

AMERICAN MUSEUM *Novitates*

PUBLISHED BY
THE AMERICAN MUSEUM
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2570

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Number 2570, pp. 1-31, figs. 1-6, tables 1, 2

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The Termite Family Serritermitidae (Isoptera)¹

ALFRED E. EMERSON² AND KUMAR KRISHNA³

ABSTRACT

The monotypic termite family Serritermitidae Holmgren and *Serritermes serrifer* (Hagen and Bates) from Brazil are described and figured, with synonymies and bibliography. The imago, soldier, worker, and nymph are compared with all other families of Isoptera and related genera. New characters of *Glossotermes* Emerson and *Macrorhinotermes* Holmgren are given. Primitive and derivative, homologous and analogous characters and their use for phylogenetic and evolutionary inference are discussed in detail. External anatomy, glands, intestines, biogeography, ecol-

ogy, nests, food, and the coevolution of termites and intestinal zooflagellates are discussed. Also included are hypotheses on the phylogeny of all termite families including Serritermitidae, genetic persistence and change in Isoptera during 200 million years, and the natural selection of unitary social populations. Hypotheses on the Mesozoic origin of termite families are presented, based upon paleogeography, continental drift, and comparative morphology of living and fossil genera.

INTRODUCTION

The monotypic termite family Serritermitidae includes only a single, small, rare, bizarre species, *Serritermes serrifer* (Hagen and Bates), known from three localities in Brazil. The purpose of the present paper is to redescribe this family and species, together with its known nutrition, nests, and ecology, to compare it with related families and genera, and to draw phylogenetic inferences.

HISTORY

Specimens of soldiers and workers were first collected from two colonies by Bates at Santarém on the Amazon River, Para, Brazil, in 1854. Bates named the species T. [= *Termes*] *serrifer* in his field notes, which were later expanded into his classic book (Bates, 1863, 1892). Hagen

¹ Study supported by a John Simon Guggenheim Foundation fellowship to Alfred E. Emerson 1926-1927 and a National Science Foundation Grant no. GB-20684 to Kumar Krishna 1970-1973.

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(1858a) transferred the species to *Calotermes*, described the soldier and nymph, and used Bates's name and his notes, translated into German. The mention of the small size of the soldier, the presence of the eye, and the name denoting serrated mandibles are deemed sufficient to warrant junior authorship to Bates. Hagen (1858a) provided a fuller description and a figure of the soldier and technically therefore is the senior author of the species name, according to modern rules of nomenclature. Wasmann (1897) placed the species in the new subgenus *Serritermes* of the genus *Calotermes*. Silvestri (1901, 1903) gave full generic status to *Serritermes* and described the imago, soldier, and worker of *S. serrifer* from his own collections from Coxipó, Mato Grosso, adding a few observations on the nest and food. Holmgren (1909, 1910a, 1910b, 1911a) recognized the affinity of this species to his newly created but misnamed Mesotermitidae, a family that in large part forms the current Rhinotermitidae (Emerson, 1971). Holmgren gave subfamily status to the Serritermitinae within the Mesotermitidae. Light (1934) and Grassé (1949) included *Serritermes* in the Rhinotermitidae. Snyder (1949), Ahmad (1950), Emerson (1955), and Harris (1961) placed the Serritermitinae in the Termitidae. Emerson (1965) raised the subfamily to family status. Krishna (1969, 1970) described key characters of the Serritermitidae. Araujo (1970, 1972) recorded its geography and ecology.

The confusion in the taxonomy of *Serritermes serrifer* for more than a century was due to changing theories of taxa and relationships within Isoptera, to nomenclatural errors, and to a lack of thorough examination and comparison of the few specimens available. The species possesses some comparatively primitive characters and some strikingly derivative ones and has no very close relative that might indicate gradations in its phylogeny.

There is no exact definition of the limits of a subfamily or a family; the category is determined by the grouped relationships of the included genera and the extent of the gap between roughly equivalent higher systematic categories (see Chatterjee and Thakur, 1964). We consider the gap sufficiently wide to include the single

known species in the monotypic family Serritermitidae.

FAMILY SERRITERMITIDAE HOLMGREN

- < Family Termitina: Hagen, 1858a, p. 4.
- < Subfamily Termitinae: Silvestri, 1903, p. 37.
- < Subfamily Calotermitinae: Silvestri, 1901, p. 1. Desneux, 1904, pp. 9, 11, 24.
- < Family Mesotermitidae Holmgren, 1909, p. 100; 1910a, p. 285; 1910b, p. 143; 1911a, pp. 13, 61; 1911b, pp. 206, 209.
- < Family Mésotermitidés: Bathellier, 1927, pp. 129, 254.
- < Family Rhinotermitidae: Light, 1934, p. 112. Grassé, 1949, p. 533.
- < Family Termitidae: Silvestri, 1901, p. 1. Snyder, 1949, pp. 5, 99. Ahmad, 1950, p. 56. Emerson, 1955, pp. 495, 497, 505, 506, 507, 510, 517. Harris, 1961, pp. 53, 64. Krishna, 1961, p. 332.
- = Subfamily Serritermitinae Holmgren, 1910a, p. 285; 1910b, p. 143; 1911a, pp. 62, 63, 82. Snyder, 1949, pp. 99, 100. Grassé, 1949, p. 534. Ahmad, 1950, pp. 56, 75. Emerson, 1955, pp. 495, 497, 505, 506, 515, 516, 517. Weidner, 1955, pp. 10, 41. Tu, 1955, pp. 33, 34, 35. Harris, 1961, pp. 53, 64; 1962, p. 195. Krishna, 1961, p. 332. Springhetti, 1963, p. 213. Sen-Sarma, 1968, p. 7.
- = Family Serritermitidae: Emerson, 1965, pp. 17, 38; 1968b, p. 4; 1971, p. 248. Krishna, 1969, pp. 3, 4; 1970, pp. 127, 130, 131, 137, 139, 140. Weesner, 1969a, p. 28. Araujo, 1970, pp. 527, 531, 533, 545; 1972, pp. 67-70. Wilson, 1971, p. 105.

Type Genus. *Serritermes* Wasmann (Holmgren, 1910a, p. 285). No other genus is included in the family.

Diagnostic Characters. The imago, worker, and nymph differ from all other termite families by the proportionally elongated sharp apical tooth of each mandible separated from a single marginal tooth near the ridged molar plate by a widely curved inner margin (fig. 2A).

The soldier has long, relatively straight apical portions of both mandibles, each with numerous proportionally coarse, large serrations on the inner apical margins behind the tips (figs. 4, 5). The pronotum is proportionally narrow, elongated, and both front and hind margins are conspicuously bilobed, each with a relatively

deeply curved concave emargination in the middle (fig. 4).

GENUS *SERRITERMES* WASMANN

< Genus *Calotermes*: Hagen, 1858a, pp. 32, 33; 1858b, p. 5. Wasmann, 1897, p. 150.

= Subgenus *Serritermes* Wasmann, 1897, p. 150.

= Genus *Serritermes*: Silvestri, 1901, p. 3; 1903, p. 40. Desneux, 1904, p. 47. Holmgren, 1909, pp. 91, 109-111, 169, 170; 1911a, pp. 62, 63, 82, 83. Bathellier, 1927, p. 130. Emerson, 1928, p. 406; 1952, p. 508; 1955, p. 515. Armbruster, 1941, p. 20. Snyder, 1949, p. 100. Ahmad, 1950, p. 74; 1958, p. 35. Harris, 1961, p. 64. Weesner, 1969a, pp. 27, 28. Krishna, 1970, p. 137. Wilson, 1971, p. 105. Araujo, 1972, pp. 67-70.

Type Species. Calotermes (Serritermes) serrifer (Bates) (Wasmann; 1897, p. 150), a synonym of *Serritermes serrifer* (Hagen and Bates), only included species in the genus.

Diagnostic Characters. The same as those of the family Serritermitidae.

Serritermes serrifer (Hagen and Bates)

Termes serrifer Bates In Hagen, 1858a, p. 73 (field notes).

Calotermes serrifer Hagen, 1858a, p. 72 (soldier, nymph), pl. 1, fig. 6 (soldier); 1858b, p. 11 (soldier, nymph).

Calotermes (Serritermes) serrifer: Wasmann, 1897, p. 150 (systematics).

Serritermes serrifer: Silvestri, 1901, p. 3; 1903, p. 41 (imago, soldier, worker), p. 112 (biology), pl. 1, figs. 39, 40, 43 (imago), figs. 41, 42 (soldier). Holmgren, 1909, pp. 91, 109-111, 169, 170 (anatomy, imago, nymph, worker, soldier), fig. 33e (worker mandible), fig. 53 (worker intestine); 1911a, p. 82, fig. 6 (nymph mandibles), pl. 6, fig. 8 (soldier). Snyder, 1949, p. 100 (synonymy). Ahmad, 1950, p. 84, fig. 17 (imago-worker mandibles). Harris, 1961, p. 43 (systematics, history). Emerson, 1965, pp. 17, 38 (imago mandibles, soldier). Araujo, 1970, pp. 533, 537, 545 (geography, ecology); 1972, pp. 67-70 (geography, ecology, bibliography).

Imago (figs. 1-3). Very small (table 1), close to the smallest living termite.

Head medium light brown to yellow; postcly-

peus slightly lighter than head; pronotum same color as head or a little lighter; wing hyaline except for opaque white costal margin and radial sector (Rs).

Head, postclypeus, labrum, and pronotum with numerous irregularly scattered medium-length thin hairs (fig. 1); forewing scale with hairs on costal margin; wings with no hairs beyond humeral suture on margins, veins, or membranes; sternites and tergites each with short hairs and a marginal row of bristles hardly longer than hairs, hairs near tip of abdomen longer; pleural membrane covered with short hairs.

Head egg-shaped from above (fig. 1). Fontanelle in small depression, white, moderate-sized, forked, with somewhat thickened arms. Y-suture vestigial, with short arms from fontanelle visible, very faint stem connecting with more distinct short stem at rear. Frontal gland beneath fontanelle possibly present but small, not seen through head chitin. Two muscle insertions in front of ocelli, each smaller than ocellus. Eye proportionally moderately large, round, about a fourth of its diameter from lower margin of head, prominent from above with convex margin. Ocellus moderately large, subtriangular, facing toward side and front, much less than width from eye. Antenna with 13 or 14 articles, third either smallest or equal to second or fourth. Antennal fossa larger than ocellus, less than width from eye. Mandibles probably close to those of nymph or worker (fig. 2). Postclypeus large, not quite so long as half its width, with median longitudinal line, profile convex, with small but distinct angle at junction with front of head. Pronotum (fig. 1) a little narrower than head, about as long as half its width, with front margin fairly straight with slight notch in middle, faint median line, sides rounded and converging, hind margin somewhat emarginate, profile evenly arched with only slight elevation behind front margin. Mesonotum and metanotum sides converging with narrow hind borders straight or barely perceptible notch (fig. 1). All tibiae with two spurs (2/2/2). Tarsi with four articles. Arolium absent. Forewing scales large, extending almost to border of mesonotum but not actually overlapping base of hind wing scale. Humeral suture of forewing sharply convex between costal

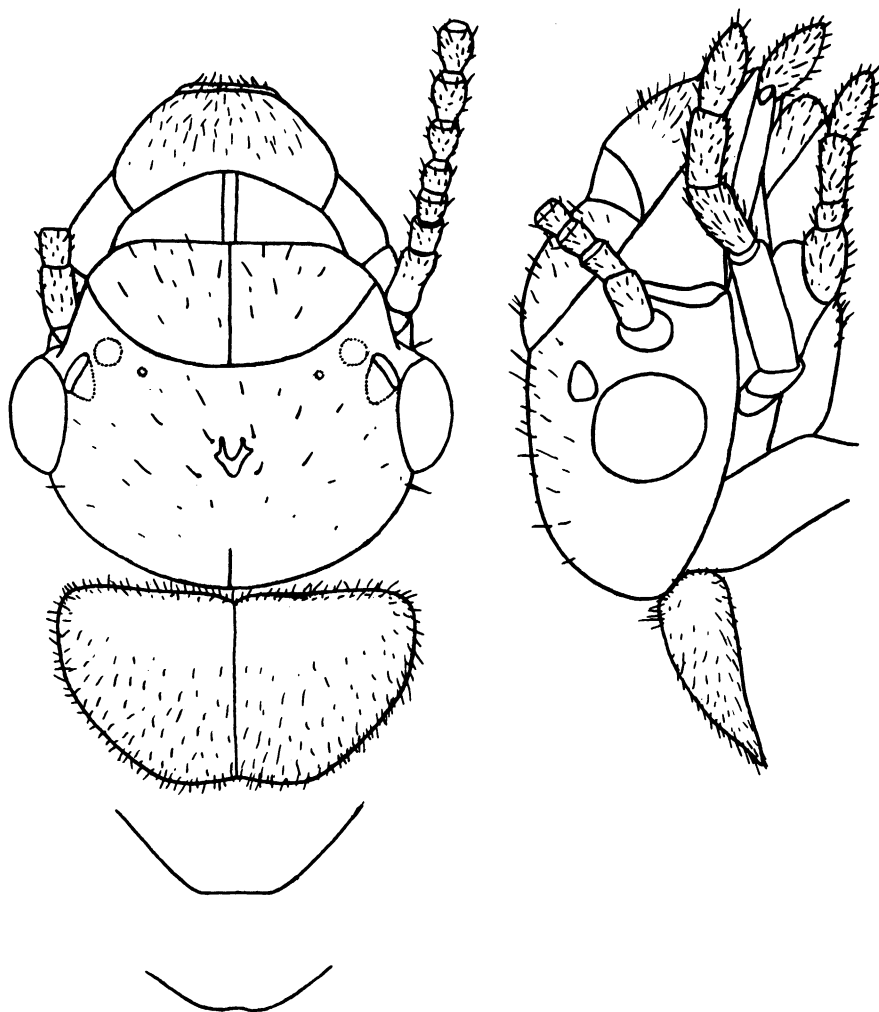


FIG. 1. Imago of *Serritermes serrifer* (Hagen and Bates) from Coxipó, Mato Grosso, Brazil, Silvestri Collection, Portici, Italy. Head, pronotum, and hind margins of mesonotum and metanotum from above; head and pronotum from side. Drawn by A. E. Emerson.

margin and radial sector (Rs), straight from Rs to inner margin. Wing membranes (fig. 3) with irregular vertical and slanting chitinizations, giving a reticulated appearance to whole wing between Rs and inner margin except at base near suture and a few cross reticulations between costal margin and Rs in apical fourth. Forewing with subcosta (Sc) and first radius (R_1); second plus third radius (R_{2+3}) absent. Radial sector (Rs)

heavy and parallel to costal margin almost to tip of wing. Media (M) weak, in one wing almost disappearing at base, with about seven to nine branches; in another wing lacking as a distinct vein and possibly coalesced with the cubitus (Cu). Cu weak with eight to nine branches and extending half length of wing. Hind wing scale smaller than forewing scale, not extending nearly to margin of metanotum; humeral suture straight

