

Phylogeny of the Nasutitermtinae
and Revision of the Neotropical
Genus *Syntermes* Holmgren
(Isoptera: Termitidae)

by Reginaldo Constantino

B. S., Universidade Estadual Paulista, 1984

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ABSTRACT

The Nasutitermitinae are one of the most diverse subfamilies of termites, with more than 80 genera and 600 known species. Soldiers of most Nasutitermitinae have their heads modified for chemical defense, with a long frontal tube connected to a reservoir of defensive secretions. These nasute soldiers are capable of squirting noxious substances on enemies and have vestigial mandibles. A group of 13 neotropical genera of Nasutitermitinae, the mandibulate nasutes, have soldiers with functional mandibles and various degrees of development of the frontal tube; they have been considered to represent intermediate stages toward the evolution of the nasute soldier, and would correspond to the basal branches of the Nasutitermitinae. This work investigates the phylogenetic relationships of the mandibulate nasutes. A cladistic analysis based on 35 morphological characters indicates that the traditional phylogenies are incorrect and that the mandibulate nasutes form a monophyletic group in which a long frontal tube evolved independently. The analysis of a fragment of the 16S rRNA gene provides some support for the same conclusion, but with lower resolution.

The taxonomy of the genus *Syntermes*, traditionally considered the most primitive of the Nasutitermitinae, is revised, and 23 species are now recognized. Six species are described as new: *S. barbatus*, *S. cearensis*, *S. crassilabrum*, *S. longiceps*, *S. nanus*, and *S. tanygnathus*; the imagoes of *S. aculeosus*, *S. chaquimayensis*, and *S. wheeleri* are described for the first time; two species, *S. bolivianus* and *S. wheeleri*, are revalidated; and six new synonyms are proposed: *S. hageni* (previously treated as a synonym of *S. dirus*) and *S. lighti* are junior synonyms of *S. grandis*; and *S. solidus*, *S. chaquimayensis parvinasus*, *S. emersoni*, and *S. robustus* are junior synonyms of *S. spinosus*. A phylogenetic analysis of the species of *Syntermes* was based on 45 characters indicates that most characters of this genus that have been considered primitive are actually derived.

Based on the cladistic analysis of the mandibulate Nasutitermitinae, *Cahuallitermes*, new genus, is described with two species from tropical North America, *C. aduncus*, new species, from southern Mexico and *C. intermedius*, new combination, from Belize and Honduras.

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INTRODUCTION

Termites comprise the relatively small order Isoptera, with about 2200 known species. Best known for their economic importance as pests of structural timber and other cellulosic materials, termites have also attracted the attention of many biologists because of their unique social systems.

Termites are primarily tropical insects, with very few species living in northern temperate zones. Far more species of termites can be found in one hectare of tropical forest or savanna than the total number found in North America north of Mexico or in Europe (Banks & Snyder 1920; Snyder 1949; Constantino 1992). Because most entomologists live in North America and Europe, the study of termites has been biased toward the few species living in northern temperate regions. Most generalizations about termite biology and social behavior are based on detailed studies of a few North American and European species belonging to the families Kalotermitidae, Termopsidae, and Rhinotermitidae. Family Termitidae, which contains about 70% of all known termite species and is almost exclusively tropical, has been far less studied.

Among the Termitidae, the Nasutitermitinae are one the most diverse subfamilies, with more than 80 genera and 600 species. Soldiers of most Nasutitermitinae show a remarkable modification of the head, which has a long frontal tube with a pore at the tip, connected to a reservoir of defensive secretion that may occupy most of the head capsule. Using this apparatus like a squirting gun, these termites are able to spread noxious substances over enemies. Coincident with the development of this defensive system there was a reduction of the mandibles, which are completely non-functional and vestigial in most genera, the so-called true nasutes. The exception is a group of 13 neotropical genera, the mandibulate nasutes, whose soldiers usually have shorter frontal tubes with a wide pore at the tip, and retain functional and well-developed mandibles.

In this dissertation I will deal with the phylogeny and systematics of this group of 13 genera, which, in traditional phylogenies, have been considered to be the basal lineages of the Nasutitermitinae, with several intermediate forms representing transitional stages in the evolution of the nasute soldier. A cladistic analysis of this group, based both on morphological data and DNA sequences, is presented in Chapter I; a complete revision of the genus *Syntermes*, traditionally considered the most primitive Nasutitermitinae and also the most diverse of the mandibulate genera, is presented in Chapter II; and the description of a new genus based on the cladistic analysis is presented in Chapter III.

CHAPTER I

PHYLOGENY OF THE NASUTITERMITINAE

Termite Phylogeny

The phylogeny of termites remains poorly understood, despite some claims to the contrary (Krishna 1970) and a quite large volume of literature on this subject. Termites were initially thought to be related to Embiidina and Psocoptera (Enderlein 1903), and Burmeister (1839) included them in a group named Corrodentia. Hagen (1869) was the first author to claim a close relationship between termites and cockroaches, a position defended by Handlirsh (1904) and Desneux (1904b), among others. Desneux (1904b) presented a detailed analysis of the available evidence, and introduced the primitive Australian genus *Mastotermes* as strong evidence for a close relationship between Isoptera and Blattodea. He claimed that the presence of an anal lobe on the hindwings of *Mastotermes* would indicate that the homonomous wings of termites are derived and that termites are direct descendants of cockroaches. Holmgren (1909: 130) thoroughly reanalyzed this question, and concluded that termites and cockroaches are sister groups, both descendants of the extinct Protoblattoidea.

Cleveland et. al. (1934), based on their studies of the wood-feeding roach *Cryptocercus punctulatus*, claimed that "the evidence is overwhelming that this roach is either the ancestor of termites or is closely related to the ancestor, which is extinct." Although the idea that a living roach could be the ancestor of an ancient and diverse order of insects is clearly unacceptable, *Cryptocercus* has been considered as an important source of evidence for the relation between termites and roaches. McKittrick (1965), based on some morphological similarities between *Cryptocercus* and *Mastotermes*, proposed that Isoptera, Blattodea and Mantodea should be treated as suborders of Dictyoptera. These three orders form a clearly monophyletic group, but the relationship among them has been obscure.

Martynov (1937) presented the idea that termites are the sister group of Blattodea + Mantodea, a hypothesis also supported by Boudreaux (1979). Hennig (1981) defended a direct sister group relationship between termites and cockroaches. A third possibility is that cockroaches are paraphyletic in relation to termites, if *Cryptocercus* is really more closely related to termites than to other cockroaches. This question was examined by Thorne & Carpenter (1992) in a formal cladistic analysis based on an extensive list of morphological and behavioral characters gleaned from the literature, and their results strongly support Martynov's hypothesis. The same results were obtained by DeSalle et al. (1992) based on DNA sequences of various insects, including a fossil *Mastotermes*, and by Kambhampati (1995) in an analysis of the phylogeny the Blattodea based on ribosomal RNA

genes. Grandcolas (1994), based on a formal cladistic analysis, concluded that *Cryptocercus* is a derived genus of Polyphagidae, and not a primitive and separate lineage of cockroaches. Unfortunately, Kambhampati's analysis did not include any Polyphagidae, and Grandcolas' results were not be tested. Nevertheless, the hypothesis of roach paraphyly in relation to termites seems unlikely, and *Cryptocercus* apparently has no special relation to termites. The monophyly of Isoptera seems to be very well supported and has never been formally questioned.

As for the relationship among different termite families, subfamilies, and genera, no recent analysis is available, and phylogenies are based on subjective interpretation of a few characters, especially the imago-worker mandibles, considered important by some authors. Krishna (1970), claiming that termite phylogeny is relatively well-known, summarized the hypotheses about phylogenetic relationships between genera, most of them produced by A.E. Emerson and his students. Ahmad (1950), one of Emerson's students, presented a phylogeny of termite genera based on a single character, the morphology of the imago-worker mandibles, which was considered conservative. Despite the evident limitations of such a study, Ahmad's work has been considered by many termitologists as the most important reference on termite phylogeny.

A few groups of termites are supported by several unique morphological characters and seem to be monophyletic. One such group is Rhinotermitidae + Serritermitidae + Termitidae, which have the following unique characters in common: 1) wing venation reduced to two sclerotized unbranched veins near the anterior border (Sc+R and Rs) and M and Cu branched and weakly sclerotized; 2) fontanelle and frontal gland present on head, sometimes reduced; 3) spherical spermatozoa (not known for *Serritermes*); 4) tibial spurs reduced to 3:2:2 or 2:2:2. Family Termitidae is a quite heterogeneous group, currently divided into four subfamilies: Macrotermitinae (fungus-growing termites of the Old World), Apicotermitinae (mostly soil-feeding termites, many of them lacking soldiers), Termitinae (a heterogeneous group, probably paraphyletic), and Nasutitermitinae (nasutes and some mandibulates from the Neotropics). Support for the monophyly of Termitidae is limited to: 1) reduction of the number of Malpighian tubules to four; and 2) reduction of the size of the forewing scale (basal portion proximal to the basal suture).

Phylogeny of the Nasutitermitinae

The Nasutitermitinae are characterized by a peculiar modification of the soldier head, which has a long frontal tube with a pore at the tip, connected to a reservoir of defensive secretion that may occupy most of the head capsule. Soldiers of some species are capable of squirting defensive secretion

on enemies. Coincident with this specialization for chemical defense, soldier mandibles became reduced or vestigial.

The current concept of the subfamily Nasutitermitinae was defined by Holmgren (1912), although he referred to it just as *Syntermes-Reihe*, included in his family Metatermitidae (equivalent to modern Termitidae). Hare (1937) introduced the name Nasutitermitinae, and mostly agreed with Holmgren's ideas about the phylogeny of the group. There are two distinct subgroups in this subfamily (Fig. 1): 1) true nasutes (pan-tropical), whose soldiers have a long frontal tube and non-functional mandibles; and 2) mandibulate nasutes (neotropical only), whose soldiers possess functional mandibles and various degrees of development of the frontal tube. According to the traditional phylogenies, mandibulate nasutes represent intermediate steps in the evolution of the nasute soldier. Both Holmgren and Hare considered the origin of the nasute soldier as monophyletic (Figs. 2 and 3).

Ahmad (1950) in his study of termite phylogeny based on imago-worker mandibles, concluded that there are two distinct lineages (Fig. 4) in the Nasutitermitinae: 1) the *Procornitermes-Nasutitermes* branch, with large apical teeth and reduced molar ridges on worker mandibles; and 2) the *Paracornitermes-Subulitermes* branch, with short apical teeth and well-developed molar ridges. Both branches included genera with mandibulate soldiers and true nasute soldiers, and, therefore, the nasute soldier would be diphyletic, a concept that has been widely accepted among termitologists. For example, Sands (1957) studied the evolution of the soldier mandibles of the Nasutitermitinae and introduced a few modifications in Ahmad's phylogeny, but agreed with a diphyletic origin of the nasutes. The idea of several independent origins of the nasutes was further extended by Sen-Sarma (1968), who concluded that the nasutes originated three times (Fig. 5), and, interestingly, assigned ancestral positions for several living genera. Krishna (1970), in a review of the ideas about termite phylogeny (Fig. 6), basically agreed with Sands. The division of the subfamily into the *Procornitermes* and the *Paracornitermes* branches clearly correlates with diet specialization, the first being composed of wood- and litter-feeders and the second of soil-feeders. Different types of worker mandibles are associated with particular feeding habits. Wood-feeders have mandibles with short apical teeth and well-developed molar ridges (Fig. 8), and soil-feeders have mandibles with large apical teeth and reduced molar ridges (Figs. 9). This is a broad generalization and there are also several intermediate types of mandible as well as some apparently specialized types. For example, the worker mandibles of litter-feeding termites like *Syntermes* and *Rhynchotermes* have long, straight cutting edges.

The hypothesis of a diphyletic origin of the nasutes was first challenged by Prestwich & Collins (1981a) based on the chemical composition of the soldier frontal gland secretion. They found that all nasutes produce diterpenes, a group of substances absent in the mandibulate nasutes or any

other group of termites. Miller (1986) conducted a cladistic analysis of the Nasutitermitinae based on a limited number of taxa and characters, which resulted in a poorly resolved cladogram (Fig. 7), but provided good support for the monophyly of the nasutes. The main apomorphies of the nasutes were: 1) vestigial soldier mandibles; 2) fontanelle of soldier very narrow; 3) defensive secretion of soldier with diterpenes; 4) first segment of hindgut cylindrical.

It is interesting that the inclusion of the neotropical mandibulate genera in the Nasutitermitinae has never been questioned, although an exhaustive search of the literature shows that little evidence has been presented to support their relationship with the true nasutes. In fact, the only evidence seems to be the long frontal tube present on the soldiers of some mandibulate genera, which is usually shorter than that of true nasutes and has a much wider opening. An alternative hypothesis would be that the frontal tube evolved independently in these two groups, and the mandibulates might be more closely related to other groups of termites than to the nasutes.

The present chapter deals with the phylogenetic relationships of the 13 genera of Nasutitermitinae with mandibulate soldiers, based both on morphological and molecular data. Two genera of nasutes were also included, to determine whether the analysis would show them to be monophyletic or diphyletic.

Taxa Included in the Analyses

Taxa included in the analysis are listed below, with some data on distribution and natural history. Comments on the monophyly of the various genera are based on a subjective evaluation of literature information and/or examination of representative species. The choice of outgroup and nasute genera was based on the material available for DNA sequencing. Among the nasutes, *Nasutitermes* represents the wood-feeding assemblage and *Cyranotermes* represents the soil-feeding assemblage. According to traditional phylogenies, these two genera are considered to have separate origins from mandibulate ancestors.

Mandibulate nasutes.

Armitermes Wasmann. 11 species; no revision. With the removal of *A. intermedius*, now transferred to *Cahuallitermes*, *Armitermes* seems to comprise a quite homogeneous group of species. But some species are poorly known and a complete revision will be necessary to determine whether it forms a monophyletic group. Present in both forests and savannas of South America, with one species found in Panama. Feeding habits not well known, but certainly include semi-decomposed wood.

Cahuallitermes Constantino. Two species; described in the third chapter and in Constantino (1994). Biology poorly known. Alates unknown.

Cornitermes Wasmann. 13 species; revised by Emerson (1952) and Canello (1989). Certainly monophyletic and very homogeneous. Found in forests and savannas of South America, with one species in Panama and Costa Rica. Feeding habits include semi-decomposed wood, litter, and grasses. Forest species tend to be subterranean, whereas savanna species build very hard, epigeic termitaria with a distinct central core made with carton material.

Curvitermes Holmgren. Three species; no revision. The description of the poorly known species *C. projectidens* suggests that it is misplaced in this genus and probably belongs to *Armitermes*, but the other two species probably form a monophyletic group. These soil-feeding termites are found only in forests and savannas of South America, in the soil or inside nests built by other termites.

Cyrelliatermes Fontes. Five species; no revision. Several species of *Cyrelliatermes* were previously included in *Curvitermes*. The unique shape of the soldier head supports the monophyly of this quite homogeneous group found in forests and savannas of South America. All species feed on humus and are usually found inside nests built by other termites.

Embiratermes Fontes. 14 species; no revision. Most species of *Embiratermes* were previously placed in *Armitermes*. The monophyly of this group is doubtful and it needs a full revision. Found in forests and savannas of South America, with one species in Panama. Mostly soil-feeding. Some species build epigeic termitaria, but most live inside nests of other species.

Ibitermes Fontes. Two species. Poorly known. One species from the Amazon and the other from the Brazilian Atlantic forest. Soil-feeding, found in forests only. Alates unknown.

Labioatermes Holmgren. Four species; revised by Emerson & Banks (1965). Apparently monophyletic, but possibly paraphyletic in relation to *Paracornitermes*. Soil-feeding termites found in forests and savannas of South America. Nests may be arboreal, epigeic, or subterranean, depending on the species.

Macuxitermes Canello & Bandeira. One species. Known only from the type material, from central Amazonia. Alates unknown.

Paracornitermes Emerson. Five species; no revision. The distinct soldier mandible suggests that it forms a monophyletic group. Soil-feeding termites found inside termitaria built by other species, in both forests and savannas of South America. Alates unknown.

Procornitermes Emerson. Five species; revised by Canello (1986). Monophyly poorly supported. Found in forests and savannas of central and southern Brazil.

Rhynchotermes Holmgren. Four species; no revision. Three species from the savannas of

central Brazil to Paraguay and one species from Panama. Feed on surface litter collected in the open at night; found inside termitaria built by other species.

Syntermes Holmgren. 23 species; complete revision in the second chapter and in Constantino (in press).

Nasutes.

Nasutitermes Dudley. Pantropical genus with more than 200 named species. Neotropical species revised by Holmgren (1910b), but that revision is outdated and of limited value. Mostly wood-feeding with some litter-feeding species. Typical nests are arboreal and made of somewhat soft carton material, but some species build hard epigeic termitaria. Possibly paraphyletic in relation to other nasute genera.

Cyranotermes Araujo. Three species from the savannas and forests of Brazil. Soil-feeding termites; live in peculiar subterranean nests.

Taxa included as outgroups.

Rhinotermitidae.

Reticulitermes Holmgren. 13 nearctic and palearctic species. Subterranean and wood-feeding.

Termitidae: Apicotermatinae.

Anoplotermes Fr. Müller. 31 neotropical species. Soldierless termites; feed on decaying wood or soil; most species are subterranean, but a few build epigeic or arboreal nests. Certainly paraphyletic in relation to several other soldierless genera. Poorly studied and diverse group.

Termitidae: Termitinae.

Amitermes Silvestri. More than 100 tropical and subtropical species. Feed on wood or litter; nesting habits variable. Certainly paraphyletic in relation to several genera.

Microcerotermes Silvestri. About 100 tropical species. Wood-feeding; nests usually arboreal, made of hard carton. Apparently monophyletic.

Cladistic Analysis I: Morphological Data

Methods

Most of the information on morphological characters was obtained from the literature

(revisions indicated in the list of taxa above and specific references in the list of characters), complemented by the study of representative species. The digestive tube of *Macuxitermes triceratops* is described in Appendix I for the first time. More detailed information on *Syntermes* and *Cahuallitermes* is presented in Chapters II and III. Characters 11, 19, 20, 22 and 30 were coded as additive because the various states form a simple linear morphocline; characters 5, 26, and 33-35 were coded as non-additive because order was unclear.

The outgroup taxon *Anoplotermes* lacks a soldier caste, which creates problems for coding characters that are only present in soldiers. Because such characters comprise almost half of the data set, coding all of them as missing or unknown may lead to many alternative placements of *Anoplotermes* and greatly decrease the overall resolution of the analysis. Thus, coding of these characters is a hypothesis of the state likely to have been present in the ancestor of *Anoplotermes* and its closest relatives that have soldiers. (Special emphasis is placed on *Speculitermes*, which has at least one species with soldiers and a majority of species that are soldierless).

List of characters

Soldier

1. Mandibles: (0) functional; (1) vestigial.
2. Left mandible: (0) with one marginal tooth or none (Figs. 14-16); (1) with two marginal teeth (Figs. 10-13).
3. Mandibles: (0) slashing type (Figs. 10-12); (1) piercing type (Figs. 13-16).
4. Cutting edge between 1st and 2nd marginal teeth on left mandible: (0) not serrated; (1) serrated (Fig. 12).
5. Molar region of mandible: (0) reduced (Figs. 10-11); (1) well-developed (Fig. 14); (2) absent (Fig. 12).
6. Marginal teeth of soldier mandibles: (0) not like a fish hook; (1) like a fish hook (Fig. 14).
7. Labrum: (0) without a well-developed exocrine gland at tip; (1) with a well-developed exocrine gland at tip.
8. Labrum: (0) uni-lobed; (1) three-lobed.
9. Labrum: (0) short (length equal to or shorter than width); (1) elongate (length greater than width).
10. Head capsule: (0) subrectangular; (1) rounded.
11. Frontal tube: (0) absent; (1) short, not reaching clypeus; (2) long, extending beyond clypeus.

12. Frontal tube: (0) conical; (1) cylindrical.
13. Pore at tip of frontal tube: (0) wide; (1) narrow (Miller 1986).
14. Anterior margin of soldier forecoxae: (0) without a spine-like protuberance; (1) with a spine-like protuberance (Mathews 1977, Figs. 101b and 102a).
15. Foretibia with: (0) 3 apical spurs; (1) 2 apical spurs.
16. Secretion of frontal gland: (0) without diterpenes; (1) with diterpenes (Prestwich & Collins 1981a).
17. Secretion of frontal gland: (0) without macrocyclic lactones; (1) with macrocyclic lactones (Prestwich & Collins 1981b).

Imago-Worker Mandibles

18. Molar region of imago mandible: (0) normal; (1) very narrow (Fig. 43).
19. Molar ridges of worker mandibles: (0) well-developed (Fig. 8); (1) reduced; (2) absent (Fig. 9).
20. Left mandible index¹: (0) less than 0.6; (1) 0.7 - 1.4; (2) more than 1.4.
21. Second marginal tooth of worker right mandible: (0) well developed (Fig. 8); (1) reduced (Fig. 9).
22. Second marginal tooth of left worker mandible: (0) present; (1) reduced; (2) absent.
23. Cutting edge of 1st + 2nd marginal tooth on left worker mandible: (0) not strongly concave; (1) strongly concave (Fig. 9).

Worker

24. Inner margin of tibiae: (0) without an aligned row of short spines; (1) with an aligned row of short spines (Emerson 1952, Fig. 3).
25. Outer margin of femur: (0) without short spines; (1) with short spines.

Digestive tube

26. Mixed segment: (0) well developed (longer than width of midgut) (Kovoor 1969, Fig. 69); (1) reduced (shorter than width of midgut) (Fontes 1987a, Figs. 46-47); (2) absent (Fontes 1987a, Figs 40-41).

¹ Left mandible index = (distance from apical tooth to 1st marginal tooth)/(distance from 1st marginal tooth to 3rd marginal tooth). This index indicates the development of the apical tooth; small values are associated with wood-feeding termites and large values with soil-feeding termites. The 2nd marginal tooth is absent in most taxa represented here.

27. Mixed segment: (0) with single mesenteric prolongation; (1) with 2 unequal prolongations (Kovoor 1969, Fig. 2).
28. Origin of the mesenteric prolongation (radial position relative to mixed segment): (0) ventral (Fig. 66); (1) dorsal (Fig. 396).
29. Mixed segment: (0) tubular (Kovoor 1969, Fig. 9); (1) dilated (Kovoor 1969, Fig 1).
30. First proctodeal segment: (0) tubular (Kovoor 1969 Fig. 9); (1) dilated; (2) strongly dilated and enlarged (Kovoor 1969, Fig 1).
31. Opening of enteric valve: (0) narrow; (1) wide.
32. Enteric valve swellings: (0) without large and thick spines; (1) with large and thick spines (Kovoor 1969, Plate II, Fig 1).
33. Enteric valve swellings: (0) without slender spines; (1) with short slender spines; (2) with long slender spines (Kovoor 1969, Plate II, Fig. 3). Treated as a separate character because both thick and slender pines may be present.
34. Enteric valve with: (0) 6 subequal swellings (Mathews 1977, Pl. 49); (1) 3 large and 3 small swellings (Mathews 1977, Pl. 50); (2) 3 swellings (Fig. 401); (3) a single swelling (Fig. 391); (4) no swellings.
35. Malpighian tubules: (0) 8 inserted radially in the midgut-hindgut junction; (1) 4 inserted on midgut (Mathews 1977, Figs. 36-37); (2) 4 inserted in two separate pairs in the midgut-hindgut junction (Fig. 399); (3) two pairs inserted together in the midgut-hindgut junction (Kovoor 1969, Fig. 6).

Data Analysis

The matrix of character states for the morphological data is presented in Table I. Computer analyses were performed with Hennig86 1.5 (Farris 1988) and with Pee-Wee 2.1 and Nona 1.1 (Goloboff 1993; 1994). Hennig86 and Nona search for most parsimonious trees, i.e., trees with the minimum number of steps or evolutionary changes using equal or pre-defined weights for characters. Hennig86 also performs successive weighting, an iterative procedure in which character weights are determined by the degree of homoplasy of each character in most parsimonious tree(s) previously found. The process of setting weights and searching for shortest trees is repeated until a stable solution is found. Goloboff (1993) pointed out several problems with the successive approximations approach, and proposed the use of implied weights, a non-iterative procedure that estimates character reliability and sets weights during tree search. This procedure is implemented in Pee-Wee, a program that searches for trees with best character fit. In Hennig86 the function mh* was initially used to

produce trees, which were submitted to the branch-swapping function *bb**. Successive approximations were performed with the function *xs w*, followed by *bb**; this process was repeated until the result became stable. In *Pee-Wee* and *Nona*, the option *mult*15* was used, followed by *max** and *jump* if necessary. Character analysis distributions shown in the cladograms (Figs. 17-21) were determined with the computer program *Clados 1.2* (Nixon 1992). Three analyses were performed. Analysis 1A used equal weights for all characters, in *Nona* and *Hennig86*. Analysis 1B applied successive weighting to the results of analysis 1A. Analysis 1C used implied weights with *Pee-Wee*.

Results based on Morphological Data

In analysis 1A, *Hennig86* found three trees while *Nona* found only one, of length = 344, $ci = 0.58$, $ri = 0.73$. However, the trees found by *Hennig86* are of quite similar topology, and their strict consensus tree is identical to the tree found by *Nona* (Fig. 17). The variations shown by *Hennig86* are not accepted by *Nona* because they are supported only under some optimizations (Goloboff 1994). In any case, the differences are only in the position of two outgroup genera, *Amitermes* and *Microcerotermes*. Analysis 1B found the same result as analysis 1A.

Analysis 1C resulted in three trees of $fit = 243.9$ (Figs. 18-20). Their strict consensus tree shows a large polytomy at the base of the clade formed by the mandibulate nasutes (Fig. 21), but the three groups of two or more genera within this polytomy are also supported in all other analyses. These trees indicate a reduction of the soldier frontal tube (character 11). Although this might be possible, I consider it unlikely because the evolution of a long frontal tube involves a specialization towards chemical defense, which seems to be more efficient than simple mechanical defense. Since *Pee-Wee* does not allow irreversible characters, it was not possible to run the analysis under implied weights and with this constraint.

All trees support the monophyly of the nasutes, represented by *Nasutitermes* (exemplar of the wood-feeding nasutes) and *Cyranotermes* (exemplar of the soil-feeding nasutes). There is also support for the monophyly of the mandibulate nasutes and for a sister group relationship between the true nasutes and the mandibulate nasutes. Characters supporting the monophyly of the mandibulate nasutes are the greatly inflated mixed segment (29) and first proctodeal segment (30), the origin of the mesenteric prolongation of the mixed segment (28), and possibly the wide opening of the pore at the tip of the frontal tube (13).

Sister group relationships between *Labiotermes* and *Paracornitermes* and between *Curvitermes* and *Cyrilliotermes* are well supported. Group *Armitermes* + *Curvitermes* + *Cyrilliotermes* is present

in every tree and is supported by the shape of the insertion of the Malpighian tubules (35). *Embiratermes* and *Ibitermes* appear as sister groups in all trees, but support for this relationship is based only on homoplasious characters. A sister group relationship between *Syntermes* and *Cornitermes* is supported by a few characters, especially the shape of the imago mandibles (18-1).

Group *Cahuallitermes* + *Procornitermes* + *Labiatermes* + *Paracornitermes* + *Syntermes* + *Cornitermes* is present in all trees from analysis 1C and is supported by the presence of two unique soldier characters: a large labral gland (7-1) and two marginal teeth on each mandible (2-1). In the same trees, the clade *Labiatermes* + *Paracornitermes* + *Syntermes* + *Cornitermes* is supported by a single unique character, the presence of two mesenteric prolongations on the mixed segment (27-1).

Cladistic Analysis II: Molecular Data

Methods

Termites.

It was not possible to obtain DNA from all taxa included in the morphological analysis. The species included in this study are listed below. Most of them were preserved in 80% ethanol, except for the *Nasutitermes*, which was kept frozen at -70°C. Sequences for *Reticulitermes flavipes* were obtained from GenBank (Kambhampati 1995). Only a few workers from each sample were destroyed, and several voucher specimens were preserved. Some belong to the collections of the Museu Paraense Emílio Goeldi (MPEG), Universidade Federal de Viçosa (MEUV), and the rest are in the author's personal collection and will eventually be deposited in a museum.

Apicotermitinae: *Anoplotermes* sp [COSTA RICA. *Guanacaste*. Palo Verde, coll. R. Constantino, 4.vi.1993, workers]; **Termitinae:** *Microcerotermes exiguus* [COSTA RICA. *Guanacaste*. Palo Verde, coll. R. Constantino, 05.vi.1993, soldiers, workers, alates]; *Amitermes beaumonti* [COSTA RICA. *Guanacaste*. Palo Verde, coll. R. Constantino, 5.vi.1993, soldiers, workers]; **Nasutitermitinae (mandibulate):** *Syntermes nanus* [BRAZIL. *Minas Gerais*. Divinópolis, coll. O.F.Souza, 04.x.93, soldiers, workers, MEUV]; *Procornitermes araujo* [BRAZIL. *Distrito Federal*. Brasília, coll. M.G. Siqueira, 03.vi.1982, soldiers, workers]; *Paracornitermes orthocephalus* [BRAZIL. *Amazonas*. Humaitá, coll. R. Constantino, 20.ix.90, soldiers, workers, MPEG]; *Labiatermes labralis* [BRAZIL. *Amazonas*. Humaitá, coll. R. Constantino, 13.ix.90, soldiers, workers, MPEG]; *Cahuallitermes intermedius* [BELIZE. *Columbia Woods*, coll. W. Steiner Jr., 11.vi.1981, soldiers, workers]; *Embiratermes* sp [PERU. *Loreto*. San Jacinto, coll. R. Leschen, 7.vii.1993,

soldiers, workers]; *Armitermes holmgreni* [BRAZIL. Amazonas. Maraã, coll. R. Constantino, 13.x.88, soldiers, workers, alates, MPEG]; *Nasutitermitinae* (nasutes): *Cyranotermes timuassu* [BRAZIL. Amazonas. Humaitá, coll. R. Constantino, 19.ix.90, soldiers, workers, MPEG]; *Nasutitermes ephratae* [COSTA RICA. Guanacaste. Palo Verde, coll. P. Bardunias, 4.vi.1993, soldiers, workers (frozen)].

DNA Extraction.

The head and thorax of 2-10 workers of the same sample were immersed in distilled water for a few minutes to remove the ethanol, and then transferred to a 1.5 ml microfuge tube containing 500 μ l STE buffer (0.1 M NaCl, 0.05 M Tris-HCl pH 7.5, 0.001 M EDTA, autoclaved) and 25 μ l 20% SDS (Sodium lauryl sulfate). A sterile plastic microfuge pestle was used to grind the tissue. Proteins were digested by adding 25 μ l of 10mg/ml proteinase-K and incubating at 56°C in a waterbath for 2 hours. A 25:24:1 mixture of phenol:chloroform:isoamyl alcohol was added to each tube, vortexed, and centrifuged at 13000 g for 10 minutes. The upper layer was transferred to a new tube, a mixture chloroform:isoamyl alcohol added, vortexed, and centrifuged again. The upper layer was transferred to a new tube, and DNA was precipitated by adding 1/10 volume 3 M sodium acetate and two volumes cold 95% ethanol, and keeping it at -20°C overnight. The samples were then centrifuged at 13000 g for 15 minutes and the alcohol was discarded. The DNA pellet was washed by adding 700 μ l 70% ethanol, centrifuging for 5 minutes, and discarding the alcohol. The DNA was dried in a vacuum centrifuge and resuspended in 100 μ l of 1/10 TE buffer (0.1 mM Tris-HCl pH 7.5, 0.01 mM EDTA, autoclaved).

DNA Amplification (PCR).

The target DNA fragment was amplified with Polymerase Chain Reaction as follows. For each sample, 10 μ l 10X TAQ buffer (Promega), 16 μ l 25 mM MgCl₂, 1 μ l of each primer, 1 μ l NTP mix (Pharmacia, 20 mM each dNTP), 1 μ l DNA, 0.5 μ l TAQ polymerase (Promega), 69.5 μ l sterile water, and one drop of mineral oil were added to a PCR tube. The PCR program was: 94°C for 30 s, 45°C for 1 min, and 72°C for 1.5 min; 40 cycles. The primers used to amplify a 415-bp fragment of the 16S rRNA gene (positions 13000-13415 of *Drosophila yakuba*) were the same as used by Kambhampati (1995).

DNA Sequencing.

The PCR product was purified using minicolumns (Wizard PCR preps, Promega), and sequenced with the cycle sequencing method (fmol Sequencing System, Promega), using ³²P as a marker. The sequencing reaction product was electrophoresed on 6% polyacrylamide gels, and

autoradiographed on X-ray film. Segments close to the primer (about 10 bases) were excluded because they were difficult to read (accurate reading would require additional sequencing with different primers).

Sequence Alignment and Data Analysis.

The sequences were read manually from the autoradiographs and aligned using ClustalW (Thompson et al. 1994) with the default parameters. Alignment was then visually inspected, but no further improvement was possible. The aligned sequences are presented in Table 2. A segment of about 55 Bp was excluded from the analysis because it was too variable to be reliably aligned (Swofford & Olsen 1990: 497). Gaps were treated as a fifth character. Computer analyses were performed with Hennig86 1.5 (Farris 1988), Pee-Wee 2.1 and Nona 1.1 (Goloboff 1993; 1994), in the same manner as the morphological data above. Character analysis distributions shown in the cladograms (Figs. 22-30) were determined with the computer program Clados 1.2 (Nixon 1992). Analysis 2A used Nona and equal weights; analysis 2B used Hennig86 and successive approximations; and analysis 2C used Pee-Wee and implied weights.

Results based on molecular data

Analysis 2A resulted in 10 trees of length 211, $ci = 0.72$, and $ri = 0.41$. Due to major differences in tree topologies (examples in Figs. 22-26), a strict consensus tree (Fig. 27) shows very little resolution. The only two groups supported are the Termitidae and *Labiotermes* + *Paracornitermes*. Analysis 2B resulted in a single tree, which is identical to one from analysis 2C (Fig. 28). Analysis 2C resulted in 4 trees (Figs. 22-23 and 28-29) of relatively similar topology, resulting in a more informative consensus tree (Fig. 30).

An inspection of the distribution of nucleotide substitutions on the various trees shows that there are few non-homoplasious changes supporting most groups. The exceptions are the two groups supported in Analysis 2A (Fig. 27). The sister group relationship of *Labiotermes* and *Paracornitermes* is also well supported by morphological data. The monophyly of Apicotermitinae + Termitinae + Nasutitermitinae in relation to Rhinotermitidae is also expected. The relationships among the other groups are not well supported. Apparently this DNA fragment does not show adequate variation for the relationships under investigation. Most parts of it are too conserved, and a few segments are too variable. With the exclusion of the most variable segment from the analysis, there are only 99 variable sites, of which 29 are autapomorphic changes that do not affect tree topology. Among the remaining possibly informative sites there is a high degree of homoplasy.

Considering only the results of analyses 2B and 2C (Figs. 22-23 and 28-30), in which differential weighting should have reduced the effect of the most homoplasious changes, the general tree topology agrees with the results based on morphological data. These results support the monophyly of the nasutes and a sister group relationship between the mandibulate nasutes and the true nasutes.

DISCUSSION

The morphological data, and to some extent the DNA data, support the hypothesis that the mandibulate nasutes are not the basal branches of the lineage with nasute soldiers, but form a group in which soldiers with a long frontal tube evolved independently. There is also support for a sister group relationship between the mandibulate nasutes and the true nasutes, both originating from an ancestor whose soldier had a short frontal tube. This hypothesis has never been proposed before in the literature, and all previous discussions of the phylogeny of the Nasutitermitinae just assumed that the nasutes originated inside this group of mandibulate nasutes, an idea originally proposed by Holmgren (1912).

It is interesting that in the debates about how many times nasute soldiers have originated, it has always been assumed that elongation of the frontal tube was correlated with a reduction of mandibles, and that mandibulate soldiers with a somewhat elongated frontal tube exemplify intermediate stages in the development of the nasute soldier. Previous authors have not mentioned the possibility that elongation of the frontal tube in mandibulate nasutitermitines may have been a distinct evolutionary event that has not led to the development of nasute soldiers.

Considering the geographical distribution of the nasutes and mandibulates (Fig. 1), the hypothesis that these groups form separate clades makes more sense. Emerson (1955) claimed that South America was the center of origin of the nasutes, which dispersed to other regions through land bridges and that "The failure of the relatively primitive mandibulate genera to move to the Old World under the same favorable climatic conditions may be explained by biotic barriers that could be penetrated only by the highly defended nasute genera." Since the notion of centers of origin in a fixed configuration of continental masses is currently unacceptable due to modern theories of continental drift and vicariance biogeography, Emerson's explanation is no longer satisfactory. The pantropical distribution of the nasutes indicates a Gondwanan or older origin, and they are probably among the oldest lineages of Termitidae. The neotropical distribution of the mandibulates could be the result of a more recent origin, when South America was isolated from other continents, or a relict distribution

resulting from differential extinction. The second possibility seems to be unlikely because the mandibulate Nasutitermitinae are a quite diverse and abundant group of termites, being dominant in several habitats in South America, and it is difficult to imagine what could have caused their extinction in all other tropical areas of the world.

If the trees based on morphological characters are close to the true phylogeny, then the mandibulate nasutes would be the sister group of the true nasutes, both descendants of an ancestor whose soldier had a short frontal tube. However, this sister-group relationship is basically supported by the presence of the frontal tube and there is still the possibility that the mandibulates are more closely related to some Termitinae not included in the analysis. In order to study the latter possibility it would be necessary to conduct a detailed study of the Termitinae, which is beyond the scope of the present work. It should also be noted that the molecular data indicate *Anoplotermes* (Apicotermitinae) as the sister group of the Nasutitermitinae, whereas the morphological data indicate the genera of Termitinae. But since the molecular data show very low resolution in this case, it seems more likely that the sister group of the Nasutitermitinae is either the Termitinae or part of it.

Support for the monophyly of the mandibulate Nasutitermitinae is based on gut morphology and the external morphology of soldiers. Particularly, the first proctodeal segment is strongly inflated in all mandibulate genera. This unique and unreversed character, along with the presence of a frontal tube with a wide opening, some other unique characters present in most genera, and their strictly neotropical distribution, seem to comprise convincing evidence that they form a monophyletic group.

As for the relationships among the various mandibulate genera, some are clearly well supported while others are doubtful. A sister group relationship between *Labiotermes* and *Paracornitermes* is very well supported both by morphological and molecular data. Based on morphology, *Curvitermes* and *Cyrillitermes* are also well supported sister groups.

Labiotermes, *Paracornitermes*, *Cornitermes* and *Syntermes* possess a mixed segment formed by two mesenteric prolongations, a unique character not found in any other group of termites. The tree in Fig. 17 shows this character (27) as evolving independently twice, which is highly unlikely. Either it was present in the ancestor of all the mandibulates and was reversed twice (adding one step to the tree) or these four genera form a monophyletic group as in Fig. 18 and this character evolved only once. *Procornitermes* also seems to be related to this group, and some characters indicate a close relationship with *Cornitermes*, particularly the soldier mandibles. It is plausible that *Procornitermes* lost one mesenteric prolongation, and in this case it could be the sister group of *Cornitermes* or of *Cornitermes* + *Syntermes*.

Cahuallitermes is a new genus described in Chapter III. One of its species, *C. intermedius*, previously had been included in *Armitermes*. It is clear that these two genera do not form a clade, and

that *Armitermes* would be polyphyletic with the inclusion of the species now included in *Cahuallitermes*. Soldiers of *Cahuallitermes* are superficially similar to those of *Armitermes*, but soldier mandibles, worker mandibles, and gut morphology are distinct and point towards other relationships.

Syntermes, which has been traditionally considered as the most primitive genus of Nasutitermitinae, appears as the sister group of *Cornitermes*. This relationship is supported only by the shape of the worker mandibles and the strongly reduced molar regions of the imago mandible. However, the shape of the worker mandibles does not seem to be a very strong evidence, since *Rhynchotermes*, a more distantly related genus, has very similar mandibles. Mandibular similarity may reflect convergence due to similar feeding habits. As mentioned above, there is also some evidence that *Procornitermes* is the true sister group of *Cornitermes*. In any case, *Syntermes* does not seem to be the most primitive genus of Nasutitermitinae, and many characters mentioned as evidence of its primitiveness, such as the large size, are clearly derived. The relationships of *Syntermes* are also discussed in Chapter II.

Embiratermes and *Ibitermes* appear as sister groups in trees based on morphological data, but support for this relationship seems to be weak. Also, it is not clear whether *Embiratermes* is monophyletic. It is likely that it is paraphyletic in relation to *Ibitermes* or other genera. A complete revision of *Embiratermes* will be necessary in order to answer this question.

The phylogenies presented here should still be considered tentative, but I hope they are pointing in the right direction. Resolution will certainly be improved by additional morphological data. Revisions of several genera would help, particularly those of doubtful status such as *Embiratermes*. The imagoes of several genera are completely unknown, and might provide further evidence once they are described. Additional molecular data may also help, but the challenge is to find a DNA fragment that shows the right amount of variation.

TABLE 1. Matrix of character states: morphological data.

	1	1	2	2	3	3		
	5	0	5	0	5	0	5	
<i>Reticulitermes</i>	00000000	100??	00000000	00000002	???	00???	0	
<i>Anoplotermes</i>	0000?	00??	00???	1???	01001	0002???	00???	1
<i>Amitermes</i>	00100?	00?	00??	00000000	2000000	101000	042	
<i>Microcerotermes</i>	000?	0000	100??	00000000	2000000	101000	042	
<i>Syntermes</i>	010000	11001	000000	010002	000010	12100	042	
<i>Cornitermes</i>	010120	11002	000100	100020	100101	12010	022	
<i>Procornitermes</i>	010120	1?002	000?00	001002	000000	12001	042	
<i>Labiotermes</i>	010000	10101	000100	001102	001010	12002?	2	
<i>Paracornitermes</i>	010000	10101	000100	001102	001010	12002	02	
<i>Rhynchotermes</i>	001000	00014	001101	000020	000000	12001	042	
<i>Embiratermes</i>	001000	00003	00?10	102102	000000	11200	122	
<i>Ibitermes</i>	001000	00003	00010??	210200	000000	11200	122	
<i>Armitermes</i>	001000	00014	000101	021020	000000	10201	013	
<i>Curvitermes</i>	001011	00014	00010?	022121	000010	2002	223	
<i>Cyrilliotermes</i>	001011	00014	10010?	022121	000011	2002	13	
<i>Cahuallitermes</i>	011000	11013	00010??	000200	000000	1200?	32	
<i>Macuxitermes</i>	001000	00014	00010??	210200	000000	11200	212	
<i>Nasutitermes</i>	10002	000014	01011	000002	000000	100000	042	
<i>Cyranotermes</i>	100?	2000014	01011	002212	100101	00010	12	

TABLE 2. cont.

R TCCCATAAAAACATCTAAGAATTTTAAGTCAAAGACCAAATTCATA-----AACCAATTCAAAA
A TCCCATAAAAACATTTAAGAATTTTAAGTCAAAGACCAAATTCATTT-----AAAT--ATCCAC
N TCCCATAAAAACATTTAAGAATTTTAAGTCAAAAACCAAATTCATTT-----AAACCAATACCT
C TCCCATAAAAACATTTAAGCATTTTAAGTCAAAAATCAAATTCATTT-----AAAT-AATACCT
M TCCCATAAAAACATCTAAGAATTTTAAGTCAAAGACCAAATTCATTT-----AAAGAAATACTTT
A TCCCATAAAAACATCTAAGAATTTTAAGTCAAAAACCAAATTCATTT-----AAACAA-TACTC
S TCCCATAAAAACATCTAAGAATTTTAAGTCAAAAACCAAATTCATTT-----AAAACCATATCC
L TCCCATAAAAACATCTGAGTATTTTAAGTCAAAAACCAAATTCATTTTATAATCCAATTTCTC
P TCCCATAAAAACATTTAAGAATTTTAAGTCAAAAACCAAATTCATTTCAATTTAATTAAC-AATACTC
E TCCCATAACAACATCTAAGTATTTTAAGTCAAACTACAAATTCATTT-----AAAACAATACCC
C TCCCATAAAAACATCTAAGAATTTTAAGTCAAAAACCAAATTCATTT-----AAA-CAATACCC
A TCCCATAAAAACATTTAAGAATTTTAAGTCAAAAACCAAATTCATTT-----TTAAC-AATACCC
***** ** * ** ***** ** * ** ***** * **

R TTAAGACAGCTTATGCCTCGTGCAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
A TTAAGACAGCTCATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
N CTAAGACAGCTTATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
C CTAAGACAGATTATGCCTCGT-CAAGCCATTCAACTAGATCACAATTAAGAAGTAATGATTA
M CTAAGACAGCTCATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
A CTAAGACAGCTCATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
S ATAAGACAGCTAATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
L CTGAGACAGTTAGTGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
P CTGAGACAGTTTGTGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
E CTAAGACAGCTTATGCCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
C CTAAGACAGCTTATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
A TTAAGACAGCTGATGTCTCGT-CAAGCCATTCAACCAGATCACAATTAAGAAGTAATGATTA
***** * ** ***** ***** ***** ***** ***** ***** *****

R TGCTACCTTTGCACGGTCAAATAACCGGGCCTTCAACAT-TCAAGGTCAGTGGGCAGGCCAT
A TGCTACCTTTGCA-GGTCAAATAACCGGGCCTTCAACA--AAAAGTCAGTGGGCAGGCCAT
N TGCTACCTTTACCGGTCAAATAACCGGGCCTTCAACT--CTAAGTCAGTGGGCAGGC-AT
C TGCTACCTTTGCACGGTCAAATAACCGGGCCTTCAACT--AAA?CTCAGTGGGCAGGCCAT
M TGCTAACTTTGCACGGTCAAATAACCGGGTCTTCAACCATAAACGTCAGTGGGCAGGCCAT
A TGCTACCTTTGCACGGTCAAATAACCGGGCCTTCAACAA-----GTCAGCGGGCAGGCCAT
S TGCTACCTTTGGACGGTCAAATAACCGGGCCTTCAACT--AATAGTCAGTGGGCAGGCCAT
L TGCTACCTTTGCACGGTCAAATAACCGGGCCTTCAACTTTTAAACGTCAGTGGGCAGGCCAT
P TGCTACCTTTGCACGGTCAAATAACCGGGCCTTCAACT--AAAACGTCAGCGGGCAGGCCAT
E TGCTACCTTTGGACGGTCAAATAACCGGGCCTTCAACT--AAAAGTCAGTGGGCAGGCCAT
C TGCTACCTTTG?ACGGTCAAATAACCGGGCCTTCAACT--CAAAGTCAGTGGGCAGGCCAT
A TGCTACCTTTGCACGGTCAAATAACCGGGCCTTCAAC--ACAAAGTCAGTGGGCAGGCCAT
***** ***** ***** ***** ***** ***** ***** *****

R ACTTCAAAAAC
A ACTTCAAAAAC
N ACTTCAAAAAC
C ACTTCAAAAAC
M ACTTCAAAAAC
A ACTTCAAAAAC
S ACTTCAAAAAC
L ACTTCAAAAAC
P ACTTCAAAAAC
E ACTTCAAAAAC
C ACTTCAAAAAC
A ACTTCAAAAAC

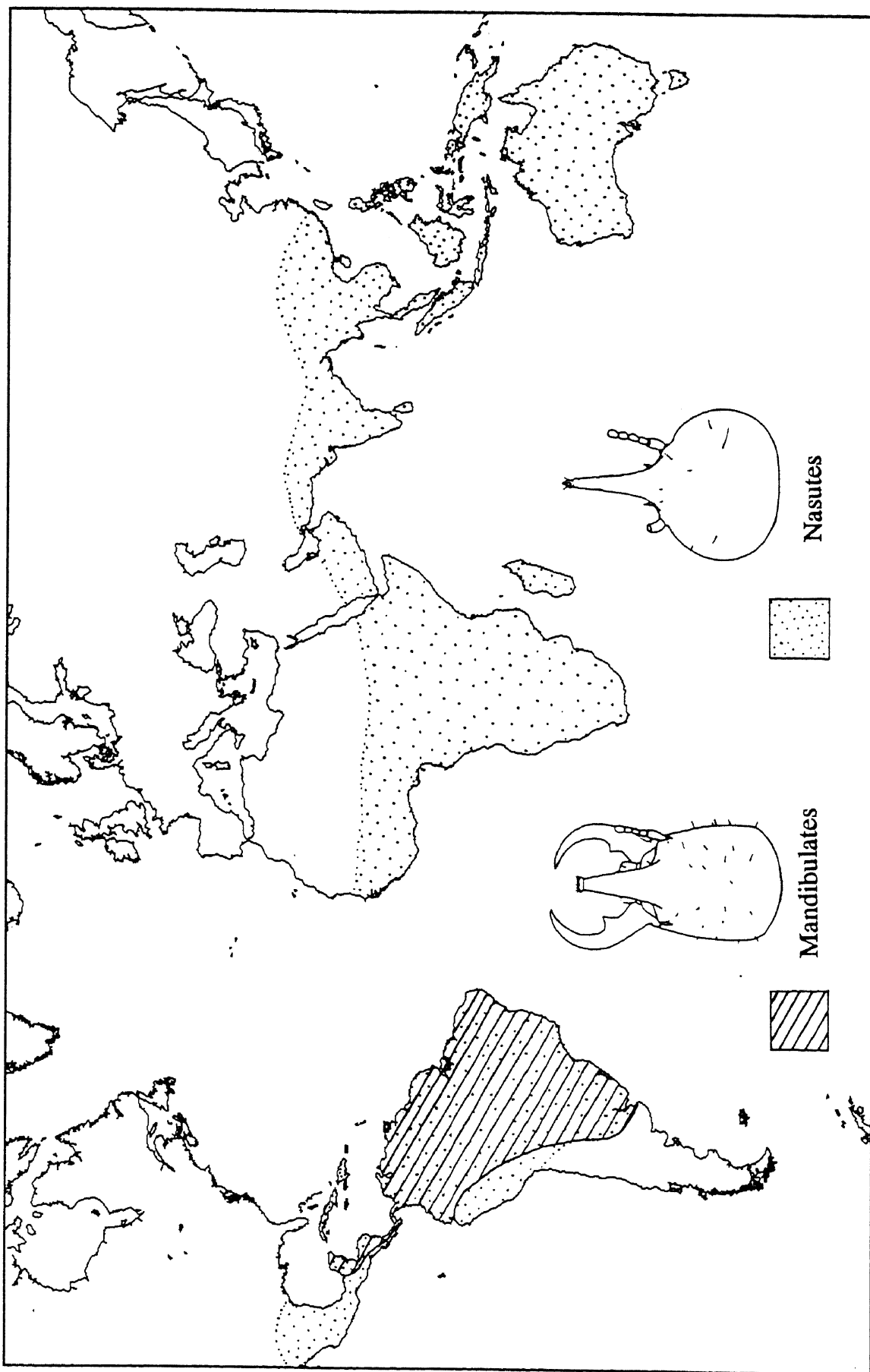
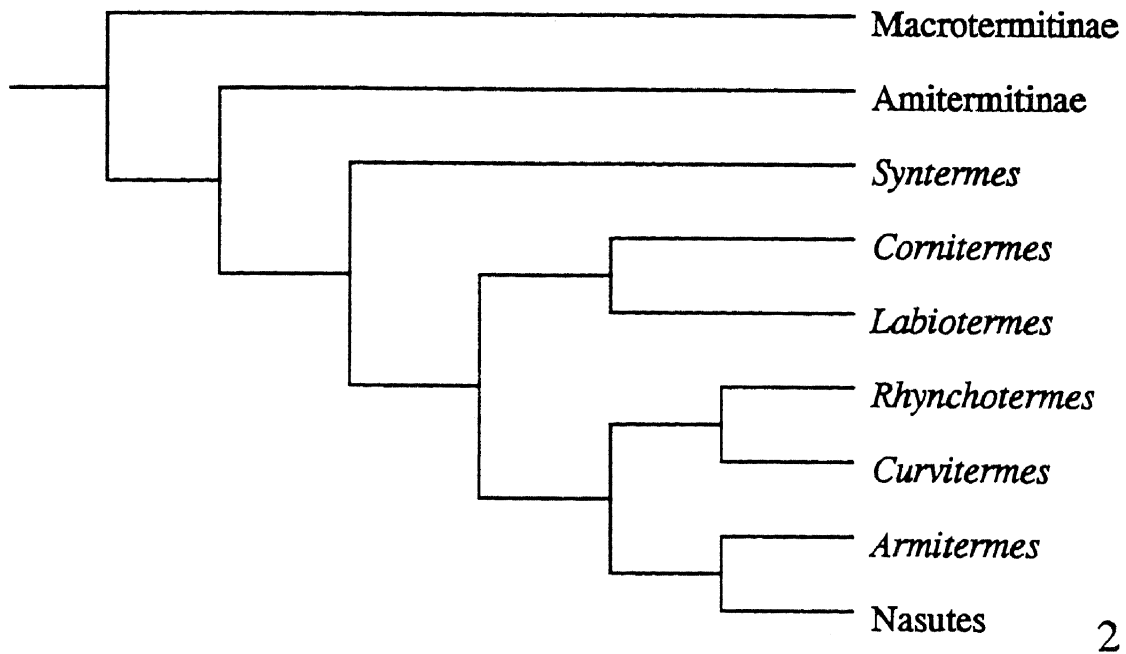
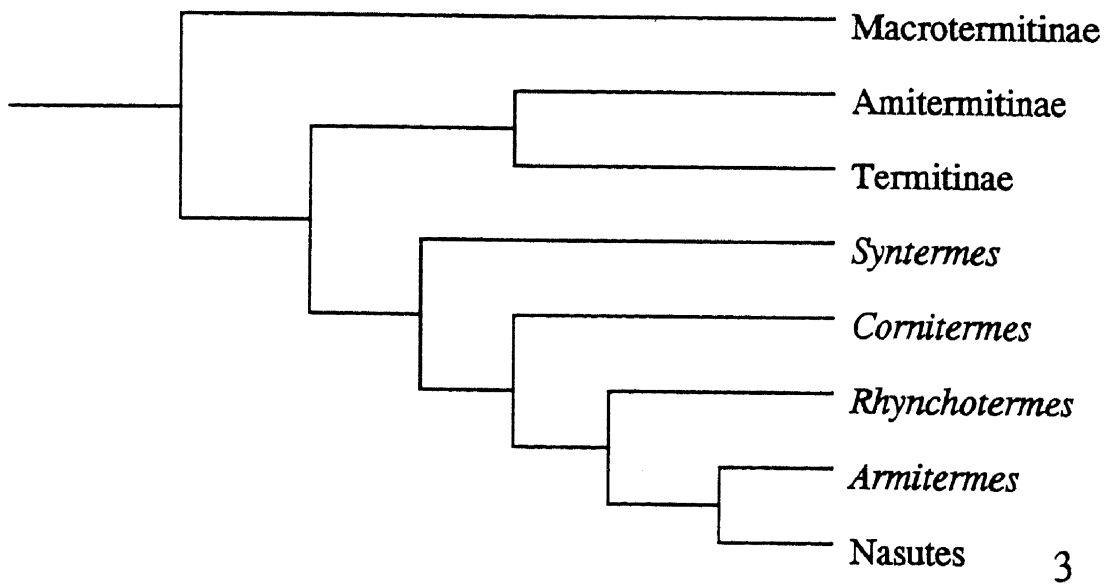


Fig. 1. Distribution of the Nasutitermitinae with nasute soldiers and with mandibulate soldiers.

Holmgren 1912

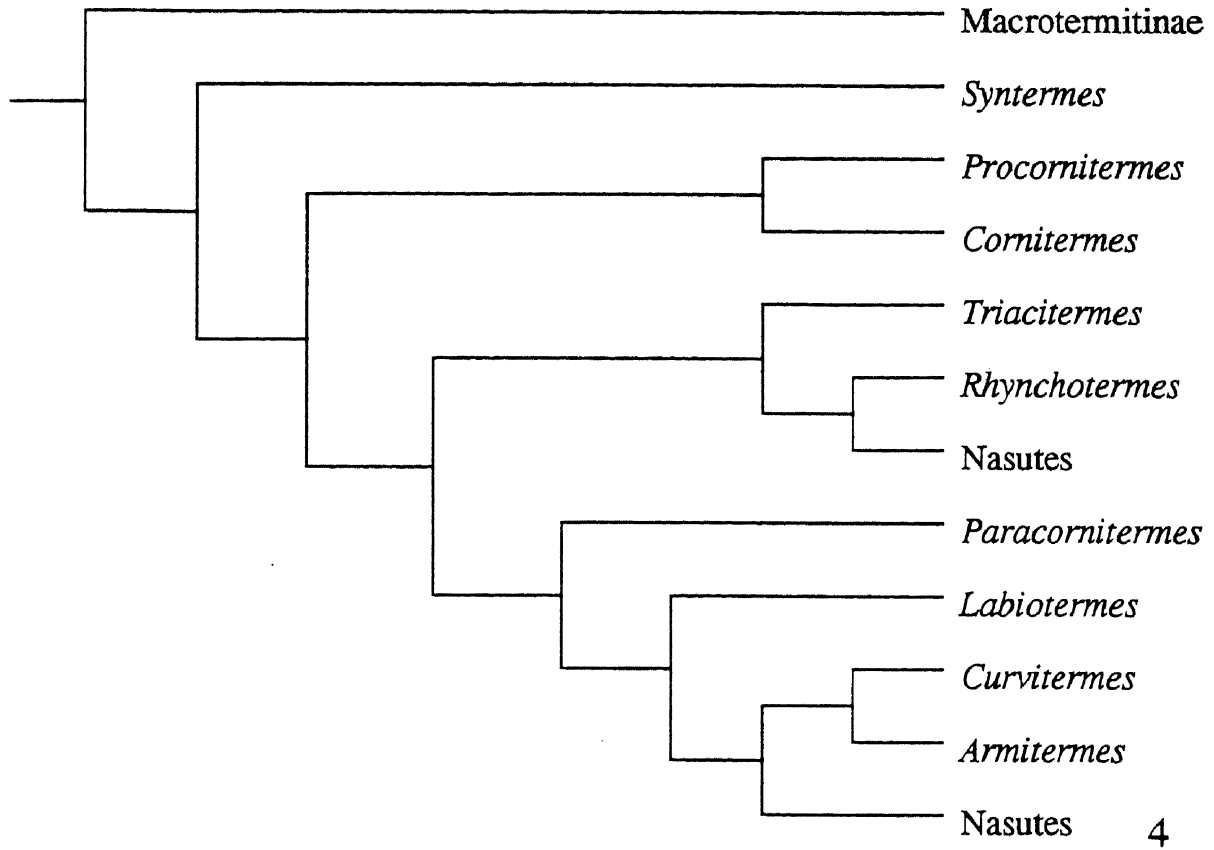


Hare 1937

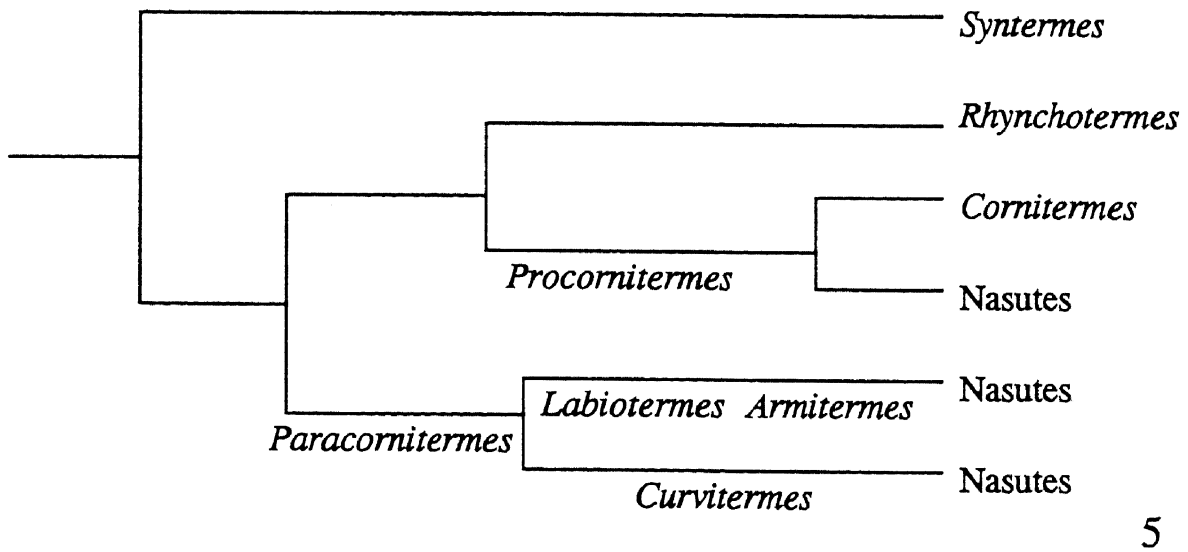


Figs. 2-3. Phylogeny of the Nasutitermitinae according to: 2. Holmgren (1912); and 3. Hare (1937).

Ahmad 1950

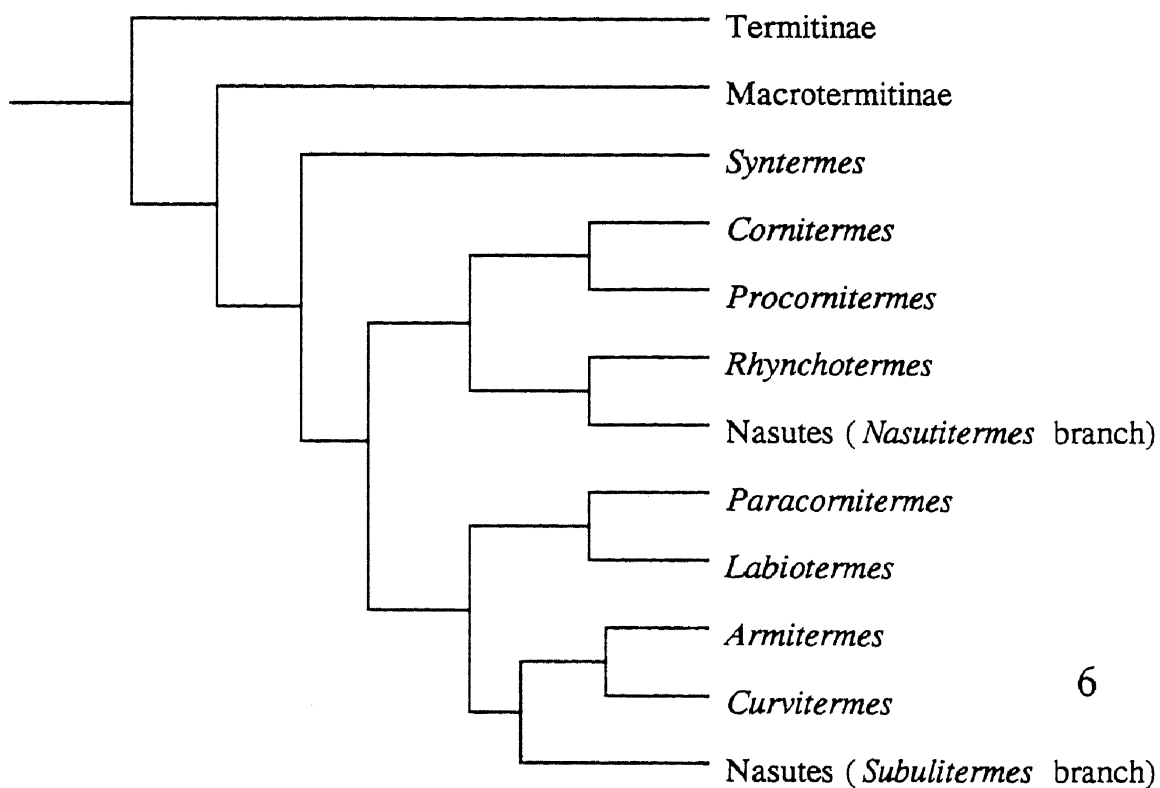


Sen-Sarma 1968

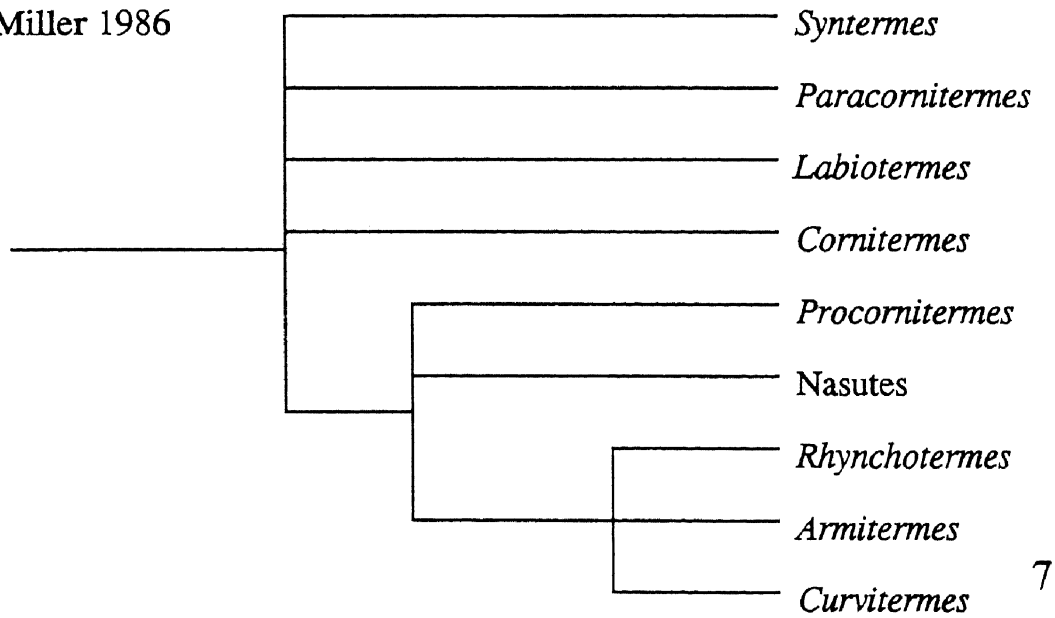


Figs. 4-5. Phylogeny of the Nasutitermitinae according to: 4. Ahmad (1950); and 5. Sen-Sarma (1968).

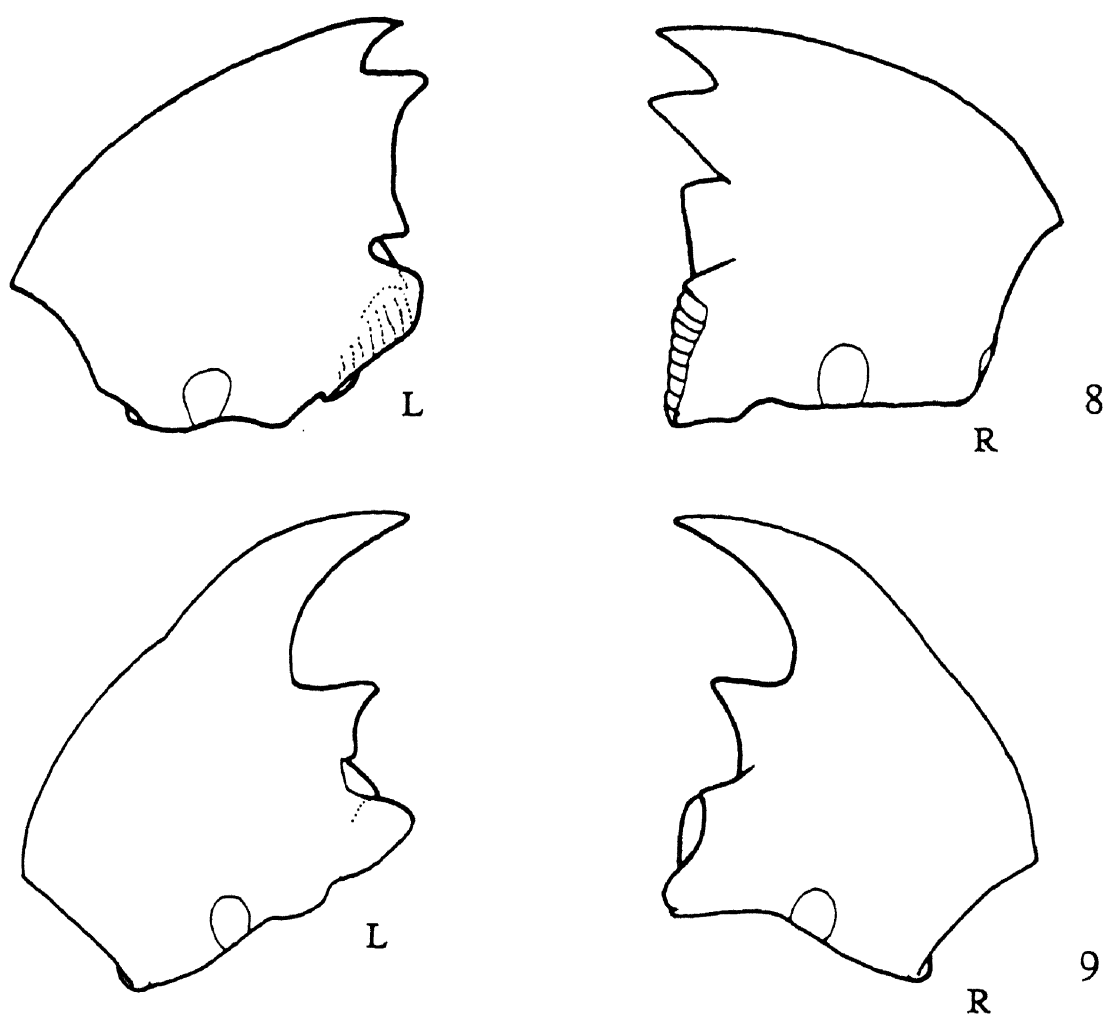
Krishna 1970



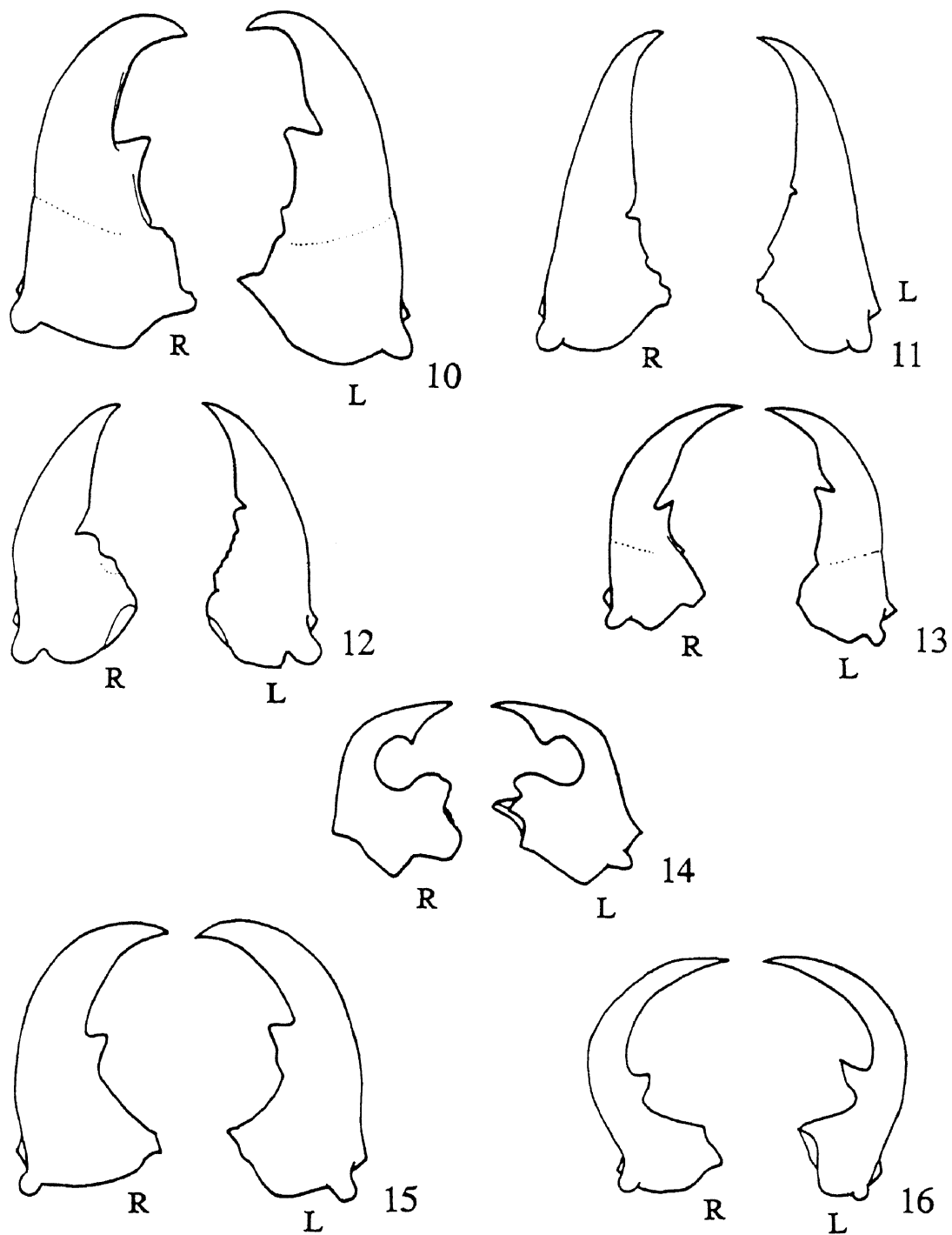
Miller 1986



Figs. 6-7. Phylogeny of the Nasutitermitinae according to: 6. Krishna (1968); and 7. Miller (1986).



