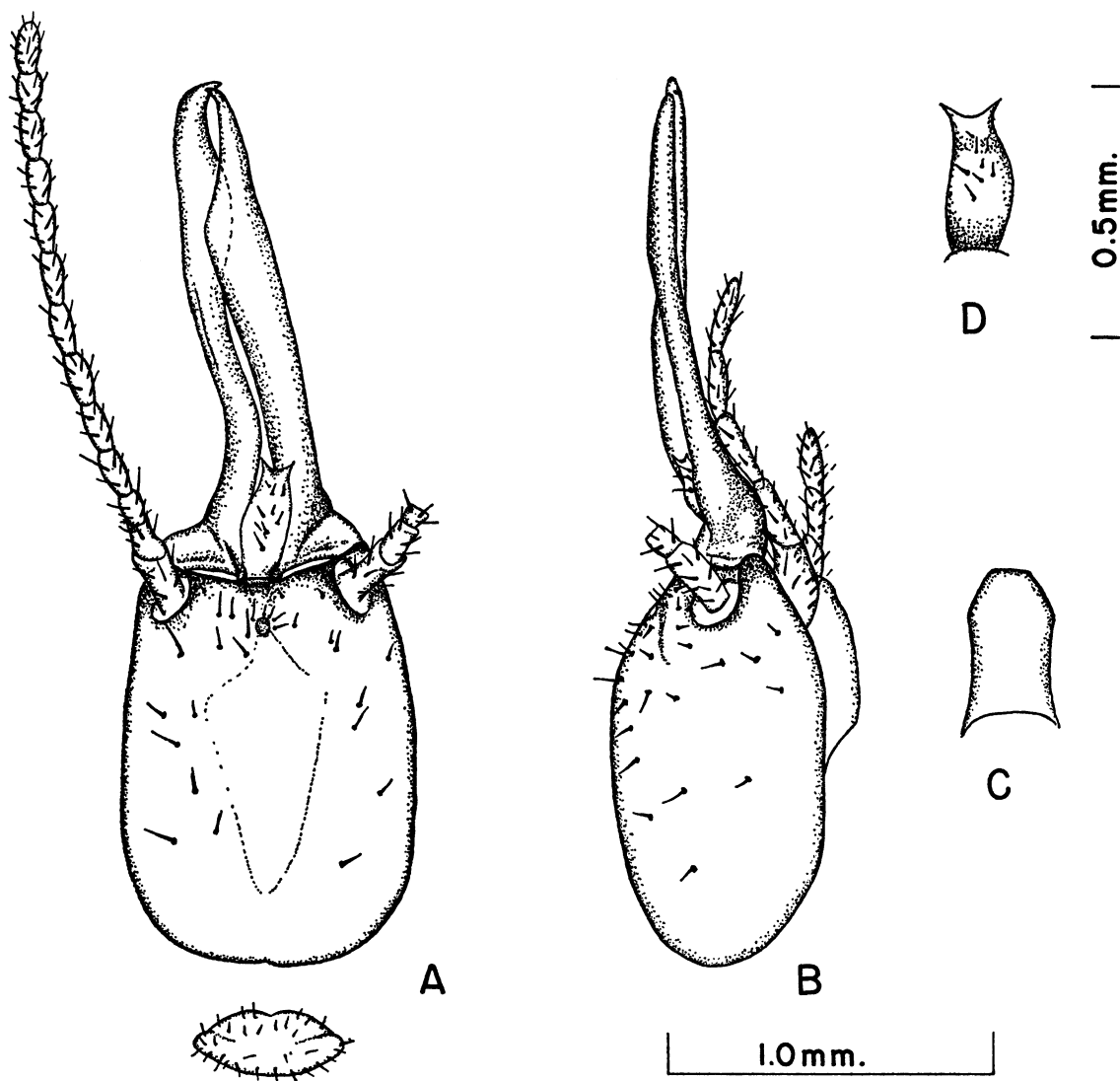


FIG. 16. Soldier of *Homallotermes foraminifer* (Haviland), cotype from type colony; Perak, Malaya. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

GENUS *DICUSPIDITERMES* KRISHNA, 1965

<Genus *Termes* (section with *T. nemorosus* for type): HAVILAND, 1898, pp. 378, 412.

<Genus *Termes*: subgenus *Eutermes*: DESNEUX, 1904, pp. 26, 28, 39, 40.

<Genus and subgenus *Capritermes*: HOLMGREN, 1912, pp. 114–118.

<Genus *Capritermes*: WASMANN, 1902, p. 125. ESCHERICH, 1911, pp. 53–56, 145, 148. HOLMGREN, 1911, p. 209; 1913, p. 242. BUGNION, 1914, p. 184. JOHN, 1925, p. 414. SNYDER, 1949, p. 192. WEID-

NER, 1955, p. 73. EMERSON, 1955, pp. 469, 478, 480, 486, 488, 489, 501, 512. HARRIS, 1957, pp. 23, 25–27. AHMAD, 1958, pp. 88, 91, 183.

= Genus *Dicuspiditermes* KRISHNA, 1965, pp. 16–18. AHMAD, 1965, pp. 8, 9, 100.

TYPE SPECIES: *Dicuspiditermes obtusus* (Silvestri).

Krishna (1965) proposed this genus for some species previously included in the genus *Capritermes* by Snyder (1949) and others.

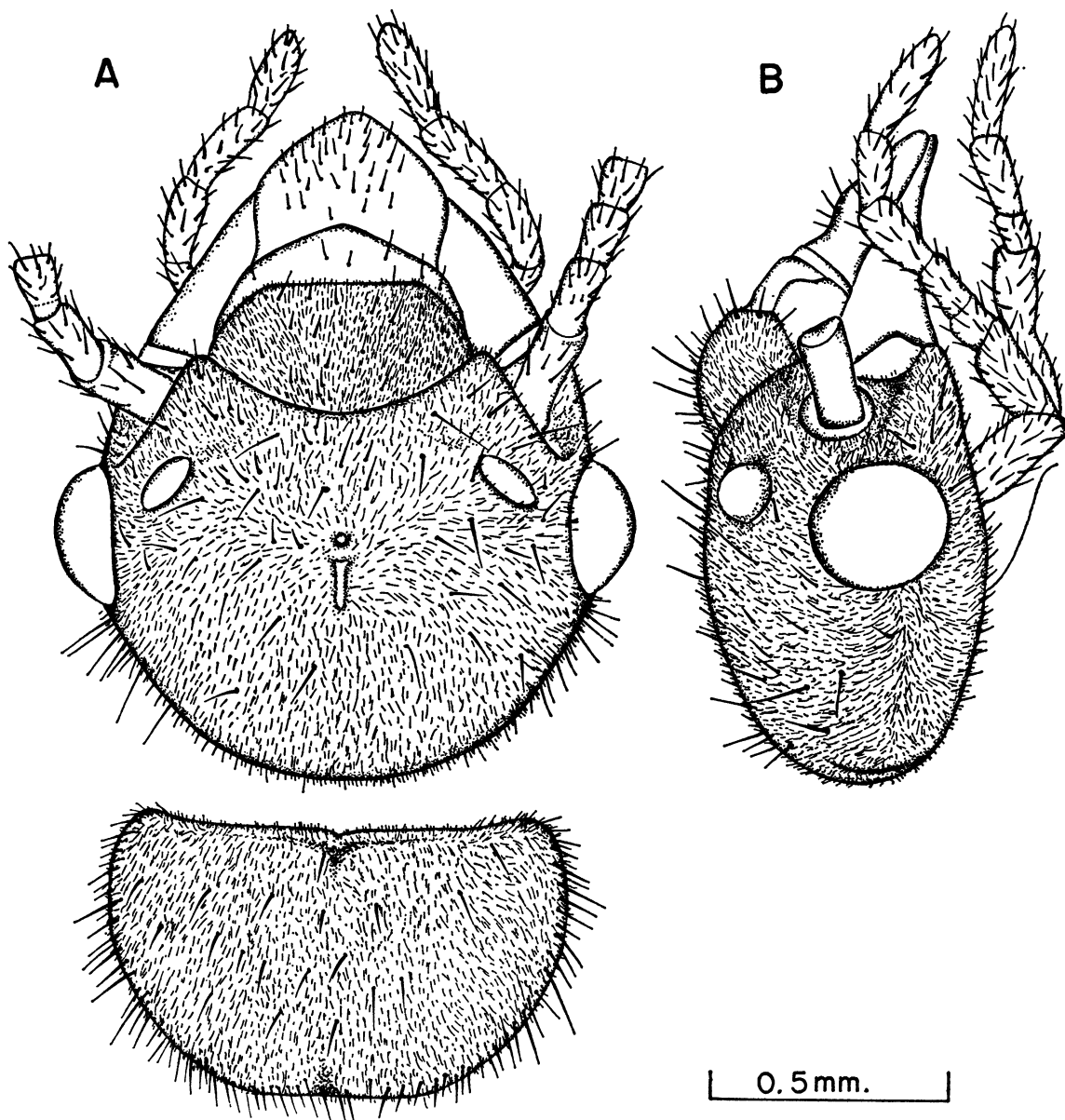


FIG. 17. Imago of *Dicuspiditermes obtusus* (Silvestri), cotype; Barkuda Island, Chilka Lake, Orissa, India, A. Head and pronotum from above. B. Head from side.

IMAGO (FIG. 17): Head and pronotum covered with numerous bristles and short hairs, the short hairs forming a conspicuous mat, contrasting with longer bristles. Fontanelle varied in size and shape, usually long, narrow, and slitlike, in some cases small and oval or indistinct. Ocellus not touching eye.

Antennae with 14 to 15 articles, third article equal to fourth, second longer than third or fourth. Mandibles as shown in figure 18. Left mandible with cutting edge of fused first plus second marginal tooth sinuate and longer than apical tooth (in *nemorosus* and *santschii* apical tooth shorter than in other

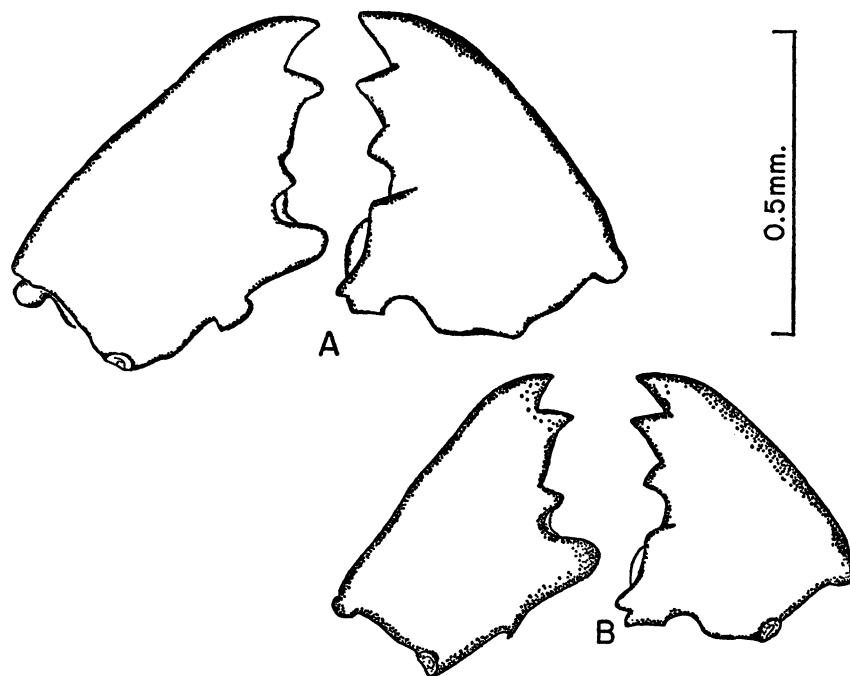


FIG. 18. Mandibles of workers. A. *Dicuspiditermes obtusus* (Silvestri).
B. *Dicuspiditermes nemorosus* (Haviland).

species included in this genus) and third marginal tooth prominent. Right mandible with second marginal tooth well developed and posterior margin of first marginal tooth long.

SOLDIER (FIG. 19): Head with scattered bristles; fontanelle surrounded by a few bristles. Head rectangular, with anterolateral corners extended into distinct, tubercle-like projections in front of and below antennal sockets. Vertex above frontal-gland opening bulging into hump, with frons in some species sloping steeply (*laetus*), in others gradually. Frontal gland large in some species, such as *laetus*, and reduced in others, such as *makhamensis*. Fontanelle transversely oval, with dorsal rim well marked and darker (in *nemorosus* and *santschii* fontanelle minute and circular, opening into capillary tube leading into frontal gland). Labrum asymmetrical, lying obliquely, with anterior margin deep and broadly or narrowly concave and anterolateral corners extended into long, pointed processes, with anterolateral margins serrated in some species. Mandibles asymmetrical. Left mandible with its tip in

form of a beak, usually with small, toothlike projection below, and its inner margin with basal projection. Right mandible bladeliike, with anterior margin concave. Antennae with 14 articles; fourth article shortest. Tibial spurs 3:2:2. Middle tibia with one or two spines.

RELATIONSHIPS AND COMPARISONS: *Dicuspiditermes* is most closely related to *Pericapritermes* and *Homallotermes*, as is indicated by the imago-worker mandible (figs. 15, 18, 21). The imagoes of *Pericapritermes* and *Dicuspiditermes* are similar. The soldier of *Pericapritermes*, however, differs from that of *Dicuspiditermes* in the following respects: the anterolateral corners of the head are not extended into tubercle-like projections; the frontal gland is much reduced; the fontanelle is small, circular, and dotlike; the frons is not raised vertically into a distinct protuberance; the anterior margin of the labrum is straight, with its anterolateral corners not extended into long, needle-like processes; and the left mandible does not have an inner basal projection.

Homallotermes can be distinguished from

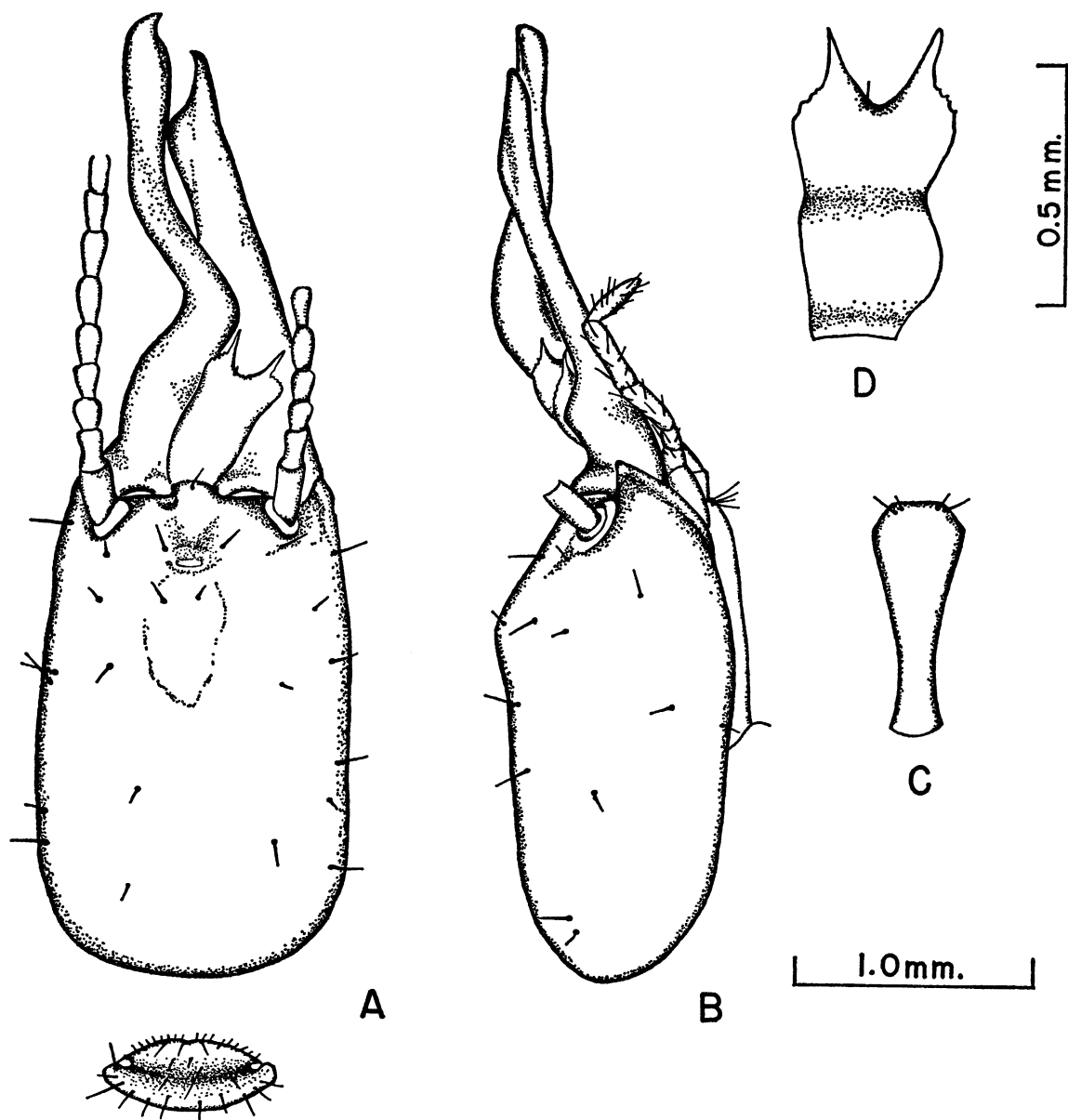


FIG. 19. Soldier of *Dicuspiditermes obtusus* (Silvestri), cotype; Barkuda Island, Chilka Lake, Orissa, India. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

Dicuspiditermes as follows: In the soldier the antennae are 13-segmented; the mandibles are slender; the head is smaller and slopes less steeply in front, with its anterolateral corners without tubercle-like processes; and the labrum has evenly rounded lateral margins and a broadly concave anterior margin. In the imago-worker mandible the posterior

margin of the second right marginal tooth is shorter.

The genus *Capritermes* (as treated in this paper) differs from *Dicuspiditermes* in that, in the imago-worker mandible, the second right marginal tooth is reduced, and the left apical tooth is proportionally longer than the cutting edge of the fused first plus second

marginal tooth. The soldier of *Capritermes* has the anterior margin of the labrum biconvex, with its anterolateral corners not so long, and no tubercle-like projections at the anterolateral corners of the head.

SPECIES INCLUDED

- D. fletcheri* (K. and N. Holmgren), 1917
D. gravellyi (Silvestri), 1922
D. hutsoni (Kemner), 1926
D. incola (Wasmann), 1893
D. cornutella (Silvestri), 1922
D. laetus (Silvestri), 1914c
 [New synonymy: *Capritermes garthwaitei* Gardner, 1944]
D. makhamensis Ahmad, 1965
D. nemorosus (Haviland), 1898
D. obtusus (Silvestri), 1923a
 [New synonymy: *Capritermes obtusus* var. *abreviatus* Silvestri, 1923a]
D. punjabensis (K. and N. Holmgren), 1917
D. santschii (Silvestri), 1922
 [New synonymy: *Capritermes padangensis* Kemner, 1930]

GEOGRAPHICAL DISTRIBUTION: Oriental Region: Borneo, Burma, Ceylon, India, Malay Peninsula, Pakistan, Sumatra.

GENUS PERICAPRITERMES SILVESTRI, 1914

<Genus *Termes* (section with *T. nemorosus* for type): HAVILAND, 1898, pp. 378, 412.

<Genus *Termes*: subgenus *Eutermes*: DESNEUX, 1904, pp. 26, 28, 39, 40.

>Genus *Pericapritermes* SILVESTRI, 1914a, p. 134; 1914b, p. 616. SJÖSTEDT, 1926, pp. 281, 282. SNYDER, 1949, p. 198. AHMAD, 1950, pp. 47, 72, 74, 75; 1965, pp. 8, 9, 98. WEIDNER, 1955, p. 73. EMERSON, 1955, pp. 469, 486, 501, 512. NOIROT AND KAVOOR, 1958, pp. 451, 453, 455, 461, 462, 466-468, 470. HARRIS, 1961, pp. 55, 64. COATON, 1962, p. 64. BODOT, 1964, p. 253. KRISHNA, 1965, p. 15. BOUILLON AND MATHOT, 1965, pp. 13, 23, 46, 83; 1966, chart.

>Subgenus *Pericapritermes* (of genus *Capritermes*): EMERSON, 1928, pp. 409, 420, 543.

<Subgenus *Capritermes* (of genus *Capritermes*): HOLMGREN, 1912, pp. 114-118; 1914, p. 278. EMERSON, 1928, pp. 409, 412, 542.