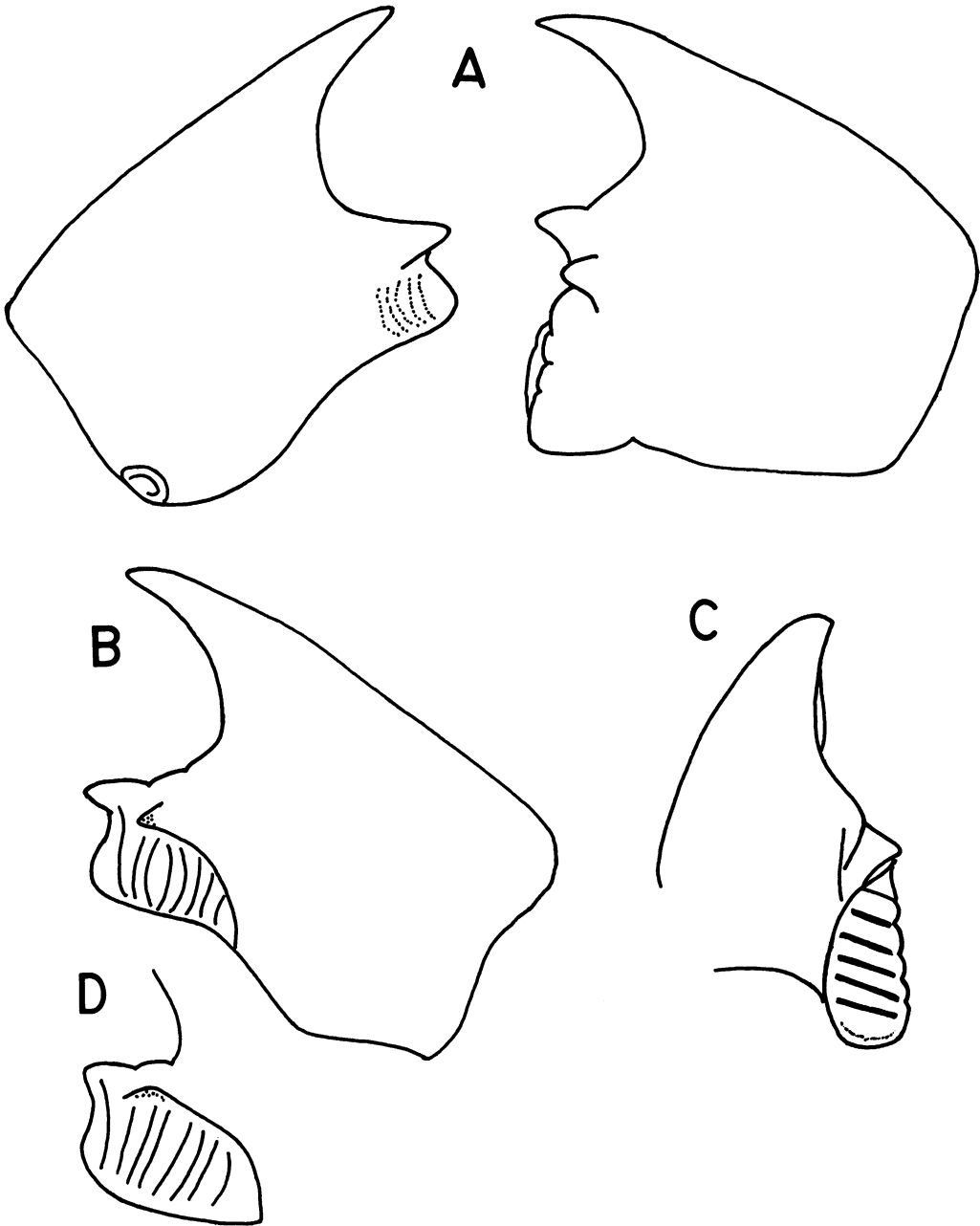


FIG. 2. Mandibles of worker of *Serritermes serrifer* (Hagen and Bates) from Coxipó, Mato Grosso, Brazil, collected and determined by F. Silvestri. A. Left and right mandible from above. B. Left mandible from below. C. Right mandible from below at angle to show molar area. D. Left mandible molar area from below at angle. Drawn by K. Krishna.

(fig. 3). Hind wing with costal margin and Rs similar to forewing. M joined to Rs near base, with 10-11 branches reaching tip and apical half of inner margin; in one hind wing (fig. 3) first branch of M sharply turned and joined to Rs in about middle of wing. (M is variable and details should not be used for specific or generic diagnosis.) Cu separate at suture with about eight branches, usually not extending beyond middle of wing (2.17 mm. from costal suture in one wing) unless it coalesces with M. Anal vein (A) absent. Spiracles on lower edge of pleural portion of tergites, separated from tergites by light bands. Seventh sternite of female with bluntly pointed hind lobe. Styli absent in both male (Holmgren, 1911a) and female. Cerci short with two articles.

Soldier (figs. 4, 5). General size very small (table 2).

Head and pronotum straw yellow; labrum yellowish white; outer portion of mandibles reddish brown with light bases.

Top of head, postmentum, postclypeus, and labrum sparsely covered with short or microscopic hairs without long bristles; tip of labrum with denser group of longer hairs; pronotum with numerous short hairs near margins but bare in middle.

Sides of head nearly straight, converging toward front; head capsule wider than length of head to base of anteclypeus, thick in proportion to length and width; hind margin flatly rounded; profile of short top flat in middle; profile of front convex with extremely slight, hardly

noticeable depression in middle at junction with postclypeus. Fontanelle small, oval, about midway between front of postclypeus and rear of head, flat without projection. Frontal gland moderately small, oval. Middle longitudinal line in rear, Y-suture absent otherwise. Postmentum

TABLE 1
Measurements (in Millimeters) of Two Female
Imagoes of *Serritermes serrifer* (Hagen and Bates)

	Range
Length with wings	6.12
Length without wings	4.16
Length of head to tip of labrum	0.89, 0.97
Width of head	0.81, 0.82
Diameter of eye	0.23
Length of ocellus	0.08
Width of ocellus	0.05
Ocellus from eye	0.02, 0.03
Length of antenna	1.39
Length of postclypeus	0.23
Width of postclypeus	0.51
Length of pronotum	0.34, 0.35
Width of pronotum	0.66, 0.68
Length of hind tibia	0.58, 0.68
Length of forewing scale costal margin	0.41
Length of forewing from suture	4.41
Width of forewing	1.35
Width of forewing at suture	0.37
Length of hind wing scale costal margin	0.28
Length of hind wing from suture	3.92
Width of hind wing	1.25
Width of hind wing at suture	0.23

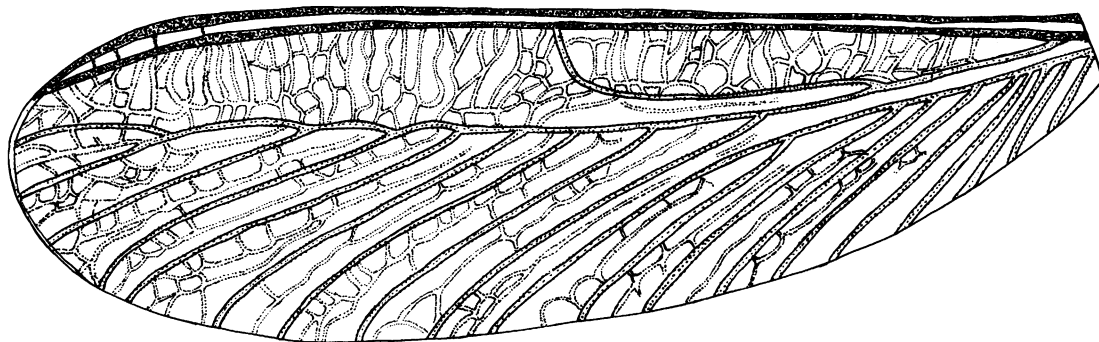


FIG. 3. Left hind wing of *Serritermes serrifer* (Hagen and Bates) from Coxipó, Mato Grosso, Brazil, collected and determined by F. Silvestri. Drawn by K. Krishna.

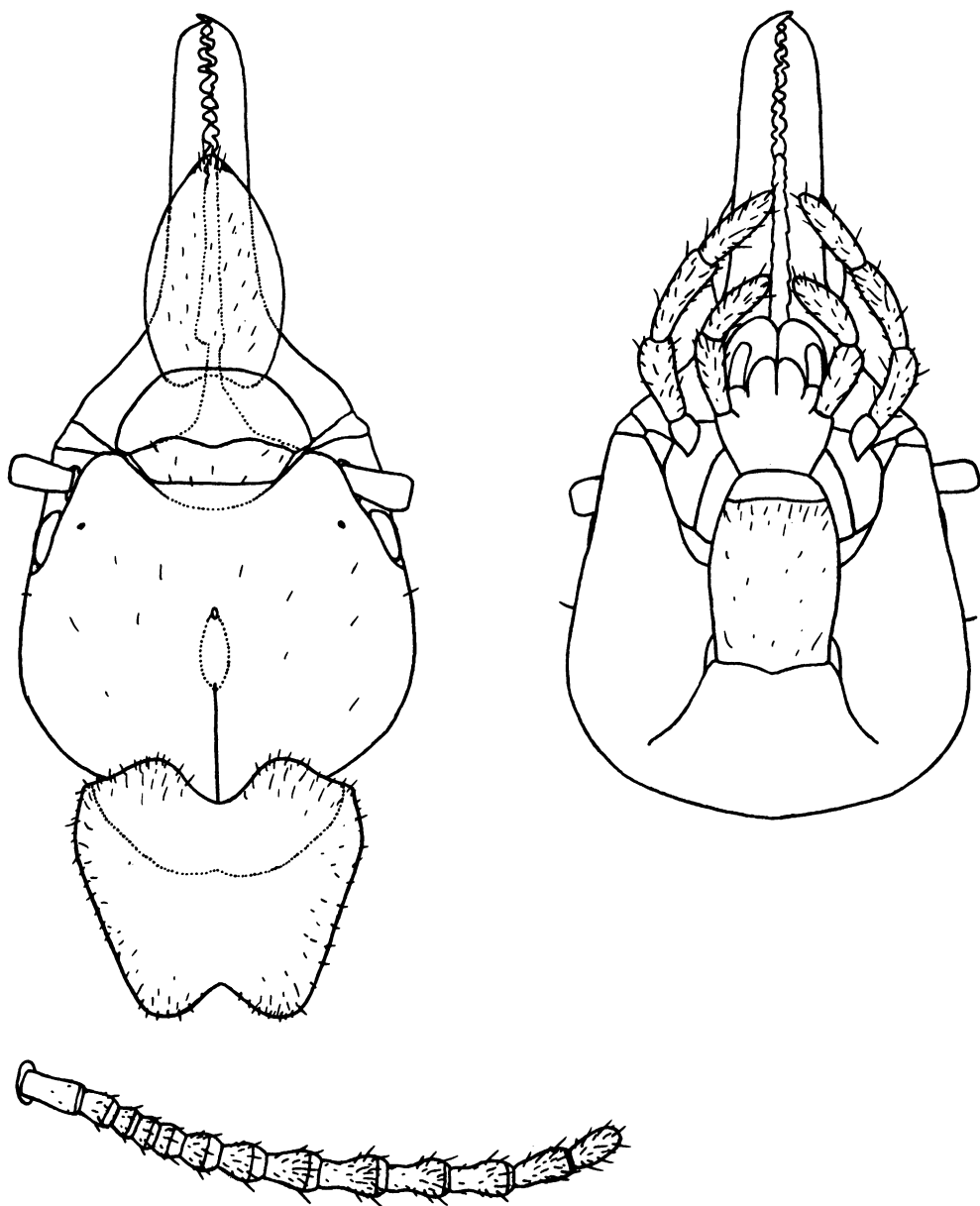


FIG. 4. Soldier of *Serritermes serrifer* (Hagen and Bates) from Coxipó, Mato Grosso, Brazil, Silvestri Collection, Portici, Italy. Head and pronotum from above; head from below; antenna. Drawn by A. E. Emerson.

(fig. 4) short, wide, its sides somewhat convex in middle, sutures slightly constricted near rear, profile strongly convex, bulging. Vestigial eyes

comparatively large, slightly convex, oval, white, almost continuous with head, slightly larger than antennal fossa; irregularities of surface

possibly due to much reduced indistinct facets; ocular suture distinct in some lights. Vestigial ocellus about two-thirds diameter of eye above eye on each side. Antenna with 12 or 13 articles, third shortest, articles 8 to 11 constricted in middle forming bulbous tips (fig. 4). Both mandibles with outer margins concave near bases, nearly straight in middle, and convex near apical ends; blades about equal width from bases to close to tips, with tips hardly hooked, each with numerous coarse inner serrations on apical third, and bases without molar ridges. Left mandible with smaller forward pointing serrations reaching almost to base, slight blunt hump in front of base, small, sharp (about 60°), toothlike projection on basal portion. Right mandible with about six smaller serrations posterior to three or four coarse apical serrations, but not reaching so close to base as on left mandible; slight, pointed hump on inner margin near base (possibly vestigial tooth but too obscure to be sure of homology); small sharp toothlike projection on base. Postclypeus short, with front concave, base straight, obscure shallow longitudinal depression in middle, suture at junction with front of head barely visible, profile flatly convex. Labrum much longer than wide, with sides evenly convex, narrowed anteriorly; tip white, obtusely pointed, narrowly convex, and slightly constricted behind; profile convex. Pronotum (fig. 4) from above elongate, with deeply indented front and hind margins; frontal lobes large and strongly convex, middle longitudinal line faint or obscure, sides moderately straight and converging toward rear; profile with large front lobes raised above straight hind portion. Mesonotum wider than pronotum, hind margin evenly curved. Metanotum wider than mesonotum, hind margin evenly curved. Coxae without conspicuous sharp ridge, right and left close but bases not touching in middle. Femora normally thicker than tibiae, not markedly swollen. Each tibia with two apical spurs (2/2/2). Tarsi with four articles, fourth longer than all others combined. Styli absent. Cerci short with two articles, first much wider than second.

Nymph and Worker. Antenna with 13 articles. Mandibles (fig. 2) most specialized of any known termite; apical portion proportionally prolonged, ending in sharp point; marginal teeth reduced to

one in each mandible with obscure homologies. Left mandible (figs. 2A, 2B, 2D) with one relatively large marginal tooth close to molar region, possibly homologous with third marginal tooth of *Coptotermes* because of its position and backward pointed direction; slight hump on cutting edge immediately anterior to marginal tooth, possibly greatly reduced second marginal tooth. (First marginal tooth of more primitive *Rhinotermitidae* proportionally smaller than second marginal tooth, and consequently possibly lost before reduction or modification of second and third marginal teeth of *Serritermes*.) Molar plate of left mandible with eight distinct molar ridges and grooves indicating some molar function. Lower edge of molar plate bounded by ridge with sharp projecting toothlike prolongation at anterior edge conforming in position to interpretation of homology of third marginal tooth in *Coptotermes*. (Holmgren [1911a, p. 82,

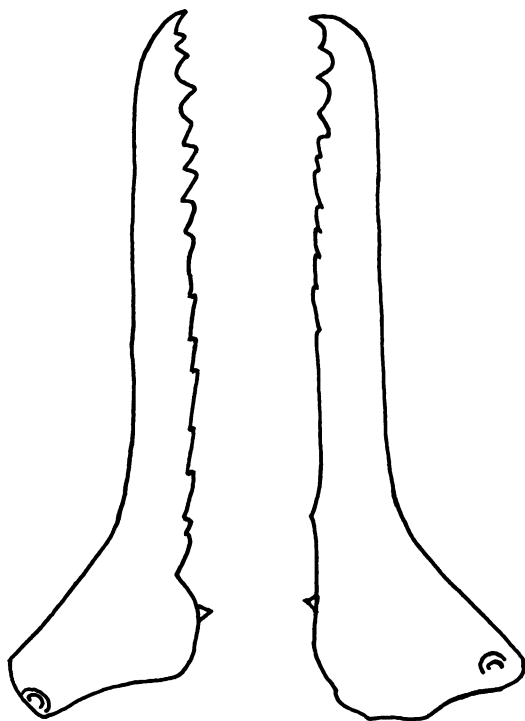


FIG. 5. Soldier mandibles of *Serritermes serriker* (Hagen and Bates) from Coxipó, Mato Grosso, Brazil.

fig. 6] showed ridges on molar surface not shown by Ahmad [1950, p. 74, fig. 17].)