Figs. 8-9. Examples of worker mandibles associated with: 8. wood-feeding (*Nasutitermes*); and 9. soil-feeding (*Cyranotermes*). L= left, R= right.



Figs. 10-16. Different types of soldier mandibles of the mandibulate Nasutitermitinae, ventral view: 10. *Syntermes*; 11. *Labiotermes*; 12. *Cornitermes*; 13. *Cahuallitermes*; 14. *Curvitermes*; 15. *Embiratermes*; 16. *Armitermes*. L= left, R= right.

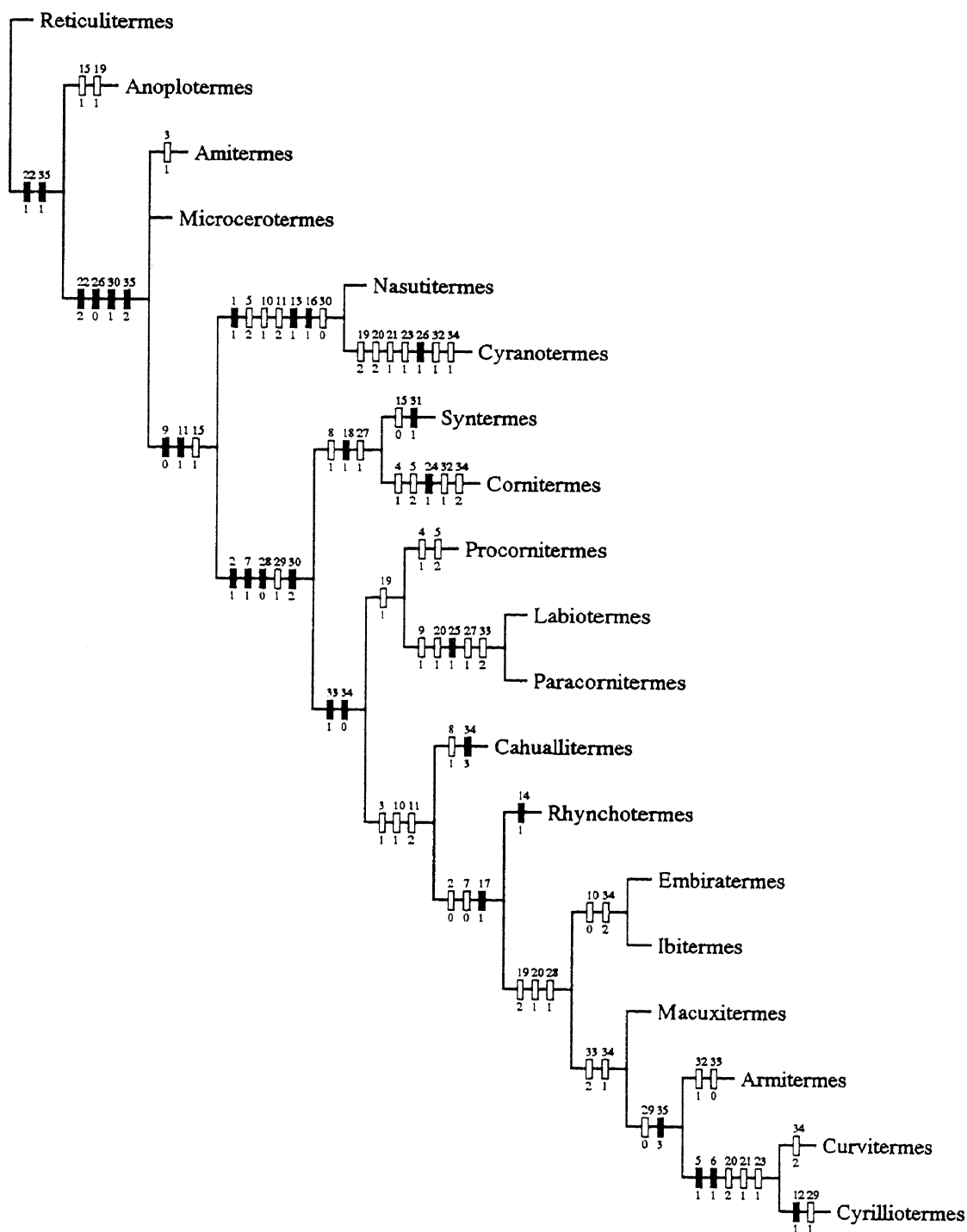


Fig. 17. Tree from analyses 1A (equal weights for all characters, length= 82, $ci = 0.58$, $ri = 0.73$) and 1B (successive approximations character weighting: length= 344, $ci = 0.76$, $ri = 0.82$), based on morphological data. Numbers above each branch refer to characters as defined in text; numbers below each branch refer to character states. Black bars indicate character states that are unique and unreversed within the clade subtended by the branch; white bars indicate characters that originate more than once on the tree or undergo reversal within the clade subtended by the branch.

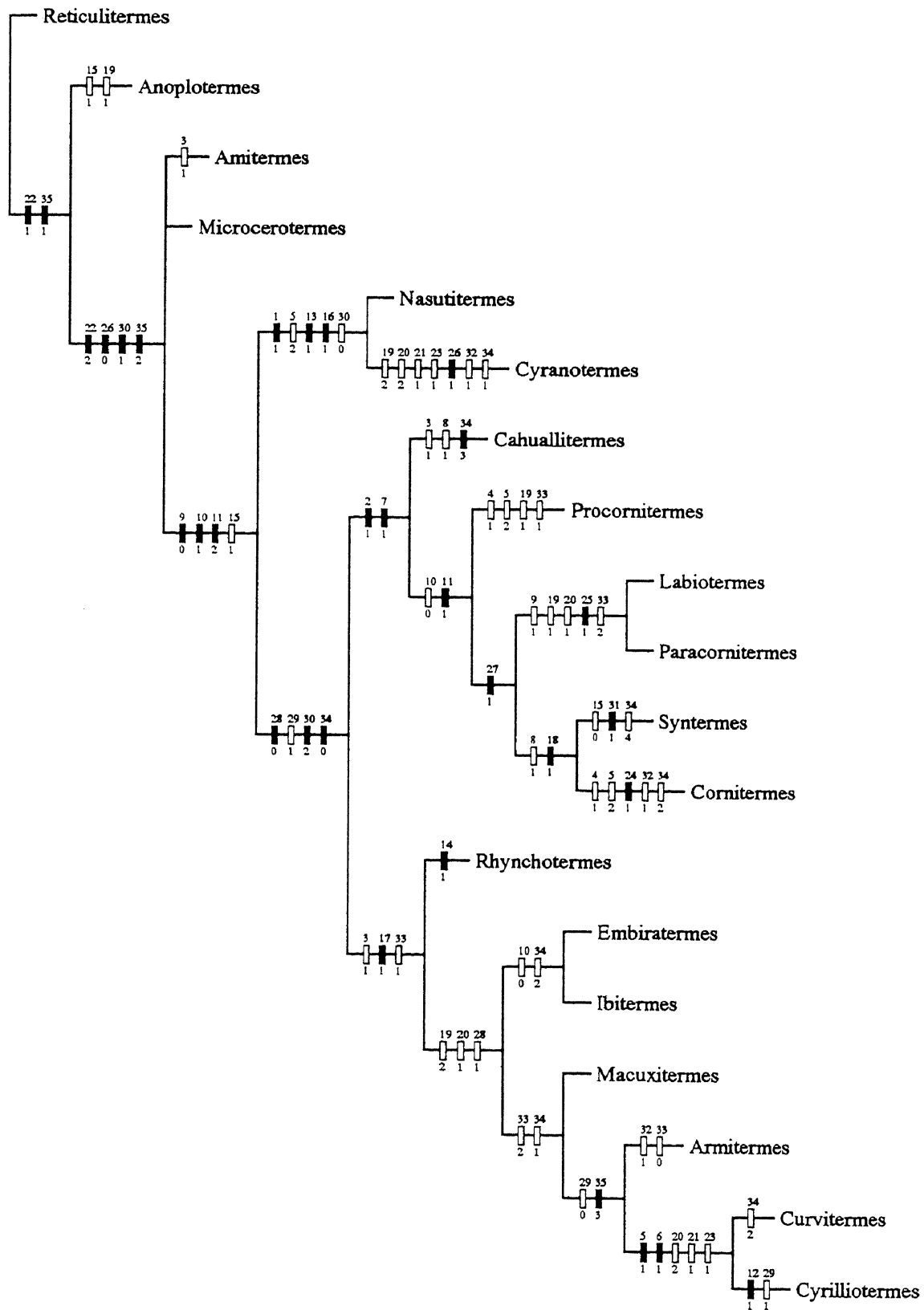


Fig. 18. Tree 1 from analysis 1C, based on morphological data; implied weights (Pee-Wee); fit=243.9. Symbols as in Fig. 17.

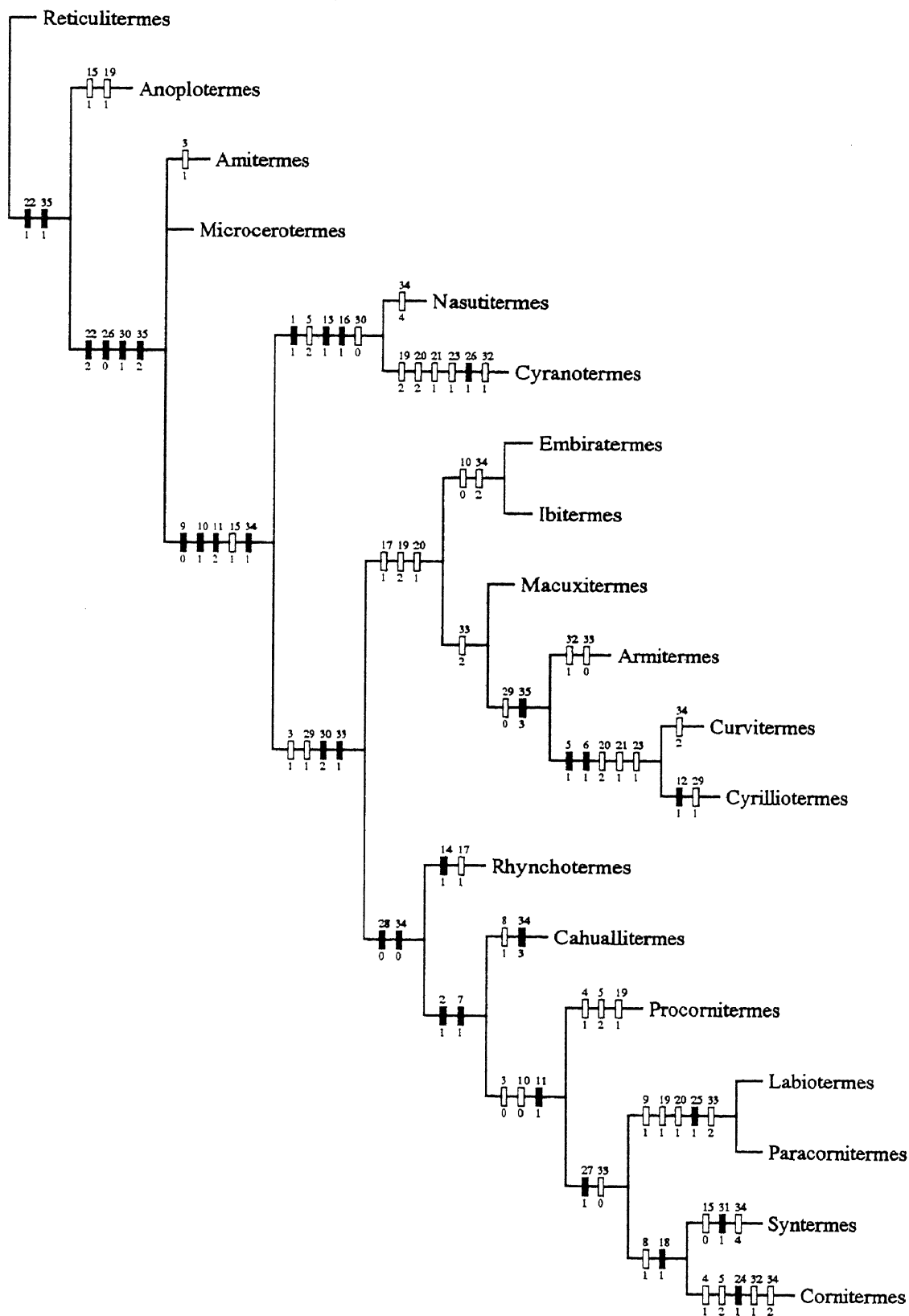


Fig. 19. Tree 2 from analysis 1C, based on morphological data; implied weights (Pee-Wee); fit= 243.9. Symbols as in Fig. 17.

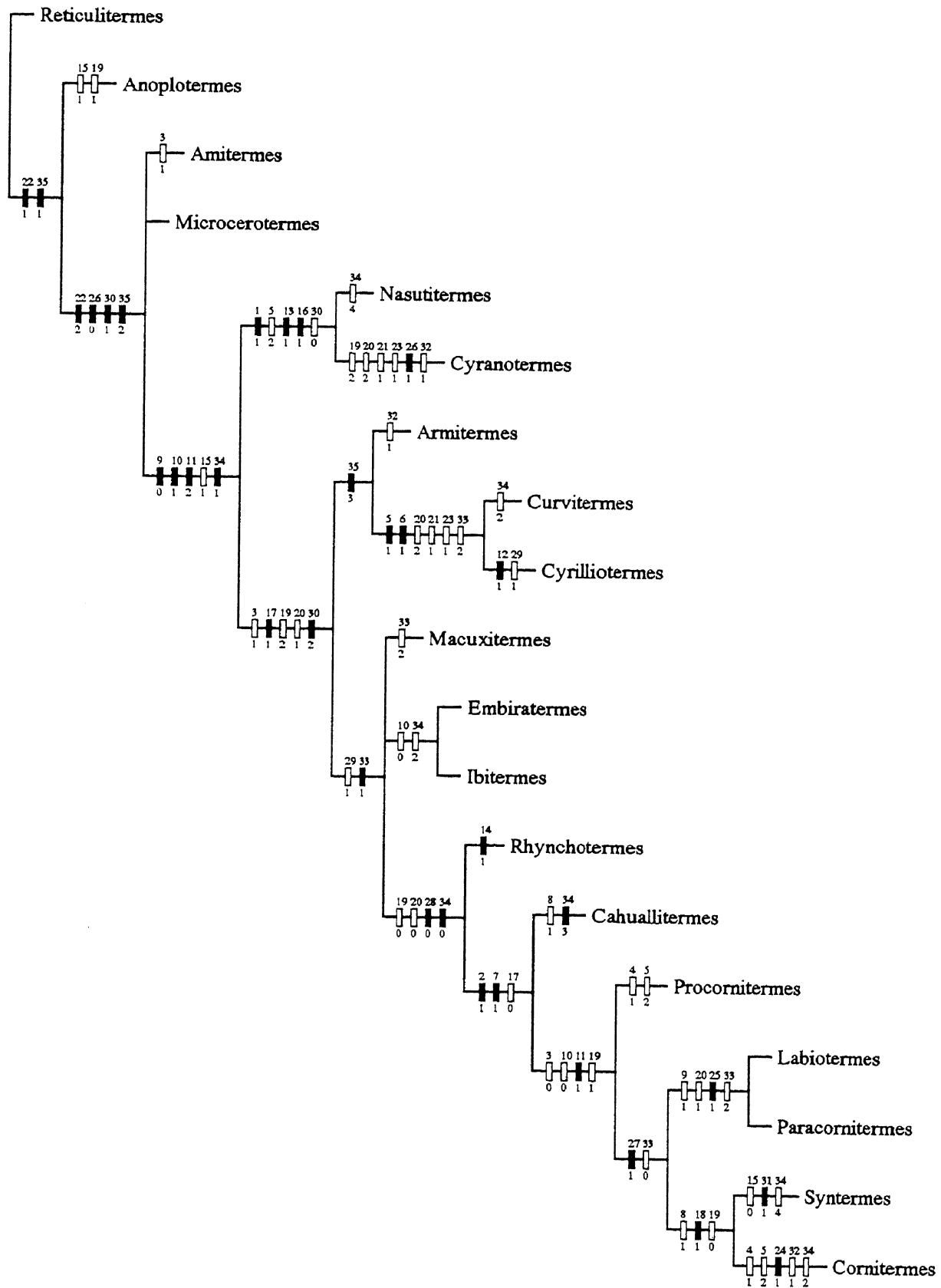


Fig. 20. Tree 3 from analysis 1C, based on morphological data; implied weights (Pee-Wee); fit= 243.9. Symbols as in Fig. 17.

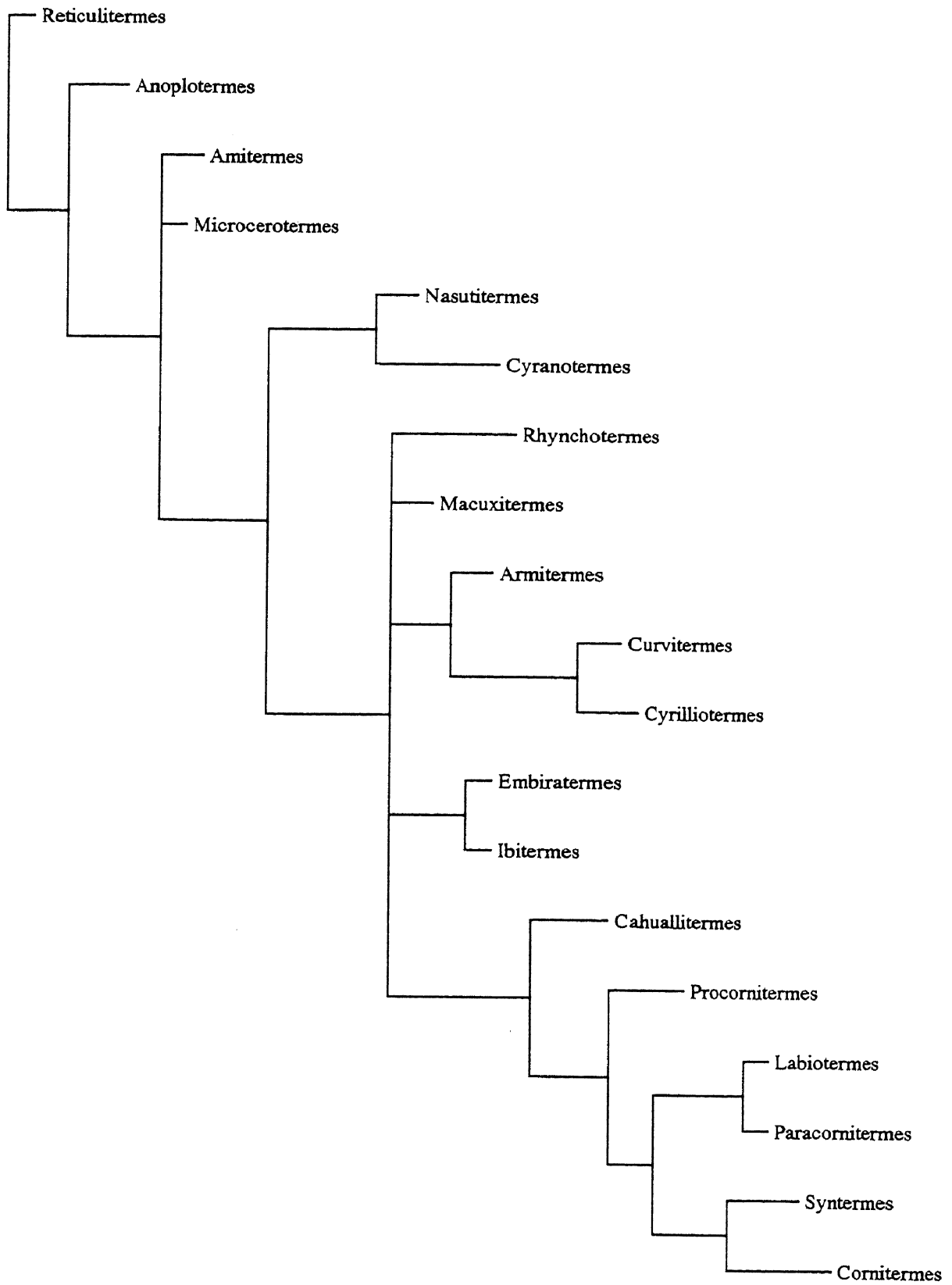


Fig. 21. Strict consensus tree from analysis 1C, based on morphological data.

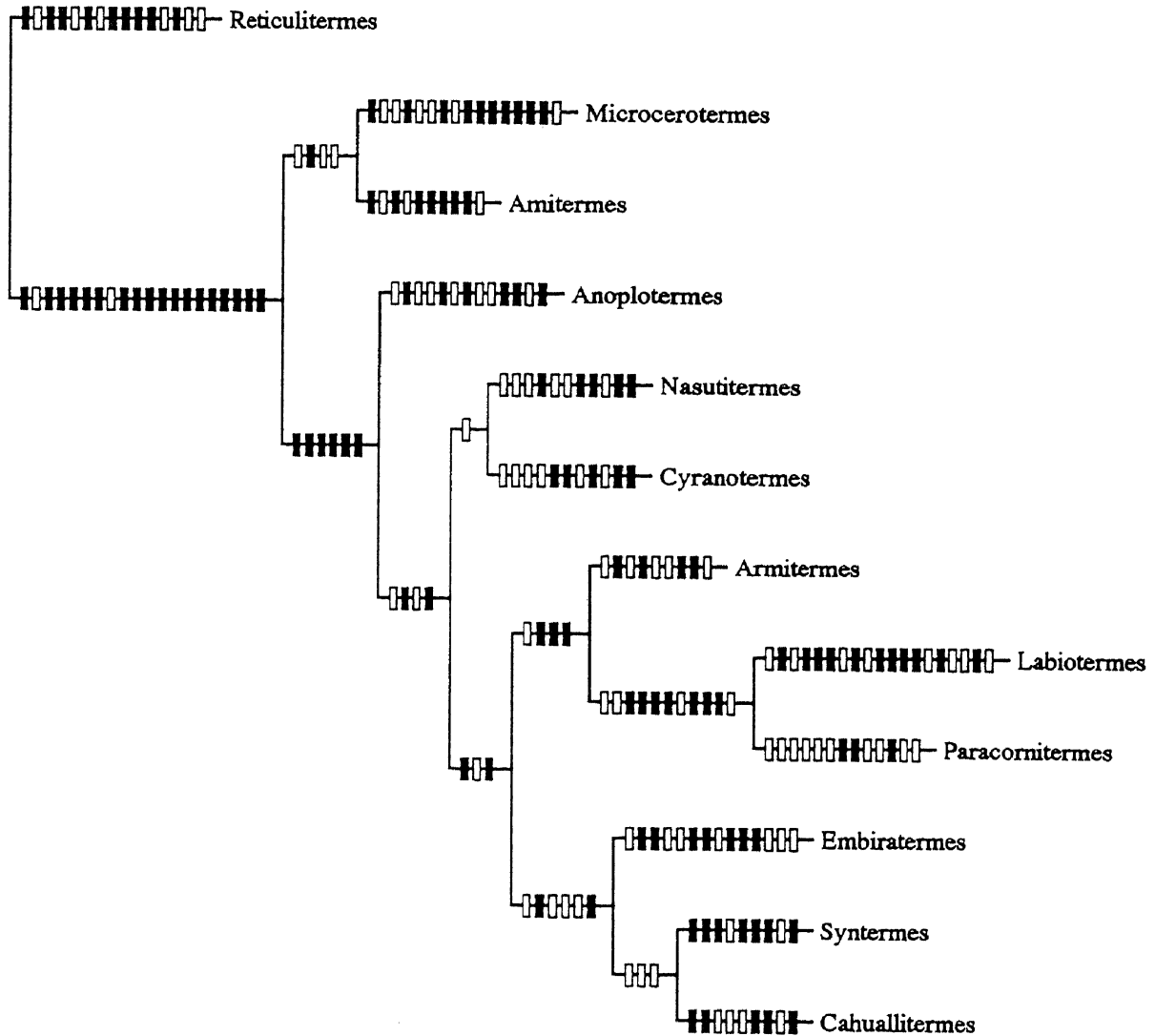


Fig. 22. Tree from analysis 2A, based on a 16S rDNA fragment; equal weights. Length= 211; $c_i = 0.72$; $r_i = 0.41$. Black bars indicate nucleotide substitutions that are unique and unreversed within the clade subtended by the branch; white bars indicate changes that originate more than once on the tree or undergo reversal within the clade subtended by the branch.

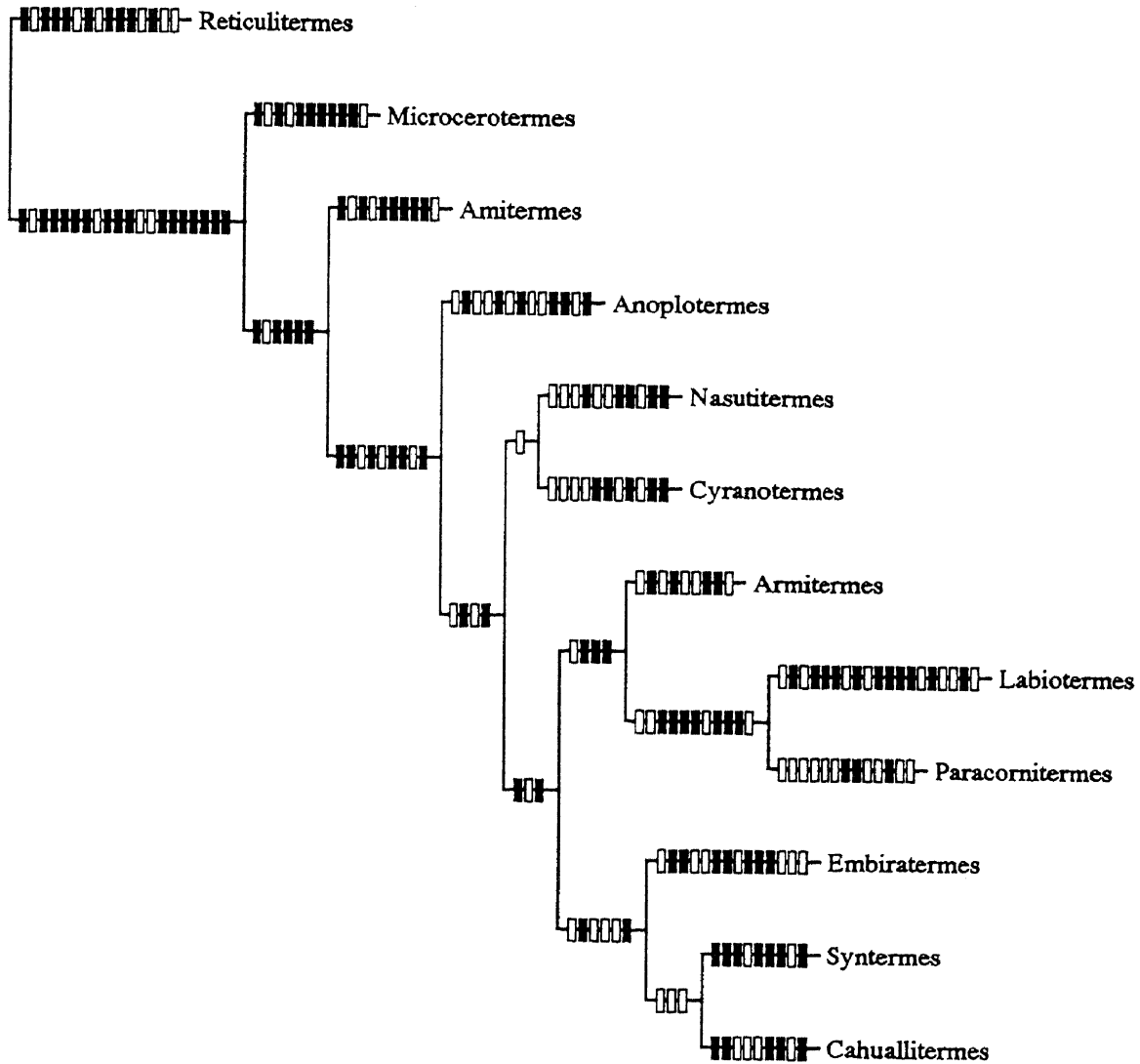


Fig. 23. Tree from analysis 2A, based on a 16S rDNA fragment; equal weights. Length= 211; $c_i = 0.72$; $r_i = 0.41$. Symbols as in Fig. 22.

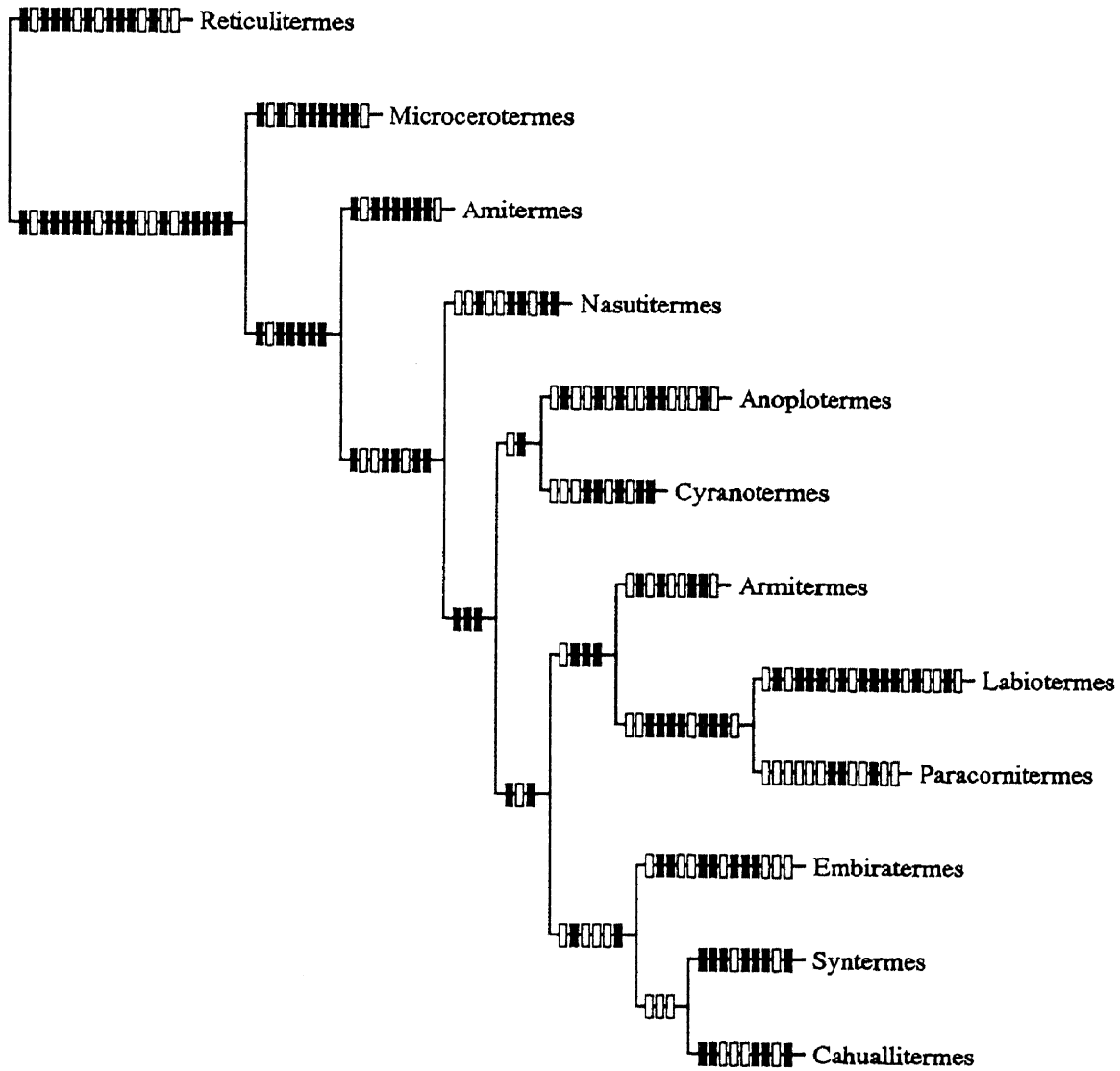


Fig. 24. Tree from analysis 2A, based on a 16S rDNA fragment; equal weights. Length= 211; $c_i = 0.72$; $r_i = 0.41$. Symbols as in Fig. 22.

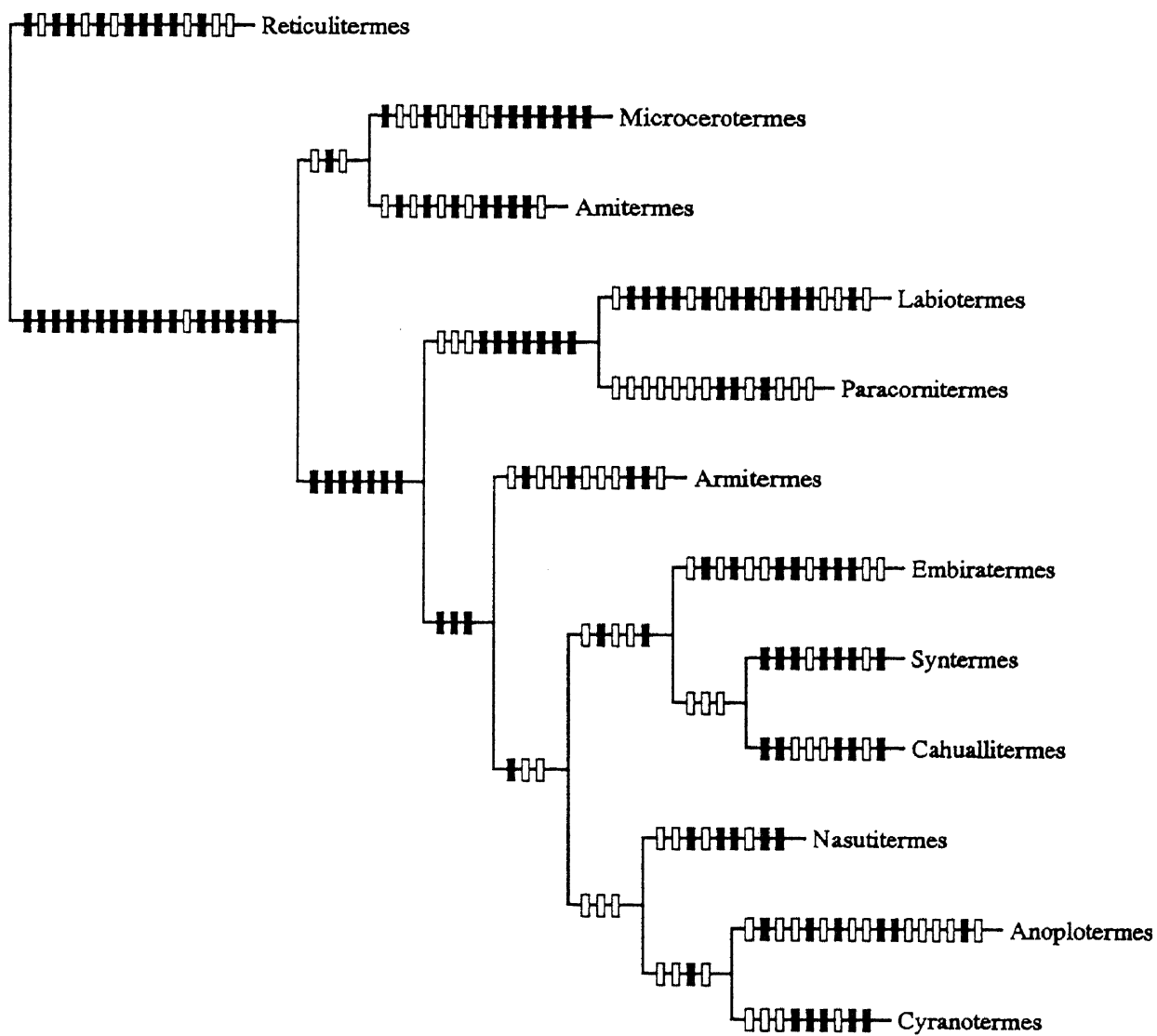


Fig. 25. Tree from analysis 2A, based on a 16S rDNA fragment; equal weights. Length= 211; $c_i = 0.72$; $r_i = 0.41$. Symbols as in Fig. 22.

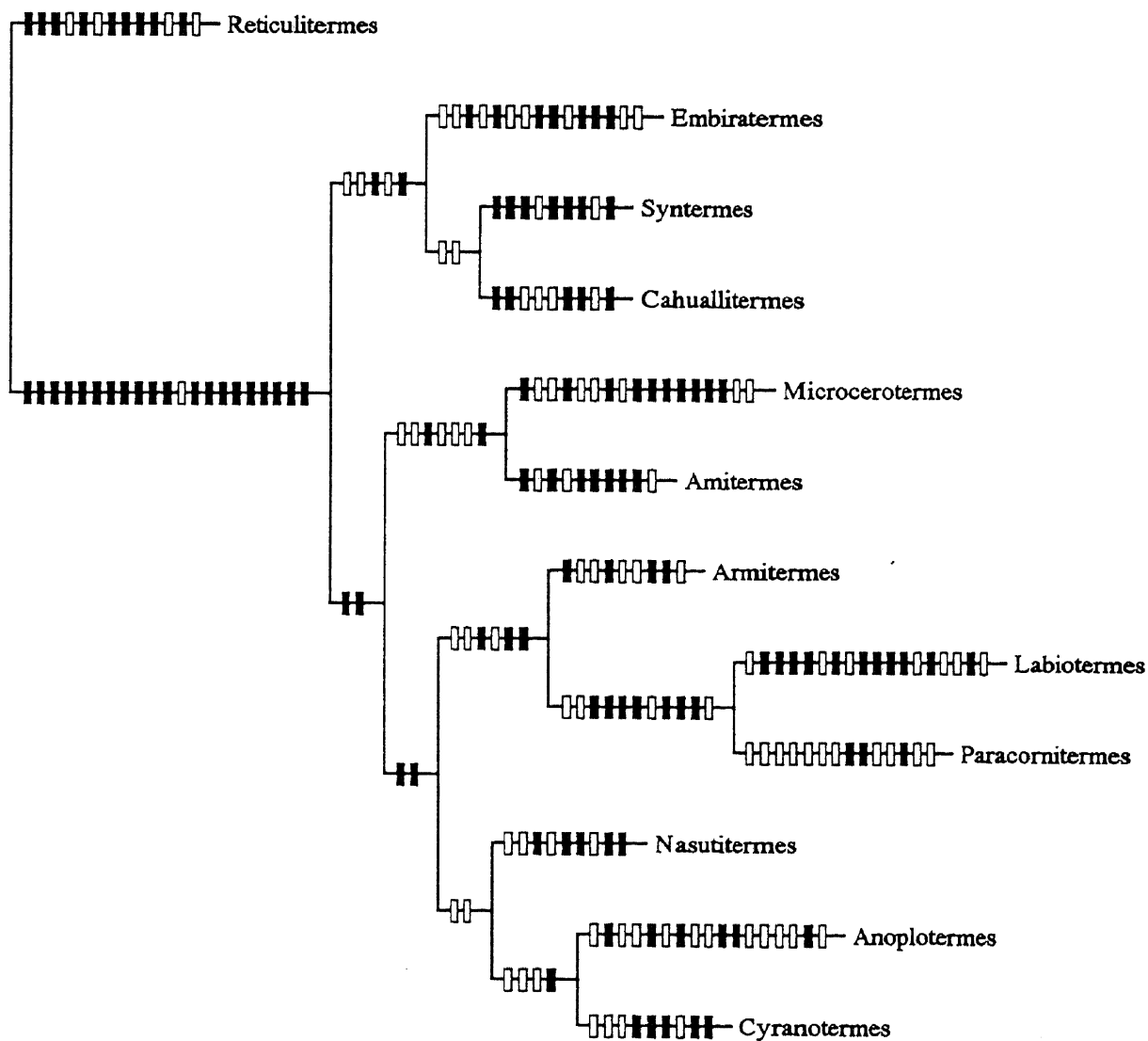


Fig. 26. Tree from analysis 2A, based on a 16S rDNA fragment; equal weights. Length= 211; $c_i = 0.72$; $r_i = 0.41$. Symbols as in Fig. 22.

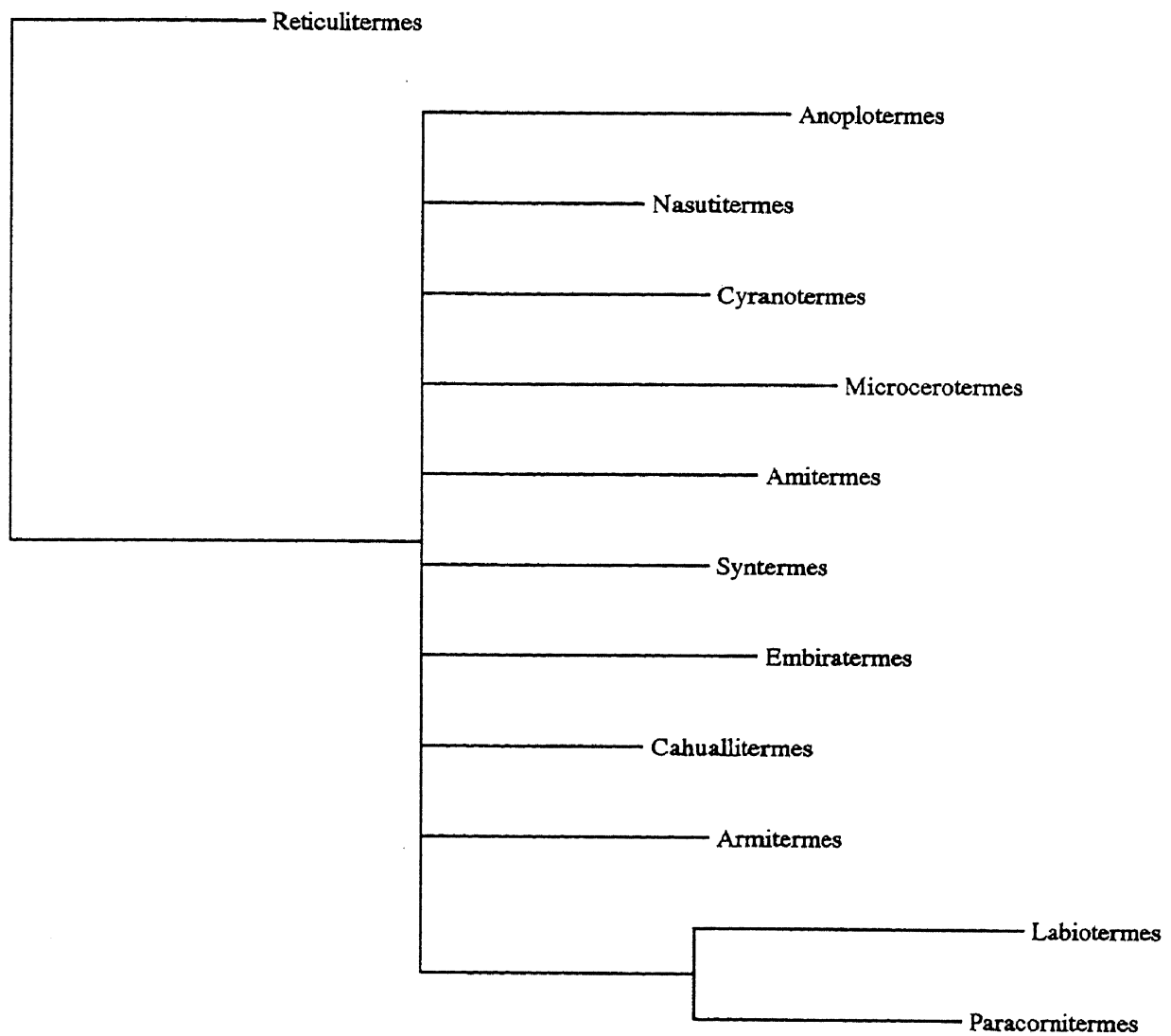


Fig. 27. Strict consensus tree from analysis 2A, based on a 16S rDNA fragment.

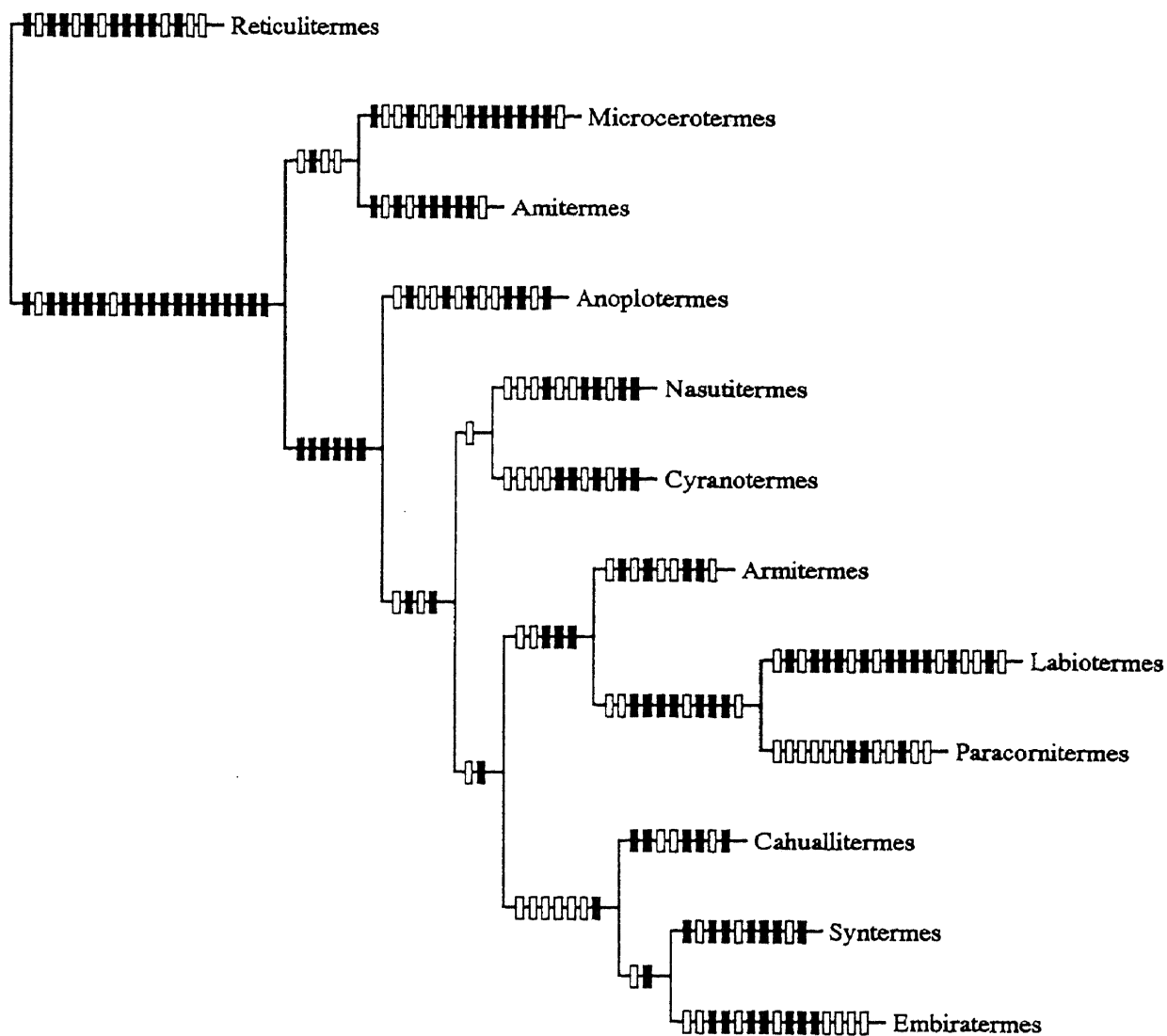


Fig. 28. Tree from analyses 2B (successive approximations character weighting: length= 1017, $c_i=0.93$, $r_i=0.75$) and 2C (implied weights: fit= 319.7), based on a 16S rDNA fragment. Symbols as in Fig. 22.

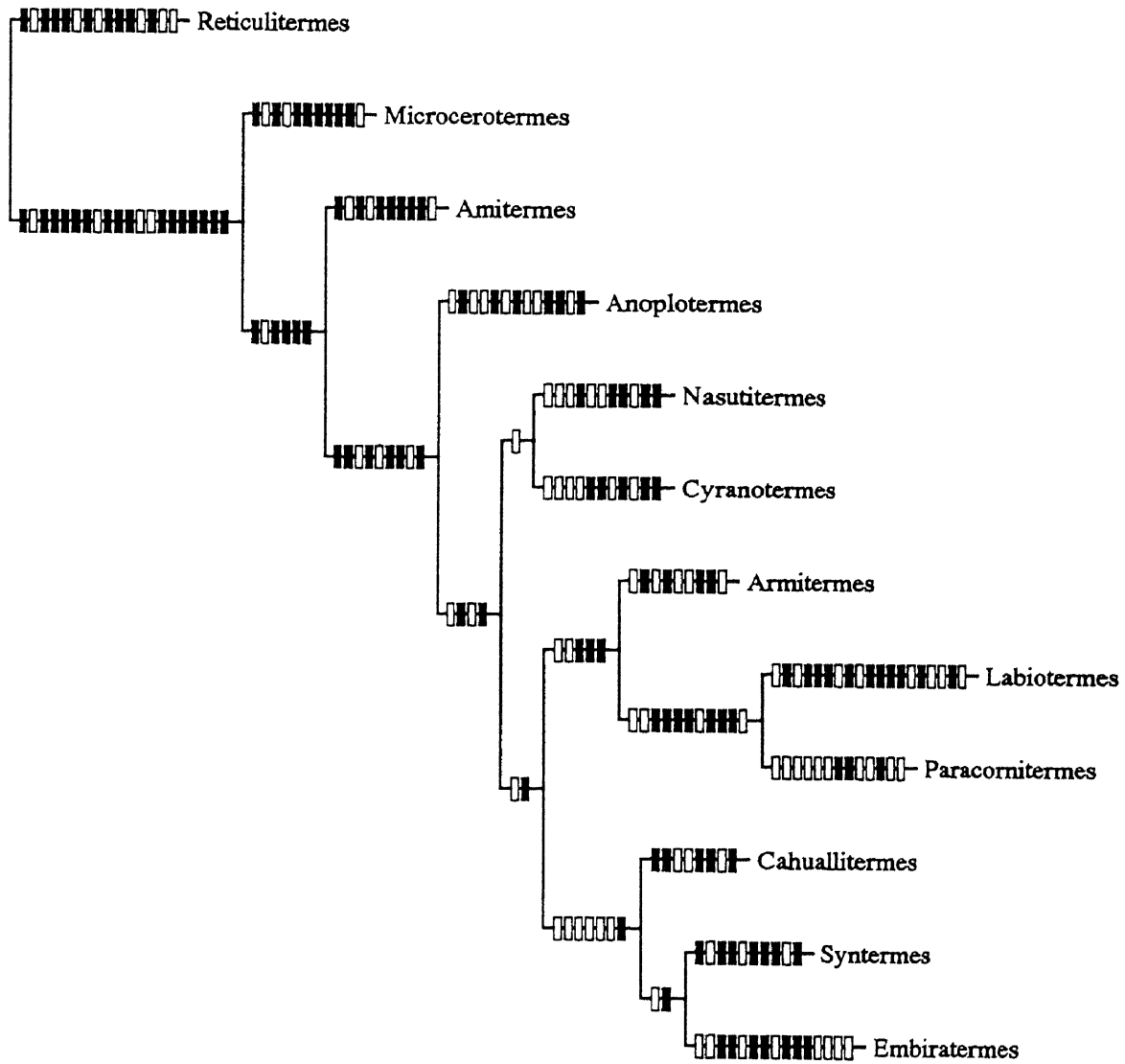


Fig. 29. Tree from analysis 2C, based on a 16S rDNA fragment; implied weights; fit= 319.7.
Symbols as in Fig. 22.

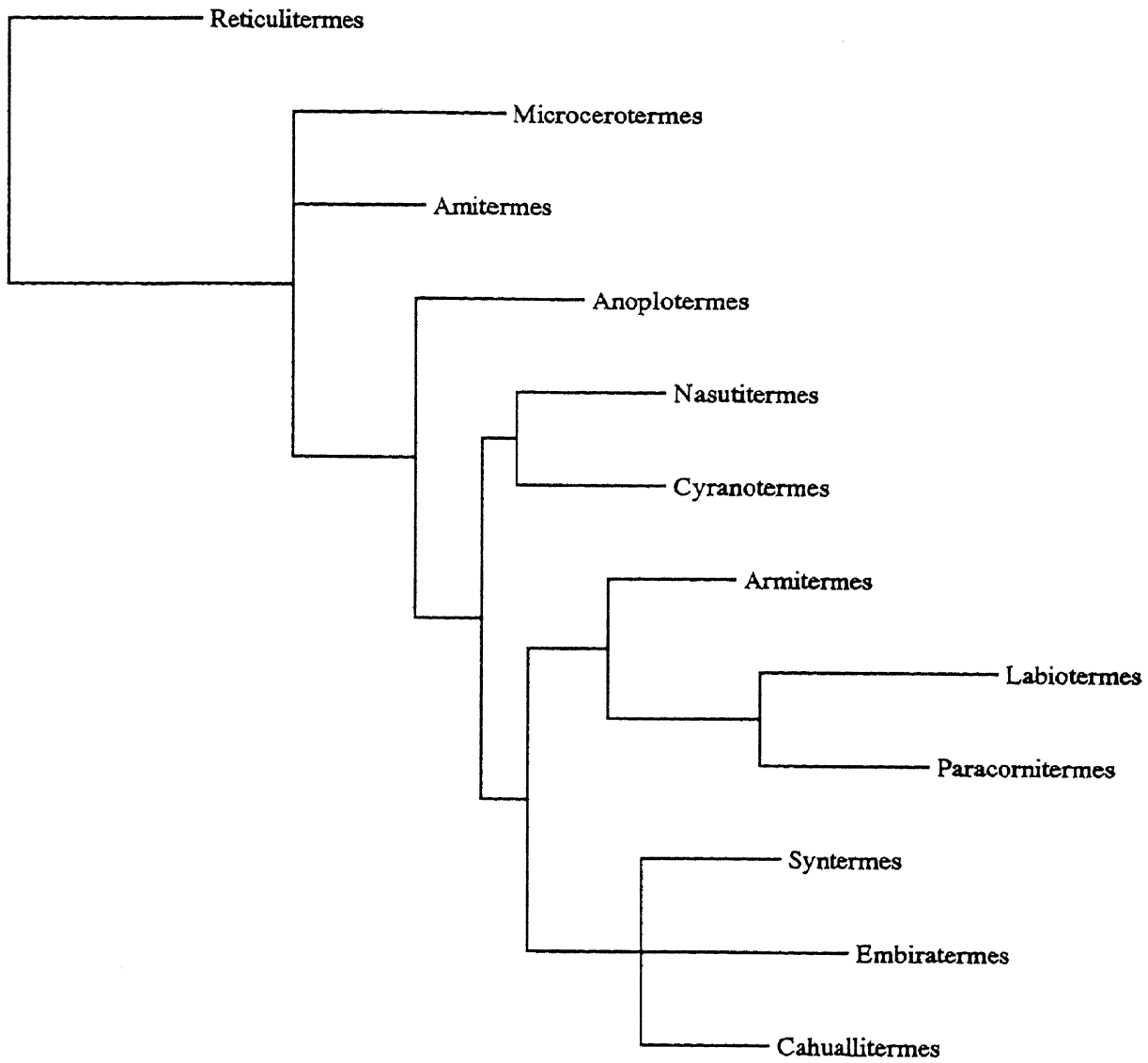


Fig. 30. Strict consensus tree for analysis 2C, based on a 16S rDNA fragment.

CHAPTER II

REVISION OF THE NEOTROPICAL TERMITE GENUS *Syntermes* HOLMGREN
(ISOPTERA: TERMITIDAE)

INTRODUCTION

The neotropical genus *Syntermes* is restricted to the forests and savannas of South America east of the Andes, from Venezuela to northern Argentina, and comprises some of the largest termites in the world. As far as their biology is known, most species live in subterranean nests and feed on leaf- or grass-litter, and a few have been recorded as pests in agriculture and forestry.

Their large size has attracted the attention of general collectors but their subterranean habits and their tendency to hide quickly underground when disturbed have resulted in meager collections. Beginning with Latreille's (1804) *Termes spinosum*, several species now assigned to *Syntermes* were originally described in the genus *Termes*. (At the time of those descriptions, *Termes* was almost synonymous with our current Order Isoptera). Early in this century, Holmgren (1910) proposed a new classification for the order Isoptera, including the new genus *Syntermes* in the subfamily Termitinae of the Metatermitidae, and designating *Termes dirus* as its type-species. Subsequently, Holmgren (1911) presented a list and a key for the identification of the nine species included in *Syntermes*, five of them new and four transferred from *Termes*. A description of the genus was given in Holmgren's (1912) monograph on family Metatermitidae, including a discussion about its phylogenetic relations and new subdivision of that family. *Syntermes* was then included in a group named "*Syntermes-Reihe*", which is synonymous with the current concept of the subfamily Nasutitermitinae. Later, Snyder (1924) presented a new taxonomic account of *Syntermes*, including a new key and the description of four new species.

Based on admittedly limited material, Emerson (1945) revised the taxonomy of *Syntermes*, recognizing 18 species, one of them divided into three subspecies. In a brief discussion about the phylogenetic relations of *Syntermes*, Emerson (1945: 441) states that it is the most primitive genus of the Nasutitermitinae and that it is somehow related to the genus *Acanthotermes* in Macrotermitinae. His argument in favor of the primitiveness of *Syntermes* was based on the presence of many characters believed to be primitive.

After Emerson's revision, Silvestri (1946) described two new species, and Araujo (1977) placed four names in synonymy, based on his own observations and on information provided by A.E. Emerson. More recently, thanks to the efforts of many termitologists and collectors, a large amount

of new material of *Syntermes* has been made available for study, including several undescribed species and castes and new data on the geographical distribution and morphological variation of most species.

Syntermes is currently included in the subfamily Nasutitermitinae, and clearly belongs to a group of 13 neotropical genera usually called the mandibulate nasutes, due to the fact that their soldiers bear both a frontal tube (sometimes very short) and functional mandibles, in contrast with the true nasutes, which have very long frontal tubes and vestigial mandibles. However, the traditional hypothesis that the mandibulate nasutes are the basal lineages of the Nasutitermitinae is not supported by a formal cladistic analysis (Chapter I), and it is possible that the presence of a frontal tube in both groups is a case of convergence or parallelism.

In the revision below, I present a review of the literature on *Syntermes*, new keys for the identification of imagoes and soldiers, a description of each species, including six new ones, new synonymies, the revalidation of two names previously treated as synonyms, and an analysis of the phylogenetic relations among the species.

BIOLOGY AND ECOLOGY OF *SYNTERMES*

Formation of sterile castes

Since the taxonomy of termites is heavily based on the morphology of sterile castes, it is important to understand their polymorphism and how they develop. In the case of *Syntermes*, this has never been fully studied, and we have to rely on fragmentary information in the literature and on the analysis of preserved material. The only published data about the formation of castes in *Syntermes* are those presented by Noirot (1969: 329) based on his analysis of *S. wheeleri*. A diagram of the most probable pathway of development of workers and soldiers is presented in Fig. 31.

The worker caste of *Syntermes* has always been described as dimorphic. Nevertheless, careful examination of large samples clearly shows that there are four different workers: two less sclerotized with white heads of different sizes; and two more sclerotized ones with yellow to yellow-brown heads. The white-head workers are females and the dark-head workers are males, both found in two sizes corresponding to third and fourth instars. The 3rd instar male worker is about the same size as the 4th instar female worker. The 4th instar male worker is much larger than the others and is also the type most commonly found in collections.

The soldier caste of *Syntermes* probably develops from the large male worker, which molts

and becomes a presoldier and then a soldier. It is believed to be monomorphic but, among the material examined in the course of the current revision, there are a few samples with two sizes of soldiers. The most probable explanation for this occurrence was presented by Silvestri (1946), based on his observations on *S. praecellens*. Young colonies of that species produce soldiers considerably smaller than and morphologically distinct from soldiers in older colonies. Silvestri called these smaller soldiers "forma prima" (first form), contrasting with "forma perfecta" (perfect form) soldiers. This phenomenon has also been observed in other genera of Termitidae (Noirot 1969). In most cases the pathway of development is the same and the soldiers are just smaller than normal, but in some species (e.g., *Pericapritermes urgens*), the first soldiers develop from an earlier instar and are morphologically very distinct. In the case of *Syntermes*, my hypothesis is that in young colonies soldiers develop from the 3rd instar male worker instead of the 4th instar and in intermediate stages both kinds of soldiers could be found in the colony, which would explain the few samples with two sizes of soldiers. As Silvestri (1946) already warned, this phenomenon is very important for taxonomy because a first form soldier could be taken as a species distinct from the normal soldier.

A relatively common phenomenon is the presence of individuals intermediate between workers and soldiers. These intercastes were first reported by Silvestri (1945a) for *S. grandis* and, according to his detailed study, are caused by a microsporid protozoan. They can easily be identified by the presence of numerous white cysts in the abdomen.

Nesting behavior

Termite nests are sometimes extremely complex structures, which can be a good source of information for taxonomic and phylogenetic studies. The nests of most species of *Syntermes* have never been adequately described in the literature (Noirot 1970: 80), probably because in most cases they are subterranean and difficult to study. Based on the descriptions available in the literature and on my own observations of several species, the nests of *Syntermes* can be divided into three main types: completely subterranean; subterranean with a pile of loose soil on the surface; and compact mound.

Several species seem to live in completely subterranean nests, and those are the most difficult to collect and to study. Some of the more common species, such as *S. molestus* and *S. nanus*, and most of the little-known species, have this type of nest. The only detailed description of a subterranean nest was that by Silvestri (1946), who discovered by chance an exposed nest of *S. praecellens* in a construction site in the city of São Paulo. The central portion (endoecie) of that nest

was found at a depth of three meters, was approximately spherical and had a diameter of about 45 cm (Fig. 34). It was composed of many thin horizontal chambers divided by vertical walls, and had a fragile structure. Silvestri also mentions that workers collect plant material on the surface and store it in subterranean chambers. The nests of *S. molestus* and *S. nanus* are certainly subterranean, but an endoecie was never found, probably because it is located deep in the soil as in *S. praecellens*, and extremely difficult to find. Darlington (1993) briefly described the subterranean galleries and storage chambers of a nest attributed to *S. molestus* (probably *S. nanus*, because it was found in cerrado vegetation). The galleries were about one centimeter in diameter and were covered with a weak lining of cemented soil particles. The storage chambers were 7-10 cm long and 1 cm high, irregularly shaped.

In his monograph on termite nests, Emerson (1938) described the nest of *Syntermes spinosus* (as *S. snyderi*), studied by himself in Guyana, as "simple excavations in the sandy-clay soil", with a pile of "excavated dirt" on the surface, and also mentioned that leaf fragments were stored in some compartments of the nest. Emerson considered the nest of *Syntermes* as primitive and used it as evidence for the primitiveness of the genus. Holmgren's (1906: 662) description of the nest of *S. chaquimayensis* seems to have been overlooked by later authors, including Emerson. According to Holmgren's description, the nest of that species is found only in rain-forest, commonly at the base of a palm or other tree, making it very difficult to study because of the presence of many roots. It also has a pile of loose soil on the surface with sparse cylindrical galleries, and a vast subterranean part with many large, flat chambers, in which he found larvae and stored plant material. He did not find the bottom of this part after having excavated to a depth of more than a meter. Like *S. spinosus* and *S. chaquimayensis*, *S. dirus* is a forest species and builds a semi-subterranean nest with a large pile of loose soil on the surface (Fig. 32). However, based on my observations, there is a clearly differentiated central portion below ground with many horizontal, thin chambers. The chamber walls are fragile and brittle, and have a color and consistency distinctly different from the surrounding soil, indicating that this part of the nest was constructed and not simply excavated. The pile of loose soil above ground lacks any internal structure, but has several galleries lined with pelleted soil and some chambers with stored leaf litter.

Holmgren (1906: 661) also presented a detailed description of the nest of *S. peruanus* (misidentified as *T. dirus*), which also has been overlooked. He described the nest of that species as a complex structure, with a true, above-ground, compact mound about 50 cm in height and 2 m or more in diameter, found only in dry areas without trees. Holmgren divided that nest into three parts: a thin external layer with few galleries; a thick layer with numerous galleries and rounded chambers between the first layer and the soil surface; and a subterranean part with many flat and wide chambers.

There is no differentiated royal cell and the queen or queens live in any chamber in the subterranean portion. Larvae and stored grass are also found in this subterranean portion. Grass is stored mainly in a concave layer of chambers at the bottom of the nest. Negret & Redford (1982: 90), briefly described the nests of *S. wheeleri* (misidentified as *S. dirus*) from the cerrado of Central Brazil as "low-domed termitaria, the major part of which are below ground level (often to a depth of 1.5 m). The galleries are large and diffuse, often containing grass stores and are lined with regurgitated soil in which individual pellets are clearly visible." However, according to my own observations of the nest of *S. wheeleri* in Central Brazil, its structure appears similar to the nest of *S. peruanus* and can be divided into three distinct parts (Fig. 33): an external, hard, thin layer without galleries; a thick layer with many galleries and storage chambers; and a central part (endoecie) with many flat, wide and thin chambers with fragile walls, which are not lined with soil pellets but have a smooth surface. Some larvae were found in this central part, but the termites, including the queen, seem to be able to escape quickly through the wide galleries. No differentiated royal chamber was found, but there is enough space for the queen in all chambers and galleries.

The nest of *S. grandis*, from the cerrado of Central Brazil and other savannas, seems to be intermediate between the mound type and the loose soil type (Coles 1980: 51, and my own observations). It is mostly subterranean but has a small, flat mound of soft consistency above ground. No description of the subterranean part is available.

A photograph of a spherical subterranean termite nest attributed to a *Syntermes* species was published by Snyder (1948: 79). That photograph was taken during a study conducted by Fonseca (1949, Fig. F), who clearly states that the spherical nest did not belong to a *Syntermes* species, although some less conspicuous galleries and chambers made by *S. molestus* can be seen in the same picture. It is important to make this correction because Noirot (1970: 80), based on that picture, suggests that the nests of *Syntermes* may have a paraecie, which is not true.

The nests of many species of *Syntermes* still remain completely unknown. However, based on the information available, it appears that the presence of a central portion with many thin, flat and wide chambers, as well as an extensive system of subterranean galleries with storage chambers, is characteristic and can possibly be considered a synapomorphy of the genus. Other related genera, such as *Cornitermes*, *Labioterme*s and *Procornitermes*, have different types of nest, with a predominance of smaller, globular cells. None of these genera is known to store plant material inside the nests.

Feeding habits

All species of *Syntermes* seem to be specialized feeders on leaf- or grass-litter, which they collect above ground in the open and store in subterranean chambers. This is supported by the facts that grass or leaf stores have been consistently found inside their nests and that the following species have been observed foraging: *S. molestus* (as *S. brasiliensis*) and *S. grandis* (Bequaert 1925); *S. praecellens* (Silvestri 1946); *S. wheeleri* (misidentified as *S. dirus*), *S. grandis*, *S. nanus* sp.n. (misidentified as *S. molestus*), and *S. barbatus* sp.n. (misidentified as *S. brevimalatus*) (Coles 1980; Negret & Redford 1982); *S. spinosus* (misidentified as *S. chaquimayensis*), *S. molestus* and *S. parallelus* (Bandeira 1991; Barbosa 1993).

Savanna species feed mostly or exclusively on grasses. They forage in the open at night and at dusk, leaving their nest from small exit holes and forming a foraging line of workers guarded by soldiers. Workers cut grass, both living and dead, into pieces, sometimes climbing up grass tussocks, and carry them to their nest. Apparently they never consume grass above ground.

Forest species forage in a similar manner, but they seem to eat only leaf litter, which they cut into circular pieces and carry to their nest. According to Barbosa (1993), *S. spinosus* and *S. molestus* forage mainly between 7 P.M. and 3 A.M. in a forest in Central Amazonia. However, some forest species have been seen foraging during the day, and I had the opportunity to observe *S. molestus* foraging around 11 A.M. in an eastern Amazonian forest.

Apparently no one has ever tried to estimate the contribution of the activities of *Syntermes* species to total litter decomposition. Luizão & Schubart (1987) estimated that termites in general are responsible for a litter weight loss of 40% or more during the wet season in some forests in Central Amazonia, referring to *Syntermes* species as the most important members of the litter-feeding termite assemblage.

Termitophiles and inquilines

Due to the subterranean habits of most *Syntermes* species, the study of termitophiles associated with them has been greatly limited. The list in Table 3 was based on the following references: Wasmann (1894), Borgmeier (1930, 1935, 1959), Reichensperger (1936), Seevers (1941, 1957), Silvestri (1945b), Dybas (1955). The identification of the host species was corrected when possible. Species marked with an asterisk were considered as probably not true termitophiles by Seevers (1957).

A termitolestic ant of the genus *Carebara* was collected by Emerson in a nest of *Syntermes*

spinosus, and described by Wheeler (1922). Both Wheeler (1936: 199) and Emerson (1945: 436) considered this finding important evidence for the relationship between *Syntermes* and the macrotermitine genera *Acanthotermes*, *Macrotermes*, and *Odonthotermes*, because *Carebara* is otherwise found only associated with the mounds of these genera. However, there are no additional records of those ants associated with *Syntermes*, and this termitolestic association is only hypothetical. The putative phylogenetic relationship between *Syntermes* and those African macrotermitine genera is not supported by a strict cladistic analysis, and if there is any association between *Carebara* and *Syntermes* species, this is probably due to ecological similarities involving nesting and feeding behavior.

Several species of termites are also frequently associated with the nests of *Syntermes*. These are usually called inquilines by termitologists, but the nature of their association is unknown. These termites are probably associated with the nest itself instead of the species that builds it, since they live in separate galleries and possibly never meet their hosts, except for some accidental encounters. In some *Cornitermes* species, it is common to find more than 10 inquiline species in a single nest (Mathews 1977). The figures are not so impressive in *Syntermes*, and usually no more than two to five inquiline species are found in a single nest. The following list was based on collectors' notes and on my own observations. Data are available for only three species, probably because they are relatively common and build conspicuous nests.

S. dirus: *Heterotermes* sp; *Anoplotermes* sp; *Neocapritermes* sp; *Orthognathotermes* sp; *Spinitermes* sp; *Procornitermes lespesii*; *Subulitermes* sp.