<Genus *Capritermes*: ESCHERICH, 1911, pp. 53, 55, 56, 145, 148. HOLMGREN, 1911, p. 209; 1913, p. 242. JOHN, 1925, p. 414. LIGHT, 1931, p. 598. KEMNER, 1934, p. 171. WU, 1935, p. 221. HILL, 1942, p. 419. SNYDER, 1949, p. 192. TU, 1955, pp. 3, 6. EMERSON, 1955, p. 512. WEIDNER, 1955, p. 73. AHMAD, 1958, pp. 88, 91, 183; 1965, pp. 8, 9, 103. CALABY AND GAY, 1959, pp. 213, 294, 324.

ROONWAL AND CHHOTANI, 1962, pp. 294, 324. TSAI AND CHEN, 1964, pp. 29, 30, 35. YU AND PING, 1964, pp. 13, 14, 16. MATHUR AND THAPA, 1965, p. 10.

TYPE SPECIES: *Pericapritermes urgens* SILVESTRI.

The genus *Pericapritermes* has been reported, from the Ethiopian Region only, by Snyder (1949) and Emerson (1955). The studies of the present author have shown that many species from the Indomalayan Region and the single species *Capritermes schultzei* from New Guinea included in the genus *Capritermes* (Snyder, 1949; Roonwal and Sen-Sarma, 1960; Roonwal and Chhotani, 1962; Mathur and Thapa, 1965) actually belong to the genus *Pericapritermes*.

Krishna (1965) included the species *Capritermes semarangi* Holmgren and *C. tetraphilus* for the first time in the genus *Pericapritermes*. Ahmad (1965) placed *C. latignathus* Holmgren as a new combination in the genus *Pericapritermes* for the first time.

Thus the distribution of this genus now is Ethiopian, Indomalayan, and Papuan rather than only Ethiopian.

IMAGO (FIG. 20): Head densely hairy. Fontanelle usually large, with short diameter 0.05-0.10 mm. Frontal suture meeting at fontanelle. Ocellus large, not touching eye. Antennae with 14 to 15 articles; fourth shortest in 14-segmented antennae. Imago-worker mandible as shown in figure 21. Apical tooth shorter than fused first plus second marginal tooth; posterior margin of fused first plus second marginal tooth elongated and sinuate; third marginal tooth prominent, but not so well developed as in *Homallotermes*. Right mandible with second marginal tooth well developed.

SOLDIER (FIG. 22): Head with scattered bristles and a few hairs. Head rectangular, frontal projection absent. Fontanelle minute, dotlike, circular, opening into small tube leading into frontal gland. Labrum with anterior margin almost straight and anterolateral corners extended into short processes. Mandibles asymmetrical. Left mandible strongly bent in middle, without either hook at tip or prominent basal projection (in a few species minute, pimple-like projection) and with rudimentary tooth in basal inner third. Right mandible blade-like, with tip

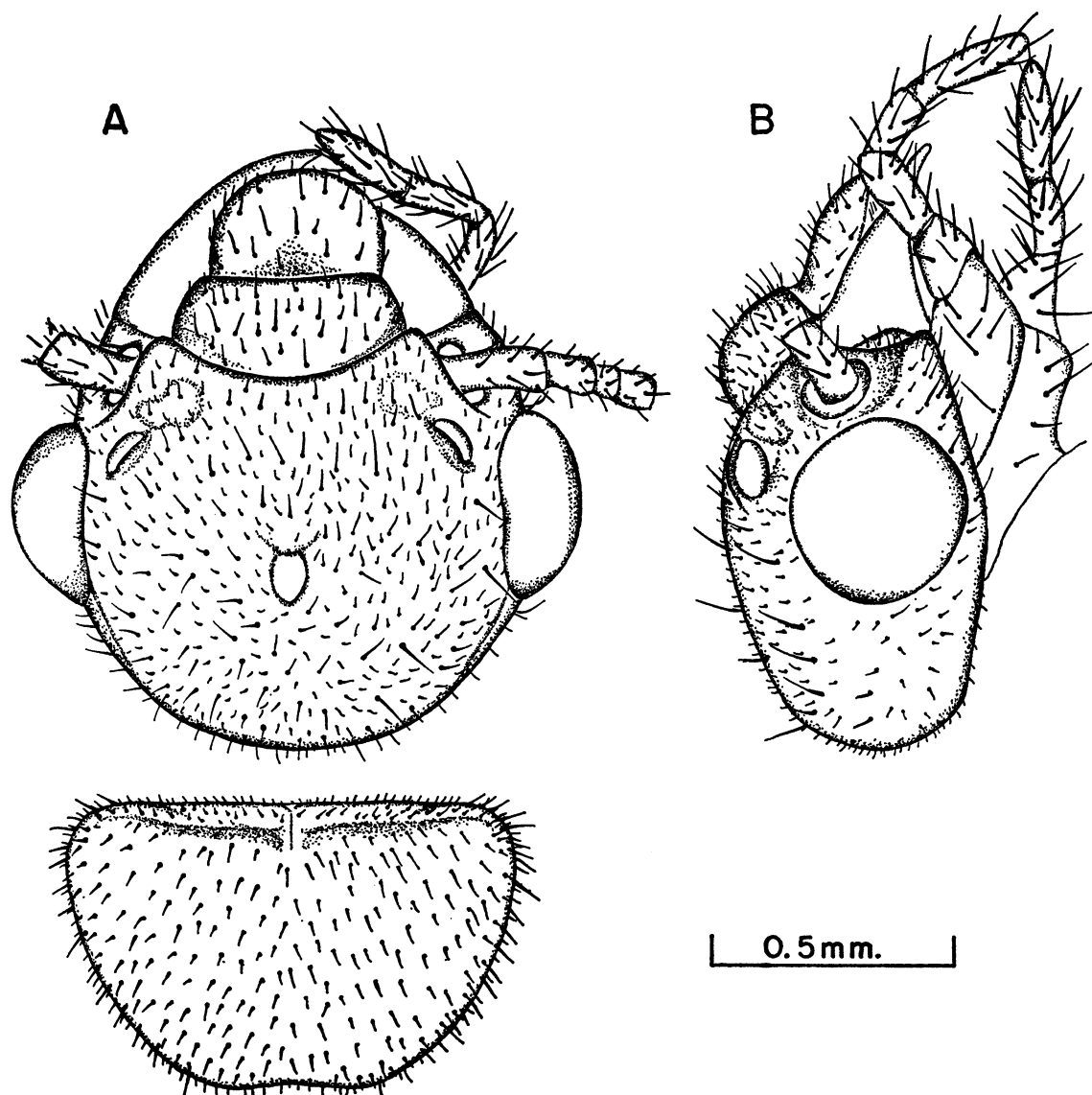


FIG. 20. Imago of *Pericapritermes urgens* Silvestri, cotype; Mamou, former French Guinea.
A. Head and pronotum from above. B. Head from side.

usually pointed and bent outward anteriorly and inner apical margin straight. Antennae with 14 articles. Tibial spurs 3:2:2. Middle tibia with one or two spines.

RELATIONSHIPS AND COMPARISONS: The genus *Pericapritermes* is more closely related to *Dicuspiditermes* and *Homallotermes* than to the genus *Capritermes* (as treated in this paper). Ahmad (1950) concluded that *Pericapritermes* probably was derived from *Ho-*

mallotermes, based on the evidence of the imago-worker mandible. The imago mandibles of *Pericapritermes*, *Dicuspiditermes*, and *Homallotermes* closely resemble one another (figs. 15, 18, 21). The imago mandible of *Pericapritermes*, however, most closely resembles that of *Dicuspiditermes*; variations within the two overlap, and it is difficult to separate the two genera from the imago-worker mandible alone. In addition, other

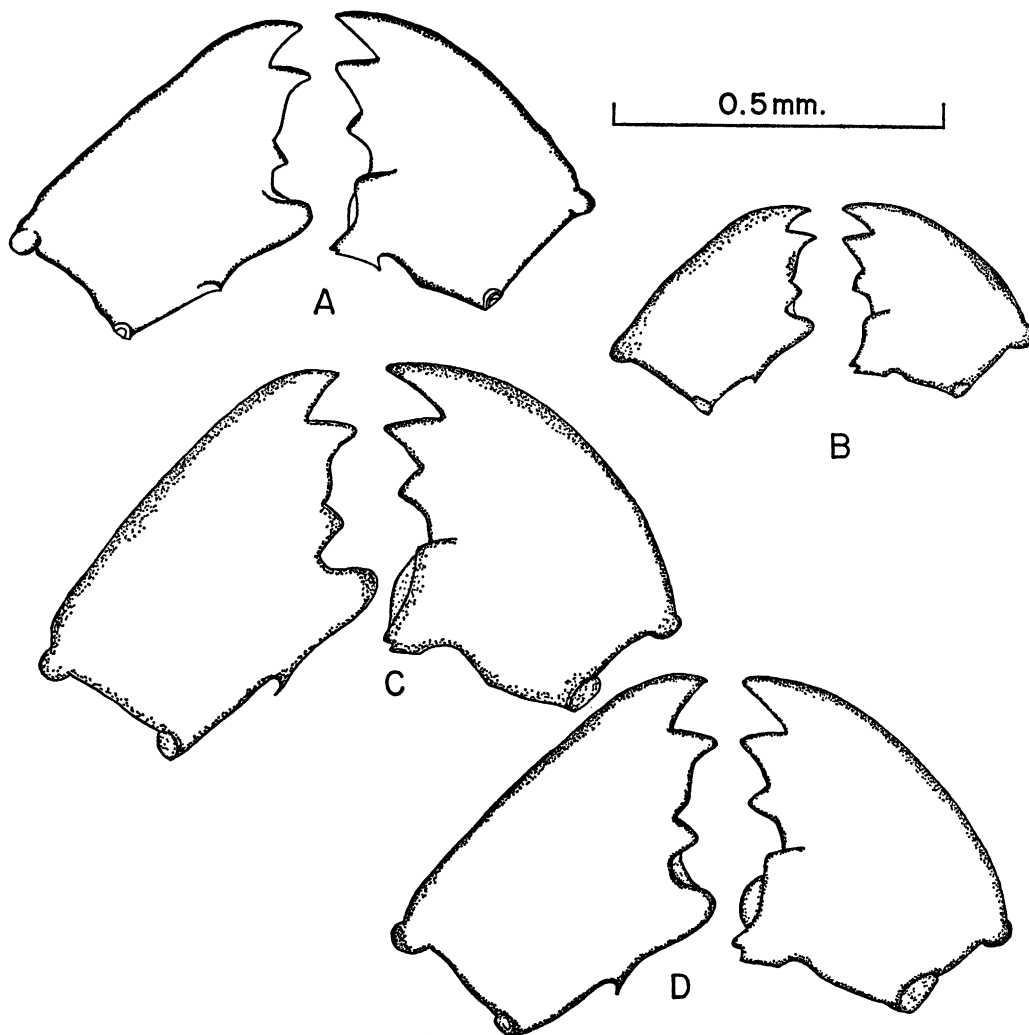


FIG. 21. Mandibles of workers. A. *Pericapritermes urgens* Silvestri. B. *Pericapritermes minimus* Weidner. C. *Pericapritermes dumicola* Harris. D. *Pericapritermes tetraphilus* (Silvestri).

characters in the imagoes are almost indistinguishable in the two genera.

The soldier of *Dicuspiditermes* is distinguished from that of *Pericapritermes* by the following characters: the anterolateral corners of the head have pointed projections in front of and below the antennal sockets; the frontal gland is well developed, with the head rising vertically above the fontanelle; the labrum is deeply concave, with its anterolateral corners projected into long, needle-like processes; and the left mandible has an inner basal projection.

The soldier of *Homallotermes* can be separated from that of *Pericapritermes* by the following characters: the frontal gland is larger; the fontanelle is large and circular; the anterior margin of the labrum is concave; the antennae are invariably 13-segmented; the mandibles are more slender and hooked at the tips; and the left mandible has a prominent projection at the base.

Also, *Capritermes* as treated in this paper differs from *Pericapritermes* as follows: in the imago-worker mandible the left apical tooth is proportionally longer than the fused first

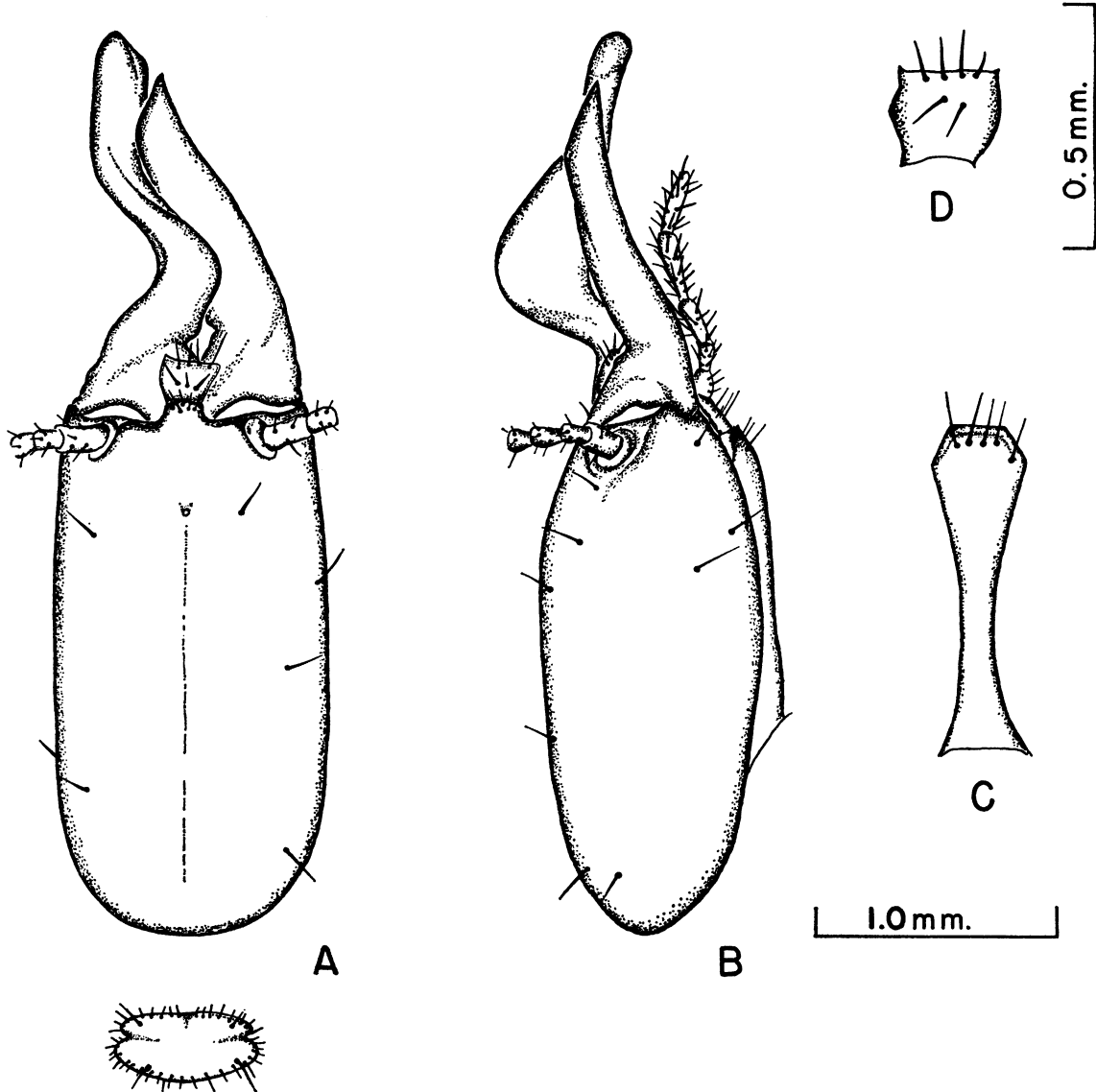


FIG. 22. Soldier of *Pericapritermes urgens* Silvestri; Bipindi, Cameroon. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

plus second marginal tooth, and the second right marginal tooth is much more reduced; in the soldier there is a rudimentary frontal projection with bristles surrounding the fontanelle, and the anterior margin of the labrum is faintly bilobed, with its anterolateral projections more prominent.

Procapritermes can be distinguished from *Pericapritermes* by the following characteristics: in the imago-worker mandible, the apical teeth are longer, and the third left

marginal tooth is more reduced; in the soldier the labrum is broadly or deeply concave, with the points at its anterolateral corners more developed, the fontanelle is larger, and the left mandible has a distinct tooth in front of the basal toothlike projection.

SPECIES INCLUDED

P. assamensis (Mathur and Thapa), new combination = *Capritermes assamensis* Mathur and Thapa, 1965

- P. appellans* Silvestri, 1914a
P. appellans Silvestri var. *metata* Silvestri, 1914a
P. brachygnathus (John), new combination = *Capritermes brachygnathus* John, 1925
P. buitenzorgi (Holmgren), new combination = *Capritermes (Capritermes) buitenzorgi* Holmgren, 1914
P. ceylonicus (Holmgren), new combination = *Capritermes ceylonicus* Holmgren, 1911
 [New synonymy: *Capritermes distinctus* Holmgren, 1911]
P. chiasognathus (Sjöstedt), 1904
 [New synonymy: *Pericapritermes cordatus* Sjöstedt, 1924]
P. desaegeri Harris, 1963
P. dolichocephalus (John), new combination = *Capritermes dolichocephalus* John, 1925
P. dumicola Harris, 1954
P. dunensis (Roonwal and Sen-Sarma), new combination = *Capritermes dunensis* Roonwal and Sen-Sarma, 1960
P. emersoni Krishna, new name for soldier of *P. socialis* (Sjöstedt), 1900 (imago = *Anoplotermes*)
P. fuscotibialis (Light), new combination = *Capritermes fuscotibialis* Light, 1931
P. gloveri Harris, 1951
P. heteronotus Silvestri, 1914a
P. latignathus (Holmgren), 1914¹
P. latignathus durga (Roonwal and Chhotani), new combination = *Capritermes latignathus durga* Roonwal and Chhotani, 1962
P. machadoi Noirot, 1955
P. magnificus (Silvestri), 1912
P. minimus Weidner, 1956
 [New synonymy: *Pericapritermes amplignathus* Harris, 1956]
P. modiglianii (Silvestri), new combination = *Capritermes modiglianii* Silvestri, 1922
P. mohri (Kemner), new combination = *Capritermes mohri* Kemner, 1934
P. nitobei (Shiraki), new combination = *Eutermes nitobei* Shiraki, 1909
 [New synonymy: *Capritermes jangtsekiangensis* Kemner, 1925]
P. paetensis (Oshima), new combination = *Capritermes paetensis* Oshima, 1920
P. schultzei (Holmgren), new combination = *Capritermes schultzei* Holmgren, 1911
P. semarangi (Holmgren), 1913²
 [New synonymy: *Capritermes sumatrensis* John, 1925]
P. silvestrianus (Emerson), 1928

- P. speciosus* (Haviland), new combination = *Termes speciosus* Haviland, 1898
P. tetraphilus (Silvestri), 1922³
 [Synonymy: *Capritermes orientalis*, Mathur and Sen-Sarma, 1961]³
P. urgens Silvestri, 1914a
P. urgens var. *confinis* Silvestri, 1914a
P. urgens var. *nigeriana* Silvestri, 1914a

GEOGRAPHICAL DISTRIBUTION: Ethiopian Region: Africa. Oriental Region: Borneo, Burma, Ceylon, China, Taiwan, Hongkong, India, Java, Malaya, Philippines, Sumatra. Papuan Region: New Guinea.

GENUS *PROCAPRITERMES* HOLMGREN, 1912

<Genus *Termes* (section with *T. setiger* for type): HAVILAND, 1898, pp. 378, 414.

<Genus *Termes*: subgenus *Eutermes*: DESNEUX, 1904, pp. 28, 29, 39, 45.

>Genus *Procapritermes* HOLMGREN, 1912, pp. 97, 113, 114, 119; 1913, p. 239. JOHN, 1925, p. 412. EMERSON, 1928, p. 409; 1955, p. 512. LIGHT, 1931, p. 595. KEMNER, 1934, p. 167. WU, 1935, p. 220. HARE, 1937, p. 478. SNYDER, 1949, p. 190. AHMAD, 1950, pp. 72, 74, 75; 1958, pp. 87, 91, 192; 1965, pp. 9, 104. TU, 1955, pp. 3, 6. WEIDNER, 1955, p. 73. HARRIS, 1961, p. 64. YU and PING, 1964, p. 13. TSAI and CHEN, 1964, pp. 29, 30.

<Subgenus *Capritermes* (of genus *Capritermes*): HOLMGREN, 1914, p. 278.

<Genus *Capritermes*: JOHN, 1925, p. 414. SNYDER, 1949, p. 192. YU and PING, 1964, p. 13.

>Genus *Pseudocapritermes* KEMNER, 1934, pp. 167-168. New synonymy (type species = *Pseudocapritermes silvaticus*).

>Genus *Pseudocapritermes*: SNYDER, 1949, p. 191. AHMAD, 1950, pp. 72, 74, 75; 1958, pp. 87, 91, 193; 1965, pp. 7, 9, 106. EMERSON, 1955, p. 512. WEIDNER, 1955, p. 73. HARRIS, 1961, p. 64. ROONWAL AND CHHOTANI, 1962, pp. 290, 291, 294. MATHUR AND THAPA, 1965, p. 12.