Right mandible of *S. serrifer* (figs. 2A, 2C) also with reduction of marginal teeth to one, and reduction of molar ridges to five. Single marginal tooth possibly homologous with first marginal tooth of *Coptotermes* because faint hump anterior to tooth possibly being reduction of subsidiary tooth of primitive Hodotermitidae and all genera of Rhinotermitidae. (In all other cases of reduced marginal teeth, first present in right mandible.) Sharp toothlike projection above molar plate possibly extension of upper side of molar plate on different level than marginal tooth (fig. 2A), perhaps adaptation for interlocking and fitting right mandible with left mandible.

In anterior intestine, crop not voluminous, probably not clearly separated from esophagus, lightly asymmetrical. Gizzard with very reduced armature, 24 longitudinal folds, slightly prominent, not chitinized. Middle intestine generalized, contact with hind intestine forming transverse circle or ring. Malpighian tubules at least six in number, but probably eight in better preserved material, according to Holmgren (1909, pp. 169, 170, fig. 53), emerging exactly at junction of middle and hind intestine. Hind intestine preceding enteric valve very short and cylindrical. Enteric valve not much differentiated, with posterior border projecting into dilated paunch, six lightly chitinized folds corresponding to six bands of longitudinal muscles, no distinct rounded swellings in lumen. Paunch very voluminous, containing flagellates. Colon and rectum simple and of normal length.¹

Sternal Glands. Noirot (personal commun.) stated that the sternal glands are at the anterior border of the fifth sternite.

Seminal Vesicles. Springhetti (1963, p. 213) described the seminal vesicle.

Abnormal Legs. Numerous individuals in a single vial (collected by F. Silvestri, Coxipó, Cuyabá, 30.VIII.1900) have abnormal hind legs. The femur, tibia, and tarsus are more or less coalesced, often with the appearance of a single

TABLE 2
Measurements (in Millimeters) of Two Soldiers of
Serritermes serrifer (Hagen and Bates)

	Range
Length of head with mandibles	1.54, 1.61
Length of head to middle front of postclypeus	0.75, 0.77
Width of head	0.77, 0.79
Maximum thickness of head without postmentum	0.48, 0.49
Maximum thickness of head with postmentum	0.61
Length of postmentum in middle	0.38
Width of postmentum	0.24, 0.26
Maximum length of eye	0.13
Length of antenna	1.13, 1.22
Maximum length of fossal suture	0.10
Length of left mandible	0.87, 0.94
Length of right mandible	0.89
Median maximum length of labrum	0.32, 0.36
Width of labrum	0.28
Length of pronotum in middle	0.36
Maximum length of pronotum with lobes	0.52, 0.55
Width of pronotum	0.56, 0.58
Length of hind tibia	0.58, 0.59

structure with normal claws at the tip. Of a total of two winged imagoes, two soldiers, 13 workers, and 10 nymphs with wing pads—one soldier, five workers, and one nymph have coalesced tibiae and tarsi of the left hind legs; one soldier and six workers have coalesced right tibiae and tarsi; two imagoes, no soldiers, two workers, and nine nymphs have normal right and left legs.

The senior author first thought this abnormality might be a Mendelian mutation analogous to some mutations of legs or antennae in *Drosophila* (Diptera), but he now interprets the abnormal legs as regenerations of injured legs in early development, and therefore epigenetic rather than genetic. It is well known that early injured structures may undergo partial regeneration in insects and other Arthropoda.

Specimens and Collections. One of the original soldiers collected by H. W. Bates and described by Hagen (1858a) as "*Calotermes serrifer*" is labeled "*T. serrifer* Bates TYPE" in the Hagen Collection, Museum of Comparative Zoology, Harvard University. This soldier was collected at Santarém, Para, Brazil, in 1854.

¹Charles Noirot examined the intestines of three workers and fixed the alcoholic specimens in Bouin's solution. The preservation was inadequate in several respects, but Noirot has given us permission to use his observations and comments.

Hagen (1858a, pp. 72-73) examined five soldiers and three nymphs from two separate colonies. According to W. A. Sands (personal commun.), specimens collected by Bates (1855, pp. 4551, 4552) and identified by Hagen were sold to the British Museum (Natural History), London, England. Bates sent his specimens to Samuel Stevens, a dealer, auctioneer, and entomologist, with a letter suggesting sale to the British Museum. They were purchased from Stevens and are labeled "Santarém on the Amazon, Bates, BM Accession No. 1865-19." We are here designating as lectotype a soldier of *Serritermes serrifer* (Hagen and Bates) from the British Museum collection, which has been selected by W. A. Sands and labeled "lectotype Soldier *Serritermes serrifer* (Hagen and Bates) Coll. H. W. Bates 19.iv.1854." Therefore, the soldier labeled TYPE at the Museum of Comparative Zoology should be labeled paralectotype. Hagen (1858a) revised the termites in the British Museum and retained one soldier in his personal collection now in the Museum of Comparative Zoology.

Specimens of imagoes, soldiers, and workers were collected by F. Silvestri, 30.VIII.1900, at Coxipó da Ponte, about 5 km. southeast of Cuiabá, Mato Grosso. Silvestri (1901, 1903) identified and described these specimens under the name *Serritermes serrifer* and deposited them in alcohol in his collection in the Scuola Agraria, Portici, Italy, from which he exchanged a few specimens. Silvestri sent specimens to N. Holmgren in Stockholm, Sweden, who gave a number of termites from around the world to A. E. Emerson in 1927, among them one imago, one soldier, and workers of *S. serrifer*, all formerly dried and shriveled. Emerson compared a soldier from Coxipó with the pinned paralectotype soldier at the Museum of Comparative Zoology, and found them specifically identical. The single soldier from Holmgren now in the American Museum of Natural History labeled homoparalectotype is included in the present article. Drawings (figs. 1, 3) and descriptions of an imago and soldier were made in Portici in 1927 when Emerson was studying Silvestri's collection. Krishna obtained exchange specimens from the Silvestri Collection in Portici, Italy, and drew the nymph-worker and soldier mandibles (figs. 2, 5), and one soldier and several nymphs or workers

from this collection are included in the foregoing description. Three worker abdomens were sent to C. Noirot for a study of intestinal structures.

Araujo (1972) collected two colonies at Curvelo, Mato Grosso, from which he compared soldiers with the Bates Collection in the British Museum (Natural History). These soldiers should be labeled "homolecotype determined, compared and collected by R. L. Araujo."

Geographical Distribution. Araujo (1972) listed all known localities in Brazil (fig. 6) as follows: Santarém, Pará (type locality), at the mouth of Rio Tapajós, 2° 24' 54" S; 54° 39' W; alt. 36 m., collected by H. W. Bates. Coxipó da Ponte, Mato Grosso, about 5 km. SE of Cuiabá (= Cuyaba), 15° 35' 38" S; 56° 05' 54" W; alt. 150 m., collected by F. Silvestri. Curvelo, Minas Gerais, 1.5 km. N of 18° 45' 40" S; 44° 24' 46" W; alt. 633 m., collected by R. L. Araujo.

Ecological Distribution. The vegetation in the vicinity of all the localities is described as tropical savanna forest, *campos* or *cerrado*, with small, scattered, low single trees or with wooded patches dotted with mound nests of *Cornitermes*, and sometimes degraded by cultivation, felling of trees or cattle grazing (Araujo, 1972). Bates specifically stated that the vicinity of Santarém on the Amazon River does not have dense high forest (rain forest). The few collections of *S. serrifer* have always been associated with other termites of various genera and species, particularly mounds of *Cornitermes* spp. (*C. cumulans* determined by Silvestri and Hagen needs reidentification). Termites of different species are commonly in close proximity and often in separate galleries within the nests of other species. With few exceptions [i.e., *Termes inquilinus* Emerson in the stored humus-like material in arboreal nests of *Constrictotermes cavifrons* (Holmgren) in Guayana], there is seldom any species-specific nest association. It is doubtful whether *Serritermes serrifer* is associated wholly with any other species or genus of termite, although a small species of this type may find the microclimatic conditions of termite mounds such as those of *Cornitermes* attractive for establishing its own colonies.

Nests. Meager notes on the nests have been published by Hagen (1858a), Bates (1892), Silvestri (1903), and Araujo (1972). *Serritermes*

occupies a small chamber measuring 3 to 4 square inches, subdivided into smaller cells, all distinctly separated from the surrounding galleries of *Cornitermes* in mounds also occupied by several other species of termites. The mounds, of course, were built by the large workers of *Cornitermes*. The five colonies so far discovered are insufficient to conclude that an inquiline association always occurs between *Serritermes* and *Cornitermes*, although attention of future collectors should be focused on this possibility, and also upon the source of the food of *Serritermes*.

Food. Bates (noted in Hagen, 1858a) recorded the nest within carton material. Silvestri (1901, 1903) thought the food was vegetable detritus. Noirot (personal commun.) described the pres-

ence of particles of mineral matter in the contents of the intestines examined under polarized light. The worker mandibles show the most extreme reduction of marginal teeth and proportional elongation of the apical portion known among worker termites, but the mandibles possess basal molar ridges that are absent in numerous species of the Termitidae that feed on humus alone. The intestinal armature described by Noirot (personal commun.) indicated a reduction in comparison with a wood-eating genus like *Reticulitermes*. William A. Sands (personal commun.) suggested that the worker mandibles might be adapted to a predatory or seminivorous (seed-eating) diet, or just possibly to a diet of soft *Cornitermes* carton. Sands is sure *Serritermes* is not a soil feeder and that the gut is too

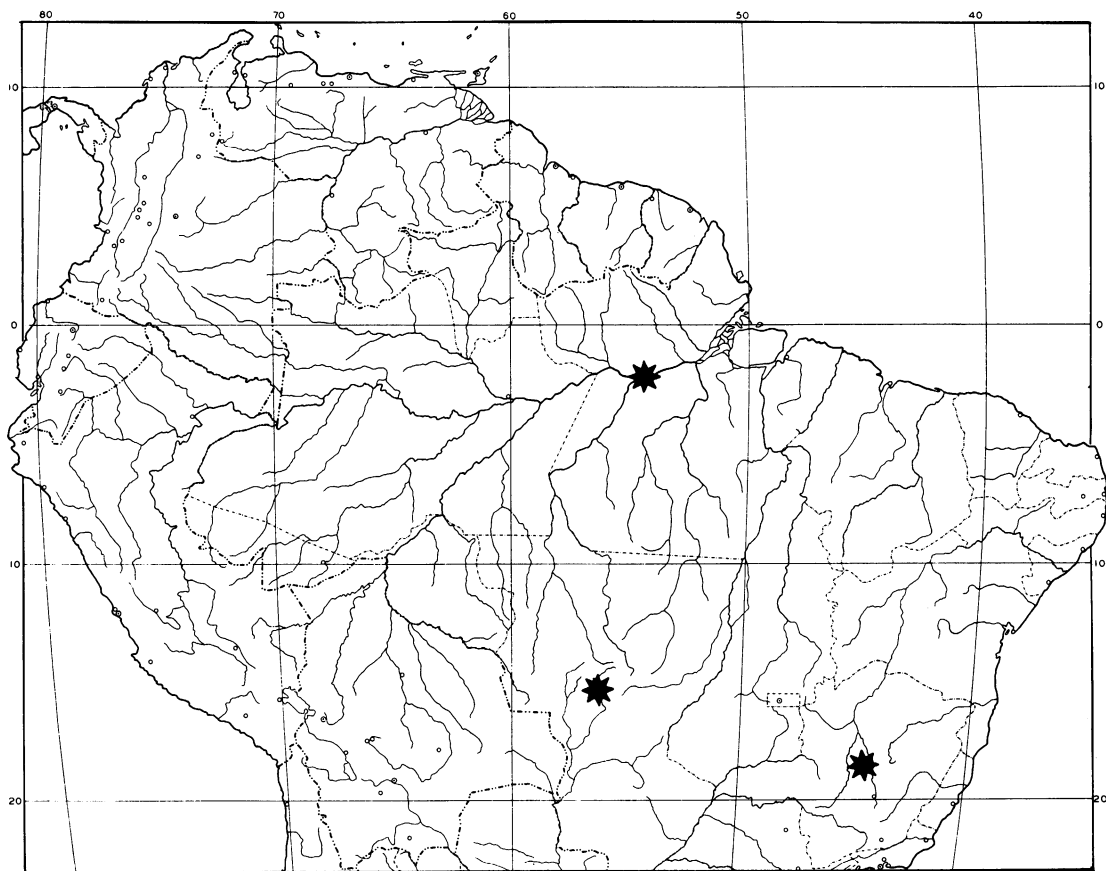


FIG. 6. Distribution of *Serritermes serrifer* (Hagen and Bates) from Brazil.

short for a humivore. *Capritermes* and related genera are thought to feed on humus and soil, and in these genera the basal ridges of the mandibles are reduced to three, four, or five in both mandibles. It remains an open question what the exact nature of the food of *Serritermes* is, and what the nutritional role of the intestinal flagellates may be.

COMPARISONS OF FAMILIES AND GENERA

Descriptions, figures, and discussions of remotely related families and genera are contained in the literature cited of the present article; among the most useful are Silvestri (1909); Emerson (1933, 1950, 1965, 1968b); Krishna (1961); and Chatterjee and Thakur (1964). Characters indicating taxonomic and phylogenetic relations were discussed by Emerson (1971, fig. 1, pp. 249-254, 265, 272-273, 277, 287-289, 291, 295). We did not examine every species in every genus, so the ranges of variation may be greater than those given below.

IMAGO

Size. The very small size of *Serritermes* is derivative compared with the moderate or large size of primitive species of the Mastotermitidae, Kalotermitidae, Hodotermitidae, Rhinotermitidae, and Termitidae (Emerson, 1933, 1965, 1969, 1971). The fossil *Reticulitermes minimus* Snyder is about as small as *Serritermes*. *Parrhinotermes* and *Termitogeton* are small, but not so small as *Serritermes*. In a few cases, notably among the Termitidae, there is a rare evolution toward larger size, but the far more obvious trend is from large to small.

Pilosity. *Mastotermes* and *Archotermopsis* have short hairs on the head and pronotum. The longer and thicker hairs and bristles of *Coptotermes* have been considered primitive among the Rhinotermitidae (Emerson, 1971), but the trend toward many short hairs and bristles and the trend toward long bristles and few short hairs may both be derivative. Sequences in allied genera indicate evolutionary trends. *Heterotermes* may be more primitive with less abundance of hairs and bristles than *Coptotermes* and more abundance than *Serritermes*, although *Serri-*

termes is closer to the head pilosity of the more primitive families. *Termitogeton* has many hairs and bristles. *Parrhinotermes* has numerous long bristles and a few microscopic hairs. *Prorrhinotermes* has a few long hairs or bristles with short hairs nearly absent on top, and *Macrorrhinotermes* and *Schedorhinotermes* have a few short bristles only, in front of the eyes. The pronotum of *Macrorrhinotermes* has a number of long bristles on the margins and a few short bristles on the disc, whereas the tergites and sternites are thickly covered with long bristles of similar length above and below. *Acorhinotermes* has long bristles on the front part of the head and no short hairs.