S. grandis: *Anoplotermes* sp; *Orthognathotermes* sp; *Subulitermes microsoma*.

S. wheeleri: *Anoplotermes* sp; *Dentispicotermes* sp; *Dihoplotermes* sp; *Spinitermes* sp; *Paracornitermes* sp.

Fossil Record

There is no positive record of any fossil *Syntermes*, but Bown & Laza (1990) described a Miocene fossil termite nest from southern Argentina which they attributed to a *Syntermes* species. However, based on their description and illustrations, I do not see any positive evidence that what they found was even a termite nest, and it does not look like any known nest of *Syntermes*. Given the facts that the descriptions of *Syntermes* nests in the literature are very poor and that those authors based their analysis on published information only, their identification should be considered doubtful.

Economic importance

There are a few records of *Syntermes* species causing damage to cultivated plants, including young *Eucalyptus* trees (Fonseca 1949), peanuts (Cruz et al. 1962), rice (Ramalho 1976), pastures (Mariconi et al. 1976), sugar-cane (Guagliumi 1971; Mendonça-Filho 1972) and yams (Veiga 1974). Most cases of damage seem to be associated with the period immediately after the conversion of natural habitats into cultivated land, when the termites, deprived of their natural food, will eat any plant material available. There are no published estimates of the economic losses and control expenses involved. Fonseca (1949) reports that *S. nanus* (as *S. molestus*) and *S. insidians* can cause considerable damage to young *Eucalyptus* trees in some areas, destroying up to 70% of them.

Several species of *Syntermes* have been reported as being used as food by native peoples of South America. Weidner (1980) mentions that soldiers and workers of *S. aculeosus* are consumed by Indians in southern Colombia. According to Dufour (1987), alates and soldiers of *Syntermes* are an important food item for the Tukanoan Indians in the Colombian Amazon. Soldiers are consumed during ritually restricted diets in which ant and termite soldiers are the only animal food permitted. One sample of *S. aculeosus* from Venezuelan Amazon has the following label information: "Indians bite off head and eat them; grind heads and mix with salt or oil and refrigerate; aphrodisiac or taste enhancer in cooking — hot and spicy like pepper." A vial with salted, pulverized soldier heads prepared by those Indians came with that sample and it tastes really hot. The spicy taste comes from the defensive secretions from the frontal gland, which have not been studied in *S. aculeosus*. In other species of *Syntermes* this gland contains a mixture of mono- and sesquiterpene hydrocarbons (Baker et al. 1981). Tukanoan Indians in the Brazilian Amazon, close to the Colombian border, use *Syntermes tanygnathus* sp.n. (and probably other species as well) as a spice, cooking whole soldiers together with fish (R.B. Barthem, personal communication). Termite alates in general are known to be part of the diet of many groups of South American Indians and *Syntermes* species, due to their large size, are probably an important component.

MATERIAL AND METHODS

About 700 samples (vials) in alcohol and a few pinned specimens were examined, from the following entomological collections: American Museum of Natural History, New York (AMNH); Università degli Studi di Napoli, Dipartimento di Entomologia e Zoologia agraria (Silvestri's collection), Portici, Italy (LEFS); Institut Royal des Sciences Naturelles de Belgique, Brussels (ISNB); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu Paraense Emílio Goeldi,

Belém, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP); Museum of Comparative Zoology, Harvard University (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde, Humboldt Universität, Berlin (ZMHU); The Natural History Museum, London (BMNH); Naturhistoriska Riksmuseet, Stockholm (NHRS); Universidad Nacional del Nordeste, Corrientes, Argentina (UNN); Universidade de Brasília, Brazil (UnB); Universidade Federal de Goiás, Goiânia, Brazil (UFG); Universidade Federal de Viçosa, Brazil (MEUV); Zoological Museum, University of Copenhagen (ZMUC); U.S. National Museum of Natural History, Washington, D.C. (USNM).

The terminology used for imago and worker mandibles is the same as that used by Krishna (1968: 265) and Fontes (1987b: 504), and is indicated in Fig. 43. Both mandibles have an apical tooth (A) and two marginal teeth. On the left mandible, the first marginal tooth is considered to be a fusion of two teeth found in other taxa and is called first plus second marginal tooth (M_{1+2}), and, consequently, the second one is referred to as the third marginal tooth (M_3). On the proximal part of the left mandible there is a molar prominence (MP_r) with ridges on its crushing surface. Under the molar prominence there is another tooth, named the molar tooth (Mt, indicated in Fig. 44). On the right mandible, the marginal teeth are named first marginal (M_1) and second marginal (M_2), and on its proximal inner part there is a molar plate (MP), which also has ridges on its crushing surface. On the proximal part of the molar plate there is a notch, named the basal notch (BN). Since soldier mandibles are derived from worker mandibles, their dentition is homologous and I use the same terminology, except for the marginal teeth of the left mandible, which I prefer to designate M_1 and M_2 (Fig. 89).

Terms used for the digestive tube are the same as those used by Noirot & Noirtot-Timotheé (1969), indicated in Figs. 58-64. Most terms used for external morphology are of common use in entomology and do not need any special explanation, with the exception of the frontal tube of the soldier and the fontanelle. The frontal tube, also called the nasus, is present only in the soldier caste of some groups of termites. It has a pore at its tip, which is connected to a reservoir of a defensive secretion inside the head. The term fontanelle has been used with two different meanings in the termite literature (Weesner 1969). In taxonomy it has been used to refer to an area of reduced sclerotization present on the top of the head of imagoes and workers of some taxa, which is associated with a pore, also called the fontanelle. I am here using the term fontanelle to refer to the area of reduced sclerotization, and the pore itself is not mentioned in the descriptions. Terms used for hair-like structures are comparative. Bristles are long, with well-marked bases, and found on the head, thoracic nota, posterior margins of tergites and sternites, and legs. Hairs are thinner and less conspicuous. Tibial spurs are thick and present on the apical part of the tibiae.

Drawings were prepared using a camera lucida coupled with a dissection microscope. Measurements were taken with a micrometric reticle on the eyepiece of the dissection microscope. Most measurements were explained and illustrated by Roonwal's (1970), and correspondence to his system is indicated by the numbers in brackets. Measurements without any equivalent in Roonwal's system are explained.

1. length of head to lateral base of mandibles, taken laterally [5].
2. maximum width of head excluding eyes, taken dorsally [17].
3. minimum width of head, at the base of the mandibles, taken dorsally [19].
4. height of head excluding postmentum, taken laterally [21].
5. length of fontanelle: length of the area of reduced sclerotization present on the top of head of imagoes and workers, taken dorsally.
6. maximum diameter of eye, taken laterally [48]
7. maximum diameter of ocellus, taken dorsally [55]
8. length of forewing from basal suture [74]
9. maximum width of forewing.
10. maximum length of pronotum, taken dorsally [65]
11. length of frontal tube: distance between the tip and the base of the frontal tube present on the top of the head of soldiers, taken laterally.
12. length of left mandible, taken dorsally [37]
13. curvature of the left soldier mandible: the distance between the tip of the mandible and a line tangential to its outer margin, taken dorsally (indicated in Fig. 53).
14. distance M_1 - M_2 on left mandible: distance between the tips of the two marginal teeth of left soldier mandible, taken ventrally (Fig. 53).
15. width of left mandible: minimum distance between the outer and inner margin of the soldier mandible between M_1 and M_2 , taken ventrally (Fig. 53).
16. length of left M_1 : distance between the tip of the first marginal tooth and the apical cutting edge of left soldier mandible, taken ventrally (Fig. 53).
17. minimum width of postmentum [63]
18. maximum width of pronotum, including spines [68]
19. maximum width of metanotum, including spines [72]
20. length of hind tibia [85]

KEY TO THE IMAGOS OF *SYNTERMES*

Note: Alates are difficult to identify and in some cases those of two different species are indistinguishable. It is important to keep in mind that the alates of several species are still unknown, and that the descriptions and the key below are, in most cases, based on limited material. Some species may show more variation than is currently known. Correct identification depends on careful comparison of descriptions, geographical distribution, and habitat. Care should also be taken with broken antennae and missing hairs, which can be easily rubbed off from the top of the head and other areas.

1. Head capsule in dorsal view² with fewer than 20 hairs posterior to clypeus (Fig. 90); eyes small, less than 0.26 width of head; wings brown 2
 Head capsule in dorsal view with more than 30 hairs posterior to clypeus (Fig. 236); eyes and wings variable 8
- 2(1). Width of pronotum more than 3.5mm; postclypeus with 6 or more hairs 3
 Width of pronotum less than 3.5mm; postclypeus with 2 or 4 hairs 6
- 3(2). Antenna with 21 articles; Colombian Amazon and westernmost Brazilian Amazon (Figs. 326-328) *S. tanygnathus*
 Antenna with 19-20 articles (3rd article sometimes partially subdivided) 4
- 4(3). Anterior margin of postclypeus with 6 long hairs; top of head with conspicuous, fairly long hairs; widely distributed in Amazonia and Mato Grosso (Figs. 314-316)
 *S. spinosus*
 Anterior margin of postclypeus with 2-4 hairs; hairs on top of head short and inconspicuous, sometimes barely visible 5
- 5(4). Ratio of length to width of pronotum less than 0.5; length of fontanelle 0.47-0.57mm; western and northern Amazonia (Figs. 90-92) *S. aculeosus*
 Ratio of length to width of pronotum more than 0.5; length of fontanelle 0.3-0.5mm; eastern

² Dorsal view assumes a prognathous orientation of the head.

- Amazonia to Brazilian Atlantic forest (Figs. 167-169) *S.dirus* or *S. cearensis*³
- 6(2). Anterior corners of pronotum nearly rounded; postclypeus with 4 hairs (Figs. 337-339) *S. territus*
 Anterior corners of pronotum distinctly angular (Figs. 216, 277); postclypeus with only two hairs on anterior margin (Figs. 214, 275) 7
- 7(6). Ratio of length of hind tibia to width of head without eyes less than 1.8; central and eastern Amazonia (Figs. 214-216) *S. longiceps*
 Ratio of length of hind tibia to width of head without eyes more than 1.8; northern Amazonia and Guianas (Figs. 275-277) *S. parallelus*
- 8(1). Width of head without eyes less than 2.8mm; anterior corners of pronotum rounded (Figs. 238, 249) 9
 Width of head without eyes more than 2.8mm; anterior corners of pronotum slightly to strongly angular (Figs. 143, 186, 297) 10
- 9(8). Width of pronotum less than 2.7mm; ratio diameter of eye to width of head 0.32-0.38mm; length of fontanelle 0.17-0.34; head and pronotum dark brown; fontanelle about the same color as head capsule or a little paler; cerrado vegetation (Figs. 247-249) . . . *S. nanus*
 Width of pronotum more than 2.7mm; ratio diameter of eye to width of head 0.28-32mm; length of fontanelle 0.34-0.45; head and pronotum chestnut brown; color of fontanelle conspicuously paler than head capsule; from Amazonia to Brazilian Atlantic forest (Figs. 236-238) *S. molestus*
- 10(8). Ratio of maximum diameter of eye to width of head without eyes less than 0.26 11
 Ratio of maximum diameter of eye to width of head without eyes more than 0.26 12
- 11(10). Fontanelle nearly triangular, length 0.2-0.3mm; wings hyaline, length of forewing 36-36.5mm; head dark brown, contrasting with much paler pronotum; anterior corners of pronotum moderately angular; southeastern Brazil (Figs. 295-297) *S. praecellens*

³ See geographical distribution. *S. cearensis* restricted to a relatively small area in northeastern Brazil.

- Fontanelle rounded, length 0.34-0.4; wings dark, length of forewing 27.5-28mm; head and pronotum light chestnut; anterior corners of pronotum distinctly angular; western Amazonia (Figs. 141-143) *S. chaquimayensis*
- 12(10). Length of ocellus 0.29-0.39; fontanelle usually elongate, roughly triangular; head chestnut-brown contrasting with paler pronotum; Central and southeastern Brazil (Figs. 353-355) *S. wheeleri*⁴
- Length of ocellus 0.37-0.45; fontanelle rounded or elongate; head dark-brown; pronotum about the same color as head 13
- 13(12). Fontanelle rounded, length less than 0.48mm; antenna with 20 articles; Central and southeastern Brazil to Guianas (Figs. 184-186) *S. grandis* or *S. magnoculus*⁵
- Fontanelle elongate, length more than 0.5mm; antenna with 21 articles; northern Argentina, Paraguay, southern Bolivia, and southwestern Brazil (Figs. 263-265) *S. obtusus*

KEY TO THE SOLDIERS OF *SYNTERMES*

Note: The terminology and measurements used in the key below are described in the Methods section. Several species are still poorly known and may show more morphological variation and wider geographical distribution than indicated in this key. The soldiers of some species show high morphological variation and may be very difficult to separate from those of other similar species because of overlap in size and morphology. Accurate identification depends on careful comparison of morphology, geographical distribution, habitat, and sometimes the nest. It is also important to keep in mind that young colonies produce, at least in some species, smaller soldiers with a somewhat different morphology. This key is based exclusively on normal soldiers (i.e., from mature colonies).

1. First marginal tooth (M1, Fig. 53) of right mandible very small or absent; angle between

⁴ The imago of *S. peruanus*, not included in this key, is very similar, but is known only from a few, poorly preserved and incompletely sclerotized specimens from southern Peru and northern Bolivia. See also remarks under *S. bolivianus*.

⁵ *S. magnoculus* known from a few localities in Central Brazil.

- right M1 and apical cutting edge more than 100°; left M1 small, not projecting much beyond apical cutting edge; a notch anterior to left M1 always present (Figs. 112, 208, 235, 274, 325) 2
- Right M1 well-developed; angle between right M1 and apical cutting edge less than 100°; left M1 variable, but always near the middle of the mandible (Figs. 117, 177, 194, 294, 305) 10
- 2(1). Left M1 very close to left M2; right M1 vestigial, very close to base of mandible, or absent (Figs. 235, 325) 3
- Distance from left M1 to left M2 more than 0.2 X the distance from A to M2; right M1 small but distinct (Figs. 208, 257) 6
- 3(2). Frontal tube very short, pore visible from dorsal view⁶; lateral margins of thoracic nota not upturned, roughly angular but not sharp (Figs. 231-235, 242-246) 4
- Frontal tube prominent, pore not visible from dorsal view; lateral margins of thoracic nota upturned, very sharp and forming spines (Figs. 269-274, 320-325) 5
- 4(3). Sides of head converging towards front; mandibles strongly hooked at tips; postmentum widening posteriorly, with only two hairs on anterior corners; maximum width of head more than 2.9mm; Amazonia to Brazilian Atlantic forest (Figs. 231-235) *S. molestus*
- Sides of head parallel and slightly convex; mandibles moderately hooked at tip; postmentum with posterior lateral margins parallel, two hairs on anterior corners and several hairs on posterior part; maximum width of head less than 2.9 mm; cerrado vegetation of central, southeastern and northeastern Brazil (Figs. 242-246) *S. nanus* sp.n.
- 5(3). Head elongate with parallel sides; width of head less than 4mm; antenna with 19 articles; spines of meso- and metanotum short and slightly upturned; Guyana, eastern Venezuela and northern Roraima (Figs. 269-274) *S. parallelus*
- Head short with sides converging towards front; width of head more than 5mm; antenna with 20-21 articles; spines of meso- and metanotum large and strongly upturned; western Amazonia (Figs. 320-325) *S. tanygnathus* sp.n.

⁶ Dorsal view assumes a prognathous orientation of the head, with top of head oriented horizontally.

- 6(2). Head elongate with parallel sides; width of head less than 0.85 X length of head; frontal tube prominent, pore not visible from dorsal view (Figs. 204, 332) 7
 Head short with sides converging towards front or nearly parallel; width of head more than 0.85 X length of head; frontal tube variable 8
- 7(6). Maximum width of head more than 4.4mm; base of mandibles and clypeal region with many hairs (Figs. 332-336) *S. territus*
 Maximum width of head less than 4.4mm; base of mandibles with scattered hairs; clypeal region with fewer than 10 hairs (Figs. 204-208) *S. longiceps*
- 8(6). Width of head less than 5.1mm; antenna with 19-20 articles 9
 Width of head more than 5.1mm; antenna with 20-21 articles (Figs. 253-262); northern Argentina, southern Bolivia, Paraguay, and southwestern Brazil *S. obtusus*
- 9(8). Sides of head converging towards front; length of left M1 more than 0.2mm; postmentum without a protuberance near anterior margin; southern Peru and northern Bolivia (Figs. 281-285) *S. peruanus*
 Sides of head parallel; left M1 very small, length less than 0.2 mm; postmentum with a small protuberance near anterior margin; southern Bolivia and northwestern Argentina (Figs. 108-112) *S. bolivianus*
- 10(1). Maximum width of head less than 4.3 mm 11
 Maximum width of head more than 4.3 mm 12
- 11(10). Antennae with 20-21 articles; length of hind tibia more than 0.8 X length of head; M1 oriented anteriorly on both mandibles; central and southeastern Brazil (Figs. 190-200) *S. insidians*
 Antennae with 19 articles; length of hind tibia less than 0.8 X length of head; M1 oriented perpendicularly on both mandibles; Brazilian Amazonia (Figs. 209-213)
 *S. longiceps* sp.n.
- 12(10). Mandibles short and robust, with inflated bases (Figs. 117, 294); length of left mandible 0.38-0.45 X length of head; notal spines short and only slightly upturned 13
 Mandibles moderately elongate (Figs. 177, 305); length of left mandible 0.45-0.58 X length of head; notal spines variable, but spines on meso- and metanotum conspicuously

- upturned 16
- 13(12). Head (at least anteriorly), thoracic nota and base of mandibles densely covered with hairs (Figs. 96, 289) 14
 Head, thoracic nota and base of mandibles with few hairs (Figs. 113, 147) 15
- 14(13). Head with long, fine, curly hairs, more numerous anteriorly and on bases of mandibles; posterior margin of head distinctly three-lobed and irregular; cerrado vegetation of central Brazil (Figs. 96-101) *S. barbatus* sp.n.
 Head with short and straight hairs, evenly distributed; posterior margin of head evenly rounded; central to southeastern Brazil (Figs. 289-294) *S. praecellens*
- 15(13). Labrum short with lateral corners forming a right angle and median lobe very short; postmentum very elongate, with two hairs on anterior corners and a few or none on posterior part; right M1 small, forming an angle of more than 90° with the apical cutting edge (Figs. 113-117) *S. brevimalatus*
 Labrum large and fleshy, with rounded corners; postmentum shorter, with numerous hairs; right M1 larger, forming an angle of about 90° with the apical cutting edge (Figs. 147-152) *S. crassilabrum*
- 16(12). Head densely covered either with long, fine, curly hairs or short, straight hairs of uniform size; pronotal spines long and conical; frontal tube prominent (Figs. 84-89, 102-106, 156-161, 301-305) 17
 Head capsule with scattered hairs of variable size; pronotal spines and frontal tube variable (Figs. 130-134, 343-347) 20
- 17(16). Head densely covered with long, fine, curly hairs (Figs. 84, 156) 18
 Head densely covered with short, straight hairs (Figs. 135, 301) 19
- 18(17). Mandibles strongly curved; apical cutting edge of both mandibles evenly curved; M1 very large on both mandibles; central and northern Amazonia (Figs. 84-89) *S. aculeosus*
 Mandibles moderately curved; apical cutting edge sigmoid on both mandibles; M1 small on both mandibles; Brazilian Atlantic forest and gallery forests along Tocantins and Araguaia rivers up to Marajó Island (Figs. 156-161) *S. dirus*

- 19(17). Width of head 5.5-6.3mm, usually less than 6.1mm; mandibles short and robust; western Amazonia (Figs. 135-140) *S. chaquimayensis*
 Width of head 5.7-7.6mm, usually more than 6.0mm; mandibles variable, but part anterior to M1 tends to be more elongate and slender; from Venezuela and Guianas to Mato Grosso (Figs. 301-305) *S. spinosus*
- 20(16). Pronotal spines well developed, distinctly conical (Fig. 159); frontal tube prominent with pore oriented anteriorly, sometimes in a small depression (Figs. 125, 157); forest species 21
 Pronotum with angular sides, without conical spines or with short conical spines (Figs. 175, 222); frontal tube short with pore clearly visible from dorsal view (Fig. 174); cerrado or savanna species 24
- 21(20). Scattered long, fine, curly hairs present on top of head (Fig. 162); sides of head nearly parallel; Brazilian Atlantic forests, from Ceará to Rio de Janeiro 22
 Long, fine, curly hairs never present on head capsule; sides of head converging towards front or nearly parallel; Guianas, Amazonia, Mato Grosso 23
- 22(21). Width of head more than 5.2mm; frontal tube prominent; length of hind tibia 5.1-6.3mm; Brazilian Atlantic forest from Bahia to Rio de Janeiro (Figs. 162-166) *S. dirus*
 Width of head less than 5.2mm; frontal tube small; length of hind tibia 4.6-5.1mm forests of Ceará and western Rio Grande do Norte (Figs. 130-134) *S. cearensis* sp.n.
- 23(21). Width of head more than 5.5mm; postmentum not inflated, only partially visible in profile; underside of head with many short, straight hairs of fairly uniform size; top of head posterior to frontal tube with many short, straight hairs; western Amazonia to Mato Grosso do Sul (Figs. 306-310) *S. spinosus*⁷
 Width of head less than 5.5mm; postmentum inflated, clearly visible in profile; underside of head with a few hairs of variable size; top of head posterior to frontal tube with very few or no hairs; Guianas and northeastern Brazilian Amazonia (Figs. 124-129) *S. calvus*
- 24(20). Apical cutting edge of left mandible evenly curved, not forming a notch anterior to M1; left

⁷ In typical soldiers of *S. spinosus*, the top of head is densely covered with short, straight hairs. However, in some specimens from western Amazonia and Mato Grosso, fewer hairs are present on head.

- M1 0.97-1.24mm; width of head more than 6mm; antenna with 21 articles (Figs. 220-224) *S. magnoculus*
- Apical cutting edge sigmoid; width of head 5-6.6mm; left M1 0.76-1.14mm; antenna with 19-20 articles 25
- 25(24). Top of head posterior to frontal tube with many hairs; sides of head nearly parallel from dorsal view; M1 rather small and forming a right angle with the apical cutting edge on both mandibles; length of left mandible 2.8-3.0mm; length of hind tibia 4.7-5.3 mm (Figs. 343-347) *S. wheeleri*
- Top of head posterior to frontal tube with few or no hairs; sides of head converging towards front or nearly parallel; M1 larger and forming an angle of less than 90° with the apical cutting edge on both mandibles; length of left mandible 3.0-3.4mm; length of hind tibia 5.3-6.9mm (Figs. 173-183) *S. grandis*⁸

TAXONOMY

Genus *Syntermes* Holmgren

Type species: *Syntermes dirus* (Burmeister), by original designation.

Termes, Burmeister 1839: 758 [part].

Termes (*Termes*), Hagen 1858: 107; Desneux 1904a: 35 [part].

Syntermes Holmgren 1910: 286 [type species designated; no description]; Holmgren 1911: 545 [taxonomic notes and key to species]; Holmgren 1912: 46 [description; phylogenetic relations]; Emerson 1945: 439 [revision]; Mathews 1977: 141 [diagnosis].

Imago. Head rounded, light chestnut to dark brown; pilosity variable, from a few very short hairs to numerous long ones. Relative size of eyes and ocelli variable. Fontanelle conspicuous, usually large and circular, flat or slightly convex; small and concave in a few species and slightly elongate in

⁸ Soldier of *S. grandis* show a lot of morphological variation and may be difficult to separate from those of *S. wheeleri*. Information on nest and geographical distribution will help identification.

others. Antenna with 19 to 21 articles. Left mandible (Fig. 43) with apical tooth (A) nearly equal to first marginal tooth (M1); second marginal tooth (M2) absent; third marginal tooth (M3) short but conspicuous; cutting edge between M1 and M3 long and straight. Right mandible with A about equal to M1, sometimes a little longer; M2 smaller than A or M1; molar plate concave, small, and very narrow, with about 7 transverse ridges (less conspicuous than in workers); basal notch distinct, forming approximately a right angle. Postclypeus weakly inflated; median line visible; length less than half width. Pronotum in most species about same width as head with eyes, but sometimes wider or narrower; anterior margin raised in middle; lateral projection flat, sharply pointed or rounded; hind margin always emarginate. Tibial spur formula 3:2:2. Wings (Figs. 35-42) dark or hyaline, with two unbranched sclerotized veins distad of basal suture, one on costal border (SC + R), the other parallel to it (Rs), and weakly sclerotized and variably branched M and Cu, with distal part sometimes barely visible. Very short R1 joining SC + R distad of the basal suture. Surface of wings covered with numerous very short hairs and fine microsculpturing.

Soldier. Head large, usually short and broad, sometimes elongate; sides straight, parallel or converging towards front; head color yellow-brown; pilosity of head variable, from a few scattered hairs to dense short or long hairs. Frontal tube very short. Labrum conspicuously three-pointed, with white area on median lobe (labral gland of unknown function, probably defensive). Antennae with 19 to 21 articles. Mandibles large and robust, of variable shape and dentition; left mandible with a marginal tooth (M1) usually near middle, sometimes close to the base; second marginal tooth (M2) small and near the base; right mandible also with two marginal teeth, usually less developed than in left mandible and sometimes vestigial or absent. Pronotum with large raised anterior lobe. Lateral edges of thoracic nota angular, usually developed into upturned sharp points or conical spines (only *S. molestus* and *S. nanus* lack spines, but sides are distinctly angular). Proximal external face of forecoxa, mesepimeron, and metepimeron with elliptic, lighter colored area with numerous pores and differentiated tissue under cuticle (exocrine glands of unknown function). Legs usually long; foretibia with numerous spine-like short bristles on inner margin, a little thicker than other leg bristles. Tibial spur formula 3:2:2.

Workers. Four forms can be recognized (Figs. 54-57): males of 3rd and 4th instars and females of 3rd and 4th instars. Male workers larger and more sclerotized, with proportionally longer mandibles with smaller molar plates (Figs. 44-47), more slender abdomens, and slightly larger notal spines (when present). Female workers pale, not differing much between instars. Male worker of 4th instar dramatically larger than that of the 3rd instar and well sclerotized, with yellow-brown head.

Head of 3rd instar male yellow with irregular longitudinal stripes of paler color. Detailed descriptions will be provided only for the 4th instar male worker because it is the form most easily collected and, for many species, it is the only one available for study.

Large worker. Head nearly rounded to moderately elongate; yellow-brown; pilosity variable from few to numerous straight hairs. Fontanelle conspicuous; paler than head capsule; rounded or slightly elongate. Mandibles similar to those of imago but with much larger and wider molar region and more conspicuous molar ridges (Fig. 44). Antenna with 19 to 21 articles. Thoracic nota with angular sides or spines similar to those of soldier of same species, but smaller. Exocrine glands same as on thorax and forecoxa of soldier. Pilosity of thorax and abdomen usually similar to that of soldier. Tibiae with two rows of spine-like short bristles on inner face, more conspicuous than in soldiers. Tibial spur formula 3:2:2.

Digestive tube. Crop small and not separate from the gizzard; both forming an oval pouch of diameter similar to that of midgut; gizzard armature well-developed, its length about 1/10 that of abdomen; stomodeal valve short. Midgut relatively short. Midgut-hindgut junction with two unequal extensions of midgut tissue into hindgut, forming a mixed segment (Figs. 62-64). Malpighian tubules inserted in two pairs at midgut-hindgut junction (Fig. 64). First segment of hindgut very large, much broader than midgut. Enteric valve very wide, lacking any sclerotized armature, but with reinforced circular musculature. Paunch also well-developed, about same volume as first segment of hindgut.

Syntermes aculeosus Emerson

Syntermes aculeosus Emerson 1945: 443 [soldier, worker]. Holotype soldier: Guyana, Oronoque River, coll. N.A. Weber, 22.vii.1936, AMNH. Paratypes: one major worker, same data as holotype.

Material examined. BRAZIL. *Amazonas*. Manaus, coll. H. Schubart, 16.iv.66, soldiers, workers [MZSP-1133]; coll. W. Paarman, 31.vii.92, alates [INPA], coll. C. Martius, 27.vii.93, one soldier, one worker [INPA]. Porto Urucu, Rio Urucu, coll. T.C.S. Pires, 19.xi.89, one soldier [MPEG-3302]. *Pará*. Faro, Rio Nhamundá, coll. T.C.S. Pires, 15.xii.88, one soldier, [MPEG-3437]; Rio Trombetas, coll. M. Lohmann, vii.94, one soldier, workers [INPA]. *Rondônia*. Presidente Médici, coll. R.B. Neto, 24.viii.84, soldiers, workers, [MPEG-2231]. U.H. Samuel, coll. A.B. Machado, 22.xi.84, soldiers, workers [MPEG-2243]. COLOMBIA. *Amazonas*, coll. S.H. Jones, soldiers [BMNH]. Bakura, coll. S.H. Jones, soldiers, alates [BMNH]. Vaupés. Querarimiri, Rio Cuduyari,

coll. D. Dufour, vii.76, soldiers, [USNM]. SURINAME. Anapaïke. Marowijne, coll. B. Malkin, 12.xi.63, one soldier, workers [MZSP-177]. VENEZUELA. Haut Orenoque: Maraca, coll. J. Lizot, 20.xii.69, soldiers [MNHN]. *Amazonas*. Movaca, coll. F.F.Y., 15.iv.65, soldiers [MZSP-9600]. Puerto Ayacucho, coll. C. Seiderman, i.1993, soldiers, [AMNH]. San Carlos de Rio Negro, coll. M. Blum, v.78, soldiers [MZSP-7592].

Imago (Figs. 90-92). Eyes small, diameter less than 1/4 width of head; ocelli small, length about 1/10 width of head; fontanelle large and rounded. Antenna with 20 articles. Anterior corners of pronotum sharply angular; lateral margins rounded and converging posteriorly. Wings relatively short; distal part of media and cubitus conspicuous. Head capsule with a few scattered very short hairs; postclypeus with 6-8 short hairs; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with line of hairs on posterior margin. Head and pronotum light chestnut; tergites dark brown; wings brown to dark brown.

Measurements (in mm) of 3 imagoes from one colony: length of head 2.70-2.95; width of head without eyes 3.10-3.50; length of fontanelle 0.47-0.57; length of pronotum 2.00-2.30; width of pronotum 4.25-4.85; length of hind tibia 6.90-7.10; maximum diameter of eye 0.69-0.72; length of ocellus 0.27-0.35; length of forewing 26.50-30.50; width of forewing 5.70. Ratios: diameter of eye to width of head 0.21-0.23; length of ocellus to width of head 0.09-0.10; length of fontanelle to width of head 0.15-0.18; width of pronotum to width of head 1.37-1.52; length of wing to width of head 8.55-8.71; length of hind tibia to width of head 2.03-2.27.

Soldier (Figs. 84-89). Head capsule short and wide; sides straight, converging towards front; posterior margin evenly rounded. Frontal tube prominent. Lateral angle of labrum obtuse. Antenna with 20 articles. Sides of posterior part of postmentum nearly parallel. Anterior margin of pronotum emarginate (visible in posterior view only; figures show dorsal view); posterior margin slightly emarginate. Thoracic spines very long and conical. Mandibles moderately elongate and robust, strongly curved; M1 on both mandibles very large near the middle, oriented anteriorly. Apical cutting edge on both mandibles evenly curved. Head capsule with a few scattered bristles and densely covered with long, fine and curly hairs. Labrum with many bristles. Base of mandible densely covered with fine, curly hairs, shorter than those on head capsule. Postmentum with one bristle on each anterior corner and numerous fine, long and curly hairs. Pronotum with numerous bristles on anterior lobe; a few bristles on posterior margin, and scattered fine, long and curly hairs. Mesonotum and metanotum with a few bristles on posterior margin and scattered fine, long hairs. Tergites with scattered bristles on surface and posterior margins and a few long, fine hairs.

Measurements (in mm) of 11 soldiers from 11 colonies: length of head 6.30-7.10; maximum width of head 6.50-7.20; height of head excluding postmentum 3.70-4.30; length of frontal tube 0.27-0.42; length of left mandible 3.20-4.00; curvature of left mandible 1.40-2.00; distance from M1 to M2 on left mandible 0.76-1.09; width of left mandible 1.06-1.24; length of left M1 0.40-0.66; minimum width of postmentum 1.00-1.10; width of pronotum 5.40-7.10; width of metanotum 5.55-7.10; length of hind tibia 6.50-7.60. Ratio length of head to maximum width of head 0.97-1.01; length of left mandible to length of head 0.46-0.57; length of hind tibia to length of head 1.01-1.15; width of pronotum to maximum width of head 0.79-1.02; distance M1-M2 to length of left mandible 0.23-0.33; height of head to maximum width of head 0.56-0.60; width to length of left mandible 0.29-0.39.

Large worker (Figs. 93-95). Head capsule covered with sparse bristles; postclypeus with about 6 bristles. Fontanelle rounded and large. Antenna with 20 articles. Thoracic spines conical and well-developed. Mandibles similar to those of *S. dirus* (Fig. 44), except that basal notch forms a right angle. Gut superficially similar to that of *S. dirus* (Figs. 71-72) (material available was poorly preserved).

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.60-3.10; maximum width of head 3.40-3.95; length of fontanelle 0.29-0.34; width of pronotum 2.85-3.45; width of metanotum 3.00-3.75; length of hind tibia 5.20-6.00.

Comparisons. Alates similar to *S. dirus*, but with a proportionally wider and shorter pronotum and larger fontanelle. Soldiers easily distinguished based on their large size, the presence of dense long, fine and curly hairs on the head, very large thoracic spines, and large teeth on the mandibles. Some of the largest specimens of *S. dirus* may be similar in size and pilosity, but they are always measurably smaller and their mandibles have smaller teeth and a distinctly sigmoid left apical cutting edge.

Distribution and Geographical Variation. Central-northwestern portion of the Amazonian region (Fig. 359). Soldiers show considerable variation in size of the thoracic spines and of the mandibular dentition, but no geographic pattern could be recognized from the material available.

Biology. It is certainly a forest species, and one sample had the note "earth pile" which indicates its nest might be similar to that of *S. dirus*.

Syntermes barbatus, new species

Syntermes brevimalatus, Coles 1980: 51, misidentification [biology] and Baker et al. 1981 [chemical composition of the frontal gland secretion].

Holotype soldier: BRAZIL. *Distrito Federal*. Brasília: Fazenda Água Limpa, coll. H.R. Coles, 30.iv.77 [MPEG-1255]. Paratypes: two vials, same data as holotype, one with 15 soldiers [MPEG-1291] and the other with 7 soldiers and one worker [MPEG-1255].

Imago. Unknown.

Soldier (Figs. 96-101). Head capsule short with parallel sides; length of head without mandibles about equal to its width; posterior margin of head conspicuously three-lobed and irregularly and coarsely rugose; frontal tube prominent, pore not visible from dorsal view. Labrum short, length about equal to width; lateral corners about right angular; median lobe short. Antenna with 19 or 20 articles. Postmentum not constricted in the middle, sides of posterior part nearly parallel. Mandibles very short and robust, with hooked tips; bases strongly inflated; first marginal tooth of both mandibles well-developed, near middle; angle between teeth and apical cutting edge obtuse; apical cutting edge of both mandibles evenly curved. Anterior margin of pronotum nearly rounded; posterior margin of pronotum conspicuously emarginate; thoracic spines weakly developed and oriented horizontally. Head capsule, base of mandibles and postmentum densely covered with long, fine, curly hairs, less dense on top and posterior part of head. Pronotum, mesonotum and metanotum with numerous hairs; tergites with many straight bristles plus variable number of long, fine hairs. Abdomen darker and more sclerotized than in most species.

Measurements (in mm) of 4 soldiers from 2 samples: length of head 6.40-6.60; maximum width of head 5.80-6.20; height of head excluding postmentum 3.40-3.60; length of frontal tube 0.27-0.29; length of left mandible 2.50-2.80; curvature of left mandible 0.85-0.90; distance from M1 to M2 on left mandible 0.59-0.60; width of left mandible 0.87-0.96; length of left M1 0.17-0.25; minimum width of postmentum 0.86-0.94; width of pronotum 3.60-4.00; width of metanotum 3.60-4.00; length of hind tibia 5.30-5.60. Ratios: length of head to maximum width of head 1.06-1.12; length of left mandible to length of head 0.39-0.42; length of hind tibia to length of head 0.82-0.85; width of pronotum to maximum width of head 0.61-0.67; distance M1-M2 to length of left mandible 0.21-0.24; height of head to maximum width of head 0.56-0.60; width to length of left mandible 0.31-0.38.

Large worker (Figs. 102-104). Head sparsely covered with straight bristles. Fontanelle rounded and small. Antenna with 20 articles. Thoracic spines very short. Mandibles in poor condition in only worker available. Worker gut not examined; soldier gut similar to that of *S. wheeleri*, but mixed segment is distinct (Figs. 36-38); major prolongation broadly rounded and strongly constricted at junction with midgut; minor prolongation elongate, inflated, oriented transversely, also strongly constricted at junction with midgut.

Measurements (in mm) of one large worker: length of head 2.85; maximum width of head 3.40; length of fontanelle 0.17; width of pronotum 2.25; width of metanotum 2.25; length of hind tibia 4.75.

Comparisons. The soldier of this species is very distinct, easily distinguished by its short mandibles, dense pilosity, rugose anterior part of head, and short thoracic spines. The gut is similar only to that of *S. praecellens*.

Distribution and Geographical Variation. Known only from the type-locality (Fig. 365).

Biology. According to Coles (1980), this species lives in completely subterranean nests, in the cerrado. Foraging behavior is similar to that of other *Syntermes* species.

***Syntermes bolivianus* Holmgren**

Syntermes bolivianus Holmgren 1911: 547-548 [soldier in key]. Lectotype soldier, here designated: Southern BOLIVIA, no data, in poor condition [AMNH]. Paralectotypes: one soldier, workers, same data as lectotype, also in poor condition [AMNH]. No types found in Holmgren's collection in NHRS.

Material examined. ARGENTINA. *Santiago del Estero*. Santiago del Estero, coll. E.R. Wagner, 1911, one pinned soldier [MNHN]. *Tucumán*. Canete, 01.ix.65, one soldier, workers [MZSP-8165].

Imago. Unknown.

Soldier (Fig. 108-112). Head capsule short, length and width of head about equal, sides

nearly parallel and slightly convex; posterior margin of head nearly rounded; frontal tube very short, pore clearly visible from dorsal view; labrum short, length about equal to width; lateral corners of labrum approximately a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle, small, not extending much beyond the apical cutting edge; first marginal tooth of right mandible small but conspicuous, angle between anterior margin and apical cutting edge obtuse; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines well-developed and upturned; pronotum with distinct but short conical spines. Head capsule from dorsal view with about 30 straight bristles; clypeal region and base of mandible with many short hairs; postmentum with two straight bristles on anterior corners plus many scattered ones. Pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior half and occasionally a few on spines and lateral margins; tergites with many bristles near hind margins.

Measurements (in mm) of 3 soldiers from 3 colonies: length of head 4.35-4.80; maximum width of head 4.20-4.45; height of head excluding postmentum 2.45-2.65; length of frontal tube 0.15-0.17; length of left mandible 2.50-2.60; curvature of left mandible 0.65-0.70; distance from M1 to M2 on left mandible 0.54-0.55; width of left mandible 0.67-0.67; length of left M1 0.13-0.15; minimum width of postmentum 0.76-0.81; width of pronotum 2.95-3.10; width of metanotum 2.95-3.05; length of hind tibia 4.45-4.45. Ratio length of head to maximum width of head 1.04-1.08; length of left mandible to length of head 0.54-0.57; length of hind tibia to length of head 1.02-1.02; width of pronotum to maximum width of head 0.70-0.70; distance M1-M2 to length of left mandible 0.22-0.22; height of head to maximum width of head 0.58-0.60; width to length of left mandible 0.27-0.27.

Large worker (Figs. 105-107). Head covered with many straight bristles. Fontanelle rounded, moderately large, and convex. Antenna with 20 articles. Mandibles similar to those of *S. wheeleri*, with wide molar region. Gut not examined; available material in poor condition.

Measurements (in mm) of 2 large workers from 2 colonies: length of head 2.60-2.70; maximum width of head 3.10-3.10; length of fontanelle 0.30-0.34; width of pronotum 2.00-2.10; width of metanotum 2.43-2.43; length of hind tibia 3.75-3.80.

Comparisons. The soldier of *S. bolivianus* has no special diagnostic character, but can be

distinguished on the basis of its relatively small size, very short frontal tube, marginal teeth weakly developed on both mandibles, and moderately developed thoracic spines. The most similar soldier is that of *S. peruanus*, which is larger and has a larger marginal tooth on the left mandible.

Distribution and Geographical Variation. Southern Bolivia and northern Argentina (Fig. 366).

Biology. No information available. Based on the geographical distribution, the most probable habitat is the chaco, an arid savanna.

Remarks. This species was considered by Emerson (1945) as a junior synonym of *S. peruanus*, based on the poor description by Holmgren (1911) and without examining any type material. Cotypes of *S. bolivianus* were later found by Emerson in Holmgren's collection and they are clearly distinct from the type of *S. peruanus*. Based on the limited material and information available, they seem to be distinct species and I am here resurrecting *S. bolivianus*. Future studies based on larger series and imagoes will be necessary to clarify the status of this species. Two undetermined alates from Argentina (Tucumán: Canete, MZSP-8164) probably belong to this species since soldiers of *S. bolivianus* were collected in the same locality. They are similar to the imagoes of *S. peruanus* and *S. wheeleri*, but I am not describing the imago of *S. bolivianus* based on that material because they were not collected with soldiers and they are not in good condition.

Syntermes brevimalatus Emerson

Syntermes brevimalatus Emerson 1945: 457 [soldier, worker]. Holotype soldier: GUYANA. Oronoque River, coll. N. Weber, 22.vii.36 [AMNH]. Paratypes: one soldier, workers, same data as holotype [AMNH]; one soldier, workers, same data [USNM].

Imago. Unknown.

Soldier (Figs. 113-117). Head capsule elongate with parallel sides; posterior margin of head rounded or weakly three-lobed; frontal tube prominent, pore not visible from dorsal view; labrum short, length about equal to width; lateral corner nearly forming a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel.

Mandibles short and robust; bases strongly inflated; tips slightly hooked; both mandibles with a well-developed first marginal tooth near middle; angle between both teeth and apical cutting edge obtuse; apical cutting edge of both mandibles evenly curved. Anterior margin of pronotum conspicuously emarginate; posterior margin nearly straight; lateral projections of thoracic nota oriented horizontally; thoracic spines weakly developed; lateral corners of pronotum sharp but not forming conical spines. Head capsule in dorsal view with only about eight short bristles on clypeal region; base of mandible without hairs; postmentum with two straight bristles on anterior corners plus a few scattered ones; pronotum with only a few bristles on anterior lobe and margins; meso- and metanotum without bristles or hairs; tergites with a few bristles near hind margin.

Measurements (in mm) of 1 soldier: length of head 7.30; maximum width of head 6.30; height of head excluding postmentum 3.90; length of frontal tube 0.32; length of left mandible 2.80; curvature of left mandible 1.05; distance from M1 to M2 on left mandible 0.76; width of left mandible 0.96; length of left M1 0.24; minimum width of postmentum 1.01; width of pronotum 4.50. Ratio length of head to maximum width of head 1.16; length of left mandible to length of head 0.38; width of pronotum to maximum width of head 0.71; distance M1-M2 to length of left mandible 0.27; height of head to maximum width of head 0.62; width to length of left mandible 0.34.

Large worker (Figs. 118-120). Head with a few scattered bristles; postclypeus with 4 bristles. Fontanelle rounded and small. Antenna with 20 articles. Thoracic spines moderately developed. Mandibles (Fig. 50) with very narrow molar plates. Gut not examined; available material in poor condition.

Measurements (in mm) of 1 large worker: length of head 2.80; maximum width of head 3.45; length of fontanelle 0.25; width of pronotum 2.50; width of metanotum 2.85; length of hind tibia 4.30.

Comparisons. The soldier of *S. brevimalatus* is very distinct and can be identified based on its elongate head with parallel sides, very short and robust mandibles, weakly developed thoracic spines and lack of hairs on most parts of the head and thorax. The most similar soldiers are those of *S. barbatus*, which is densely covered with hairs and has strongly hooked mandibles, and *S. crassilabrum*, which has longer mandibles, a large and fleshy labrum and more hairs on the head.

Distribution and Geographical Variation. Known only from the type series, a single colony from Guyana (Fig. 366).

Biology. Little information available. Field notes from the type material state: "Nesting in

clay at base of tree. Openings one centimeter in diameter leading to horizontal galleries in top ten to thirty centimeters of soil." This implies that the nest is completely subterranean, since no epigeal portion is mentioned. It can also be inferred that *S. brevimalatus* lives in a forest habitat, since specimens of *S. aculeosus*, a forest species, were present in the same vial.

Syntermes calvus Emerson

Syntermes calvus Emerson 1945: 463 [soldier, worker]. Holotype soldier: GUYANA. Kartabo, coll. A.E. Emerson, 19.iv.24 [AMNH]. Paratypes: one soldier, workers, same data as holotype [AMNH].

Material examined. BRAZIL. *Pará*. Bujaru, coll. A.G. Bandeira, 22.v.79, soldiers, workers [MPEG-718]. Marituba, coll. Wygodzinsky, 10.xi.63, soldiers, workers [AMNH]. Serra dos Carajás, coll. T.P. Chaves, 22.v.84, soldiers, one worker [MPEG-2197]. Tucuruí: Chiqueirinho, coll. A.L. Nunes, 03.iv.84, soldiers [MPEG-2198]. FRENCH GUIANA. Euclare, piste à St. Eloit, coll. C. Snyder, 3.v.91, soldiers, workers [AMNH].

Imago. Unknown.

Soldier (Figs. 124-129). Head capsule short, length and width about equal; sides converging towards front; posterior margin of head nearly rounded; frontal tube moderately prominent, pore not visible from dorsal view, usually in a small depression; labrum short, length about equal to width; lateral corners of labrum forming an obtuse angle; median lobe of labrum elongate, longer than lateral ones. Antenna with 19 or 20 articles. Postmentum strongly inflated, sides of posterior part nearly parallel or slightly concave. Mandibles curved and elongate; tip slightly hooked; first marginal tooth of left mandible near the middle and small, not extending much beyond the apical cutting edge; first marginal tooth of right mandible small; angle between apical cutting edge and M1 obtuse; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum slightly emarginate; posterior margin of pronotum nearly straight; lateral projections of thoracic nota strongly upturned; thoracic spines well-developed but slender. Head capsule in dorsal view with about 30 scattered, short bristles, more numerous laterally; base of mandibles without hairs; postmentum with two straight bristles on anterior corners plus many scattered ones; pronotum with many bristles on anterior lobe and margins;

meso- and metanotum with numerous bristles on posterior margin and a few on spines and side margins; tergites with many bristles near hind margin.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 5.20-5.50; maximum width of head 4.80-5.10; height of head excluding postmentum 2.80-3.00; length of frontal tube 0.08-0.25; length of left mandible 2.80-3.00; curvature of left mandible 0.95-1.15; distance from M1 to M2 on left mandible 0.62-0.69; width of left mandible 0.76-0.82; length of left M1 0.17-0.22; minimum width of postmentum 1.01-1.14; width of pronotum 3.60-3.85; width of metanotum 3.70-4.30; length of hind tibia 5.10-5.20. Ratio length of head to maximum width of head 1.04-1.15; length of left mandible to length of head 0.51-0.58; length of hind tibia to length of head 0.94-0.98; width of pronotum to maximum width of head 0.74-0.77; distance M1-M2 to length of left mandible 0.21-0.25; height of head to maximum width of head 0.56-0.59; width to length of left mandible 0.26-0.27.

Worker (Figs. 121-123). Head capsule very large relative to that of soldier (when compared to this proportion in other species of *Syntermes*); with many scattered bristles; postclypeus with about 10 bristles. Fontanelle large and rounded. Antenna with 20 articles. Thoracic spines moderately developed. Mandibles very similar to those of *S. spinosus* (Fig. 49), with well defined basal notch forming a right angle. Gut similar to that of *S. dirus* (Figs. 71-72), but minor mesenteric prolongation of mixed segment more elongate.

Measurements (in mm) of 2 large workers from 2 colonies: length of head 3.10; maximum width of head 3.50-3.55; length of fontanelle 0.30-0.42; width of pronotum 2.75-2.85; width of metanotum 2.85-2.90; length of hind tibia 4.85-4.90.

Comparisons. The soldier of *S. calvus* can be distinguished based on its elongate mandibles with relatively small teeth, conspicuously inflated postmentum, long and slender thoracic spines, and sparse head pilosity. The most similar soldiers are those of *S. peruanus*, which has a shorter frontal tube and more hairs on top of head, and *S. cearensis*, which has shorter mandibles with more conspicuous right M1 and less inflated postmentum, and usually some long, fine and curly hairs on head.

Distribution and Geographical Variation. Guianas and northeastern Brazilian Amazonia (Fig. 360). The limited material available does not allow a clear definition of geographical patterns of variation, but soldiers from Carajás and Tucuruí were a little smaller, with sides of head converging less towards front.

Biology. Very limited information available. Based on distribution and field notes, it seems to be a forest species. No nest information available; most probably completely subterranean.

Syntermes cearensis, new species

Holotype soldier: BRAZIL. Ceará. Chapada do Araripe, coll. R.L. Araujo, 21.xii.76 [MZSP-7241]. Paratypes: BRAZIL. Ceará. Seven soldiers, 6 alates and many workers, same data as holotype [MZSP-7241]. Crato, coll. R.L. Araujo, 10.xi.75, soldiers, workers [MZSP-6394]. Itapipoca, coll. C.R. Gonçalves, 12.xii.48, soldiers, workers [MZSP-3143]. Rio Grande do Norte. Martins, coll. C.R. Gonçalves, 31.v.56, soldiers [MZSP-1838].

Imago. Identical to that of *S. dirus*.

Measurements (in mm) of 2 imagoes from one colony: length of head 2.60-2.65; width of head without eyes 3.05; length of fontanelle 0.34-0.45; length of pronotum 2.00-2.15; width of pronotum 3.65-3.85; length of hind tibia 5.60; maximum diameter of eye 0.67; length of ocellus 0.25-0.27; length of forewing 30.00; width of forewing 7.70. Ratios: diameter of eye to width of head 0.22; length of ocellus to width of head 0.08-0.09; length of fontanelle to width of head 0.11-0.15; width of pronotum to width of head 1.20-1.26; length of wing to width of head 9.84; length of hind tibia to width of head 1.84.

Soldier (Fig. 130-134). Head capsule slightly elongate, sides nearly parallel; posterior margin of head nearly rounded; frontal tube prominent, pore not visible or barely visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum forming an obtuse angle; median lobe short. Antenna with 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle, small, not extending much beyond apical cutting edge; first marginal tooth of right mandible well developed; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible nearly straight, except for curved distal portion. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; lateral projections of thoracic nota strongly upturned; thoracic spines well-developed, but slender. Head capsule in dorsal view with scattered long, fine hairs, some longer and curved; base of mandibles with a few to many hairs; postmentum with many fine, long hairs; pronotum with many bristles on anterior lobe and margins; meso- and

metanotum with numerous bristles on posterior margin and a few on spines and side margins; tergites with many bristles near hind margin.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 4.90-5.30; maximum width of head 4.60-5.00; height of head excluding postmentum 2.60-2.90; length of frontal tube 0.18-0.25; length of left mandible 2.40-2.80; curvature of left mandible 0.90-1.15; distance from M1 to M2 on left mandible 0.59-0.69; width of left mandible 0.77-0.81; length of left M1 0.20-0.25; minimum width of postmentum 0.89-0.97; width of pronotum 3.60-4.00; width of metanotum 3.60-4.10; length of hind tibia 4.60-5.10. Ratio length of head to maximum width of head 1.04-1.10; length of left mandible to length of head 0.46-0.57; length of hind tibia to length of head 0.94-0.96; width of pronotum to maximum width of head 0.74-0.83; distance M1-M2 to length of left mandible 0.24-0.27; height of head to maximum width of head 0.56-0.58; width to length of left mandible 0.28-0.34.

Large worker. Apparently identical to that of *S. dirus*. Gut apparently also very similar to *S. dirus*, but material was too poorly preserved for detailed study.

Measurements (in mm) of 4 large workers from 2 colonies: length of head 2.55-2.85; maximum width of head 3.10-3.25; length of fontanelle 0.24-0.30; width of pronotum 2.15-2.45; width of metanotum 2.25-2.60; length of hind tibia 3.90-4.30.

Comparisons. Alates are apparently indistinguishable from those of *S. dirus*. Soldiers are conspicuously smaller than those of *S. dirus* and less hairy, and the sides of the head are more straight and parallel.

Distribution and Geographical Variation. Restricted to patches of forest in the caatinga vegetation zone in Ceará and part of Rio Grande do Norte, Brazil (Fig. 359). Little morphological variation is present in the material available.

Biology. Certainly a forest species; field notes indicate that the nest has a pile of loose soil above ground, as in *S. dirus*. One sample had workers that were parasitized by microsporid protozoans but had an otherwise normal aspect. These parasites often cause soldier-worker intercastes, as described by Silvestri (1945a) for *S. grandis*.

Syntermes chaquimayensis (Holmgren)

Termes chaquimayensis Holmgren 1906: 547 [soldier, worker], 662 [nest]. Lectotype soldier, here designated: PERU. Llinquipata, coll. N. Holmgren, xi.1904 [AMNH]. Paralectotypes: one soldier, same data as holotype [AMNH].

Syntermes chaquimayensis, Holmgren 1911: 548 [soldier, in key].

Syntermes chaquimayensis chaquimayensis, Emerson 1945: 447 [soldier, worker].

Material examined. BOLIVIA. No data, coll. Mulford Exploration, soldiers, workers [BMNH]. *Beni*. Huachi, coll. W.M. Mann, ix.1920, soldiers, workers [two vials in USNM and two vials in AMNH]. BRAZIL. *Acre*. Vila Taumaturgo, coll. Pe. L. Herbst, ii.62, one soldier [MZSP-147]. COLOMBIA. *Meta*. Mico, coll. J. Hendrickson, 27.xi.50, one soldier, workers [AMNH]. EQUADOR. *Napo*. Cuyabeno, coll. E. Asanza, 20.viii.81, soldiers, alates [MZSP-8868]. Limoncocha, coll. M.G. Nauman, 29.vi.71, soldiers, workers, in two vials [SEM]; coll. K. Riede, vii.1983, soldiers, workers [MNHN]. PERU. No data, one soldier, workers [ISNB]. *Cuzco*. Quillabamba, coll. W.A. Sands, 27.iv.71, soldiers, workers [BMNH]. *Huanuco*. Pampayacu, coll. R. Kaneshiro, 25.i.27, soldiers [USNM]; Tingo Maria: Rio Huallaga, coll. Vegrauil, soldiers, workers [MZSP-1815]. *Junin*. Perene, vi.1926, one soldier, workers [LEFS]; coll. J.C. Bradley, 26.vi.20, soldiers, workers in two vials [AMNH]. *Madre de Dios*. Valle Chanchamayo, 800 m, coll. Weynrauch, 1939, soldiers, workers [AMNH]. *Puno*. Chaquimayo, coll. Holmgren, soldiers, workers [ZMHU].

Imago (Figs. 141-143). Eyes small, less than 1/4 width of head without eyes; ocelli small; fontanelle large and rounded. Antenna with 20 articles. Anterior corners of pronotum angular, with sharp points; lateral margins of pronotum nearly straight and converging posteriorly. Wings (Fig. 35) relatively short and dark; distal part of media and cubitus conspicuous. Head capsule covered with numerous long hairs; postclypeus with about 16 hairs; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with many hairs from middle to posterior margin. Head light chestnut; pronotum light chestnut; tergites chestnut-brown; sternites light chestnut.

Measurements (in mm) of 4 imagoes from one colony: length of head 2.60-2.75; width of head without eyes 3.05-3.25; length of fontanelle 0.34-0.40; length of pronotum 2.10-2.30; width of pronotum 4.00-4.30; length of hind tibia 6.30-6.80; maximum diameter of eye 0.67-0.72; length of ocellus 0.32-0.34; length of forewing 27.50-28.00; width of forewing 6.70-7.60. Ratios: diameter of eye to width of head 0.22-0.23; length of ocellus to width of head 0.10-0.11; length of fontanelle to

width of head 0.11-0.13; width of pronotum to width of head 1.31-1.35; length of wing to width of head 8.62-9.03; length of hind tibia to width of head 2.00-2.13.

Soldier (Figs. 135-140). Head capsule short, length and width about equal, sides converging towards front; posterior margin nearly rounded or weakly three-lobed; frontal tube prominent, pore not visible in dorsal view. Labrum short, length about equal to width; lateral corners about equal to a right angle; median lobe short. Antenna with 19 to 20 articles. Postmentum not constricted, sides of posterior part nearly parallel or slightly concave; mandibles short, curved, robust; tip slightly hooked; first marginal tooth of left mandible usually small, not extending much beyond apical cutting edge, sometimes larger; first marginal tooth of right mandible well-developed; angle between right M1 and apical cutting edge acute; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible slightly sigmoid or nearly straight. Anterior and posterior margin of pronotum slightly emarginate; lateral projections of thoracic nota strongly upturned; thoracic spines well-developed. Head capsule densely covered with short, straight bristles; base of mandibles with numerous short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 5 soldiers from 5 colonies: length of head 5.60-6.20; maximum width of head 5.60-6.10; height of head excluding postmentum 3.05-3.50; length of frontal tube 0.13-0.22; length of left mandible 2.70-3.30; curvature of left mandible 1.25-1.50; distance from M1 to M2 on left mandible 0.59-0.79; width of left mandible 0.94-1.11; length of left M1 0.25-0.40; minimum width of postmentum 0.89-1.06; width of pronotum 4.20-4.80; width of metanotum 4.30-4.85; length of hind tibia 5.40-5.80. Ratio length of head to maximum width of head 0.97-1.02; length of left mandible to length of head 0.45-0.59; length of hind tibia to length of head 0.90-0.95; width of pronotum to maximum width of head 0.75-0.81; distance M1-M2 to length of left mandible 0.22-0.28; height of head to maximum width of head 0.53-0.57; width to length of left mandible 0.31-0.40.

Large worker (Figs. 144-146). Head capsule with several scattered straight bristles; postclypeus with about 12 bristles. Fontanelle large and rounded. Antenna with 19 or 20 articles. Thoracic spines well developed. Mandibles very similar to those of *S. spinosus*. Gut apparently similar to that of *S. dirus*, but material was poorly preserved.

Measurements (in mm) of 4 large workers from 4 colonies: length of head 2.60-2.85;

maximum width of head 3.25-3.55; length of fontanelle 0.22-0.32; width of pronotum 2.50-2.80; width of metanotum 2.50-3.05; length of hind tibia 4.40-4.80.

Comparisons. The imago of *S. chaquimayensis* is similar to those of *S. dirus* and *S. spinosus*, but has a distinct pilosity on the head capsule. The most similar soldier is that of *S. spinosus*, which is usually larger and has longer mandibles with larger teeth. However, soldiers of *S. spinosus* show wide variation and there seems to be some size overlap.

Distribution and Geographical Variation. A narrow zone, from Colombia to Bolivia, parallel to the Andes (Fig. 361). Apparently this species is limited to a certain range of altitude, around 300 to 800 m.

Biology. *S. chaquimayensis* is a rain forest species and, according to Holmgren's (1906: 662) description, its nest is similar to that of *S. dirus*.

Syntermes crassilabrum, new species

Holotype soldier. BRAZIL. Amazonas. Manaus: Reserva Ducke, coll. F.B. Apolinario, 23.i.91 [INPA-895]. Paratypes: BRAZIL. Rondônia. Indeterminate locality, 1985, one soldier, workers [MPEG-3923].

Imago. Unknown.

Soldier (Figs. 147-152). Head capsule elongate with sides slightly converging towards front or nearly parallel; posterior margin of head nearly rounded; frontal tube prominent, pore not visible in dorsal view; labrum large and fleshy, longer than width, with rounded corners, median lobe short. Antenna with 19 to 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles short and robust; bases strongly inflated; tip slightly hooked; first marginal tooth of left mandible large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible slightly sigmoid; apical cutting edge of right mandible evenly curved. Anterior and posterior margins of pronotum slightly emarginate. Lateral projections of thorax slightly upturned; thoracic spines small but conspicuous. Head capsule in dorsal view with 30-40 scattered short, straight bristles, more

numerous laterally and anteriorly; clypeal region with about 12 hairs; base of mandible with a few short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 2 soldiers from 2 colonies: length of head 6.30-6.80; maximum width of head 5.90-6.20; height of head excluding postmentum 3.30-3.80; length of frontal tube 0.25-0.29; length of left mandible 2.60-2.70; curvature of left mandible 1.05-1.10; distance from M1 to M2 on left mandible 0.72-0.72; width of left mandible 0.99-1.06; length of left M1 0.32-0.35; minimum width of postmentum 1.06-1.06; width of pronotum 4.00-4.40; width of metanotum 4.00-4.40; length of hind tibia 5.80-5.90. Ratio length of head to maximum width of head 1.07-1.10; length of left mandible to length of head 0.40-0.41; length of hind tibia to length of head 0.85-0.94; width of pronotum to maximum width of head 0.65-0.75; distance M1-M2 to length of left mandible 0.27-0.28; height of head to maximum width of head 0.56-0.61; width to length of left mandible 0.37-0.41.

Large worker (Fig. 153-155). Head capsule with scattered straight bristles. Postclypeus with about 10 bristles. Fontanelle large and rounded. Thoracic spines weakly developed. Mandibles similar to those of *S. spinosus*, with a 90° basal notch. Gut superficially similar to that of *S. dirus*, but material available was poorly preserved; mesenteric prolongations of mixed segments touch one another.

Measurements (in mm) of 2 large workers from 1 colony: length of head 2.70-2.70; maximum width of head 3.35-3.45; length of fontanelle 0.34-0.34; width of pronotum 2.35-2.35; width of metanotum 2.65-2.65; length of hind tibia 4.50-4.50.

Comparisons. The most similar soldier is that of *S. brevimalatus* which has shorter mandibles, a more elongate head, fewer hairs on head and thorax, and smaller marginal teeth on both mandibles. A distinctive character of the soldier of *S. crassilabrum* is the large and fleshy labrum.

Distribution and Geographical Variation. Known from only two localities in central and western Brazilian Amazonia (Fig. 366).

Biology. No information available. Based on the localities, it is probably a rain forest species.

Syntermes dirus (Burmeister)

Termes dirus Burmeister 1839: 766 [alate, soldier]. Lectotype alate ♀, here designated: BRAZIL. Rio (probably Rio de Janeiro), coll. V. Olfers. Nr. 2763 [ZMHU]. Paralectotypes: two alates ♀, same data as lectotype [ZMHU]; two alates and one soldier, "Brazil, Winthem" [MCZ]. The syntype soldier in ZMHU is not *S. dirus*.

Syntermes dirus, Holmgren 1911: 545 [key]; Emerson 1945: 459 [redescription, part].

Termes obscurum Blanchard 1840: 47 [alate]. From Rio de Janeiro, Brazil. Type not located, but based on the description and the locality there is little doubt that this is *S. dirus*. Synonymized by Hagen (1858: 151).

Termes dubius Rambur 1842: 309 [soldier]. From Brazil. Type not located. Synonymized by Hagen (1858: 155).

Syntermes hageni, Snyder 1924: 28, Fig. 21, misidentification [soldier].

Syntermes sp.n., Baker et al. 1981, misidentification [chemical composition of the frontal gland secretion].

Material examined. BRAZIL. *Bahia*. Andaraí, coll. E.M. Canello, 13.xii.90, soldiers, workers [MZSP-9743 and 9745]. Iguassu, coll. A. Roman, 31.vii.24, one soldier, workers [AMNH]. Ilhéus, coll. Jacques Labie, 22.xii.86, soldiers, workers [MZSP-8996]. Itabuna, coll. R.L. Araujo, 25.ii.72, one soldier, workers [MZSP-5010]. Itapetinga, coll. R.L. Araujo, 28.ii.72, soldiers, workers [MZSP-5009]. Olivença, coll. R.L. Araujo, 26.ii.72, soldiers, workers [MZSP-5006]. Poções, coll. R.L. Araujo, 22.xii.76, soldiers, workers [MZSP-7255]. São José, Rio Utinga, coll. A.G. Bandeira, 29.xii.94, soldiers, workers [UFPB]. Urucuca, coll. R.L. Araujo, 22.ii.72, soldiers, workers [MZSP-5008]. Vila Nova, coll. E. Gorbe, 1908, soldiers, workers [MZSP-1850]. *Distrito Federal*. Brasília: Fazenda Água Limpa, coll. D. Brandão, 1981, soldiers, one worker [UFG-153]. *Espírito Santo*. coll. H. Fruhstorfer, one alate [BMNH]; soldiers, workers [LEFS]; coll. E. Garbe, ii.1906, soldiers, workers, one alate [MZSP-1142]; coll. A.N. Ab'Saber, 15.xi.69, soldiers [MZSP-4739]. Aracruz, coll. R.L. Araujo, 27.v.54, soldiers [MZSP-4169]. Chapada de Carapina, coll. R.L. Araujo, 29.v.54, soldiers, workers [MZSP-4181]. S.J. de Petrópolis, coll. R.L. Araujo, 25.v.54, soldiers, workers [MZSP-4131]. *Goiás*. Goiânia, coll. A. Barcelos, 30.iii.90, soldiers, workers [UFG-378]. Ilha do Bananal, coll. D. Brandão, 01.x.87, soldiers, workers [UFG-331]. *Maranhão*. Montes Altos, coll. A.G. Bandeira, 10.i.77, soldiers, workers [MPEG-217]. *Mato Grosso do Sul*. Costa Rica, expedição IQUSP, 12.ii.86, soldiers, workers, alates [MZSP-8769]. *Minas Gerais*. Belo Horizonte, coll. R.L. Araujo, 23.xii.51, soldiers, workers, alates [MZSP-3422]; coll. R.L. Araujo, 30.xii.53,

soldiers, workers [MZSP-4034]. Coronel Fabriciano, coll. A.B. Pereira, ix.55, soldiers [MZSP-1860]. Francisco Sá, coll. R.L. Araujo, 18.xii.75, soldiers, workers [MZSP-5919 and 5929]. Machacalis, coll. F.S. Pereira, xii.54, one soldier, workers [MZSP-1839]. Montezumia, coll. R.L. Araujo, 16.xii.50, one soldier, one worker [AMNH]; coll. R.L. Araujo, 12.i.52, soldiers, workers [MZSP-3406]. Rio Preto, coll. C.R. Goncalves, 22.i.68, soldiers [MZSP-370]. Viçosa, coll. B. Nogueira, iii.72, soldiers, workers [MZSP-5349]; coll. H.R. Coles, 07.xi.76, soldiers [MZSP-9294], coll. O.F. Souza, 15.xii.93, one soldier, one worker [MEUV]. *Pará*. Marajó Isl., Anajás, coll. W.L. Overal, 09.xii.82, soldiers [MPEG-1449]. Tucuruí, Canoal, coll. A.G. Bandeira, 28.iii.84, one soldier, workers [MPEG-1990]. *Rio Grande do Sul*. Porto Alegre, coll. C.H. Reiniger, 2.i.40, one soldier [AMNH]. Rio Grande, coll. H.v. Ihering, one soldier [MCZ]. *Rio de Janeiro*. Campo Grande, coll. A.G. Araujo e Silva, 17.ii.44, soldiers, workers [MZSP-4659]. Duque de Caxias, coll. Jose Amancio, soldiers, workers [MZSP-4657]. Ilha Grande, coll. Muth & Sick, iv.43, one soldier, one worker [AMNH]. Ilha do Governador, coll. G. Pabst, ix.67, soldiers, workers [MZSP-374]; coll. M.L. Oliveira, vi.29, soldiers, workers [MZSP-2961]. Itaguaí, coll. R.L. Araujo, 15.iii.68, soldiers, workers [MZSP-1846]. Jacarepaguá, coll. F.M. Oliveira, 25.iii.68, one soldier, workers [MZSP-1814]. Rio de Janeiro, coll. Wygodzinsky, 5.xi.63, soldiers, workers [AMNH]; coll. H. Schubart, 09.viii.62, soldiers, workers [MZSP-65]; coll. R.L. Araujo, 18.ii.64, soldiers, one worker [MZSP-157]; coll. Lima & Garcia, 09.xi.70, alates [MZSP-4853]. S.J. da Barra, coll. M.M. Chaves, 06.ix.63, soldiers, workers [MZSP-1818]. Santa Cruz, coll. Costa Lima, 30.ix.36, one soldier, one worker [AMNH]. *São Paulo*. Nova Europa, coll. K. Lenko, 26.iv.68, soldiers, workers [MZSP-1827, MZSP-1828 and MZSP-1829]; coll. K. Lenko, 18.vi.65, soldiers, workers [MZSP-1832]. Rincão, i.45, alates [MZSP-2722]. São Paulo, coll. Stevens, one alate [BMNH].

Imago (Figs. 167-169). Eyes small, less than 1/4 width of head without eyes; ocelli small; fontanelle rounded and large. Antenna with 20 articles. Anterior corners of pronotum angular, with sharp points; lateral margins slightly sigmoid, with anterior half nearly parallel. Wings (Fig. 36) dark and relatively short; distal part of media and cubitus conspicuous. Head capsule with scattered very short hairs, sometimes barely visible; postclypeus with 6-8 short hairs; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with very short hairs on posterior margin; head and pronotum light chestnut; tergites chestnut-brown; sternites light chestnut.

Measurements (in mm) of 7 imagoes from 4 colonies: length of head 2.45-2.90; width of head without eyes 3.05-3.40; length of fontanelle 0.30-0.50; length of pronotum 2.20-2.40; width of pronotum 3.90-4.45; length of hind tibia 6.00-6.60; maximum diameter of eye 0.71-0.74; length of ocellus 0.25-0.37; length of forewing 29.50-34.00; width of forewing 6.90-8.10. Ratios: diameter of

eye to width of head 0.21-0.23; length of ocellus to width of head 0.08-0.11; length of fontanelle to width of head 0.10-0.15; width of pronotum to width of head 1.21-1.33; length of wing to width of head 8.94-10.33; length of hind tibia to width of head 1.88-2.10.

Soldier (Figs. 156-166). Head capsule short, length and width of head about equal; sides nearly parallel or converging slightly towards front; posterior margin of head nearly rounded or weakly three-lobed; frontal tube prominent and broad, pore not visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible small but conspicuous; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible slightly sigmoid. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; lateral projections of thorax strongly upturned; thoracic spines long and conical. Head capsule covered with variable number of long, fine, curly hairs and some straight hairs; base of mandibles with numerous short hairs; postmentum densely covered with fine, long, curly hairs; pronotum with numerous hairs; meso- and metanotum with numerous hairs near hind and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 19 soldiers from 18 colonies: length of head 5.10-7.00; maximum width of head 4.80-6.70; height of head excluding postmentum 2.70-3.80; length of frontal tube 0.24-0.37; length of left mandible 2.70-3.10; curvature of left mandible 0.85-1.50; distance from M1 to M2 on left mandible 0.62-0.94; width of left mandible 0.77-1.04; length of left M1 0.18-0.35; minimum width of postmentum 0.79-1.09; width of pronotum 3.50-5.00; width of metanotum 3.60-5.70; length of hind tibia 4.80-6.80. Ratio length of head to maximum width of head 0.98-1.10; length of left mandible to length of head 0.44-0.56; length of hind tibia to length of head 0.87-1.02; width of pronotum to maximum width of head 0.66-0.84; distance M1-M2 to length of left mandible 0.22-0.30; height of head to maximum width of head 0.54-0.60; width to length of left mandible 0.27-0.34.