TYPE SPECIES: *Procapritermes setiger* (Haviland).

Holmgren (1913) described the genus *Procapritermes* for Haviland's "section for *T. setiger* for type" (1898) and included in it three species, namely, *P. atypus* Holmgren, *P. minutus* Haviland, and *P. setiger*. Since Holmgren's report, five other species have been included in *Procapritermes* (Snyder, 1949; Ahmad, 1965; Tsai and Chen, 1963).

Kemner (1934) created the genus *Pseudocapritermes* for the single species *Pseudo-*

¹ Ahmad (1965, p. 98) transferred this species to *Pericapritermes* for the first time.

² Krishna (1965) transferred this species to *Pericapritermes* for the first time.

³ Krishna (1965) treated *Capritermes orientalis* as a synonym of *P. tetraphilus*.

capritermes silvaticus Kemner. Since Kemner, six other species have been included in this genus (Snyder, 1949; Roonwal and Chhotani, 1962; Ahmad, 1965; Mathur and Thapa, 1962, 1965).

The present study has shown that the genera *Procapritermes* and *Pseudocapritermes* are not sharply separated and that they intergrade with each other in most characters.

Until now, *Procapritermes* has been dis-

tinguished from *Pseudocapritermes* by the following characteristics: in the left imago-worker mandible, the apical tooth is proportionally longer, and the cutting edge of the fused first plus second marginal tooth is angular and short (long and almost straight in *Pseudocapritermes*; fig. 26); the soldier mandibles are not strongly asymmetrical: the left mandible is not strongly bent in the middle, and its tip is hooked and narrow

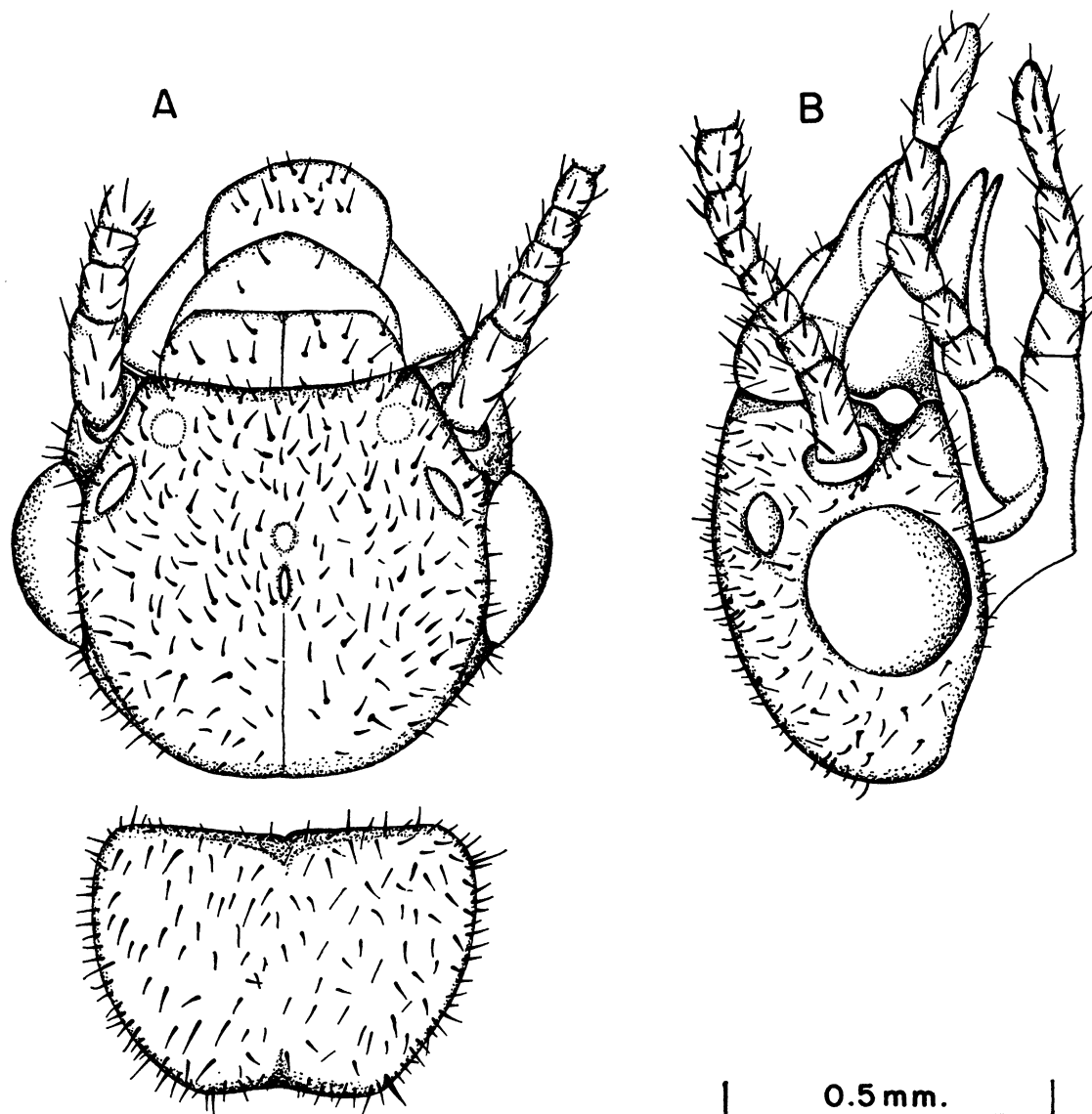


FIG. 23. Imago of *Procapritermes setiger* (Haviland), cotype from colony 343; Sarawak, Borneo.
A. Head and pronotum from above. B. Head from side.

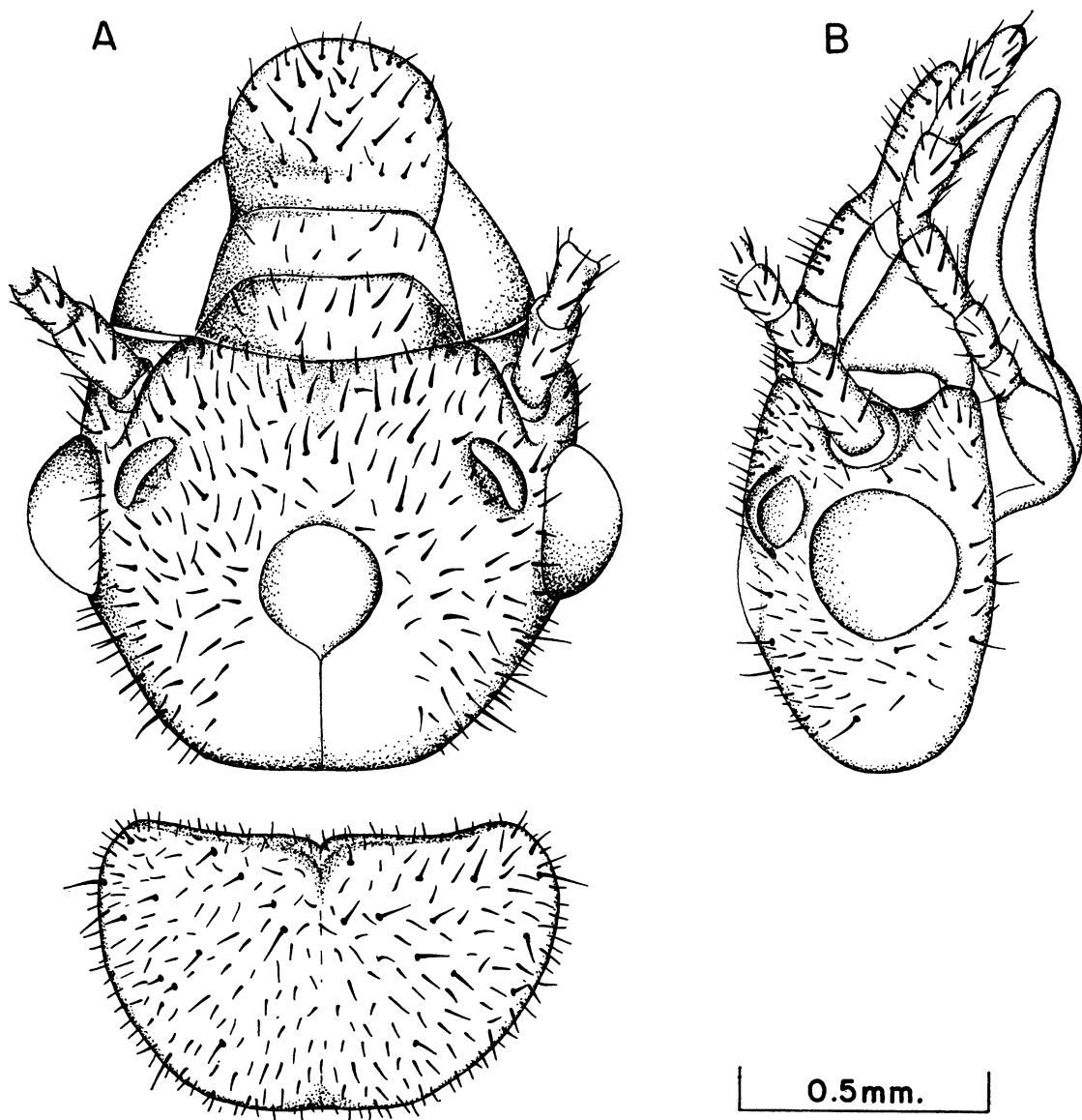


FIG. 24. Imago of *Procapritermes angustignathus* (Holmgren), cotype; Penang, former Straits Settlements, Malaya. A. Head and pronotum from above. B. Head from side.

(fig. 30A, B, F) (more strongly bent with its tip hooked and broad in *Pseudocapritermes*).

However, the imago-worker mandible is variable among the species hitherto included in the genus *Procapritermes* (fig. 25A–C, F). As can be seen by a comparison of the imago-worker mandibles of the species included in *Procapritermes* (fig. 25) with those of *Pseudocapritermes* (fig. 26), there is overlapping variation between the genera.

Also, the soldier mandibles of the species hitherto included in *Procapritermes* (fig. 30A–F) do not show a sharp demarcation from those of *Pseudocapritermes* (fig. 30G–I). The left soldier mandible of *Procapritermes setiger* is rodlike, very slightly bent in the middle, with its outer lower margin very slightly concave (fig. 30B), whereas the soldier mandibles of *Pseudocapritermes angustignathus* and *Pseudocapritermes silvaticus* are more sharply

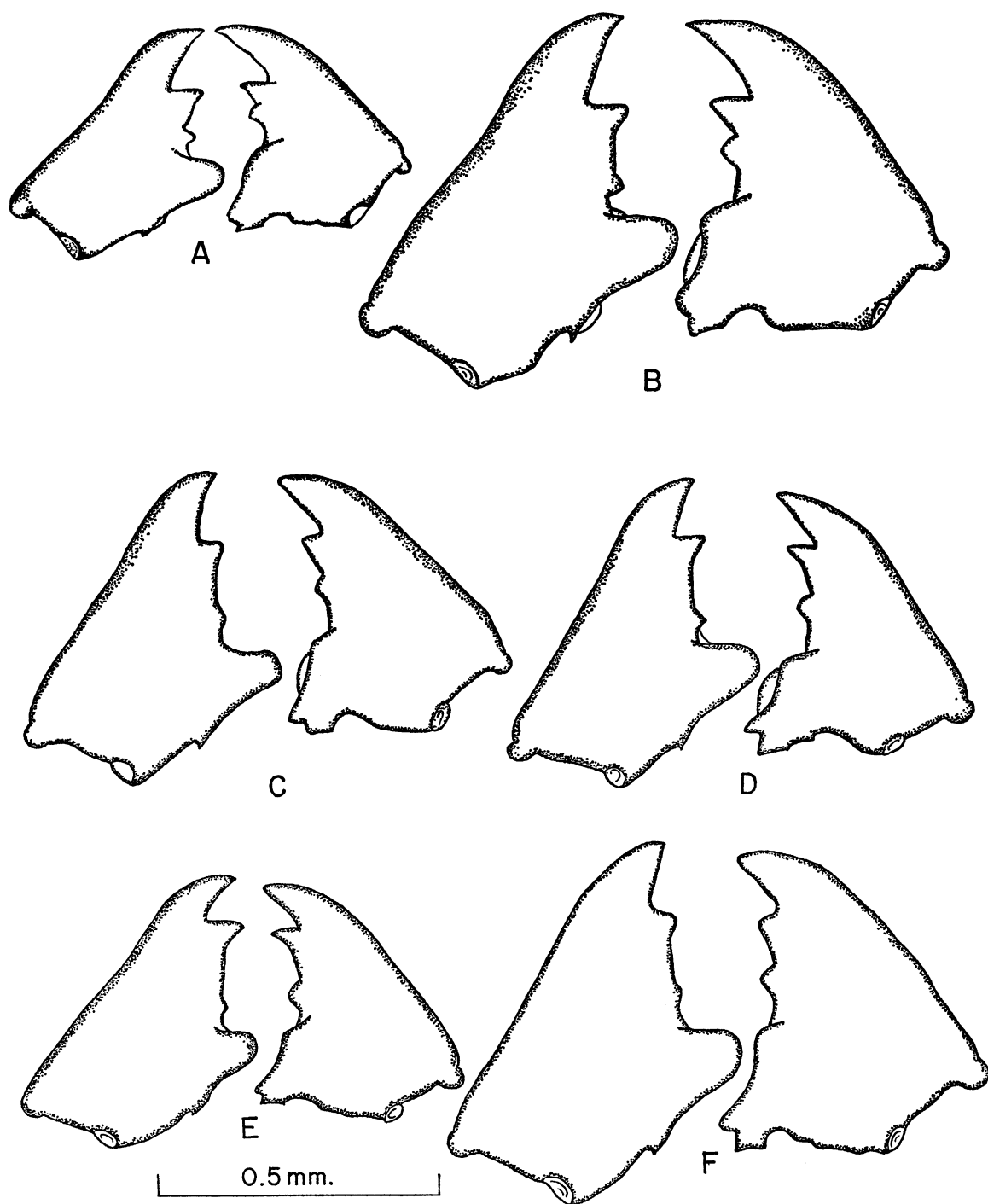


FIG. 25. Mandibles of workers. A. *Procapritermes setiger* (Haviland). B. *Procapritermes atypus* Holmgren. C. *Procapritermes prosetiger* Ahmad. D. *Procapritermes*, new species I; Sarawak. E. *Procapritermes*, new species; Thekaday, Kerala, India. F. *Procapritermes sowerbyi* (Light).

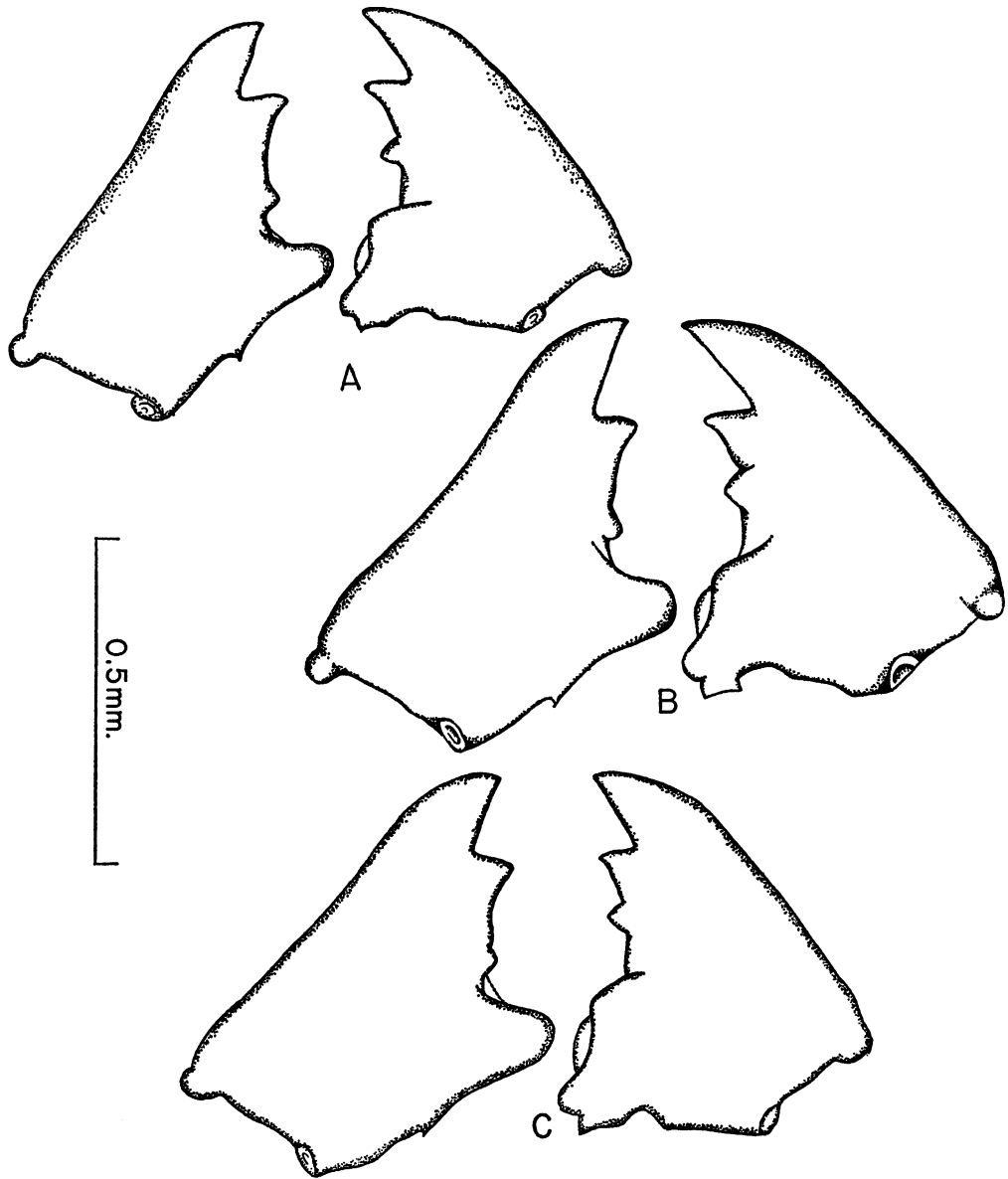


FIG. 26. Mandibles of workers. A. *Procapritermes silvaticus* Kemner. B. *Procapritermes angustignathus* (Holmgren). C. *Procapritermes tikadari* (Roonwal and Chhotani).

bent in the middle, with their outer lower margins more deeply concave (fig. 30G, I). Between these two extremes are the mandibles of *Procapritermes sowerbyi* and *Procapritermes atypus*, in which the outer concavity of the left mandible is intermediate (fig. 30E, F). Thus the mandibles of the species from *Procapritermes prosetiger* (fig. 30A) to *Pseudocapritermes silvaticus* (fig. 30I)

form a continuous, intergraded series, and there is no correlation between their taxonomic characters.

Therefore, there is not a single character that clearly separates the genus *Procapritermes* from *Pseudocapritermes*. From the above evidence it is clear that the two genera are congeneric and that, consequently, *Pseudocapritermes* should be treated as a synonym of

Procapritermes, as the latter is the older name.

I am also transferring the species *greeni*, hitherto included in the genus *Capritermes* (Snyder, 1949) to *Procapritermes*. It is true that *greeni* is distinct from all other species included in *Procapritermes* in that the left soldier mandible is extremely bent in the middle, the tip is without a beak, and the inner margin near the tip is hollowed. There is also present in our collection a new species from Sarawak, Borneo, which has mandibles similar to those of *greeni*. However, in all other characters (dentition of the imago-worker mandible, fig. 27; anterior margin of labrum; and so on) it is *Procapritermes*-like.

I do not think that this single character is enough to justify erecting a new genus for these two species at the present time. I am therefore tentatively including them in *Procapritermes*.