The wing pilosity of *Mastotermes*, *Archotermopsis*, and *Zootermopsis* is the most primitive, with few hairs on the costal margins and an occasional hair on the strong veins, and without hairs on the weaker veins, inner margins, and membranes. *Parastylotermes robustus* (Rosen) is equally primitive. *Coptotermes*, *Heterotermes*, *Termitogeton*, and other relatively primitive rhinotermitids have numerous hairs on the costal and inner wing margins, veins, and membranes—in *Heterotermes*, varying in abundance from species to species. The absence of hairs on the costal margins, inner margins, membranes, and strong veins beyond the humeral suture in *Stylotermes*, *Prorrhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Serritermes* is now considered derivative in contrast to the earlier interpretation by Emerson (1971, pp. 252, 253, tables 1, 2).

Head Capsule. The comparatively wide oval head of *Coptotermes* is considered primitive among the Rhinotermitidae. The slightly narrower and less widely oval head of *Serritermes* is hardly of phylogenetic significance. The wide, angular, short and small head of *Termitogeton* is unique among the Rhinotermitidae. The sides of the head of *Prorrhinotermes* and *Parrhinotermes* are straighter near the eyes. The head of *Macrorrhinotermes* is proportionally wider, the front is arched in profile from the side and rear, and is similar to the profile of *Schedorhinotermes* except for the clypeus. *Parrhinotermes*, *Macrorrhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes* have several small ridges or wrinkles behind and at the sides of the fontanelle, and a shallow groove extending from the

fontanelle through the middle of the postclypeus. *Heterotermes* and *Reticulitermes* have proportionally narrower heads with straighter sides than in *Serritermes*.

The fontanelle of *Coptotermes*, *Termitogeton*, *Stylotermes*, and *Prorhinotermes* is small, oval, and more primitive than the thicker portions of the fontanelle of *Serritermes*. The fontanelle and associated frontal gland originated with the Rhinotermitidae and are lacking in the Mastotermitidae, Kalotermitidae, and Hodotermitidae. The frontal gland is large and derivative in *Prorhinotermes*. The position of the fontanelle of *Coptotermes*, *Termitogeton*, and *Serritermes* in back of the level of the antennal fossae and ocelli is primitive compared to the forward position in the more derivative genera of the Rhinotermitinae. The fontanelle of *Parrhinotermes*, *Macrorhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes* is close to the level of the ocelli and is surrounded by a shallow depression slightly concave in profile. The more complete and distinct the epicranial suture (Y-suture), the more primitive the genera and species. *Mastotermes* and *Archotermopsis* in particular have a primitive, complete Y-suture (Emerson, 1933). Some species of *Coptotermes* have a distinct forked fontanelle indicating the vestigial arms of the Y-suture, and the stem is distinct, but *C. testaceus* lacks both the fork and the stem. The distinct arms of the Y-suture of *Termitogeton* form an angle greater than a right angle. *Stylotermes chakratensis* Mathur and Thapa (= *Sarvaritermes faveolus* Chatterjee and Thakur) has a complete Y-suture, whereas *Stylotermes fletcheri* and *Parastylotermes robustus* do not. The stem and arms of the Y-suture are barely distinguishable in *Prorhinotermes*. The arms are distinct in *Parrhinotermes*, but the stem is indistinct or absent. The Y-suture of *Serritermes* is partially regressed.

Compound Eye. The lenticular flatly convex eyes of *Archotermopsis* and *Ulmeriella* are blattoid in shape and are the most primitive among termites (Emerson, 1933, 1968b). The rounded eye of *Serritermes* is proportionally larger than that of *Coptotermes*, *Stylotermes*, *Termitogeton*, and *Psammotermes*, and the convex projecting eye of these genera and *Mastotermes* is probably primitive, although the flat eye of *Archotermopsis* is more primitive. The eye of *Prorhino-*

termes is moderately large and flatter than that of *Coptotermes*. The eye of *Parrhinotermes* is round, convex, and relatively large. The eye of *Macrorhinotermes* is large, oval, and proportionally similar to *Serritermes* although the size of the head is much larger (width of head with eyes 2.74 mm.). The proportions and convexity of the eye of *Rhinotermes* (except *R. nasutus*), *Dolichorhinotermes*, and *Acorhinotermes* are similar to *Coptotermes*. The proportionally smaller, triangular, flat eyes of *Heterotermes* and *Reticulitermes* are derivative. The trend is from a large, primitive eye toward a small, derivative eye, but there are numerous exceptions.

Ocelli. The Hodotermitidae lack ocelli—a derivative character compared with their presence in the Blattodea, Mastotermitidae, Kalotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae. Ocellus-like spots in some Hodotermitidae are not near the tips of the branches of the Y-suture and are probably muscle insertions. The ocellus is large, distinct, and close to the eye in *Coptotermes*, *Termitogeton*, *Prorhinotermes*, and *Parrhinotermes*. In *Serritermes* the position is similar but it faces forward and sideways compared with *Coptotermes*. A distinct, small projection is present on the dorsal margin of the ocellus in *Termitogeton*. The ocellus is proportionally farther from the eye in *Psammotermes allocerus*, *Stylotermes*, *Parastylotermes*, *Macrorhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*. The distance of the ocellus from the eye often varies from species to species within a single genus. Some species of *Heterotermes* have the ocelli reduced or absent.

Antennae. In any sequence of related genera or species, the more primitive taxa have the largest number of antennal articles, although reduction may be analogous rather than homologous. *Coptotermes* has 18-22, *Psammotermes* has 15 or 16, *Heterotermes* has 13-19, *Reticulitermes* has 13-20, *Termitogeton* has 17, *Stylotermes* has 20-22, *Prorhinotermes* has 18, *Macrorhinotermes* has 20, *Rhinotermes* has 20, *Dolichorhinotermes* has 20, and *Serritermes* has 13 or 14. Nearly all species of the Rhinotermitidae have more antennal articles than *Serritermes*, but a rare exception is the fossil *Reticulitermes minimus* with 13 or 14 (Emerson, 1971, p. 280). *Mastotermes* has 30 or 31, *Ulmeriella* has 27-29,

and *Archotermopsis* has 23-27. In some cases there is a correlation between the number of antennal articles and general size, but in several genera the number does not vary with the relative size of the head.

The third article is shorter than or equal to the fourth in *Mastotermes*, *Archotermopsis*, *Ulmeriella*, *Coptotermes*, *Psammotermes*, *Heterotermes*, *Reticulitermes*, *Termitogeton* (some specimens), *Stylotermes*, and *Parastylotermes*. The third article of *Serritermes* is equally primitive. The third article is longer than the fourth in *Termitogeton* (some specimens), *Prorhinotermes*, *Parrhinotermes*, *Macrorhinotermes*, *Schedorhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*—a derived character. Since the third article is the one that divides, variation in its relative length often relates to the number of articles in individuals of the same species or genus.

Mandibles. The most archaic termite mandibles are those of *Archotermopsis*, with three distinct marginal teeth and 10 molar ridges on the left mandible and two distinct marginal teeth, a subsidiary tooth on the front base of the first marginal tooth, and 12 molar ridges on the right mandible. All genera of the Rhinotermitidae have dentition strikingly homologous to that of *Archotermopsis* (Emerson, 1933, 1971; Ahmad, 1950). The first and second marginal teeth of the left mandible are approximately equal in *Archotermopsis* and *Reticulitermes*, but these proportions may not be of phylogenetic significance in *Reticulitermes*, which is not primitive among the Rhinotermitidae. Because of the numerous primitive characters of *Coptotermes*, its mandibles are also considered primitive among the Rhinotermitidae and are the type from which the mandibles of *Serritermes* probably were derived. The left mandible of *Coptotermes* has three marginal teeth, the first smaller than the second and the second smaller than the third. The molar plate has 13 or 14 ridges and is bordered below by a sharp ridge extending to the base of the third marginal tooth, with a blunt angle (close to a right angle) below the front end of the molar ridges. The right mandible has a large, sharp first marginal tooth, a subsidiary tooth or hump on the front margin near its base, and a blunt second marginal tooth with a long posterior cutting edge between its rounded tip and the base. The molar

plate has about 15-18 ridges and a rounded ridge above the molar plate without a toothlike projection. The proportions of the marginal teeth of the left mandible of *Coptotermes*, *Psammotermes*, *Heterotermes*, *Termitogeton*, and *Prorhinotermes* are similar, but there are small variations in the number of molar ridges (seven or eight in *Heterotermes*). The first marginal tooth of the left mandible is larger than the second in *Stylotermes*, *Parrhinotermes*, *Macrorhinotermes*, *Schedorhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*. The smaller number of molar ridges is derivative in *Serritermes*, but the presence of a few molar ridges is primitive compared with some genera of the Termitidae, particularly in the *Subulitermes* branch of the Nasutitermitinae, in which they are regressed in association with a humivorous diet.

Postclypeus. The short, flat postclypeus of *Mastotermes* and *Archotermopsis* is more primitive than that of any genus of the Rhinotermitidae. The relatively long-arched postclypeus not projecting over the base of the labrum is derivative in *Serritermes* compared with the relatively short (length less than half width) convex postclypeus of *Archotermopsis*, *Coptotermes*, *Psammotermes*, *Heterotermes*, *Reticulitermes*, *Termitogeton*, *Stylotermes*, and *Parastylotermes*. In *Prorhinotermes* and *Parrhinotermes* the postclypeus is wider than long, but is long compared with *Coptotermes*. It has a distinct convex longitudinal median line in *Heterotermes*, *Prorhinotermes*, *Parrhinotermes*, *Schedorhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*. The anteclypeus does not project over the base of the labrum in *Prorhinotermes* and *Parrhinotermes* in which the profile is in line with the top of the head. The sclerotized postclypeus of *Macrorhinotermes* is slightly arched in profile and joins the front of the head with hardly an indentation in the middle which has a shallow groove and a short longitudinal line. The front is nearly straight, and the front of the anteclypeus is rounded and projects over the base of the labrum. The postclypeus is longer than the membranous and softer anteclypeus. The angle between the anteclypeus and labrum is slightly less than a right angle in profile. The anteclypeus projects over the base of the labrum much more in *Schedorhinotermes*, *Rhinotermes*, *Dolichorhino-*

termes, and *Acorhinotermes*. The profile of the junction of the postclypeus with the front of the head is without an angle in *Archotermopsis*, shows a small or slight angle in *Coptotermes*, *Psammotermes*, *Heterotermes*, *Reticulitermes*, *Stylotermes*, *Parastylotermes*, and *Serritermes*, and is without an angle in *Prorhinotermes*, *Parrhinotermes*, *Macrorhinotermes*, and *Schedorhinotermes*. The distinct angle in *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes* is secondarily derivative.

Pronotum. The relatively wide, flatly arched pronotum of the Blattodea, Mastotermitidae, and Kalotermitidae is more primitive than that of the Hodotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae. The most primitive pronotum among the Rhinotermitidae is that of *Coptotermes*, where it is occasionally wider than the head but usually narrower. The width in *Stylotermes*, *Prorhinotermes*, and *Serritermes* is only slightly less primitive compared with *Coptotermes*. The widely concave front margin and the rounded sides of the pronotum of *Mastotermes* and the Kalotermitidae is the most primitive among termites. *Archotermopsis* has a pronotum narrower than the head, sides somewhat convex and angular, and a low ridge behind an indented and slightly lobed front margin—probably more derivative than either *Mastotermes*, *Ulmeriella*, or *Coptotermes*. In *Coptotermes* the front margin is slightly indented as in *Heterotermes* and *Prorhinotermes*, the frontal lobes are not so prominent as in *Serritermes*, there is a low ridge behind the front margin, and the sides are rounded from above as in *Prorhinotermes*, *Parrhinotermes*, and *Serritermes*. *Heterotermes* has more prominent rounded frontal lobes. The front margin has a median projection in *Termitogeton* and an analogous, convex slightly lobed front margin in *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*. The hind margin is straight without an indentation in *Prorhinotermes*, is shallowly concave in *Parrhinotermes* and *Rhinotermes*, and is shallowly indented in *Serritermes*, but no obvious phylogenetic sequence is apparent.

Tibial Spurs. The larger number of tibial spurs are often associated with the inner and outer lateral tibial spines in the Mastotermitidae, Kalotermitidae, and Hodotermitidae that antedate the loss of lateral spines in the Rhinotermitidae. The

prothoracic, mesothoracic, and metathoracic spurs are 3/4/3-4 in *Mastotermes*, 3-5/3/2-3 in *Archotermopsis*, and 3/2/2 in *Coptotermes*, *Psammotermes*, *Heterotermes*, *Reticulitermes*, *Stylotermes*, *Prorhinotermes* (some species), *Macrorhinotermes*, and some specimens of *Parrhinotermes*. The outer spur is shorter than either of the inner spurs in *Prorhinotermes* and *Parrhinotermes* (outer spur not seen in all specimens). The spurs are 2/2/2 in *Termitogeton*, *Parastylotermes*, and some species of *Prorhinotermes*, and in *Rhinotermes*, *Dolichorhinotermes*, *Acorhinotermes*, and *Serritermes*. The 3/2/2 formula is considered primitive in the Rhinotermitidae, and is also primitive in the Termitidae.

Tarsi. The tarsus has four articles in all but two genera of the Rhinotermitidae; five articles in the Mastotermitidae, the primitive Termopsinae, and *Ulmeriella* of the Hodotermitidae; four articles in the Serritermitidae and Termitidae; and only three articles in *Stylotermes* and *Parastylotermes* of the Rhinotermitidae; and rarely in the Termitidae (*Indotermes*). The three-jointed tarsus is used as evidence of family rank by some authors, but does not warrant such a category unless associated with many other sharply defined characters without known intergradations.

A projecting arolium between the tarsal claws is a primitive character of *Archotermopsis*, *Mastotermes*, and numerous genera and species of the Kalotermitidae, but is absent in the Rhinotermitidae, Serritermitidae, and Termitidae.

Wing Scales. The base of the wing behind the humeral suture is retained in all termites when the wings are shed after the colonizing flight. The forewing scale of *Mastotermes*, Kalotermitidae, and *Ulmeriella* conspicuously overlaps the hind margin of the mesonotum and the base of the hind wing scale. The forewing scales of *Archotermopsis* are large, but do not overlap the base of the hind wing scales, whereas in *Coptotermes* the forewing scales slightly overlap the base of the hind wing scales and extend beyond the hind margin of the mesonotum. In some species of *Heterotermes*, they overlap the base of the hind scales, but not the hind margin of the mesonotum. They overlap one-fourth to one-half the length of the hind scales in *Prorhinotermes*, *Parrhinotermes*, *Macrorhinotermes*, *Schedorhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and

Acorhinotermes. The forewing scale is proportionally short in *Psammotermes*, *Reticulitermes*, *Termitogeton*, and all the Termitidae. The proportions in *Serritermes* are intermediate compared with the genera of the Rhinotermitidae. The proportional reduction of the size of the forewing scales is always derivative, but is also a parallel analogy in several independent branches of the Rhinotermitidae.

Wing Membrane. *Archotermopsis*, *Mastotermes*, *Prohrinotermes*, the advanced genera of the Rhinotermitinae, and *Serritermes* lack punctations on the wing membrane. *Coptotermes*, *Psammotermes*, *Heterotermes*, *Termitogeton*, *Stylotermes*, and *Parastylotermes* have rounded punctations or micrasters differing in density, size, and darkness in different species. Although indicating relationships between genera, punctations are probably derivative compared with the ancestry of the Rhinotermitidae, but are associated with other primitive characters in the most primitive genera of the Rhinotermitidae.