Worker (Figs. 170-172). Head capsule covered with numerous short, straight hairs. Postclypeus with about 12 hairs. Fontanelle large and rounded. Thoracic spines well developed. Antenna with 20 articles. Mandibles (Fig. 44) with relatively narrow molar plate and basal notch forming an obtuse angle. Gut described in detail by Kovoov (1969: 198). Large midgut prolongation

of the mixed segment tongue-shaped and very narrow (Fig. 71); small prolongation shaped like a golf club (Fig. 72).

Measurements (in mm) of 9 large workers from 9 colonies: length of head 2.65-2.85; maximum width of head 3.20-3.40; length of fontanelle 0.24-0.34; width of pronotum 2.30-2.75; width of metanotum 2.40-2.85; length of hind tibia 4.30-4.80.

Comparisons. The imago of *S. dirus* is indistinguishable from that of *S. cearensis*, and very similar to those of *S. aculeosus*, *S. spinosus*, *S. chaquimayensis* and *S. tanygnathus*. *S. aculeosus* has wider pronotum and larger fontanelle; *S. spinosus* and *S. chaquimayensis* have longer and more numerous hairs on head; and *S. tanygnathus* has antenna with 21 articles. The soldier of *S. dirus* can be distinguished by the numerous long, fine and curly hairs on head, the long and conical thoracic spines, the prominent and wide frontal tube, and the well marked notch anterior to left M1. Density of long, fine hairs is variable, however.

Distribution and Geographical Variation. *S. dirus* is common on the Brazilian Atlantic forests, from Bahia to Rio Grande do Sul, but it is also found in gallery forests in Central Brazil and along the Tocantins and Araguaia rivers, with one record from the Marajó Island (Fig. 359). Soldiers from Rio de Janeiro to Bahia tend to be a little smaller and with less numerous hairs on the head than those of other regions, but with some overlap. The number of alates available for study is rather small, and they do not show any geographical pattern of variation.

Biology. Although *S. dirus* is a common species in densely populated areas of the Brazilian Coast, the biology of this species is still very poorly known. It is certainly a forest species, but may occasionally be found in pastures. Its nest (Fig. 32) is described in detail here for the first time (see section on nests above).

Remarks. Klug was considered for some time as the author of this species, but, as already noted by Snyder (1924: 26), his was just a manuscript name and was never published. The type series was apparently a mixture of alates and soldiers collected separately, and at least two of those soldiers were not *S. dirus*, but *S. wheeleri* instead. The fact that Burmeister did describe the soldier caste seems to have been ignored by earlier authors, but it is not possible to determine whether he based his description on the *S. wheeleri* specimens, the *S. dirus* ones, or both. *Termes cephalotes* Rambur 1842: 309 was listed by Emerson (1945: 460) as a possible synonym of *S. dirus*, but since the type seems to be lost and the description is useless, that name should be considered of uncertain position. Based

on Rambur's description, it is impossible to tell whether *T. cephalotes* is a *Syntermes* species, or whether it refers to soldier or imago caste.

***Syntermes grandis* (Rambur)**

Termes grandis Rambur 1842: 306 [alate]. Holotype alate: FRENCH GUIANA. Cayenne. No data, in poor condition [ISNB]. No paratypes or syntypes known.

Syntermes grandis, Holmgren 1911: 547 [key]; Emerson 1945: 451 [imago, soldier]; Baker et al. 1981 [chemical composition of the frontal gland secretion].

Termes decumanus Erichson 1848: 582 [alate only, but lectotype soldier is *S. spinosus*].

Syntermes dirus f. *hageni* Holmgren 1911: 547 [soldier]. Holotype soldier: "T. Hageni n. sp. revid. Hagen 1856, Brazil", in poor condition [AMNH].

Syntermes hageni, Emerson 1945: 454 [soldier].

Syntermes lighti Emerson 1945: 453 [soldier]. Holotype soldier: BOLIVIA. Beni. Villa Bella, coll. J.D. Haseman, 9.x.1909 [AMNH].

Material examined. BOLIVIA. Beni. Villa Bela, coll. J.D. Haseman, 9.x.09, soldiers [AMNH]. BRAZIL. Amapá. Aporema, coll. R. Constantino, 26.x.89, one soldier, workers [MPEG-3234]. Curiaú, coll. R. Constantino, 18.x.89, soldiers, workers [MPEG-3168]. Amazonas. Humaitá, coll. R. Constantino, 18.ix.90, soldiers, workers [MPEG-3755 and MPEG-3757]; coll. R. Constantino, 20.ix.90, soldiers, workers [MPEG-3788 and MPEG-3797]. Distrito Federal. Brasília, coll. H.R. Coles, 26.viii.77, soldiers, workers, alates [UnB]; coll. R.L. Araujo, x.61, soldiers, workers, alates [MZSP-153]; coll. H.R. Coles, 28.iv.77, soldiers, workers [MPEG-2707]. Goiás. Goiânia, coll. D. Brandão, 24.iii.83, one soldier, workers [UFG-34]; coll. D. Brandão, 05.v.83, soldiers, workers [UFG-49; UFG-51]; coll. D. Brandão, xi.84, soldiers, workers [UFG-184]; coll. A.M. Curado, 28.v.86, soldiers, workers [UFG-229]. Parque Nacional das Emas, coll. K. Redford, ix.1981, soldiers, workers [MZSP-9780]. Mato Grosso. Caiçara, coll. Natterer, one soldier, one worker [AMNH]. Xavantina, coll. A.G.A. Mathews, 29.ix.68, soldiers [BMNH]; coll. A.G.A. Mathews, 24.x.68, large series with many soldiers, workers, alates and a queen, in several vials [BMNH]; coll. A.G.A. Mathews, xi.67, alates [BMNH]; coll. A.G.A. Mathews, one soldier, workers [BMNH]; coll. H.R. Coles, i.77, soldiers, workers [MZSP-9295]; coll. H. Sick, 30.xi.46, alates [AMNH]. Mato Grosso do Sul. 18°20'S 52°50'W, coll. A.E. Mill, 07.vii.80, soldiers [MZSP-8404]; coll. Mill & Redford, 09.vii.80, soldiers [MZSP-8405]. Campo Grande, coll. R.L. Araujo, 25.x.53,

soldiers, workers [MZSP-3983]. Três Lagoas, coll. K. Lenko, 28.iii.65, one soldier, workers [MZSP-1010]; coll. F. Silvestri, 26.vii.35, soldiers, workers [LEFS]. *Minas Gerais*. Sete Lagoas, coll. G. Cosenza, xi.71, soldiers, workers [MZSP-8566]. Uberaba, coll. R.L. Araujo, 09.xi.72, soldiers, workers [MZSP-5696]. *Paraná*. coll. L. Zolessi, vii.54, one soldier [MZSP-1813]. *Pará*. Areia, coll. C.R. Goncalves, 29.viii.47, one soldier, one worker [MZSP-4660]. João Pessoa, coll. A. Macedo, soldiers, one worker [MZSP-4658]. Santarém, coll. Thayer Expedition, soldiers [MCZ; AMNH; USNM]; coll. H.W. Bates, soldiers, workers [BMNH]; coll. Stevens, 1854, alates [BMNH]. *Pernambuco*. Engenho Camorim, coll. B. Dantas, 06.viii.58, soldiers, workers [MZSP-4687]. Jaboatão, coll. J. Rangel, 02.ii.52, soldiers [MZSP-1849]. Usina Aliança, coll. C.R. Goncalves, x.67, soldiers [MZSP-1861]. *Roraima*. Coll. B. Bentley, 1974, soldiers, workers [AMNH]; coll. K. Kityama, 19.iii.72, soldiers, workers [MZSP-5312]. Arabupu, Mt. Roraima, coll. G.H. Tate, xii.1927, soldiers, workers [AMNH]. Boa Vista, coll. C.R. Goncalves, 09.vii.53, soldiers, workers [MZSP-4662]; coll. C.R. Goncalves, 09.xi.53, soldiers, workers [MZSP-4666]. Ireng River, 1911, soldiers [AMNH]. Monte Roraima, coll. J.G. Myers, soldiers, workers [USNM]. Vista Alegre, one soldier, workers [AMNH]; coll. Bequaert, one soldier, workers [USNM]. *Sergipe*. Estância, coll. R.L. Araujo, 23.xi.75, one soldier, workers [MZSP-6449]. *São Paulo*. Agudos, coll. W.K., 31.v.52, soldiers, workers [MZSP-1840]. Itu, coll. Kloss & Silva, 05.xi.61, alates [MZSP-1865]. Ribeirão Preto, coll. R. Castro, 27.vi.83, soldiers, workers [MZSP-8268]. S.J. do Rio Preto, coll. Machado, 08.vi.66, soldiers, workers [MZSP-1831]. S.J. dos Campos, coll. F. Mariconi, 26.iv.65, soldiers, workers [MZSP-1816 and MZSP-1830]; coll. F. Mariconi, 30.vii.65, soldiers, workers [MZSP-1799]. **FRENCH GUIANA**. Cayenne, soldiers [ISNB]; 1905, soldiers [MNHN]. **GUYANA**. Lethem, coll. G.K. Rutherford, 1956, soldiers, workers [BMNH]. Pakaraima Mts., Upper Ireng R., coll. J.G. Myers, soldiers, workers [USNM]. **SURINAME**. Coesoewijne Savanne, coll. Geijskes, 7.ii.57, soldiers, workers [MZSP-9764]. Jodensavanne, coll. M.A. Knoppe, vi.57, soldiers, workers [MZSP-9767]. **VENEZUELA**. *Bolivar*. Akuriman, coll. Anduze, xi.40, soldiers, workers [AMNH]. Santa Elena de Vairen, coll. P.E. Vanzolini, 16.xii.88, one soldier, workers [MZSP-9122].

Imago (Figs. 184-186). Eyes large, diameter more than 1/4 width of head to about 1/3 width of head; ocelli relatively large; fontanelle rounded and small to medium. Antenna with 20 articles. Anterior corners of pronotum rounded to moderately angular; lateral margins of pronotum straight and nearly parallel in anterior half to rounded and converging posteriorly. Wings long; distal part of media and cubitus inconspicuous. Head capsule densely covered with straight bristles; postclypeus with about 16 bristles; pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head dark brown; pronotum chestnut-brown; tergites dark brown;

sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 9 imagoes from 6 colonies: length of head 2.90-3.10; width of head without eyes 3.30-3.70; length of fontanelle 0.32-0.47; length of pronotum 2.15-2.40; width of pronotum 3.65-4.25; length of hind tibia 6.30-7.10; maximum diameter of eye 0.92-1.08; length of ocellus 0.37-0.44; length of forewing 29.50-32.00; width of forewing 6.90-7.70. Ratios: diameter of eye to width of head 0.27-0.33; length of ocellus to width of head 0.11-0.13; length of fontanelle to width of head 0.10-0.14; width of pronotum to width of head 1.09-1.23; length of wing to width of head 8.55-9.55; length of hind tibia to width of head 1.84-2.12.

Soldier (Figs. 173-183). Head capsule short, length and width of head about equal, sides converging slightly to strongly towards front; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners nearly equal to a right angle; median lobe of labrum short. Antenna with 20 articles. Postmentum slightly constricted near the middle, sides of posterior part concave. Mandibles curved and moderately elongate; tip slightly to conspicuously hooked; first marginal tooth of left mandible near the middle and large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge less than 90°; apical cutting edge of left mandible conspicuously sigmoid; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin nearly straight; thoracic spines small and strongly upturned; pronotum with or without distinct conical spines. Head capsule with many short, straight bristles, more numerous laterally; base of mandibles with many short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 28 soldiers from 28 colonies: length of head 5.60-6.80; maximum width of head 5.65-6.60; height of head excluding postmentum 3.10-3.70; length of frontal tube 0.08-0.30; length of left mandible 3.00-3.40; curvature of left mandible 1.20-1.60; distance from M1 to M2 on left mandible 0.67-0.92; width of left mandible 0.89-1.14; length of left M1 0.25-0.47; minimum width of postmentum 0.82-1.04; width of pronotum 3.45-4.30; width of metanotum 3.55-4.35; length of hind tibia 5.30-6.90. Ratio length of head to maximum width of head 0.94-1.12; length of left mandible to length of head 0.48-0.57; length of hind tibia to length of head 0.84-1.10; width of pronotum to maximum width of head 0.58-0.74; distance M1-M2 to length of left mandible 0.22-0.28; height of head to maximum width of head 0.51-0.59; width to length of left mandible 0.28-0.35.

Worker (Figs. 187-189). Head capsule with many straight bristles; postclypeus with about 10 bristles. Fontanelle small and slightly elongate. Antenna with 20 or 21 articles. Thoracic spines weakly developed. Mandibles (Fig. 48) very similar to those of *S. wheeleri*, with wide molar plate. Gut similar to that of *S. wheeleri*, but major midgut prolongation of mixed segment is smaller, and minor prolongation is longer and tongue shaped.

Measurements (in mm) of 20 large workers from 20 colonies: length of head 2.85-3.40; maximum width of head 3.40-3.90; length of fontanelle 0.25-0.40; width of pronotum 2.15-2.70; width of metanotum 2.30-2.90; length of hind tibia 4.40-5.50.

Comparisons. The most similar imagoes are those of *S. magnoculus* and *S. obtusus*, of which the former seems to be indistinguishable from *S. grandis*. The imago of *S. obtusus* has conspicuously larger eyes and elongate fontanelle. The soldier of *S. magnoculus* is similar, but larger and with larger marginal teeth on both mandibles and apical cutting edge not sigmoid. The soldier of *S. wheeleri* is also similar and may be sometimes difficult to distinguish from *S. grandis*. It is smaller, with sides of head more parallel, straighter mandibles with smaller marginal teeth, and more numerous hairs on head.

Distribution and Geographical Variation. This species shows a considerable morphological variation among different regions. It occurs in the cerrado of central and southeastern Brazil and in the various Amazonian savannas, including the Guianas (Fig. 362). The variation seems to be continuous and I was not able to find any consistent character that could support the distinction between *S. grandis*, *S. hageni* and *S. lighti*. They seem to be part of the same continuum, and a large series collected by A. Mathews in Mato Grosso contains different soldiers that could be identified as all three species based on Emerson's descriptions. Soldiers from the Guianas, Venezuela, and most Amazonian savannas have the sides of the head more strongly converging towards the front, the apical cutting edge of both mandibles more conspicuously sigmoid and hooked at the tip, and smaller thoracic spines (Figs. 173-177). Specimens from central and southeastern Brazil tend to have larger thoracic spines and the sides of the head converging slightly (Figs. 178-183). Soldiers from the caatinga region of northeastern Brazil have a less sigmoid apical cutting edge on both mandibles. Some populations from isolated patches of Amazonian savanna show some morphological differentiation, but collections in those areas are still very limited and the patterns are not very clear. Soldiers from Humaitá, for instance, have mandibles with larger teeth.

Biology. *S. grandis* lives exclusively in grasslands and savannas. Its nest is mostly

subterranean, with a small epigeal portion of soft consistency. According to Baker et al. (1981) the soldier defensive secretion of this species lacks terpenes, in contrast to all other examined species of the genus.

Remarks. Emerson (1945) recorded *S. lighti* from a locality named Caiçara, which he incorrectly identified as being on the Amazon. That locality, sometimes also mentioned as Caissara, was an old cattle ranch on the Paraguai River, where Natterer, the famous Austrian collector, spent one year (Araujo, 1958: 219). Natterer's specimens were studied by Hagen (1858: 156), who identified them as *T. dirus*. *S. hageni* was described from a single pinned soldier from Hagen's collection, with locality information limited to "Brazil". The type soldier of *S. hageni* is very similar to the paratypes of *S. lighti* from Caiçara, and it is likely that it was also collected by Natterer at that locality. Araujo (1977: 53), based exclusively on the literature and the study of non-type material, concluded that *S. hageni* was synonymous with *S. dirus*, and incorrectly mentioned the type locality of *S. hageni* as being Rio de Janeiro, Brazil, and the type depository as the Carnegie Museum. Apparently he arrived at that conclusion based on an erroneous redescription of *S. hageni* presented by Snyder (1924: 28), based on a misidentified specimen of *S. dirus*, and not on any type material. Snyder's mistake has already been pointed out by Emerson (1945: 461).

Syntermes insidians Silvestri

Syntermes insidians Silvestri 1946: 12 [soldier, worker]. Lectotype soldier, here designated: BRAZIL. São Paulo. Pitangueira (near Guarani), coll. J.P. da Fonseca, 1937 [LEFS]. Paralectotypes, same data as lectotype: one soldier, workers [AMNH]; workers [LEFS].

Material examined. BRAZIL: *Mato Grosso*. Chapada dos Guimarães, coll. M.A. Drumond, 01.xii.84, soldiers [UFG-143 and 145; MZSP-9890, 9891 and 9892]; coll. E.E.B., 02.xii.84, soldiers, workers [MZSP-9895]; coll. J. Dalponte, 28.ii.88, soldiers, workers [MZSP-9911]; coll. J. Dalponte, 04.xi.84, soldiers, workers [MZSP-9912]. *Mato Grosso do Sul*. Três Lagoas, coll. C. Flechtmann, 5.iii.93, one soldier [MZSP-9829]. *Minas Gerais*. Bom Despacho, soldiers, workers [MZSP-7375]; coll. E. Vilela, 22.vi.77, soldiers, workers [MZSP-9760].

Imago. Unknown.

Soldier (Figs. 190-200). Head capsule elongate with parallel sides; posterior margin of head rounded; frontal tube prominent, sometimes in a small depression; pore not visible in dorsal view; labrum moderately elongate; lateral corners of labrum about equal to a right angle; median lobe of labrum elongate, longer than lateral lobes. Antenna with 20 or 21 articles. Postmentum constricted near the middle. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible near the middle and large, extending well beyond apical cutting edge; first marginal tooth of right mandible conspicuous; angle between right M1 and apical cutting edge less than 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved or nearly straight with curved tip. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin of pronotum slightly emarginate; thoracic spines weakly developed and slightly upturned, located anteriorly; lateral corners of pronotum sharp but not forming conical spines. Head capsule with numerous short, straight bristles, more numerous laterally; base of mandibles with numerous short hairs; postmentum with many short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 5 soldiers from 4 colonies: length of head 4.50-4.80; maximum width of head 3.55-3.80; height of head excluding postmentum 2.25-2.40; length of frontal tube 0.17-0.22; length of left mandible 2.20-2.35; curvature of left mandible 0.55-1.00; distance from M1 to M2 on left mandible 0.50-0.60; width of left mandible 0.60-0.64; length of left M1 0.17-0.21; minimum width of postmentum 0.59-0.76; width of pronotum 2.38-2.60; width of metanotum 2.35-2.45; length of hind tibia 3.95-4.10. Ratio length of head to maximum width of head 1.22-1.32; length of left mandible to length of head 0.47-0.51; length of hind tibia to length of head 0.84-0.88; width of pronotum to maximum width of head 0.64-0.71; distance M1-M2 to length of left mandible 0.22-0.27; height of head to maximum width of head 0.63-0.66; width to length of left mandible 0.26-0.28.

Worker (Figs. 201-203). Head capsule with many short, straight bristles. Postclypeus with four bristles. Fontanelle small and slightly elongate. Antenna with 20 or 21 articles. Thoracic nota with angular sides but lacking distinct spines. Mandibles with narrow molar plate and well marked basal notch of about 90°. Gut similar to that of *S. dirus*, but major mesenteric prolongation of mixed segment is wider and minor prolongation is more transversely elongate.

Measurements (in mm) of 5 large workers from 4 colonies: length of head 2.50-2.65; maximum width of head 2.90-3.15; length of fontanelle 0.12-0.17; width of pronotum 1.55-1.80; width

of metanotum 1.55-1.85; length of hind tibia 3.65-4.05.

Comparisons. The soldier of *S. insidians* can be distinguished based on its elongate head with parallel sides, thoracic spines weakly developed and situated anteriorly, and marginal teeth well developed on both mandibles. *S. longiceps* is superficially similar, but has antenna with only 19 articles, more robust mandibles with smaller marginal teeth, larger thoracic spines, and a quite different geographic distribution.

Distribution and Geographical Variation. Known from a few localities in central and southeastern Brazil (Fig. 365). Specimens from Chapada dos Guimarães are a little smaller, with less numerous hairs on the head, and frontal tube in a small depression.

Biology. Seems to be associated with a particular kind of cerrado on very poor, sandy soils (Fonseca 1949, and field notes from J. Dalponte), where it may be abundant. Apparently the nest is completely subterranean. Reported as a pest of *Eucalyptus* in several locations.

Syntermes longiceps, new species

Holotype soldier: BRAZIL. *Roraima*. S. Luís do Guar, coll. P.E. Vanzolini, 07.ii.90 [MZSP-9340]. Paratypes: No label, soldiers, alates [BMNH]. "Amaz." (probably Amazonia), coll. Saunders, one soldier [BMNH]. BRAZIL. *Amazonas*. Manaus: Reserva Ducke, coll. F.B. Apolinrio, 7.viii.90, one soldier, workers [INPA-891]; coll. F.B. Apolinrio, 15.i.91, soldiers, workers [INPA-892; INPA-893 and INPA-894]; coll. W. Paarman, 17.vi.92, one alate [INPA]. Manaus: INPA, coll. C. Martius, 20.iv.91, one alate [INPA]. Silves: Fazenda Aruan, coll. A.G. Bandeira, 23.v.77, one soldier, workers [MPEG-161]. *Par*. Benevides: Fazenda Morelndia, coll. R.B. Neto, 17.ix.80, one soldier, workers [MPEG-988]. bidos, coll. E.E. Austen, 2.ii.1896, alates [BMNH]. Tucuru: Arapari, coll. W.L. Overal, 03.iii.84, soldiers, workers [MPEG-1947]. *Roraima*. S. Lus do Guar, coll. P.E. Vanzolini, 07.ii.90, one soldier, workers, same colony as holotype [MZSP-9340].

Imago (Figs. 214-216). Eyes small, less than 1/4 width of head; ocelli relatively large; fontanelle large and rounded. Antenna broken in all specimens available. Anterior corners of pronotum angular, with sharp points; lateral margins straight and nearly parallel in anterior half. Wings short (Fig. 37); distal part of media and cubitus conspicuous. Head capsule with scattered

short, straight hairs; postclypeus with two short hairs on anterior margin; pronotum with many hairs on outer margin; tergites with a line of hairs on posterior margin. Head, pronotum and tergites chestnut-brown; sternites brownish yellow; wings brown to dark brown.

Measurements (in mm) of 2 imagoes from one colony: length of head 2.25-2.35; width of head without eyes 2.70-2.80; length of fontanelle 0.32-0.35; length of pronotum 1.65-1.70; width of pronotum 2.90-3.00; length of hind tibia 4.50; maximum diameter of eye 0.59-0.60; length of ocellus 0.30-0.34; length of forewing 23.00; width of forewing 1.03-1.03. Ratios: diameter of eye to width of head 0.21-0.22; length of ocellus to width of head 0.11-0.13; length of fontanelle to width of head 0.11-0.13; width of pronotum to width of head 1.04-1.11; length of wing to width of head 8.21-8.21; length of hind tibia to width of head 1.61-1.67.

Soldier (Figs. 204-213). Head capsule elongate with parallel sides; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum elongate, longer than lateral lobes. Antenna with 19 articles. Postmentum elongate and not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately robust; tip slightly hooked; first marginal tooth of left mandible variable: small, not extending much beyond apical cutting edge to large, extending well beyond the apical cutting edge; first marginal tooth of right mandible conspicuous and also variable; angle between right M1 and apical cutting edge more than 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines weakly developed and slightly upturned; lateral corners of pronotum sharp but not forming conical spines. Head capsule with scattered straight bristles, more numerous laterally; base of mandibles with variable number of short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half. Head pale yellow-brown; thorax pale yellow-brown; tergites and sternites yellowish, semi-transparent; legs pale yellow-brown.

Measurements (in mm) of 7 soldiers from 7 colonies: length of head 4.65-5.50; maximum width of head 3.35-4.20; height of head excluding postmentum 2.30-2.90; length of frontal tube 0.18-0.30; length of left mandible 2.05-2.45; curvature of left mandible 0.55-0.85; distance from M1 to M2 on left mandible 0.37-0.62; width of left mandible 0.62-0.76; length of left M1 0.11-0.27; minimum width of postmentum 0.69-0.81; width of pronotum 2.40-3.10; width of metanotum 2.30-3.00; length of hind tibia 3.20-3.80. Ratio length of head to maximum width of head 1.22-1.40;

length of left mandible to length of head 0.42-0.51; length of hind tibia to length of head 0.67-0.72; width of pronotum to maximum width of head 0.68-0.82; distance M1-M2 to length of left mandible 0.18-0.27; height of head to maximum width of head 0.64-0.72; width to length of left mandible 0.26-0.33.

Worker (Figs. 217-219). Head capsule with scattered straight bristles. Postclypeus with about six bristles. Fontanelle rounded and small. Antenna with 19 articles. Thoracic spines weakly developed, similar to those of soldier. Mandibles (Fig. 51) with narrow molar plate and well marked basal notch of a little more than 90°. Gut distinct (Figs. 73-79), with first proctodeal segment enlarging abruptly on mixed segment; loop formed by anterior part of colon elongate; enteric valve located posteriorly; first proctodeal segment distinctly larger than paunch; major mesenteric prolongation of mixed segment relatively small, with inflated and blunt tip; minor prolongation large and tongue-shaped, touching the major one.

Measurements (in mm) of 5 large workers from 4 colonies: length of head 2.15-2.30; maximum width of head 2.65-2.80; length of fontanelle 0.18-0.22; width of pronotum 1.80-2.05; width of metanotum 1.80-2.25; length of hind tibia 3.20-3.40.

Comparisons. The alate of this species seems to be indistinguishable from that of *S. parallelus*, with both sharing the following combination of characters: small size, sharp anterior corners of pronotum, small eyes, postclypeus with only two short bristles, and dark wings. The soldier can be distinguished by its relatively small size; elongate head with parallel sides; antenna with 19 articles; thoracic spines weakly developed; and relatively short legs. It is also similar to *S. parallelus*, but is larger and the mandibles are more robust and curved, with larger marginal teeth located more distally. Some of the largest soldiers of *S. longiceps* may be similar to the smallest of *S. territus*, but the latter are always larger and have small marginal teeth on both mandibles.

Distribution and Geographical Variation. Northern to northeastern Brazilian Amazonia (Fig. 365). The soldiers of this species show a large variation between different localities, but they seem to be part of the same continuum, although the material available is rather limited for a clear definition of patterns. Soldiers from the Manaus area are a little larger with conspicuously larger marginal teeth. Specimens from Pará are smaller, but otherwise identical to the type. It may be possible that there is more than one species involved here, and more collecting and field observations are necessary for a better characterization of this species. Apparently *S. longiceps* is the sister species of *S. parallelus*, which has a more northern distribution.

Biology. No information available. Certainly a forest species; nest probably completely subterranean.

Syntermes magnoculus Snyder

Syntermes magnoculus Snyder 1924: 22 [imago, soldier]; Emerson 1945: 445 [redescription].

Holotype imago ♀: BRAZIL. *Mato Grosso*. Chapada dos Guimarães, coll. H.H. Smith, Oct., [MCZ]. Paratypes: One alate ♂, same data as holotype [USNM]; one soldier, same locality and collector, but collected in "July" [MCZ].

Material examined. BRAZIL. *Goiás*. Padre Bernardo, coll. H.R. Coles, 14.vii.77, soldiers, workers [MPEG-2714]; coll. H.R. Coles, 30.xii.76, soldiers [MZSP-9298]. Senador Canedo, coll. D. Brandão, 01.vi.83, soldiers, workers [UFG-63]. *Mato Grosso*. Chapada dos Guimarães, coll. R.L. Araujo, 12.ii.76, soldiers, workers [MZSP-6511]; coll. R.L. Araujo, 7.ii.76, soldiers, workers [MZSP-6506].

Imago (Figs. 225-227). Eyes large, more than 1/3 width of head; ocelli large; fontanelle rounded and relatively small. Antenna with 20 articles. Anterior corners of pronotum moderately angular; lateral margins of pronotum straight and nearly parallel in anterior half. Wings long; distal part of media and cubitus inconspicuous. Head capsule and postclypeus with numerous long bristles (many lost in type specimen); pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head, pronotum, and tergites dark brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of the holotype ♀: length of head to base of mandibles 3.2; width of head 3.47; length of fontanelle 0.33; length of pronotum 2.27; width of pronotum 4.2; length of hind tibia 5.2; maximum diameter of eye 1.2; length of ocellus 0.4.

Soldier (Figs. 220-224). Head capsule short, length and width of head about equal; sides converging towards front; posterior margin of head rounded; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to or a little more than a right angle; median lobe of labrum moderately large, length about equal to lateral lobes. Antenna with 21 articles. Postmentum not constricted, sides of posterior part nearly parallel; mandibles curved and moderately elongate; tip of mandibles slightly hooked; first marginal

tooth of both mandibles large, extending well beyond apical cutting edge; angle between marginal teeth and apical cutting edge less than 90°; apical cutting edge of both mandibles about evenly curved. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines moderately developed and strongly upturned; lateral corners of pronotum sharp but usually not forming conical spines or forming short one. Head capsule with many short, straight bristles, more numerous laterally; base of mandibles with numerous short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 6.10-6.70; maximum width of head 6.30-7.00; height of head excluding postmentum 3.40-3.70; length of frontal tube 0.17-0.25; length of left mandible 3.20-3.70; curvature of left mandible 1.40-1.90; distance from M1 to M2 on left mandible 0.97-0.97; width of left mandible 0.97-1.24; length of left M1 0.40-0.52; minimum width of postmentum 0.87-1.08; width of pronotum 4.10-4.60; width of metanotum 4.30-4.90; length of hind tibia 5.80-6.70. Ratio length of head to maximum width of head 0.96-1.05; length of left mandible to length of head 0.51-0.55; length of hind tibia to length of head 0.91-1.00; width of pronotum to maximum width of head 0.60-0.71; distance M1-M2 to length of left mandible 0.28-0.28; height of head to maximum width of head 0.53-0.56; width to length of left mandible 0.30-0.35.

Worker (Figs. 228-230). Head capsule with numerous short, straight bristles. Postclypeus with about 10 bristles. Fontanelle slightly elongate and relatively small. Thoracic spines weakly developed. Mandibles and gut very similar to those of *S. grandis*, with wide molar plate on right mandible.

Measurements (in mm) of 2 large workers from 2 colonies: length of head 3.35-3.40; maximum width of head 3.95-4.00; length of fontanelle 0.37-0.39; width of pronotum 2.65-2.75; width of metanotum 2.70-2.80; length of hind tibia 4.85-5.10.

Comparisons. The alate is apparently indistinguishable from that of *S. grandis*. The soldier can be differentiated by its large size, mandibles with large marginal teeth and evenly curved apical cutting edge, and relatively short thoracic spines.

Distribution and Geographical Variation. Known from a few localities in Central Brazil (Fig. 360). Specimens from Goiás have smaller marginal teeth on both mandibles, but material is too

limited to recognize any geographic pattern.

Biology. *S. magnoculus* is a cerrado species. No information about nest is available; probably completely subterranean.

Remarks. The fact that Snyder (1924) described this species from alates and soldiers collected separately poses a difficult taxonomic question. Without new material with soldiers and imagoes from the same colony, it is impossible to tell whether they really belong to the same species. Even if such material becomes available, it may be still impossible to solve the problem because alates of different species are sometimes indistinguishable, and the type is an old pinned specimen in imperfect condition. Soldiers from some samples are partially intermediate between *S. grandis* and *S. magnoculus*, and, given the similarity of alates and workers, the study of larger series might eventually show that they are just variations of the same species.

Syntermes molestus (Burmeister)

Termes molestus Burmeister 1839: 766 [imago]. Lectotype alate ♀, here designated: BRAZIL. Bahia.

Coll. Gomez, pinned, [ZMHU]. Paralectotype alate ♀: same data as lectotype [ZMHU].

Syntermes molestus, Holmgren 1911: 547 [key]; Emerson 1945: 467 [part].

Syntermes brasiliensis Holmgren 1911: 548 [soldier, in key]. Lectotype soldier, here designated: Brazil, no data, "*Syntermes* n.sp." [AMNH]. Synonymized by Emerson (1945).

Material examined. BOLIVIA. *Chuquisaca*. Tumupasa, coll. W.M. Mann, xii.1921, soldiers, workers [AMNH]. BRAZIL. *Amapá*. Macapá, coll. A.L. Henriques, 21.v.89, soldiers, workers [MPEG-3109]; coll. R. Constantino, 28.x.89, soldiers, workers [MPEG-3238]. Mazagão, coll. R. Constantino, 20.x.89, soldiers, workers [MPEG-3194]. *Amazonas*. Anavilhanas, coll. A.E.Mill, 23.iv.81, soldiers, workers [BMNH]; coll. G.R. Kloss, 20.iv.67, soldiers, workers [MZSP-1804]. E. Benjamin Constant, coll. T.C.S. Pires, 08.xii.89, soldiers, workers [MPEG-3304]. Humaitá, coll. R. Constantino, 15.ix.90, one soldier, one worker [MPEG-3730]; coll. R. Constantino, 17.ix.90, soldiers, workers [MPEG-3742 and 3747]. Manaus, coll. A.G. Bandeira, 17.viii.76, soldiers, workers [MPEG-5]; coll. R.S. Bradley, 18.ix.78, soldiers, workers [MPEG-494]; coll. Og Souza, 30.vii.86, soldiers, workers [MEUV]; coll. A.G. Bandeira, 06.vi.81, soldiers, workers [MPEG-1343]; coll. S.A. Marques, 05.viii.80, soldiers, workers [MPEG-1426 and 1427]; coll. E.N.

Palheta, 05.iv.91, soldiers, workers [MZSP-9472]; coll. A.G. Bandeira, 06.iv.79, soldiers, workers [MPEG-610]; coll. Og Souza, 6.viii.86, soldiers, workers [MEUV]. Maués, coll. Flavio, 06.vi.57, soldiers [MZSP-9341]. Nova Olinda, coll. E.P.A., 20.ii.72, soldiers, one worker [MZSP-5434]. Porto Urucu: Rio Urucu, coll. T.C.S. Pires, 19.xi.89, soldiers, workers [MPEG-3300]. Silves: Fazenda Aruanã, coll. A.G. Bandeira, 21.v.77, soldiers, workers [MPEG-135]. *Bahia*. Coll. G. Bondar, 1925, soldiers, one worker, alates [MZSP-1844]. Andaraí, coll. E.M. Canello, 13.xii.90, soldiers, workers [MZSP-9738]; coll. E.M. Canello, 13.xii.90, two alates [MZSP-9737 and MZSP-9739]. Itaberaba, coll. E.M. Canello, xii.90, soldiers [MZSP-9741]. Itaité, coll. E.M. Canello, 18.i.80, soldiers, workers [MZSP-7917]; coll. E.M. Canello, 13.i.80, soldiers, workers [MZSP-7918 and MZSP-7916]; coll. E.M. Canello, 13.i.80, one alate [MZSP-7968]. Jacobina, coll. E.M. Canello, 16.x.80, soldiers, workers [MZSP-7908]. Maracas, coll. E.M. Canello, 24.xii.90, soldiers, workers [MZSP-9740 and MZSP-9742]. Marambaia, coll. C. Schofield, 30.iv.77, soldiers, workers [BMNH]. Sta. Rita de Cassia, coll. C.R.F. Brandão, 18.vii.91, soldiers, workers [MZSP-9733]. *Distrito Federal*. Brasília, coll. H.R. Coles, 14.ix.79, soldiers, workers [BMNH]. *Goiás*. Anápolis, coll. W.W. Kempf, 12.ii.58, soldiers [MZSP-1857]; coll. C.R. Gonçalves, 06.iii.43, soldiers, workers [MZSP-4663]. Goiás Velho, coll. A.E. Mill, 10.ii.80, soldiers [BMNH]. Goiânia, coll. D. Brandão, 16.iii.83, soldiers, workers [UFG-13 and 17]; coll. D. Brandão, xi.84, soldiers, workers [UFG-142]. Ilha do Bananal, coll. D. Brandão, 01.x.87, soldiers, workers [UFG-340]. Parque Nacional do Araguaia, coll. A. Raw, 15.vi.79, soldiers [BMNH]. Rio Paranã, coll. H.R. Coles, 30.i.77, soldiers, workers [BMNH]. *Maranhão*. Cajazeiras, coll. Reichardt, 17.vi.66, soldiers, workers [MZSP-1821]. Imperatriz, coll. G.M. Oliveira, 18.xii.72, soldiers, workers [MZSP-6335 and MZSP-6307]. *Mato Grosso*. Barra dos Bugres, coll. Braulio Dias, 13.viii.73, soldiers, workers [MZSP-7332]. Chapada dos Guimarães, coll. W.L. Overall, 17.xi.82, one alate [MPEG-3898]. Cuiabá, coll. J.C. Trager, 17.xii.84, soldiers [MZSP-8588]. E.E. Iquê-Juruena, coll. A.E. Mill, 13.vi.80, soldiers, workers [3 vials, BMNH]. Parque Índigena do Xingu, coll. R.G. Kloss, soldiers, workers [MZSP-5292]. Utiariti, coll. K. Lenko, 03.xi.65, soldiers, workers [MZSP-1807]. Xavantina, coll. A.G.A. Mathews, 12.x.68, soldiers, workers [BMNH]. *Mato Grosso do Sul*. Três Lagoas, coll. K. Lenko, 28.v.64, soldiers, one worker [MZSP-1806]. *Minas Gerais*. Francisco Sá, coll. R.L. Araujo, 16.vii.75, soldiers [MZSP-5932]; coll. R.L. Araujo, 18.vii.75, one soldier, workers [MZSP-6140]. Montes Claros, coll. R.L. Araujo, 08.i.52, soldiers [MZSP-4329]. Paracatu, coll. T.Ivanauskas, 1931, soldiers, workers, alates [AMNH and BMNH]. Pedra Azul, coll. E.M. Canello, 21.xi.90, one soldier, workers [MZSP-9730]. Rio Pardo, coll. R.L. Araujo, 10.i.52, soldiers [MZSP-3411]. Teófilo Otoni, coll. R.L. Araujo, 27.vi.70, soldiers, workers [MZSP-4774]; coll. R.L. Araujo, 25.xii.76, soldiers, workers [MZSP-7256]. *Pará*. Canindé, coll. R. Malkin, iv.63, soldiers [MZSP-144]. Conceição do Araguaia,

coll. A.Y. Harada, 31.i.83, soldiers, one worker [MPEG-2337]. Parque Nacional da Amazônia, coll. A.G. Bandeira, 23.viii.78, soldiers, workers [MPEG-422]. Santarém, Serra do Uratinga, coll. J.R. Lopes, i.1950, soldiers, workers, alates [USNM]. Serra dos Carajas, coll. R.B. Neto, 22.x.84, soldiers, workers [MPEG-2350]; coll. A.G. Bandeira, 28.i.86, one soldier, workers [MPEG-2446]. Tucuruí, coll. A.G. Bandeira, 21.iv.79, soldiers, workers [MPEG-618]; coll. W.L. Overall, 22.vi.84, soldiers, workers [MPEG-2273]. *Rio de Janeiro*. Rio de Janeiro, coll. J. Smith, one soldier [BMNH]. *Rondônia*. 1985, soldiers, workers [MPEG-3920, MPEG-3921 MPEG-3922]. Ouro Preto do Oeste, coll. F. Ramos, 26.iii.85, soldiers, workers [MPEG-2287]; coll. R.B. Neto, 26.iii.85, soldiers, workers [MPEG-2286]; coll. J.O. Dias, 26.iii.85, soldiers [MPEG-2288]. *Roraima*. Ilha de Maracá, coll. A.G. Bandeira, 23.ii.88, soldiers, workers [INPA-673]; coll. Carmozing, 13.v.88, soldiers, workers [MZSP-9471]; coll. A.G. Bandeira, 04.ii.88, one soldier, workers [INPA-382 and INPA-425]; coll. S. Ferraz, 16.ii.88, soldiers, workers [INPA-763]; coll. A.G. Bandeira, 21.xi.78, soldiers, workers [MPEG-3467]. Vista Alegre, Rio Branco, coll. J. Bequaert, 6.ix.24, soldiers, workers [AMNH]. *São Paulo*. São Paulo, one soldier, one worker [BMNH]. *COLOMBIA*. Meta. Villavicencio, coll. C.H. Seevers, 16.vii.38, soldiers, workers, queen and king [AMNH].

Imago (Figs. 236-238). Eyes moderately large, more than 1/4 width of head; ocelli large; fontanelle rounded and large. Antenna with 20 articles. Anterior corners of pronotum rounded; lateral margins rounded and converging posteriorly. Wings long; distal part of media and cubitus inconspicuous. Head capsule with numerous long bristles; postclypeus with two bristles on anterior margin and two near middle; pronotum with many hairs on outer margin and only a few scattered ones on surface; tergites with a line of hairs on posterior margin. Head and pronotum light chestnut; tergites chestnut-brown; sternites brownish yellow; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 5 imagoes from 5 colonies: length of head 2.15-2.25; width of head without eyes 2.35-2.55; length of fontanelle 0.34-0.45; length of pronotum 1.60-1.75; width of pronotum 2.95-3.05; length of hind tibia 4.00-4.50; maximum diameter of eye 0.69-0.81; length of ocellus 0.27-0.34; length of forewing 22.00-26.50; width of forewing 6.00-7.00. Ratios: diameter of eye to width of head 0.28-0.32; length of ocellus to width of head 0.11-0.13; length of fontanelle to width of head 0.13-0.18; width of pronotum to width of head 1.18-1.26; length of wing to width of head 9.36-10.39; length of hind tibia to width of head 1.60-1.76.

Soldier (Figs. 231-235). Head capsule elongate with sides converging towards front; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible

in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum large. Antenna with 19 or 20 articles. Postmentum slightly constricted near the middle, usually with a pimple-like projection near anterior end. Mandibles slender and elongate; tip strongly hooked; first marginal tooth of left mandible near the base and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial or absent; apical cutting edge of left mandible evenly rounded, but forming a notch anterior to M1; cutting edge of right mandible mostly straight, with evenly curved distal portion. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines absent, lateral margins of nota angular and not upturned. Head capsule with scattered short, straight bristles, more numerous laterally; base of mandibles without hairs; postmentum with only two straight bristles on anterior corners; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on lateral margins; tergites with many bristles near hind margin.

Measurements (in mm) of 10 soldiers from 10 colonies: length of head 3.75-4.30; maximum width of head 3.00-3.65; height of head excluding postmentum 1.80-2.25; length of frontal tube 0.03-0.08; length of left mandible 2.05-2.20; curvature of left mandible 0.70-0.98; distance from M1 to M2 on left mandible 0.17-0.25; width of left mandible 0.50-0.60; length of left M1 0.07-0.08; minimum width of postmentum 0.49-0.66; width of pronotum 1.75-2.10; width of metanotum 2.20-2.65; length of hind tibia 3.30-3.80. Ratio length of head to maximum width of head 1.17-1.25; length of left mandible to length of head 0.49-0.59; length of hind tibia to length of head 0.79-0.95; width of pronotum to maximum width of head 0.53-0.60; distance M1-M2 to length of left mandible 0.08-0.12; height of head to maximum width of head 0.60-0.63; width to length of left mandible 0.23-0.29.

Large worker (Figs. 239-241). Head capsule with many short, straight bristles; postclypeus with about 14 bristles. Fontanelle rounded and relatively large. Antenna with 19 or 20 articles. Lateral margins of thoracic nota angular, but lacking spines. Mandibles similar to those of *S. nanus* (Fig. 52); left apical tooth short; cutting edge of left M1 slightly undulate; right A and M1 about the same size; molar plate narrow with well marked basal notch of about 90°. Gut (Figs. 65-70) less voluminous than in *S. dirus*; mixed segment plus first proctodeal segment broadly tubular, without any abrupt enlargement; major midgut prolongation of mixed segment elongate, with conspicuously inflated distal portion; minor prolongation tongue-shaped and relatively large, touching the major prolongation.

Measurements (in mm) of 4 large workers from 4 colonies: length of head 2.00-2.15; maximum width of head 2.45-2.60; length of fontanelle 0.20-0.27; width of pronotum 1.35-1.53; width

of metanotum 1.65-1.80; length of hind tibia 2.60-2.85.

Comparisons. All castes are close to *S. nanus* and distinct from all other species of *Syntermes*. The alate can be distinguished by its small size, large eyes, rounded corners of pronotum, long and hyaline wings, and postclypeus with only four bristles. The imago of *S. nanus* is smaller and darker colored, and has a smaller fontanelle and a narrower pronotum. The soldier can be distinguished by its small size, elongate mandibles with reduced marginal dentition and strongly hooked tip, and the absence of thoracic spines. The soldier of *S. nanus* is smaller, the sides of the head are parallel, the mandibles are less hooked, and some hairs are present on the posterior part of the postmentum.

Distribution and Geographical Variation. This is the species of *Syntermes* with the widest distribution, from southeastern Brazil to Colombia and the Guianas (Fig. 363). Although there is some morphological variation, there is no clear geographic pattern, and specimens from Bahia, near the Atlantic coast, are very similar to those from Colombia.

Biology. *S. molestus* is a forest species, and its nest is completely subterranean. It may be found foraging on the forest floor even during the day, leaving the underground galleries through small circular openings.

Remarks. Many of the references about *S. molestus* in the literature actually refer to *S. nanus*. Apparently, soldiers of *S. nanus* collected by Silvestri (1903) in Paraguay and Mato Grosso, erroneously determined as *S. molestus*, became reference ("morphotypes") because only the alates of *S. molestus* were previously known. Holmgren (1911) was able to distinguish the two species, but, because he used Silvestri's morphotypes for comparison, he described the true soldiers of *S. molestus* as a new species, *S. brasiliensis*. Emerson (1945) considered the two forms as variations of the same species, probably due to limited material and biological information. Although both species show considerable variation with a little overlap in some characters, their size distribution is clearly bimodal, both soldiers and imagoes are different, and there is a clear habitat separation.

Syntermes nanus, new species

Termes molestus, Silvestri 1903: 51, misidentification [part]; 116 [biology]; plate II: figs. 84 [imago]

and 86 [soldier].

Syntermes molestus, Emerson 1945: 467, misidentification [part].

Holotype soldier: BRAZIL. *São Paulo*. Pirassununga, coll. O. Schubart, 1954, [MZSP-4239].
 Paratypes: BRAZIL. *Amazonas*. Humaitá, coll. R. Constantino, 18.ix.90, soldiers, workers [MPEG-3763]. *Bahia*. Salvador, coll. R.L. Araujo, 02.vii.70, soldiers, one worker [MZSP-4832].
Ceará. Crato, coll. R.L.A., 10.xi.75, one soldier, workers [MZSP-6454]. *Distrito Federal*. Brasília, coll. H.R. Coles, 14.ix.79, soldiers, workers [two vials, BMNH]; coll. A.E.Mill, 11.iii.80, soldiers, workers [BMNH]; coll. H.R. Coles, 30.iv.77, soldiers, workers [BMNH]; coll. H.R. Coles, 06.xi.76, soldiers, workers [MZSP-9300]; coll. M.G. Siqueira, 03.vi.82, soldiers, workers [two vials, UnB]; coll. M.G. Siqueira, 24.vi.82, soldiers, workers [two vials, UnB]. *Goiás*. Alvorada do Norte, coll. C.R.F. Brandão, 9.vii.91, one soldier, workers [MZSP-9731]; coll. Amarante, vii.91, soldiers, workers [MZSP-9732]. Formosa, coll. Goodland, 12.xii.65, soldiers, workers [MZSP-1169]. Goiânia, coll. R.F. Souza, 18.vii.91, one soldier, workers [UFG-439]. Parque Nacional das Emas, coll. Mill & Redford, 9.vii.80, soldiers, one worker [BMNH]. Padre Bernardo, coll. H.R. Coles, 17.xii.77, soldiers, workers [BMNH]. *Mato Grosso*. Aquidauana, coll. R.L. Araujo, 26.x.53, soldiers, workers [MZSP-3937]. Cáceres, coll. M. Zanuto, 02.iii.85, soldiers, workers [MPEG-2327]. Chapada dos Guimarães, coll. W.L. Overal, 17.xi.82, soldiers [MPEG-2742]; coll. W.L. Overal, 18.xi.82, one soldier, workers [MPEG-2774]. Coxipó, coll. R.L. Araujo, 18.ii.76, soldiers, workers [MZSP-6677]. Cuiabá, 22.xi.84, soldiers, workers [MZSP-9893]; coll. J.C. Dalponte, 11.ix.82, soldiers, workers [MPEG-3895]. Diamantino, coll. H. Reichardt, 10.viii.73, soldiers, workers [MZSP-5235]. Utiariti, coll. Lenko & Pereira, 29.xi.66, soldiers, workers [MZSP-1802]. Xavantina, coll. H.R. Coles, 01.iv.78, soldiers, workers [BMNH]; coll. H.R. Coles, 12.i.77, soldiers, workers [BMNH]; coll. A.G.A.Mathews, 18.ix.68, soldiers, workers [5 vials, BMNH]; coll. A.G.A.Mathews, 12.ii.68, one soldier, workers [BMNH]. *Mato Grosso do Sul*. Corumbá, one soldier, workers [ZMUC]; coll. F. Silvestri, 1900, one soldier, workers [ISNB]; coll. R.L. Araujo, 29.x.53, soldiers, workers [MZSP-3955 and 3959; AMNH]. Rio Paraguai, coll. G. Schaller, soldiers, workers [AMNH]; coll. G. Schaller, iv.78, soldiers [AMNH]. Três Lagoas, coll. K. Lenko, 20.v.64, soldiers, workers [MZSP-1803]; coll. F. Lane, iv.66, soldiers, workers [MZSP-1034]. *Minas Gerais*. Araxá, coll. R.L. Araujo, 10.xi.73, soldiers, workers [MZSP-5748]. Belo Horizonte, coll. R.L. Araujo, 15.i.54, soldiers, workers [MZSP-4109]; coll. R.L. Araujo, 04.i.54, soldiers [MZSP-4063]. Bom Sucesso, soldiers, workers [MZSP-7374]. Capitão Eneias, coll. R.L. Araujo, 15.vii.75, soldiers, workers [MZSP-6249]. Divinópolis, coll. O.F. Souza, 04.x.93, soldiers, workers [MEUV]. Lagoa Santa, coll. R.L. Araujo, 17.viii.71, soldiers, workers [MZSP-4951]. Montes Claros, coll. R.L. Araujo, 17.xi.72,

soldiers, workers [MZSP-5834]. Tiradentes, coll. R.L. Araujo, 30.vii.75, soldiers, workers [MZSP-5962]. Uberaba, coll. R.L. Araujo, 22.iv.72, soldiers, workers [MZSP-4990]. *Paraíba*. Independencia, soldiers, workers [MZSP-1845]. *Pernambuco*. Engenho do Rio Morto, coll. B. Dantas, 06.viii.58, soldiers, workers, one alate [MZSP-4688]. *Rio Grande do Norte*. Natal, Paranamirim Field, coll. H.T. Dalmat, 26.ii.45, alates [AMNH]. *Rio de Janeiro*. S.J. da Barra, coll. M.M. Chaves, 06.ix.63, soldiers, one worker [MZSP-1823]. *Rondônia*. Vilhena, coll. A.E. Mill, 06.x.80, 3 vials with soldiers, workers and alates [BMNH]; coll. A.E. Mill, 23.vii.80, soldiers, workers [MPEG-1267]. *Sergipe*. Estância, coll. R.L. Araujo, 23.xi.75, soldiers, workers [MZSP-6452]. Sto. Amaro das Brotas, coll. F. Val, 9.ii.88, soldiers, workers [MZSP-9751]. *São Paulo*. Agudos, coll. W. Kempf, 08.v.52, soldiers, workers [MZSP-1100]. Guarani, coll. J.V. Pinheiro, ii.43, one soldier, workers [MZSP-2786]; coll. J.P. Fonseca, 06.xi.43, soldiers, workers [MZSP-2911 and 2912]; no data, soldiers, one worker [MZSP-3782]. Itirapina, coll. C.R.F. Brandão, 19.x.90, soldiers, workers [MZSP-9415]. Jacareí, coll. R.L. Araujo, 27.ii.57, soldiers, workers [MZSP-3312]. Pirassununga, coll. O. Schubart, 25.iv.53, soldiers, one worker [AMNH]; coll. O. Schubart, 1954, soldiers, workers, same colony as holotype [MZSP-4239]; coll. D. Braz, 28.ix.47, soldiers, one worker [MZSP-3064]. Ribeirão Preto, coll. M.C. Rigo, 07.vii.67, soldiers, workers [MZSP-1801]. S.J. do Rio Preto, coll. I. Watanabe, ii.72, alates [MZSP-5178]. S.J. dos Campos, coll. A. Sanches, 17.v.53, soldiers [MZSP-3846]. PARAGUAY. Monte Sociedad, coll. Ternetz, 1895, soldiers, workers [AMNH].

Imago (Figs. 247-249). Eyes very large, more than 1/3 width of head; ocelli large; fontanelle small, rounded and concave. Antenna with 19 or 20 articles. Anterior corners of pronotum rounded; lateral margins of pronotum rounded and converging posteriorly. Wings very long (Fig. 38); distal part of media and cubitus inconspicuous. Head capsule with numerous long hairs; postclypeus with two hairs on anterior margin and two near middle; pronotum with many hairs on outer margin and a few scattered ones on surface; tergites with a line of hairs on posterior margin. Head, pronotum, and tergites dark brown; sternites brownish yellow; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 6 imagoes from 5 colonies: length of head 1.90-2.10; width of head without eyes 2.15-2.40; length of fontanelle 0.17-0.34; length of pronotum 1.33-1.50; width of pronotum 2.35-2.55; length of hind tibia 3.65-4.10; maximum diameter of eye 0.76-0.82; length of ocellus 0.30-0.40; length of forewing 24.50-26.00; width of forewing 6.20-6.40. Ratios: diameter of eye to width of head 0.32-0.38; length of ocellus to width of head 0.13-0.17; length of fontanelle to width of head 0.07-0.14; width of pronotum to width of head 1.02-1.14; length of wing to width of

head 10.21-11.86; length of hind tibia to width of head 1.59-1.88.

Soldier (Figs. 242-246). Head capsule elongate with nearly parallel sides; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum elongate, longer than width; lateral corners of labrum forming an obtuse angle; median lobe of labrum elongate, longer than lateral lobes. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles slender and elongate; tip moderately hooked; first marginal tooth of left mandible near base and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial or absent; apical cutting edge of left mandible evenly rounded and finely serrated, forming a notch anterior to M1; cutting edge of right mandible straight with evenly curved tip. Anterior margin of pronotum slightly emarginate (visible in posterior view only); posterior margin of pronotum nearly straight; thoracic spines absent, lateral margins of nota angular and not upturned. Head capsule in dorsal view with numerous straight, short bristles, more numerous laterally; base of mandibles with a few hairs; postmentum with two straight bristles on anterior corners plus some on posterior part; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 11 soldiers from 11 colonies: length of head 2.85-3.65; maximum width of head 2.20-2.85; height of head excluding postmentum 1.45-1.85; length of frontal tube 0.05-0.10; length of left mandible 1.65-1.95; curvature of left mandible 0.38-0.55; distance from M1 to M2 on left mandible 0.15-0.20; width of left mandible 0.35-0.49; length of left M1 0.03-0.06; minimum width of postmentum 0.45-0.60; width of pronotum 1.35-1.60; width of metanotum 1.53-2.05; length of hind tibia 2.50-3.00. Ratio length of head to maximum width of head 1.22-1.31; length of left mandible to length of head 0.49-0.61; length of hind tibia to length of head 0.78-0.91; width of pronotum to maximum width of head 0.56-0.61; distance M1-M2 to length of left mandible 0.09-0.11; height of head to maximum width of head 0.62-0.69; width to length of left mandible 0.20-0.27.

Large worker (Figs. 250-252). Head capsule with many straight bristles; postclypeus with about six bristles. Fontanelle small and slightly elongate. Antenna with 19 or 20 articles. Thoracic nota with angular sides but lacking spines. Mandibles (Fig. 52) with left apical tooth small; cutting edge of left M1 slightly undulate; right A and M1 nearly equal; molar plate narrow, with well marked basal notch of about 90°. Gut very similar to that of *S. molestus* (Figs. 65-70).

Measurements (in mm) of 4 large workers from 4 colonies: length of head 1.90-2.10;

maximum width of head 2.30-2.50; length of fontanelle 0.15-0.22; width of pronotum 1.20-1.30; width of metanotum 1.45-1.55; length of hind tibia 2.30-2.80.

Comparisons. The closest species is *S. molestus*. The alate of *S. nanus* is smaller, darker colored, with proportionally narrower pronotum and smaller fontanelle. The soldier of *S. nanus* is smaller, with sides of head parallel, less hooked mandibles, and some bristles on posterior part of postmentum. See also comparisons under *S. molestus*.

Distribution and Geographical Variation. Most parts of Brazil except Amazonia and southernmost states; a few records in Paraguay and northern Argentina (Fig. 364). There is considerable morphological variation, but no clear geographic pattern. Soldiers from Mato Grosso do Sul seem to be a little larger.

Biology. *S. nanus* lives in savannas and grasslands, where it feeds on grasses. The nest is completely subterranean and has never been described.

Remarks. See remarks under *S. molestus*.

Syntermes obtusus Holmgren

Termes grandis, Silvestri 1903: 49, misidentification [imago, workers]; 116 [biology]; plate II; fig. 79 [imago].

Syntermes obtusus Holmgren 1911: 547 [imago, in key]; Emerson 1945: 444 [redescription].
Lectotype imago ♂, here designated: PARAGUAY. Villa Rica, coll. F. Silvestri, 8.x.1900 [AMNH]. Paralectotypes: Four workers, same data as lectotype [AMNH]. Other syntypes not found in LEFS or NHRS.

Termes dirus, Silvestri 1903: 48, misidentification [soldier, worker], 115 [biology]; type material of *S. silvestrii*.

Syntermes silvestrii Holmgren 1911: 548 [soldier]; Emerson 1945: 462 [redescription]; synonymized by Araujo 1977: 6. Lectotype soldier, here designated: BRAZIL. Mato Grosso. Cuiabá, coll. F. Silvestri, 6.ix.1900 [AMNH].

Material examined. ARGENTINA. *Corrientes*. San Miguel: San Antonio, coll. G. Torales,

soldiers, workers [UNN]. *Misiones*. Loreto, coll. F. Silvestri, 27.vi.35, soldiers, workers [AMNH]; coll. Kuznesov, 20.vii.49, soldiers, workers [AMNH]; coll. Cernovitov, soldiers, workers [BMNH]; coll. Silvestri, 28.vi.35, soldiers, workers [MZSP-1859]. Southern BOLIVIA. Coll. Hill, one soldier, one worker [AMNH]. BRAZIL. *Goiás*. Parque Nacional das Emas, coll. K. Redford, ix.1981, soldiers, workers [MZSP-9781]. *Mato Grosso*. Chapada dos Guimarães, coll. M.A. Drumond, 01.xii.84, one soldier, workers [UFG-144]; coll. M.A. Drumond, 7.xii.84, soldiers, workers [MZSP-9896]. Cuiabá, coll. W.L. Overal, 19.ii.85, soldiers, workers [MPEG-2308]. Jaraguá, coll. R.L. Araujo, 24.x.53, soldiers, workers [MZSP-3927]. *Mato Grosso do Sul*. Campo Grande, coll. G. Muller, 06.vi.52, one soldier [MZSP-1868]; coll. R.L. Araujo, 25.x.53, soldiers, workers [MZSP-3924]; coll. R.L. Araujo, 20.ii.76, soldiers, workers [MZSP-6505]. *São Paulo*. Itapetininga, coll. Rabello, 09.viii.67, soldiers, workers [MZSP-1843]. Tatuí, coll. J.P. Fonseca, viii.56, soldiers, workers [MZSP-3221]. PARAGUAY. San Bernardino, coll. Fiebrig, one soldier, one worker [AMNH].

Imago (Figs. 263-265). Eyes large, more than $\frac{1}{4}$ width of head; ocelli large; fontanelle elongate and moderately large. Antenna with 21 articles. Anterior corners of pronotum moderately angular; anterior half of lateral margins of pronotum straight and nearly parallel. Head capsule with numerous long hairs; postclypeus with many hairs; pronotum with many hairs on margins and entire surface; tergites with many hairs from middle to posterior margin. Head dark brown; pronotum chestnut-brown; tergites dark brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of the holotype ♂: length of head 3.10; width of head without eyes 3.45; length of fontanelle 0.52; length of pronotum 2.50; width of pronotum 4.25; length of hind tibia 6.50; maximum diameter of eye 1.23; length of ocellus 0.45. Ratios: diameter of eye to width of head 0.36; length of ocellus to width of head 0.13; length of fontanelle to width of head 0.15; width of pronotum to width of head 1.23; length of hind tibia to width of head 1.88.

Soldier (Figs. 253-262). Head capsule short, length and width of head about equal, sides slightly to conspicuously converging anteriorly; posterior margin of head rounded or weakly three-lobed; frontal tube short, pore clearly visible in dorsal view or a little prominent and oriented anteriorly; labrum short, length about equal to width; lateral corners forming an obtuse angle; median lobe short. Antenna with 20 or 21 articles. Postmentum constricted near the middle. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible small, not extending much beyond apical cutting edge; first marginal tooth of right mandible reduce or vestigial; apical

cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible straight, except for curved tip. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines moderately developed and strongly upturned; lateral corners of pronotum sharp, sometimes forming short conical spines. Head capsule in dorsal view with many short, straight bristles, more numerous laterally; postclypeus densely covered with short hairs; base of mandibles with numerous short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with many bristles near hind margin.

Measurements (in mm) of 8 soldiers from 8 colonies: length of head 5.60-6.50; maximum width of head 5.25-6.20; height of head excluding postmentum 2.80-3.40; length of frontal tube 0.05-0.25; length of left mandible 2.90-3.25; curvature of left mandible 0.75-1.10; distance from M1 to M2 on left mandible 0.42-0.64; width of left mandible 0.76-0.87; length of left M1 0.12-0.22; minimum width of postmentum 0.76-0.96; width of pronotum 3.40-4.20; width of metanotum 3.30-4.10; length of hind tibia 4.90-6.10. Ratio length of head to maximum width of head 0.98-1.07; length of left mandible to length of head 0.49-0.55; length of hind tibia to length of head 0.84-1.09; width of pronotum to maximum width of head 0.63-0.71; distance M1-M2 to length of left mandible 0.14-0.20; height of head to maximum width of head 0.53-0.56; width to length of left mandible 0.25-0.28.

Large worker (Figs. 266-268). Head capsule covered with numerous short, straight bristles. Postclypeus with many short bristles. Fontanelle large and roughly triangular. Antenna with 20 or 21 articles. Thoracic spines moderately developed. Mandibles similar to those of *S. grandis*, with wide molar plate. Gut similar to that of *S. wheeleri*, but with major midgut prolongation of mixed segment proportionally smaller, and minor prolongation larger.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.70-3.00; maximum width of head 3.35-3.60; length of fontanelle 0.27-0.37; width of pronotum 2.10-2.40; width of metanotum 2.15-2.50; length of hind tibia 4.00-4.75.

Comparisons. The imago of *S. obtusus* can be distinguished by its large size and very large eyes; the most similar imagoes are those of *S. grandis* and *S. magnoculus*. The most similar soldier is that of *S. wheeleri*, which has larger marginal teeth located more distally on both mandibles.

Distribution and Geographical Variation. Northern Argentina, Paraguay, southwestern

Brazil, and also one record from southern Bolivia and two isolated records from southeastern Brazil (Fig. 366). Soldiers from the vicinities of Cuiabá, Brazil (type locality of *S. silvestrii*) have a more elongate head with sides converging towards front, larger thoracic spines, and more prominent frontal tube.

Biology. *S. obtusus* lives in savannas and grasslands. According to Silvestri (1903: 116), the nest is completely subterranean, but he was able to find only galleries and storage chambers with grasses. He also mentions that only the large workers collect grasses on the surface.

Remarks. *S. obtusus* was first described from the imago, and *S. silvestrii* from the soldier. The synonymy of those species was based on a series in Silvestri's collection with soldiers and a queen from the same colony, which was determined both by Silvestri and Emerson as *S. obtusus*. I was not able to examine the queen from that series, but I did examine some soldiers, which are not identical to the type of *S. silvestrii*. There are some intermediate forms, and they may be extremes of a continuum of variation, but the material available is still limited. Therefore, this synonymy should be treated with a certain amount of caution and there is some possibility that there are two species involved.

Syntermes parallelus Silvestri

Syntermes parallelus Silvestri 1923: 318, pl. XV: figs. 1-10 [imago, soldier, worker]; Emerson 1945: 466 [redescription]. Lectotype soldier, here designated: GUYANA. Cattle Trail Survey, Canister Falls, coll. A.A. Abraham, vi.1920 [AMNH]. Paralectotype: one worker, same data as lectotype [AMNH]. No other syntype found in LEFS, except for a slide with a pair of wings.

Syntermes colombianus Snyder 1924: 29, pl. 4: fig 24 [soldier]. Holotype soldier: COLOMBIA. Coll. Winthem, one pinned soldier [MCZ]. Synonymized by Emerson (1945).

Syntermes calvus, Mill 1984a: 406, misidentification, and 1984b: 131 [biology].

Material examined. BRAZIL. *Roraima*. Ilha de Maracá, coll. C.F. Sena, 4.ii.88, one soldier [INPA-393]; coll. A.G. Bandeira, 23.ii.88, soldiers, workers [INPA-672]; coll. F. Luizão, iii.88, one soldier, workers [INPA-748]; coll. A.E. Mill, 09.v.81, soldiers, workers [MPEG-1327]; coll. A.E. Mill, 06.vi.81, one soldier, workers [MPEG-1335]. GUYANA. Kartabo, coll. A.E.

Emerson, 2.vi.24, one alate [AMNH]. Oronoque River, coll. N. Weber, 21.vii.36, one soldier [AMNH]. Rupununi Savannahs, coll. J.G. Myers, 1932, one soldier, workers [USNM]. VENEZUELA. Coll. Chaper, 1885, one pinned soldier [MNHN]. *Sucre*. El Rincón, coll. E.M. Canello, 01.xi.86, soldiers, workers [MZSP-9596, MZSP-9598 and MZSP-9599].

Imago (Figs. 275-277). Eyes small, less than $\frac{1}{4}$ width of head; ocelli large; fontanelle small and rounded. Antenna with 19 articles. Anterior corners of pronotum angular, with sharp points; anterior half of lateral margins of pronotum straight and nearly parallel. Wings short, distal part of media and cubitus conspicuous. Head capsule with a few scattered short hairs; postclypeus with two short hairs on anterior margin; pronotum with many hairs on outer margin; tergites with a line of hairs on posterior margin. Head, pronotum and tergites chestnut-brown; sternites brownish yellow; wings brown.

Measurements (in mm) of 2 imagoes from 2 colonies: length of head 2.15-2.25; width of head without eyes 2.55-2.60; length of fontanelle 0.25-0.29; length of pronotum 1.60-1.75; width of pronotum 2.75-3.05; length of hind tibia 4.85-5.10; maximum diameter of eye 0.55-0.59; length of ocellus 0.29-0.29; length of forewing 20.00-21.50; width of forewing 5.50-5.70. Ratios: diameter of eye to width of head 0.22-0.23; length of ocellus to width of head 0.11-0.11; length of fontanelle to width of head 0.10-0.11; width of pronotum to width of head 1.08-1.17; length of wing to width of head 7.84-8.27; length of hind tibia to width of head 1.90-1.96.

Soldier (Figs. 269-274). Head capsule elongate with parallel sides; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view. Labrum short, length about equal to width; lateral corners about equal to or a little more than a right angle; median lobe of labrum relatively large. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles elongate and straight, except for slightly hooked tip; first marginal tooth of left mandible near the base and small, not extending beyond apical cutting edge; first marginal tooth of right mandible very small and close to the base; apical cutting edge of left mandible evenly curved, except for notch anterior to M1; apical cutting edge of right mandible straight, except for curved tip. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; thoracic spines weakly developed and slightly upturned; lateral corners of pronotum sharp but not forming conical spines. Head capsule with scattered short bristles, more numerous laterally; base of mandibles without hairs; postmentum with two straight, very short bristles on anterior corners plus many scattered ones; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles

on posterior half. Head and thorax pale yellow-brown; tergites and sternites yellowish, semi-transparent.

Measurements (in mm) of 5 soldiers from 5 colonies: length of head 4.00-4.90; maximum width of head 2.95-3.65; height of head excluding postmentum 1.95-2.50; length of frontal tube 0.20-0.27; length of left mandible 2.10-2.40; curvature of left mandible 0.35-0.65; distance from M1 to M2 on left mandible 0.20-0.32; width of left mandible 0.54-0.64; length of left M1 0.07-0.10; minimum width of postmentum 0.62-0.76; width of pronotum 2.20-2.60; width of metanotum 2.20-2.60; length of hind tibia 3.10-3.55. Ratio length of head to maximum width of head 1.26-1.37; length of left mandible to length of head 0.49-0.55; length of hind tibia to length of head 0.71-0.78; width of pronotum to maximum width of head 0.70-0.76; distance M1-M2 to length of left mandible 0.10-0.13; height of head to maximum width of head 0.64-0.68; width to length of left mandible 0.25-0.27.

Large worker (Figs. 278-280). Head capsule with a few scattered bristles; postclypeus with 4 bristles. Fontanelle rounded and small. Antenna with 19 articles. Thoracic spines weakly developed. Mandibles similar to those of *S. longiceps*, with narrow molar plate. Gut also similar to that of *S. longiceps*, but material was poorly preserved.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.05-2.25; maximum width of head 2.50-2.80; length of fontanelle 0.15-0.22; width of pronotum 1.60-1.70; width of metanotum 1.65-1.90; length of hind tibia 2.90-3.20.

Comparisons. See comparisons under *S. longiceps*.

Distribution and Geographical Variation. Northern Amazonia, including Colombia, Venezuela, Guyana and northern portion of Roraima, Brazil (Fig. 365). Soldiers show some size variation, and specimens from Roraima are a little smaller than average but otherwise there is no evident geographic pattern.

Biology. *S. parallelus* is a rainforest species. The nest is probably completely subterranean.

Syntermes peruanus Holmgren

Termes dirus, Holmgren 1906: 545, misidentification [imago, soldier, worker].

Syntermes peruanus Holmgren 1911: 548 [imago, soldier, in key]. Lectotype soldier, here designated: BOLIVIA. La Paz. Mojós, coll. N. Holmgren, with broken mandibles [AMNH]. Paralectotypes: two workers in poor condition and 6 whitish alates, also in poor condition [AMNH]. Although the species name refers to Peru, no material from that country was found in Holmgren's collection in NHRS, and part of the type material seems to have been lost. However, Mojós is very close to the Peruvian border and to Holmgren's collection sites in Peru (Fig. 366).

Imago (Figs. 286-288). Eyes moderately large, more than 1/4 width of head; ocelli small; fontanelle roughly triangular and elongate. Antenna with 20 articles. Anterior corners of pronotum moderately angular. Head capsule with many long hairs (but most hairs lost in paratype alates); pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Specimens incompletely sclerotized.

Measurements (in mm) of one alate: length of head to base of mandibles 2.6; width of head 2.9; length of fontanelle 0.37; length of pronotum 1.9; width of pronotum 3.65; length of hind tibia 6.0; maximum diameter of eye 0.84; length of ocellus 0.3.

Soldier (Figs. 281-285). Head capsule short, length and width of head about equal; sides slightly converging anteriorly; posterior margin of head rounded or weakly three-lobed; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 to 20 articles. Postmentum constricted near the middle. Mandibles curved and moderately elongate; tip of mandibles slightly hooked; first marginal tooth of left mandible small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible straight, except for curved tip. Anterior margin of pronotum slightly emarginate; posterior margin of pronotum nearly straight; lateral projections of pronotum strongly upturned; thoracic spines moderately developed and strongly upturned; pronotum with distinct conical spines; head capsule in dorsal view with many short, straight bristles, more numerous laterally; base of mandibles with a few short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on anterior lobe and margins, and a few on posterior surface; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of the lectotype soldier: length of head 5.10; maximum width of head 5.00; height of head excluding postmentum 2.70; length of frontal tube 0.12; distance from M1 to M2

on left mandible 0.59; width of left mandible 0.77; length of left M1 0.22; minimum width of postmentum 0.86; width of pronotum 3.30; width of metanotum 3.40; length of hind tibia 4.80. Ratio length of head to maximum width of head 1.02; length of hind tibia to length of head 0.94; width of pronotum to maximum width of head 0.66; height of head to maximum width of head 0.54.