IMAGO (FIGS. 23 AND 24): Head moderately to densely hairy. Fontanelle size variable, smallest in *setiger* (short diameter, 0.01 mm.), largest in *angustignathus* (short diameter, 0.19 mm.), raised in *angustignathus*, *silvaticus*, and some other species. Antennae with 15 articles; third article shorter than or as long as fourth. Imago-worker mandibles with dentition variable (figs. 25–27): in *setiger*, *minutus*, and *atypus*, fused first plus second left marginal tooth small, with its posterior mar-

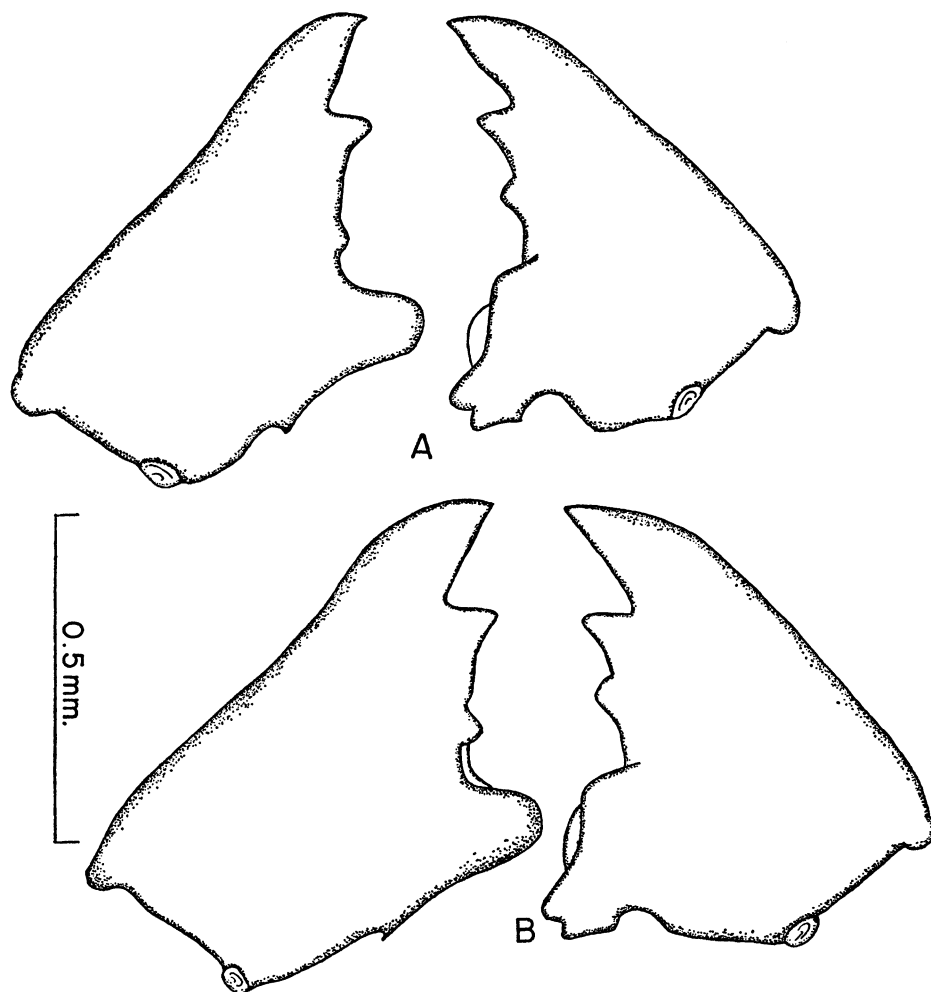


FIG. 27. Mandibles of workers. A. *Procapritermes*, new species II; Sarawak. B. *Procapritermes greeni* (John).

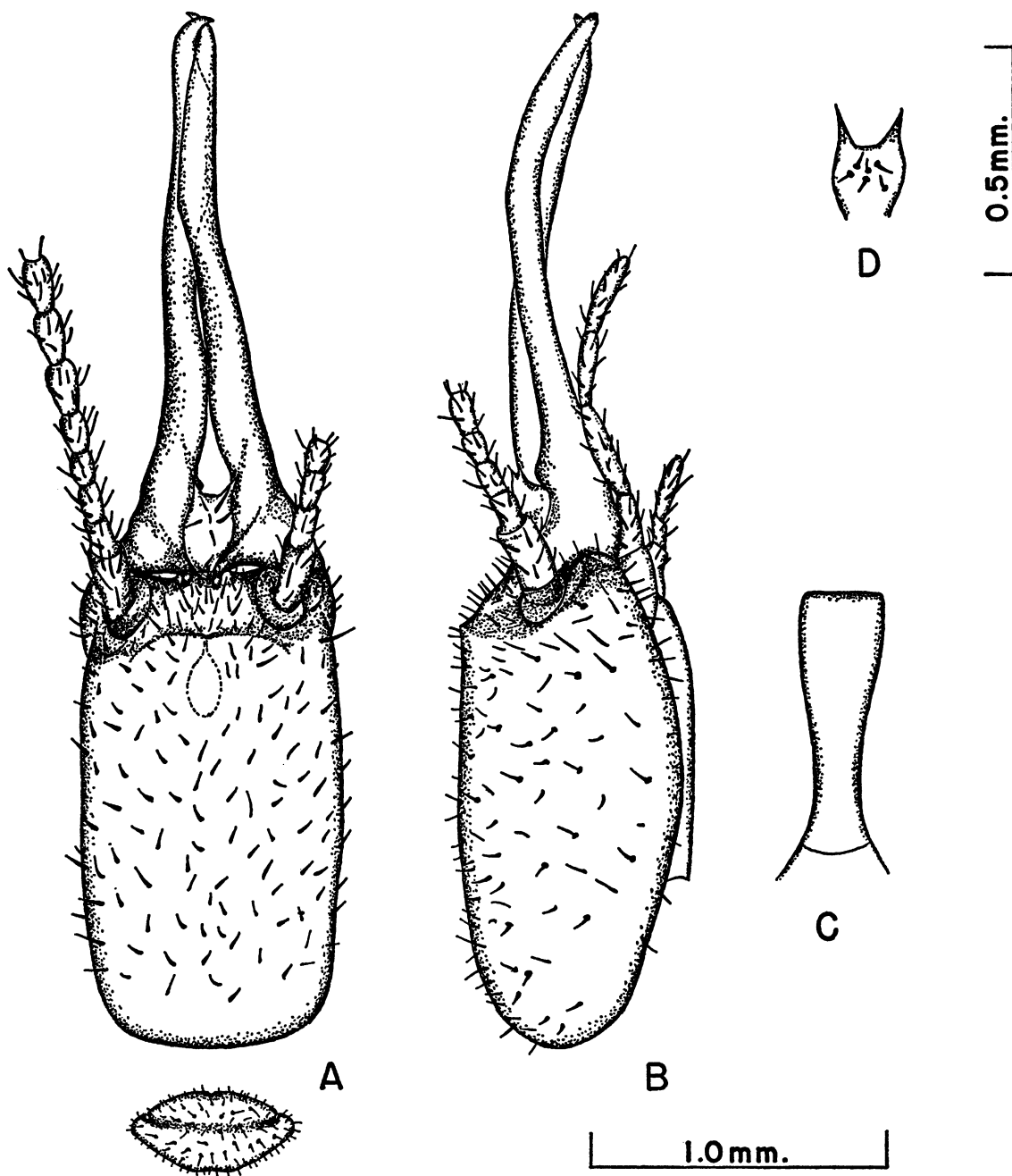


FIG. 28. Soldier of *Procapritermes setiger* (Haviland), cotype 343; Sarawak, Borneo. A. Head and pronotum from above. B. Head from above. C. Postmentum from below. D. Labrum from above.

gin short, and left apical tooth long; in *greeni*, *angustignathus*, *silvaticus*, and *tikadari*, posterior margin of fused first plus second left marginal tooth longer and third left marginal

tooth variable; in *sowerbyi* and other species, third marginal tooth much reduced.

SOLDIER (FIGS. 28 AND 29): Head with a few scattered bristles, more dense around

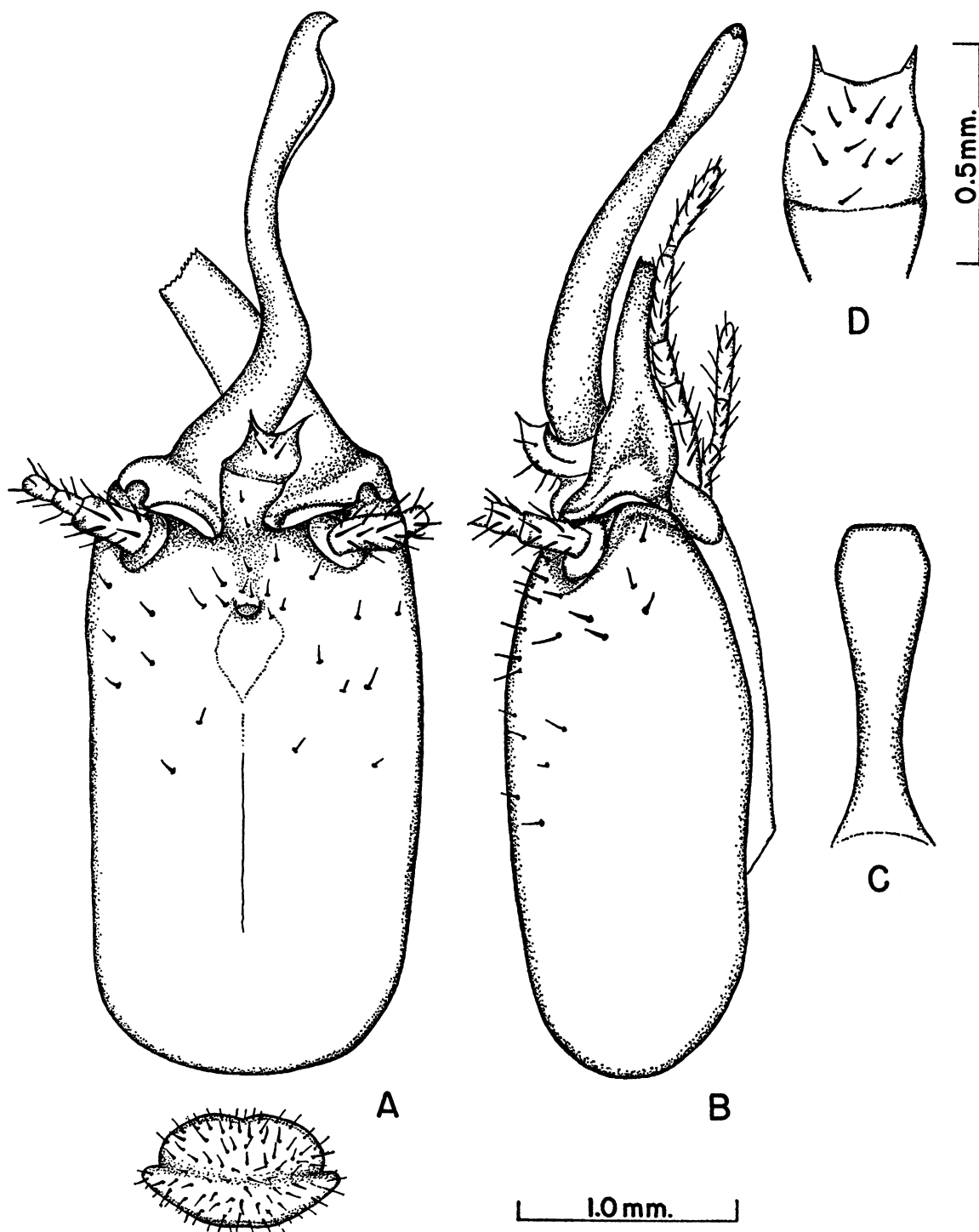


FIG. 29. Soldier of *Procapritermes angustignathus* (Holmgren), cotype; Penang, former Straits Settlements, Malaya. A. Head and pronotum from above. B. Head from sides. C. Postmentum from below. D. Labrum from above.

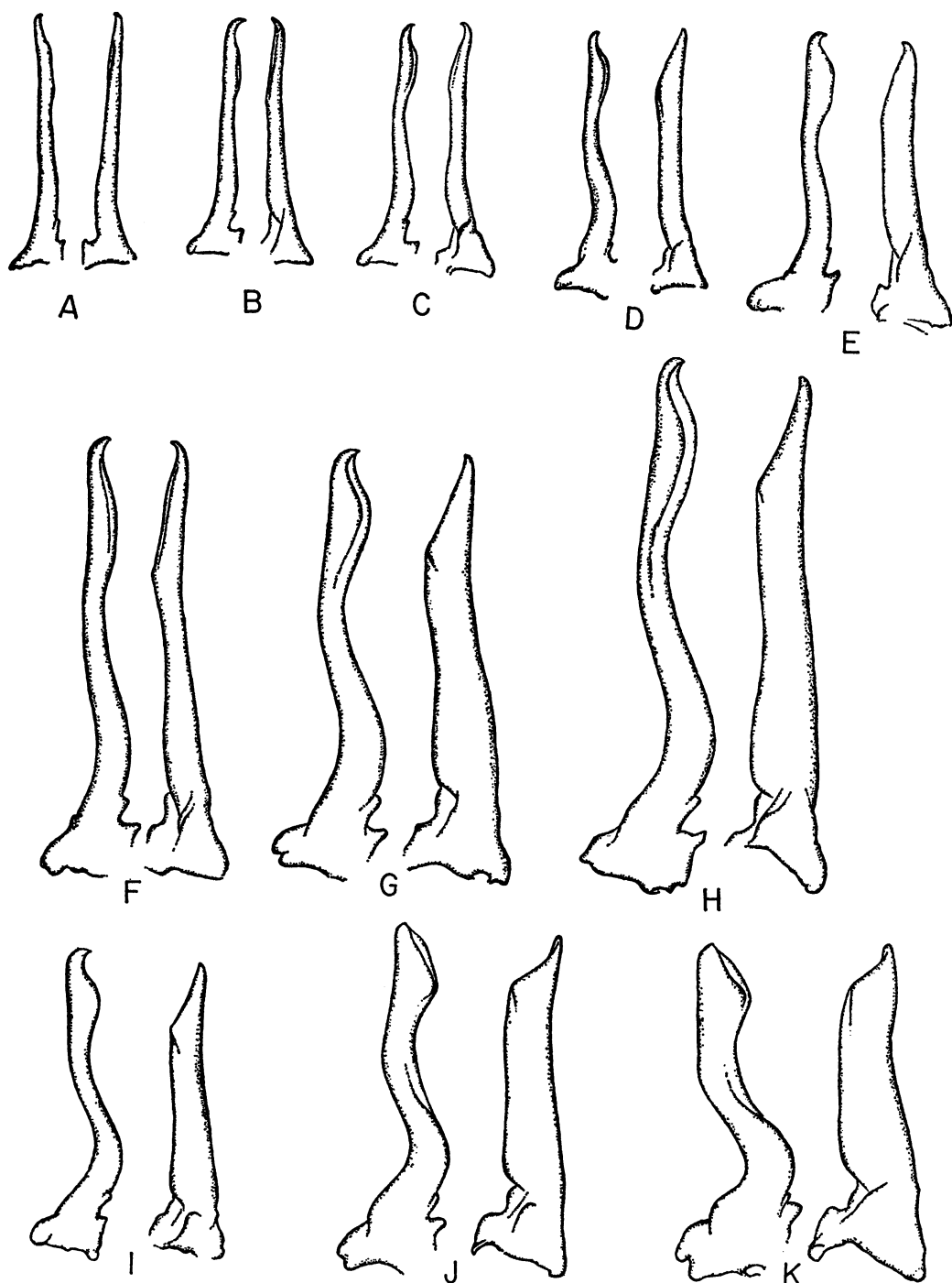


FIG. 30. Mandibles of soldiers. A. *Procapritermes prosetiger* Ahmad. B. *Procapritermes setiger* (Haviland). C. *Procapritermes*, new species I; Sarawak. D. *Procapritermes*, new species II; Sarawak. E. *Procapritermes sowerbyi* (Light). F. *Procapritermes atypus* Holmgren. G. *Procapritermes angustignathus* (Holmgren). H. *Procapritermes*, new species III; Sarawak. I. *Procapritermes silvaticus* (Kemner). J. *Procapritermes*, new species IV; Sarawak. K. *Procapritermes greeni* (John).

fontanelle. Head subrectangular, without frontal projection, in some with faint ridge on frons, as in *setiger* and a new species from Malaya. Labrum with anterior margin deeply, broadly, or sinuously concave, with its anterolateral corners extended into longish, thin, hyaline processes. Mandibles asymmetrical. Left mandible bent and curved in lower half: least bent in *setiger* (fig. 30B); most bent in *greeni* (fig. 30K); between these two extremes in other species. Prominent basal projection with a tooth in front of it in left mandible. Antennae with 14 articles, articles elongated. Tibial supurs 3:2:2. Middle tibia with one or two spines.

RELATIONSHIPS AND COMPARISONS: Holmgren (1912) stated that *Procapritermes*, by way of *Protocapritermes*, forms a link between *Mirotermes* (= *Termes*), a genus with symmetrical soldier mandibles, and *Capritermes*, a genus with asymmetrical soldier mandibles; that *Procapritermes* is derived from a *Protocapritermes*-like ancestor, with a gradual loss of the frontal projection and a gradual increase in the mandibular asymmetry; and that the genus *Capritermes*, as hitherto treated, has evolved from a *Procapritermes*-like ancestor. Kemner (1934) mentioned that the genus *Pseudocapritermes* (treated as a synonym in the present paper) is most closely related to *Capritermes*. Ahmad (1950), on the evidence of the imago-worker mandible, concluded that *Procapritermes* and *Capritermes* are closely related and that *Pseudocapritermes* is more advanced than *Procapritermes*.

The concept of the genus *Capritermes* held by Holmgren, Kemner, Ahmad, and others is very different from the concept of this genus in the present paper. *Capritermes* as I am treating it is more closely related to *Quasitermes* than to *Procapritermes*. *Procapritermes* as treated in this paper is most closely related to *Mirocapritermes* and *Labiocapritermes*. The imago-worker mandibles of *Mirocapritermes* and *Labiocapritermes* are more specialized than those of *Procapritermes* in that the third left marginal tooth is much more reduced (figs. 32, 35). The soldier of *Mirocapritermes* differs from that of *Procapritermes* in having a frontal projection, which is absent from *Procapritermes* and *Labiocapritermes*. Also, the soldier of *Procapritermes* differs from that of *Labiocapritermes* in the following respects:

the labrum is large, asymmetrical, and swollen (fig. 33D); the mandibles are extremely asymmetrical, with the left strongly bent in the middle.

Capritermes as treated in the present paper is not closely related to *Procapritermes* and differs from it in the following respects: in the imago-worker mandible the second right marginal tooth is much more reduced; in the soldier there is a rudimentary frontal projection, and the anterior margin of the labrum is bilobed, with its anterolateral corners not so prominent.

In *Homallotermes* the imago-worker mandibles are different (fig. 15): in the left imago mandible the apical tooth is shorter, and the third marginal tooth is more prominent. In the soldier, the antennae are 13-segmented, the fontanelle is larger and circular, the anterior margin of the labrum is broadly concave, and the mandibles are more slender.

Pericapritermes can be distinguished from *Procapritermes* by the following characteristics: in the soldier, the anterior margin of the labrum is straight, the fontanelle is small and dotlike, and the left mandible is extremely bent in the middle; in the imago-worker mandible the third left marginal tooth is well developed.

SPECIES INCLUDED

- P. albipennis* Tsai and Chen, 1963
- P. angustignathus* (Holmgren), new combination = *Capritermes* (*Capritermes*) *angustignathus* Holmgren, 1914
- P. atypus* Holmgren, 1912
- P. fontanellus* Mathur and Thapa, new combination = *Pseudocapritermes fontanellus* Mathur and Thapa, 1961
- P. greeni* (John), new combination = *Capritermes greeni* John, 1925
- P. longignathus* Ahmad, 1965
- P. minutus* (Haviland), 1898
- P. mushae* Oshima and Maki, 1919
- P. parasilvaticus* (Ahmad), new combination = *Pseudocapritermes parasilvaticus* Ahmad, 1965
- P. parvulus* Krishna, new name and new combination for *Capritermes minutus* Tsai and Chen, 1963
- P. prosetiger* Ahmad, 1965
- P. pseudolaetus* Tsai and Chen, new combination = *Capritermes pseudolaetus* Tsai and Chen, 1963
- P. setiger* (Haviland), 1898

P. silvaticus (Kemner), new combination =
Pseudocapritermes silvaticus Kemner, 1934

P. sowerbyi (Light), 1924

P. tikadari (Roonwal and Chhotani), new combination = *Pseudocapritermes tikardi* Roonwal and Chhotani, 1962

[New synonymy: *Pseudocapritermes planus* Mathur and Thapa, 1965]

GEOGRAPHICAL DISTRIBUTION: Oriental Region: Borneo, China (mainland), Taiwan, India, Java, Malay Peninsula, Sumatra, Thailand.

LABIOCAPRITERMES, NEW GENUS

<Genus *Capritermes*: SNYDER, 1949, p. 192. EMERSON, 1955, pp. 469, 478, 480, 486, 488, 489, 501-503, 512. AHMAD, 1958, pp. 88, 91, 183, 184, 188.

TYPE SPECIES: *Labiocapritermes distortus* (Silvestri) (= *Capritermes distortus* Silvestri).