Chitinized vertical, parallel, or irregular reticulations between the veins in the apical seven-eighths of the wing are characteristic of primitive and advanced genera, including *Mastotermes*, *Archotermopsis*, *Psammotermes*, *Stylotermes*, *Parastylotermes*, *Dolichorhinotermes*, and *Serritermes* (fig. 3). Pseudo-cross veins or veinlets between the branches of the radial sector (Rs) and the costal margin in the apical fourth of the wing are found in the primitive and advanced genera, and often in those genera in which the reticulations are found only in the apical two-thirds of the wing, such as *Reticulitermes* and *Prohrinotermes*, or are reduced as in *Coptotermes*, *Heterotermes*, *Termitogeton*, and *Schedorhinotermes*.

Wing Venation. The subcosta (Sc) occurs in the forewing of the Hodotermitidae, Mastotermitidae, and Kalotermitidae, and also may be present in the hind wing of the most primitive Mastotermitidae (*Spargotermes*, Emerson, 1965) and Hodotermitidae (*Archotermopsis* and *Zootermopsis*, Emerson, 1933). The more primitive genera of the Rhinotermitidae such as *Stylotermes*, *Parastylotermes*, and some species of *Prohrinotermes*, *Rhinotermes*, and *Dolichorhinotermes* possess a short Sc in the forewing only. *Coptotermes*, *Psammotermes*, *Heterotermes*, *Termito-*

togeton, *Parrhinotermes*, some species of *Dolichorhinotermes*, and *Serritermes* lack Sc beyond the humeral suture, doubtless independently reduced in the different phylogenetic branches.

The radius (R) and radial sector (Rs) have numerous branches joining the costal margin in the Mastotermitidae (*Spargotermes* and *Mastotermes*), nearly all genera of the Kalotermitidae, and in the Termopsinae. An unbranched Rs is close and parallel to the costal margin in all the Rhinotermitidae and Serritermitidae, although there is a little more separation in *Stylotermes* and a slight divergence in the fossil *Parastylotermes*.

The media (M) is a distinct, separated vein at the humeral suture of the forewing and is joined to the Rs a short distance beyond the suture in the hind wing. The position in the middle of the wing tends to be closer to the Rs or about halfway between the Rs and Cu in *Mastotermes*, *Heterotermes*, and *Reticulitermes* but is closer to the Cu in *Archotermopsis*, *Coptotermes*, and other genera of the Rhinotermitidae. The M is more branched in the primitive genera, the branches usually ending near the tip or on the inner margin in the outer half of the wing, but in some cases the branches end in the membrane or occasionally join the Rs or Cu in some specimens. The M is more uniform in *Coptotermes*, *Heterotermes*, and *Reticulitermes*, but is variable and sometimes absent as a distinct vein in some specimens of *Psammotermes*, *Stylotermes*, *Prohrinotermes*, and *Serritermes*. The M is absent in *Termitogeton*. Variability is derivative compared with more uniformity in some genera.

The Mastotermitidae have an anterior cubitus (CuA, or Cu in higher families) and a posterior cubitus (CuP) that is lost in other families. The Cu is unique in *Termitogeton* in having costal branches that fill the area occupied by the M in other genera.

The anal vein (A_1) has numerous short inner branches in the Mastotermitidae, is reduced to two branches or a single vein (A) in the Termopsinae, and is a short single vein in the hind wings of all except one genus of the Kalotermitidae and in *Reticulitermes*, *Stylotermes*, *Parastylotermes*, *Parrhinotermes*, and *Schedorhinotermes*. The hind wing of *Rhinotermes* has a diffuse chitin-

ized area that may be a vestigial anal vein. The A is absent or indistinct in the hind wings of *Coptotermes*, *Psammotermes*, *Heterotermes*, *Pro-rhinotermes*, *Dolichorhinotermes* (similar to *Rhinotermes*), and *Serritermes*. The anal veins in the anal lobe are branched and radiating in the hind wing in some Blattodea, *Spargotermes*, and *Mastotermes*.

Styli. The presence of styli in the male is a primitive character—the more distinct and long the more primitive (*Archotermopsis*, Emerson, 1933, p. 174, fig. 16; *Mastotermes*, Silvestri, 1909, pl. 16, fig. 13). *Coptotermes*, *Psammotermes*, *Heterotermes*, *Reticulitermes*, and *Pro-rhinotermes* have short styli in the male. *Termitogeton*, *Stylotermes*, *Parrhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, and *Serritermes* lack styli—probably an analogous regression in relatively independent phylogenetic branches.

Cerci. Cerci with more than two articles are found only in the most primitive termites, like *Mastotermes* and *Archotermopsis*. Two articles—an apical, and a bulbous basal article—are found in the Rhinotermitidae, Serritermitidae, and Termitidae.

SOLDIER

Size. Large relative soldier size is characteristic of nearly all primitive genera in all families of termites. *Mastotermes* is moderately large. *Archotermopsis* is very large. *Psammotermes allocerus* has robust, large soldiers with a gradation of sizes within the same colony. *Psammotermes hybostoma* has a relatively thicker head than does *P. allocerus*, but the general size of the largest soldiers is not so great as in *P. allocerus*. *Rhinotermes* has moderately large major soldiers. The size is more uniform and relatively smaller in *Heterotermes* (length of head to side base of mandibles, 1.15-2.72 mm.; width of head, 0.68-1.40 mm.), *Stylotermes*, *Pro-rhinotermes*, *Parrhinotermes*, and the major soldier of *Dolichorhinotermes*. The elongated head of *Glossotermes* is moderately small (thickness of head without postmentum, 0.76 mm.; with postmentum, 0.82 mm.). In *Heterotermes* the thickness of the head with postmentum ranges from 0.66 mm. to 1.27 mm. *Serritermes* has a comparatively small, short, thick head.

Soldier Castes. Monomorphic soldiers with biting mandibles are found in all primitive families, although gradation of sizes occurs in *Archotermopsis* and *Psammotermes* and the more primitive genera of the Rhinotermitidae. A sharp dimorphism with a major and minor soldier occurs in *Schedorhinotermes* with a sequence of reduced mandibles in the minor soldier from *Schedorhinotermes* through *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*, the latter genus having a monomorphic minor soldier only with the absence of the biting major soldier. *Serritermes*, with a monomorphic biting soldier, is apparently most closely related to *Glossotermes* in this particular, although few specimens have been collected.

Pilosity. Scattered short hairs on the heads of *Archotermopsis*, *Mastotermes*, and *Serritermes* are considered primitive. *Glossotermes* and *Stylotermes* have scattered, contrasting bristles, which are lacking in *Serritermes*, and the short hairs are reduced. *Glossotermes* has microscopic hairs in the middle of the labrum and two conspicuous short bristles at the tip. *Psammotermes* has microscopic hairs on the top of the head, with relatively long bristles on the ventral side and postmentum. *Heterotermes*, *Pro-rhinotermes*, and *Parrhinotermes* have numerous long bristles on the head with few microscopic hairs. *Termitogeton* has many hairs and numerous bristles. *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes* have long bristles only. The evolution of bristles and reduction of short hairs is considered derivative, although not necessarily homologous in widely separated genera.

Head Capsule. The relatively thick elongated heads of *Mastotermes*, *Glossotermes*, *Heterotermes*, *Reticulitermes*, *Pro-rhinotermes*, and some species of *Parrhinotermes* are considered primitive. The head is relatively wide in *Pro-rhinotermes*, *Rhinotermes*, and *Dolichorhinotermes*. The flattened heads of *Archotermopsis*, some species of *Psammotermes*, *Termitogeton*, and some species of *Parrhinotermes*, that in extreme cases may be lobed at the sides in the rear, are derivative and usually convergent. Both *Glossotermes* and *Serritermes* have convex fronts of the heads in profile, with a shallow concave junction with the vertex and also with the postclypeus. The flatter or very slightly convex front in

Archotermopsis and *Mastotermes* is considered primitive, and increased convexity, ridges, grooves, and lateral humps are deemed derivative in *Psammotermes*, *Heterotermes*, *Reticulitermes*, *Prorethra*, *Schedorhinotermes*, *Rhinotermes*, and *Dolichorhinotermes*. Within the Rhinotermitidae and Serritermitidae, the irregular, flat front of *Psammotermes* and *Termitogeton* and the slightly to more strongly convex front and vertex of *Glossotermes*, *Stylotermes*, *Prorethra*, and *Serritermes* are primitive, but derivative compared with the Mastotermitidae and Hodotermitidae. The shallow longitudinal groove in the front and convex humps on the sides are more developed in *Glossotermes* than in *Serritermes* and even more developed in *Heterotermes* and *Reticulitermes*. The head above the antennal fossae is more convex and bluntly projecting in *Glossotermes* than in *Psammotermes*. Conspicuous protuberances are present above the fossae of *Archotermopsis* (Emerson, 1933, fig. 17). Low ridges above the fossae occur in *Mastotermes*, *Psammotermes*, *Termitogeton*, and *Stylotermes* with some reduction in many other genera of the Rhinotermitidae.

The frontal gland and its fontanelle opening are absent in the Mastotermitidae, Kalotermitidae, and Hodotermitidae. The frontal gland and fontanelle are homologous in the Rhinotermitidae, Serritermitidae, and Termitidae, with a defensive function of the glandular secretion in the soldier caste (see Quennedey, 1973). A relatively small, pear-shaped or oval gland and a fontanelle placed to the rear of the level of the antennal fossae with a angle close to a right angle between the fontanelle and the fossae are characteristic of the more primitive genera such as *Psammotermes*, *Glossotermes* (size of gland unknown), *Heterotermes*, *Termitogeton*, and *Stylotermes*. The frontal gland of *Termitogeton* is pear-shaped but proportionally wider and longer than that of *Serritermes*. *Serritermes* is related to this group of genera, although the fontanelle of *Psammotermes* is slightly larger with a dark edge. The forward position of the large fontanelle and the enlarged frontal gland extending into the abdomen are unique and analogously derived in *Coptotermes*. The fontanelle is placed in a more forward position starting with *Prorethra* and ending with the extreme enlargement of the gland and

far forward position of the fontanelle in the minor soldiers of *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes* in which the gland extends into the abdomen and the secretion functions as a gaseous repellent defense with associated frontal, clypeal, and labral grooves, dispersion hairs, and reduced mandibles.

The Y-suture of the soldiers is distinct and entire in *Mastotermes* and *Archotermopsis*. It tends toward reduction in part or in whole in the Rhinotermitidae with gradations of arms and stem forming evolutionary sequences. In *Termitogeton* the arms are distinct, but the stem is absent. The median stem is distinct in the major soldier of *Dolichorhinotermes*, but the arms are absent (some species). The vestige of the stem at the rear of the head of *Serritermes* (fig. 4) is more primitive than the absence of the Y-suture in such genera as *Glossotermes*, *Heterotermes*, *Prorethra*, *Rhinotermes*, and *Dolichorhinotermes* (some species). The reduction of the Y-suture is probably convergent in several genera.

Postmentum. The proportionally more elongated postmentum of *Glossotermes* (Emerson, 1950, fig. 1), *Heterotermes*, *Termitogeton*, *Prorethra*, *Parrhinotermes*, major soldier of *Schedorhinotermes*, *Rhinotermes*, and *Dolichorhinotermes*, constricted from below and less bulbous in profile, is considered more primitive than that of *Serritermes* (fig. 4). The shape of the postmentum is probably correlated with the relative length of the head.

Compound Eye. Eye spots narrower than the antennal fossae, but with visible ocular sutures, are found in *Mastotermes*, *Archotermopsis*, *Psammotermes*, *Glossotermes* (length of eye 0.13 mm., width of eye 0.10 mm., eye from fossa 0.74 mm., length of fossa 0.15 mm., width of fossa 0.13 mm.), *Heterotermes* (most species), *Termitogeton*, *Stylotermes*, and *Prorethra*. In *Parrhinotermes* the eye spot is present, but irregular and indistinct. In *Rhinotermes* and *Dolichorhinotermes* both major and minor soldiers have very small, light eye spots. The monomorphic minor soldier of *Acorhinotermes* has a distinct, small eye spot. Distinctive pigmented, faceted eyes are present and possibly functional in the Hodotermitinae. Pigmentation and facets are regressed in *Mastotermes* and *Archotermopsis*. Pigmentation and facets show grada-

tions of reduction in the Kalotermitidae, with pigmented facets in *Pterotermes occidentis* that are more reduced in *Neotermes mona* and *N. jouteli*. One undescribed species of *Heterotermes* from New Guinea has a small, pigmented eye spot without a distinct ocular suture and may be primitive in this respect. Facets are vestigial in all the Rhinotermitidae, although some irregularities of the surface may be the last indications of regressed facets. In general, the proportionally larger oval eye with an ocular suture in *Serritermes* is more primitive than in any genus of the Rhinotermitidae.

Ocelli. The presence of vestigial ocelli in *Glossotermes*, some species of *Stylotermes* and *Pro-rhinotermes*, the major soldier of *Dolichorhinotermes*, and in *Serritermes* is a primitive character compared with their absence in *Psammotermes*, *Termitogeton*, *Pro-rhinotermes inopinatus*, *Par-rhinotermes*, major and minor soldiers of *Rhinotermes*, *Dolichorhinotermes* (some species), and the minor soldier of *Acorhinotermes*.

Antennae. The number of antennal articles is greater in primitive genera and reduced in derivative genera. Without exhaustively counting all species of each genus, the approximate ranges are *Mastotermes* 23 or 24, *Archotermopsis* 22-27, *Coptotermes* 14-16, *Psammotermes* 12 or 13, *Glossotermes* 13, *Heterotermes* 12-18, *Termitogeton* 13 or 14, *Stylotermes* 13-19, *Pro-rhinotermes* 16-18, *Parrhinotermes* 13, *Schedorhinotermes* 15 or 16, *Rhinotermes* major soldier 15-17 and minor soldier 15 or 16, *Dolichorhinotermes* major soldier 16 and minor soldier 14-16 (young colony 12), *Acorhinotermes* 15, and *Serritermes* 12 or 13. The comparative reduction of antennal articles in imagoes is correlated with the soldiers that invariably have fewer articles than imagoes of the same genus or species. There is some correlation between the size of the soldier and the number of antennal articles, but in general the trend is toward evolutionary reduction, with only a few exceptions in genera of the Termitidae. It is fairly obvious that reduction has occurred independently in several phylogenetic branches, but the small number in *Psammotermes*, *Glossotermes*, and *Serritermes* possibly is homologous.

The third article is either the shortest or about equal to the short fourth article in the Mastoter-

mitidae, Hodotermitidae, primitive genera of the Rhinotermitidae such as *Coptotermes* and *Heterotermes*, and in *Serritermes*. In *Glossotermes* the third article is about equal to the second and is slightly longer than the fourth. In *Termitogeton* the third may be shorter or longer than the fourth. The third article is conspicuously longer than the fourth in *Psammotermes*, *Stylotermes*, the major and minor soldier of *Rhinotermes*, the major and minor soldier of *Dolichorhinotermes*, with equal length in some minor soldiers, and the minor soldier of *Acorhinotermes*. The antenna is moniliform in termites with the attachments of the articles thicker toward the base than in the more flexible outer portion. In *Serritermes* (fig. 4), the bulging end of the middle articles is unique.