Large worker. Because the material available is in very poor condition (just fragments), no description is presented here.

Comparisons. Given the extremely limited material available for study, it is difficult to present a good diagnosis for this species. The imago seems similar to that of *S. wheeleri*, but smaller. The soldier of *S. bolivianus* is smaller, with proportionally smaller marginal teeth on the mandibles, and the sides of the head more parallel. Soldiers of *S. wheeleri* and *S. obtusus* are larger, with shorter thoracic spines.

Distribution. Holmgren (1906) records this species (misidentified as *T. dirus*) from four localities in a small area in southern Peru and northern Bolivia (Fig. 366).

Biology. According to Holmgren (1906: 661), *S. peruanus* (as *T. dirus*) lives in dry areas with open vegetation, and builds a conspicuous epigeal nest (see section on nests above).

Remarks. The type material of *S. peruanus* was first identified by Holmgren (1906) as *Termes dirus*, as indicated by Holmgren (1911). Unfortunately most specimens from that series seem to have been lost.

Syntermes praecellens Silvestri

Syntermes praecellens Silvestri 1946: 2, fig. I: 1-14 [imago, soldier, workers]; 6 [biology, nest].

Lectotype soldier, here designated: BRAZIL. *São Paulo*. São Paulo, coll. F. Silvestri, ii. 1937 [LEFS]. Silvestri's label: "Brasile: Jabaquara (S. Paolo) Febbraio 1937". Paralectotypes: 5 soldiers, workers, same data as lectotype [LEFS]. Four imagoes, also from S. Paulo, no date, "cotypi! Brasile: S. Paolo: Ypiranga" [LEFS]. One soldier, one nymph, workers, same data as lectotype [AMNH].

Material examined. BRAZIL. *Distrito Federal*. Brasília, coll. H.R. Coles, 27.i.77, soldiers [MZSP-9297]. *Minas Gerais*. Passa Quatro, coll. E. R. Wagner, one soldier, one worker [ISNB]. Rio Preto, coll. C.R. Goncalves, 08.i.68, soldiers, workers [MZSP-371]; coll. C.R. Goncalves, 08.i.68, soldiers, alates [MZSP-1866]. *Paraná*. Lapa, coll. C.R. Goncalves, 20.x.54, soldiers, workers [MZSP-4664]. *Santa Catarina*. Nova Teutonia, coll. F. Plaumann, ii.60, one soldier [MZSP-1853]. *São Paulo*. Atibaia, coll. R.L. Araujo, 19.iii.46, soldiers, workers [MZSP-2929]. Ibiuna, coll. U. Kawazoe, 08.iii.70, soldiers [MZSP-4759]. S.J. dos Campos, coll. D.L. Tiemann, 26.x.69, soldiers, workers [MZSP-4743]. Santo Andre, coll. L. Stowbnenko, ii.62, soldiers, workers [MZSP-1858]. São Paulo, coll. Silvestri, 07.ix.37, soldiers, workers [MZSP-1835]; coll. L.C. Almeida, 17.viii.60, soldiers, workers [MZSP-1848]; coll. Silvestri, 09.x.37, alates [MZSP-2945]; coll. E. Rabello, soldiers, workers [MZSP-3827]; coll. R.L. Araujo, 05.iii.74, one soldier, workers [MZSP-5347]; coll. R.L. Araujo, 29.ix.70, alates [MZSP-5393]; coll. R.L. Araujo, 28.ii.75, soldiers, workers [MZSP-5898]; coll. L.R. Fontes, 03.i.79, soldiers, workers [MZSP-7727]; coll. C.R.F. Brandão, 21.ii.83, soldiers, workers [MZSP-8385]; coll. E.M. Canello, 27.xi.86, alates [MZSP-8997]; coll. E.P. Teixeira, 29.xi.87, soldiers, workers [MZSP-9757].

Imago (Figs. 295-297). Eyes small, less than 1/4 width of head; ocelli small; fontanelle nearly triangular and small. Antenna with 20 articles. Anterior corners of pronotum moderately angular. Wings very long (Fig. 39); distal part of media and cubitus inconspicuous. Head capsule with numerous straight bristles; postclypeus with about 14 bristles; pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head dark brown; pronotum light chestnut, contrasting with head; tergites chestnut-brown; sternites light chestnut and chestnut-brown, darker near lateral margins; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 4 imagoes from 3 colonies: length of head 2.75-2.90; width of head without eyes 3.20-3.40; length of fontanelle 0.20-0.30; length of pronotum 1.95-2.10; width of pronotum 3.65-3.75; length of hind tibia 5.20-6.20; maximum diameter of eye 0.74-0.82; length of ocellus 0.27-0.32; length of forewing 36.00-36.50; width of forewing 8.40-8.50. Ratios: diameter of eye to width of head 0.22-0.24; length of ocellus to width of head 0.08-0.10; length of fontanelle to width of head 0.06-0.09; width of pronotum to width of head 1.07-1.17; length of wing to width of head 10.75-10.90; length of hind tibia to width of head 1.53-1.85.

Soldier (Figs 289-294). Head capsule elongate with sides parallel; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view; labrum short, length about equal to

width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum slightly constricted in the middle. Mandibles short and robust, with inflated bases; tip of mandibles slightly hooked; first marginal tooth of left mandible near the middle and large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge a little more than 90° ; apical cutting edge of left mandible sigmoid but not forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded to slightly emarginate; posterior margin nearly straight; thoracic spines weakly developed and not upturned; lateral corners of pronotum sharp but not forming conical spines; head capsule and postmentum densely covered with very short, straight bristles; postclypeus densely covered with short hairs; base of mandibles with numerous short hairs; pronotum with many short bristles on entire surface, more numerous on anterior lobe; mesonotum, metanotum and tergites densely covered with short, straight bristles.

Measurements (in mm) of 6 soldiers from 6 colonies: length of head 5.40-5.80; maximum width of head 4.60-5.00; height of head excluding postmentum 2.90-3.10; length of frontal tube 0.22-0.27; length of left mandible 2.30-2.50; curvature of left mandible 0.65-0.80; distance from M1 to M2 on left mandible 0.45-0.67; width of left mandible 0.77-0.87; length of left M1 0.13-0.20; minimum width of postmentum 0.76-0.87; width of pronotum 2.90-3.20; width of metanotum 2.80-3.30; length of hind tibia 4.60-5.30. Ratio length of head to maximum width of head 1.10-1.21; length of left mandible to length of head 0.41-0.45; length of hind tibia to length of head 0.82-0.98; width of pronotum to maximum width of head 0.63-0.67; distance M1-M2 to length of left mandible 0.20-0.28; height of head to maximum width of head 0.61-0.65; width to length of left mandible 0.33-0.35.

First form soldier. Described by Silvestri (1946: 5, Fig. I, 6-9). No material examined. Smaller than normal soldier, with fewer hairs on head and more slender mandibles.

Large worker (Figs. 298-300). Head capsule and postclypeus densely covered with short bristles. Fontanelle small and rounded. Antenna with 20 articles. Thoracic spines weakly developed. Mandibles similar to those of *S. dirus*, with narrow molar plate and basal notch forming an obtuse angle. Gut very similar to that of *S. barbatus*; major midgut prolongation of mixed segment a little more elongate; minor prolongation identical.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 2.50-2.75; maximum width of head 3.10-3.30; length of fontanelle 0.24-0.25; width of pronotum 1.80-1.90; width of metanotum 1.90-2.10; length of hind tibia 3.80-4.05.

Comparisons. The imago of *S. praecellens* is not particularly similar to the imago of any other species of *Syntermes* and can be identified by its very long and hyaline wings, small triangular fontanelle, numerous bristles on top of head, relatively small eyes, and dark brown head contrasting with chestnut pronotum. The soldier is very distinct with its elongate head densely covered with short bristles, short and robust mandibles, and weakly developed thoracic spines. The most similar soldier is that of *S. territus*, which has a less elongate head with fewer bristles and smaller mandibular teeth.

Distribution and Geographical Variation. Except for the isolated record from Brasília, all samples come from a narrow band along the coastal mountain range of southern Brazil (Fig. 361). Apparently this species is associated with a particular kind of habitat that occurs on mountain slopes. Unfortunately, most samples come from urban areas and it is difficult to determine which habitat was there prior to urbanization. Most likely it was a kind of grassland that occurs at some elevation. There is little morphological variation between most areas, but soldiers from Minas Gerais have less numerous hairs on the head. The single sample from Brasília has somewhat different soldiers, with less numerous hairs on the head, and slightly longer mandibles.

Biology. The nest (Fig. 34) is subterranean (see section about nests for more information), but some label notes indicate that sometimes there are small piles of soil on the surface. All samples were collected in grassland areas.

Syntermes spinosus (Latreille)

Termes spinosum Latreille 1804: 62 [soldier]. Holotype soldier: "Afrique (?)", unknown locality, probably French Guyana, labelled by A.E. Emerson as the holotype of *S. spinosus* based on a statement by J. Desneux; pinned and in poor condition [ISNB]. No paratypes known.

Syntermes spinosus, Araujo 1977: 54 [catalog].

Termes costatus Rambur 1842: 305 [imago]. Holotype imago: FRENCH GUIANA: Cayenne, coll. Serville. [ISNB], not examined. Synonymized by Emerson in Araujo (1977: 54).

Termes decumanus Erichson 1848: 582 [soldier only]. Lectotype soldier, here designated: GUYANA, coll. Schomburgk [ZMHU]. Alates of the same series are *S. grandis*.

Syntermes snyderi Emerson 1925: 358, fig. 44 [imago, soldier]; Emerson 1945: 446 [redescription]. Holotype soldier: GUYANA. Kartabo, coll. A.E. Emerson, 1919 [AMNH]. Synonymized by Emerson in Araujo (1977: 54).

Syntermes solidus Emerson 1945: 447, fig. 6 [soldier]. Holotype soldier: FRENCH GUIANA, St.

Jean, Moroni R., coll. Le Moulton [AMNH].

Syntermes chaquimayensis parvinasus Emerson 1945: 450, fig. 7 [soldier]. Holotype soldier: COLOMBIA. *Vaupés*. Rio Uaupés, 1906 [AMNH].

Syntermes robustus Constantino 1991: 221, fig. 31-34 [imago, soldier]. Holotype soldier: BRAZIL. *Amazonas*. Maraã, coll. R. Constantino, 17.x.1988 [MPEG-2885].

Syntermes lighti, Mill 1984b: 132, misidentification [biology].

Material examined. BRAZIL. *Amazonas*. Manaus, coll. R.S. Bradley, 18.ix.78, one soldier, workers [MPEG-493]; coll. A.G. Bandeira, 16.viii.76, soldiers, workers [MPEG-2]; coll. T.C. Fletcher, 19.i.1863, alates [MCZ]; coll. O.F. Souza, 21.v.86, soldiers, workers [MEUV]; coll. O.F. Souza, soldiers, one worker [MEUV]. Manaus: Reserva Ducke, coll. R.I. Barbosa, 7.vi.92, soldiers, workers [INPA-1]. Maranhoto: Rio Jau, coll. H.O. Schubart, 06.iv.77, soldiers, workers [MPEG-74]. Porto Urucu: Rio Urucu, coll. T.C.S. Pires, 22.xi.89, soldiers, workers [MPEG-3297]; coll. T.C.S. Pires, 26.xi.89, soldiers, workers [MPEG-3299]; coll. T.C.S. Pires, 19.xi.89, soldiers, workers [MPEG-3308 and MPEG-3309]. *Mato Grosso*. Chapada dos Parecis, coll. E.Z.F. Setz, 24.i.80, soldiers [MZSP-8766]. Iquê-Juruena, coll. A.E. Mill, 04.viii.80, one soldier, workers [MPEG-1302]; coll. A.E. Mill, 10.viii.80, soldiers, one worker [MZSP-8401]. Xavantina, coll. A.G.A. Mathews, iv.68, soldiers, workers [BMNH]; coll. A.G.A. Mathews, 8.xii.67, alates [BMNH]. *Pará*. Monte Dourado, coll. W.L. Overal, 02.xi.79, one soldier, workers [MPEG-3896]. Serra dos Carajás, 26.x.83, soldiers, workers [MPEG-3897]; coll. M.F. Torres, 16.iv.83, one soldier [MPEG-1528]; coll. A.G. Bandeira, 13.ix.83, soldiers, one worker [MPEG-1604]; coll. R. Moraes, 11.vi.85, soldiers [MPEG-2372]. Tucuruí: Chiqueirinho, coll. M.F. Torres, 06.iv.84, soldiers, workers [MPEG-2131]. *Roraima*. Ilha de Maracá, coll. A.G. Bandeira, 19.ii.88, soldiers, workers [MZSP-9120]; coll. A.G. Bandeira, 23.x.87, soldiers, workers [INPA-212 and 326]; coll. A.G. Bandeira, 11.ii.88, one soldier, workers [INPA-455]; coll. A.G. Bandeira, 12.ii.88, soldiers, workers [INPA-497, 499 and 511]; coll. C.F. Sena, 17.ii.88, soldiers, workers [INPA-619]; coll. A.G. Bandeira, 19.ii.88, soldiers, workers [INPA-669]. Ireng River, viii.11, soldiers [AMNH]. COLOMBIA. *Vaupés*. Yebaka, coll. S.H. Jones, soldiers, alates [BMNH]. Rio Uaupés, 1906, two soldiers, paratypes of *S. chaquimayensis parvinasus* [AMNH]; two other vials with many soldiers, same data but not labelled as paratypes [AMNH]. Yapú: Rio Papuri, coll. D. Dufour, 12.vi.77, soldiers [USNM]; coll. D. Dufour, 27.iv.77, soldiers, one worker [USNM]; coll. D. Dufour, 27.iii.77, soldiers [USNM]. FRENCH GUIANA. Coll. Desutter & Gran, 1.vii.88, one soldier [MNHN]. Cayenne, one soldier [ISNB]. Oiapoque, coll. J. Gray, 1900, one soldier [MNHN]. GUYANA. Coll. R. Schomburgk, one soldier [BMNH]. Bartica District, coll. A.E. Emerson, 1919, one soldier, one alate [AMNH]. Demerara, coll. Bowerbank, one

soldier [BMNH]. SURINAME. Jodensavanne, coll. M.A. Knoppe, vi.57, soldiers, workers [MZSP-9765]. Oelemarie, coll. Raatzerer, 1938, soldiers [AMNH]. VENEZUELA. Sarare, coll. F. Gray, 1893, one soldier [ISNB]; coll. J. Gray, 1895, one soldier [MNHN].

Imago (Figs. 314-316). Eyes small, less than 1/4 width of head; ocelli small; fontanelle rounded and moderately large. Antenna with 20 articles. Anterior corners of pronotum angular, with sharp points; lateral margins of pronotum slightly sigmoid, with anterior half nearly parallel. Wings short, distal part of media and cubitus conspicuous. Head capsule with a few scattered bristles; postclypeus with 6-8 bristles; pronotum with many hairs on outer margin and a few scattered ones on surface; tergites with many hairs near posterior margin and scattered very short hairs on posterior half. Head and pronotum light chestnut; tergites chestnut-brown; sternites light chestnut; wings brown to dark brown.

Measurements (in mm) of 7 imagoes from 5 colonies: length of head 2.65-3.05; width of head without eyes 3.00-3.40; length of fontanelle 0.37-0.54; length of pronotum 2.00-2.40; width of pronotum 3.70-4.55; length of hind tibia 6.40-7.10; maximum diameter of eye 0.67-0.72; length of ocellus 0.29-0.35; length of forewing 26.00-30.00; width of forewing 6.60-7.70. Ratios: diameter of eye to width of head 0.20-0.24; length of ocellus to width of head 0.09-0.10; length of fontanelle to width of head 0.11-0.16; width of pronotum to width of head 1.23-1.36; length of wing to width of head 8.51-9.03; length of hind tibia to width of head 1.97-2.20.

Soldier (Figs. 301-310). Head capsule short to moderately elongate, sides converging towards front; posterior margin of head rounded; frontal tube prominent, or short, in a small depression, pore usually not visible in dorsal view. Labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 or 20 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible large, extending well beyond apical cutting edge; first marginal tooth of right mandible large; angle between right M1 and apical cutting edge less than 90°; apical cutting edge of left mandible sigmoid; apical cutting edge of right mandible slightly sigmoid or straight, except for curved tip. Anterior margin of pronotum slightly emarginate; posterior margin slightly emarginate; thoracic spines well-developed and strongly upturned; pronotum with distinct, large conical spines. Head capsule densely covered with short, straight bristles; clypeal region densely covered with short hairs; base of mandibles with numerous short hairs; postmentum densely covered with short, straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous hairs near hind and lateral margins

and some on spines; tergites with numerous bristles on posterior half.

Measurements (in mm) of 22 soldiers from 20 colonies: length of head 5.45-7.20; maximum width of head 5.10-7.60; height of head excluding postmentum 2.90-4.10; length of frontal tube 0.15-0.30; length of left mandible 3.00-3.60; curvature of left mandible 1.00-2.10; distance from M1 to M2 on left mandible 0.66-1.09; width of left mandible 0.87-1.26; length of left M1 0.25-0.55; minimum width of postmentum 0.87-1.13; width of pronotum 4.30-5.70; width of metanotum 4.30-5.70; length of hind tibia 5.80-6.50. Ratio length of head to maximum width of head 0.93-1.11; length of left mandible to length of head 0.46-0.59; length of hind tibia to length of head 0.86-1.12; width of pronotum to maximum width of head 0.70-0.89; distance M1-M2 to length of left mandible 0.21-0.33; height of head to maximum width of head 0.51-0.60; width to length of left mandible 0.27-0.40.

First form soldier (Figs. 311-313). Conspicuously smaller than the normal soldier, and with more elongate mandibles with smaller marginal teeth. Pilosity and thoracic spines similar to those of normal soldier.

Large worker (Figs. 317-319). Head capsule and postclypeus with many straight bristles. Fontanelle rounded and relatively small. Antenna with 20 articles. Thoracic spines well developed. Mandibles (Fig. 49) with relatively narrow molar plate and basal notch of a little more than 90°. Gut similar to that of *S. dirus*, but major midgut prolongation of mixed segment is wider.

Measurements (in mm) of 13 large workers from 11 colonies: length of head 2.80-3.15; maximum width of head 3.35-3.80; length of fontanelle 0.25-0.34; width of pronotum 2.55-3.10; width of metanotum 2.75-3.40; length of hind tibia 4.45-5.25.

Comparisons. The imago of *S. spinosus* is similar to those of *S. dirus*, *S. cearensis*, *S. aculeosus*, *S. chaquimayensis* and *S. tanygnathus*, and it is difficult to distinguish from some of these species. *S. dirus*, *S. cearensis* and *S. aculeosus* have shorter hairs on the head, and *S. aculeosus* also has a larger fontanelle and different pronotum; *S. tanygnathus* has an antenna with 21 articles; *S. chaquimayensis* has longer and more numerous bristles on the head. The soldier is most similar to that of *S. chaquimayensis*, but is usually conspicuously larger, with more elongate mandibles and larger marginal teeth. However, *S. spinosus* shows considerable morphological variation and may be difficult to separate from *S. chaquimayensis*.

Distribution and Geographical Variation. *S. spinosus* occurs in most parts of Amazonia,

from Venezuela to Mato Grosso, Brazil, including the Guianas, and there is also one isolated southern record near the Paraná River (Fig. 361). The long list of synonyms is a good indication of how variable this species is. Soldiers from Suriname and French Guiana tend to be larger than elsewhere, with proportionally wider head and thorax, and prominent frontal tube, and some would correspond to Emerson's *S. solidus*. Specimens from Guyana and Venezuela are intermediate, and would closely fit the description of *S. snyderi*. Those from Colombia are also larger than average, with less numerous hairs on the head and a smaller frontal tube located in a small depression, and would correspond to *S. chaquimayensis parvinasus*. Specimens from central Amazonia are a little smaller, with slightly elongate head and short frontal tube, and correspond to *S. robustus*. However, the study of large series indicates that the variation is continuous, and all these forms belong to the same species. Some soldiers from Mato Grosso also have less numerous hairs on the head.

Biology. *S. spinosus* is a forest species which seems to be very common in the Amazon region. Its nest was described by Emerson (1938) and is similar to that of *S. dirus* (see section about nests above).

Remarks. The smaller soldiers were present in a few samples mixed with normal soldiers, and in some cases without the normal soldiers. They are here interpreted as first form soldiers, which appear in young colonies. Although there is no direct evidence that they are from young colonies, the facts that they were collected with normal soldiers of *S. spinosus*, have pilosity and thoracic nota similar to normal soldiers and fit the expected size and morphology of a first form soldier (based on the first form soldier of *S. praecellens*) support this interpretation. Also, there is no evidence of parasitism or disease, which could also cause the appearance of abnormal soldiers. There is, however, a remote possibility that they belong to a different species.

Syntermes tanygnathus, new species

Holotype soldier: BRAZIL. *Amazonas*. Aldeia São João, Rio Tiquié, coll. R.B. Barthem, 01.i.91 [MPEG-3805]. Paratypes. Seven soldiers, same data as holotype [MPEG-3805]. COLOMBIA. Ohea (?), coll. S.H. Jones, soldiers, one worker, alates [BMNH]. *Amazonas*. Chorrera, coll. J. Gashe, four pinned soldiers [MNH]. *Vaupés*. Yapú, Rio Papuri, coll. D. Dufour, 23.v.77, soldiers, one worker, in two vials [USNM].

Imago (Figs. 326-328). Eyes small, less than 1/4 width of head; ocelli small; fontanelle rounded and moderately large. Antenna with 21 articles. Anterior corners of pronotum angular, with sharp points; lateral margins of pronotum slightly sigmoid. Wings long (Fig. 40); distal part of media and cubitus conspicuous. Head capsule with a few scattered hairs; postclypeus with 6-8 hairs; pronotum with many hairs on outer margin; tergites with many hairs near posterior margin and scattered very short hairs on posterior half. Head and pronotum light chestnut; tergites chestnut-brown; sternites light chestnut; wings brown.

Measurements (in mm) of 2 imagoes from one colony: length of head 2.75-2.95; width of head without eyes 3.30-3.40; length of fontanelle 0.34-0.50; length of pronotum 2.20-2.30; width of pronotum 3.80-4.15; length of hind tibia 6.70-6.90; maximum diameter of eye 0.71-0.72; length of ocellus 0.25-0.30; length of forewing 30.00-32.00; width of forewing 7.60-7.70. Ratios: diameter of eye to width of head 0.21-0.22; length of ocellus to width of head 0.08-0.09; length of fontanelle to width of head 0.10-0.15; width of pronotum to width of head 1.15-1.22; length of wing to width of head 9.09-9.41; length of hind tibia to width of head 2.03-2.03.

Soldier (Figs. 320-325). Head capsule short, length and width of head about equal, sides converging towards front; posterior margin of head conspicuously three-lobed; frontal tube prominent, pore not visible in dorsal view. Labrum short and distinctly three-lobed; lateral corners of labrum forming an acute angle; median lobe of labrum not elongate. Antenna with 20-21 articles. Postmentum relatively short and wide; slightly constricted in the middle. Mandibles slender and elongate; tip of mandibles slightly hooked; first marginal tooth of left mandible near the base and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial and close to the base; apical cutting edge of left mandible straight except for curved tip and notch anterior to M1; apical cutting edge of right mandible slightly sigmoid. Anterior margin of pronotum slightly emarginate; posterior margin nearly straight; lateral projections of pronotum strongly upturned; thoracic spines well-developed and strongly upturned; pronotum with distinct conical spines. Head capsule with a few scattered, short bristles; postclypeus with only 4 hairs; base of mandibles without hairs; postmentum with scattered short, straight bristles; pronotum with many bristles on anterior lobe and posterior margin, plus scattered ones near posterior margin and on spines; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with a few bristles near hind margin.

Measurements (in mm) of 4 soldiers from 4 colonies: length of head 5.90-6.30; maximum width of head 5.70-6.30; height of head excluding postmentum 3.30-3.40; length of frontal tube 0.15-0.22; length of left mandible 3.80-4.10; curvature of left mandible 0.80-1.00; distance from M1

to M2 on left mandible 0.34-0.45; width of left mandible 0.82-0.87; length of left M1 0.15-0.18; minimum width of postmentum 1.02-1.14; width of pronotum 4.30-4.60; width of metanotum 4.50-4.60; length of hind tibia 7.00-7.20. Ratio length of head to maximum width of head 1.00-1.05; length of left mandible to length of head 0.63-0.67; length of hind tibia to length of head 1.14-1.20; width of pronotum to maximum width of head 0.73-0.77; distance M1-M2 to length of left mandible 0.09-0.11; height of head to maximum width of head 0.54-0.58; width to length of left mandible 0.21-0.22.

Large worker (Figs. 329-331). Head capsule large, with scattered straight hairs. Fontanelle rounded and small. Antenna with 20-21 articles. Mandibles similar to those of *S. dirus*, with relatively narrow molar plate and a basal notch of a little more than 90°. Gut (examined in a soldier) similar to *S. dirus*, but mixed segment with relatively larger midgut prolongations; minor prolongation more elongate; mixed segment with a conspicuous protuberance on the opposite side of the insertion of Malpighian tubules (Fig. 83).

Measurements (in mm) of 1 large worker: length of head 3.10; maximum width of head 3.75; length of fontanelle 0.34; width of pronotum 2.80; width of metanotum 2.80; length of hind tibia 5.60.

Comparisons. The alate is very similar to that of *S. spinosus*, which has the antenna with only 20 articles. The soldier is very distinct and can be easily identified by its short head with conspicuously three-lobed posterior margin, very elongate mandibles with reduced marginal teeth, well-developed thoracic spines, and relatively long legs.

Distribution. Apparently limited to a small region of western Amazonia, near the border between Brazil and Colombia (Fig. 360). The few samples available do not show much variation.

Biology. The limited information available indicates that this is a forest species. One label indicates an "earth pile", and the nest may be similar to that of *S. dirus*.

Remarks. Soldiers of *S. tanygnathus* are consumed by indigenous peoples of the region where this species occurs.

Syntermes territus Emerson

Syntermes territus Emerson 1925: 359, fig. 45 [imago, soldier]; Emerson 1945: 464 [redescription].

Holotype soldier: GUYANA. Kartabo, coll. A.E. Emerson, 1919 [AMNH]. Paratypes: one soldier, 5 alates, one worker, same data as holotype [AMNH].

Material examined. BRAZIL. *Amazonas*. Cururuzinho, R. Autaz, coll. A. Roman, 22.x.14, one soldier, workers [AMNH]. *Ceará*. Guaramiranga, coll. C.R. Gonçalves, 26.xii.48, soldiers, one worker [AMNH]; coll. C.R. Gonçalves, 18.i.45, soldiers [MZSP-2927]; coll. C.R. Gonçalves, 25.xii.48, soldiers, workers [MZSP-3148]. *Pará*. Serra dos Carajás, coll. R. Moraes, 11.vi.85, one soldier [MPEG-3461]. GUYANA. Bartica District, coll. A.E. Emerson, soldiers, workers [AMNH]. Kamakusa, coll. H. Lang, xi.22, soldiers, workers [BMNH]; coll. H. Lang, xii.1922, soldiers, one worker [AMNH]. Kartabo, coll. A.E. Emerson, 5.iv.24, one soldier, workers, queen, king [AMNH].

Imago (Figs. 337-339). Eyes small, less than 1/4 width of head; ocelli small; fontanelle rounded and relatively small. Antenna with 19 or 20 articles. Anterior corners of pronotum moderately angular. Wings short (Fig. 41), distal part of media and cubitus conspicuous. Head capsule with a few scattered short bristles; postclypeus with two hairs on anterior margin and two near middle; pronotum with many hairs on outer margin and an occasional one on surface; tergites with a line of hairs on posterior margin. Head, pronotum and tergites chestnut-brown; sternites brownish yellow; wings brown.

Measurements (in mm) of 3 imagoes from 2 colonies: length of head 2.15-2.50; width of head without eyes 2.60-2.85; length of fontanelle 0.25-0.30; length of pronotum 1.75-1.90; width of pronotum 3.03-3.25; length of hind tibia 5.00-5.40; maximum diameter of eye 0.59-0.67; length of ocellus 0.25-0.30; length of forewing 25.00; width of forewing 6.50. Ratios: diameter of eye to width of head 0.21-0.24; length of ocellus to width of head 0.10-0.11; length of fontanelle to width of head 0.09-0.12; width of pronotum to width of head 1.07-1.17; length of wing to width of head 8.77; length of hind tibia to width of head 1.75-1.96.

Soldier (Figs. 332-336). Head capsule elongate with nearly parallel sides; posterior margin of head rounded; frontal tube prominent, pore not visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 articles. Postmentum not constricted, sides of posterior part nearly parallel. Mandibles short and robust, with inflated bases; tip slightly hooked; first marginal tooth of left

mandible near the middle and small, not extending much beyond apical cutting edge; first marginal tooth of right mandible vestigial; apical cutting edge of both mandibles evenly rounded except for notch anterior to left M1. Anterior margin of pronotum slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines weakly developed and slightly upturned; lateral corners of pronotum sharp but not forming conical spines. Head capsule with scattered short, straight bristles, more numerous laterally; base of mandibles with many short hairs; postmentum with numerous short, straight bristles; pronotum with many bristles on anterior lobe and margins; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with many bristles near hind margin.

Measurements (in mm) of 5 soldiers from 5 colonies: length of head 5.60-6.20; maximum width of head 4.50-5.20; height of head excluding postmentum 3.00-3.30; length of frontal tube 0.24-0.30; length of left mandible 2.40-2.55; curvature of left mandible 0.80-0.90; distance from M1 to M2 on left mandible 0.47-0.59; width of left mandible 0.76-0.82; length of left M1 0.12-0.15; minimum width of postmentum 0.77-0.94; width of pronotum 3.30-3.80; width of metanotum 3.10-3.70; length of hind tibia 4.00-4.40. Ratio length of head to maximum width of head 1.19-1.28; length of left mandible to length of head 0.41-0.43; length of hind tibia to length of head 0.68-0.77; width of pronotum to maximum width of head 0.67-0.78; distance M1-M2 to length of left mandible 0.18-0.24; height of head to maximum width of head 0.63-0.67; width to length of left mandible 0.30-0.34.

Large worker (Figs. 340-342). Head capsule with a few scattered short bristles; postclypeus with four bristles. Fontanelle rounded and small. Antenna with 19 to 20 articles. Thoracic spines moderately developed. Mandibles very similar to those of *S. longiceps*. Gut also similar to that of *S. longiceps*.

Measurements (in mm) of 4 large workers from 4 colonies: length of head 2.40-2.60; maximum width of head 2.85-3.10; length of fontanelle 0.22-0.27; width of pronotum 2.05-2.15; width of metanotum 2.15-2.55; length of hind tibia 3.65-3.90.

Comparisons. The alate of *S. territus* is most similar to those of *S. parallelus* and *S. longiceps*, which are smaller, with anterior corners of pronotum more distinctly angular, and only two bristles on postclypeus. The soldier can be distinguished by its elongate head with nearly parallel sides, robust mandibles with weak dentition, and weakly developed thoracic spines. Some soldiers of *S. longiceps* from central Amazonia are similar, but are smaller and with more conspicuous marginal teeth on both mandibles.

Distribution and Geographical Variation. Sparse records from Guyana to northeastern Brazil and central Amazonia (Fig. 364). Soldiers from Ceará are almost identical to those from Guyana, and apparently there is little variation. There is some size variation, but without any geographic pattern.

Biology. According to Emerson (1945), *S. territus* inhabits forests and its nest is completely subterranean.

Syntermes wheeleri Emerson

Syntermes wheeleri Emerson 1945: 455, fig. 10 [soldier]. Holotype soldier: BRAZIL. "Rio, Bras.", pinned [MCZ]. Part of the type series of *S. dirus*. See comments about type locality below. *Syntermes dirus*, Negret & Redford 1982, misidentification [biology, nest]; Baker et al. 1981 [chemical composition of frontal gland secretions]; Brandão 1991 [ecology].

Material examined. BRAZIL. *Bahia*. Vitória da Conquista, coll. R.L. Araujo, 30.vi.70, soldiers, workers [MZSP-4799]. *Distrito Federal*. Brasília, 20.ii.78, soldiers [UnB]; coll. A.E. Mill, 12.iv.80, soldiers, workers [MPEG-1333]; coll. A.E. Mill, 6.iii.80, soldiers, workers [two vials, BMNH]; coll. H.R. Coles, 04.ii.77, soldiers [MZSP-9301 and UnB]; coll. H.R. Coles, 08.ii.77, soldiers, workers [3 vials, UnB]; coll. H.R. Coles, 12.xii.76, soldiers [MZSP-9291]; coll. H.R. Coles, 20.x.76, soldiers [MZSP-9290]; coll. H.R. Coles, 24.iii.77, soldiers, workers [two vials, UnB]; coll. H.R. Coles, 27.i.77, soldiers [MZSP-9296 and MZSP-9299]; coll. H.R. Coles, 28.v.77, soldiers, workers [UnB]; coll. H.R. Coles, 29.iv.77, soldiers, workers [UnB]; coll. H.R. Coles, vi.77, soldiers, workers [4 vials, BMNH]; coll. H.R. Coles, xi.76, soldiers [MZSP-9292 and UnB]; coll. K. Kitayama, xii.74, soldiers, workers [MZSP-7331]; coll. M.G. Siqueira, 03.ix.82, soldiers, workers [two vials, UnB]; coll. M.G. Siqueira, 03.vi.82, soldiers, workers [five vials, UnB]; coll. R. Constantino, 02.iii.86, soldiers, workers [MPEG-2615]; coll. R. Constantino, 17.x.86, alates [MPEG-2702]; coll. R. Constantino, 24.x.86, alates [MPEG-2699]; Brasília: Fazenda Água Limpa, coll. H.R. Coles, 15.vii.77, soldiers, workers [MPEG-1269 and MPEG-1287]; coll. D. Brandão, 1981, alates [UFG-154]. *Goiás*. Anápolis, coll. H.F. Cunha, 12.vii.92, one soldier, workers [UFG-441]. Goiânia, coll. D. Brandão, 9.iii.83, soldiers, workers [UFG-4]; coll. R.F. Souza, 17.v.91, soldiers, workers [UFG-430]; coll. R.F. Souza, 06.vii.91, soldiers, workers [UFG-440]. Padre Bernardo, coll. H.R. Coles, vii.1977, four first form soldiers, workers [MZSP]. Parque Nacional das

Emas, coll. K. Redford, 3.vi.80, soldiers, workers, [two vials, BMNH]. *Mato Grosso do Sul*. Três Lagoas, coll. F. Lane, vi.67, soldiers, workers [MZSP-1811]; coll. F. Lane, vi.66, soldiers, workers [MZSP-1833]. *Minas Gerais*. Barbacena, coll. F. Silvestri, 22.viii.45, soldiers, workers [LEFS]. Belo Horizonte, coll. Schreiber, vii.68, soldiers, one worker [MZSP-1808]; coll. R.L. Araujo, 28.vii.53, soldiers, workers [MZSP-4020]; coll. R.L. Araujo, 01.xi.56, soldiers, alates [MZSP-4479]; coll. D. Lavallo, 1969, one soldier, workers [MZSP-4741]; coll. F. Avila-Pires, ii.71, alates [MZSP-8567]. Bocaiuva, coll. R.L. Araujo, 25.vii.75, soldiers, workers [MZSP-5918]. Bom Sucesso, coll. R.L. Araujo, 12.xi.72, soldiers, workers [MZSP-5795]. Campanha, coll. R.L. Araujo, 28.vii.54, soldiers, workers [MZSP-4227]. Curvelo, soldiers, workers [MZSP-4439]; coll. R.L. Araujo, 14.xi.72, alates [MZSP-5595]. Diamantina, coll. R.L. Araujo, 23.viii.71, soldiers, workers [MZSP-4950 and MZSP-4955]. Guanhães, coll. R.L. Araujo, 02.iii.72, soldiers, workers [MZSP-5003 and MZSP-5004]. Lagoa Santa, coll. R.L. Araujo, 07.i.54, soldiers, workers [MZSP-4073]; coll. R.L. Araujo, 03.i.57, soldiers, workers [MZSP-4543]; coll. Reinhardt, 20.iii.89, one soldier, workers [ZMUC]. Lavras, coll. R.L. Araujo, xi.72, soldiers, workers [MZSP-5594]. Paracatu, coll. K. Kitayama, 19.ii.72, soldiers, workers [MZSP-7335]. Serra do Cipó, coll. R.L. Araujo, 04.iii.72, soldiers, workers, one alate [MZSP-5032]. Uberaba, coll. Goodland, v.65, soldiers, workers [MZSP-1171]. *São Paulo*. Artur Alvim, coll. V. Autuori, 20.vi.53, soldiers, workers [MZSP-3841]. Barueri, coll. K. Lenko, 19.vii.67, soldiers, workers [MZSP-1867]. Conceição de Itanhaém, coll. Silvestri, soldiers [MZSP-1841]. Congonhas, coll. R.L. Araujo, 26.vi.57, soldiers, workers [MZSP-3370]. Itupeva, coll. F. Mariconi, 10.xi.74, soldiers, workers, alates [MZSP-6876]. Palestina, coll. E. Amante, 27.ix.74, soldiers [MZSP-5889]. São Miguel Paulista, coll. R.L. Araujo, 31.x.50, soldiers, one worker, alates [MZSP-3261]. São Paulo, coll. H. Luederwaldt, 16.x.07, one soldier, workers, one alate [MZSP-1150]; coll. Silvestri, soldiers, workers, alates [MZSP-1834]; coll. R.L. Araujo, 31.x.50, soldiers, workers [MZSP-3259].

Imago (Figs. 353-355). Eyes moderately large, more than 1/4 width of head; ocelli small; fontanelle slightly elongate, sometimes nearly triangular. Antenna with 20 articles. Anterior corners of pronotum moderately angular. Wings long (Fig. 42); distal part of media and cubitus inconspicuous. Head capsule and postclypeus with many bristles; pronotum with many hairs on outer margin and surface; tergites with many hairs from middle to posterior margin. Head chestnut-brown; pronotum light chestnut; tergites chestnut-brown; sternites light chestnut; wings hyaline, except for brownish proximal and costal areas.

Measurements (in mm) of 6 imagoes from 3 colonies: length of head 2.85-3.10; width of head without eyes 3.30-3.65; length of fontanelle 0.32-0.55; length of pronotum 2.15-2.30; width of

pronotum 3.90-4.20; length of hind tibia 5.90-7.10; maximum diameter of eye 0.91-1.04; length of ocellus 0.29-0.39; length of forewing 32.00-33.00; width of forewing 7.40-7.80. Ratios: diameter of eye to width of head 0.27-0.30; length of ocellus to width of head 0.09-0.11; length of fontanelle to width of head 0.09-0.16; width of pronotum to width of head 1.12-1.23; length of wing to width of head 9.14-9.57; length of hind tibia to width of head 1.67-2.06.

Soldier (Figs. 343-347). Head capsule short, length and width of head about equal; sides converging slightly anteriorly or nearly parallel; posterior margin rounded; frontal tube very short, pore clearly visible in dorsal view; labrum short, length about equal to width; lateral corners of labrum about equal to a right angle; median lobe of labrum short. Antenna with 19 to 20 articles. Postmentum constricted near the middle, or not constricted with sides of posterior part nearly parallel. Mandibles curved and moderately elongate; tip slightly hooked; first marginal tooth of left mandible moderately large, usually extending a little beyond apical cutting edge; first marginal tooth of right mandible conspicuous; angle between right M1 and apical cutting edge about 90°; apical cutting edge of left mandible conspicuously sigmoid, forming a notch anterior to M1; apical cutting edge of right mandible evenly curved. Anterior margin of pronotum nearly rounded or slightly emarginate; posterior margin of pronotum nearly straight; thoracic spines weakly developed and upturned; lateral corners of pronotum sharp but usually not forming conical spines, although sometimes forming short spines. Head capsule with many straight bristles, more numerous laterally; postclypeus densely covered with hairs; base of mandibles with a few hairs; postmentum with numerous straight bristles; pronotum with many bristles on entire surface, more numerous on anterior lobe; meso- and metanotum with numerous bristles on posterior margin and a few on spines and lateral margins; tergites with numerous bristles on posterior half.

Measurements (in mm) of 10 soldiers from 10 colonies: length of head 5.10-5.90; maximum width of head 5.10-5.80; height of head excluding postmentum 2.80-3.10; length of frontal tube 0.15-0.25; length of left mandible 2.80-3.00; curvature of left mandible 0.80-1.10; distance from M1 to M2 on left mandible 0.59-0.76; width of left mandible 0.76-0.92; length of left M1 0.18-0.31; minimum width of postmentum 0.81-0.96; width of pronotum 3.10-3.80; width of metanotum 3.30-4.00; length of hind tibia 4.70-5.30. Ratio length of head to maximum width of head 0.98-1.12; length of left mandible to length of head 0.49-0.56; length of hind tibia to length of head 0.82-0.93; width of pronotum to maximum width of head 0.60-0.70; distance M1-M2 to length of left mandible 0.21-0.25; height of head to maximum width of head 0.53-0.59; width to length of left mandible 0.27-0.31.

First form soldier (Figs. 348-352). Smaller than the normal soldier and with more elongate head and mandibles; smaller marginal teeth closer to the base on both mandibles.

Measurements (in mm) of 3 soldiers from 1 colony: length of head 4.45-4.80; maximum width of head 3.90-4.30; height of head excluding postmentum 2.30-2.55; length of frontal tube 0.17-0.22; length of left mandible 2.70-2.85; curvature of left mandible 0.80-0.95; distance from M1 to M2 on left mandible 0.44-0.47; width of left mandible 0.71-0.77; length of left M1 0.13-0.17; minimum width of postmentum 0.67-0.74; width of pronotum 2.45-2.80; width of metanotum 2.60-2.70; length of hind tibia 4.50-4.75. Ratio length of head to maximum width of head 1.12-1.17; length of left mandible to length of head 0.57-0.61; length of hind tibia to length of head 0.94-1.01; width of pronotum to maximum width of head 0.63-0.65; distance M1-M2 to length of left mandible 0.16-0.17; height of head to maximum width of head 0.59-0.62; width to length of left mandible 0.26-0.28.

Large worker (Figs. 356-358). Head capsule and postclypeus densely covered with short, straight bristles. Fontanelle slightly elongate and moderately large. Antenna with 19 to 20 articles. Thoracic spines weakly developed. Mandibles very similar to those of *S. grandis*, with broad molar plate. Gut (Figs. 58-64) very large, with strongly inflated 1st and 3rd segments of hindgut; mixed segment with major midgut prolongation very large and wide, and minor prolongation rounded, small, and slightly inflated.

Measurements (in mm) of 5 large workers from 5 colonies: length of head 3.05-3.20; maximum width of head 3.50-3.73; length of fontanelle 0.25-0.39; width of pronotum 2.20-2.55; width of metanotum 2.40-2.70; length of hind tibia 4.15-4.40.

Comparisons. The alate is similar to that of *S. peruanus*, but is larger. Alates of *S. grandis* and *S. magnoculus* are also superficially similar, but are usually larger and have proportionally larger eyes and ocelli, and a rounded fontanelle. The soldier of *S. wheeleri* is most similar to that of *S. obtusus*, which has the first marginal tooth of the right mandible vestigial and a smaller tooth on the left mandible. Soldiers of *S. grandis* are usually larger, with larger marginal teeth on both mandibles and a more strongly sigmoid apical cutting edge of the left mandible, but there is considerable variation and possibly some overlap. I was not able to find a good external character to separate the soldier of *S. grandis* from *S. wheeleri*, but they may be easy to identify based on nest differences.

Distribution and Geographical Variation. Central and southeastern Brazil, in the southern portion of the cerrado region (Fig. 366). Soldiers show considerable morphological variation, but

there is no clear geographic pattern.

Biology. *S. wheeleri* lives in the cerrado and some areas of grassland. Its nest (Fig. 33) is described in the section on nests above.

Remarks. Araujo (1977: 6), based on the study of non-type material, erroneously concluded that *S. wheeleri* was a synonym of *S. dirus*. These two species are quite distinct, except for a very superficial similarity of soldiers. Apparently Araujo arrived at his conclusion based on the fact that the type locality is the same for both species (Rio de Janeiro), and he was not able to find *S. wheeleri* there, after years of observation and collecting. However, I suspect that the label information of the type specimen may be incorrect. *S. wheeleri* is clearly a cerrado and grassland species, a kind of habitat not present in the vicinity of Rio de Janeiro. The first form soldier was described from material not collected with normal soldiers and there is no direct information on the age of the colony. Therefore, it is possible that it actually belongs to a different species. However, it seems to fit the morphological pattern of first form soldiers, the material was collected in a region where *S. wheeleri* is abundant, and the workers are identical to those of *S. wheeleri*, including gut morphology.

PHYLOGENETIC RELATIONS OF THE SPECIES OF *SYNTERMES*

Emerson (1945: 441) briefly discusses the phylogenetic relationships of the genus *Syntermes*, claiming that it is the most primitive member of the Nasutitermitinae, a position maintained in all traditional phylogenies. Both Holmgren (1912: 47) and Emerson (1945) advocate a relationship between *Syntermes* and the macrotermite genus *Acanthotermes*, based primarily on the common presence of thoracic spines in the soldier caste. The latter hypothesis seems to have supported the idea of a sister group relationship between the Nasutitermitinae and the Macrotermitinae. However, these hypotheses are not supported by a formal cladistic analysis, the Macrotermitinae seem to form a separate clade in relation to all other members of the family Termitidae, and *Syntermes* is probably not the most basal lineage of the Nasutitermitinae, possibly forming a clade with the genera *Cornitermes*, *Procornitermes*, *Labiotermes* and *Paracornitermes* (see Chapter I). Among the characters mentioned by Emerson (1945) as evidence for the primitiveness of *Syntermes* and its putative relationship with *Acanthotermes*, some can be dismissed because they were based on grades (for Emerson, some characters were always primitive, e.g. large size). The evidence against the hypothesis of homologous thoracic spines in *Syntermes* and *Acanthotermes* is: 1) not all species of *Syntermes* bear

spines; 2) the spines are in different positions in the two genera, specially on the pronotum; 3) *Pseudacanthotermes*, which is clearly closely related to *Acanthotermes*, lacks the lateral spines; 4) other characters, specially the digestive tube, indicate a distant relationship between these two genera. The short R_1 joining the costal border, mentioned by Emerson as a primitive character in *Syntermes*, is also present in many related genera, although it may be difficult to detect in small species. The presence of a third apical spur on the foretibia is the only character that could possibly indicate that *Syntermes* is the basal lineage of the Nasutitermitinae, if the loss of this spur is a synapomorphy for the rest of the subfamily. The problem with this hypothesis is that some species of *Procornitermes*, a closely related genus, have three spurs on the foretibia; this character is also somewhat variable in other groups of termites.

No hypothesis about the phylogenetic relationships among the species of *Syntermes* has ever been proposed, except for some vague comments included in taxonomic descriptions. The number of valid species recognized in this work is 23, six of them known from soldiers and workers only. Within the limitations of the material available for study, the morphology of all the species of *Syntermes* was exhaustively studied. Unfortunately, there is much missing information for many species, which resulted in many question marks in the data matrix and certainly reduced resolution.

I included as many characters as possible, excluding only obvious autapomorphies and characters that seemed too variable to be phylogenetically informative. Some of the included characters show no variation in *Syntermes*, but they provide information about the relationship of *Syntermes* to the outgroup taxa, and of outgroup taxa to one another. Multi-state characters were coded as additive when the various states could clearly be ordered in an evolutionary sequence, and coded as non-additive when order was unclear.

The choice of the outgroup was based on my analysis of the subfamily Nasutitermitinae in Chapter I, which indicated that *Syntermes* is closely related to *Cornitermes*, *Labiotermes*, *Paracornitermes* and *Procornitermes*. *Paracornitermes* was not included because it is so close to *Labiotermes* that most characters would be identical, and increasing the number of taxa would make the analysis more time-consuming. Data on the outgroups were obtained from Emerson (1952), Emerson & Banks (1965), Kovoov (1969), Canello (1986), and Canello (1989).

The present analysis included 26 taxa and 45 characters, 21 from soldiers, 10 from imagoes, 12 from workers, and 2 behavioral / ecological (Table 4), and was performed with the computer programs Hennig86 1.5 (Farris 1988) and Pee-Wee 2.1 (Goloboff 1993; 1994). Hennig86 searches for most parsimonious trees, i.e., trees with minimum number of steps or evolutionary changes using equal or pre-defined weights for characters. It also performs successive weighting, an iterative procedure in which character weights are determined by the degree of homoplasy of each character

in most parsimonious tree(s) previously found. The process of setting weights and searching for shortest trees is repeated until a stable solution is found. Goloboff (1993) pointed out several problems with the successive approximations approach, and proposed the use of implied weights, a non-iterative procedure that estimates character reliability and sets weights during tree search. This procedure is implemented in Pee-Wee, a program that searches for trees with best character fit. In Hennig86 the function mh* was initially used to produce trees, which were submitted to branch-swapping bb*. Successive approximations were performed with the function xs w, followed by bb*; this process was repeated until the result became stable. In Pee-Wee, the option mult*15 was used, followed by max* and jump if necessary. Character analysis distributions shown in the cladograms (Figs. 367-372) were determined with the computer program Clados 1.2 (Nixon 1992). The following analyses were performed:

Analysis 3A included all taxa and used Hennig86. Four trees of length 124, consistency index (ci) 0.50, and retention index (ri) 0.76 were found.

Analysis 3B was made by applying successive weighting to the results of analysis 1A, and resulted in a single tree of length 444, ci= 0.69, and ri= 0.87.

Analysis 3C was made using Pee-Wee. It resulted in a single tree of fit= 335.5.

Analysis 4A was performed like 3A but included only the species with known alates, thus reducing the number of question marks in the data matrix. Species excluded are *S. barbatus*, *S. bolivianus*, *S. brevimalatus*, *S. calvus*, *S. crassilabrum*, *S. insidians*. It resulted in three trees of length 109, ci= 0.56, ri= 0.78.

Analysis 4B was like 3B but with the smaller matrix. It resulted in two trees of length 450, ci= 0.78, and ri= 0.91.

Analysis 4C used Pee-Wee and the smaller matrix. It resulted in a single tree of fit 355.2.

List of characters

Soldier

1. Left mandible with: (0) M1 close to M2 (Figs. 235, 274). (1) M1 distant from M2 (Figs. 89, 177, 294).

2. Cutting edge between M1 and M2 on left mandible: (0) Not serrated (all *Syntermes* species). (1) Serrated (*Cornitermes* and *Procornitermes*).

3. Left mandible: (0) With a notch anterior to M1 (Figs. 161, 235, 347). (1) Without a notch

anterior to M1 (Figs. 89, 101).

4. Molar plate and molar prominence: (0) Vestigial. (1) Absent. Soldier mandibles of all *Syntermes* and *Labiotermes* species have very reduced but conspicuous molar regions. In soldiers of *Cornitermes* and *Procornitermes* this structure is not visible.

5. Mandibles: (0) Moderately elongate (Figs. 89, 177). (1) Short and robust. (2) Slender and elongate (Figs. 235, 325). Coded as non-additive because evolutionary order is unclear.

6. Tip of mandibles: (0) Slightly or not hooked (Figs. 89, 112). (1) Strongly hooked (Figs. 235, 246).

7. Left M1: (0) Small, not extending beyond apical cutting edge (Figs. 112, 257). (1) Large (Figs. 89, 177).

8. Right M1: (0) Small (Figs. 112, 208). (1) Large (Figs. 89, 161, 177). (2) Vestigial (Figs. 235, 325). Coded as non-additive.

9. Angle between right M1 and longitudinal axis of mandible: (0) About 90 degrees (Figs. 134, 152). (1) Less than 90 degrees (Figs. 89, 177). (2) More than 90 degrees (257, 336). Coded as non-additive.

10. Base of mandibles: (0) Not inflated (Fig. 112). (1) Inflated (Fig. 101).

11. Head size: (0) Small (length of head x width of head less than 20mm²). (1) Medium (20 - 35mm²). (2) Large (more than 35mm²). Coded as additive. This character was included in this analysis because the large size of most *Syntermes* species seems to be a derived condition. Emerson (1945) argued that large size is primitive.

12. Head capsule: (0) Elongate (Fig. 204). (1) Short (Fig. 84).

13. Sides of head: (0) Nearly parallel (Figs. 242, 269). (1) Converging anteriorly (Figs. 84, 231).

14. Frontal tube: (0) Very short, pore visible from dorsal view (Figs. 231, 281). (1) Short, pore not visible from dorsal view (Figs. 84, 269). (2) Moderately elongate (*Cornitermes* and *Procornitermes*). Coded as additive.

15. Soldier antenna with: (0) 13-16 articles. (1) 19 articles. (2) 20-21 articles. Coded as additive. The number of antennal articles sometimes show intra-specific variability and is difficult to code. Nevertheless I believe it has some phylogenetic information since some species consistently have 19 articles, while other have 20-21. The few species with antenna variable in the range 19-20 were coded as variable (question mark in the matrix). Only one species has only 21 articles and none vary from 19 to 21. Most have either 19 or 20-21.

16. Sides of thoracic nota: (0) Rounded (*Cornitermes*, *Labiotermes*, and *Procornitermes*). (1) Moderately angular (Fig. 233). (2) Distinctly angular and sharp; sides of pronotum not ending in

conical spines (Figs. 175). (3) With distinct conical spines in all segments (Figs. 87). Coded as additive.

17. Lateral projections of meso- and metanotum: (0) Horizontal. (1) Slightly upturned. (2) Strongly upturned. Coded as additive.

18. Head capsule: (0) Without long, fine, curly hairs. (1) With long, fine, curly hairs (Figs. 84, 96).

19. Head capsule: (0) Without numerous short, straight hairs. (1) With numerous short, straight hairs (Figs. 135, 289).

20. Clypeal region with: (0) 4 hairs (Fig. 242). (1) Many hairs.

21. Hairs on posterior surface of pronotum: (0) Absent (Fig. 233). (1) Present (Fig. 99).

Imago

22. Eyes: (0) Large (Figs. 236, 263). (1) Small (Figs. 167, 275).

23. Ocelli: (0) Large (Fig. 225). (1) Small (Fig. 353).

24. Fontanelle: (0) Rounded or elliptic (Fig. 90). (1) Nearly triangular (Fig. 295).

25. Anterior corners of pronotum: (0) Rounded (Fig. 238). (1) Moderately angular (Fig. 355). (2) Angular with sharp points oriented laterally (Fig. 92). (3) Angular with sharp points oriented anteriorly (Fig. 216). Coded as nonadditive.

26. Wings: (0) Hyaline. (1) Brown.

27. Wings relatively: (0) Short. (1) Long. Wings with length less than 9 times width of head were considered short.

28. Head capsule with: (0) Fairly long hairs. (1) Very short hairs. These very short hairs are present in *S. aculeosus*, *S. cearensis* and *S. dirus*, and are barely visible under a magnification of 60x.

29. Head capsule with: (0) Few hairs (Fig. 90). (1) Many hairs (Fig. 141).

30. Postclypeus with: (0) 4 hairs (Fig. 337). (1) 2 hairs (Fig. 275). (2) Many hairs (Fig. 184). Coded as non-additive.

31. Surface of pronotum with: (0) No hairs or a few scattered hairs (Fig. 169). (1) Numerous hairs (Fig. 265).

Worker

32. Molar plate: (0) Moderately wide. (1) Very wide.

33. Cutting edge between M_{1+2} and M_3 on left mandible: (0) Perfectly straight (Fig. 44). (1) Slightly undulated (Fig. 52).
34. Cutting edge $M1 - M3$ on left mandible: (0) Parallel to the line $M3 - A$ (Fig. 48). (1) Forming an angle to the line $M3 - A$ (Fig. 50).
35. Apical tooth of left mandible: (0) Not reduced (Fig. 44). (1) Reduced (Fig. 52).
36. Proximal border of the apical ridge of molar plate: (0) Slightly concave. (1) Strongly concave. The first ridge (most distal, also called apical thickening) of the molar plate is distinctly more curved in some species of *Syntermes*.
37. Major prolongation of mixed segment: (0) Tongue-shaped (Fig. 71). (1) Nearly circular with constricted connection to midgut (Fig. 80). (2) Elongate with nearly rectangular tip (Fig. 77).
38. Tip of major prolongation of mixed segment: (0) Not inflated. (1) Inflated. In some species the major mesenteric prolongation of the mixed segment is distinctly swollen, while in most species it is flat.
39. Minor prolongation of mixed segment: (0) Elongate longitudinally (Fig. 70). (1) Shaped like a golf club, enlarged towards the Malpighian tubules (Fig. 72) (2) Elongate transversely, with constricted connection to midgut (Fig. 81). (3) Small, circular, and inflated (Fig. 63). Coded as non-additive.
40. Widening of the gut in the mixed segment: (0) Gradual (Figs. 69-70). (1) Abrupt (Figs. 77-79). In most species the mixed segment widens gradually towards the hindgut. In *S. longiceps*, *S. parallelus*, and *S. territus* the first part of the mixed segment is nearly cylindrical, about the same width as the midgut, and enlarges suddenly into a pouch.
41. Enteric valve located on: (0) Posterior left side (Figs. 60). (1) Posterior right side (Figs. 73-76). In *S. longiceps*, *S. parallelus*, and *S. territus* the gut has a distinct arrangement, with a larger first segment of the hindgut, pushing the location of the enteric valve to the other side of the abdomen.
42. Enteric valve: (0) With sclerotized armature. (1) Without sclerotized armature. The absence of spines on the enteric valve is characteristic of all *Syntermes*. The primitive condition seems to be the presence of six plates (or swellings) with numerous sclerotized spines.
43. Enteric valve: (0) Narrow. (1) Very wide. All *Syntermes* species have a very wide enteric valve; in other genera the gut is much more constricted near the valve.

Behavior and Ecology

44. Nest: (0) Completely subterranean (Fig. 34). (1) Mostly subterranean with a pile of loose soil above ground (Fig. 32). (2) Epigeal and compact (Fig. 33). (3) Mostly subterranean with a soft,

flat, epigeal portion. Coded as non-additive because order is unclear; nest of type (2) could have evolved from type (1), but it could also have originated from a type (0). This is still a crude classification of the nests of *Syntermes*, but it carries some information.

45. Habitat: (0) Savanna. (1) Forest. Habitat fidelity seems to be high in *Syntermes*, and no species is known to live in both kinds of habitats. Habitat association involves differences in diet (grass-litter or leaf-litter) and probably also adaptations to different microclimates and biological interactions (e.g. with predators).

Results and Discussion

Analysis 3A resulted in four different trees, but there are basically two distinct topologies (Figs. 367 and 368). The other two trees, which are not illustrated, differ only in the relative position of *S. wheeleri*, *S. bolivianus* and *S. peruanus* and are otherwise identical to the tree shown in Fig. 368. Although few trees were found in this analysis, they are quite different in the mid-level branching and therefore the strict consensus tree (Fig. 369) shows a large polytomy.

The application of successive weighting (analysis 3B) to the results of analysis 3A resulted in a single tree, very similar to the one in Fig. 367. The only difference was a reversal in the relative position of *S. tanygnathus* and *S. calvus*. The use of implied weights (analysis 3C) also generated a single tree, with groups of species similar to those found in analyses 3A and 3B, but with a major difference in the position of these groups (Fig. 370).

Analysis 4A included only the species with known alates, and resulted in three different trees. The strict consensus tree is shown in Fig. 371. The differences among the three trees are in the relative position of *S. grandis*, *S. magnoculus* and *S. obtusus*. The basic topology of these trees is stable to successive approximation (analysis 4B), which resulted in two trees, one of them identical to their strict consensus tree (Fig. 372). Analysis 4C, with implied weights, resulted in a single tree, identical to the strict consensus of analysis 4B (Fig. 372).

Although the results of different analyses show some variation, several groups are stable and seem to be well supported. The *molestus* group, with two species, is clearly monophyletic and consistently appears as the most basal branch of *Syntermes*. The main characters supporting this group are: (6-1) the strongly hooked soldier mandible; (8-2) marginal dentition reduced on both mandibles; (35-1) reduced apical tooth of the worker mandibles; and (38-1) the inflated major mesenteric prolongation of the mixed segment.

The *parallelus* group, including three species, is also very well supported, particularly by a

distinctive gut pattern (characters 37-1, 38-1, 40-1 and 41-1). Some imago characters are derived only under some tree topologies, but at least one is constant, the very short wings (27-0). *S. parallelus* consistently appears as the sister species of *S. longiceps*, a relationship supported by two imago characters: (25-3) the shape of the pronotum, and (30-1) the presence of only two hairs on the postclypeus.

The *grandis* group includes six savanna species. Although this group is stable in all analyses, most characters supporting it are not constant. Two characters of the worker mandibles are always present: (32-1) the broad molar plate and (34-0) the orientation of the cutting edge of left mandible. The relationships among the various species in this group are not clear. A sister group relationship between *S. wheeleri* and *S. peruanus* appears in several trees, and is supported by a similar nest type (44-2). *S. grandis* and *S. magnoculus* are other possible sister species. There are many unknown character states in this group, particularly for *S. peruanus* and *S. bolivianus*, which is one of the causes of the low resolution.

The *dirus* group contains six species, is well supported, and all species relationships are stable, except for the position of *S. tanygnathus*. It is not clear whether *S. calvus* belongs to this group or not, since the alate of that species is unknown. All species in this group have similar imagoes, with small eyes and ocelli, dark wings (26-1), and anterior corners of pronotum distinctly angular (25-2); also, they are all forest species (45-1), build similar nests (44-1), and the soldiers have large thoracic spines (16-3). The polarity of the imaginal characters varies with tree topology, but some are probably derived. The nest type and the large thoracic spines of soldiers appear as derived in all trees. The group of five species excluding *S. tanygnathus* is supported by two characters: (36-1) a strongly convex apical ridge of the molar plate of the worker mandible, and (39-1) a minor mesenteric prolongation of the mixed segment shaped like a golf club. The sister-group relationship between *S. spinosus* and *S. chaquimayensis* is consistently supported by a single character, the presence of dense, short, straight hairs on the soldier head (19-1). The group *dirus* + *aculeosus* + *cearensis* is supported by two characters: (18-1) long, fine, curly hairs on soldier head, and (28-1) very short hairs on imago head. The sister-group relationship between *dirus* and *cearensis* is supported by a similar marginal tooth on left soldier mandible (9-0).

The four species of the *brevimalatus* group are characterized by very robust and short soldier mandibles (5-1) with inflated bases (10-1), more or less hooked tips (6-1), and no notch anterior to M_1 (3-1). A sister-group relationship between *S. praecellens* and *S. barbatus* is supported by a distinctive configuration of the mixed segment (37-1 and 39-1). *S. brevimalatus* and *S. crassilabrum* are also stable as sister species, but this relationship should be treated with caution because there are many unknown character states for both species, and they share no clear synapomorphy.

The position of *S. insidians* is uncertain. It appears associated with the *brevimalatus* group in many trees, but there is no clear synapomorphy supporting the inclusion of *insidians* in any group. Hopefully, the imago of *insidians* will provide some informative characters, but it is not known yet.

One of the sources of conflict in the mid-level branching seems to be a set of imaginal characters common to the *parallelus* and *dirus* groups, which include small eyes and ocelli (22-1), dark wings (26-1), and few hairs on head capsule (29-0). Imaginal characters would favor a tree topology similar to that in Fig. 367. On the other hand, soldier characters would indicate a different position of the *S. territus* group, as in Fig. 368.

The fact that analysis 2, including only the species with known imagoes, resulted in a tree distinct from the ones obtained in analyses 3B and 3C can be interpreted in two different ways. The many unknown character states of the species with unknown imagoes could cause the programs to converge to incorrect trees. In this case the tree in Fig. 372 would be closer to reality. It should be noted that the trees from analysis 2 are compatible with one of the trees from analysis 3A (Fig. 368). Another possibility is that the removal of several species would reduce information by eliminating some intermediate states or combinations of characters. If this is true, then the intermediate branching should be considered unknown, as in Fig. 369. This phylogeny will certainly be improved with more data, as soon as the unknown imagoes are described and more information on nests and biology is accumulated.

An interesting question is how many times there was a change in habitat, from savanna to forest or vice-versa. However, the polarity of this character (designated as 45 on the cladograms) is unclear because all outgroup genera have both savanna and forest species. And the most basal lineage, the *molestus* group, has one savanna and one forest species. The results indicate three or four changes, depending on the tree topology, either considering savanna or forest as the primitive habitat. The trees in Figs. 367-372 show only the character distribution considering savanna as the ancestral habitat, i.e., 45-1 on a branch indicates a change from savanna to forest habitat.

The large size and the thoracic spines of soldiers of *Syntermes*, which were considered by Emerson (1945) as primitive characters, consistently appear as derived characters in some species of the genus, and cannot even be considered diagnostic for *Syntermes*.

TABLE 3. List of termitophiles associated with *Syntermes* species.

Termitophile	Hosts
THYSANURA: Lepismatidae	
<i>Grassiola praestans</i> Silvestri	<i>S. dirus</i> ; also <i>Cornitermes</i> , <i>Nasutitermes</i> , <i>Spinitermes</i> , <i>Anoplotermes</i> , <i>Embiratermes</i>
<i>Gastrotheus synterminus</i> Silvestri	<i>S. dirus</i>
COLEOPTERA: Staphylinidae	
Aleocharinae	
<i>Chaetonannus fragilicornis</i> Borgmeier	? <i>S. molestus</i>
<i>Termitonannus validus</i> Silvestri	<i>S. wheeleri</i>
<i>Termitopelta fulgens</i> Borgmeier	<i>S. molestus</i>
<i>Termitophagus synterminus</i> Silvestri	<i>S. wheeleri</i>
<i>Iheringocantharus ypiranganus</i> Bernhauer	<i>S. wheeleri</i>
<i>Atheta convivens</i> Silvestri *	<i>S. wheeleri</i>
<i>Atheta syntermitis</i> Silvestri *	<i>S. wheeleri</i>
<i>Atheta silvestrii</i> Seevers *	<i>Syntermes</i> sp.; also <i>Anoplotermes</i>
<i>Atheta termitobia</i> Wasmann *	<i>S. dirus</i>
Staphylininae	
<i>Belonuchus penetrans</i> Silvestri *	<i>S. obtusus</i>
Paederinae	
<i>Termitosaurus insinuatus</i> Silvestri *	<i>S. wheeleri</i>
Tachyporinae	
<i>Termitoplus grandis</i> Silvestri	<i>S. wheeleri</i> ; <i>S. obtusus</i>
COLEOPTERA: Ptiliidae	
<i>Urotriainus grandis</i> Silvestri	<i>S. wheeleri</i>
<i>Urotriainus grandis</i> var. <i>robustior</i> Silvestri	<i>S. dirus</i>
<i>Urotriainus molesti</i> Silvestri	<i>S. molestus</i>
<i>Pycnopteryx schmidti</i> Dybas	<i>S. molestus</i>
<i>Pycnopteryx</i> sp.	<i>S. spinosus</i>
COLEOPTERA: Histeridae	
<i>Cossyphodister schwarzaieri</i> Reichensperger	<i>Syntermes</i> sp.
<i>Scapolistes sternalis</i> Borgmeier	<i>S. molestus</i>
COLEOPTERA: Scarabaeidae	
<i>Acanthocerus termiticola</i> Wasmann	<i>S. dirus</i>
DIPTERA: Phoridae	
<i>Cryptophora coeca</i> Borgmeier	<i>S. molestus</i>
<i>Cryptophora colombicae</i> Seevers	<i>S. molestus</i>
<i>Syntermophora microphtalma</i> Seevers	<i>S. molestus</i>

* Considered as probably not true termitophiles by Seevers (1957).

TABLE 4. Matrix of character states for analyses 3 and 4.

	5	1	1	2	2	3	3	4	4
	5	0	5	0	5	0	5	0	5
<i>Labiotermes</i>	0000	2000	0000	?10000	??00??	000000	?111	10000	?0000??
<i>Cornitermes</i>	0101	2000	0000	?20000	???0000	??0?21	?0?000	000000	0000??
<i>Procornitermes</i>	0101	2000	000000	0200000	?0?1000	101???	11100?	?0?0100	??
<i>S. aculeosus</i>	1010	0011	1021	11?3	2101	1110	2101	02000	10100?001111
<i>S. barbatus</i>	1010	1111	2121	1011	2110	11????	??????	00100	102001100
<i>S. bolivianus</i>	1000	0000	2011	1001	2200	11????	??????	10000	?????11?0
<i>S. brevimalatus</i>	1010	1111	2120	0112	1001	0?????	??????	00100	?????11?1
<i>S. calvus</i>	1000	0001	2011	111?3	2001	0?????	??????	00100	0000011?1
<i>S. cearensis</i>	1000	0001	0011	1012	3210	?111	0211	102000	101001001111
<i>S. chaquimayensis</i>	1000	00?1	1021	111?3	2011	1111	0211	1012000	10100?001111
<i>S. crassilabrum</i>	1010	1?11	1012	1?11	2200	10????	??????	00100	0010011?1
<i>S. dirus</i>	1000	00?1	0021	1112	3210	1111	0211	102000	101001001111
<i>S. grandis</i>	1000	0011	1021	1102	2200	1100	0101	0121	10000000001130
<i>S. insidians</i>	1000	0011	1000	0122	1001	1?????	??????	00100	001001100
<i>S. longiceps</i>	?000	00?0	?0?0	0011	2100	1011	0310	001000	1002101111?1
<i>S. magnoculus</i>	1010	0011	1021	1102	2200	1100	0101	0121	100000000011?0
<i>S. molestus</i>	0000	2102	?000	1011	1000	0000	0000	10100	01110010001101
<i>S. nanus</i>	0000	2102	?000	0011	1000	0000	0000	10100	01110010001100
<i>S. obtusus</i>	?000	0000	0202	1??2	2200	1100	1101	0121	10000001001100
<i>S. parallelus</i>	0000	0000	0200	0112	1001	0110	3100	0100	1002101111?1
<i>S. peruanus</i>	1000	00?0	2011	110?3	2001	1011	1010	121???	00?????1120
<i>S. praecellens</i>	1010	1111	1011	0011	2101	1111	1101	0121	100100102001100
<i>S. spinosus</i>	1000	0011	1021	111?3	2011	1111	0211	1002000	101001001111
<i>S. tanygnathus</i>	0000	2002	2021	1112	3200	1111	0211	1000000	100000001111
<i>S. territus</i>	?000	0000	0211	1001	1210	0001	1011	0000000	100210111101
<i>S. wheeleri</i>	1000	00?1	0011	110?2	2001	1011	1010	1211	0000003001120

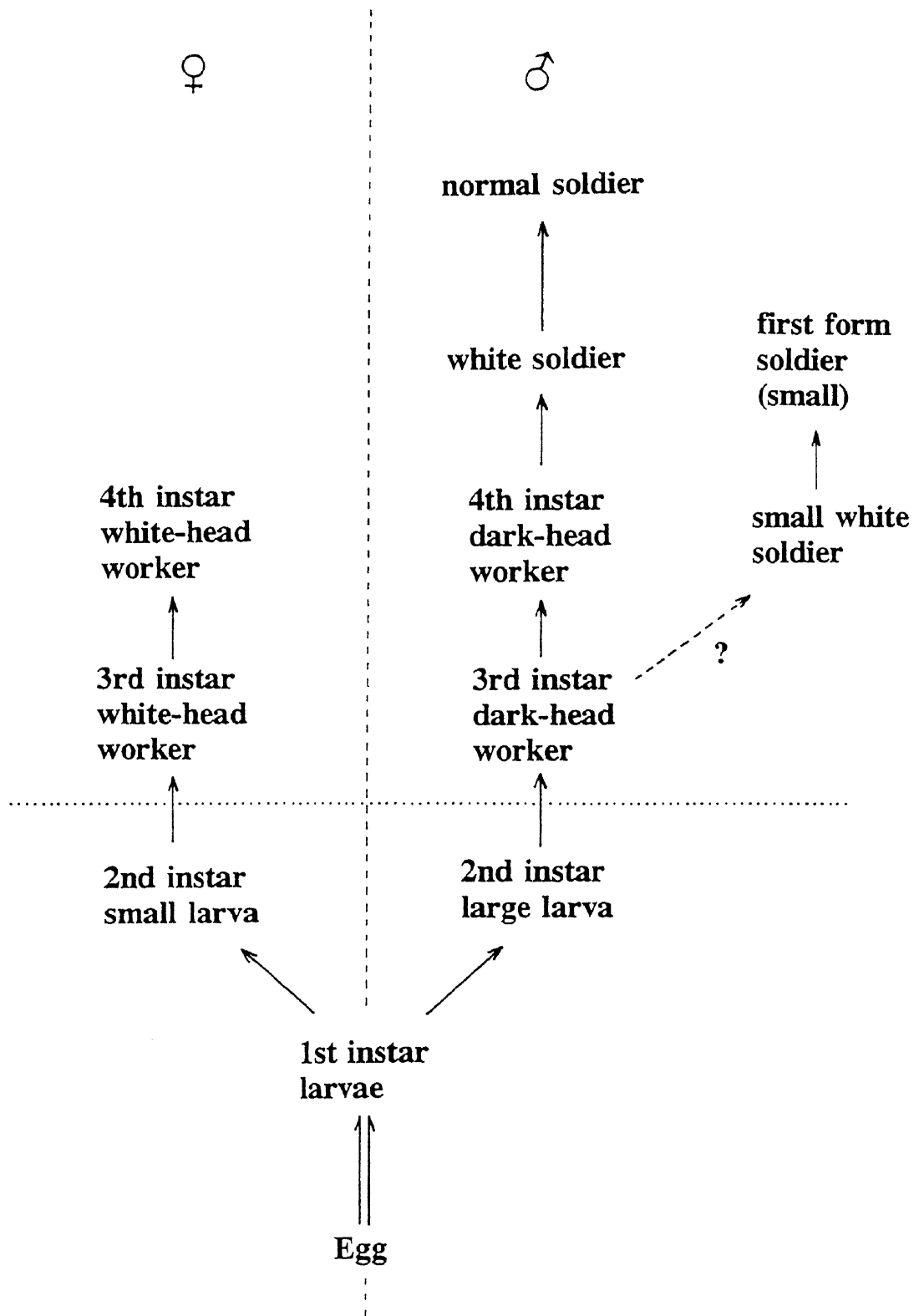


Fig. 31. Most likely developmental pathways of the sterile castes of *Syntermes*. Modified from Noirot (1969: 329 and personal communication), and Silvestri (1946).