This new monotypic genus is proposed for the species described by Silvestri under the name *Capritermes distortus*. This new genus is distinct from *Capritermes* (as treated in this paper) and differs from it in the following respects: In the soldier the frontal projection is totally absent (rudimentary in *Capritermes*); the mandibles are not hooked at the tips, and the left mandible is strongly bent in the middle; the labrum is asymmetrical, large, and swollen, with its front margin broadly concave and its sides strongly convex. In the imago-worker mandible the third left marginal tooth is greatly reduced, and the second right marginal tooth is more prominent. Also,

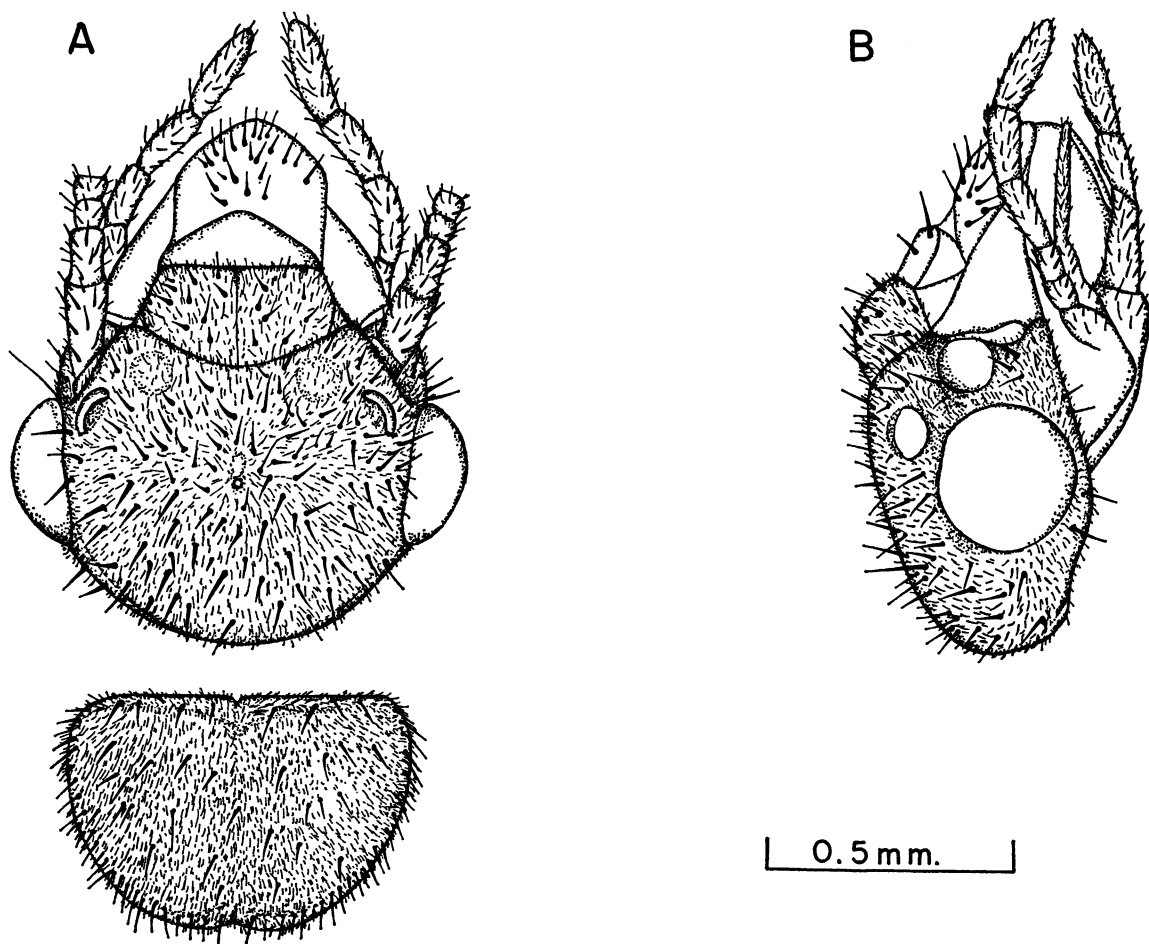


FIG. 31. Imago of *Labiocapritermes distortus* (Silvestri); cotype from type colony; Karalai, Kerala, India. A. Head and pronotum from above. B. Head from side.

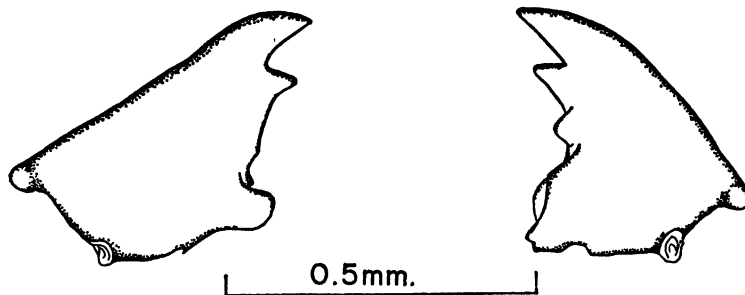


FIG. 32. Mandibles of worker of *Labiocapritermes distortus* (Silvestri), cotype colony; Karalai, Kerala, India.

in the imago the fontanelle is very minute.

IMAGO (FIG. 31): Small. Head and pronotum densely covered with fine hairs and numerous, scattered, long bristles. Eyes large. Ocellus not touching eye. Postclypeus twice as wide as long, prominently arched, in profile elevated above level of upper margin of head. Fontanelle small, ovoid. Imago-worker mandible as shown in figure 32. Left mandible with apical tooth robust, posterior margin of fused first plus second marginal tooth long, and third marginal tooth greatly reduced, almost rudimentary.

SOLDIER (FIG. 33): Head with a few scattered bristles; fontanelle surrounded by a few bristles. Head small, frontal projection absent and with frontal gland small. Fontanelle minute, situated on frontal slope. Labrum whitish, large, swollen, asymmetrical, its sides convex, anterior margin broadly concave (fig. 33 D), and anterolateral corners pointed. Mandibles short, asymmetrical. Left mandible strongly bent and twisted in middle, with tip blunt and without a beak, inner margin with pointed basal projection, and tooth in front of projection rudimentary or almost absent. Right mandible flat, much shorter than left mandible, its inner margin indented and grooved anteriorly, near tip. Antennae with 14 articles, fourth shortest. Tibial spurs 3:2:2. Middle tibia with two spinelike bristles.

RELATIONSHIPS AND COMPARISONS: The new genus *Labiocapritermes* is most closely related to *Procapritermes* (as treated in this paper). In the imago-worker mandible of both genera the apical tooth is long and the posterior margin of the fused first plus second left marginal tooth is elongated. From the

soldier of both genera, the frontal projection is absent. However, *Labiocapritermes* differs from *Procapritermes* as follows: In the imago-worker mandible the third left marginal tooth is much more reduced; the postclypeus is swollen and longer (length/width index, 0.50; in *Procapritermes* not swollen and short, length/width index, 0.27–0.33); and the fontanelle is minute (like a pinpoint) and circular. In the soldier the labrum is greatly swollen, with its anterolateral corners not so pointed and prominent; the left mandible is blunt at the tip (generally hooked at the apex in all species of *Procapritermes* except *P. greeni* and a new species from Sarawak); and the right mandible is much shorter than the left mandible.

The imago mandible of *Labiocapritermes* is almost identical with that of *Mirocapritermes*. The third left marginal tooth is greatly reduced in both *Mirocapritermes* and *Labiocapritermes*, but much more so in *Labiocapritermes*. The soldier of *Mirocapritermes* has a distinct frontal projection, its labrum is not swollen, and its left mandible is hooked at the apex and not bent so much in the middle.

SPECIES INCLUDED

L. distortus (Silvestri), new combination = *Capritermes distortus* Silvestri, 1922

GEOGRAPHICAL DISTRIBUTION: Oriental Region: India.

GENUS **MIROCAPRITERMES** HOLMGREN, 1914

= Genus *Mirocapritermes* HOLMGREN, 1914, p. 277. KEMNER, 1934, pp. 167, 168.

= Genus *Microcapritermes* (misspelling): EMERSON, 1928, p. 408. YU AND PING, 1964, p. 13. AHMAD, 1965, pp. 96, 97.

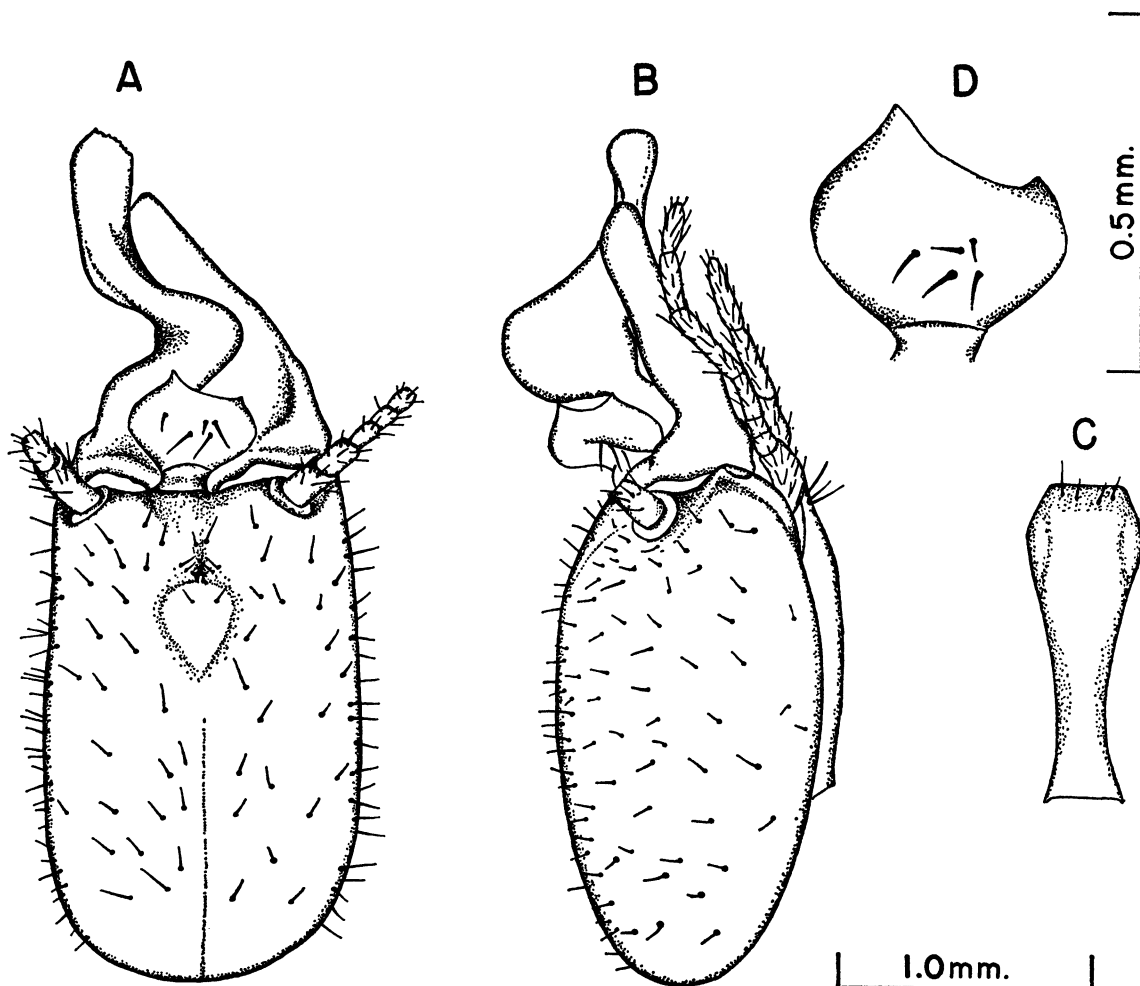


FIG. 33. Soldier of *Labiocapritermes distortus* (Silvestri); Thekaday Forest Preserve, Kerala, India. A. Head from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

= Genus *Mirocapritermes*: SNYDER, 1949, p. 189. EMERSON, 1950, pp. 12-15; 1955, p. 512. AHMAD, 1950, pp. 45, 72, 74; 1958, pp. 91, 182; 1965, pp. 8, 95. WEIDNER, 1955, p. 72. HARRIS, 1961, p. 64.

TYPE SPECIES: *Mirocapritermes connectens* (Holmgren).

The genus *Mirocapritermes* was first described by Holmgren in 1914 for the single species *Mirocapritermes connectens* Holmgren. Only recently, four additional species have been added by Krishna (1965) and Ahmad (1965).

IMAGO: Unknown.

SOLDIER (FIG. 34): Head covered with a number of hairs and bristles, with frontal

projection more hairy than rest of head. Head small; frontal gland well developed; frontal projection prominent, obtuse-angled from above, with tip blunt and rounded. Fontanelle small, circular, situated below projecting frontal process. Labrum with anterior margin shallowly or deeply concave, its anterolateral corners projected as short, spinelike processes. Mandibles asymmetrical. Left mandible moderately bent in middle, hooked at tip, with blunt tooth and prominent basal projection in inner margin. Antennae with 14 articles; fourth article shortest. Tibial spurs 3:2:2. Middle tibia with one or two outer spines.

WORKER: Mandibles as shown in figure 35.

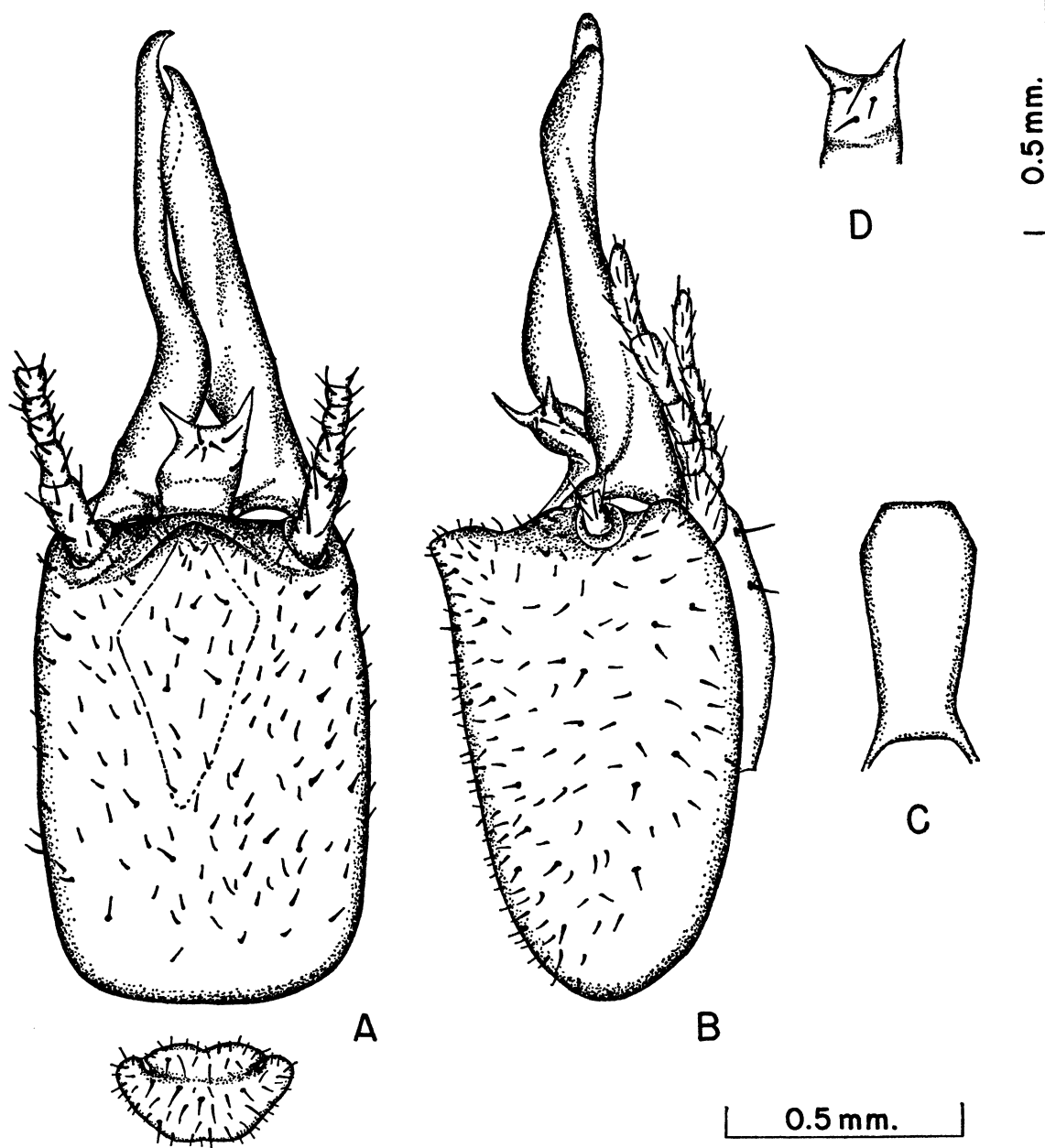


FIG. 34. Cotype soldier of *Mirocapritermes connectens* (Holmgren); Tandjang, Slamet, Sumatra. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

Left mandible with apical tooth long, cutting edge of fused first plus second marginal tooth long, and second marginal tooth greatly reduced.

RELATIONSHIPS AND COMPARISONS: Holm-

gren (1914) concluded, from the characters of the soldier caste (mandible, frontal projection), that the genus *Mirocapritermes* is closely related to the genus *Capritermes* (as treated by him) and that it occupies an inter-

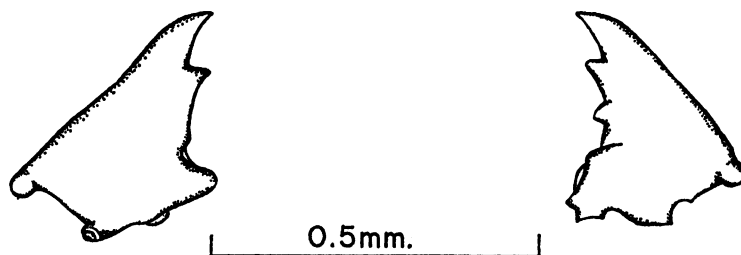


FIG. 35. Mandibles of worker of *Mirocapritermes connectens* (Holmgren); Buloh Forest Preserve, Malaya.

mediate position between *Capritermes* and *Mirotermes* (= *Termes*), forming a link between these two. He also stated that *Mirocapritermes* is not closely related to *Procapritermes*, as the soldier of *Procapritermes* does not have a frontal projection, and its mandibles are not so asymmetrical. Ahmad (1950) and Emerson (1950) also grouped *Mirocapritermes* with genera having a prominent frontal projection in the soldier caste, namely, *Paracapritermes*, *Quasitermes*, and *Cornicapritermes*.

However, the genus *Mirocapritermes* is actually more closely related to *Procapritermes* (as treated in this paper) and *Labiocapritermes* than to *Paracapritermes* or *Quasitermes*.

The imago-worker mandibles of *Mirocapritermes*, *Procapritermes*, and *Labiocapritermes* have the following similarities: the apical tooth is long and robust, and the posterior margin of the fused first plus second marginal tooth is long. *Procapritermes* and *Labiocapritermes* differ, however, from *Mirocapritermes* in the following ways: In *Procapritermes* the imago-worker mandible is more primitive, as in many species the third left marginal tooth is prominent, though there is a gradual reduction of this characteristic within the genus (in *Mirocapritermes* this character is extremely reduced). The *Procapritermes* soldier does not have a frontal projection (in *P. setiger* and a new species from Malaya there is a ridge in the frontal region), and its fontanelle is larger and usually in a depression. In the *Labiocapritermes* soldier the frontal projection is totally absent; the mandibles are not hooked at the tips; the left mandible is strongly bent in the middle; and the labrum is greatly enlarged. The imago-worker mandible of *Labiocapritermes* has the third left marginal tooth slightly

more reduced; otherwise the dentitions of *Mirocapritermes* and *Labiocapritermes* are identical.

Cornicapritermes differs from *Mirocapritermes* in the following respects: The soldier has a more prominent frontal projection, its mandibles are not hooked at the tips, and the left mandible is more strongly bent in the middle. The third left marginal tooth is absent from the imago-worker mandible of *Cornicapritermes*, and the second right mandible tooth is greatly reduced.

In the soldier of *Paracapritermes* and *Quasitermes*, the frontal projection is pointed at the tip; the anterior margin of the labrum is straight or biconvex, with its anterolateral points not so prominent as those of *Mirocapritermes*; and the left mandible does not have a tooth in front of the prominent basal toothlike projection. In the imago-worker mandible of *Quasitermes* and *Paracapritermes*, the third left marginal tooth is more prominent, the posterior margin of the fused first plus second left marginal tooth is shorter, and the second right marginal tooth is reduced.

SPECIES INCLUDED

- M. concaveus* Ahmad, 1965
- M. connectens* Holmgren, 1914
- M. latignathus* Ahmad, 1965
- M. prewensis* Ahmad, 1965
- M. valeriae* Krishna, 1965

GEOGRAPHICAL DISTRIBUTION: Oriental Region: Borneo, Burma, Thailand.

GENUS *CORNICAPRITERMES* EMERSON, 1950

= Genus *Cornicapritermes* EMERSON, 1950, pp. 12-15; 1955, pp. 495, 512. AHMAD, 1950, pp. 47, 72, 74. WEIDNER, 1955, p. 73.