Postclypeus. The postclypeus is separated from the front of the head by a complete, more or less distinct suture in *Mastotermes*, *Archotermopsis*, *Coptotermes*, *Glossotermes*, *Psammotermes hybostoma*, *Heterotermes*, *Stylotermes*, *Pro-rhinotermes*, and *Serritermes*. In *Psammotermes allocerus*, the suture with the front of the head is distinct at the sides but indistinct in the middle. In *Termitogeton* the postclypeus is short, but fused with the front. In *Par-rhinotermes*, the postclypeus is fused with the front of the head. The shape is short and flat in *Mastotermes*, *Archotermopsis*, *Coptotermes*, and *Serritermes*, relatively short and more or less convex in *Psammotermes* and *Glossotermes*, and proportionally longer in *Heterotermes*, *Stylotermes*, *Pro-rhinotermes*, and *Schedorhinotermes*. A shallow longitudinal groove occurs in the middle in *Archotermopsis*, *Psammotermes*, and *Glossotermes*. The groove is more distinct, deeper, narrower, and continuous from the fontanelle to the tip of the labrum in *Parrhinotermes*, *Schedorhinotermes*, the major soldier of *Rhinotermes*, the major soldier of *Dolichorhinotermes* and particularly in the minor soldier of *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*, in which the groove is in an elevated ridge and functions for the dispersion of the frontal gland secretion. This groove is absent in *Coptotermes*, *Termitogeton*, and *Serritermes*, and the front of the postclypeus is emarginate (fig. 4) in contrast to the straight or slightly convex front margin in *Psammotermes*, *Glossotermes*, *Heterotermes*,

Stylotermes, *Prorhinotermes*, and in the major and minor soldiers of *Schedorhinotermes*. The postclypeus and front of the head of *Coptotermes* is highly derivative in association with the forward position of the large fontanelle and the enlargement of the frontal gland. The postclypeus of *Glossotermes* appears to be the most primitive among the Rhinotermitidae, is slightly less primitive in *Psammotermes*, and in somewhat different characteristics is less primitive in *Coptotermes*. *Serritermes* is most closely related to that of *Glossotermes*.

Labrum. The labrum of *Mastotermes* and *Archotermopsis* has a wide, moderately straight front margin, with somewhat convex sides. The labrum of *Prorhinotermes* and *Stylotermes* is tongue-shaped, with a broad, convex front margin without a white lip. It is derivative in *Glossotermes* (Emerson, 1950, fig. 1), particularly in the broadly convex, whitish anterior lip, the horizontal, brownish yellow band in the middle, and the slight constriction of the sides behind the tip. The much more constricted sides, the distinctive smaller tip, and the wider middle portion in *Psammotermes* indicate relationship to *Glossotermes*. The tip of the labrum of *Termitogeton* has a small, pointed hyaline tip, with a slight constriction behind. Although derivative and unique in its shape, the labrum of *Serritermes* (fig. 4) may be remotely related to that of *Glossotermes* and possibly to *Termitogeton*. The elongated narrowly convex or pointed tip of *Coptotermes* and *Heterotermes* is probably analogous to *Serritermes*. The concave or bilobed tip of the elongated labra of *Parrhinotermes*, *Schedorhinotermes*, *Rhinotermes*, and *Dolichorhinotermes* indicates divergent evolution in a separate phylogenetic branch. The major soldier of *Rhinotermes* has a wide labrum with a convex, slightly bilobed front margin, whereas the labrum is narrow and distinctly bilobed in the *Dolichorhinotermes* major mandibulate soldier and extremely narrow, elongate, and bilobed in the minor soldier with vestigial mandibles in *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*.

Mandibles. *Archotermopsis* has the most primitive mandibles among living genera (Emerson, 1933, fig. 20). The marginal teeth and molar plates are easily homologized with the

archaic imago mandibles. The left mandible of the soldier of *Mastotermes* and the primitive Kalotermitidae has three marginal teeth in contrast to the fused first and second of the imago. We assume that the soldier mandibles of the ancestral Rhinotermitidae had three marginal teeth on the left mandible and two distinct marginal teeth on the right mandible. The major soldier of *Dolichorhinotermes* has two distinct marginal teeth on both right and left mandibles and a small toothlike projection on the base of each mandible, but no molar ridges. Two distinct marginal teeth on the left mandible and one on the right mandible are seen in *Parrhinotermes*, *Schedorhinotermes*, and *Rhinotermes* (a small hump close to the base may be a vestigial third marginal on the left mandible, and a minute vestige of the second marginal occurs on the right mandible), but other genera show varying degrees of reduction of marginal teeth, probably analogous in separate subfamilies. The basal portion of the mandible is distinct, with a notch on the outer margin at the junction with the apical portion in the more primitive genera and in *Parrhinotermes*, but less distinct in various derivative genera. Molar ridges are present in *Archotermopsis* and *Parrhinotermes*, but are lacking in all other rhinotermitids and in *Serritermes*. The left mandible of *Glossotermes* has a sharp (60° angle) basal, toothlike projection that is bluntly convex in *Stylotermes* and may be homologous with the smaller, sharper projection in *Serritermes*. The left mandible of *Termitogeton* has a finger-like projection basal to a slight hump that may be a vestigial marginal tooth. The left mandible of *Prorhinotermes* resembles *Stylotermes* with a reduced third marginal and other teeth minute or absent. The right mandible of *Termitogeton* has minute inner serrations, three slightly more visible than others. The right mandible of *Prorhinotermes* has a minute, pointed basal projection and vestigial first and second marginal teeth near the base. The blades of both mandibles curve inward, more so near the tip, and taper to a sharp pointed tip not markedly hooked. *Serritermes* shares a series of serrations with *Glossotermes* and *Psammotermes* with different numbers, proportions, and positions in each genus. Conspicuous serrations are derivative, contrary to Emerson (1971, p. 254, table 2).

all undulations of the inner margin near the apex in some rhinotermitids may be reduced to marginal teeth rather than serrations. *Glossotermes* and *Psammotermes* have tapering blades, which are hooked at the tips in contrast to *Serritermes* (fig. 5). A tooth near the base of the right mandible of *Glossotermes*, together with a small, low, slightly pointed hump between the tip of the marginal tooth and the cutting edge of the blade (not shown by Emerson, 1950, fig. 1) may be homologous with the marginal teeth of *Parrhinotermes*. The outer margins of the base of each mandible of *Glossotermes* and *Psammotermes* are convex. The left mandible of *Glossotermes* possibly indicates the separation of the base from the toothed cutting edge seen in *Parrhinotermes*. The 10 to 12 serrations on the basal two-thirds of the left mandible of *Glossotermes* (Emerson, 1950, fig. 1) are not readily homologized with the marginal teeth of other genera; the inner margin of the blade is concave from the notch to the slightly hooked and upwardly curved tip. The outer margin of the right mandible of *Glossotermes* has a sharp but wide notch at the junction of the blade and base and an evenly convex outer edge behind the slightly hooked tip. The lower edge of the base of the right mandible has a large, blunt, toothlike projection that is probably homologous with the sharp, minute tooth on the base of *Serritermes* (fig. 5). A small, slightly convex hump at the apical portion of the large basal projection of *Glossotermes* is absent in *Serritermes*. In *Glossotermes*, a sharp, deep notch with an angle greater than a right angle is between the inner margin of the blade and the base of the right mandible. The serrations of *Psammotermes* are larger and coarser than in *Glossotermes*, but in both genera the serrations diminish in size from the base to the apex, whereas the reverse is true for *Serritermes* (fig. 5). The bases of the mandibles of *Psammotermes* are proportionally large and primitive. The outer margins have less distinct angles at the junctions of the bases and blades in *Psammotermes hybostoma* compared with those of *P. allocerus*. The concave area between the lower base and upper ridge of *P. hybostoma* is not as marked or sharp as in *P. allocerus*.

Pronotum. The wide, saddle-shaped pronotum of *Mastotermes* and the narrower, angular pronotum

of *Archotermopsis* are both probably derivative from the wider, somewhat arched and flatter pronotum with rounded sides characteristic of several genera of the Kalotermitidae, and with some resemblances to the pronota of many cockroaches. Among the Rhinotermitidae, the most primitive pronotum is that of *Coptotermes* and *Prorrhinotermes* (Silvestri, 1909, fig. 59) with an indented front margin, slightly convex frontal lobes, slightly convex sides, and slightly concave hind margin. The pronotum of *Heterotermes* is narrow, with variations from rounded to straight front lobes, and its sides and hind margin are sometimes emarginate. The pronotum of *Termitogeton* has a bluntly angular, somewhat raised median projection. The pronotum of *Stylotermes* is similar to that of *Prorrhinotermes*, but proportionally longer. Those of *Glossotermes* and *Parrhinotermes* are proportionally narrower than the head. In *Glossotermes* (Emerson, 1950, fig. 1), the frontal lobes are proportionally narrower and more convex than in *Prorrhinotermes*, and the sides are convex, evenly joining the slightly indented hind margin. The pronotum of *Parrhinotermes* is strongly convex in front with a small median indentation, its sides flatly convex, and a hind margin straight, with no indentation. In the major soldier of *Rhinotermes* and *Dolichorhinotermes*, the middle of the front margin is conspicuously raised with a convex lobe which is narrower and more sharply convex in the minor soldier of *Rhinotermes*, *Dolichorhinotermes*, and *Acorhinotermes*. The pronotum of *Psammotermes allocerus* is wide and relatively long, with a small notch in the middle of the front margin, and somewhat concave in the middle of the hind margin. It is about as wide as the head, and the frontal lobes are raised and overlap the back of the flat head. The sides are moderately convex in front, concave or almost straight in the middle, and evenly convex as they join the hind margin. The pronotum of *P. hybostoma* is flatter than that of *P. allocerus*, with less prolonged frontal lobes. *Serritermes* has a unique and highly derived pronotum (fig. 4), but possibly is remotely related to that of *Glossotermes*.

Legs. The close proximity of the right and left coxae is primitive in termite soldiers, including *Mastotermes*, and *Archotermopsis*. The striking bladelike protuberance on the front coxa of *Mas-*

totermes is unique and probably derivative. The separation of the right and left coxae of *Termitogeton* is derivative. The normal relative sizes of the coxae, femora, and tibiae of *Archotermopsis* are primitive and similar to those of *Glossotermes* and *Serritermes*. The coxae of *Prorhinotermes* are moderately swollen, the prothoracic and mesothoracic coxae are close, but the metathoracic coxae are a little farther apart. The coxae of *Parrhinotermes* are similar to those of *Prorhinotermes* except that they are not so swollen. The coxae of all thoracic segments are more separated in *Rhinotermes*. The front coxae of *Acorhinotermes* are close, but the mesothoracic and metathoracic coxae are more separated. The coxae of *Glossotermes* and *Stylotermes* are closer together than those of *Serritermes*. Those of *Glossotermes* are proportionally larger and more swollen than those of *Serritermes*. The markedly swollen femora or tibiae of *Psammotermes*, *Termitogeton*, and *Stylotermes* are derivative and possibly an adaptation to fossorial burrowing. The tibiae of *Glossotermes* are more slender, less wide, and with far less convex margins than the robust tibiae of *Psammotermes*.

The inner and outer spines on the tibiae of the primitive genera *Mastotermes* and *Archotermopsis* are similar to those of the imago caste. Secondary rows of short spines on the front tibiae of some genera of the Rhinotermitidae and Termitidae are derivative and often more developed in the soldier and worker than in the imago. The tibial spurs on the legs of the prothorax, mesothorax, and metathorax have the same formulae as in the imago, and show the same regressions in evolutionary sequences discussed under the imago caste. The tibial spurs are 2/2/2 in the soldier of *Glossotermes*, characteristics that may be a regression homologous with those of *Serritermes*, but as in the imago, reduction of numbers may be analogous on separated branches of the phylogenetic tree. The front tibial spurs of *Psammotermes hybostoma* are thicker than those of *Glossotermes*, but not so dark, thick, and robust as those of *Psammotermes allocerus*. *Psammotermes* is confined to arid steppe and desert soils, and the legs may be derivative adjustments to digging.

The tarsal articles are the same in the soldier as in the imago and follow the same evolutionary trends toward reduction.

Styli. The presence of styli in the soldiers is primitive, the longer and more conspicuous the more primitive. Styli are present in *Mastotermes*, *Archotermopsis*, *Psammotermes*, *Heterotermes* (some species), and *Prorhinotermes*, and absent in *Termitogeton*, *Stylotermes*, *Parrhinotermes*, *Rhinotermes*, *Dolichorhinotermes*, *Acorhinotermes*, *Glossotermes*, and *Serritermes*. Loss of styli in separate branches of the phylogenetic tree is probably analogous, but may be homologous in closely allied genera within the same subfamily.

Cerci. The cercus has five to seven articles in *Archotermopsis* and is twice the length of the stylus. It is moderately long, with five articles in *Mastotermes*, the length about the same as the stylus. In the Rhinotermitidae, Serritermitidae, and Termitidae the cercus is reduced to two articles, the basal one swollen in comparison to the thinner terminal article or joint.

WORKERS AND NYMPHS

Intestines. We include comparisons with other termites described by Noirot and Noirot-Timothee (1965, 1969), with comments based on information supplied by Charles Noirot (personal commun.). The comparisons are confined to the lower families that show relationships to the Serritermitidae. The intestines of the Termitidae are much more varied, doubtless due to the more varied substances ingested and also probably to more varied digestive physiology. Few genera of the Rhinotermitidae have been examined for their intestinal structures, and the few that have are uniform, without much generic variation.

The crop is symmetrical in the Rhinotermitidae, but is slightly asymmetrical in *Serritermes*.

The armature of the gizzard of *Coptotermes* and *Reticulitermes* consists of sclerotized surfaces of 24 folds divided into three types or orders (Noirot and Noirot-Timothee, 1969, pp. 54-55, fig. 2). Twenty-four small folds of the fourth order do not have sclerotized cuticles. In the anterior region of the gizzard, the six folds of the first order and six folds of the second order have thick cuticles and partial sclerotization, but in the posterior region, the first order folds are prolonged, and have a thick but unsclerotized

cuticle. The 12 folds of the third order protrude less in the posterior region than in the anterior region, but their cuticle is sclerotized in both regions. The folds of the gizzard of *Serritermes* are reduced to 24, but project very little and have no sclerotization. Those present have very reduced cuticular armature in comparison with *Reticulitermes*, but possibly are homologous with the first, second, and third order folds, whereas the 24 fourth-order folds are absent. The reduction of the armature has no equivalent among the lower families of termites.

The middle intestine shows no differences between the Rhinotermitidae and Serritermitidae.

The Mastotermitidae has 12-15 Malpighian tubules, whereas the Termopsinae (Hodotermitidae), *Anacanthotermes*, (Hodotermitinae, Hodotermitidae), *Kalotermes* (Kalotermitidae), and *Coptotermes*, *Reticulitermes*, and *Rhinotermes* (Rhinotermitidae) have eight. The Serritermitidae have eight, whereas the known genera of the Termitidae have two or four, usually four.

The hind intestine is similar to that of the lower termites below the Termitidae, although the enteric valve differs.

In the opinion of Charles Noirot (personal commun.), the characters of the digestive tube by themselves do not warrant family status, but are not incompatible with family rank. The discovery of flagellates in the intestines by Noirot is consistent with a relationship to the lower families of termites (Krishna, 1970, p. 139). Emerson (1971) has discussed the correlations of the taxonomy of the flagellates and their hosts. Alcoholic preservation does not allow exact description and classification of the flagellates, but R. L. Araujo (personal commun.) has preserved specimens of *Serritermes* in Schaudinn's fluid, and it is hoped that this material will enable accurate determinations and comparisons of genera and species of flagellates.