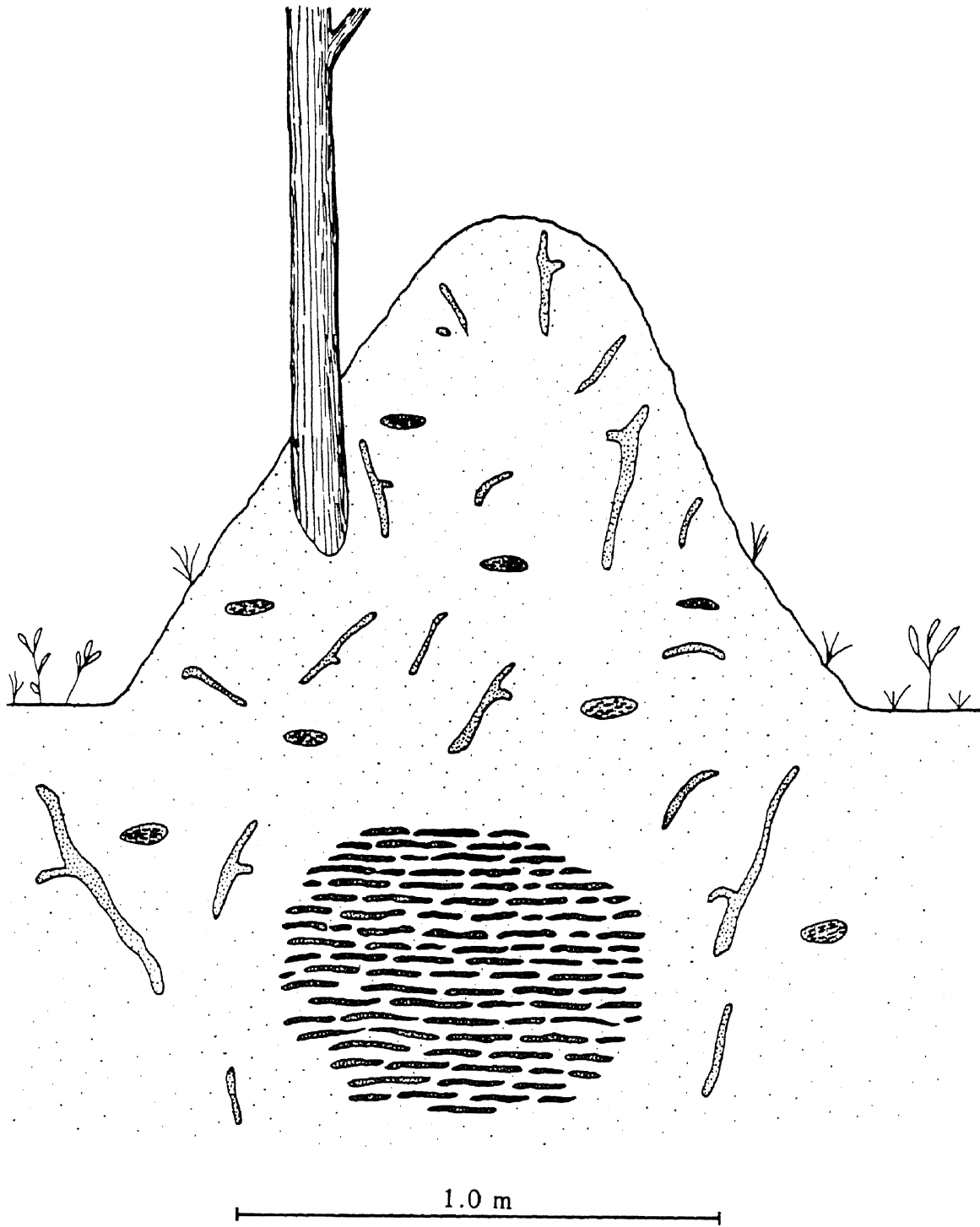


Fig. 32. Nest of *Syntermes dirus* from the Brazilian Atlantic forest. Above-ground portion is soft.

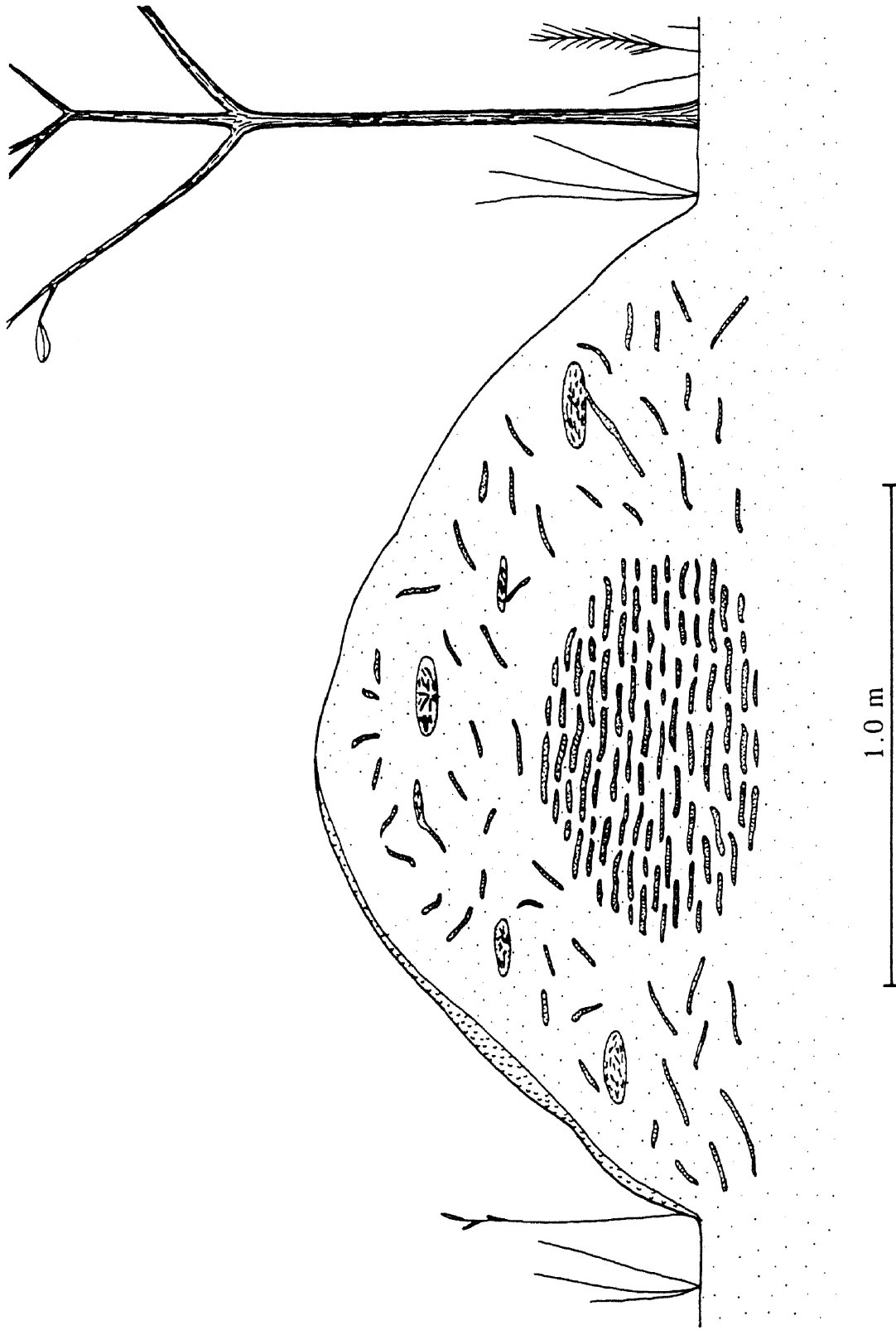


Fig. 33. Nest of *Syntermes wheeleri* from the cerrado vegetation of Central Brazil. Above-ground portion is hard.

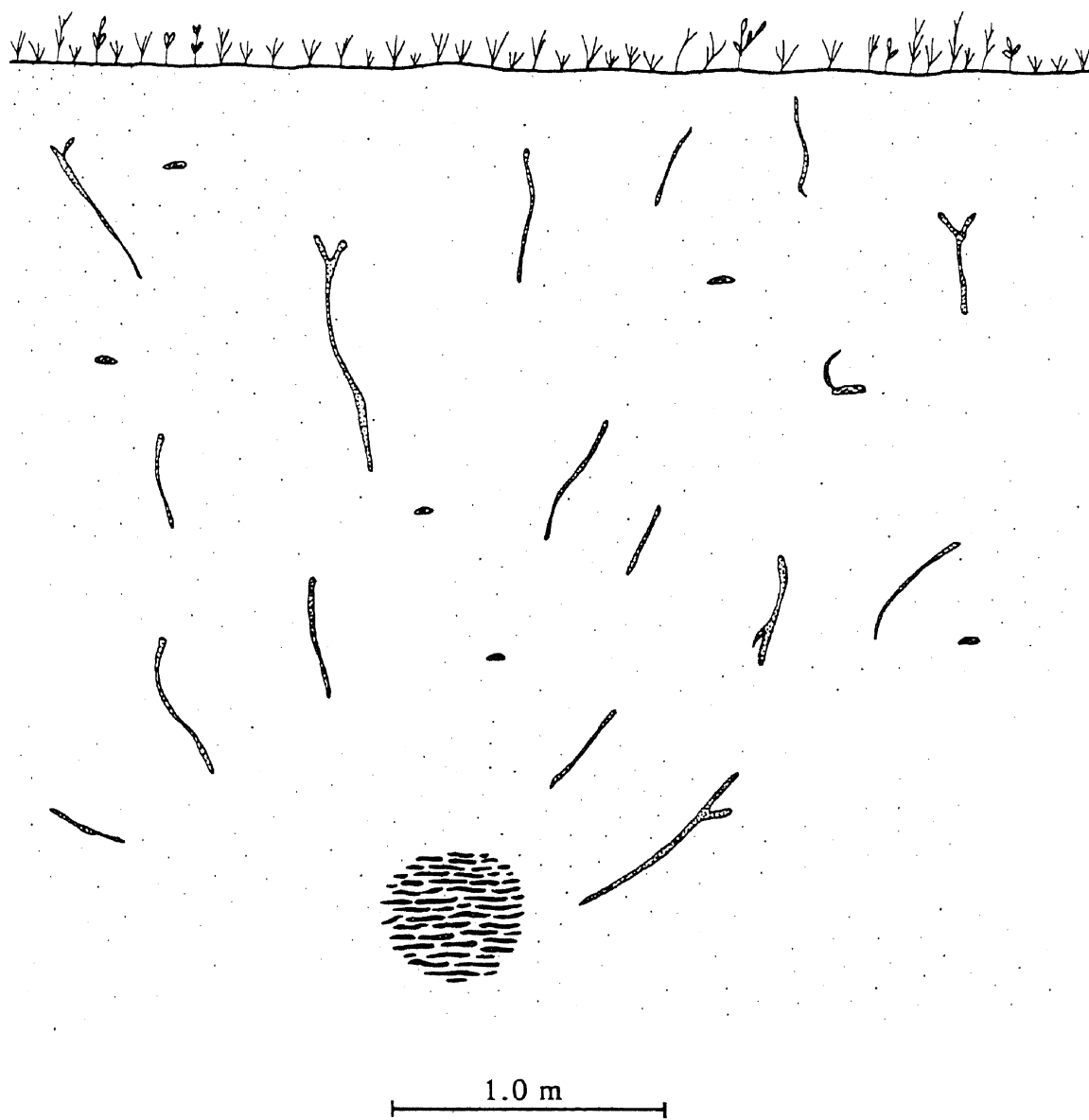
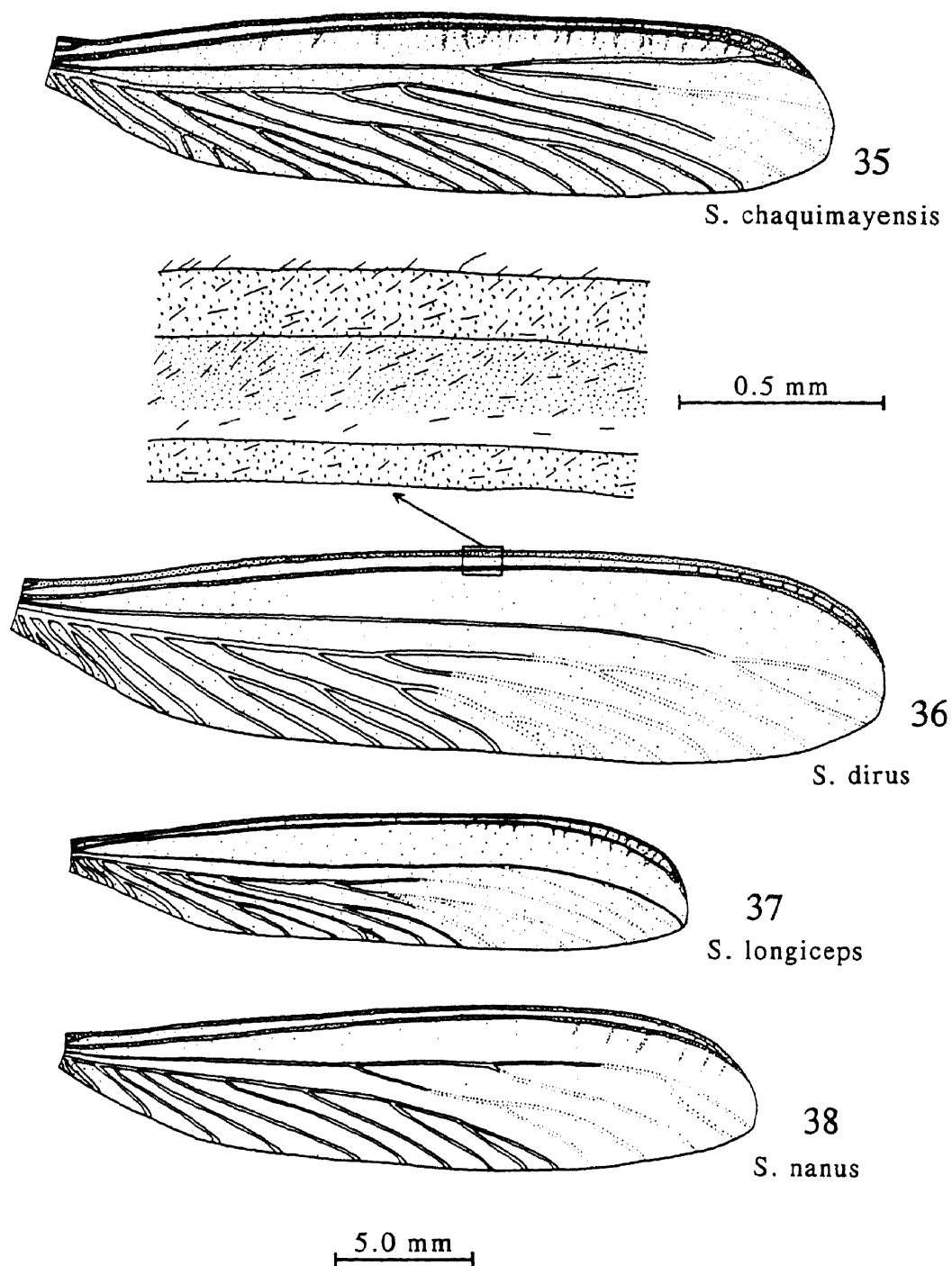
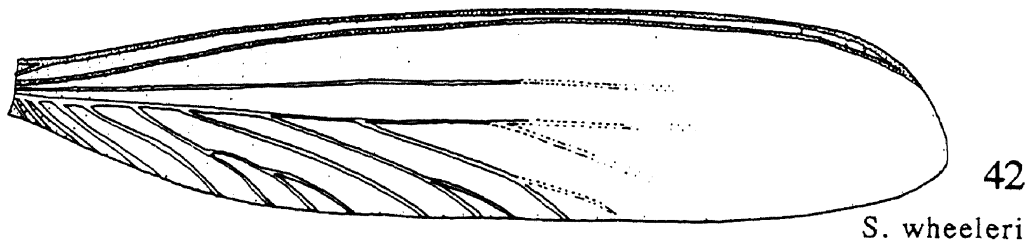
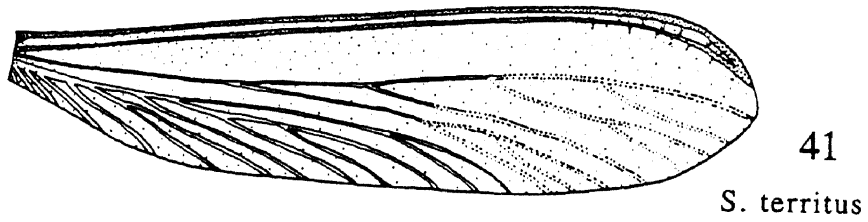
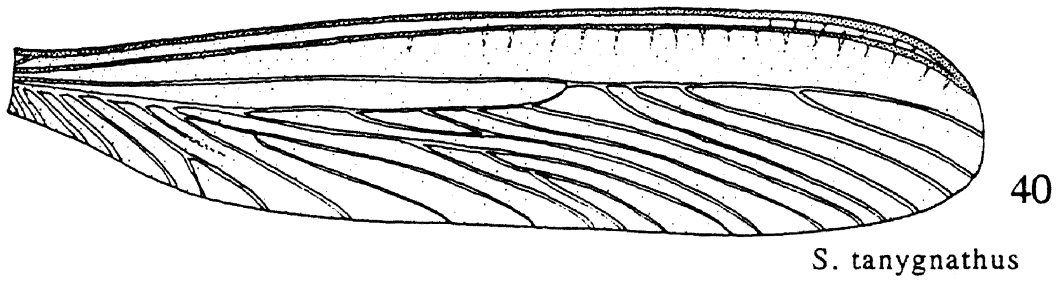
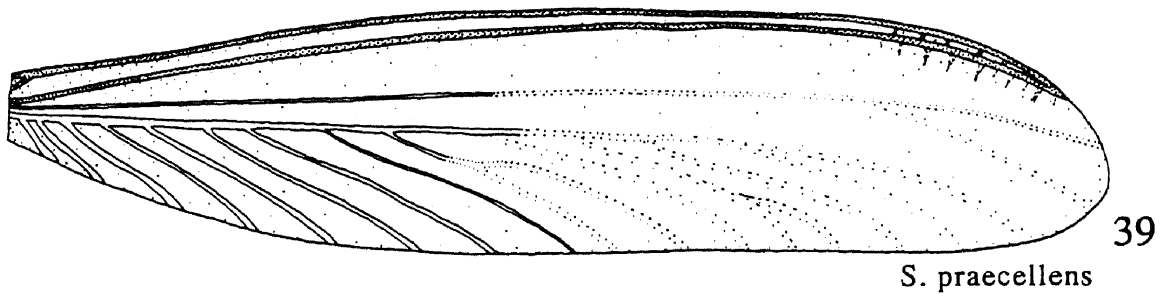


Fig. 34. Nest of *Syntermes praecellens*. After Silvestri (1946).

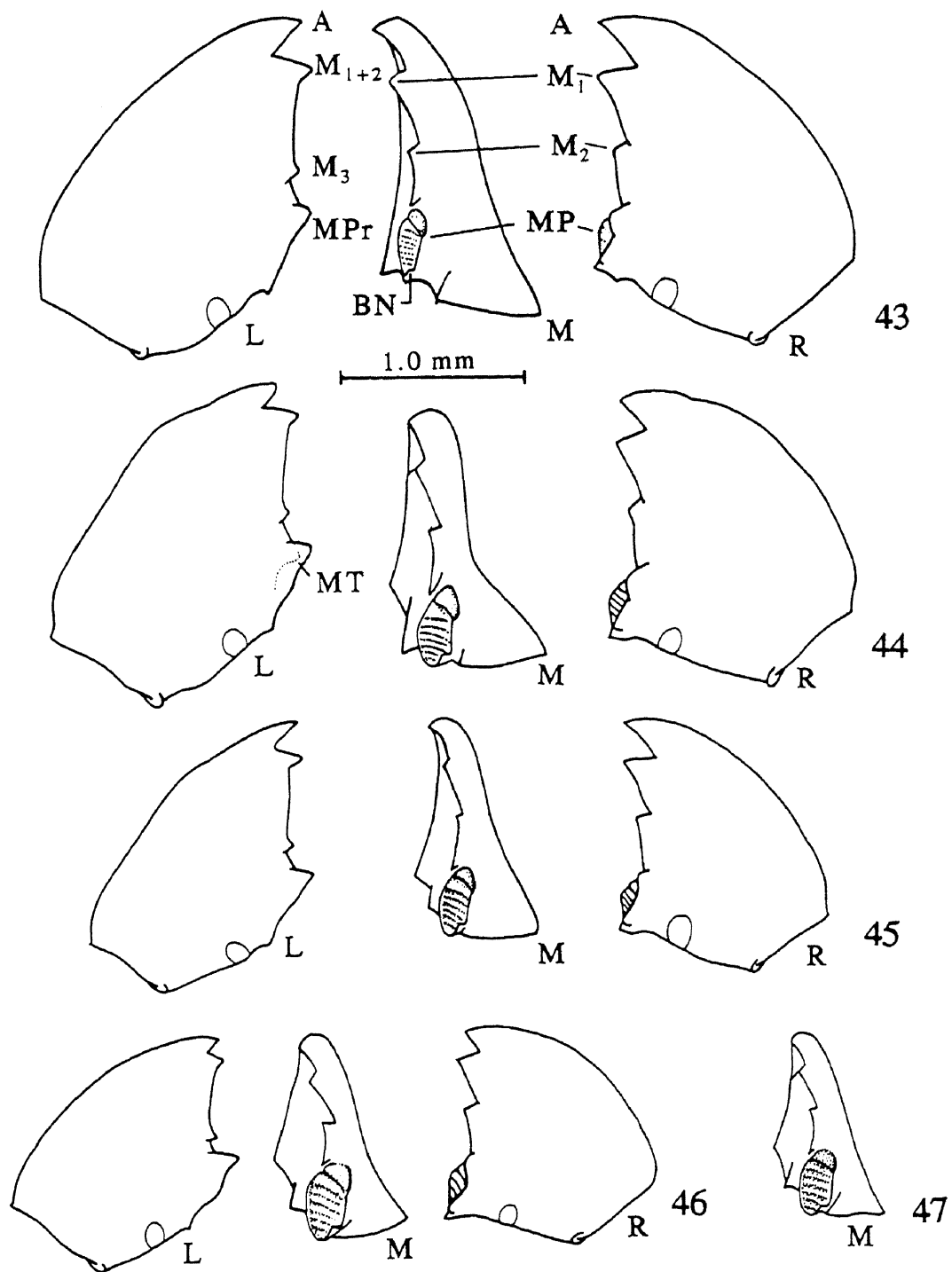


Figs. 35-38. Forewing of various *Syntermes*: 35. *S. chaquimayensis*; 36. *S. dirus*; 37. *S. longiceps*, sp.n.; 38. *S. nanus*, sp.n.

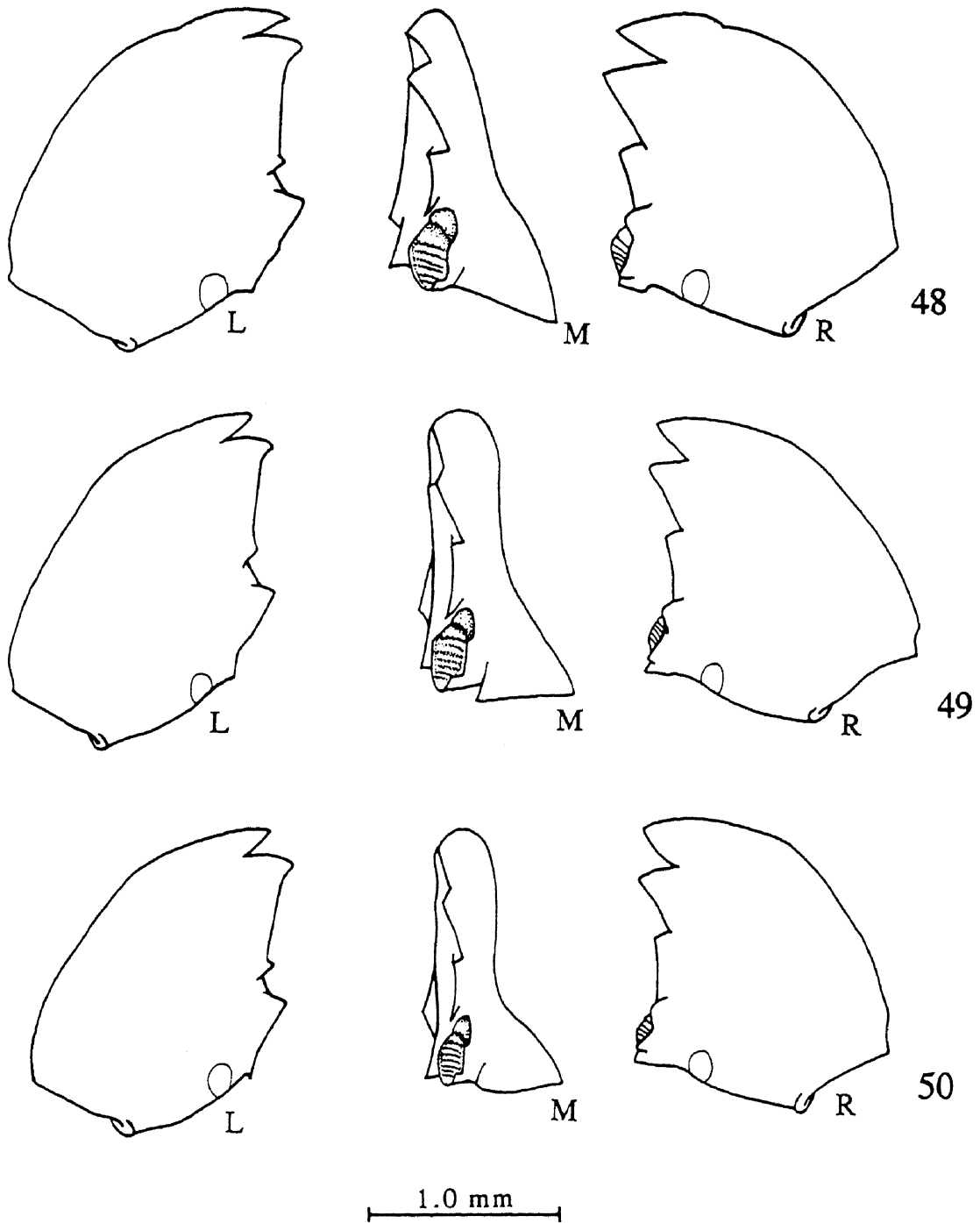


5.0 mm

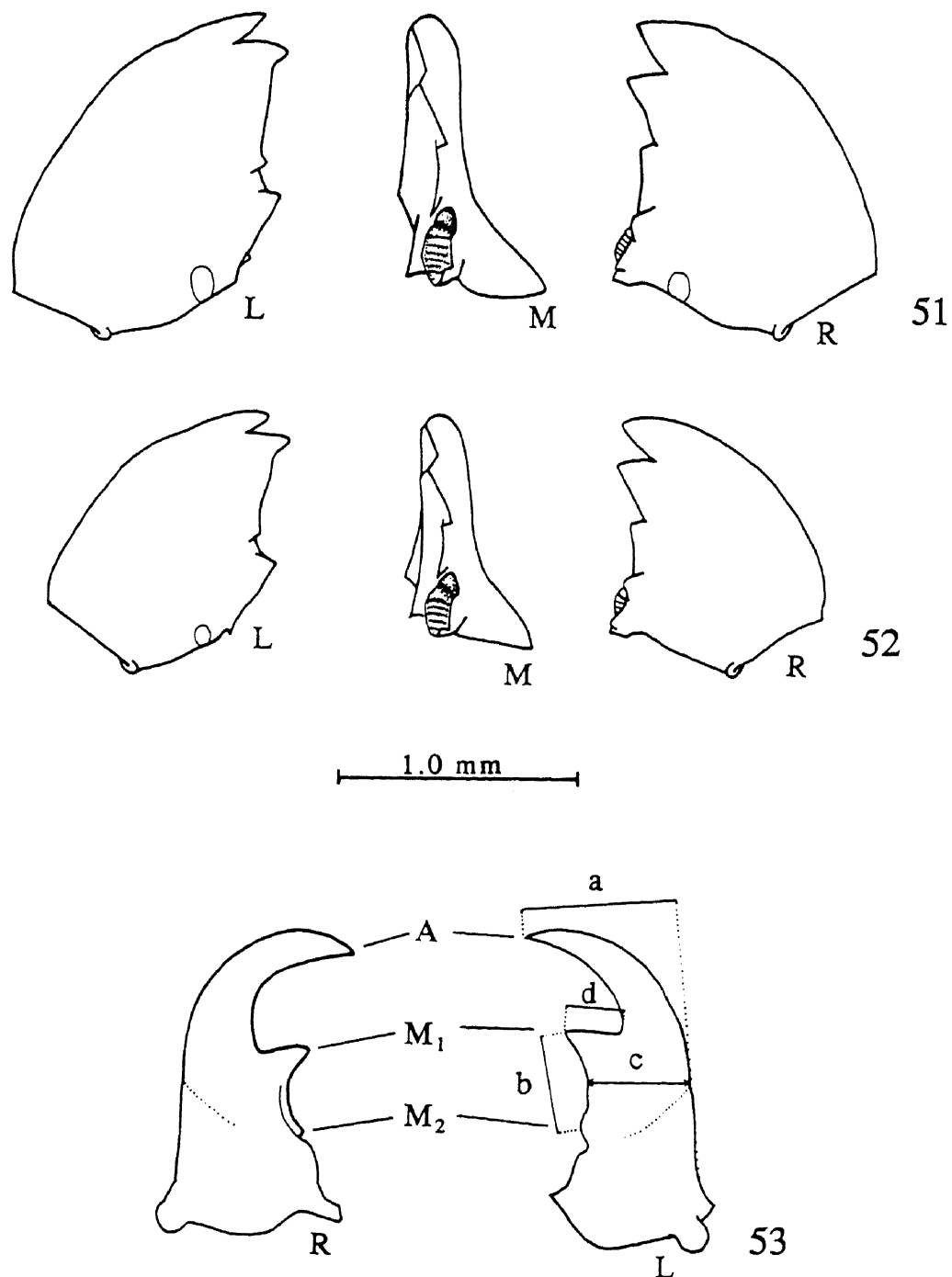
Figs. 39-42. Forewing of various *Syntermes*: 39. *S. praecellens*; 40. *S. tanygnathus*, sp.n.; 41. *S. territus*; 42. *S. wheeleri*.



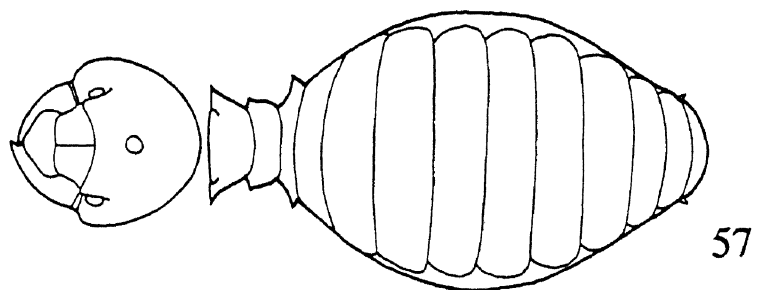
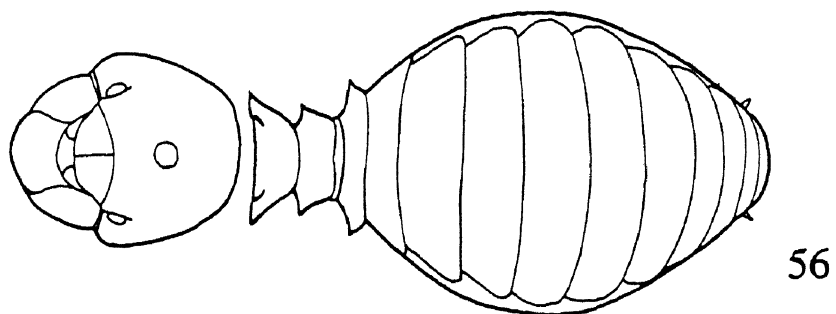
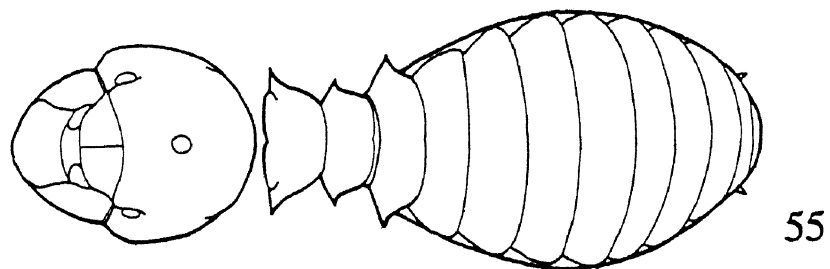
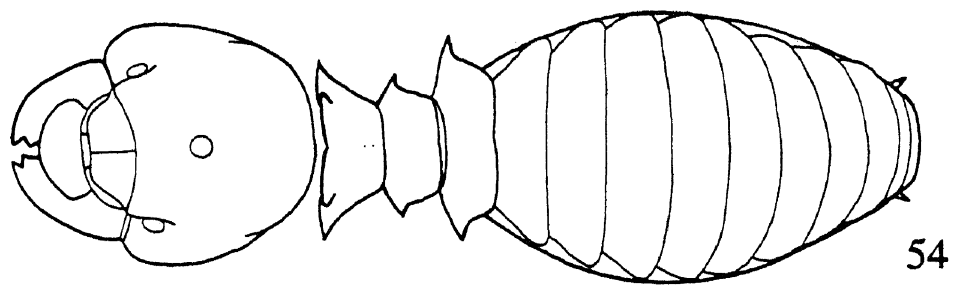
Figs. 43-47. *Syntermes dirus*, imago-worker mandibles: from left to right, left mandible from dorsal view, mesal face of right mandible, and right mandible in dorsal view. 43. imago; 44. 4th instar male worker; 45. 3rd instar male worker; 46. 4th instar female worker; 47. 3rd instar female worker. L= left mandible, dorsal view; M= right mandible, mesal face; R= right mandible, dorsal view; A= apical tooth; BN= basal notch; M₁, M₂, M₃= marginal teeth; MP= molar plate; MP_r= molar prominence; MT= molar tooth.



Figs. 48-50. Mandibles of large workers: 48. *Syntermes grandis*; 49. *S. spinosus*; 50. *S. brevimalatus*.
 L= left mandible, dorsal view; M= right mandible, mesal face; R= right mandible, dorsal view.

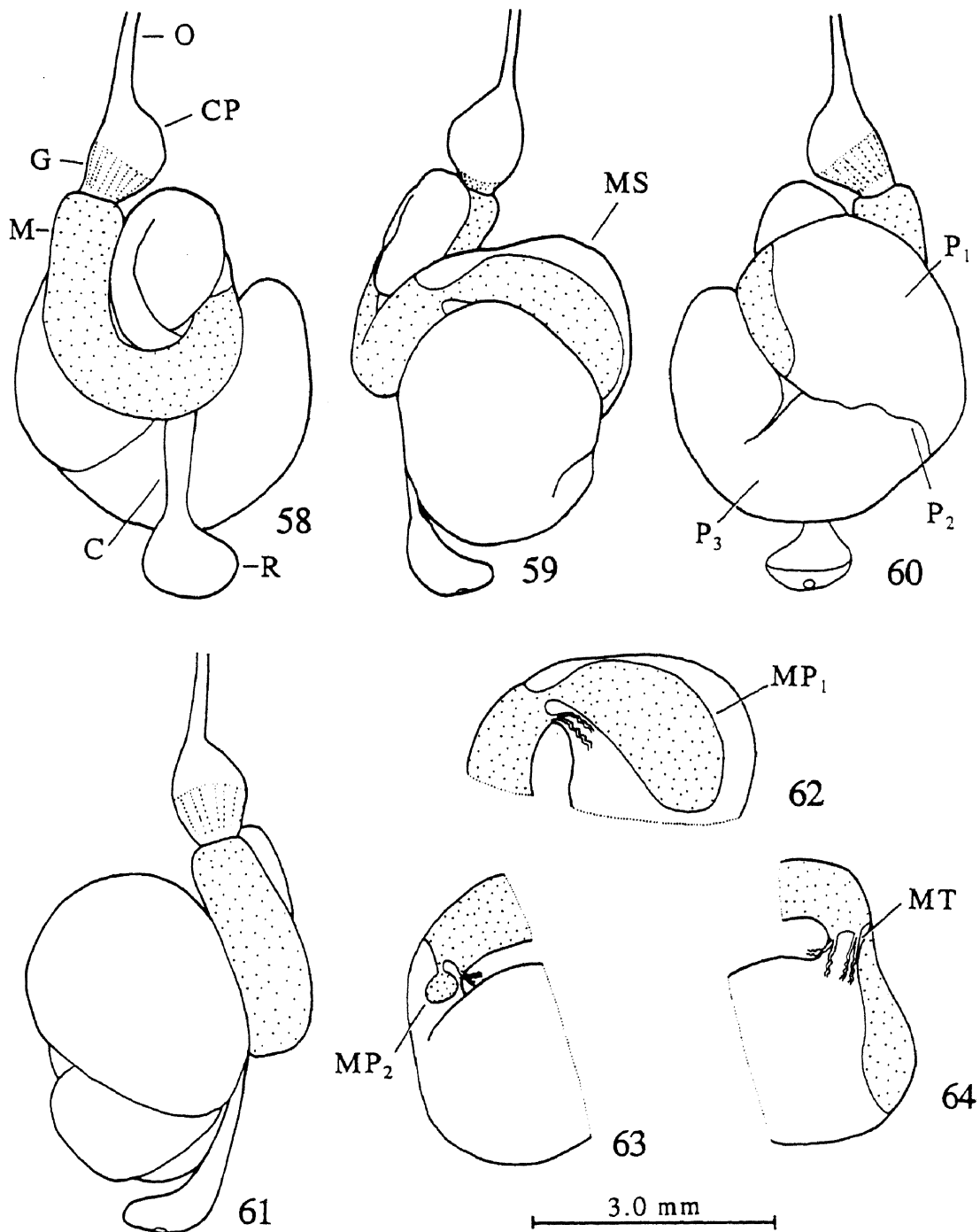


Figs. 51-53. Mandibles: 51. *Syntermes longiceps*, sp.n., large worker; 52. *S. nanus*, sp.n., large worker. 53. Soldier mandibles, ventral view: R= right mandible; M= right mandible, mesal face; L= left mandible; A= apical tooth; M₁= first marginal tooth; M₂= second marginal tooth. Measurements: a= curvature; b= distance from tip of M₁ to tip of M₂; c= width of mandible; d= length of M₁.

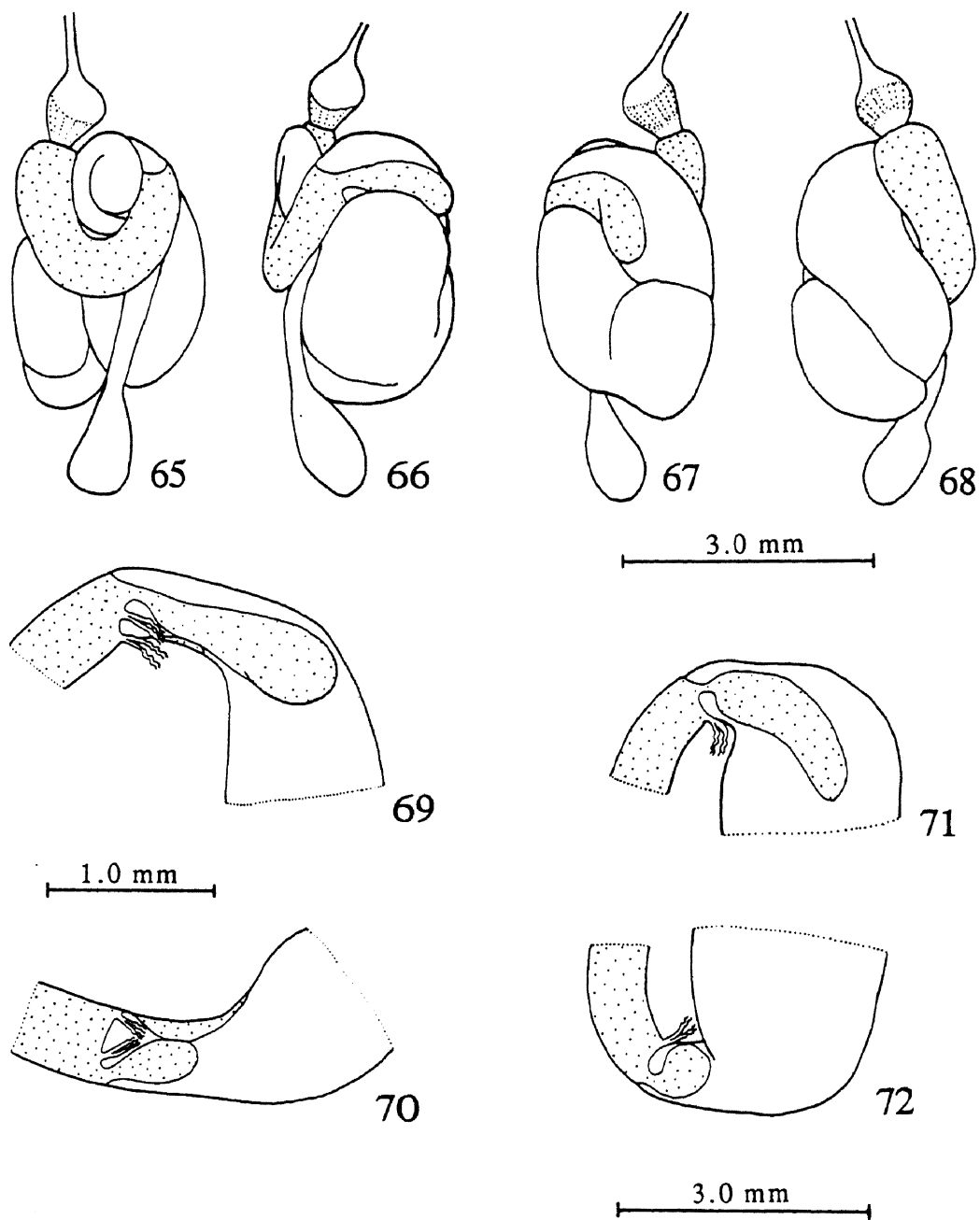


3.0 mm

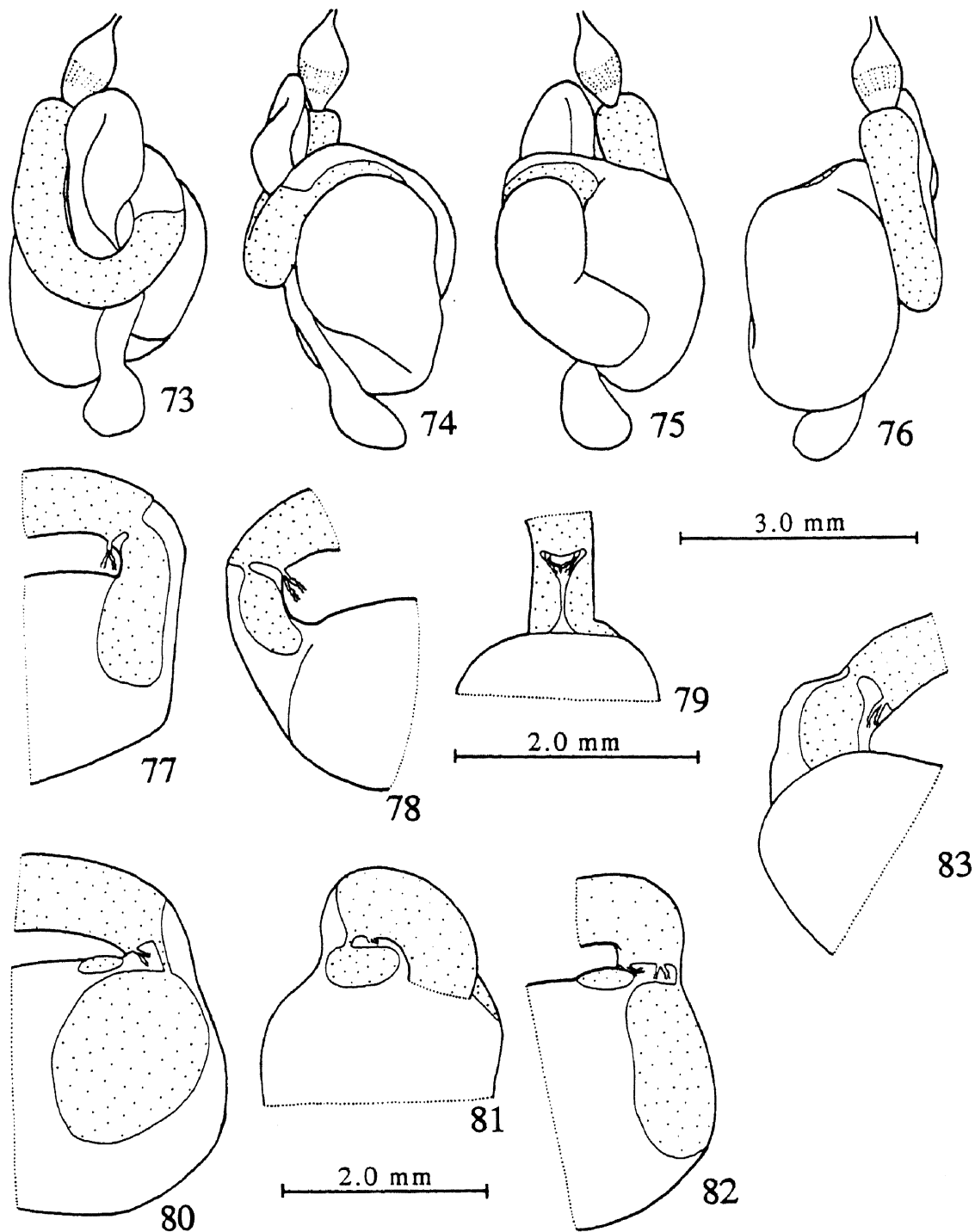
Figs. 54-57. *Syntermes dirus*, workers: 54. 4th instar male ("large worker"); 55. 3rd instar male; 56. 4th instar female; 57. 3rd instar female.



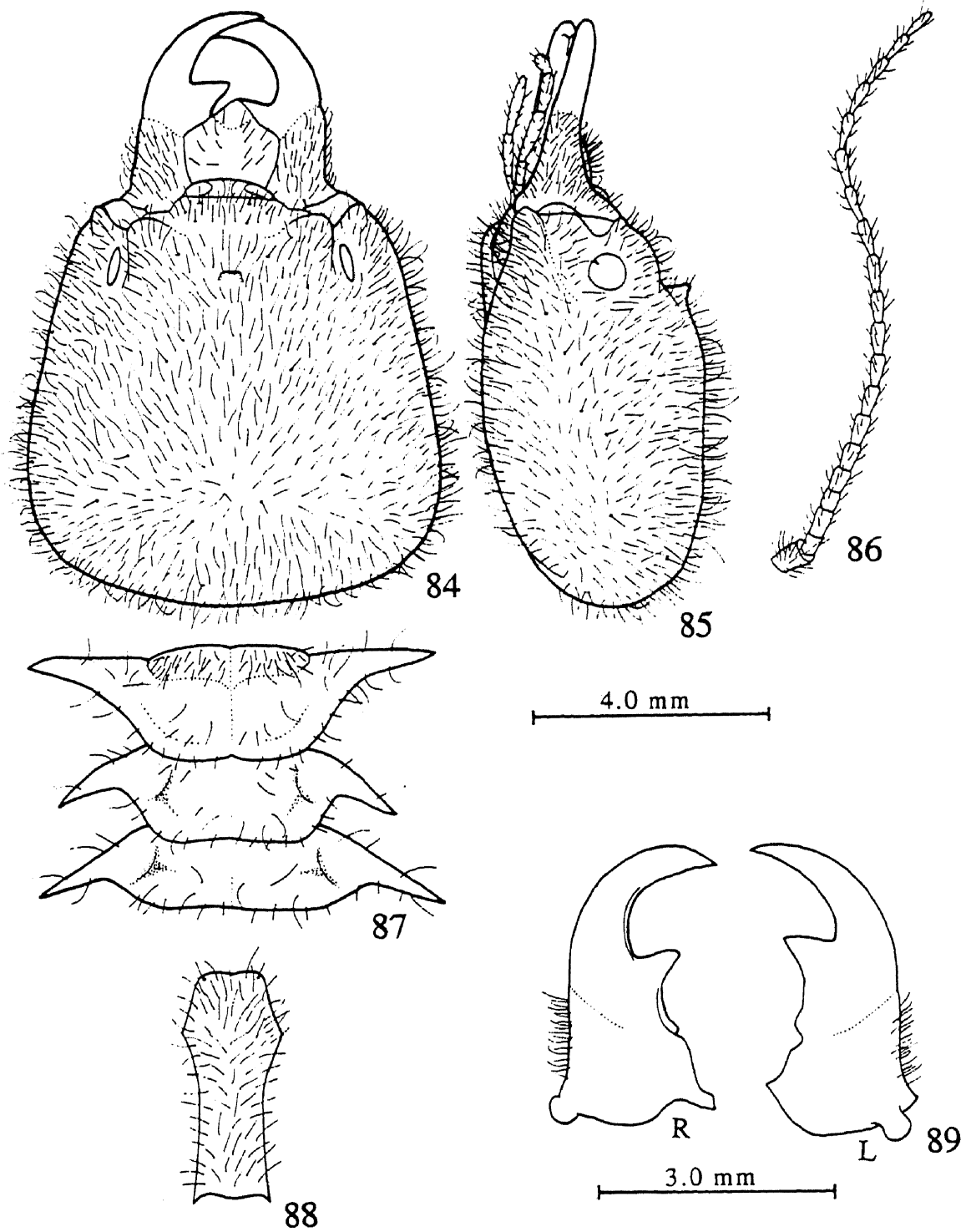
Figs. 58-64. Digestive tube: *Syntermes wheeleri*. 58. dorsal; 59. right; 60. ventral; 61. left; 62., 63., 64. mixed segment and insertion of Malpighian tubules. C= colon; CP= crop; G= gizzard; M= midgut; MP₁, MP₂= mesenteric prolongations on mixed segment; MS= mixed segment; MT= Malpighian tubules; O= oesophagus; P₁= first proctodeal segment; P₂= enteric valve; P₃= third proctodeal segment (paunch); R= rectum.



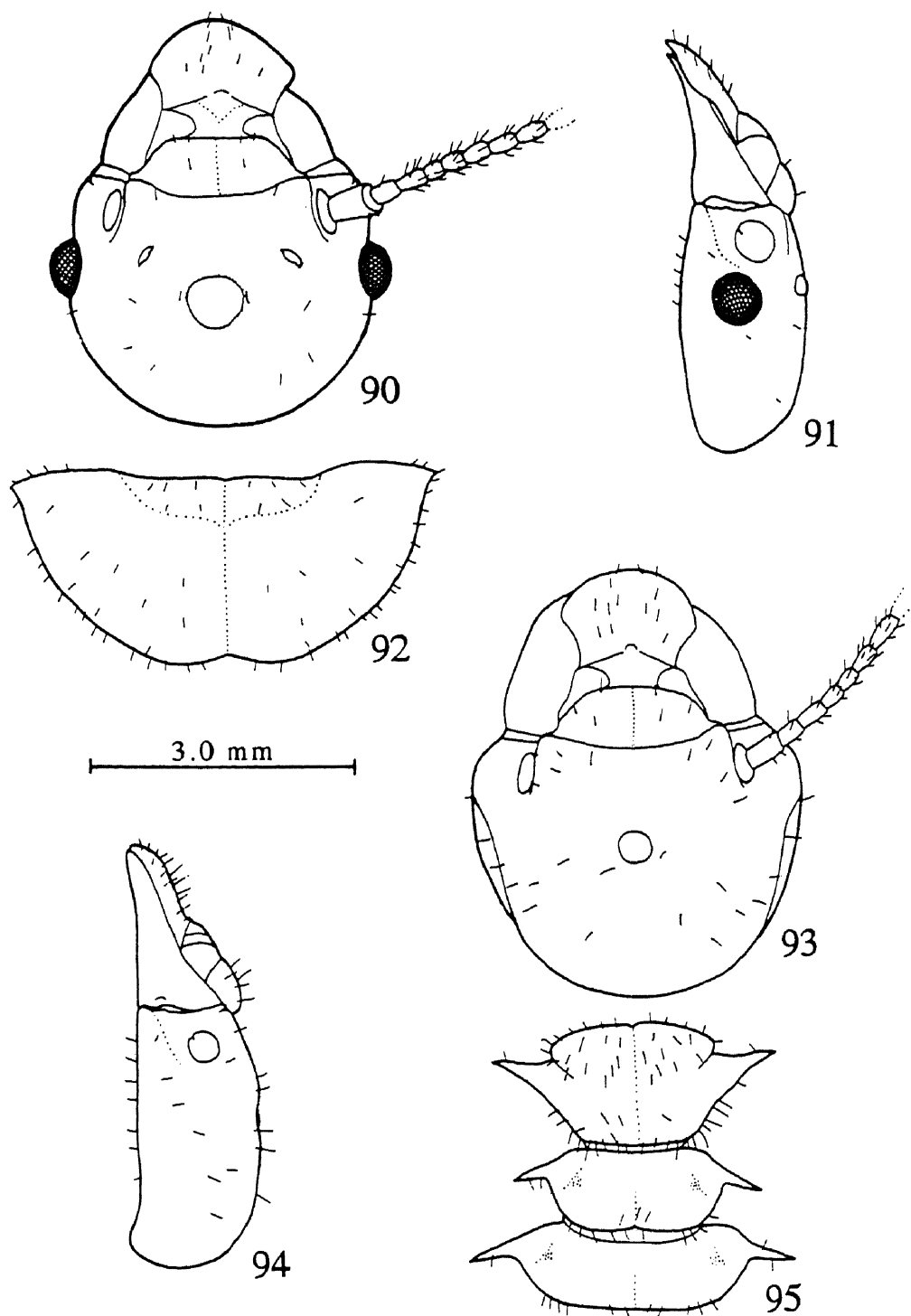
Figs. 65-72. Digestive tube: *Syntermes molestus*. 65. dorsal; 66. right; 67. ventral; 68. left; 69. major mesenteric prolongation of mixed segment; 70. minor mesenteric prolongation of mixed segment and insertion of Malpighian tubules. *S. dirus*. 71. major mesenteric prolongation of mixed segment; 72. minor mesenteric prolongation of mixed segment.



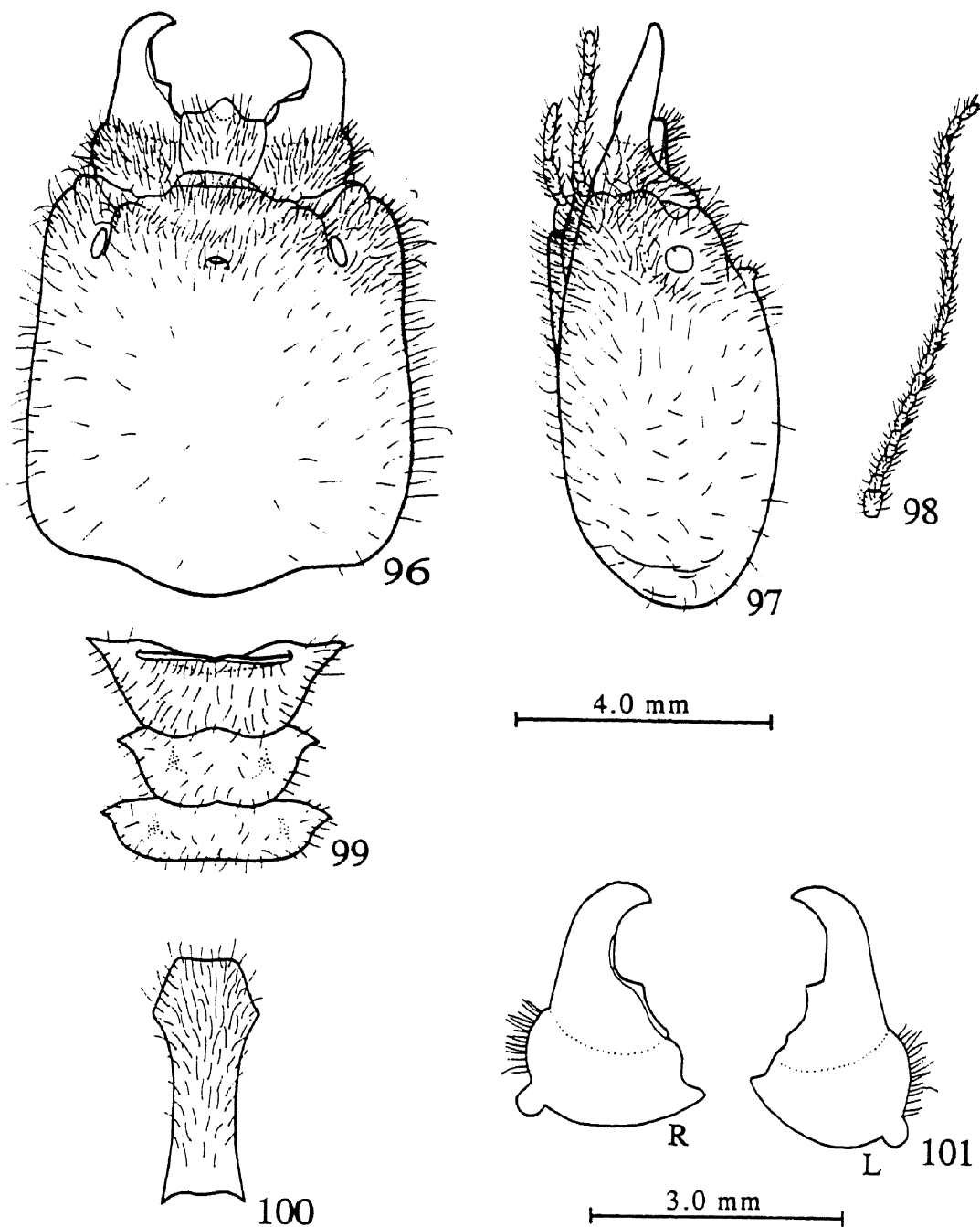
Figs. 73-83. Digestive tube: *Syntermes longiceps*, new species. 73. dorsal; 74. right; 75. ventral; 76. left; 77. major mesenteric prolongation of mixed segment; 78. minor mesenteric prolongation of mixed segment; 79. insertion of Malpighian tubules. *S. barbatus*, new species 80. major mesenteric prolongation of mixed segment; 81. minor mesenteric prolongation of mixed segment; 82. insertion of Malpighian tubules; *S. tanygnathus*, new species 83. mixed segment, showing minor mesenteric prolongation and dilation on the opposite side of the insertion of Malpighian tubules.



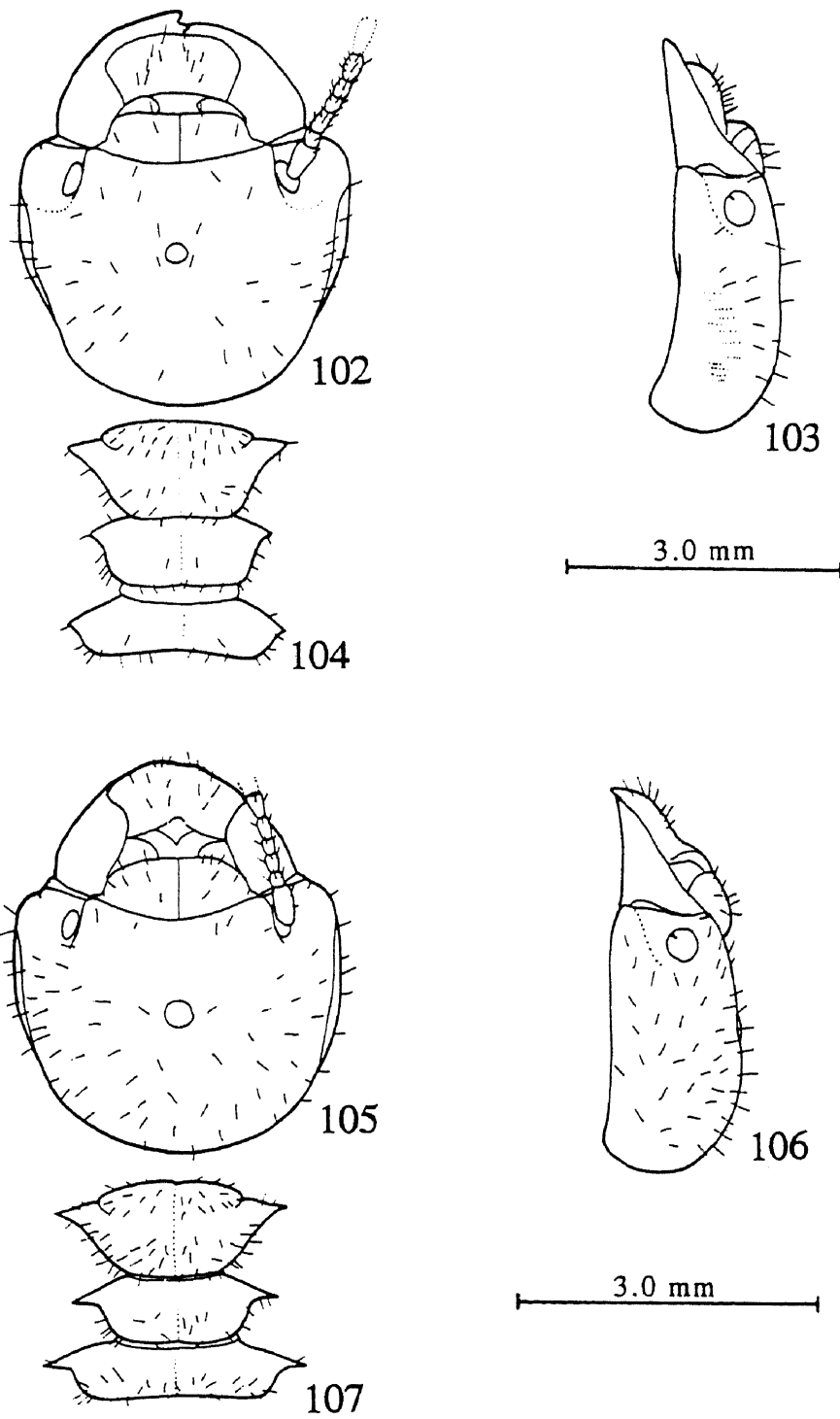
Figs. 84-89. *Syntermes aculeosus*, soldier. 84. head, dorsal view; 85. head, lateral view; 86. antenna; 87. thorax, dorsal view; 88. postmentum; 89. mandibles, ventral view.



Figs. 90-95. *Syntermes aculeosus*. Imago: 90. head, dorsal view; 91. head, lateral view; 92. pronotum. Large worker: 93. head, dorsal view; 94. head, lateral view; 95. thorax.

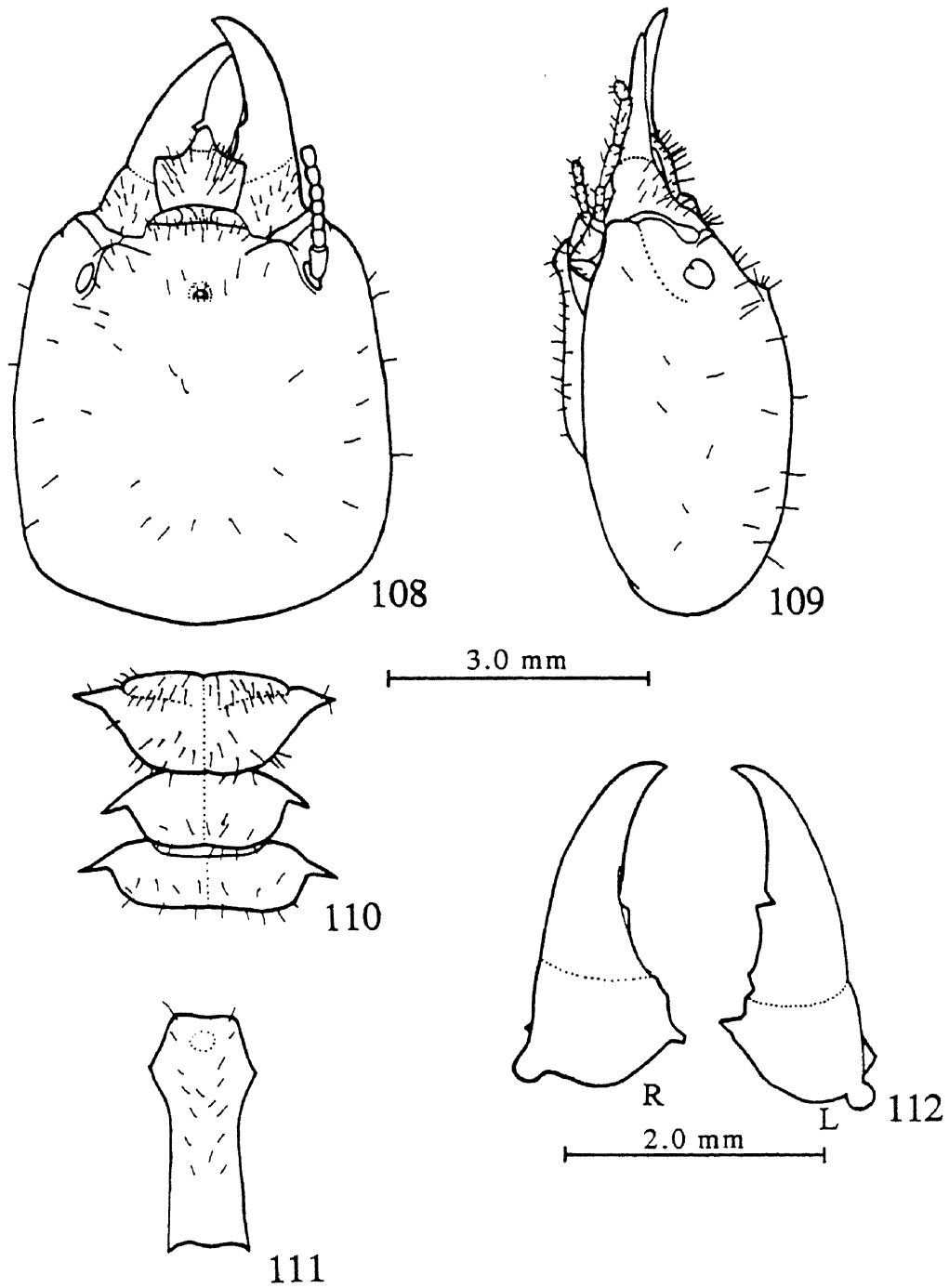


Figs. 96-101. *Syntermes barbatus*, new species, soldier. 96. head, dorsal view; 97. head, lateral view; 98. antenna; 99. thorax, dorsal view; 100. postmentum; 101. mandibles, ventral view.

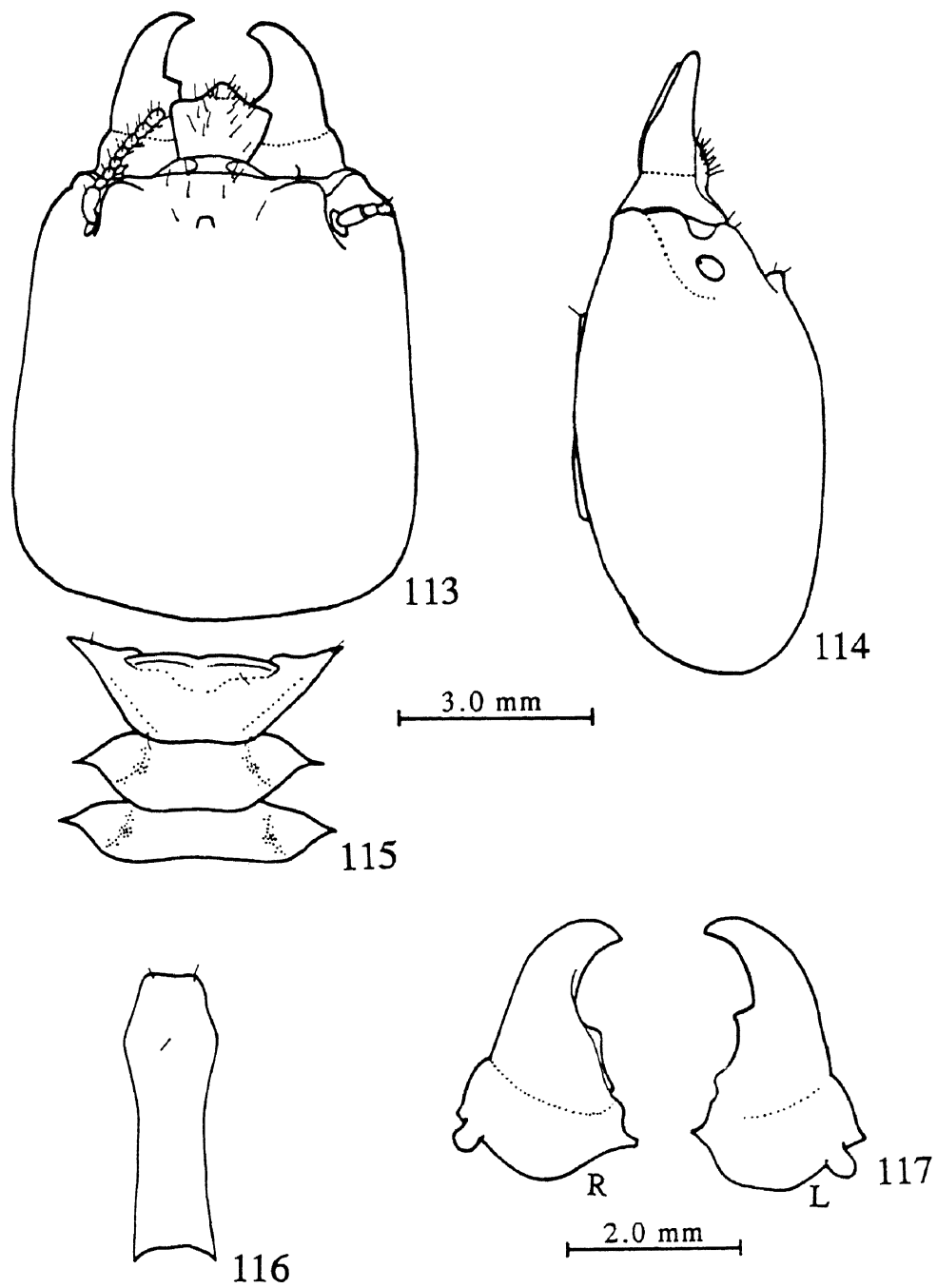


Figs. 102-104. *Syntermes barbatus*, large worker: 102. head, dorsal view; 103. head, lateral view; 104. thorax.