TYPE SPECIES: *Cornicapritermes mucronatus* Emerson.

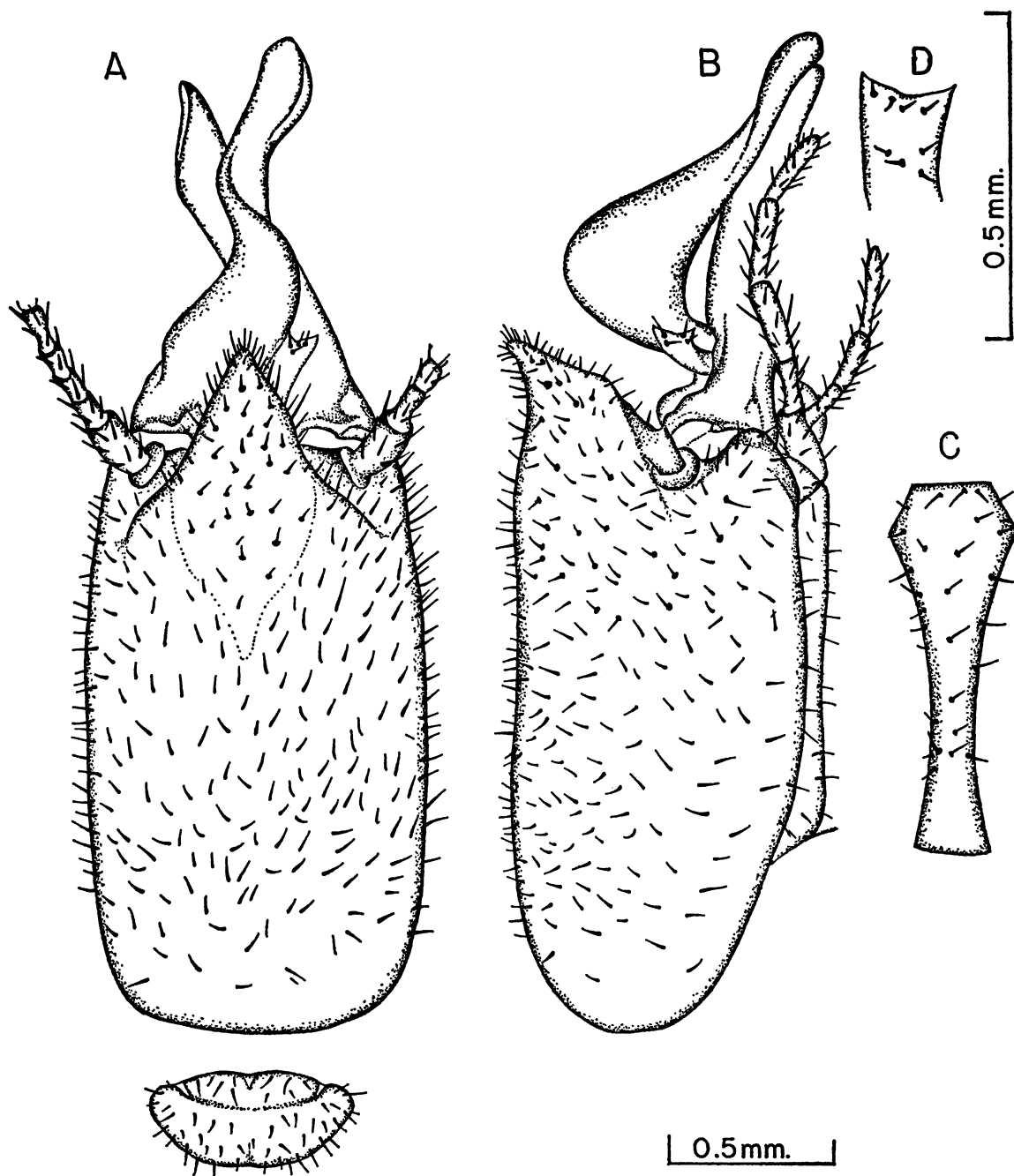


FIG. 36. Soldier of *Cornicapritermes mucronatus* Emerson, paratype; Itabu Creek, Guyana. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

The genus *Cornicapritermes* was first described by Emerson (1950) for the single species *C. mucronatus*. As a detailed description of the genus was given by Emerson, I

mention only the diagnostic characteristics.
IMAGO: Unknown.

SOLDIER (FIG. 36): Head covered with numerous bristles, more dense on frontal pro-

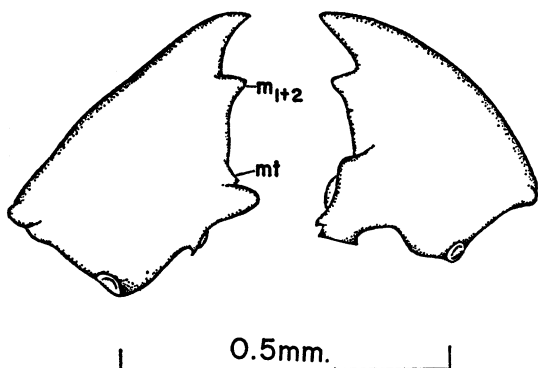


FIG. 37. Mandibles of worker of *Cornicapritermes mucronatus* Emerson, type colony; Guyana.

Abbreviations: m_{1+2} , fused first plus second left marginal tooth; mt, molar tooth.

jection. Head thick, elongate, with sides faintly convex; frontal projection prominent, extending well beyond base of mandibles, pointed in front, and in profile upturned at tip; frontal gland opening below projection, on small bump. Labrum slightly asymmetrical, its anterior margin broadly V-shaped. Mandibles asymmetrical. Left mandible strongly bent and twisted in middle, with blunt tip and prominent projection at inner region of base. Left mandible straight, its anterior inner margin with concavity. Antennae with 14 articles; second article subequal to third, fourth slightly shorter than third. Tibial spurs 3:2:2. Middle tibia with two spinelike bristles.

WORKER: Mandibles as shown in figure 37. Left mandible with apical tooth long, posterior margin of fused first plus second marginal tooth long, third marginal tooth absent, and inner molar tooth partially visible and partially covered by molar plate.¹ Right mandible with second marginal tooth extremely rudimentary.

RELATIONSHIPS AND COMPARISONS: Emerson (1950) and Ahmad (1950) maintained that *Cornicapritermes* is most closely related to the genera with a frontal projection in the soldier, namely, *Paracapritermes*, *Quasitermes*, and *Mirocapritermes*. However, *Corni-*

¹ Ahmad (1950) has mistakenly referred to this inner molar tooth as the third left marginal tooth. In all genera of this group except *Dihoplotermes* the inner molar tooth is not visible when viewed from the top, as it is covered by the molar plate.

capritermes is actually more closely related to *Dihoplotermes* (a genus described by Araujo in 1961), as is indicated by the imago-worker mandible, than to the above-mentioned three genera. The imago-worker mandibles of *Cornicapritermes* and *Dihoplotermes* are similar in many respects: the second marginal tooth in the right mandible is rudimentary or almost absent in *Cornicapritermes* and completely absent from *Dihoplotermes*; in the left mandible of both genera, the apical tooth is long, the posterior margin of the fused first plus second marginal tooth is long, the third marginal tooth is absent, and the inner molar tooth is partially visible. The soldiers of *Cornicapritermes* and *Dihoplotermes* also have similar characteristics. In both, the frontal projection is conical and prominent, and the postmentum narrows considerably from the wide anterior region. *Dihoplotermes*, however, is more specialized than *Cornicapritermes*, as its soldiers are dimorphic. Further, in the major soldier there is a small, distinct spine near the side base of the mandibles; the frontal projection is longer, with its upper margin markedly concave; the posterior half of the left mandible is straight, and the anterior third is bent inward, with a beak at the apex. In *Cornicapritermes* the spine is absent, the posterior half of the left mandible is strongly bent and twisted, with its tip blunt and without a beak; and the anterior margin of the labrum is broadly V-shaped.

SPECIES INCLUDED

C. mucronatus Emerson, 1950

GEOGRAPHICAL DISTRIBUTION: Neotropical Region: Guyana.

GENUS *DIHOPLOTERMES* ARAUJO, 1961

= Genus *Dihoplotermes* ARAUJO, 1961, p. 108.

TYPE SPECIES: *Dihoplotermes inusitatus* Araujo.

Araujo (1961) described this specialized monotypic genus for *D. inusitatus*. This is the only genus in this group with asymmetrical soldier mandibles that has dimorphic soldiers.

IMAGO (FIG. 38): Head and pronotum densely covered with hairs and bristles. Head depressed around fontanelle. Fontanelle small, oval, without plate. Ocellus not touching eye. Antennae with 15 articles; third article smallest. Imago-worker mandible as

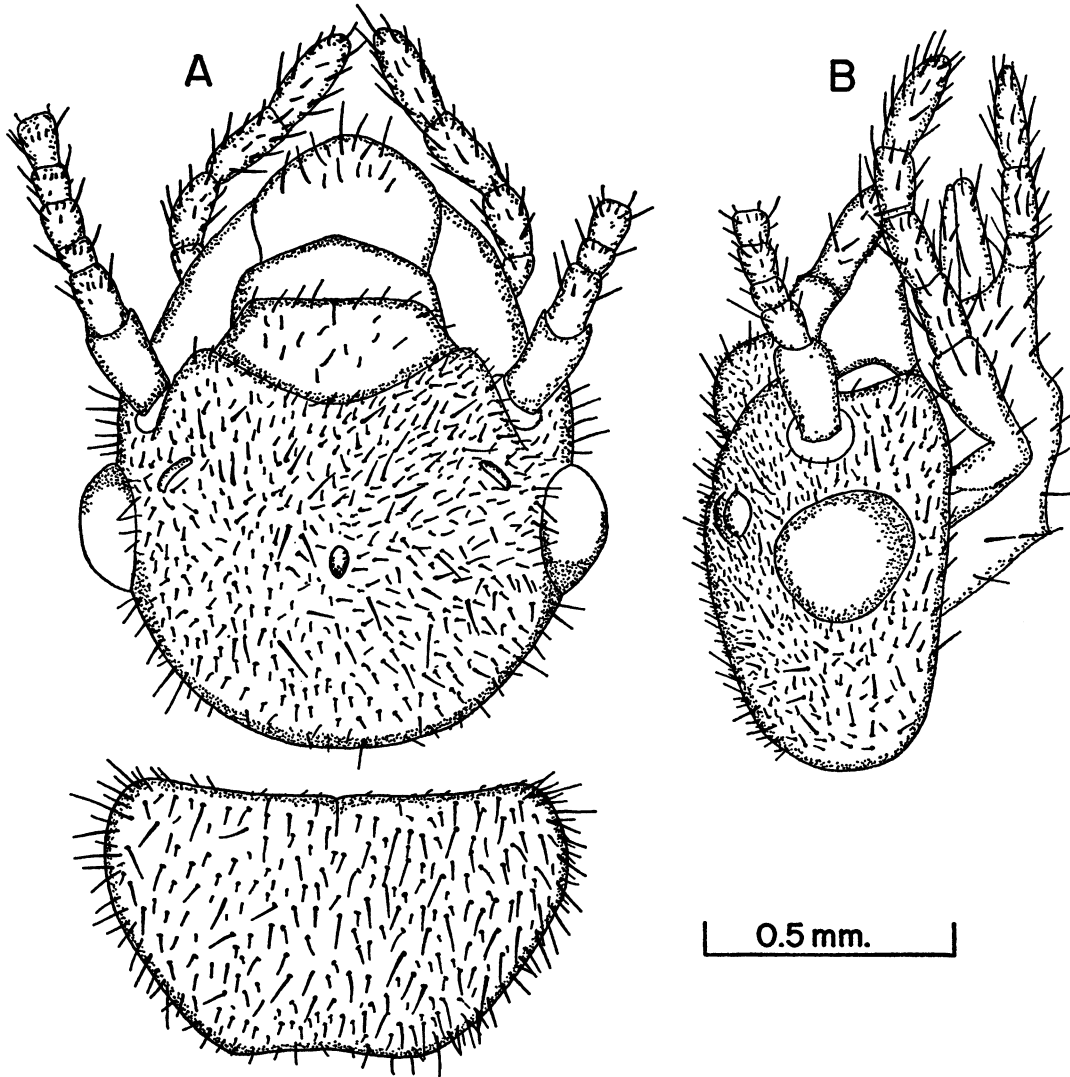


FIG. 38. Imago of *Dihoplotermes inusitatus* Araujo, type colony; Morumbi, São Paulo, Brazil. A. Head and pronotum from above. B. Head from side.

shown in figure 39. Left mandible with apical tooth long, posterior margin of fused first plus second marginal tooth long, third marginal tooth absent, and inner molar tooth partially visible and partially covered by molar plate.¹ Second marginal tooth completely absent from right mandible.

¹ Araujo (1961) has mistakenly referred to this inner molar tooth as the third marginal tooth. In all genera of this group except *Cornicapritermes* the inner molar tooth is not visible when viewed from the top, as it is covered by the molar plate.

MAJOR SOLDIER (FIG. 40): Head moderately covered with hairs, denser on frontal projection. Head long and narrow, with sides parallel; small distinct spine projecting in front near side base of mandibles; frontal projection prominent, pointed forward, extending approximately to half of length of mandibles and covering labrum; tip turned upward in profile; and frontal gland opening below, on a small bump. Labrum with anterior margin bilobed, indented in middle. Mandibles asymmetrical. Left mandible with

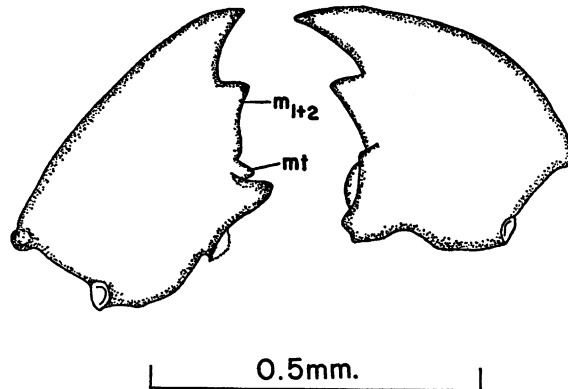


FIG. 39. Mandibles of worker of *Dihoplotermes inusitatus* Araujo, type colony; Morumbi, São Paulo, Brazil.

Abbreviations: m_{1+2} , fused first plus second left marginal tooth; mt, molar tooth.

posterior half straight or faintly bent, anterior third distinctly bent inward, with beak at apex, and inner margin excavated. Right mandible straight. Antennae with 14 articles; third article subequal to fourth. Tibial spurs 3:2:2. Middle tibia with one extra spine.

MINOR SOLDIER (FIG. 41): Head shorter than major soldier, with sides almost parallel, slightly rounded; small distinct spine projecting in front near side base of mandibles; frontal projection prominent, its tip bent upward. Labrum bisinuate, with anterolateral margins faintly angular. Mandibles less asymmetrical than those of major soldier. Left mandible with anterior expanded region bent inward and outer margin sinuate. Right mandible bladeliike, with anterior inner margin grooved. Antennae with 14 articles; second subequal to third, fourth slightly shorter than second or third. Tibial spurs 3:2:2. Middle tibia with one spinelike bristle.

RELATIONSHIPS AND COMPARISONS: See discussion under *Cornicapritermes*.

SPECIES INCLUDED

D. inusitatus Araujo, 1961

GEOGRAPHICAL DISTRIBUTION: Neotropical Region: Brazil.

GENUS *NEOCAPRITERMES* HOLMGREN, 1912

<Genus *Termes*: subgenus *Eutermes*: HAGEN, 1858a, pp. 107, 108, 186. DESNEUX, 1904, pp. 26, 28, 39, 40.

<Genus *Termes*: subgenus *Entermes* (misspelling): HAGEN, 1858b, pp. 16, 26.

<Genus *Termes*: subgenus *Capritermes*: WASMANN, 1897, pp. 150, 151.

<Genus *Capritermes*: SILVESTRI, 1901, pp. 4-5; 1903, p. 63. HOLMGREN, 1906, p. 37; 1912, pp. 114, 115. EMERSON, 1928, pp. 412, 542.

<Gruppe *Capritermes*: SJÖSTEDT, 1926, p. 281.

=Subgenus *Neocapritermes* (of genus *Capritermes*) HOLMGREN, 1912, pp. 97, 115, 116. SNYDER, 1926b, p. 64. EMERSON, 1928, p. 409.

<Subgenus *Neocapritermes* (of genus *Capritermes*): EMERSON, 1925, pp. 310, 445.

=Genus *Neocapritermes*: SJÖSTEDT, 1926, pp. 281, 286-287. HARE, 1937, pp. 462, 463, 478. SNYDER, 1949, p. 200. GRASSÉ, 1949, p. 539. AHMAD, 1950, pp. 47, 65, 68, 69, 77. EMERSON, 1950, pp. 14, 15; 1952, p. 508; 1955, pp. 469, 495, 512; 1959, pp. 7, 15. WEIDNER, 1955, p. 73. HARRIS, 1961, pp. 55, 64. KRISHNA AND ARAUJO, 1968, pp. 87-89.

TYPE SPECIES: *Neocapritermes opacus* (Hagen).

Krishna and Araujo (1968) have revised this genus and have given a full description of it. I am therefore citing only a few diagnostic features here.

IMAGO (FIG. 42): Fontanelle plate sclerotized, without visible opening. Antennae with 16 or 17 articles. Mandibles as shown in figure 43. Left mandible with apical tooth small, posterior margin of fused first plus second marginal tooth long, and third marginal tooth well developed. Right mandible with posterior margin of second marginal

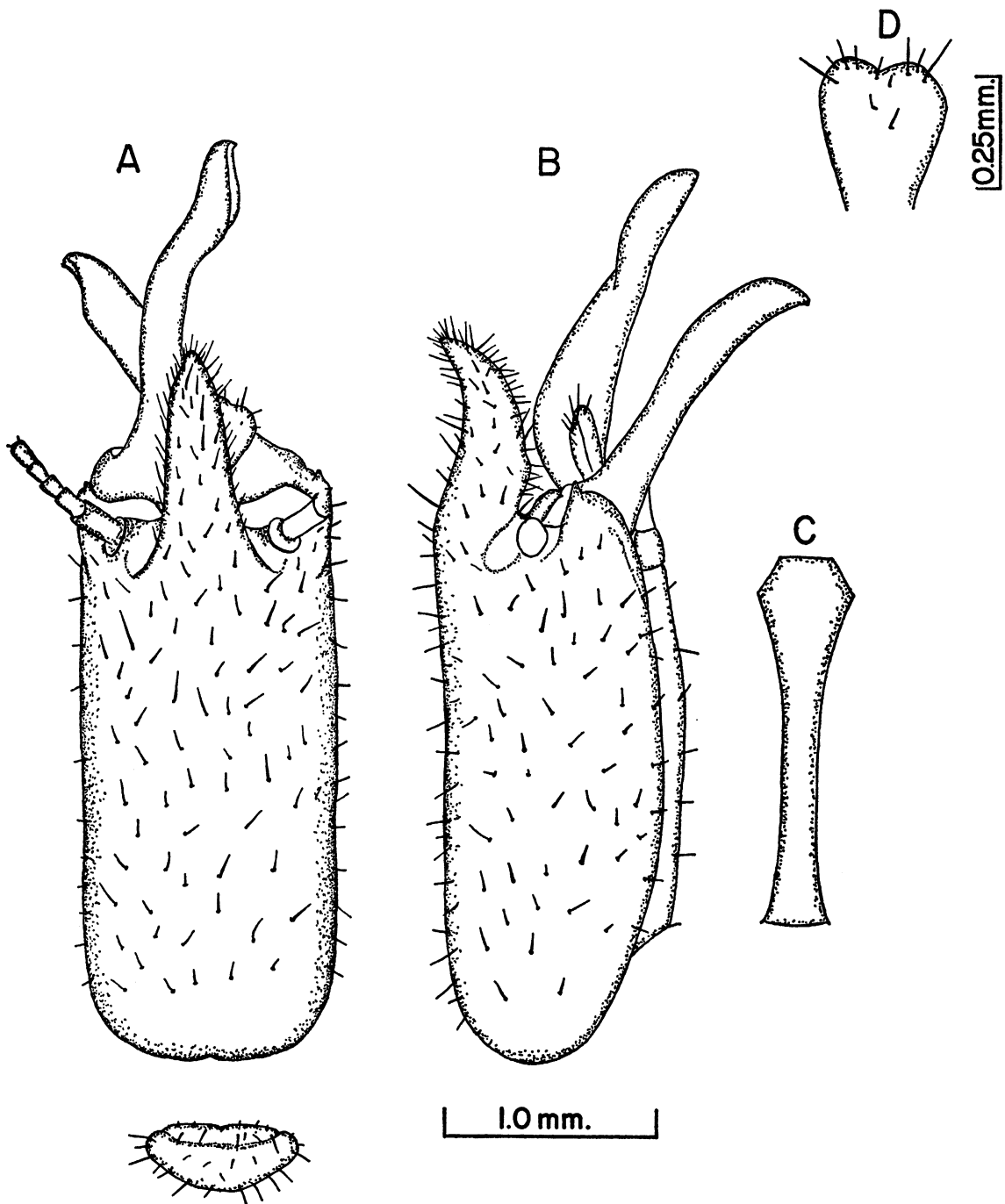


FIG. 40. Major soldier of *Dihoplotermes inusitatus* Araujo, paratype from type colony; Morumbi, São Paulo, Brazil. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