Sternal Glands. The sternal glands are on the third, fourth, and fifth sternites of *Mastotermes* (Noirot and Noirot-Timothee, 1965). They are on the fourth sternite only in *Stolotermes*, *Porotermes*, and the Hodotermitinae. They are at the anterior border of the fifth sternite only in the Termopsinae (Hodotermitidae), Kalotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae. The position on the fifth sternite is

possibly an analogous reduction in the Kalotermitidae, and a homologous reduction in the Termopsinae and the more advanced families. The comparative ultrastructure and histochemistry of a related series of genera may provide further evidence of systematic relationships (see Quennedey, 1969, 1971b, 1972).

Seminal Vesicles. The presence of seminal vesicles in the lower families including the Serritermitidae and their absence in the Termitidae (Weesner, 1969b, p. 153) indicate an evolutionary reduction, but the details of the structure in related series are insufficient for adequate comparison between taxa.

PHYLOGENETIC INFERENCES AND INTERPRETATIONS

The principles of phylogenetic inference from taxonomic data are summarized for the Kalotermitidae by Krishna (1961, pp. 309-310, fig. 81) and for the Rhinotermitidae by Emerson (1971, pp. 248-254, 265-266, tables 1, 2, fig. 1). In the present attempt to postulate the ancestry of the Serritermitidae, a few points need emphasis.

Nearly every individual organism combines ancient homologous monophyletic primitive characters with derived characters of comparatively more recent origin. Homologous characters in compared organisms seldom have 100 percent identity. Derived characters may be homologous, but are often analogues without shared genetic origin. In termites, derived characters are more often regressions or losses, but some are progressive adaptations, particularly the defensive functions of the soldiers or the nutritive and nest-building functions of the worker-like nymphs or the true sterile workers. Since the genome is usually identical through equational mitosis in a single individual organism, the explanation of differences in rates of evolution of primitive and derived characters is found in the ontogenetic expression of gene systems under different physiological, developmental, or environmental conditions. Of course the ontogenetic lability may be based upon homologous genetic capacities to react to different stimuli.

The castes in the same colony are epigenetic modifications resulting from highly similar genomes from the same king and queen. Deriva-

tions of multiple gene epigenetic characters gradually evolve with many gradations. A homologous derivative character can be considered primitive when compared with even more derived types. Comparative indications of the phylogeny of the reproductive imago caste and the sterile soldier caste provide fine examples of the genetic evolution of epigenetic enhancement or inhibition during development. (In the most primitive termites, soldiers occasionally lay unfertilized eggs which may hatch into parthenogenetic nymphs.)

In the case of the frontal gland of the higher families, the defensive function is largely confined to the soldier so far as is known, although poorly developed glandular tissues opening through distinct fontanelles are found in the imagoes and workers including those of the soldier-less genera of the Termitidae. More histological and biochemical study of possible glandular defensive functions of imagoes and workers is needed. It is probable that the defensive frontal gland is selected primarily in the soldier, but is genetically transmitted only in the reproductive caste. This is a strong indication of the selection of the population unit as a whole, thus illustrating a connecting principle between the genetic unity within an individual and a genetic unity of a social population of individuals, a principle that is basic to the concept of the social supraorganism. The significance of the above homology and the much more common analogy between an individual and a population has been negated, attacked, or severely criticized by numerous distinguished biologists, but upheld by others who may, however, use different terms for social unitary systems.

It is obvious that the structures of the soldier are much farther removed from the ancestral blattoid insect than are those of the imago. For this reason, soldier traits more often are derivative regressions or are adaptively progressive with a greater possibility that similarities between different taxa are parallel or convergent rather than genetically homologous. Nevertheless, comparative soldier structures can be postulated to be primitive or derivative, and the consistent constellation of many characters often is correlated with phylogenetic inferences drawn from the imago caste.

The retention of primitive characters by several taxa allows the postulation of the unknown ancestral stem, whereas derivative characters indicate the branching of the phylogenetic tree. Primitive characters may be assumed to be homologous (Emerson, 1961), but derivative characters may be either homologous or analogous. It is often difficult to determine whether they are monophyletic or polyphyletic. Difficulties of interpretation result from the extinction of intergrades without many known fossils, the few samples examined for many important and unrecorded characters, and the complicated mixture of homology and analogy in derived characters. However, once a primitive character is lost or reduced, it is almost never regained or redeveloped in later more advanced taxa (Dollo's Rule). As we know that the genetic capacity for the development of a compound eye is unimpaired in the reproductive imagoes of all termites, one might expect that the regression of the soldier eye could be reversed by relatively simple ontogenetic changes in phyletic sequences, but no such case of reappearance is known, and many other comparative regressions follow a similar unidirectional evolution. The most plausible explanation is that there are multiple gene effects upon both regressive inhibition and complex progressive functional adaptations, although regression often is more simple genetically than progression (Emerson, 1961).

Evidence is increasingly convincing that effective parts of gene systems have a high order of identity over periods of time encompassed by the evolution of the Isoptera from ancestral cockroaches. This genetic identity does not negate a great deal of genetic change, and it is the relation between identity and change that we attempt to elucidate in this study of the ancestry of the Serritermitidae.

THE ISOPTERAN STEM

By combining the primitive characters in the Mastotermitidae and Hodotermitidae, one can postulate the characters of the unknown ancestral termite which arose from a blattoid ancestor closely similar to the living cockroach *Cryptocercus punctulatus* Scudder of North America. Like all living primitive forms, *Cryptocercus* has

some derivative characters, in this case exemplified by the loss of wings.

The hypothetical ancestral isopteran imago was of large size; had the head and wing pilosity of *Mastotermes* and *Archotermopsis*; a complete epicranial suture (Y-suture); the large lenticular eye of *Archotermopsis* and *Ulmeriella* (Emerson, 1968b); the two ocelli of *Mastotermes*; antennae with 30 or more articles and a short third article; mandible dentition close to *Cryptocercus* and *Archotermopsis*; a short flat postclypeus; a wide pronotum with the concave front margin and rounded sides of *Mastotermes*; up to five spurs on some of the tibiae; two rows of lateral inner and outer spines on the middle tibiae; a five-jointed tarsus with an arolium between the claws; humeral sutures separating the basal scales from the apical portions of both wings (weaker in the hind wing); the forewing scale large and overlapping the hind wing scale; no punctations on the wing membrane; chitinous reticulations covering seven-eighths of each wing between the veins; wing venation resembling the forewing of *Mastotermes* (Silvestri, 1909, figs. 10, 12) with the Sc, R₁, R₂, R₃, Rs, M, and Cu separated beyond the suture; the hind wing resembling that of *Spargotermes* (Emerson, 1965, fig. 4), with separated Sc, R₁, R₂, R₃, Rs, the M joined with the Rs close to but beyond the humeral suture, anterior Cu, posterior Cu, first anal (A₁), radiating branches of the anal field with many secondary branches in a large anal lobe; long styli in the male and also probably in the female; many-jointed cerci with at least nine articles; and blattoid-like male and female reproductive organs and appendages (Browman, 1935). A large monomorphic soldier was the only nonreproductive caste, resembling *Archotermopsis* (Emerson, 1933, figs. 17-20) more closely than any other living termite, with short scattered hairs on the head; large size; a thick head without hind lobes, a pigmented and faceted, reduced eye, resembling that of the soldiers of the Hodotermitinae; a vestigial ocellus, resembling that of *Mastotermes*, primitive rhinotermitids, and *Serritermes*, but lost in the Kalotermitidae, higher Rhinotermitidae, and Termitidae; 27 or more antennal articles, with the third short; a short postclypeus; a tongue-shaped labrum with a straight or slightly convex front margin; elongated mandibles with

dentition easily homologized with that of the imago and resembling that of *Archotermopsis*, with many molar ridges on the bases; a flatly arched pronotum; the left and right coxae nearly touching; normal unswollen proportions of the femora and tibiae; numerous tibial spines and spurs; a five-jointed tarsus without arolium; long styli; many-jointed cerci; and reduced organs of reproduction. A true sterile worker caste was absent, but the pseudergate nymph had at least 12-15 Malpighian tubules, sternal glands on the third, fourth, and fifth sternites, seminal vesicles, and the hind gut filled with many genera of wood-ingesting zooflagellates. This archaic ancestor probably lived in wet logs, used its excrement to build partitions between the excavated galleries in logs, and inhabited temperate latitudinal or altitudinal climates similar to the ecology of *Cryptocercus*, *Archotermopsis*, and *Porotermes* on the continuous land mass of Pangaea before the split in Permian or lower Triassic times into southern and northern continental masses.

Of the 64 independently variable characters compared in all castes and nymphs of *Mastotermes* and *Archotermopsis*, 18 are more primitive in *Mastotermes*, 34 are about equally primitive in both genera, four are equally derivative compared with the blattoids and the Hodotermitinae, and eight are more primitive in *Archotermopsis*. Not only do these two genera show many primitive characters in the living species, but each has a long history possibly as far back as the Triassic. *Mastotermes* fossils occur in the Eocene, *Archotermopsis* in Baltic amber of late Eocene or early Oligocene age (Emerson, 1933, 1965), and an advanced hodotermitid, *Cretatermes*, is known from the mid-Cretaceous (Emerson, 1968a).

THE MASTOTERMITIDAE-KALOTERMITIDAE STEM

The possible homologous derivative characters of the Mastotermitidae-Kalotermitidae branch from the primitive isopteran stem are a fused first and second marginal tooth of the left imago mandible, a rounded eye with a flat anterior margin, and the position of the media vein (M) which ends close to the tip of the wing and tends to be halfway between the radial sector (Rs) and

the cubitus (Cu) or closer to the Rs than to the Cu in the middle of the wing. A number of homologous characters (at least six), including a wide, flatly arched pronotum with a concave front margin in the Mastotermitidae and Kalotermitidae, differ from the derived characters in the Hodotermitidae-Rhinotermitidae branch (Silvestri, 1909; Krishna, 1961; Emerson, 1969, pp. 4-7, 10, figs. 1, 2).

As the Kalotermitidae branched from the common stem of the Mastotermitidae-Kalotermitidae, eight regressions in the imago, analogous to similar reductions in the advanced genera of the Hodotermitidae-Rhinotermitidae branch, occurred. These include a lesser number of antennal articles (24-26 in *Prokalotermes*, Emerson, 1969, p. 12), a four-jointed tarsus, consolidation of portions of the wing venation, loss of the posterior cubitus (CuP), loss of the lobe of the hind wing with its branched anal veins, a two-jointed cercus, eight Malpighian tubules, and the sternal glands confined to the fifth sternite. The soldier of the Kalotermitidae lost the ocellus spot, but in some genera retained three marginal teeth in the left mandible, which can also be detected in *Mastotermes*. This is a rare case of a character more primitive in the soldier than in the imago of the same species.

Where the reduction resulted in a similarity of derived characters in other branches from the primitive isopteran stem, these characters are guessed to be analogous, but it should be emphasized that such postulates rest upon meager data with alternative hypotheses possible if homology and analogy have been confused. An alternative hypothesis is the separate radiation of the Mastotermitidae and Kalotermitidae from the primitive isopteran stem with the retention of many homologous primitive characters and parallel reduction of numerous analogous derivative characters.

THE HODOTERMITIDAE-RHINOTERMITIDAE STEM

The hypothetical ancestor of the Hodotermitidae and Rhinotermitidae possessed most of the characters of the primitive isopteran stem including the blattoid lenticular eye, two ocelli, and blattoid dentition of the left mandible.

However, it also had the following derivative characters: a reduction of the radius (R), loss of the posterior cubitus (CuP) and the anal lobe of the hind wing, the media (M) closer to the Cu than to the Rs in the middle of the wing, and the sternal glands on the third sternite possibly lost. An alternative hypothesis is the independent radiation of the four more primitive families from the primitive isopteran stem.

As the Hodotermitidae branched from the Hodotermitidae-Rhinotermitidae stem, the ocelli were lost, the pronotum became narrower, the front margin became less concave, and the Malpighian tubules were reduced to eight (possibly independently of the reduction to eight in the Kalotermitidae).

An early splitting of the Hodotermitidae probably occurred, as the Stolotermitinae, Porotermitinae, and Hodotermitinae retained sternal glands on the fourth sternite only, whereas the Termopsinae retained sternal glands on the fifth sternite only, a character that also occurs in the Rhinotermitidae—possibly a homologous reduction. If so, the loss of the ocelli in all subfamilies of the Hodotermitidae may not be homologous in every case.

THE RHINOTERMITIDAE STEM

A number of primitive characters were retained in the ancestral Rhinotermitidae as it separated from the Hodotermitidae-Rhinotermitidae stem, notably the head shape of *Mastotermes*, the archaic blattoid dentition of the left imago mandible, the subsidiary tooth on the front base of the first marginal tooth of the right mandible seen in *Archotermopsis* and all the Rhinotermitidae, the two ocelli of the Mastotermitidae, a short third antennal article, the head and wing pilosity close to *Archotermopsis*, a short, flat postclypeus, a wide pronotum with rounded sides, a large forewing scale overlapping the hind wing scale, chitinous reticulations covering seven-eighths of the length of the wing, a monomorphic thick-headed soldier, eye and ocellus spots in the soldier, sternal glands on the fifth sternite of the worker, seminal vesicles, and wood-ingesting zooflagellates. Symbiotic cellulose-digesting flagellates are found in all families of termites except the Termitidae, and

coevolve with their hosts (Emerson, 1971).

The derivative characters of the imago (Emerson, 1971, pp. 243-254, table 2) have included a trend toward some reduction of the Y-suture; a rounded eye; some reduction in the number of antennal articles (22 or less); a straighter front margin of the pronotum with a small median indentation; the loss of all lateral tibial spines; reduction of the spurs to 3/2/2; reduction of tarsal articles to four; loss of the arolium; shortening of the male styli; strengthening of the humeral suture of the hind wing; reduction of the Sc in the hind wing; and loss of R_1 , R_2 , and R_3 in the forewing. The facets of the eye of the soldier have become vestigial, the third marginal tooth of the left mandible has been reduced, and the soldier styli shortened. In addition to these regressive reductions and losses, the soldier acquired a defensive frontal gland and fontanelle opening at the junction of the arms of the Y-suture. There is also some indication that the queen became larger with a greater reproductive capacity of her ovaries, the social life of the colony became more complex, the worker caste more differentiated from the pseudergate nymphs (a true worker caste seems to have evolved independently in the Hodotermitinae), excrement was used more for nest and tunnel building, and the moist tropical soil and soil-connected wood were invaded; this group was later to be superseded to a large degree by its more advanced descendants, the Termitidae.

The closest living hodotermitid with many features of the ancestral rhinotermitid is *Archotermopsis*, which, however, evolved some independent derivative characters. Comparison of the 53 independently variable characters of all castes in *Archotermopsis* with those in the hypothetical primitive rhinotermitid, shows 17 to be clearly more primitive in *Archotermopsis*, 23 equivalently primitive in both (four of which are equally derivative compared with *Mastotermes*), seven more clearly derivative in *Archotermopsis* and more primitive in the ancestral rhinotermitid, and six characters to have inconclusive phyletic trends.

It is tentatively postulated that the ancestral rhinotermitid branched off from the primitive isopteran stem or the more advanced hypothetical ancestor of the Hodotermitidae-Rhino-

termitidae branch. No living or fossil genus of the Rhinotermitidae possesses all the postulated primitive characters, and each subfamily has derived characters not shared with other subfamilies (Emerson, 1971, pp. 251, 254, 256, fig. 1). The relative degree of primitiveness or derivativeness of living subfamilies or genera is statistical. Relations between some genera are better understood than others, and in one case (*Schedorhinotermes*) the living genus is very close to the ancestor of another (*Rhinotermes*).