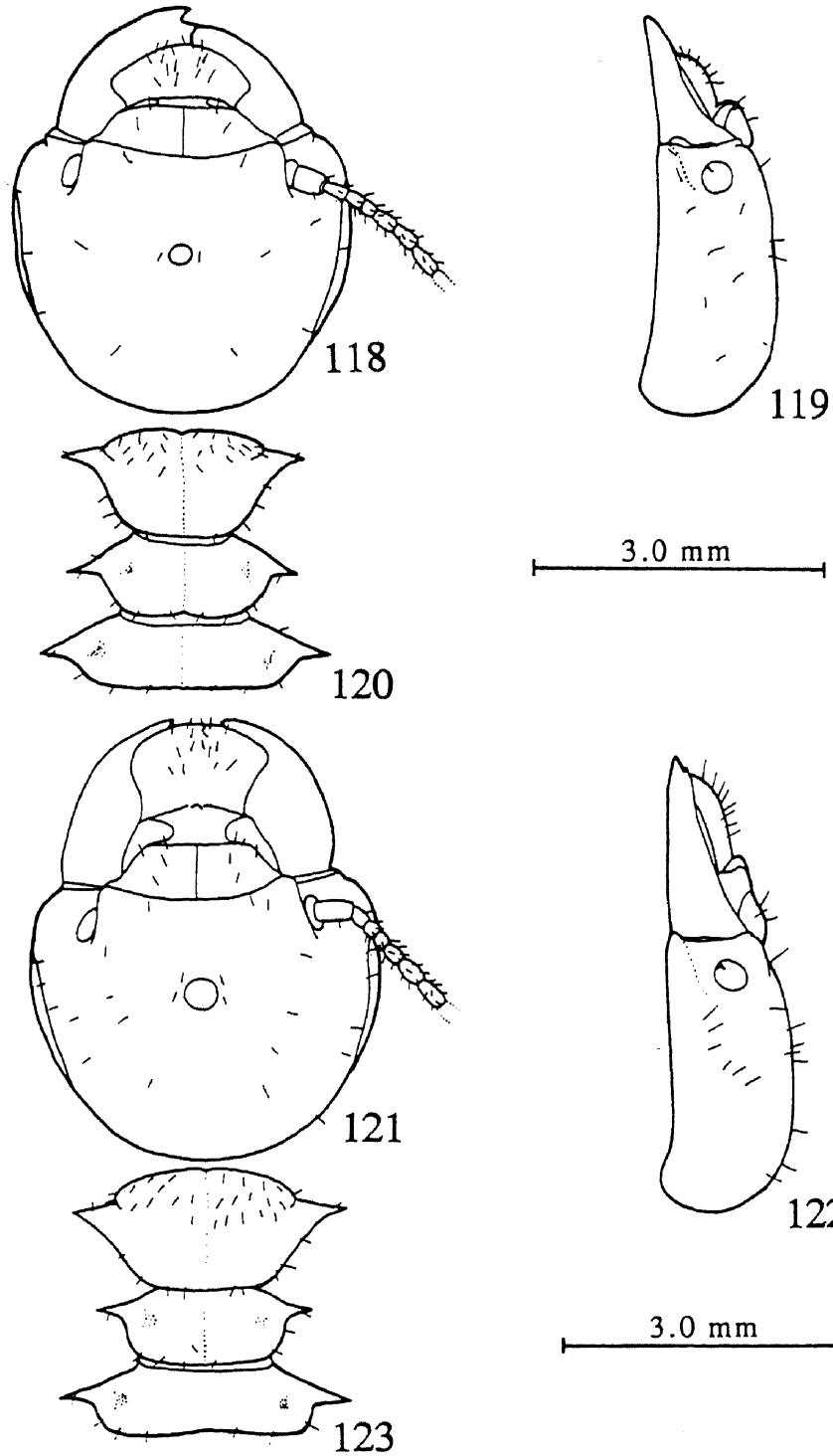
Figs. 105-107. *Syntermes bolivianus*. Large worker: 105. head, dorsal view; 106. head, lateral view; 107. thorax.



Figs. 108-112. *Syntermes bolivianus*, soldier. 108. head, dorsal view; 109. head, lateral view; 110. thorax, dorsal view; 111. postmentum; 112. mandibles, ventral view.

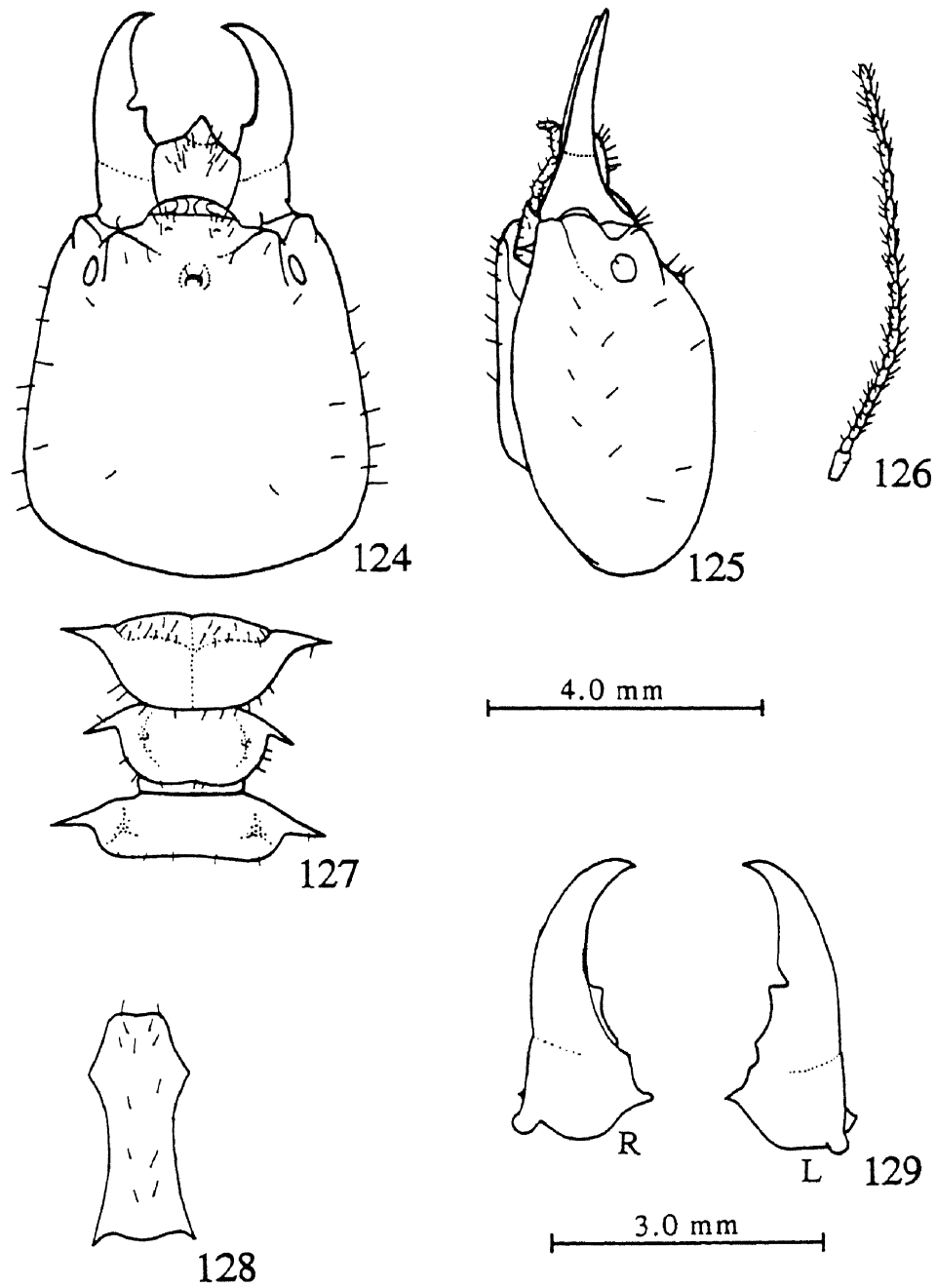


Figs. 113-117. *Syntermes brevimalatus*, soldier. 113. head, dorsal view; 114. head, lateral view; 115. thorax, dorsal view; 116. postmentum; 117. mandibles, ventral view.

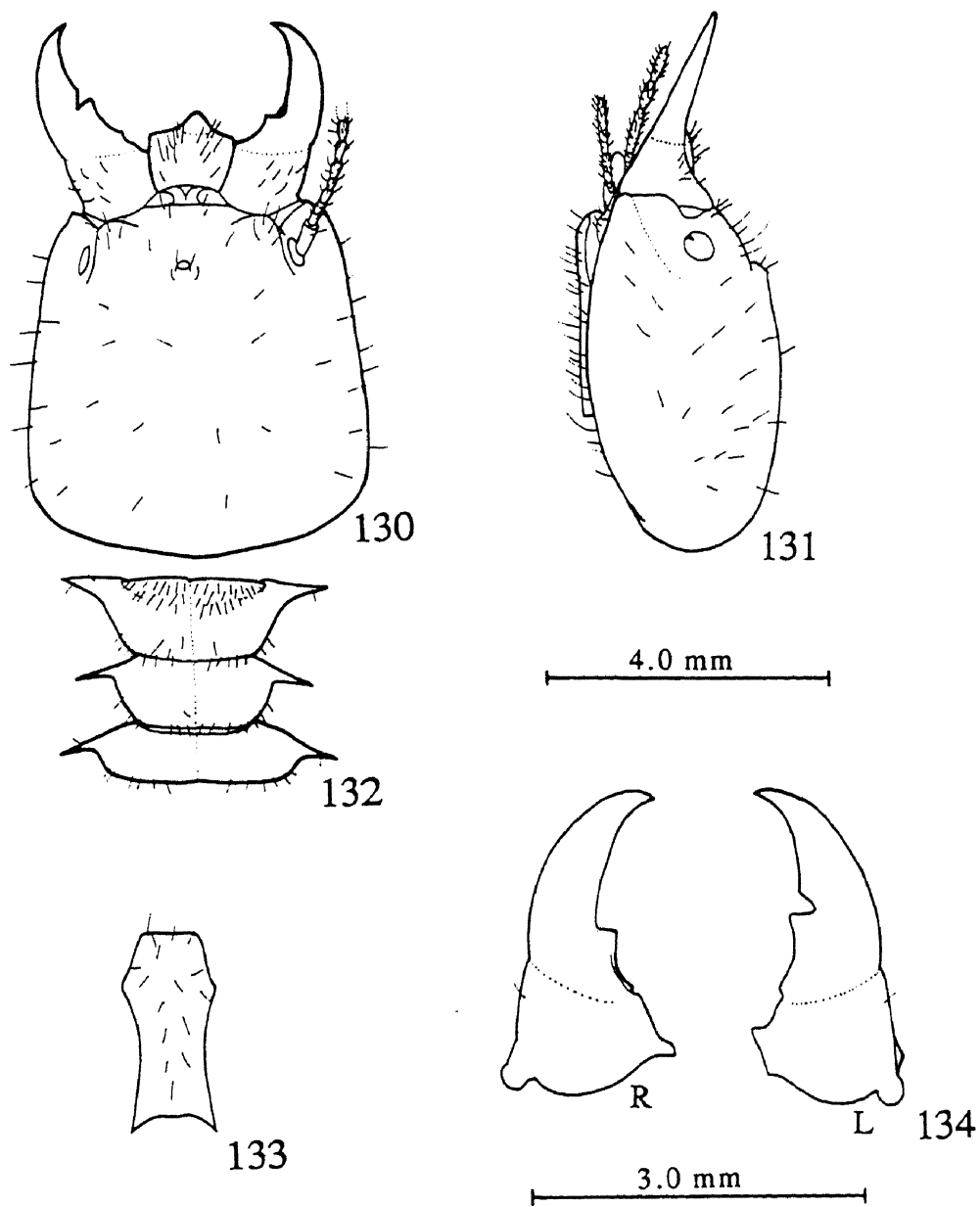


Figs. 118-120. *Syntermes brevimalatus*. Large worker: 118. head, dorsal view; 119. head, lateral view; 120. thorax.

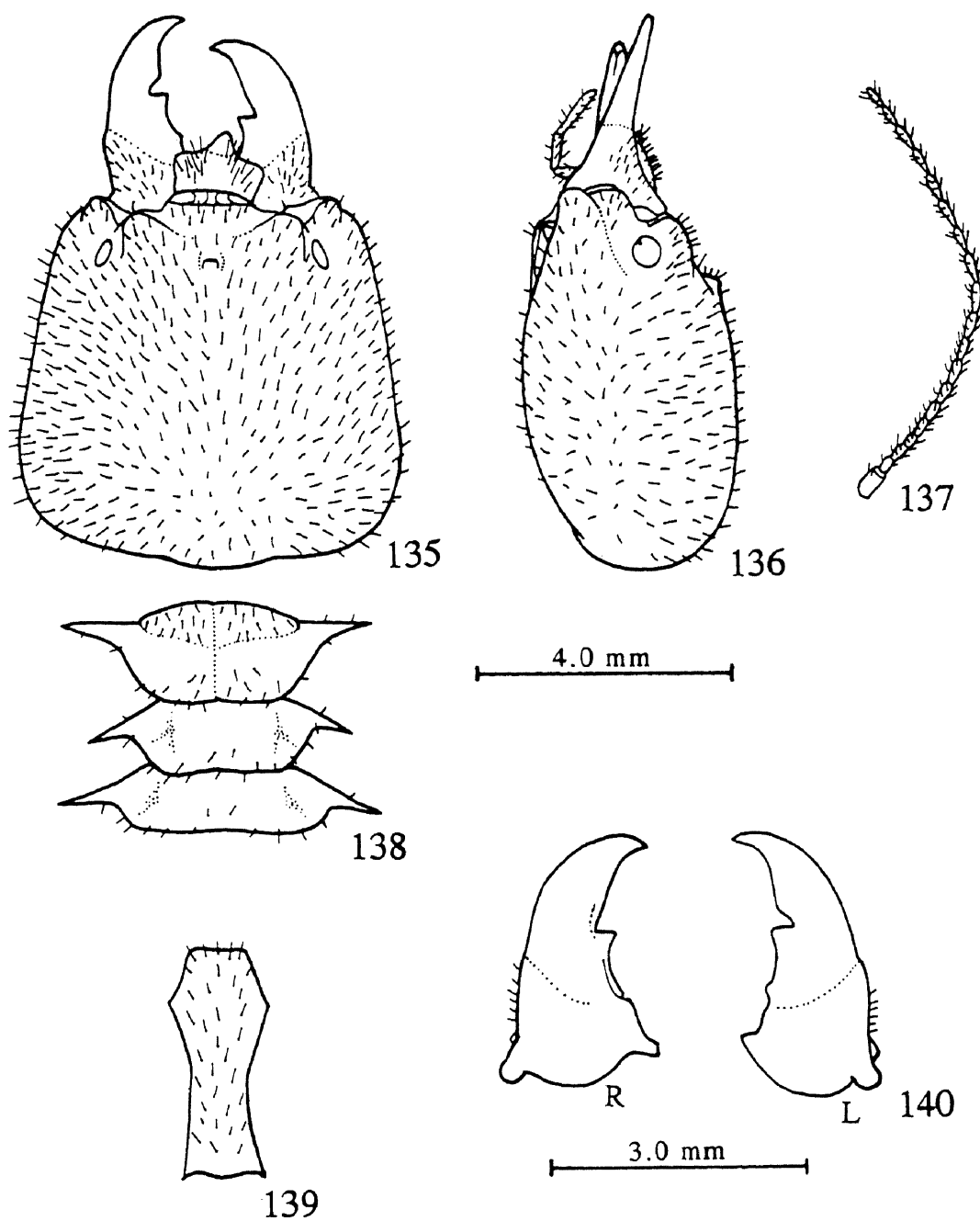
Figs. 121-123. *Syntermes calvus*. Large worker: 121. head, dorsal view; 122. head, lateral view; 123. thorax.



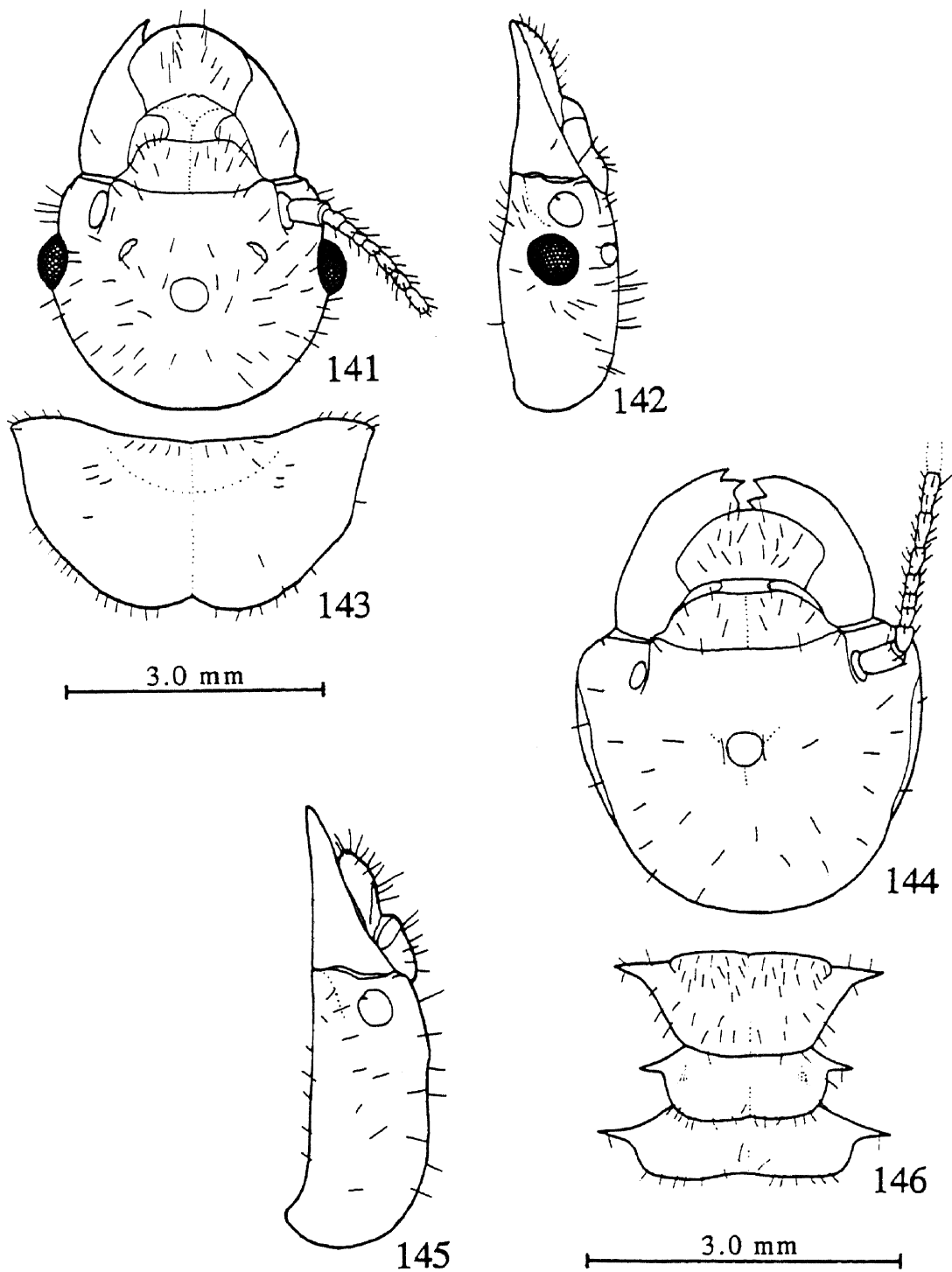
Figs. 124-129. *Syntermes calvus*, soldier. 124. head, dorsal view; 125. head, lateral view; 126. antenna; 127. thorax, dorsal view; 128. postmentum; 129. mandibles, ventral view.



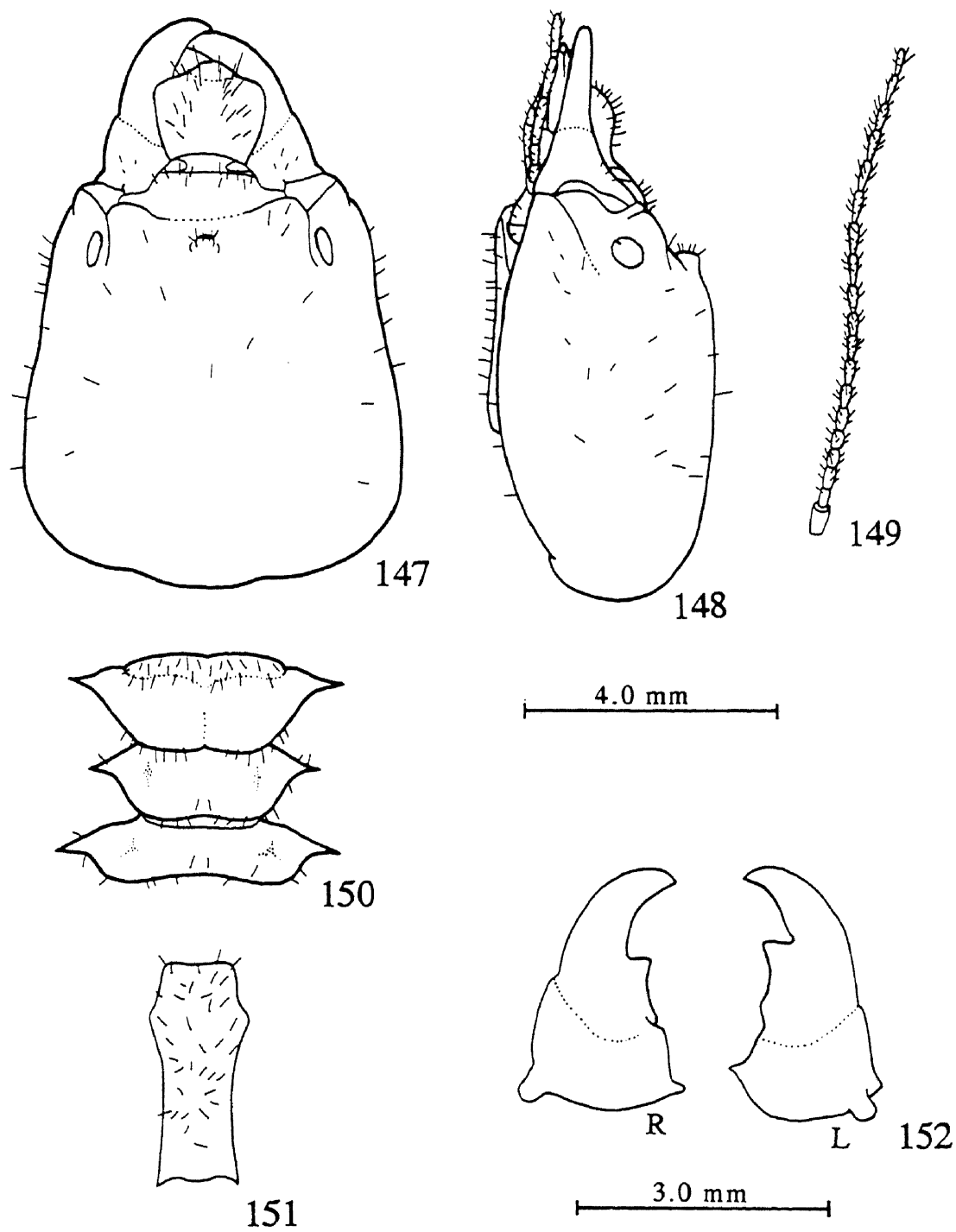
Figs. 130-134. *Syntermes cearensis*, sp.n., soldier. 130. head, dorsal view; 131. head, lateral view; 132. thorax, dorsal view; 133. postmentum; 134. mandibles, ventral view.



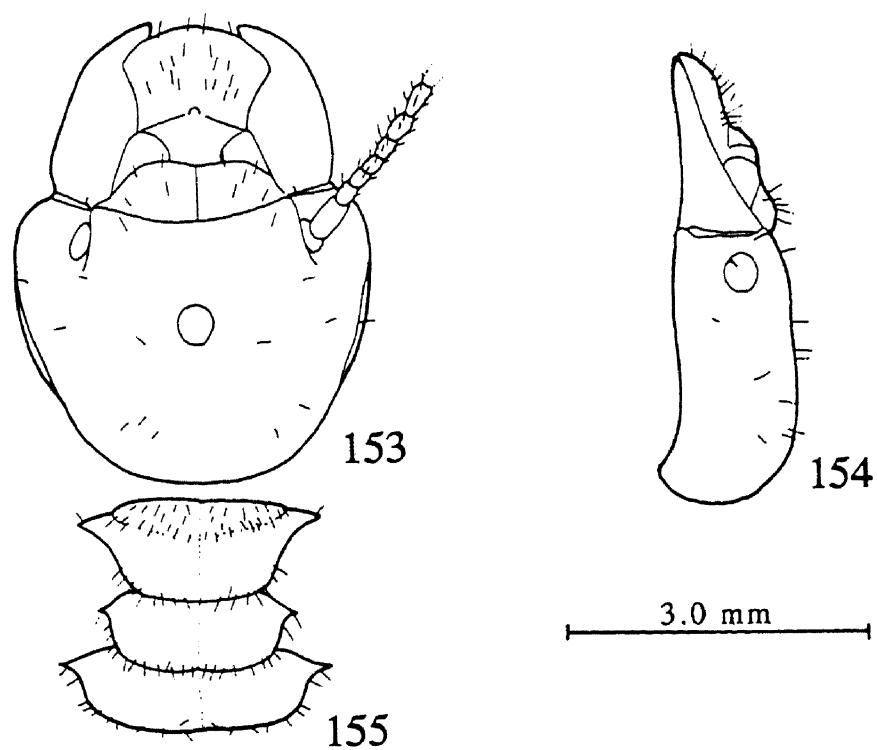
Figs. 135-140. *Syntermes chaquimayensis*, soldier. 135. head, dorsal view; 136. head, lateral view; 137. antenna; 138. thorax, dorsal view; 139. postmentum; 140. mandibles, ventral view.



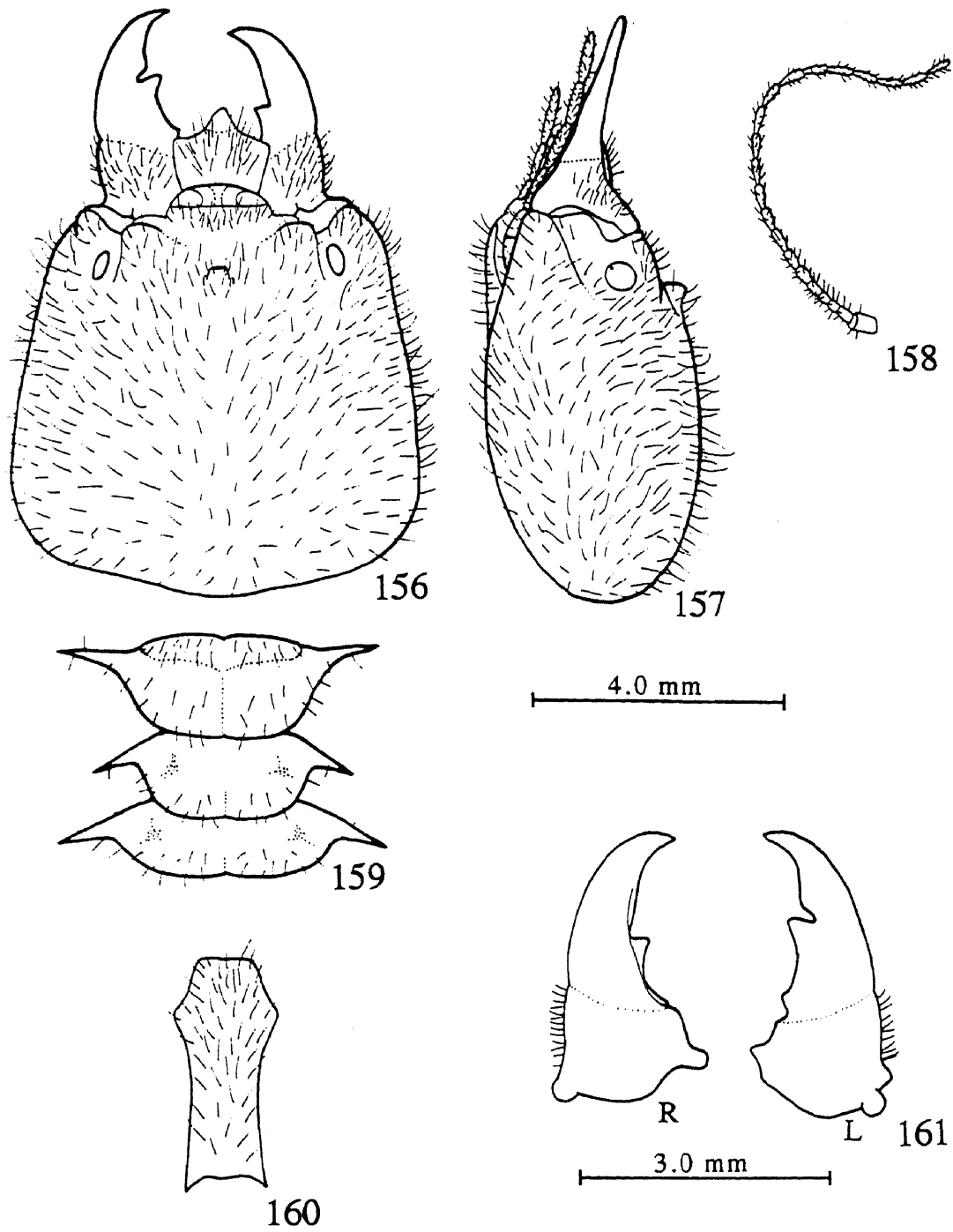
Figs. 141-146. *Syntermes chaquimayensis*. Imago: 141. head, dorsal view; 142. head, lateral view; 143. pronotum. Large worker: 144. head, dorsal view; 145. head, lateral view; 146. thorax.



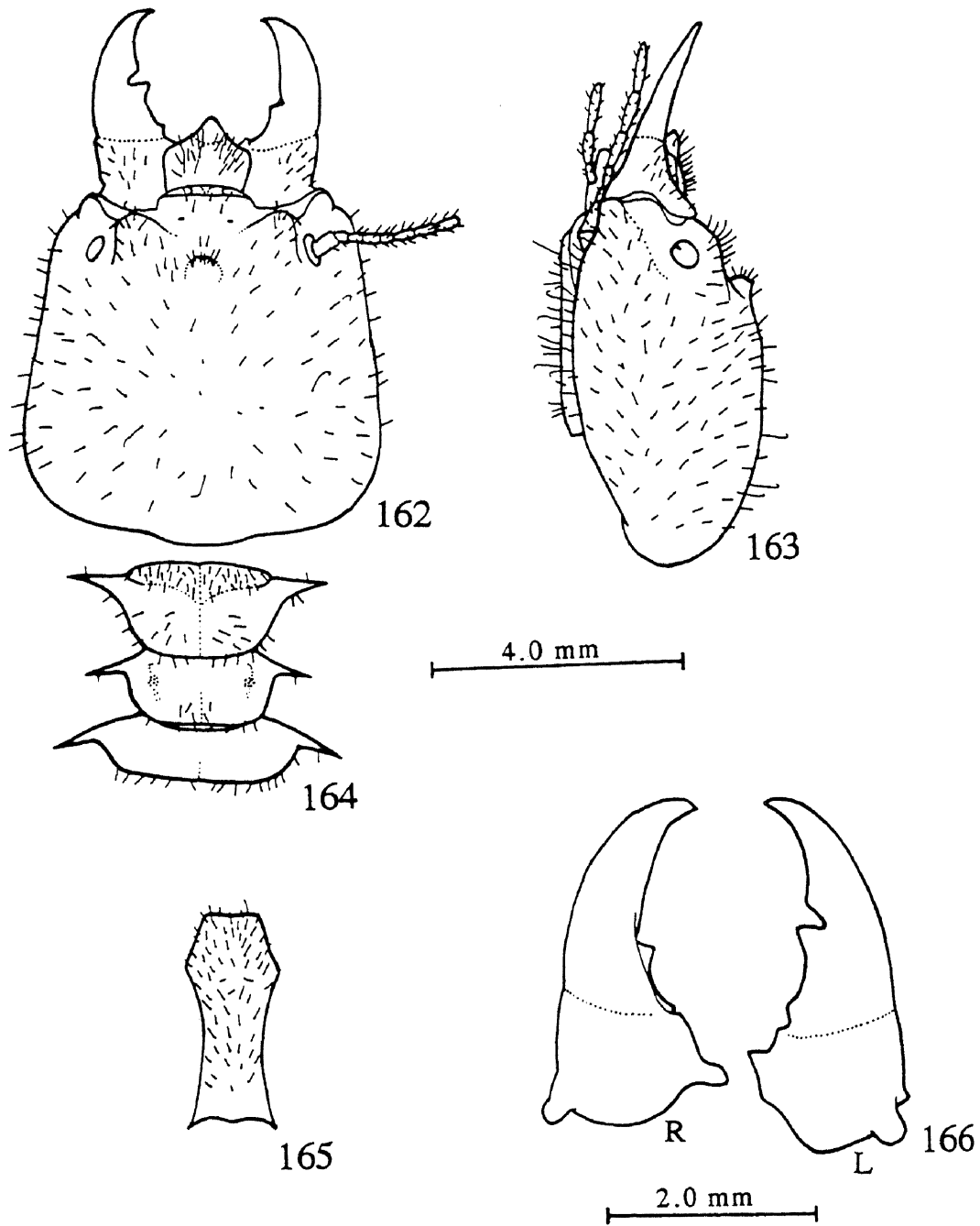
Figs. 147-152. *Syntermes crassilabrum*, new species, soldier. 147. head, dorsal view; 148. head, lateral view; 149. antenna; 150. thorax, dorsal view; 151. postmentum; 152. mandibles, ventral view.



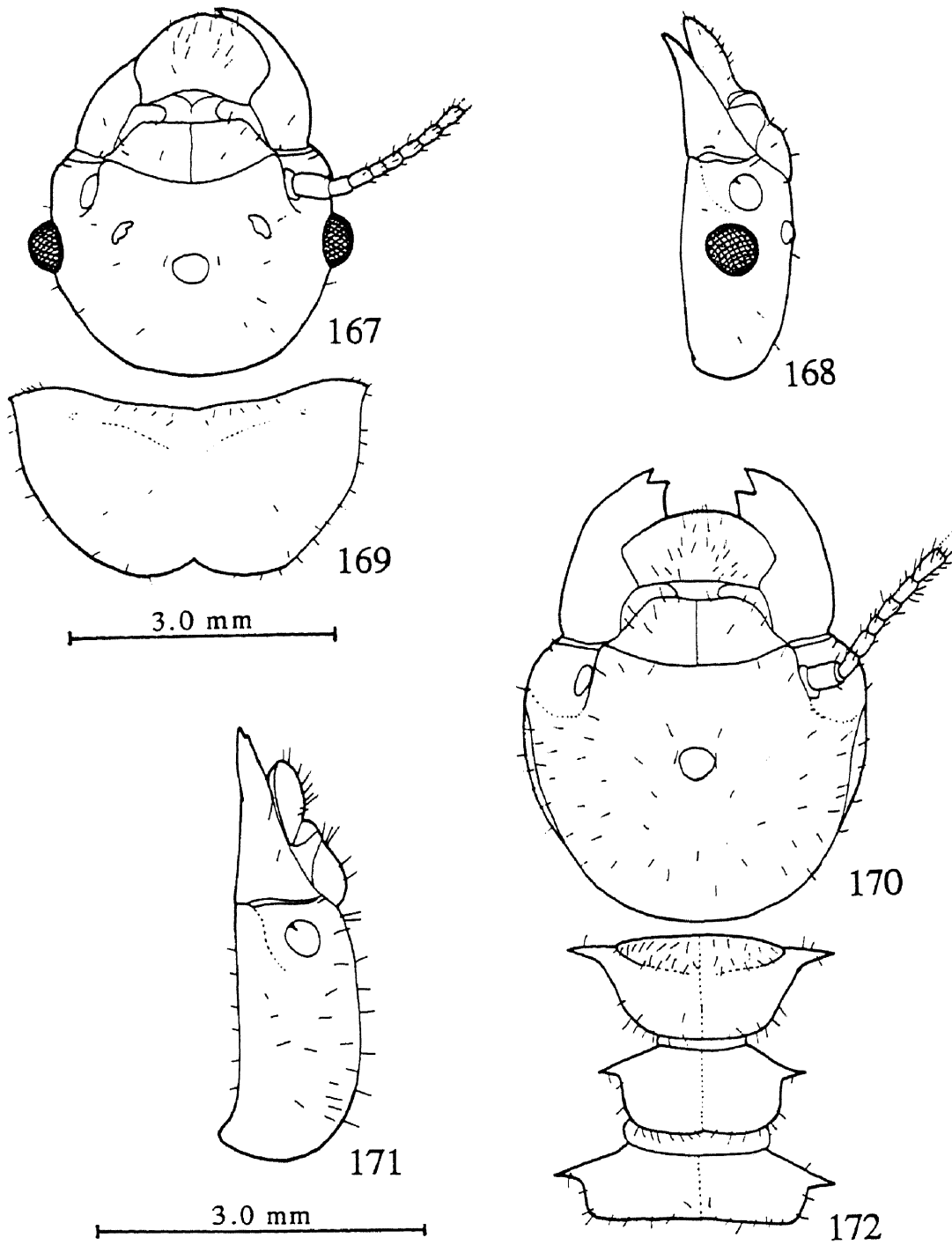
Figs. 153-155. *Syntermes crassilabrum*. Large worker: 153. head, dorsal view; 154. head, lateral view; 155. thorax.



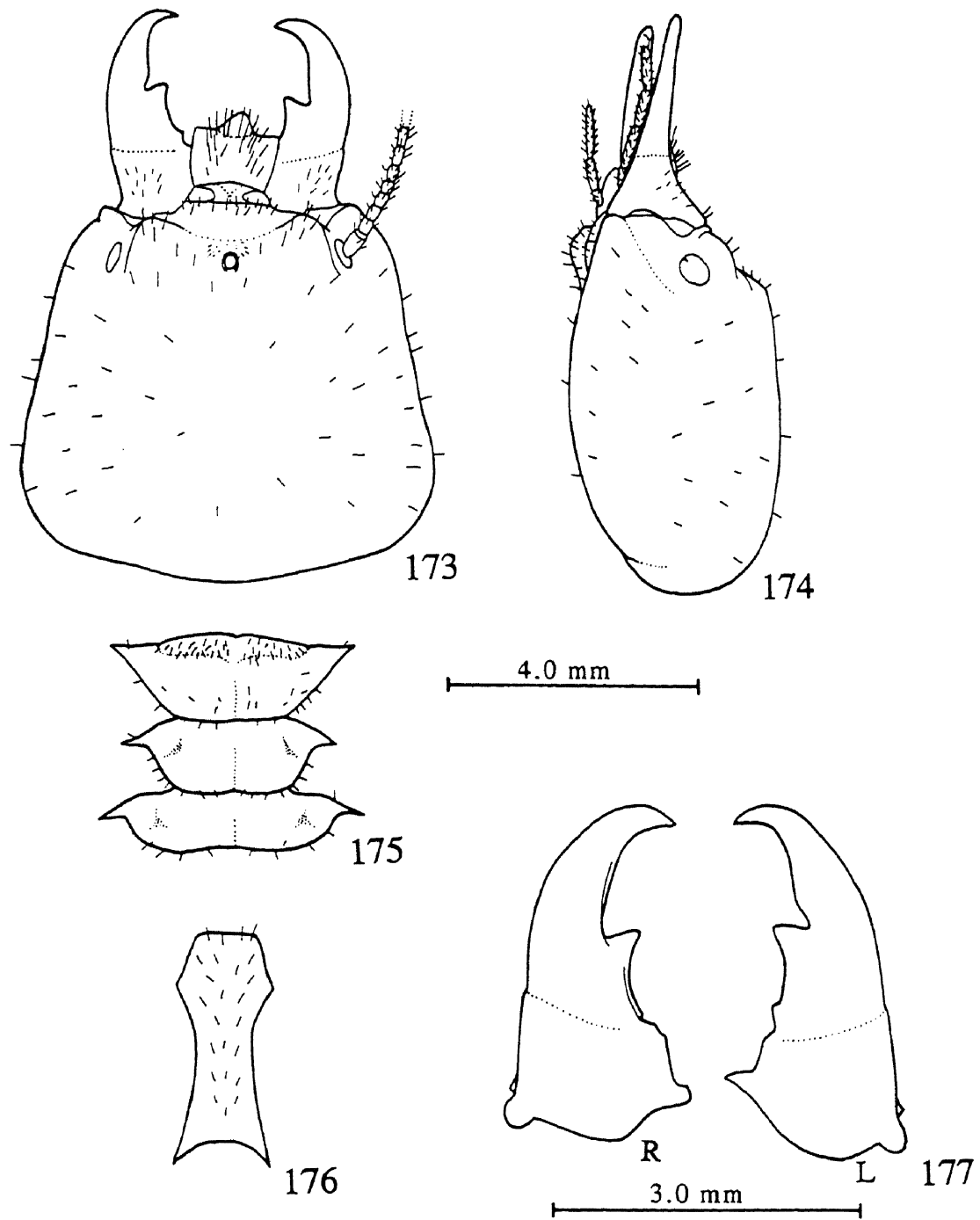
Figs. 156-161. *Syntermes dirus*, soldier. 156. head, dorsal view; 157. head, lateral view; 158. antenna; 159. thorax, dorsal view; 160. postmentum; 161. mandibles, ventral view.



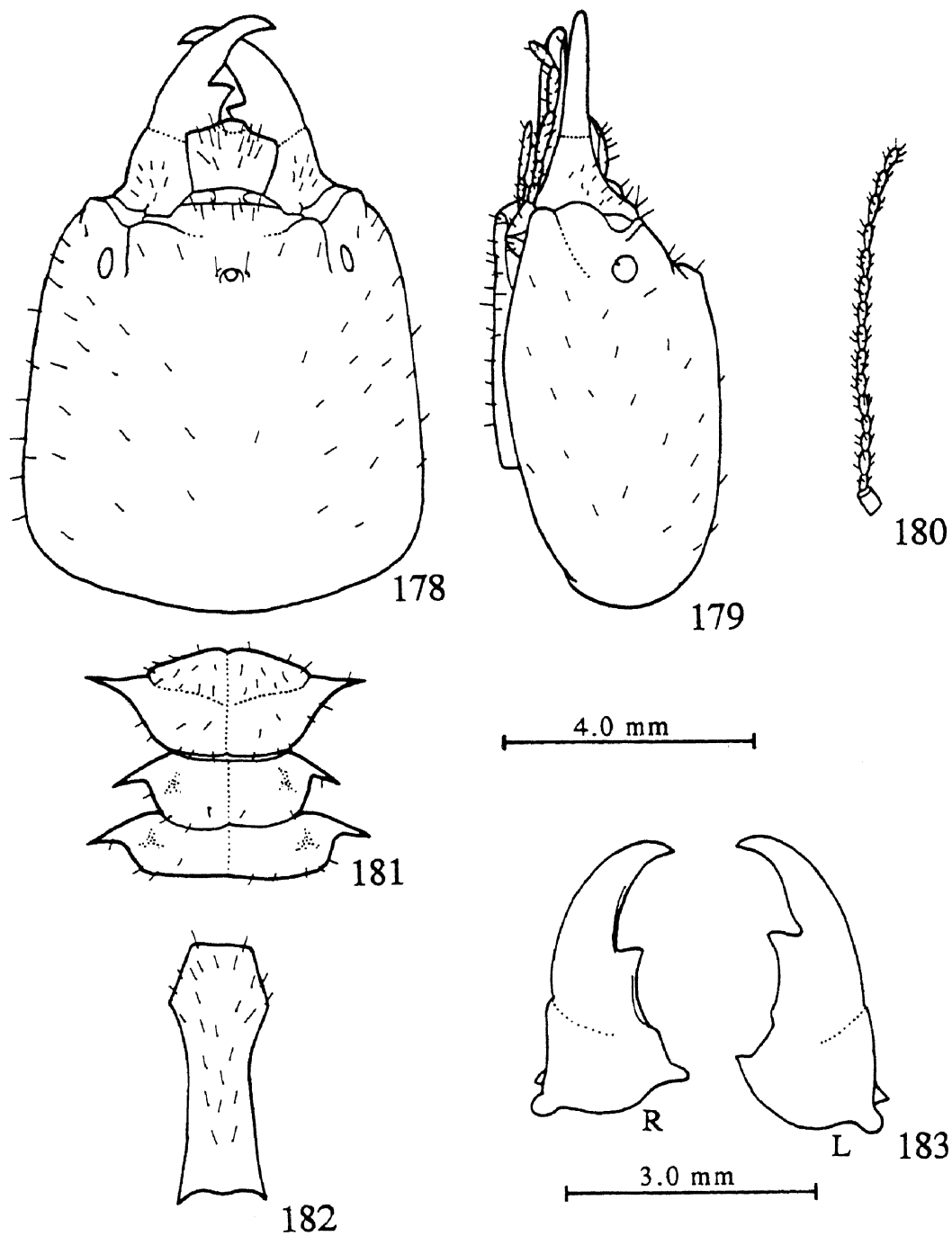
Figs. 162-166. *Syntermes dirus*, soldier from a different colony. 162. head, dorsal view; 163. head, lateral view; 164. thorax, dorsal view; 165. postmentum; 166. mandibles, ventral view.



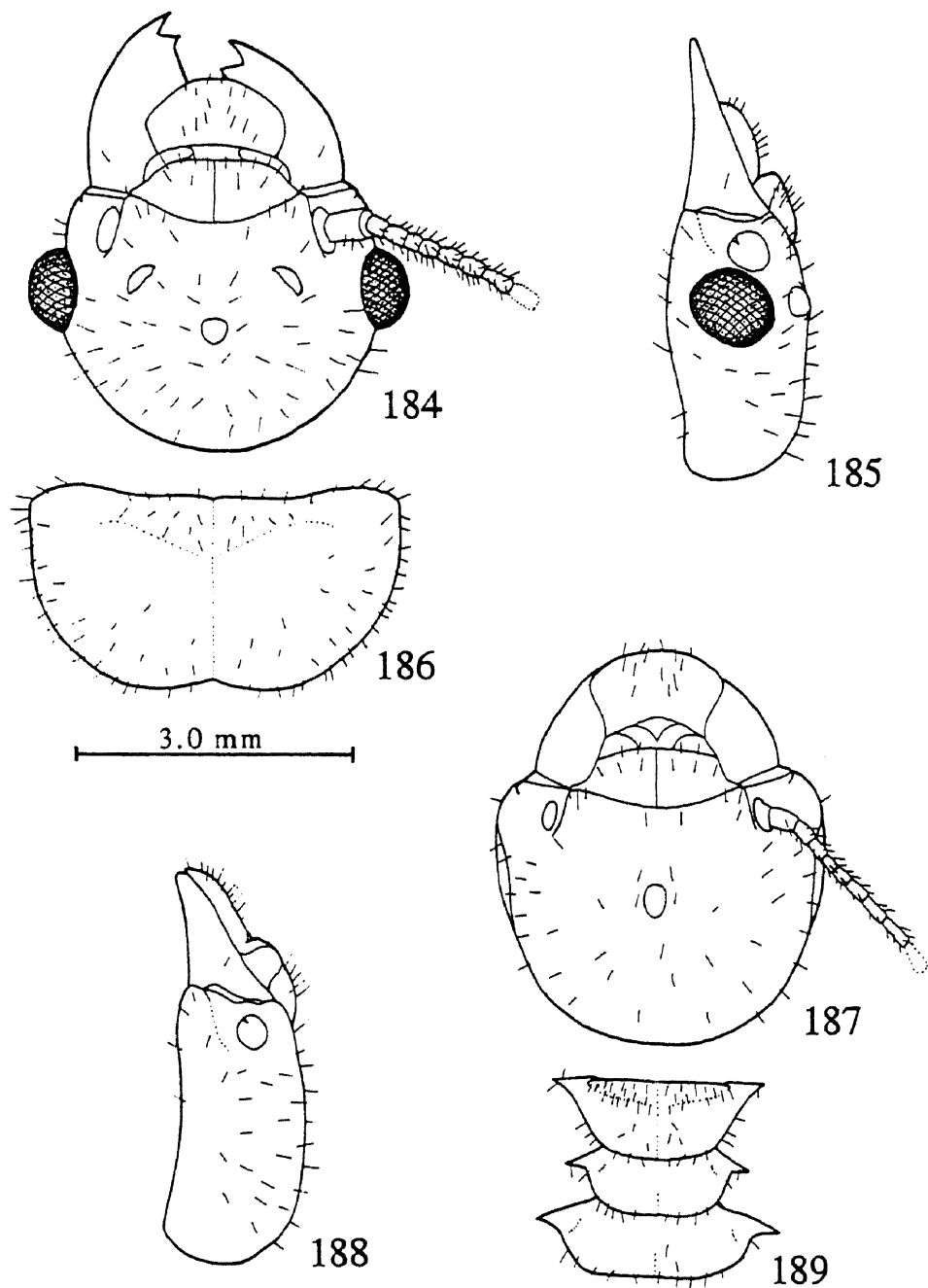
Figs. 167-172. *Syntermes dirus*. Imago: 167. head, dorsal view; 168. head, lateral view; 169. pronotum. Large worker: 170. head, dorsal view; 171. head, lateral view; 172. thorax.



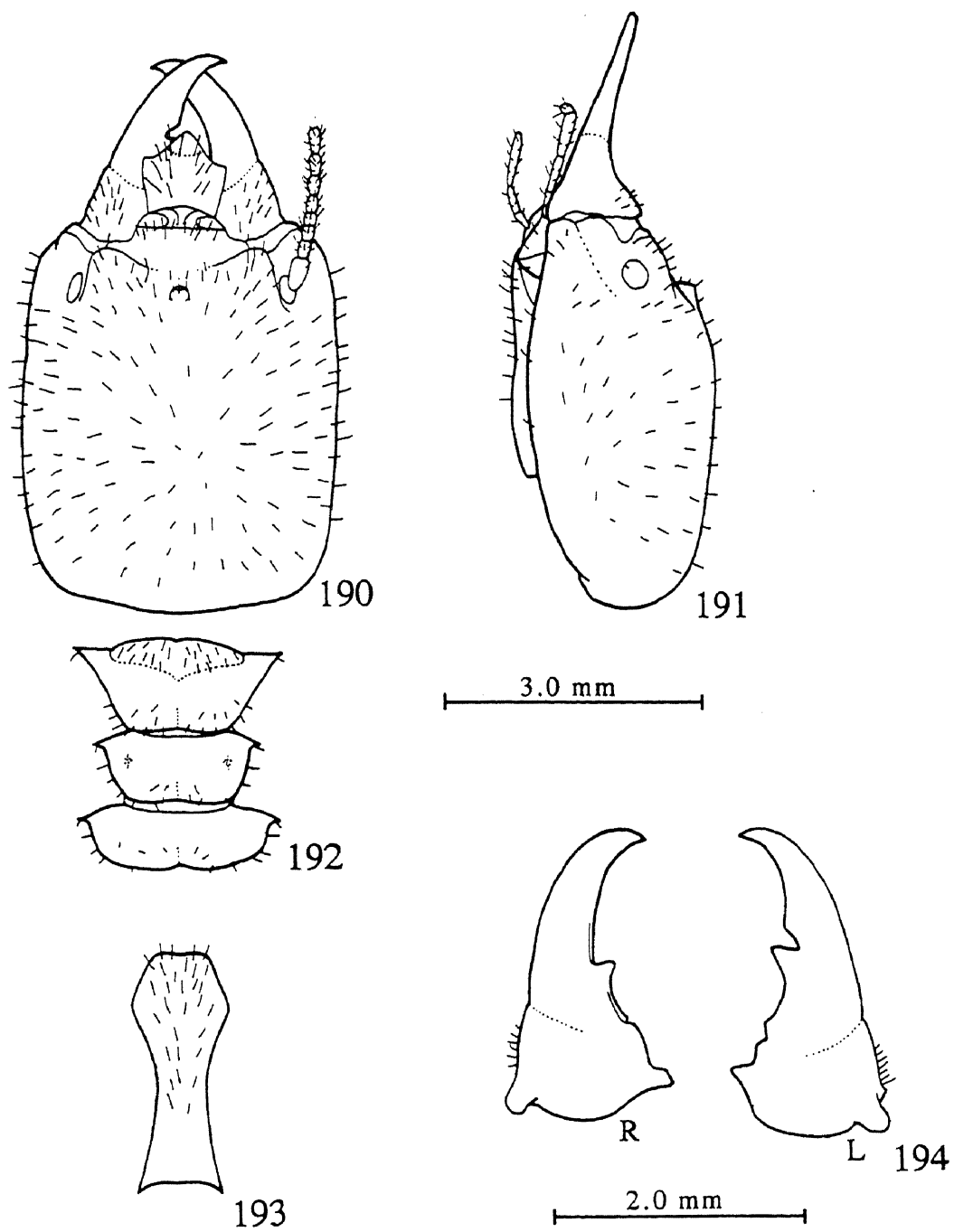
Figs. 173-177. *Syntermes grandis*, soldier from Suriname. 173. head, dorsal view; 174. head, lateral view; 175. thorax, dorsal view; 176. postmentum; 177. mandibles, ventral view.



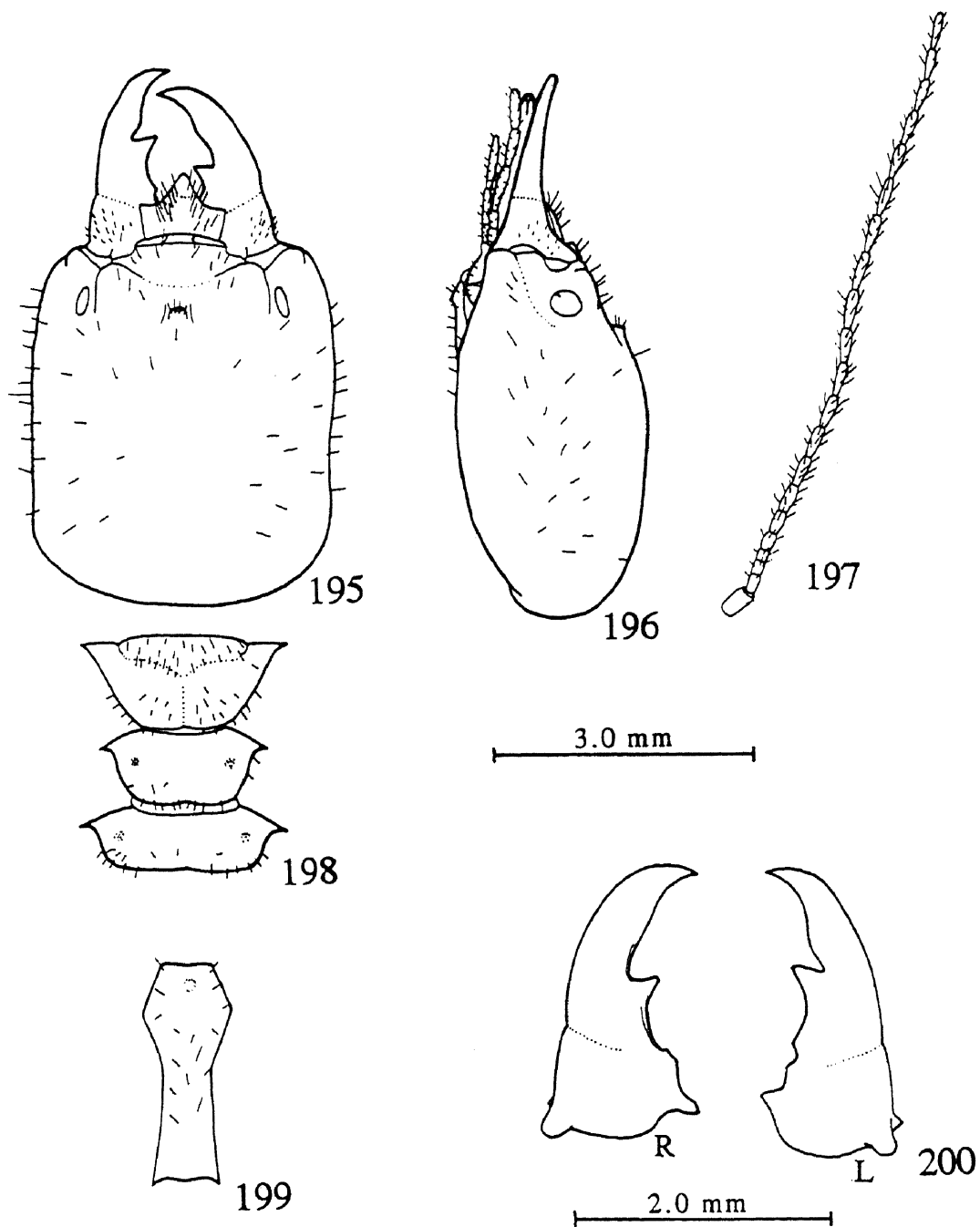
Figs. 178-183. *Syntermes grandis*, soldier from Bolivia, paratype of *S. lighti*. 178. head, dorsal view; 179. head, lateral view; 180. antenna; 181. thorax, dorsal view; 182. postmentum; 183. mandibles, ventral view.



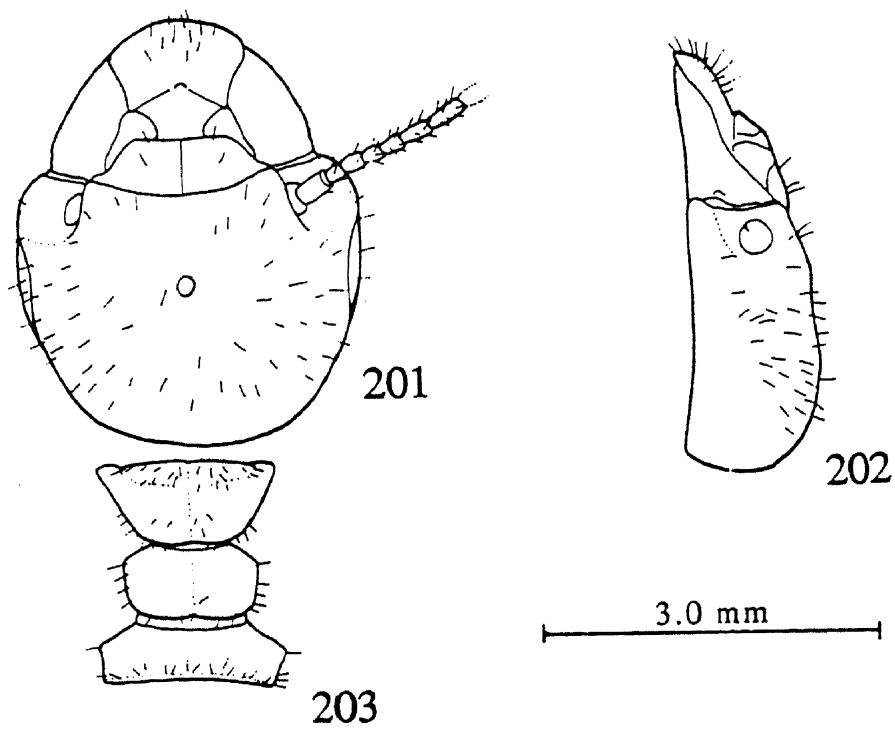
Figs. 184-189. *Syntermes grandis*. Imago: 184. head, dorsal view; 185. head, lateral view; 186. pronotum. Large worker: 187. head, dorsal view; 188. head, lateral view; 189. thorax.



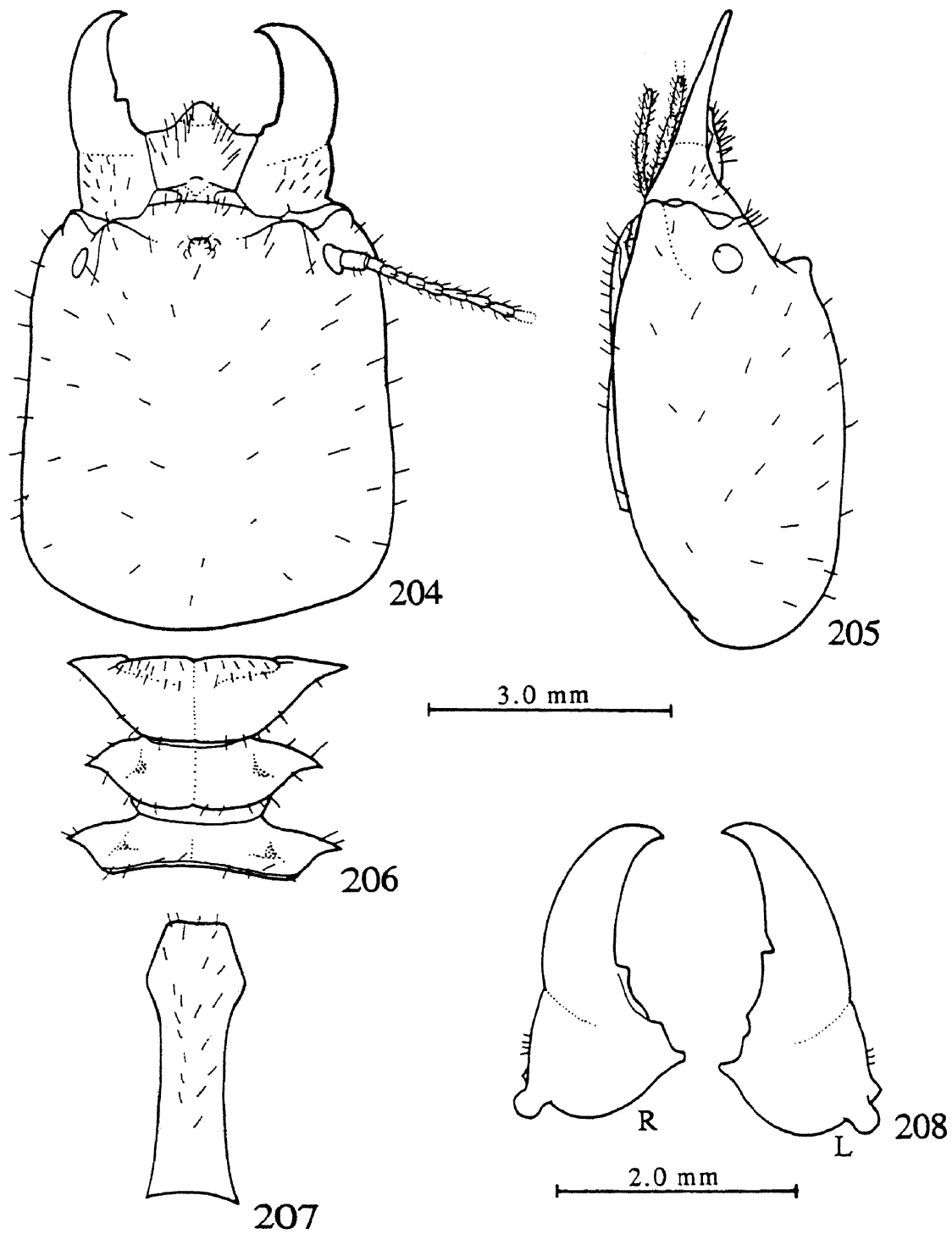
Figs. 190-194. *Syntermes insidians*, soldier from Minas Gerais. 190. head, dorsal view; 191. head, lateral view; 192. thorax, dorsal view; 193. postmentum; 194. mandibles, ventral view.



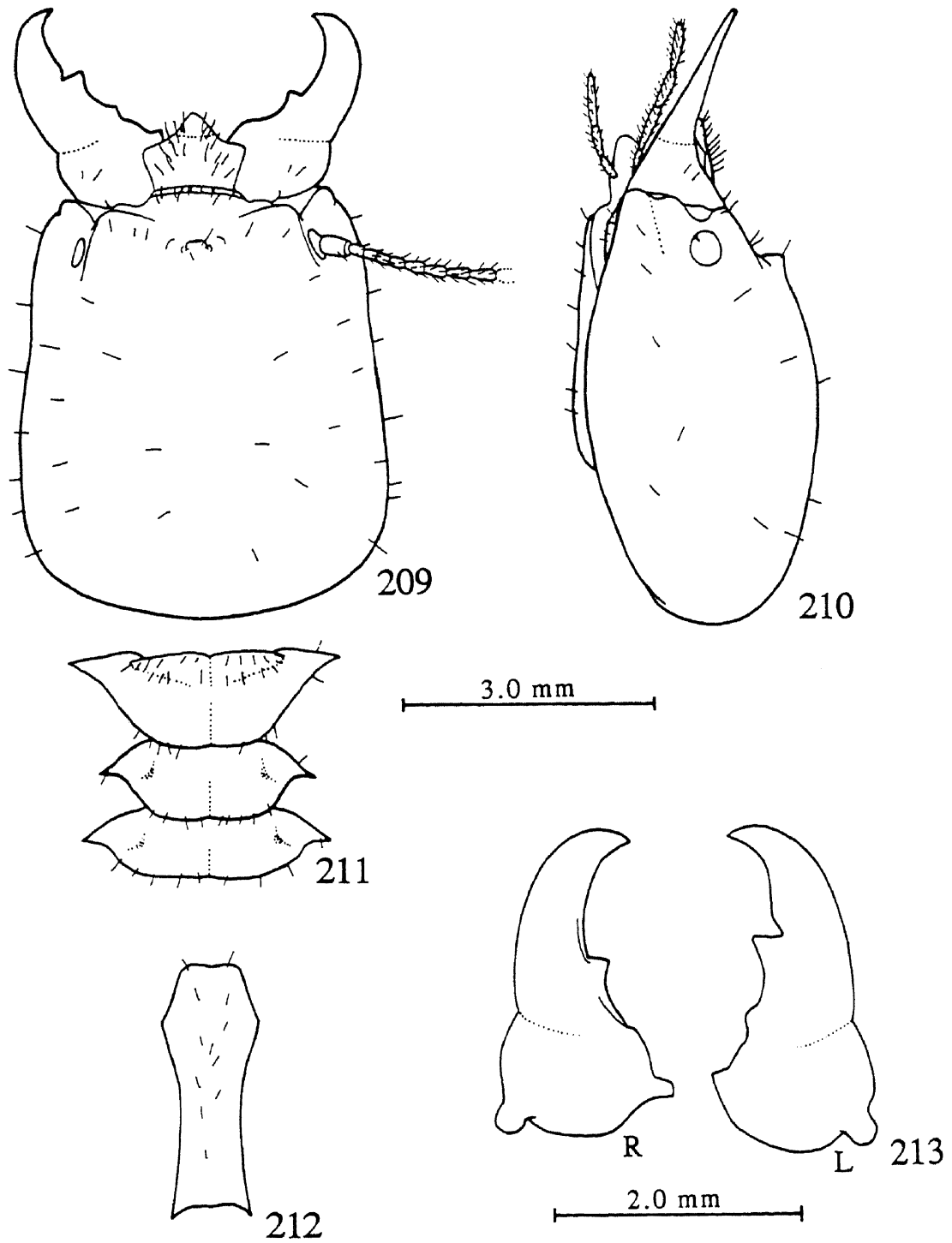
Figs. 195-200. *Syntermes insidians*, soldier from Mato Grosso. 195. head, dorsal view; 196. head, lateral view; 197. antenna; 198. thorax, dorsal view; 199. postmentum; 200. mandibles, ventral view.



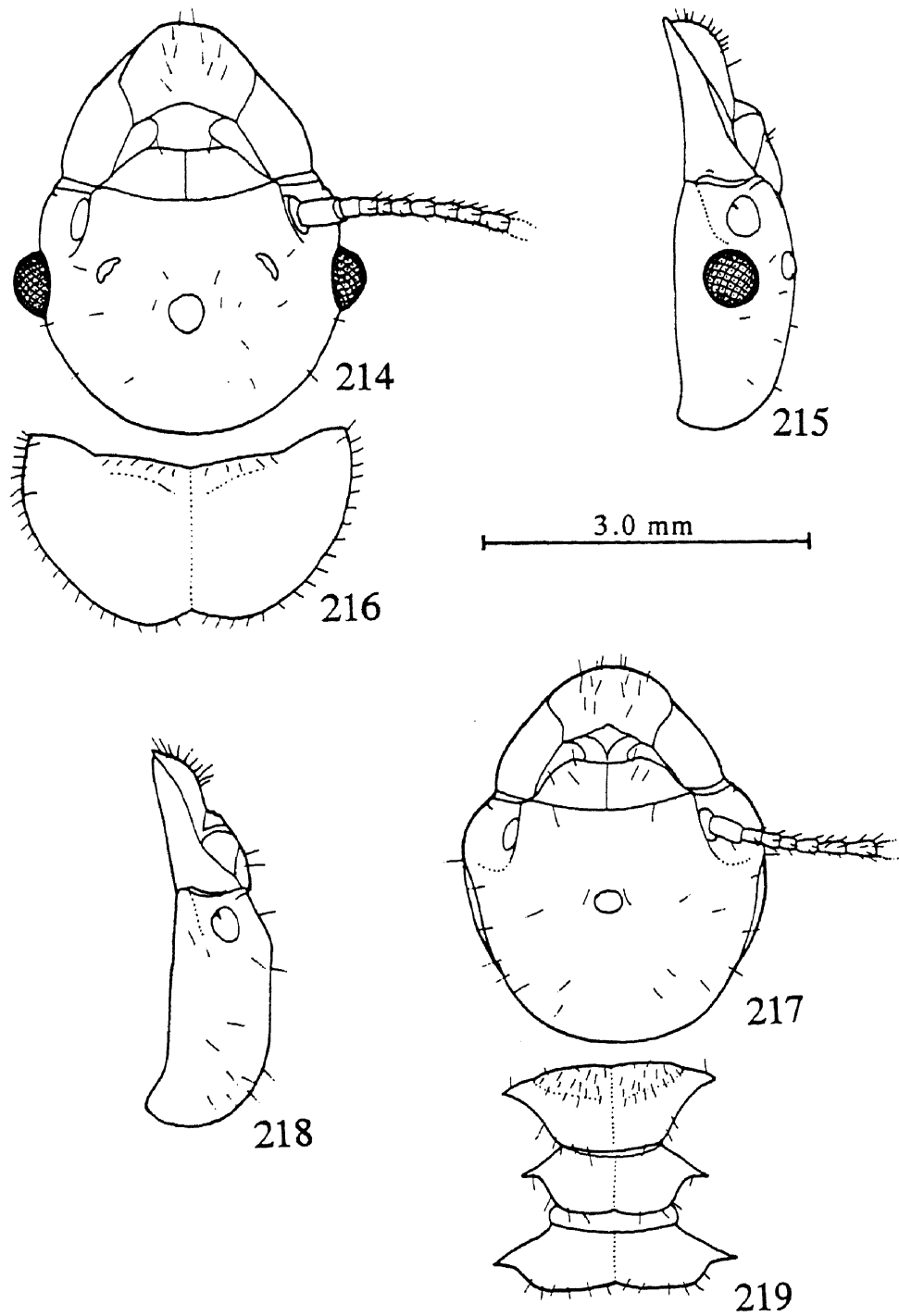
Figs. 201-203. *Syntermes insidians*. Large worker: 201. head, dorsal view; 202. head, lateral view; 203. thorax.