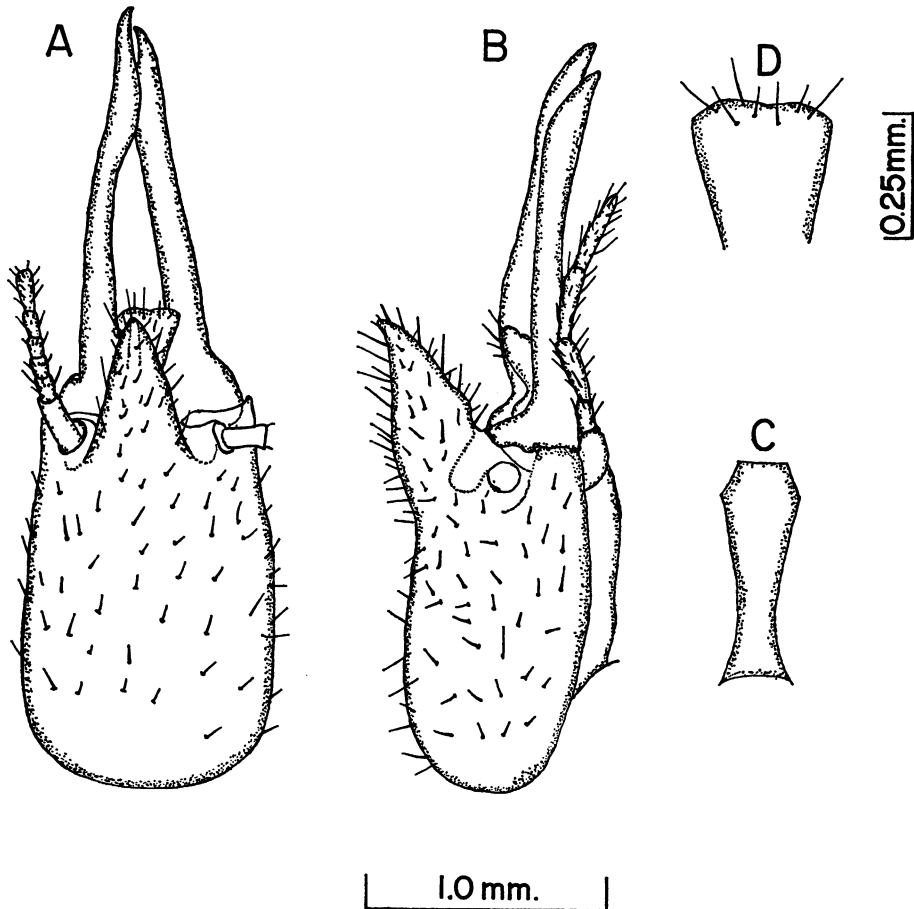


FIG. 41. Minor soldier of *Dihoplotermes inusitatus* Araujo, paratype from type colony; Morumbi, São Paulo, Brazil. A. Head from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

tooth straight. Tibial spurs 3:2:2, except in *Neocapritermes bodkini*, in which 2:2:2.

SOLDIER (FIG. 44): Head with posterior margin evenly rounded (in *Neocapritermes bodkini* slightly indented in middle); frontal gland absent; fontanelle small, circular; postclypeus distorted and in some cases drawn into a spinelike protuberance projecting upward. Labrum tongue-shaped, with tip rounded or three-lobed. Mandibles asymmetrical. Antennae with 15 or 16 articles.

RELATIONSHIPS AND COMPARISONS: Holmgren (1912) offered the tentative opinion that *Capritermes* and *Neocapritermes* are closely related and derived from a common stem, basing his suggestion on the similarity between the soldiers, although he recognized

that the imagoes of these two genera were very different. Ahmad (1950) stated that *Neocapritermes* and *Planicapritermes* had the most primitive imago-worker mandibles in the Termitinae, the apical tooth being small and the posterior margin of the second right marginal tooth straight, and placed these genera of a separate branch, before the *Hoplognathotermes-Allognathotermes* branch, at the bottom of the Termitinae phylogenetic tree, rather than at the top with the *Capritermes* branch. He thought that the strongly asymmetrical snapping soldier mandibles had evolved convergently twice in the Termitinae—once in the *Neocapritermes-Planicapritermes* branch and again independently in the *Capritermes* branch.

The present author is inclined to agree with Holmgren (1912) and Emerson (1959, p. 15) and to place *Neocapritermes* and *Planicapritermes* on the same ancestral branch as the other genera with asymmetrical snapping soldier mandibles (*Capritermes* and others). It is true that the imago of *Neocapritermes*

has unique characteristics not found in genera of the *Capritermes* complex: the 16- or 17-segmented antennae (14- or 15-segmented in all other genera of the *Capritermes* complex), and the sharp angle between the right first and second marginal tooth (curved margin in all other genera of the *Capritermes* complex).

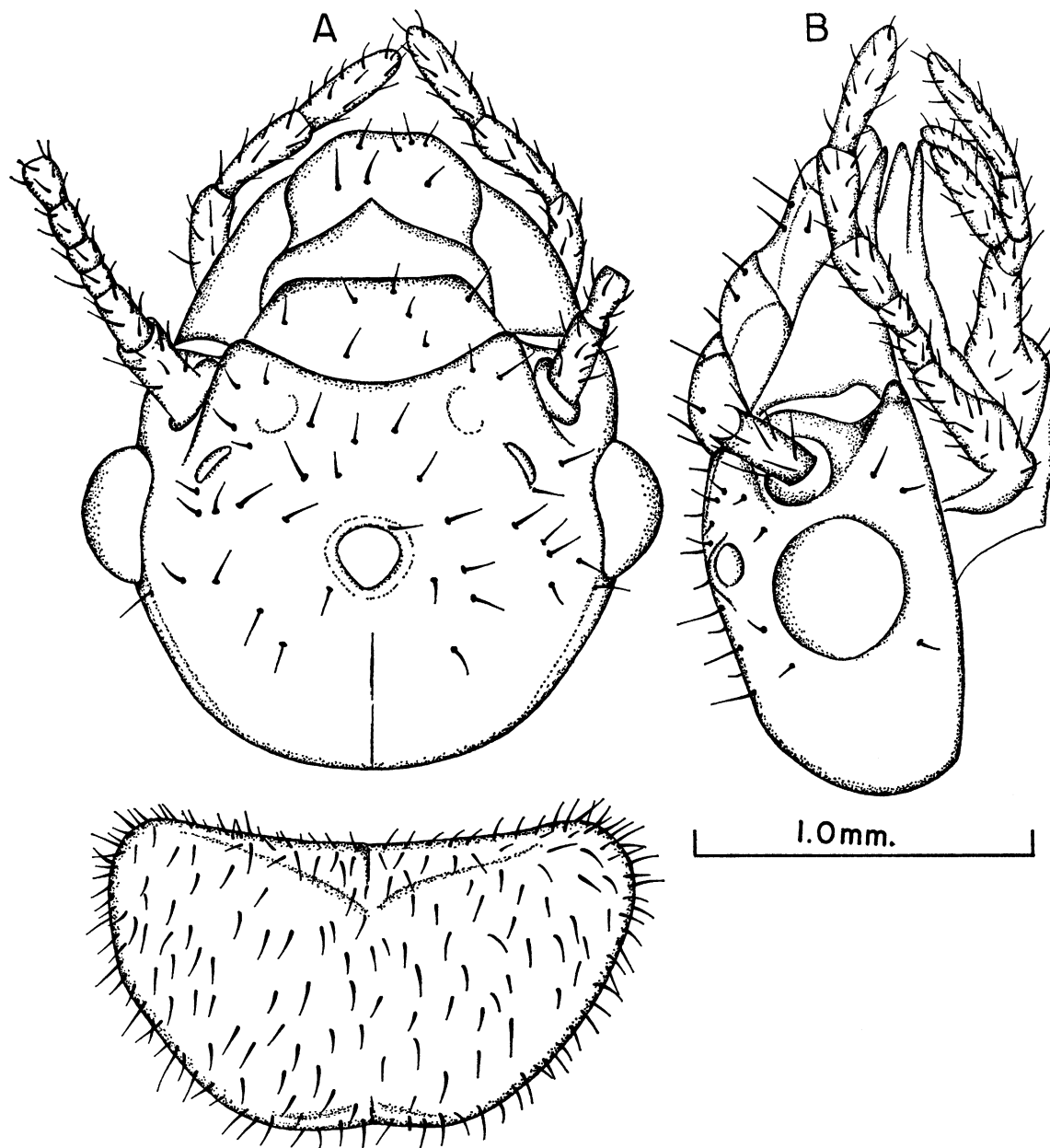


FIG. 42. Imago of *Neocapritermes opacus* (Hagen), plesiotype; Tukurupucu, Paraguay. A. Head and pronotum from above. B. Head from side.

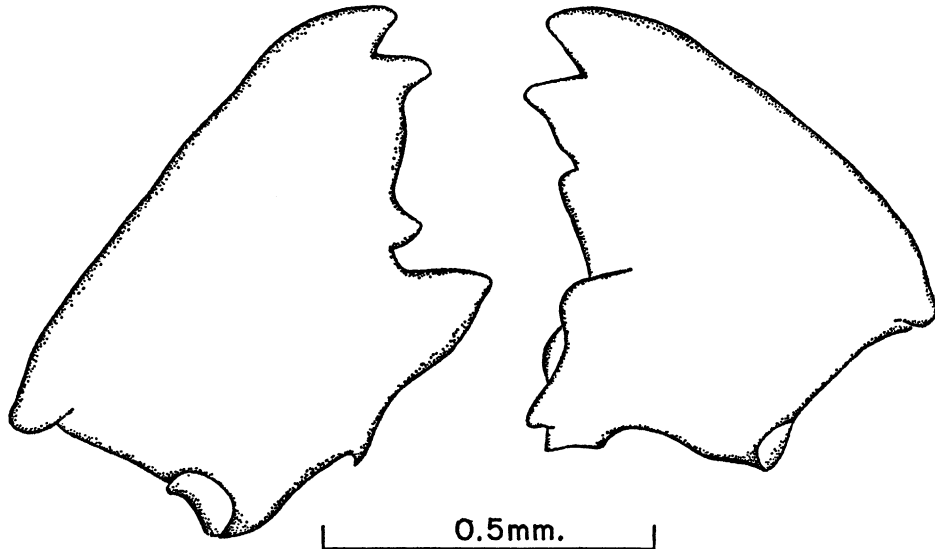


FIG. 43. Mandibles of worker of *Neocapritermes opacus* (Hagen); São Paulo, Brazil.

The soldier, however, suggests that *Neocapritermes* and the other genera of the *Capritermes* complex have evolved from a common ancestor. It is hard to conceive that such a complex adaptation as the asymmetrical snapping mandibles could have evolved more than once, particularly as no phylogenetic gradations leading up to this character in *Neocapritermes* are known, whereas almost all gradations leading up to it in genera of the *Capritermes* complex are known. In view of this fact and of the fact that the small apical tooth is also found in some genera of the *Capritermes* complex, such as *Pericapritermes*, we must conclude that this "primitive" dentition in the imago mandible is actually a derived character.

Although it is not certain exactly how *Neocapritermes*, along with *Planicapritermes*, fits into the *Capritermes* complex, it seems that the *Neocapritermes*-*Planicapritermes* branch diverged early from the main stem that later gave rise to the other genera with asymmetrical snapping mandibles in the soldier.

Neocapritermes is the genus most closely related to *Planicapritermes*. The imago-worker mandibles of the two genera are identical. (The imago of *Planicapritermes* is unknown, so comparison of the imagoes is impossible.) The soldier of *Planicapritermes* resembles

most closely that of *Neocapritermes*. In *Planicapritermes*, however, the soldier head is much broader and very flat with its posterior margin having one median and two lateral lobes (in *Neocapritermes* it is either evenly rounded or faintly indented in the middle); the antennae are 14-segmented (15- or 16-segmented in *Neocapritermes*); and the pronotum is much narrower in comparison with the head.

SPECIES INCLUDED

N. angusticeps (Emerson), 1925
N. araguaia Krishna and Araujo, 1968
N. bodkini (Silvestri), 1923b
N. brasiliensis (Snyder), 1926b
N. centralis (Snyder), 1932
N. guyana Krishna and Araujo, 1968
N. longinotus (Snyder), 1926a
N. opacus (Hagen), 1858a
N. parvus (Silvestri), 1901
N. talpa (Holmgren), 1906
N. talpoides Krishna and Araujo, 1968
N. taracua Krishna and Araujo, 1968
N. utiariti Krishna and Araujo, 1968
N. villosus (Holmgren), 1906

GEOGRAPHICAL DISTRIBUTION: Neotropical Region: Costa Rica, Panama, South America.

GENUS **PLANICAPRITERMES** EMERSON, 1949

<Genus *Capritermes*: EMERSON, 1925, p. 445.

<Subgenus *Neocapritermes*: EMERSON, 1925, p. 445. SNYDER, 1926b, p. 64.

= Genus *Planicapritermes* EMERSON, 1949, pp. 202, 375; 1952, p. 508; 1955, p. 512. WEIDNER, 1955, p. 73. HARRIS, 1961, p. 64.

TYPE SPECIES: *Planicapritermes planiceps* (Emerson).

IMAGO: Unknown.

SOLDIER (FIG. 45): Head and pronotum moderately covered with bristles. Head very flat, with sides converging toward front;

posterior margin three-lobed, middle lobe not so prominent; fontanelle small and circular; and frontal gland absent. Labrum asymmetrical, curved or wrapped around base of mandibles, and tongue-shaped, its sides converging anteriorly into blunt point. Mandibles asymmetrical. Left mandible strongly bent in middle, with base thick, its outer region with ridge and concavity; anterior

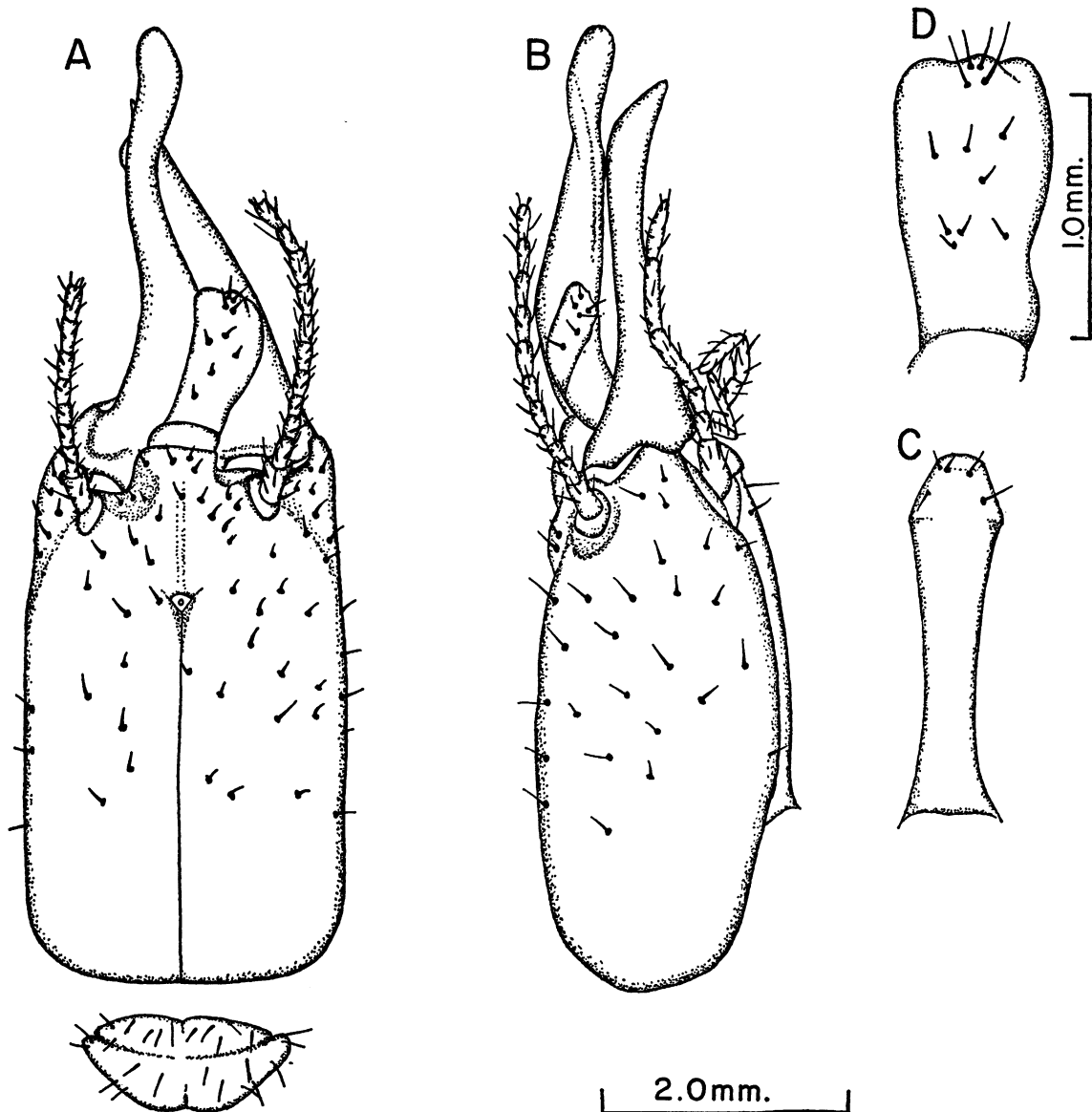


FIG. 44. Soldier of *Neocapritermes opacus* (Hagen), plesiotype; Tucurupucu, Paraguay. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

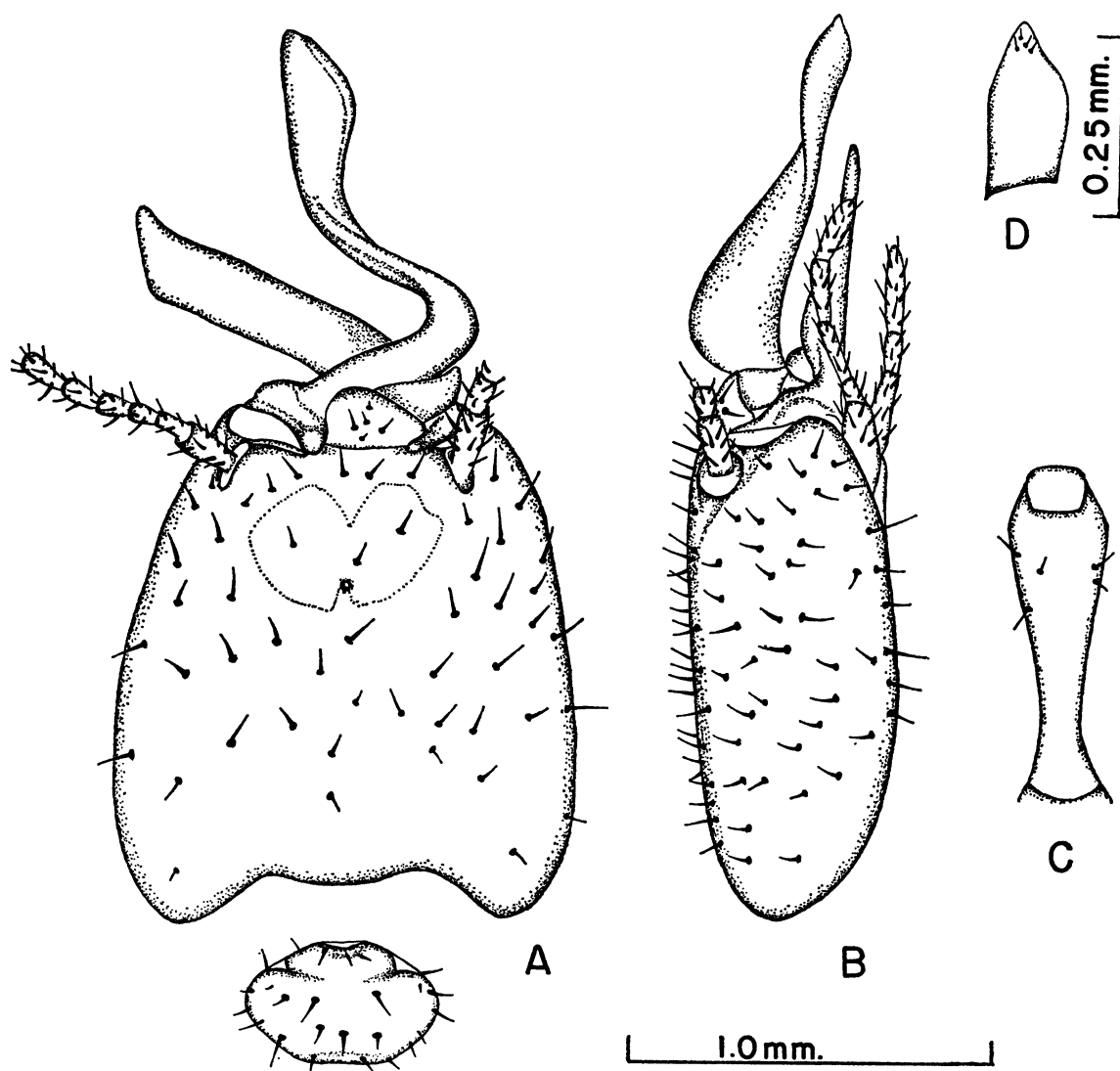


FIG. 45. Soldier of *Planicapritermes planiceps* (Emerson), holotype; Kartabo, Guyana. A. Head and pronotum from above. B. Head from side. C. Postmentum from below. D. Labrum from above.

region spatulate; apex blunt; and inner basal region with toothlike projection, fitting into corresponding excavation in right mandible. Right mandible flat and straight. Antennae with 14 articles. Pronotum much narrower than head, with anterior lobe very slightly turned up. Tibial spurs 2:2:2. Middle tibia without spines.