THE SERRITERMITIDAE BRANCH

Of 63 characters of the ancestral rhinotermitid and the castes of *Serritermes* compared, 24 are more primitive in the ancestral rhinotermitid; 32 are equally primitive in both families, although several of these are derivative compared with the lower families; no characters are more derivative in the ancestral rhinotermitid than in *Serritermes*, although the soldier eye is proportionally larger in *Serritermes* than in any known genus of living Rhinotermitidae and was as large presumably in the ancestral rhinotermitid; and seven compared characters do not show obvious or clear phyletic trends.

Of the 43 compared characters of the imago, workers, and nymphs of *Coptotermes* and *Serritermes*, 13 are more primitive in *Coptotermes*, 17 are equally primitive in both genera, two are equally derivative in both genera but not necessarily homologous, five are more primitive in *Serritermes*, and the trend is not clear in six characters. Of the 24 compared characters of the soldier, five are more primitive in *Coptotermes*, five are equally primitive in both genera, three are equally derivative in both, five are more primitive in *Serritermes*, and the trend is not clear in six characters. *Coptotermes*, combining 67 characters of all castes, has a generally more primitive imago, but a markedly derivative soldier that is not closely related to any other rhinotermitid genus. It could not possibly be very close to the ancestor of *Serritermes*.

Of the 56 compared characters of the imago and soldier of *Psammotermes* and *Serritermes*, 12 are more primitive in *Psammotermes*, 16 are equally primitive in both genera, nine are equally derivative in both genera of which six are

possibly homologous, 11 are more primitive in *Serritermes*, and the trend is unknown or not clear in eight characters. *Psammotermes* and *Serritermes* seem to be remotely related, but neither could have evolved directly from the other. The imago of *Psammotermes* in general has more derivative characters than *Coptotermes*, but more primitive characters than *Serritermes*.

The imago of the Heterotermitinae (*Heterotermes* and *Reticulitermes*) has fewer primitive characters and more derivative characters than either the Coptotermitinae or Psammotermitinae and, with the soldier characters added, is less close to the ancestry of the Serritermitidae than to the Psammotermitinae (Emerson, 1971, pp. 265, 272).

Among the rhinotermitid genera, the soldiers of *Psammotermes* and *Glossotermes* are most closely related, each with distinctions in both primitive and derivative characters, but both included in the subfamily Psammotermitinae.

Unfortunately, the imago of *Glossotermes* is unknown. Of the 45 compared soldier characters of *Glossotermes* and *Serritermes*, 16 are more primitive in *Glossotermes*, 11 are equally primitive in both genera, seven are equally derivative in both genera and all are possibly homologous regressions, seven are more primitive in *Serritermes*, and the trend is unknown (size of frontal gland of *Glossotermes*) or not clear in four characters.

Comparisons of soldiers are not so indicative of phyletic trends as are comparisons of imagoes with additional worker-nymph characters. However, *Glossotermes* is more closely related to *Serritermes* than to the soldier of any other rhinotermitid genus. Because of this, it is possible to divide some characters into independent variables (labrum, mandibles, and pronotum in particular). The Neotropical distribution of both genera may not be a coincidence. The serrated mandibles of *Psammotermes* (Ethiopian, Malagasy, Oriental, and Palaearctic), *Glossotermes* (Neotropical), and *Serritermes* (Neotropical) are considered derivative compared with mandibles having larger and more distinct marginal teeth. The mandibles of *Glossotermes* are more primitive than those of *Psammotermes*. The mandibles of *Serritermes* may have evolved from an ancestral genus remotely related to *Glossotermes*. The

highly derived *Serritermes* could not have evolved directly from *Glossotermes*, and the gap is sufficient to warrant different family status. The Serritermitidae could have originated from an unknown genus related to *Glossotermes* and also related to the common ancestor of *Glossotermes*, *Psammotermes*, and possibly to the highly derived *Termitogeton*. When the imago of *Glossotermes* is discovered and compared, the relations with *Serritermes* and other genera will be better understood.

We draw the tentative conclusion that the Serritermitidae can be traced backward to an origin from the base of the Psammotermitinae, and in sequence back to the primitive rhinotermitid stem, to the hodotermitid-rhinotermitid stem, or to the primitive isopteran stem that arose from primitive blattoids possibly as early as Permian times.

A large number of characters, including the dentition of the imago and soldier mandibles, the marked differences in the intestinal structures, the reduction of the Malpighian tubules to four and in some cases to two, the loss of xylophagous flagellates, and the retention of the frontal gland and sternal glands on the fifth sternite, strongly indicate the separate origin of the Termitidae from the Rhinotermitidae independently of the Serritermitidae.

TIME OF ORIGIN OF TERMITE FAMILIES

The constellation of primitive and derivative characters of each family, the coevolution of flagellates and termitophilous beetles, and the geographical distribution related to continental drift provide some evidence for the time of origin of each known family (Emerson, 1971, pp. 255-257). The Mastotermitidae possibly branched off early in the Mesozoic. The Hodotermitidae probably appeared by Triassic or early Jurassic times before the breakup of the southern continents from Gondwana. The Kalotermitidae probably originated before Africa and South America were separated in mid-Jurassic or Lower Cretaceous times. The Rhinotermitidae probably appeared in late Jurassic or Early Cretaceous (Emerson, 1971, fig. 1), and the Termitidae in the Cretaceous when northern tropical connec-

tions between Asia and the Americas existed. The primitive Rhinotermitidae originated in tropical Asia, and ultimately gave rise to the Neotropical Serritermitidae, but family distinctions may not have evolved until the Tertiary. The most specialized Termitidae of the subfamilies Termitinae and Nasutitermitinae had arisen by mid-Cretaceous before the Old World and New World tropics were separated by sea barriers. The data are insufficient for more than speculation about the time of origin of each family, but the geographic patterns of related taxa make some postulates more probable than others, and increasing information should provide some tests of alternative hypotheses.

LITERATURE CITED

- 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 (Lahore)*, vol. 4, pp. 33-198, i-xii.
- Araujo, R. L.
1970. Termites of the Neotropical region. In Krishna, K., and Frances M. Weesner, *Biology of termites*. New York and London, Academic Press, vol. 2, pp. 527-576.
1972. Notes on the geographical distribution of *Serritermes* (Isoptera). *Rev. Brasileira Ent.*, vol. 19, no. 9, pp. 67-70.
- Armbruster, L.
1941. Über Insektenstaaten der Vorwelt. 1. Miocene Randeker Termiten. *Arch. f. Bienenkunde*. Leipzig und Berlin, vol. 22, pp. 3-43.
- Bates, H. W.
1855. Proceedings of Natural-History Collectors in Foreign Countries [Communicated by Mr. S. (Samuel) Stevens]. *Zoologist*, vol. 13, ser. 1, pp. 4549-4553.
1863. *The naturalist on the River Amazons*. London, John Murray, 2 vols.
1892. *The naturalist on the River Amazons*. London, John Murray, 2 vols. (reprint).
- Bathellier, J.
1927. Contribution à l'étude systématique et biologique des termites de l'Indochine. In Gruvel, A., *Faune des colonies françaises*. Paris, vol. 1, no. 4, pp. 125-365.
- Browman, L. G.
1935. The chitinous structures in the posterior abdominal segments of certain female termites. *Jour. Morph.*, vol. 57, pp. 113-129.
- Chatterjee, P. N., and M. L. Thakur
1964. *Sarvitermes faveolus* gen. et. sp. nov. from Kulu Valley (Punjab: India) [Isoptera], with a discussion on the systematic position and relationship of the family Stylotermitidae. *Zool. Anz.*, vol. 173, pp. 149-162.
- Desneux, J.
1904. Isoptera. Fam. Termitidae. In Wytsman, P. A. G., *Genera insectorum*. Brussels, fasc. 25, pp. 1-52.
- Emerson, A. E.
1928. Termites of the Belgian Congo and the Cameroon. *Bull. Amer. Mus. Nat. Hist.*, vol. 57, pp. 401-574.
1933. A revision of the genera of fossil and recent Termopsinae (Isoptera). *Univ. California Publ. Ent.*, vol. 6, pp. 165-196.
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.
1961. Vestigial characters of termites and processes of regressive evolution. *Evolution*, vol. 15, pp. 115-131.
1965. A review of the Mastotermitidae (Isoptera), including a new fossil genus from Brazil. *Amer. Mus. Novitates*, no. 2236, pp. 1-46.
1968a. Cretaceous insects from Labrador 3. A new genus and species of termite (Isoptera: Hodotermitidae). *Psyche*, vol. 74, pp. 276-289.
1968b. A revision of the fossil genus *Ulmeriella* (Isoptera, Hodotermitidae, Hodotermitinae). *Amer. Mus. Novitates*, no. 2332, pp. 1-22.
1969. A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). *Ibid.*, no. 2359, pp. 1-57.

1971. Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera, and reciprocal phylogeny of associated Flagellata (Protozoa) and the Staphylinidae (Coleoptera). *Bull. Amer. Mus. Nat. Hist.*, vol. 146, pp. 243-303.
- Grassé, P. -P.
1949. Ordre des isoptères ou termites. In Grassé, P. -P., *Traité de zoologie*. Paris, Masson et Cie., vol. 9, pp. 408-544.
- Hagen, H. A.
1858a. Monographie der Termiten. Part 2. *Linnaea Ent.*, vol. 12, pp. 1-342, 459.
1858b. Catalogue of the specimens of neuropterous insects in the collection of the British Museum. Part 1. Termitina. London, Taylor and Francis, pp. 1-34.
- Harris, W. V.
1961. Termites. Their recognition and control. London, Longmans, Green and Co., 187 pp.
1962. Classification of the phytophagous Isoptera. *Symposia Genetica et Biologica Italica. Atti Congresso De l'Union Internationale L'Étude des Insectes Sociaux*, Pavia, 9-14 Settembre 1961, vol. 11, pp. 193-201.
- Holmgren, N.
1909. Termitenstudien. 1. Anatomische Untersuchungen. *K. Svenska Vetensk.-Akad. Handl.*, vol. 44, no. 3, pp. 1-215, 76 figs., 3 pls.
1910a. Das System der Termiten. *Zool. Anz.*, vol. 35, pp. 284-286.
1910b. The Percy Sladen Trust Expedition to the Indian Ocean in 1905. No. 8, *Isoptera. Trans. Linnean Soc. London, Zool.*, ser. 2, vol. 14, pt. 1, pp. 135-148.
1911a. Termitenstudien. 2. Systematik der Termiten. Die Familien Mastotermitidae, Protermitidae und Mesotermitidae. *K. Svenska Vetensk.-Akad. Handl.*, vol. 46, no. 6, pp. 1-88.
1911b. Ceylon-Termiten. In Escherich, K., *Termitenleben auf Ceylon*. Jena, G. Fischer, pp. 185-212.
- Krishna, K.
1961. A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). *Bull. Amer. Mus. Nat. Hist.*, vol. 122, pp. 303-408.
1969. Introduction. In Krishna, K., and Frances M. Weesner, *Biology of termites*. New York and London, Academic Press, vol. 1, pp. 1-17.
1970. Taxonomy, phylogeny, and distribution of termites. In Krishna, K., and Frances M. Weesner, *ibid.* New York and London, Academic Press, vol. 2, pp. 127-152.
- Light, S. F.
1934. A world view of termites. In Kofoid, C. A., et al., *Termites and termite control*. Second edition. Berkeley University of California Press, chap. 10, pp. 108-117.
- Mathur, R. N., and O. B. Chhotani
1959. Revision of *Styloterms* Holmgren and Holmgren (Isoptera: Rhinotermitidae: Stylotermitinae). *Zool. Anz.*, vol. 163, pp. 40-53.
- Noirot, C., and C. Noirot-Timothee
1965. La glande sternale dans l'évolution des termites. *Insectes Sociaux*, vol. 12, pp. 265-272.
1969. The digestive system. In Krishna, K., and Frances M. Weesner, *Biology of termites*. New York and London, Academic Press, vol. 1, pp. 49-88.
- Quennedey, A.
1969. Innervation de type neurosécréteur dans la glande sternale de *Kaloterms flavicollis* (Isoptera). Étude ultrastructurale. *Jour. Insect Physiol.*, vol. 15, pp. 1807-1814.
1971a. Les glandes exocrines des termites I. Étude histochimique et ultrastructurale de la glande sternale de *Kaloterms flavicollis* Fab. (Isoptera, Kalotermitidae). *Zeitschr. Zellforsch.*, vol. 121, pp. 27-49.
1971b. Les glandes exocrines des termites II. Organisation de la glande sternale des Rhinotermitidae. Étude ultrastructurale préliminaire. *Compt. Rendus Séances Acad. Sci. (Paris)*, vol. 273, pp. 376-379.
1972. Les glandes exocrines des termites III. Structure fine de la glande sternale de *Trinervitermes geminatus* Wasmann (Termitidae, Nasutitermitinae). *Zeitschr. Zellforsch.*, vol. 130, pp. 205-218.
1973. La glande frontale des soldats de *Schedorhinoterms putorius* (Isoptera): Analyse chimique et fonctionnement. *Insect Biochem.*, vol. 3, pp. 67-74.
- Sen-Sarma, P. K.
1968. Phylogenetic relationship of the termite

- genera of the subfamily Nasutitermitinae (Isoptera, Termitidae). *Oriental Insects*, vol. 2, pt. 1, pp. 1-34.
- Silvestri, F.
 1901. Nota preliminare sui Termitidi sud-americani. *Boll. Mus. Zool. Anat. Comp. Torino*, vol. 16, no. 389, pp. 1-8.
 1903. Contribuzione alla conoscenza dei Termitidi e Termitofili dell-America meridionale. *Redia*, vol. 1, pp. 1-234.
 1909. Isoptera. In Michaelson, W., and R. Hartmeyer, *Die Fauna Südwest-Australiens*. Jena, G. Fischer, vol. 2, pt. 17, pp. 279-314.
- Snyder, T. E.
 1949. Catalog of the termites (Isoptera) of the world. *Smithsonian Misc. Coll.*, vol. 112, pp. 1-490.
- Springhetti, A.
 1963. Sulla struttura della vescicole seminali delle Termiti. *Atti Accad. Naz. Italiana Ent. Rend.*, vol. 11, pp. 212-219.
- Tu, T.
 1955. The termites of China. *Jour. Formosan Sci.*, vol. 9, no. 1, pp. 30-39.
- Wasmann, E.
 1897. Termiten von Madagaskar und Ostafrika. *Abhandl. Senckenbergischen Nat. Gesell.*, vol. 21, pp. 137-182.
- Weesner, Frances M.
 1969a. External anatomy. In Krishna, K., and Frances M. Weesner, *Biology of termites*. New York and London, Academic Press, vol. 1, pp. 19-47.
 1969b. The reproductive system. In Krishna, K., and Frances M. Weesner, *ibid.* New York and London, Academic Press, vol. 1, pp. 125-160.
- Weidner, H.
 1955. Körperbau, Systematik und Verbreitung der Termiten. In Schmidt, H., *Die Termiten*. Leipzig, Akad. Verlagsgesellschaft, Geest und Portig, pp. 5-81.
- Wilson, E. O.
 1971. *The insect societies*. Cambridge, Mass., Belknap Press of Harvard Univ. Press, x+548 pp.