WORKER: Mandibles as shown in figure 46. Left mandible with apical tooth small, posterior margin of fused first plus second mar-

ginal tooth long, third marginal tooth well developed. Right mandible with posterior margin of second marginal tooth straight and acute angle between first and second marginal teeth.

RELATIONSHIPS AND COMPARISONS: The specialized genus *Planicapritermes* is most closely related to *Neocapritermes* and is probably derived from it. The imago-worker mandibles of these two genera are identical. The soldier of *Neocapritermes*, however,

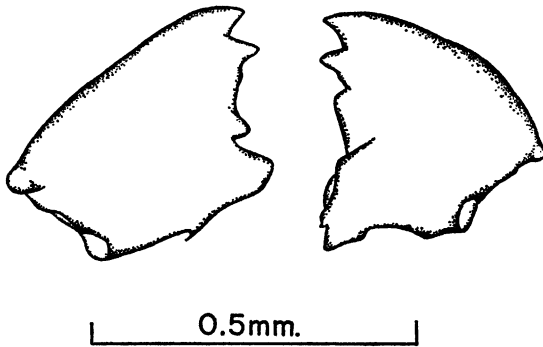


FIG. 46. Mandibles of worker of *Planicapritermes planiceps* (Emerson), type colony; Kartabo, Guyana.

differs from that of *Planicapritermes* in the following respects: the head is thicker, with

its posterior margin evenly rounded or with a faint indentation in the middle (in *Planicapritermes* the head is very flat, and the posterior margin is distinctly three-lobed); the antennae are 15- or 16-segmented (14-segmented in *Planicapritermes*); the pronotum is distinctly saddle-shaped, with its anterior lobe distinctly turned upward (in *Planicapritermes* the pronotum is almost flat); and the tibial spurs are 3:2:2 in number, except for *N. bodkini*, which has 2:2:2 (in *Planicapritermes* 2:2:2).

SPECIES INCLUDED

P. planiceps (Emerson), 1925

GEOGRAPHICAL DISTRIBUTION: Neotropical Region: Guyana.

SUMMARY

THE TERMITE GENERA with asymmetrical snapping mandibles in the soldier (*Paracapritermes* Hill, *Protocapritermes* Holmgren, *Quasitermes* Emerson, *Capritermes* Wasmann, *Homallotermes* John, *Dicuspitermes* Krishna, *Pericapritermes* Silvestri, *Procapritermes* Holmgren, *Labiocapritermes*, new genus, *Mirocapritermes* Holmgren, *Cornicapritermes* Emerson, *Dihoplotermes* Araujo, *Neocapritermes* Holmgren, and *Planicapritermes* Emerson) are described and illustrated, and their phylogenetic relationships are discussed. A key to these genera is given.

The genus *Capritermes* is treated in an entirely new sense. In it is now included only the single species *C. capricornis* (Wasmann) from Madagascar. The other species previ-

ously placed in *Capritermes* are now included in other genera.

The genera *Pseudocapritermes* Kemner and *Microcapritermes* Mathur and Thapa are now considered synonyms of *Procapritermes* and *Homallotermes*, respectively.

A new genus, *Labiocapritermes*, from India is described and illustrated, with its type species designated as *L. distortus* Silvestri, a species previously placed in *Capritermes*.

The genus *Pericapritermes*, previously reported from the Ethiopian Region only, now includes species from the Oriental and Papuan regions that were previously placed in *Capritermes*.

Twelve species names are included as new synonyms.

BIBLIOGRAPHY

- AHMAD, M.
 1950. The phylogeny of termite genera based on imago-worker mandibles. *Bull. Amer. Mus. Nat. Hist.*, vol. 95, pp. 37-86.
 1958. Key to the Indomalayan termites. *Biologia*, vol. 4, nos. 1, 2, pp. 33-198 + xii.
 1965. Termites (Isoptera) of Thailand. *Bull. Amer. Mus. Nat. Hist.*, vol. 131, art. 1, pp. 1-114.
- ARAUJO, R. L.
 1961. New genus and species of Brazilian termite (Isoptera, Termitidae, Termitinae). *Rev. Brasileira Biol.*, vol. 21, no. 1, pp. 105-111.
- BODOT, P.
 1964. Etudes écologiques et biologiques des termites dans les savanes de Basse Côte d'Ivoire. In Bouillon, A. (ed.), *Etudes sur les termites Africains*. UN Colloque International Université Louvanium, May 1-16, 1964, Léopoldville. Paris, Masson et Cie, pp. 251-262.
- BOUILLON, A., AND G. MATHOT
 1965. Quel est ce termite Africain? *Zooleo*, Université Léopoldville, no. 1, pp. 1-115.
 1966. Quel est ce termite Africain? *Ibid.*, no. 1 (suppl. no. 1), pp. 1-23.
- BUGNION, E.
 1914. La biologie des termites de Ceylan. *Bull. Mus. Natl. d'Hist. Nat.*, Paris, no. 4, pp. 170-204.
- CACHAN, P.
 1949. Les termites de Madagascar. *Mém. Inst. Sci. Madagascar*, ser. A, vol. 3, no. 2, pp. 177-275.
1951. Les termites de Madagascar. Premier supplement. *Ibid.*, ser. A, vol. 5, no. 1, pp. 1-8.
- CALABY, J. H., AND F. J. GAY
 1959. Aspects of the distribution and ecology of Australian termites. In Keast, A., R. L. Crocker, and C. S. Christian, *Biogeography and ecology in Australia*. Monogr. Biol., The Hague, vol. 8, pp. 211-223.
- COATON, W. G. H.
 1962. Nesting habits and mounds of the termites of Northern Rhodesia. *African Wild life*, vol. 16, pp. 61-70.
- DESNEUX, J.
 1904. Isoptera, family Termitidae. In Wytsman, P., *Genera insectorum*. Brussels, fasc. 25, pp. 1-52.
- EMERSON, A. E.
 1925. The termite of Kartabo, Bartica District, British Guiana. *Zoologica*, vol. 6, pp. 291-459.
 1928. Termites of the Belgian Congo and the Cameroon. *Bull. Amer. Mus. Nat. Hist.*, vol. 57, pp. 401-574.
 1929. Communication among termites. *Trans. Fourth Internatl. Congr. Ent.*, vol. 2, pp. 722-727.
 1949. In Snyder, T. E., *Catalog of the termites (Isoptera) of the world*. Smithsonian Misc. Coll., vol. 112, pp. 1-490.
 1950. Five new genera of termites from South

- America and Madagascar (Isoptera, Rhinotermitidae, Termitidae). Amer. Mus. Novitates, no. 1444, pp. 1-15.
1952. The Neotropical genera *Procornitermes* and *Cornitermes* (Isoptera, Termitidae). Bull. Amer. Mus. Nat. Hist., vol. 99, pp. 475-540.
1955. Geographical origins and dispersions of termite genera. Fieldiana: Zool., vol. 37, pp. 465-521.
- ESCHERICH, K.
1911. Termitenleben auf Ceylon. Jena, pp. 1-179.
- FROGGATT, W. W.
1897. Australian Termitidae. Part 3. Proc. Linnean Soc. New South Wales, vol. 22, pt. 4, pp. 721-758.
- GARDNER, J.
1944. New Termitidae from India and Burma (Isoptera). Indian Jour. Ent., vol. 6, pp. 103-110.
- GAY, F. J.
1956. New species of termites from Australia. Proc. Linnean Soc. New South Wales, vol. 80, pt. 3, pp. 207-213.
- GRASSÉ, P. P.
1949. Traité de zoologie. Paris, Insectes, vol. 9, pp. 1-1117.
- GREEN, E. E.
1913. Catalogue of Isoptera (termites) recorded from Ceylon. Spolia Zeylanica, vol. 9, pp. 7-15.
- HAGEN, H. A.
- 1858a. Monographie der Termiten. Part 2. Linnaea Ent., vol. 12, pp. 1-342.
- 1858b. Catalogue of the specimens of neuropterous insects in the collection of the British Museum. London, pt. 1, Termitina, pp. 1-34.
- HARE, L.
1937. Termite phylogeny as evidenced by soldier mandible development. Ann. Ent. Soc. Amer., vol. 37, pp. 459-486.
- HARRIS, W. V.
1951. Further records of East African termites. Proc. Roy. Ent. Soc. London, ser. B, vol. 20, pts. 1-2, pp. 25-28.
1954. Further records of East African termites. *Ibid.*, vol. 23, pts. 7-8, pp. 127-137.
1956. Results from the Danish Expedition to the French Cameroons, 1949-50. Bull. Inst. Française Afrique Noire, ser. A, vol. 18, no. 3, pp. 926-937.
1957. An introduction to Malayan termites. Malayan Nat. Jour., vol. 12, no. 1, pp. 20-32.
1961. Termites, their recognition and control. London, Longmans, Green & Co., xii+187 pp.
1963. Isoptera. In Exploration du Parc National de la Garamba Mission H. de Saeger. Brussels, Institut des Parcs Nationaux du Congo Belge, fasc. 4, vol. 42, pp. 1-43.
- HAVILAND, G. D.
1898. Observations on termites: with descriptions of new species. Jour. Linnean Soc. London, vol. 26, pp. 358-442.
- HILL, G. F.
1927. Termites from the Australian region. Part I. Mem. Nat. Mus., Melbourne, no. 7, pp. 5-120.
1942. Termites (Isoptera) from the Australian region. Melbourne, Australian Council for Scientific and Industrial Research, pp. 1-479.
- HOLMGREN, N.
1906. Studien über süd amerikanische Termiten. Zool. Jahrb., Abt. Syst., vol. 23, pp. 521-676.
1911. Ceylon—Termiten. In Escherich, K., Termitenleben auf Ceylon. Jena, pp. 185-212.
1912. Termitenstudien. 3. Systematik der Termiten. Die Familie Metatermitidae. K. Svenska Vetensk.-Akad. Handl., vol. 48, no. 4, pp. 1-166.
1913. Termitenstudien. 4. Versuch einer systematischen Monographie der Termiten der orientalischen Region. *Ibid.*, vol. 50, no. 2, pp. 1-276.
1914. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien, ausgeführt im Auftrage der Kgl. Preuss. Akad. Wissenschaft. Berlin von H. V. Buttel-Reepen. III. Termiten aus Sumatra, Java, Malacca und Ceylon. Gesammelt von Herrn Prof. Dr. v. Buttel-Reepen in der Jahren 1911-1912. Zool. Jahrb., Abt. Syst., vol. 36, pp. 229-290.
- HOLMGREN, K., AND N. HOLMGREN
1917. Report on a collection of termites from India. Mem. Dept. Agr. India, vol. 5, no. 3, pp. 138-171.
- JOHN, O.
1925. Termiten von Ceylon, der Malayischen Halbinsel, Sumatra, Java und der Aru Inseln. Treubia, vol. 6, nos. 3-4, pp. 360-419.
- KEMNER, N. A.
1925. Zwei neue chinesische Termiten aus der Sammelausbeute der Kolthoffschen Expedition nach China 1921-1922. Arkiv Zool., vol. 17A, no. 28, pp. 1-6.

1926. Some termites from Ceylon. Bull. Ent. Res., vol. 16, pt. 4, pp. 379-392.
1930. Fauna Sumatrensis (Bijdrage no. 66). Termitidae. Tijdschr. Ent., vol. 73, nos. 3-4, pp. 298-324.
1934. Systematische und biologische Studien über die Termiten Javas und Celebes. K. Svenska Vetensk.-Akad. Handl., ser. 3, vol. 13, no. 4, pp. 1-241.
- KRISHNA, K.
1965. Termites (Isoptera) of Burma. Amer. Mus. Novitates, no. 2210, pp. 1-34.
- KRISHNA, K., AND R. L. ARAUJO
1968. A revision of the Neotropical termite genus *Neocapritermes* (Isoptera, Termitidae, Termitinae). Bull. Amer. Mus. Nat. Hist., vol. 138, pp. 83-138.
- LIGHT, S. F.
1924. The termites (white ants) of China, with descriptions of six new species. China Jour. Sci. and Arts, vol. 2, nos. 1-4, pp. 50-60, 140-142, 242-254, 354-358.
1930. Notes on Philippine termites. IV. Philippine Jour. Sci., vol. 42, no. 1, pp. 13-58.
1931. Present status of our knowledge of the termites of China. Lingnan Sci. Jour. (1929), vol. 7, pp. 581-600.
- MATHUR, R. N., AND P. K. SEN-SARMA
1961. *Capritermes orientalis*, a new species from Burma (Isoptera: Termitidae: Termitinae). Bull. Ent., Madras, no. 2, pp. 1-4.
- MATHUR, R. N., AND R. S. THAPA
1961. *Pseudocapritermes fontanellus* sp. nov. from South India. Jour. Timber Dryers Preservers Assoc., Dehradun, India, vol. 7, no. 3, pp. 1-4.
1962. *Microcapritermes* gen. n. from India (Isoptera: Termitidae: Termitinae). Indian Forester, vol. 88, no. 4, pp. 370-375.
1965. Some termites from Assam (India) with descriptions of three new species. Bull. Ent. Loyola College, Madras, no. 6, pp. 1-14.
- NOIROT, C.
1955. Termites du centre et du sud-ouest de l'Angola récoltés par A. Barros Machado. Publ. Cult. Co. Diam. Angola, Lisbon, no. 27, pp. 139-150.
- NOIROT, C., AND J. KAVOOR
1958. Anatomie comparée du tube digestif des termites I. Sous-famille des "Termitinae." Insectes Sociaux, vol. 5, no. 4, pp. 440-471.
- OSHIMA, M.
1920. Philippine termites collected by R. C. McGregor with descriptions of one new genus and nine new species. Philippine Jour. Sci., vol. 17, no. 15, pp. 489-512.
- OSHIMA, M., AND M. MAKI
1919. On a new species of termite from Taiwan. Dobutsugaku Zasshi, vol. 31, pp. 313-316.
- ROONWAL, M. L., AND O. B. CHHOTANI
1962. Termite fauna of Assam region, eastern India. Proc. Natl. Inst. Sci. India, vol. 28B, no. 4, pp. 281-406.
- ROONWAL, M. L., AND P. K. SEN-SARMA
1960. Contributions to the systematics of Oriental termites. New Delhi, Indian Council of Agricultural Research, 407 pp., 65 pls.
- SHIRAKI, T.
1909. On the Japanese termites. Trans. Ent. Soc. Japan, vol. 2, pp. 229-242.
- SILVESTRI, F.
1901. Nota preliminare sui Termitidi sud-americani. Bol. Mus. Zool. Anat. Comp. Torino, vol. 16, no. 389, pp. 1-8.
1903. Contribuzione alla conoscenza dei Termiti e Termitofili dell'America meridionale. Redia, vol. 1, pp. 1-234.
1909. Isoptera. In Michaelsen, W., and R. Hartmeyer, Die Fauna Südwest-Australiens. Jena, Gustav Fischer, vol. 2, Lief. 17, pp. 279-314, pls. 16-21.
1912. Termiti raccolte da L. Fea alla Guinea Portoghese e alla isole S. Thomé, Annobon, Principe e Fernando Poo. Ann. Mus. Civ. Stor. Nat. Genova, ser. 3, vol. 5, no. 45, pp. 211-255.
- 1914a. Contribuzione alla conoscenza dei Termitidi e Termitofili dell'Africa occidentale. I. Termitidi. Boll. Lab. Zool. Gen. Agr., Portici, vol. 9, pp. 1-146.
- 1914b. Contribuzione alla conoscenza Termitidi e Termitofili dell'Africa occidentale. I. Termitidi. Ann. R. Scuola Sup. Agr., Portici, vol. 12, pp. 475-616.
- 1914c. Zoological results of the Abor Expedition, 1911-12. XXXII. Termitidae. Rec. Indian Mus., vol. 8, pt. 5, no. 32, pp. 425-435.
1922. Descriptions of some Indo-Malayan species of *Capritermes* (Termitidae). *Ibid.*, vol. 24, pt. 4, pp. 535-546.
- 1923a. The termites of Barkuda Island. The fauna of an island in the Chilka Lake. *Ibid.*, vol. 25, pt. 2, pp. 221-232.
- 1923b. Descriptiones Termitum in Anglorum Guiana repertorum. Zoologica, vol. 3, pp. 307-321.
- SJÖSTEDT, Y.
1900. Monographie der Termiten Afrikas. K.

- Svenska Vetensk.-Akad. Handl., vol. 34, no. 4, pp. 1-236.
1904. Monographie der Termiten Afrikas. Nachtrage. *Ibid.*, vol. 38, no. 4, pp. 1-20.
1924. Neue Afrikanische Termiten. Rev. Zool. Africaine, vol. 12, no. 4, pp. 490-494, 495-497.
1926. Revision der Termiten Afrikas. 3. Monographie. K. Svenska Vetensk.-Akad. Handl., ser. 3, vol. 3, no. 1, pp. 1-419.
- SNYDER, T. E.
- 1926a. New termites from Guatemala, Costa Rica and Colombia. Jour. Washington Acad. Sci., vol. 16, no. 1, pp. 18-28.
- 1926b. Termites collected on the Mulford Biological Exploration to the Amazon Basin, 1921-1922. Proc. U. S. Natl. Mus., vol. 68, art. 14, pp. 1-76.
1932. Two new termites from Costa Rica. Proc. Ent. Soc. Washington, vol. 34, no. 6, pp. 98-100.
1934. New termites from India. Indian Forest Rec., ent. ser., vol. 20, pt. 2, pp. 1-28.
1949. Catalog of the termites (Isoptera) of the world. Smithsonian Misc. Coll., vol. 112, pp. 1-490.
- TSAI, PAN-HUA, AND NING-SHENG CHEN
1963. New termites from South China. Acta Ent. Sinica, vol. 12, no. 2, pp. 167-195.
1964. Problems on the classification and fauna of termites in China. *Ibid.*, vol. 13, no. 4, pp. 25-37.
- TU, T.
1955. The termites of China. Jour. Formosan Sci., vol. 9, no. 1, pp. 30-39.
- WASMANN, E.
1893. Einige neue Termiten aus Ceylon und Madagaskar mit Bemerkungen über deren Gäste. Weiner Ent. Zeitg., vol. 12, no. 17, pp. 239-247.
1897. Termiten von Madagaskar und Ostafrika. Abhandl. Senckenberischen Nat. Gesellsch., vol. 21, pp. 137-182.
1902. Termiten, Termitophilen and Myrmekophilen, gesammelt auf Ceylon von Dr. W. Horn, 1899, mit andern ostindischen Material bearbeitet. 129. Beitrag zur Kenntnis der Myrmekophilen und Termitophilen. Zool. Jahrb., Syst., Jena, vol. 17, no. 1, pp. 99-164.
1911. Zur Kenntnis der Termiten und Termitengäste von Belgischen Kongo. Rev. Zool. Africaine, vol. 1, fasc. 2, pp. 145, 176.
- WEIDNER, H.
1955. Körperbau, Systematik und Verbreitung der Termiten. In Schmidt, H. (ed.), Die Termiten. Leipzig, pp. 5-81.
1956. Beiträge zur Kenntnis der Termiten Angolas, hauptsächlich auf Grund der Sammlungen und Beobachtungen von A. de Barros Machado (I. Beitrag). Publ. Cult. Co. Diam. Angola, Lisbon, no. 29, pp. 55-106.
- WU, CHENFU F.
1935. Catalogus insectorum Sinensium (Catalog of Chinese insects). Peiping (Order V, Isoptera), vol. 1, pp. i-iv, 217-222.
- YU, SWETT T., AND CHENG-MING PENG
1964. Studies on the faunal regions of Isoptera in China. Acta Ent. Sinica, vol. 13, no. 1, pp. 1-24.