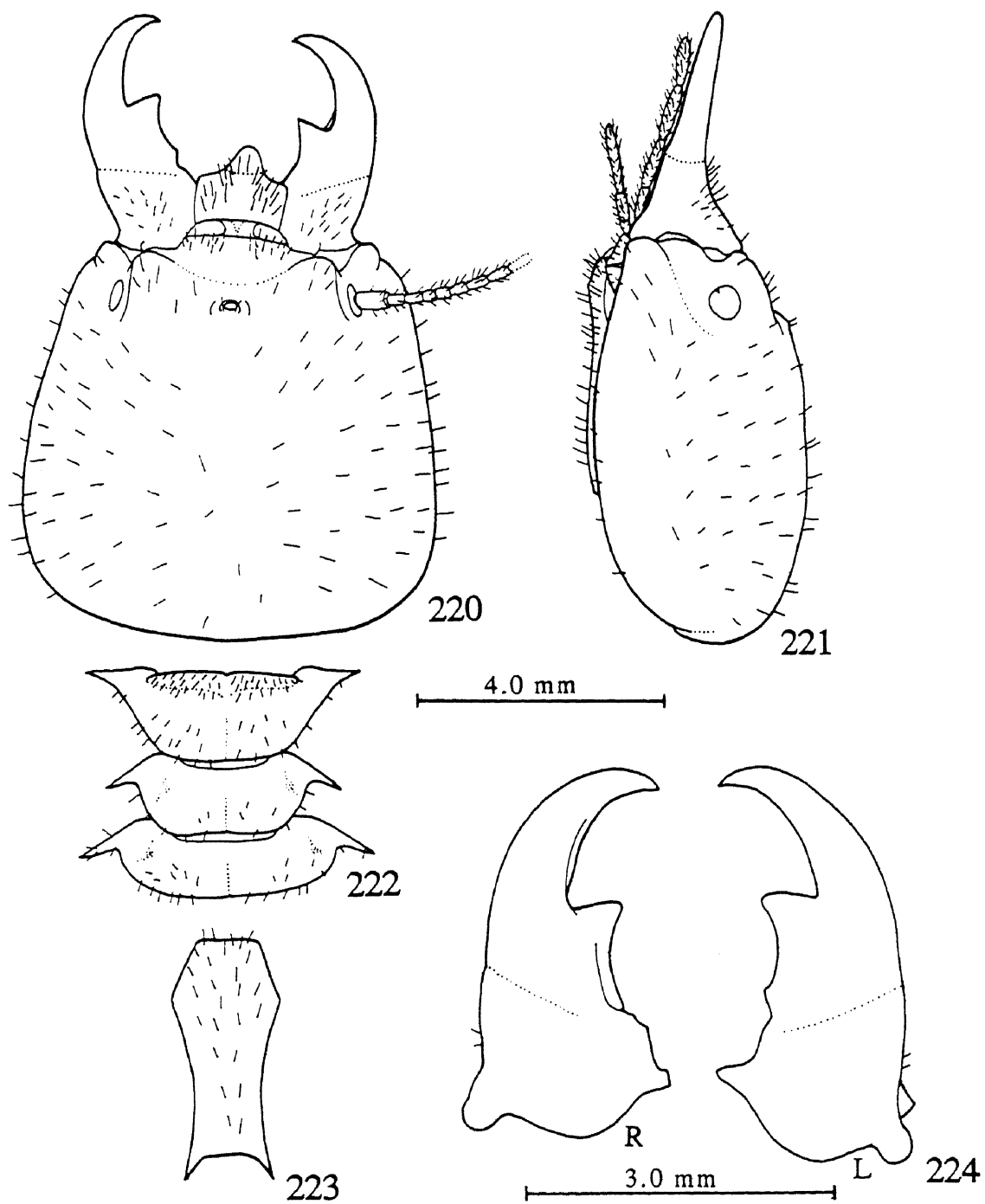
Figs. 204-208. *Syntermes longiceps*, new species, soldier from Roraima. 204. head, dorsal view; 205. head, lateral view; 206. thorax, dorsal view; 207. postmentum; 208. mandibles, ventral view.



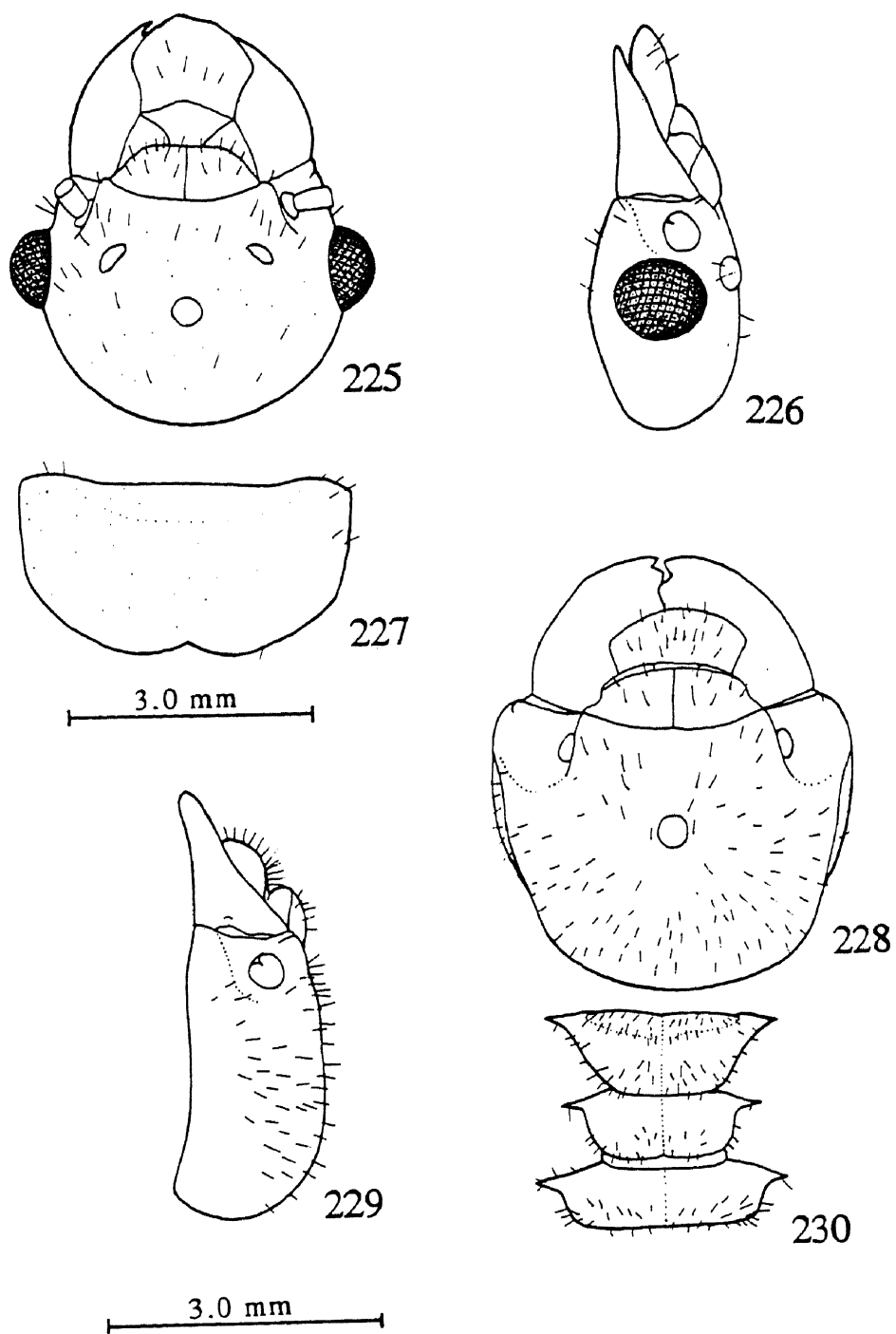
Figs. 209-213. *Syntermes longiceps*, new species, soldier from Manaus. 209. head, dorsal view; 210. head, lateral view; 211. thorax, dorsal view; 212. postmentum; 213. mandibles, ventral view.



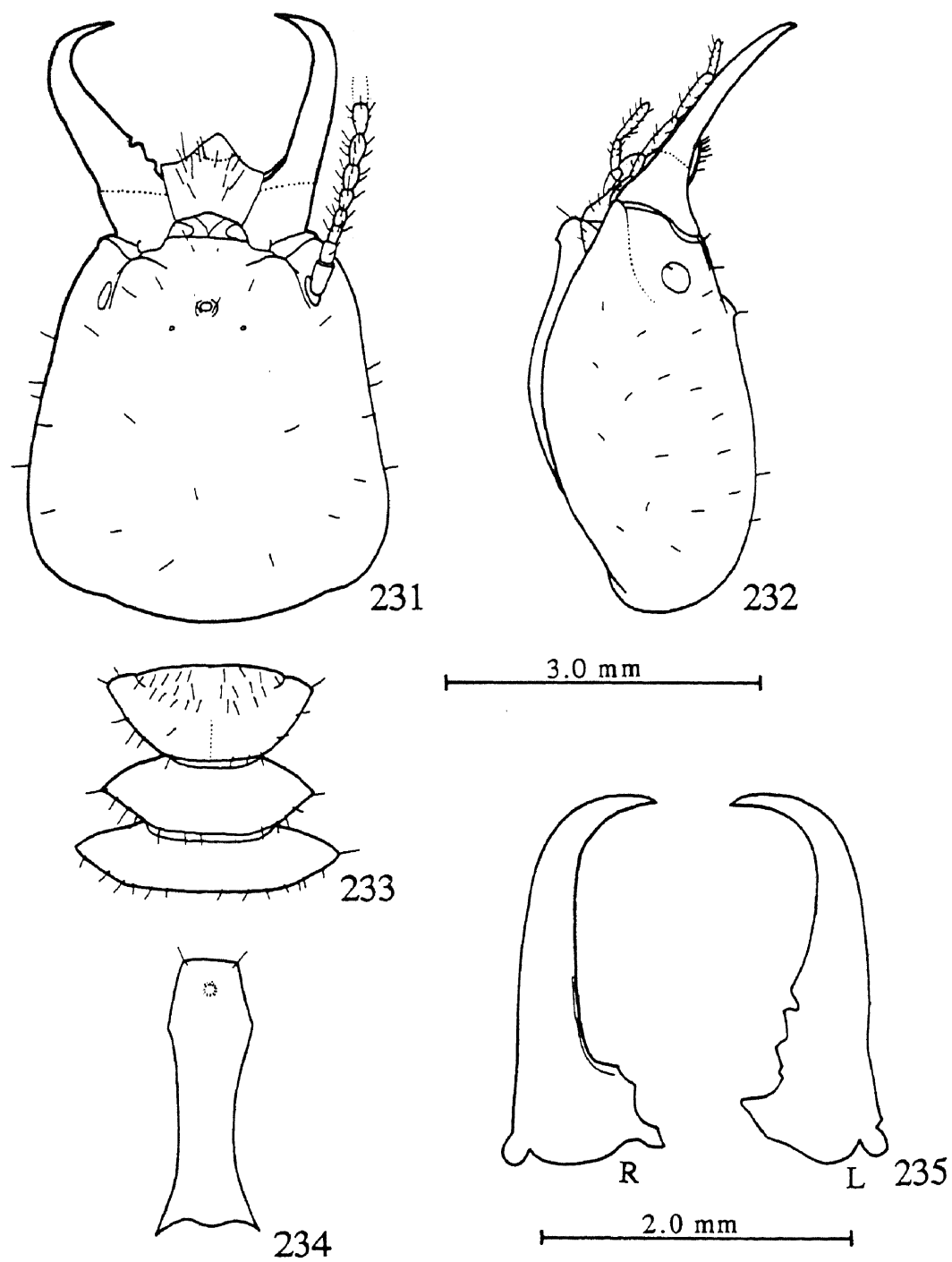
Figs. 214-219. *Syntermes longiceps*, new species. Imago: 214. head, dorsal view; 215. head, lateral view; 216. pronotum. Large worker: 217. head, dorsal view; 218. head, lateral view; 219. thorax.



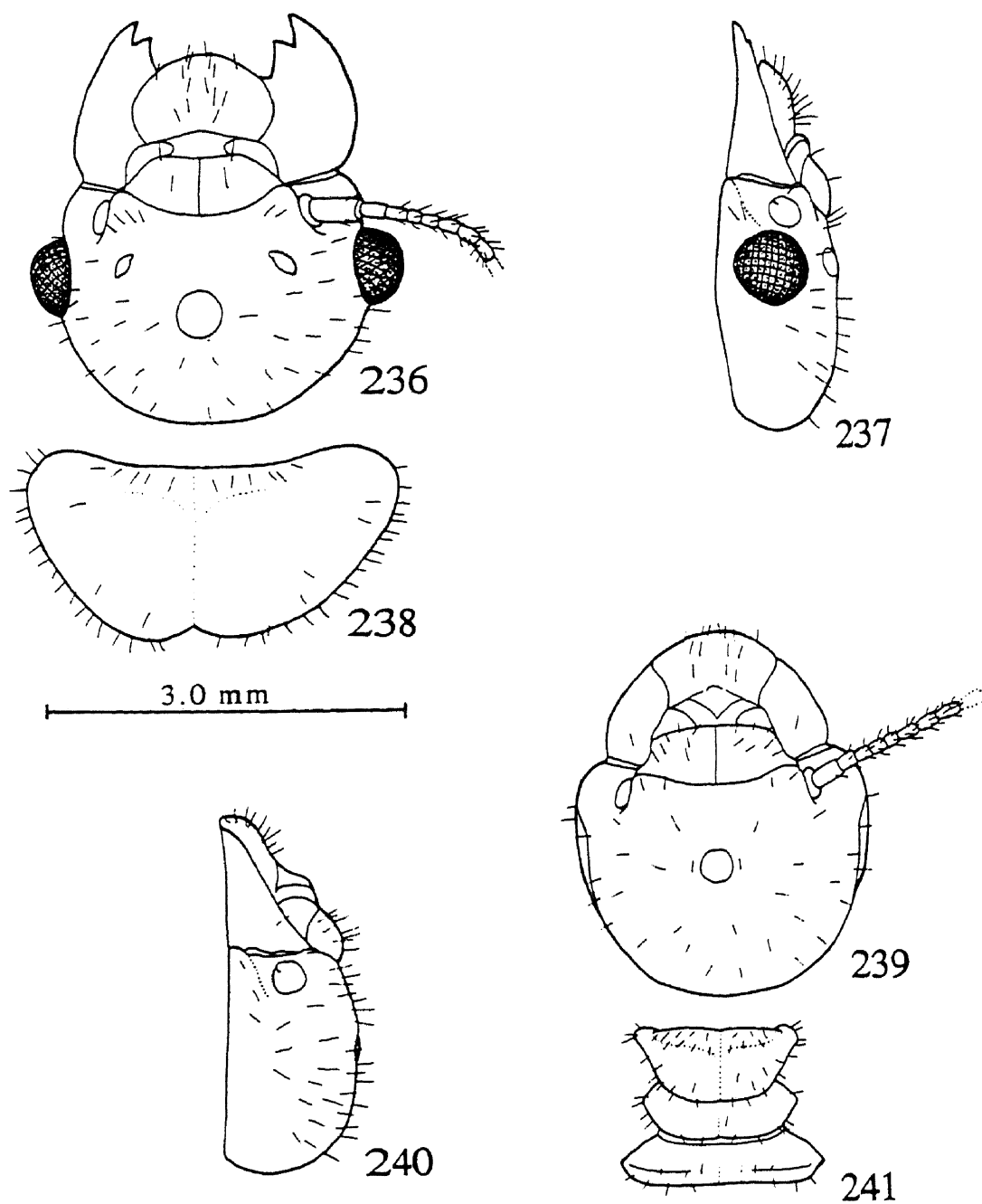
Figs. 220-224. *Syntermes magnoculus*, soldier. 220. head, dorsal view; 221. head, lateral view; 222. thorax, dorsal view; 223. postmentum; 224. mandibles, ventral view.



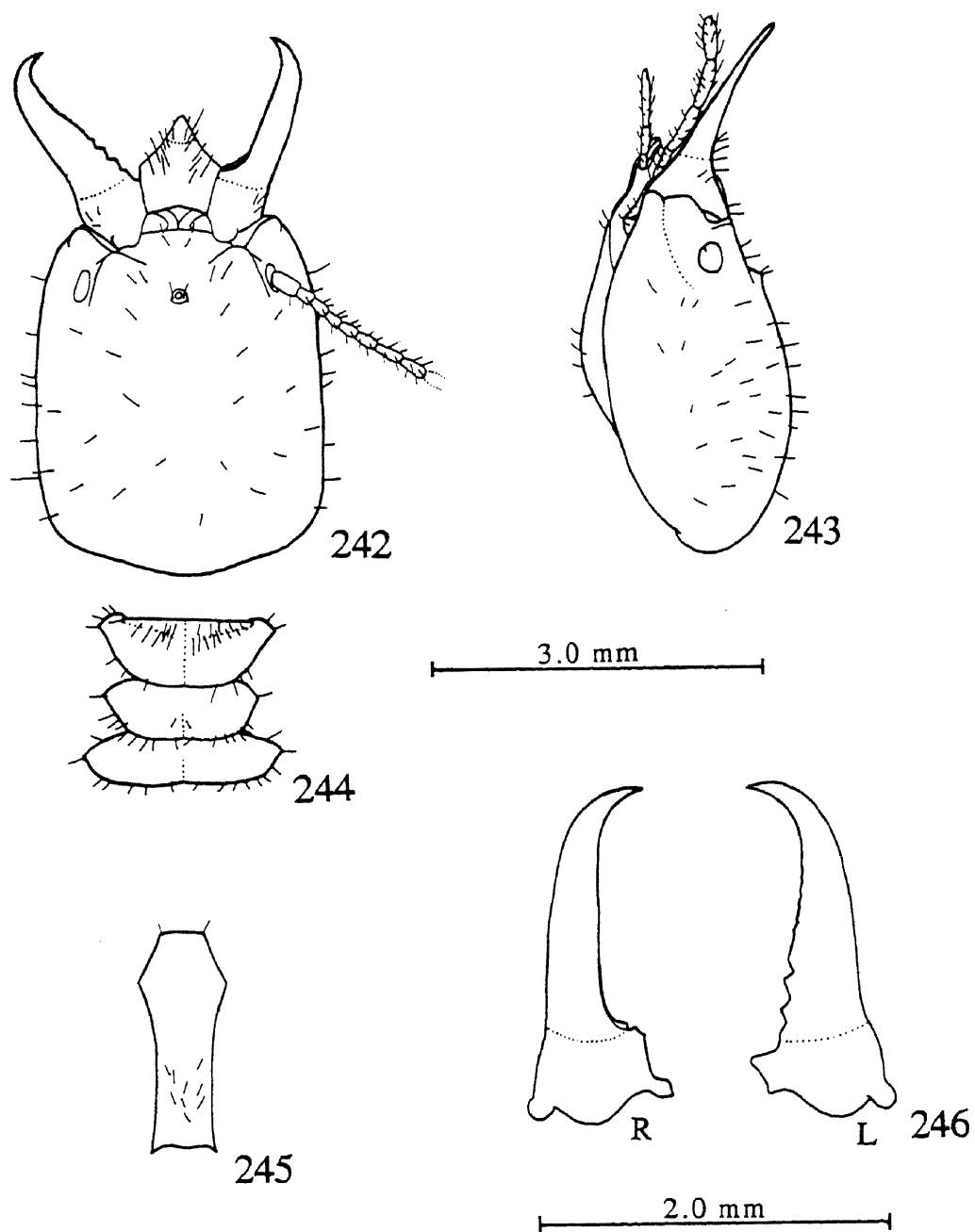
Figs. 225-230. *Syntermes magnoculus*. Holotype imago: 225. head, dorsal view; 226. head, lateral view; 227. pronotum. Large worker: 228. head, dorsal view; 229. head, lateral view; 230. thorax.



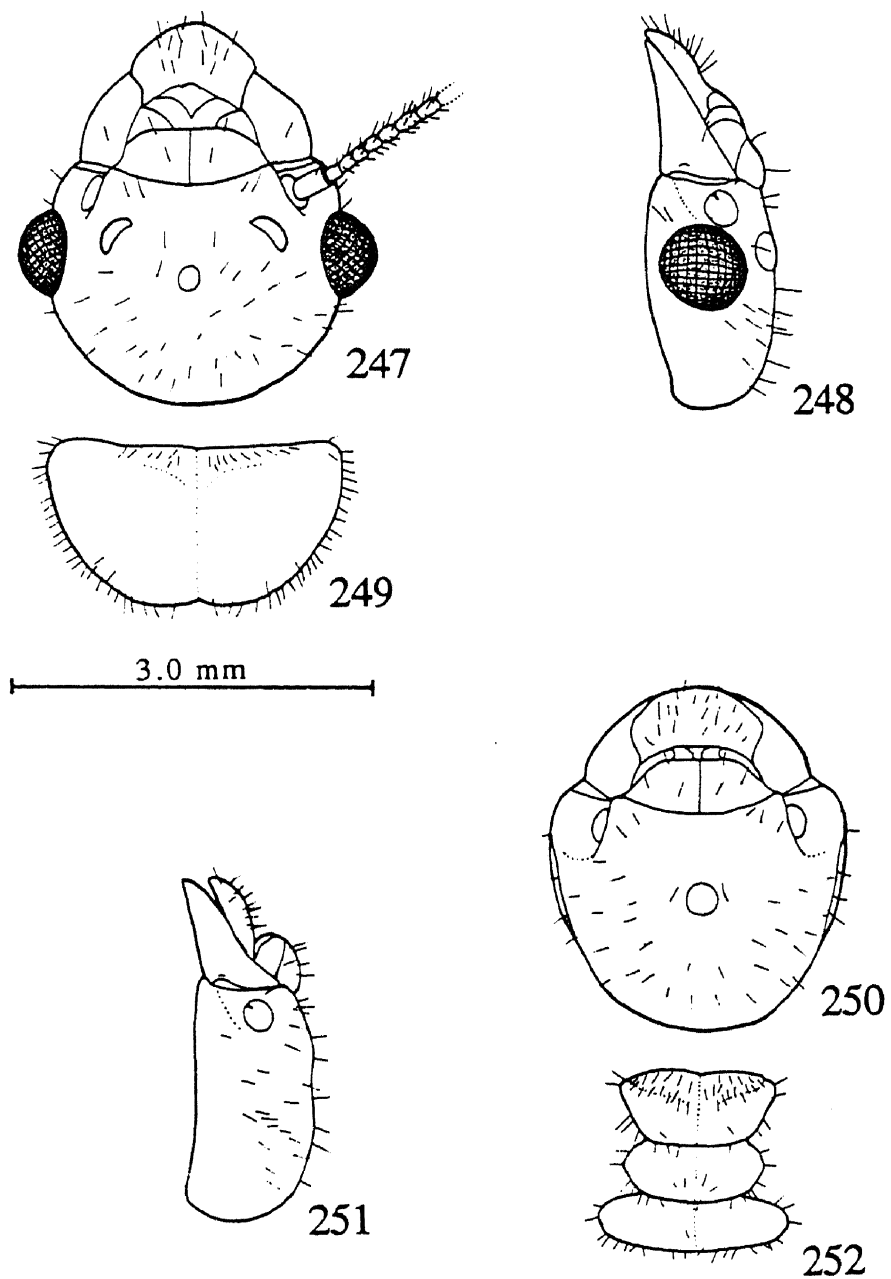
Figs. 231-235. *Syntermes molestus*, soldier. 231. head, dorsal view; 232. head, lateral view; 233. thorax, dorsal view; 234. postmentum; 235. mandibles, ventral view.



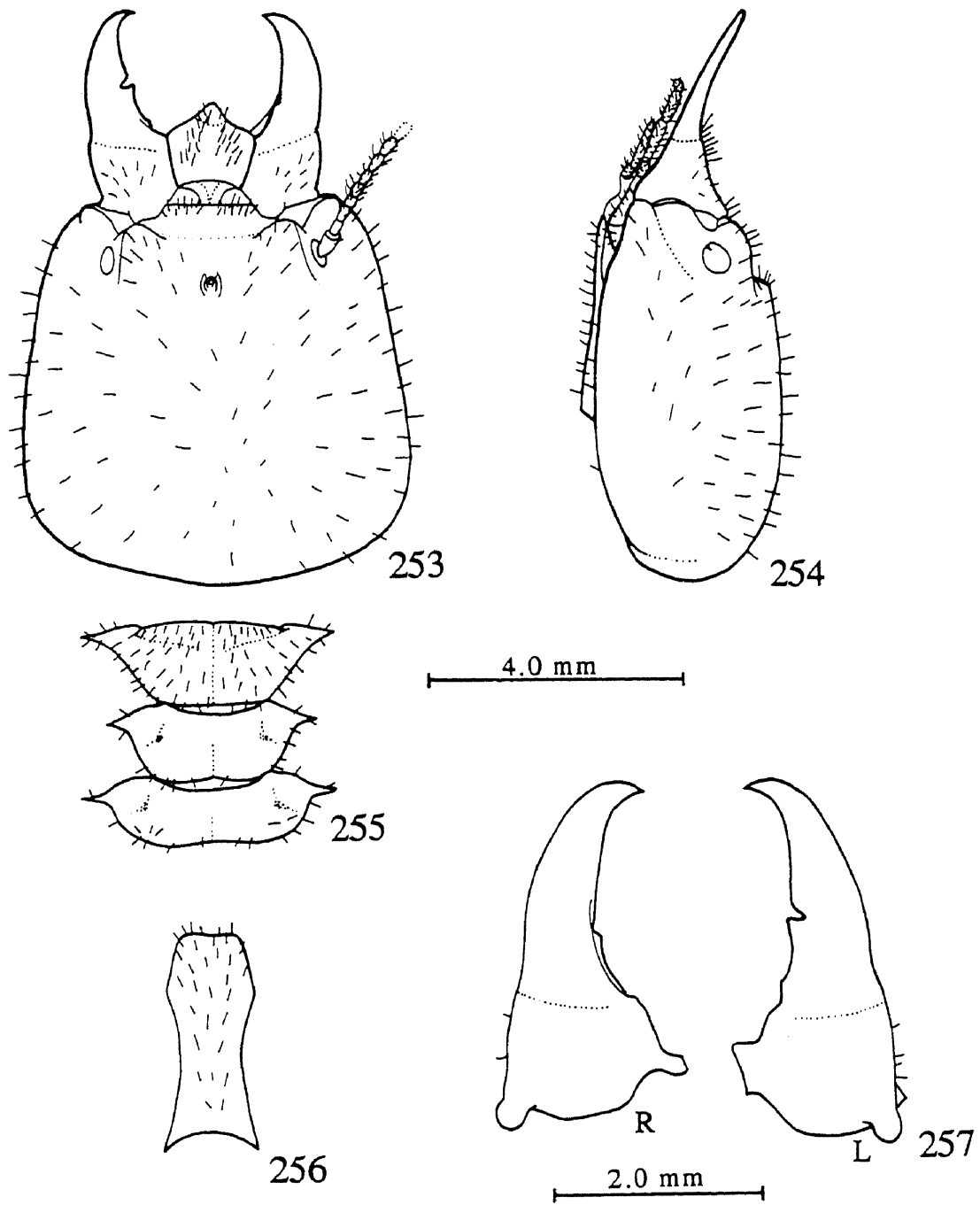
Figs. 236-241. *Syntermes molestus*. Imago: 236. head, dorsal view; 237. head, lateral view; 238. pronotum. Large worker: 239. head, dorsal view; 240. head, lateral view; 241. thorax.



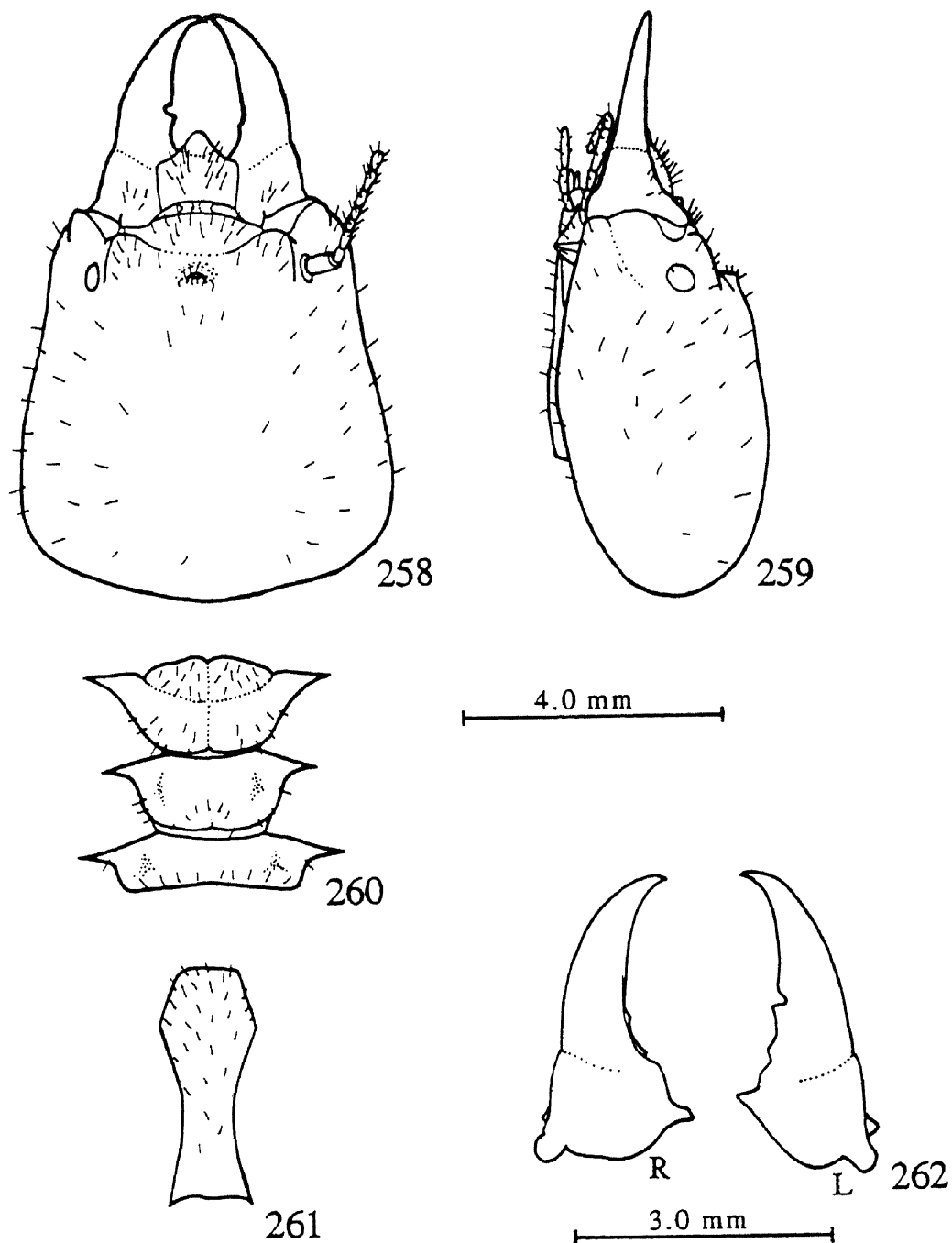
Figs. 242-246. *Syntermes nanus*, new species, soldier. 242. head, dorsal view; 243. head, lateral view; 244. thorax, dorsal view; 245. postmentum; 246. mandibles, ventral view.



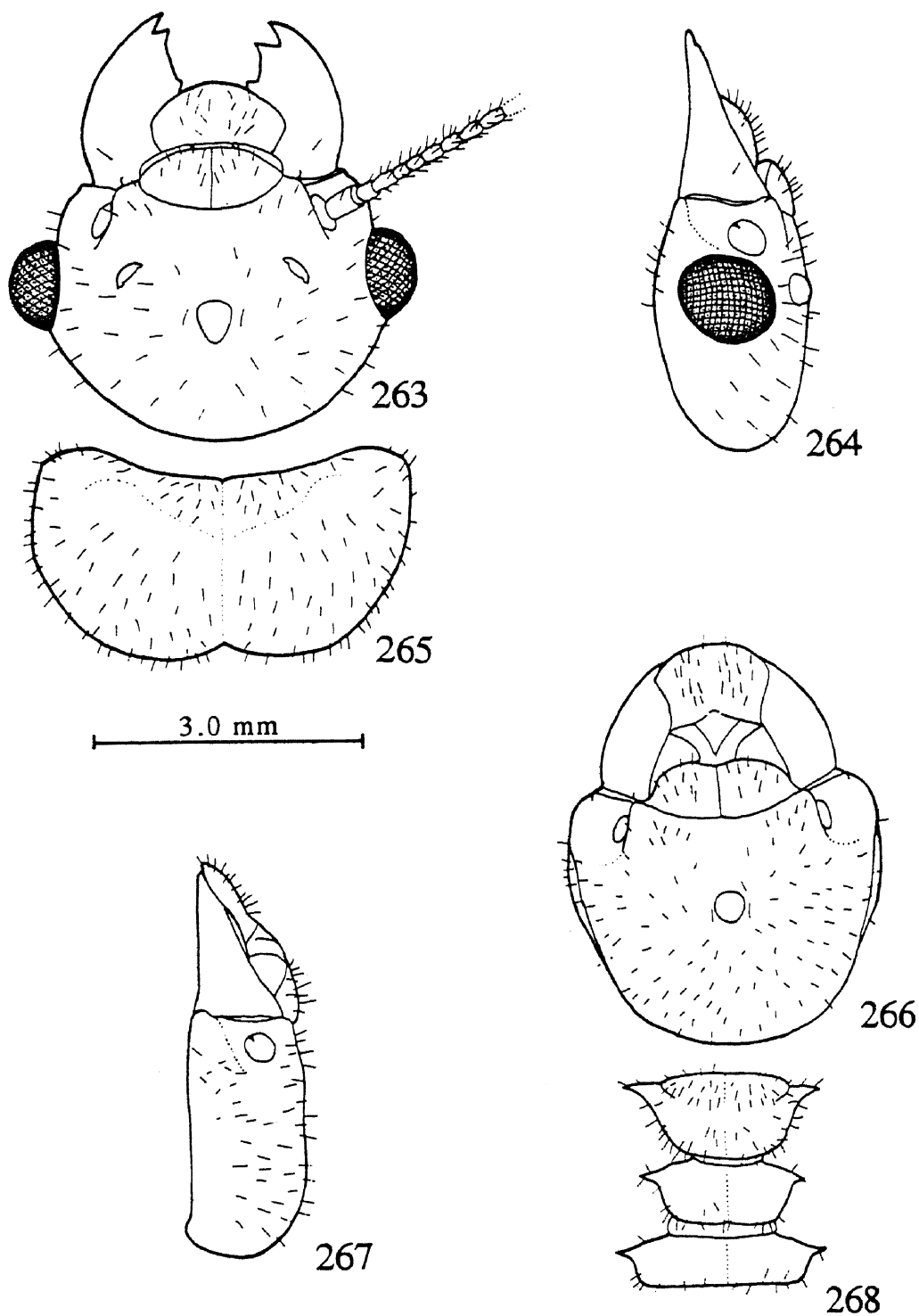
Figs. 247-252. *Syntermes nanus*, new species. Imago: 247. head, dorsal view; 248. head, lateral view; 249. pronotum. Large worker: 250. head, dorsal view; 251. head, lateral view; 252. thorax.



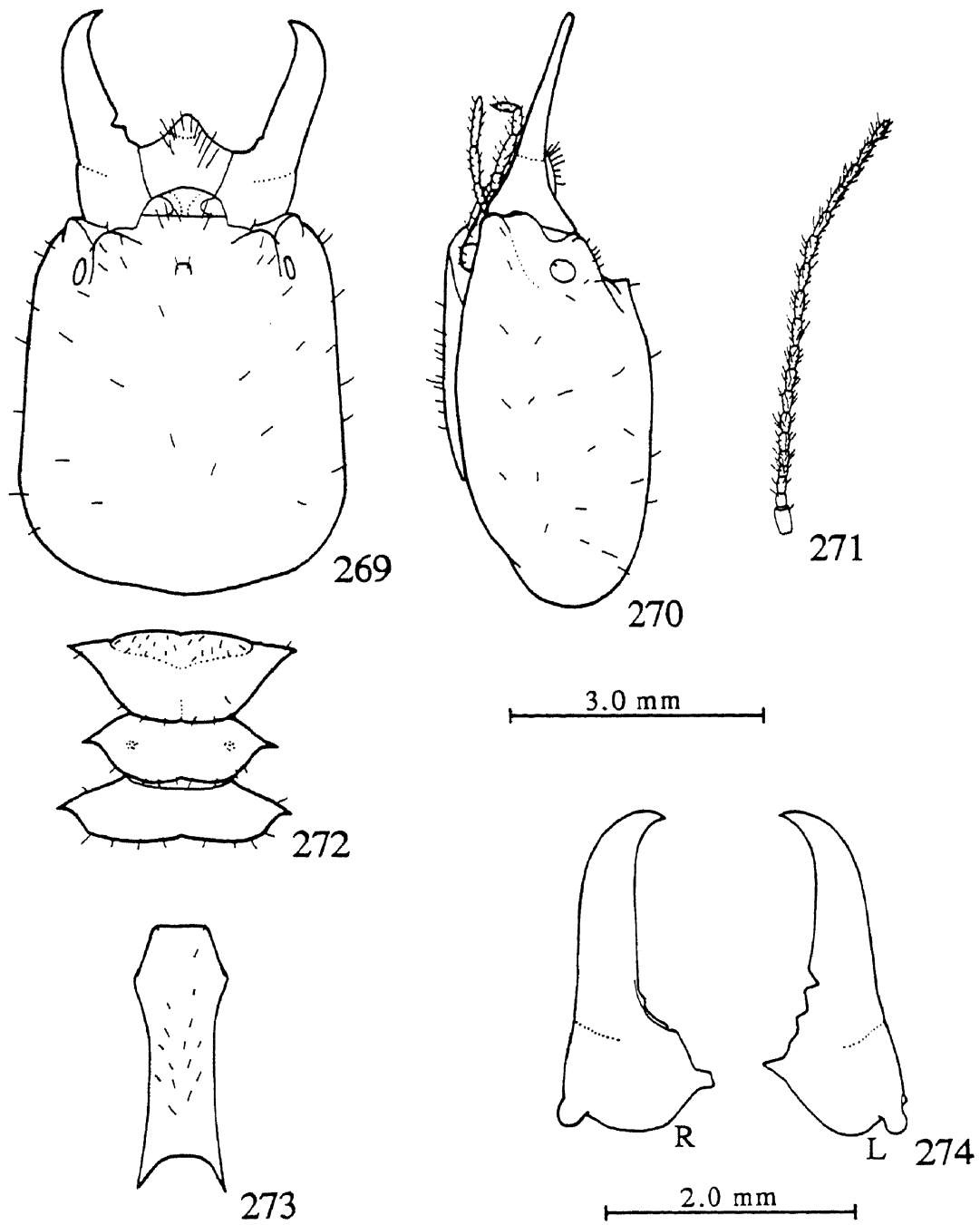
Figs. 253-257. *Syntermes obtusus*, soldier from Argentina. 253. head, dorsal view; 254. head, lateral view; 255. thorax, dorsal view; 256. postmentum; 257. mandibles, ventral view.



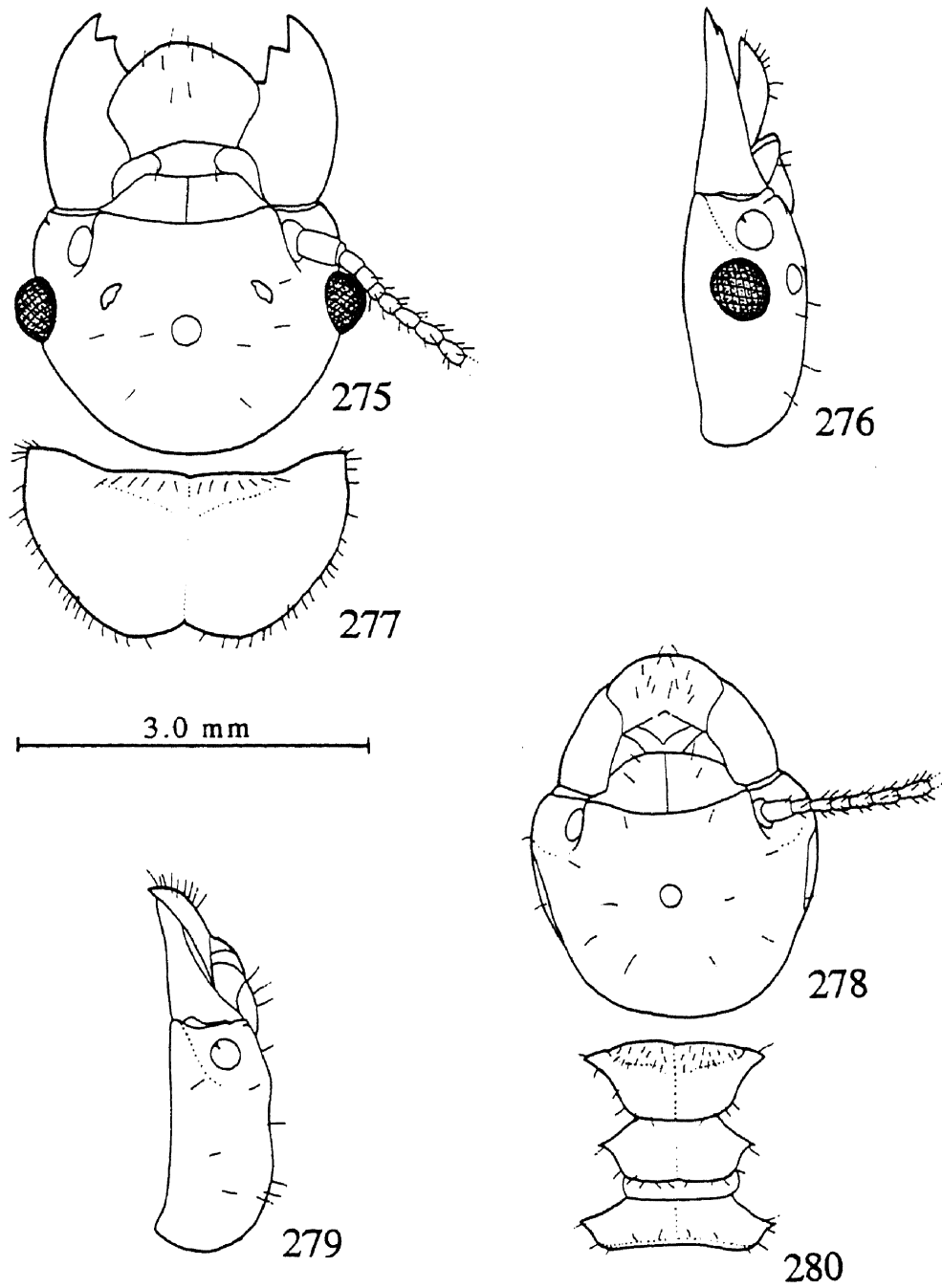
Figs. 258-262. *Syntermes obtusus*, soldier from Cuiabá, lectotype of *S. silvestrii*. 258. head, dorsal view; 259. head, lateral view; 260. thorax, dorsal view; 261. postmentum; 262. mandibles, ventral view.



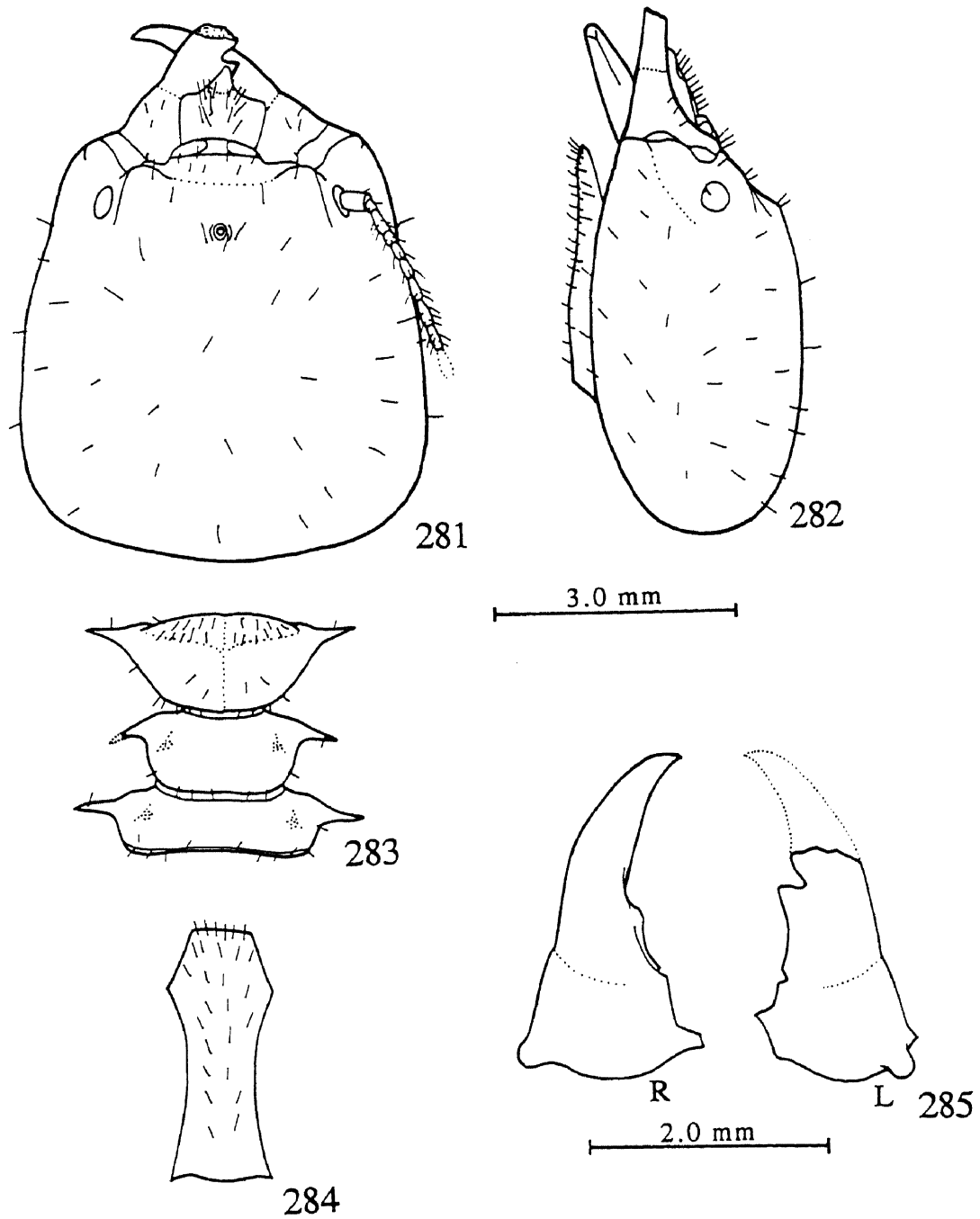
Figs. 263-268. *Syntermes obtusus*. Lectotype imago: 263. head, dorsal view; 264. head, lateral view; 265. pronotum. Large worker: 266. head, dorsal view; 267. head, lateral view; 268. thorax.



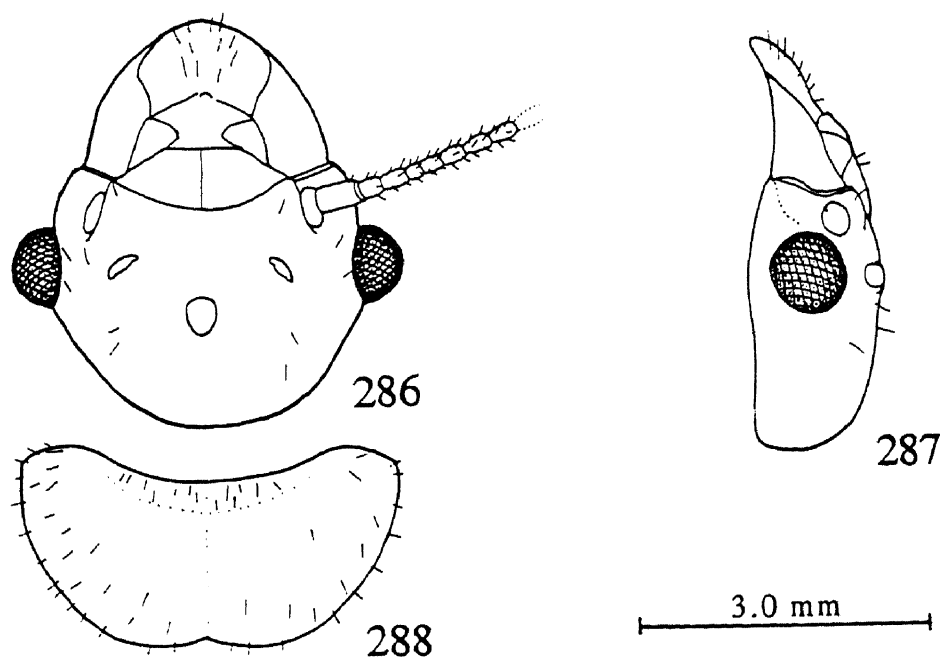
Figs. 269-274. *Syntermes parallelus*, soldier. 269. head, dorsal view; 270. head, lateral view; 271. antenna; 272. thorax, dorsal view; 273. postmentum; 274. mandibles, ventral view.



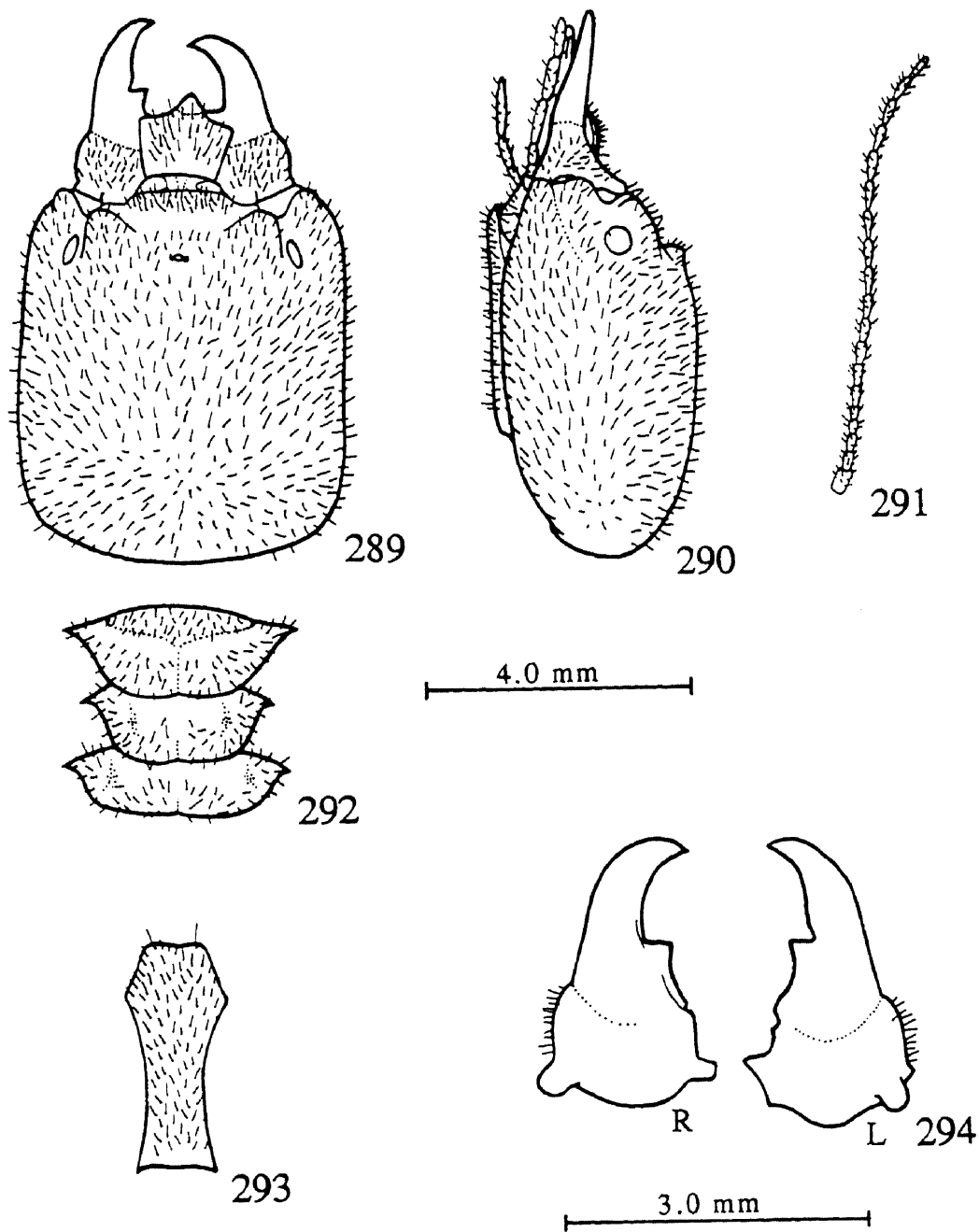
Figs. 275-280. *Syntermes parallelus*. Imago: 275. head, dorsal view; 276. head, lateral view; 277. pronotum. Large worker: 278. head, dorsal view; 279. head, lateral view; 280. thorax.



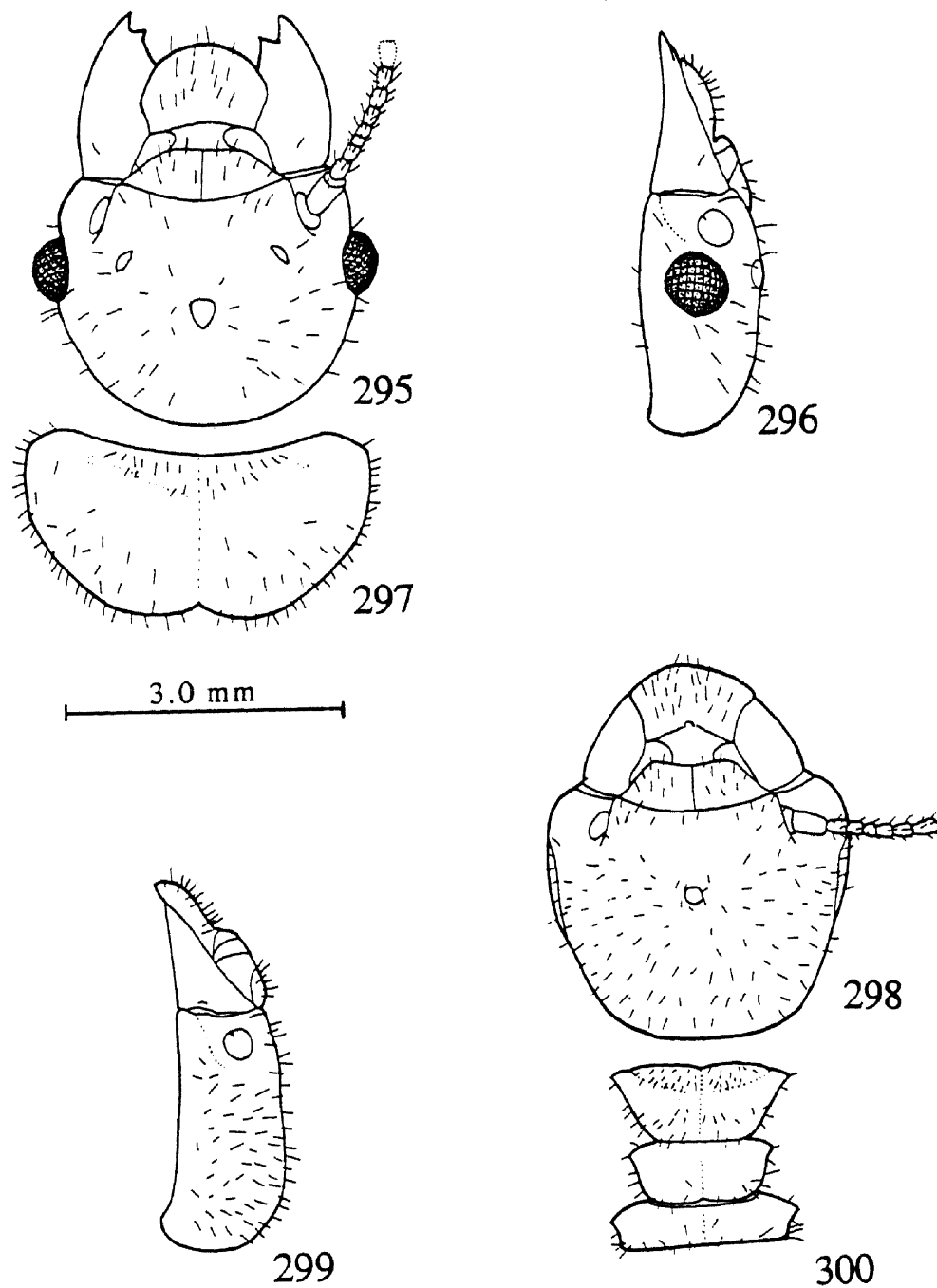
Figs. 281-285. *Syntermes peruanus*, lectotype soldier. 281. head, dorsal view; 282. head, lateral view; 283. thorax, dorsal view; 284. postmentum; 285. mandibles, ventral view.



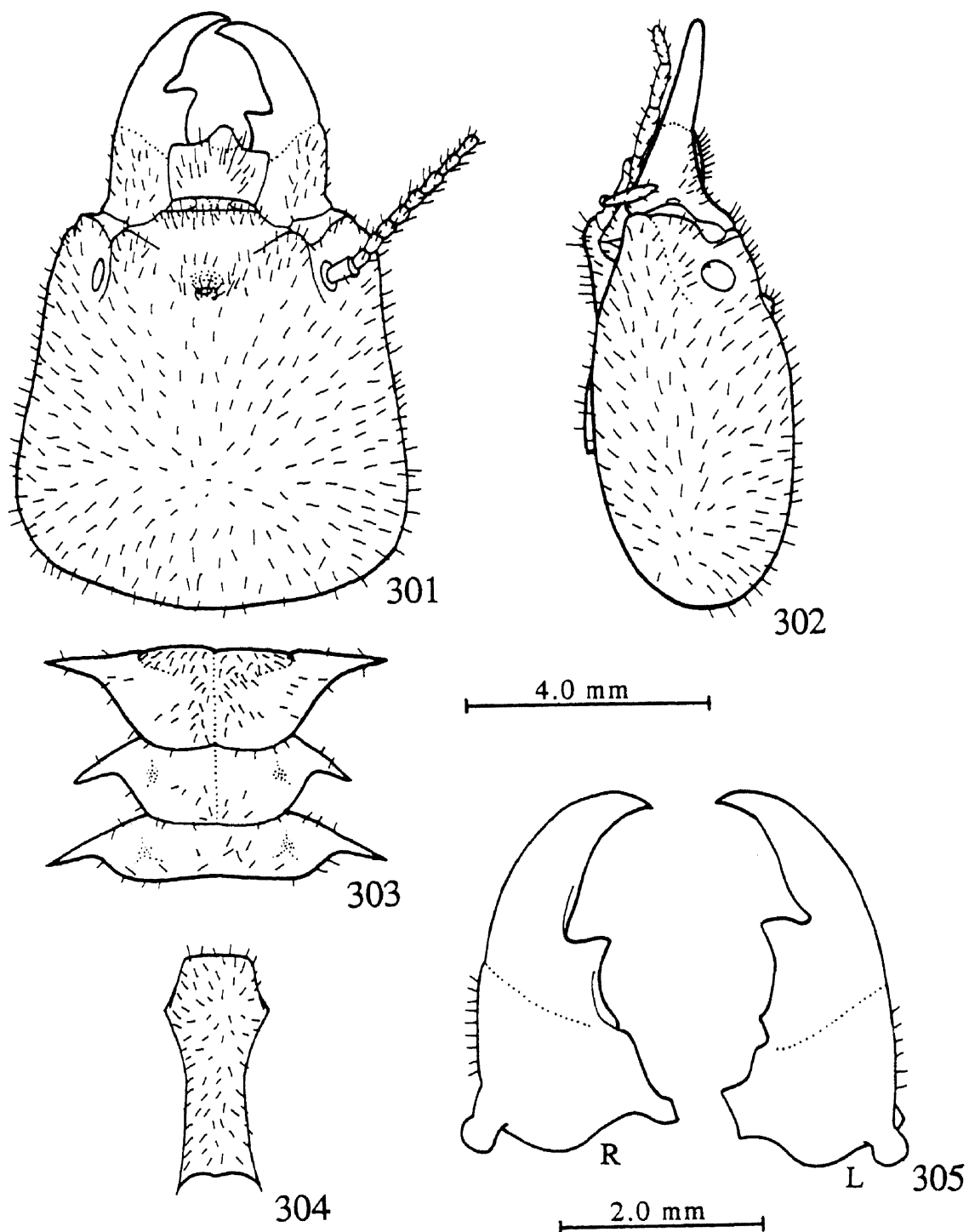
Figs. 286-288. *Syntermes peruanus*, imago: 286. head, dorsal view; 287. head, lateral view; 288. pronotum.



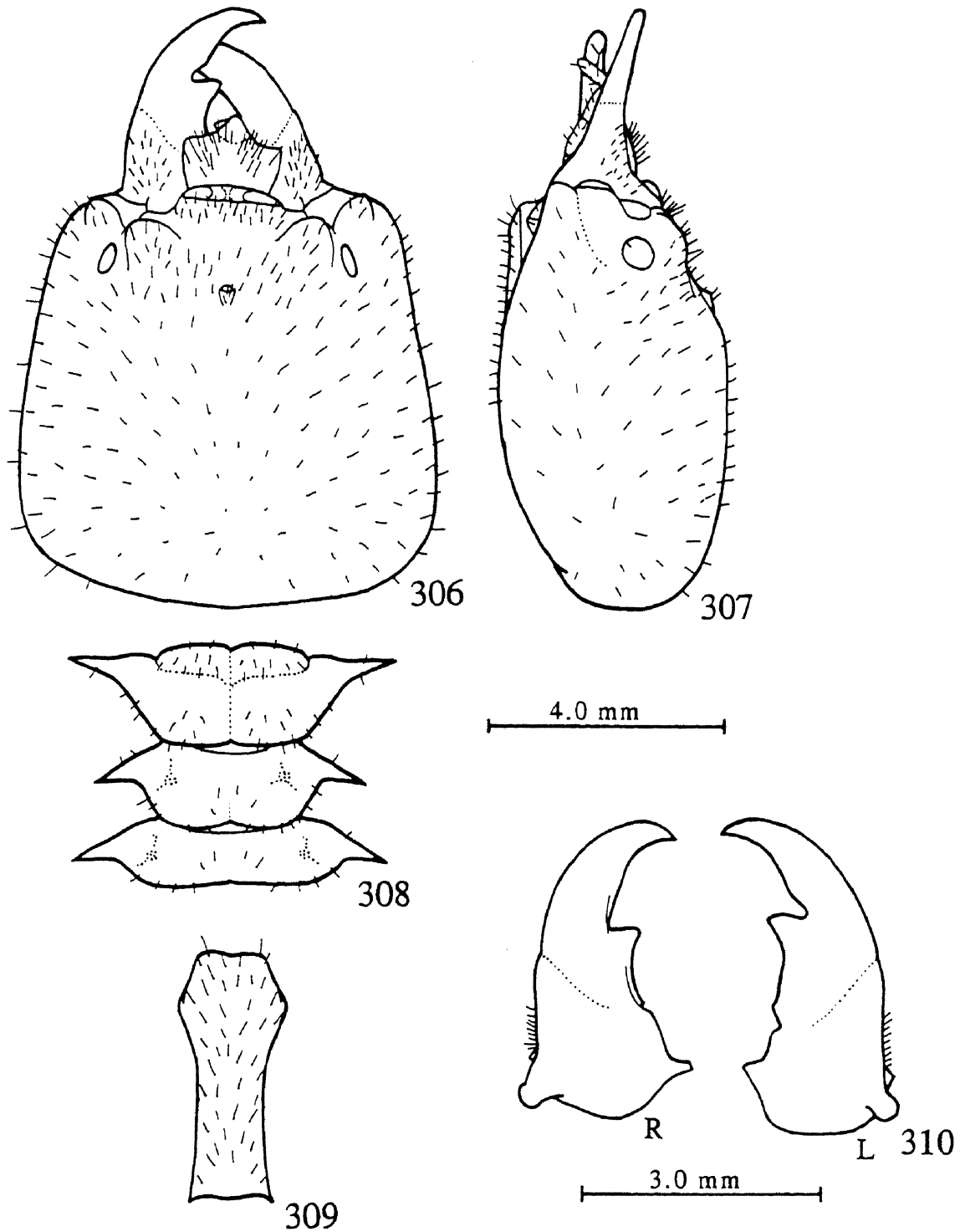
Figs. 289-294. *Syntermes praecellens*, soldier. 289. head, dorsal view; 290. head, lateral view; 291. antenna; 292. thorax, dorsal view; 293. postmentum; 294. mandibles, ventral view.



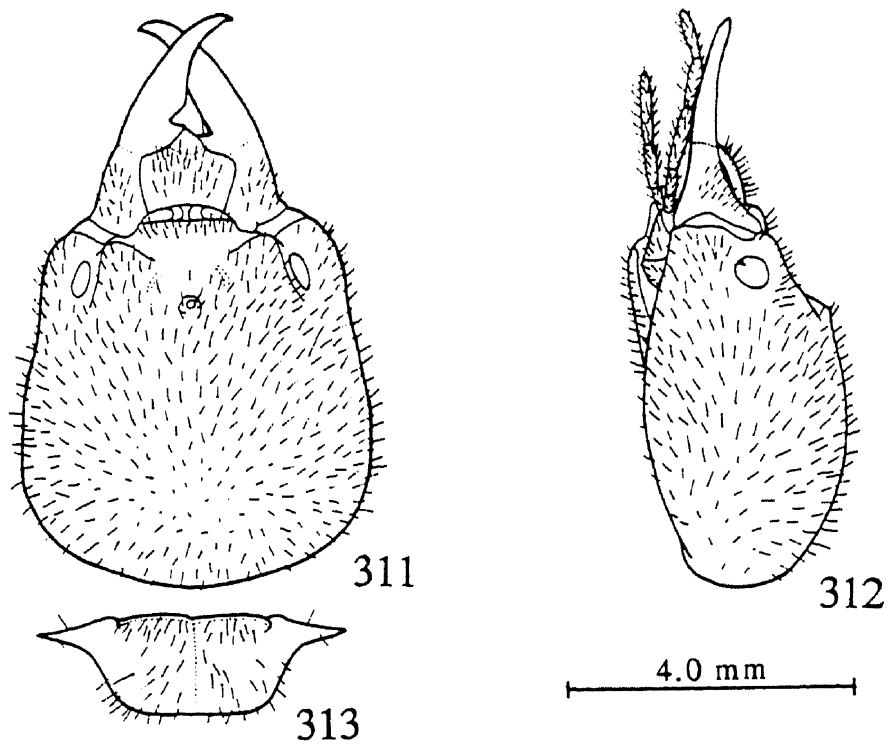
Figs. 295-300. *Syntermes praecellens*. Imago: 295. head, dorsal view; 296. head, lateral view; 297. pronotum. Large worker: 298. head, dorsal view; 299. head, lateral view; 300. thorax.



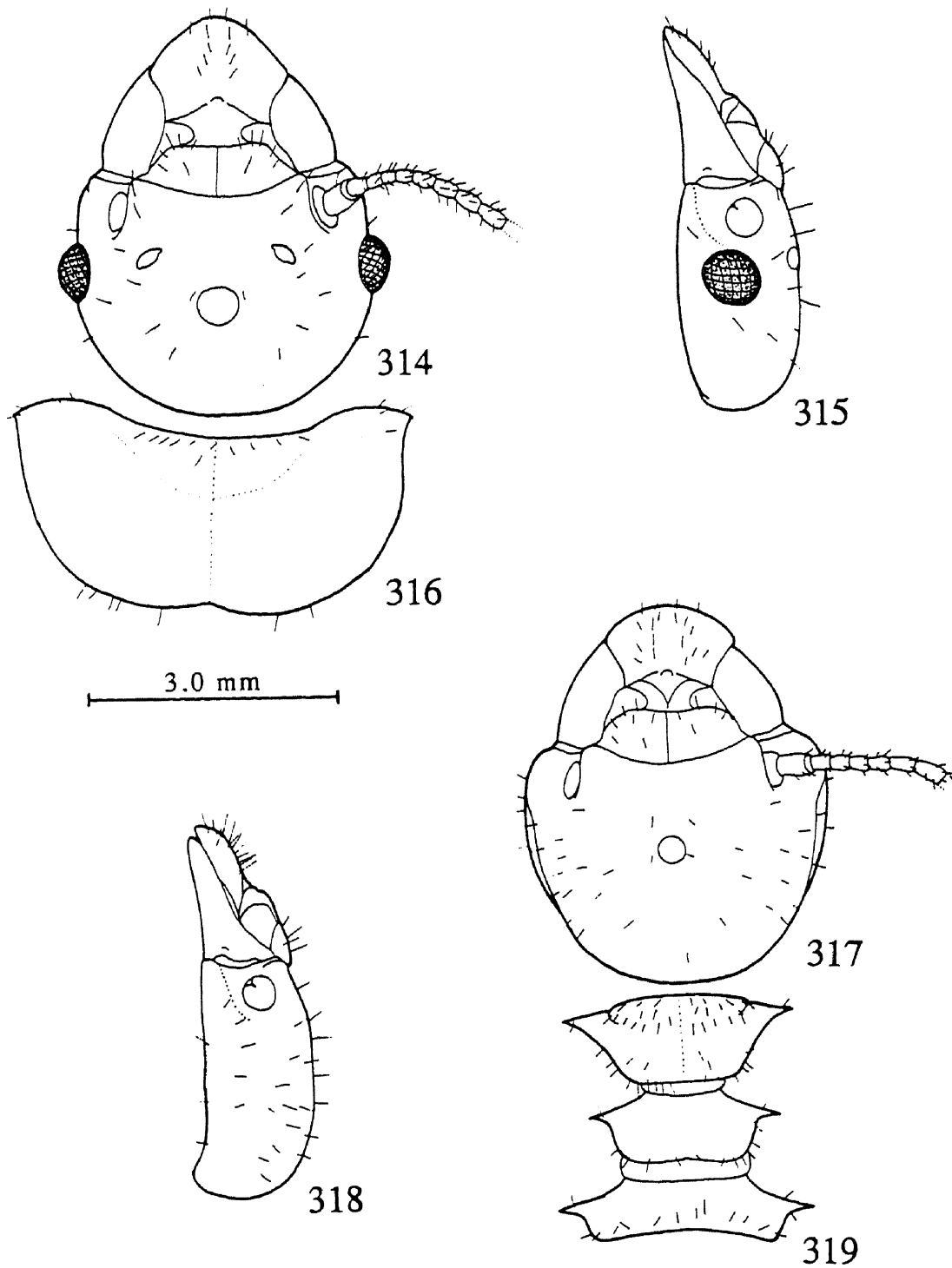
Figs. 301-305. *Syntermes spinosus*, soldier from central Amazonia. 301. head, dorsal view; 302. head, lateral view; 303. thorax, dorsal view; 304. postmentum; 305. mandibles, ventral view.



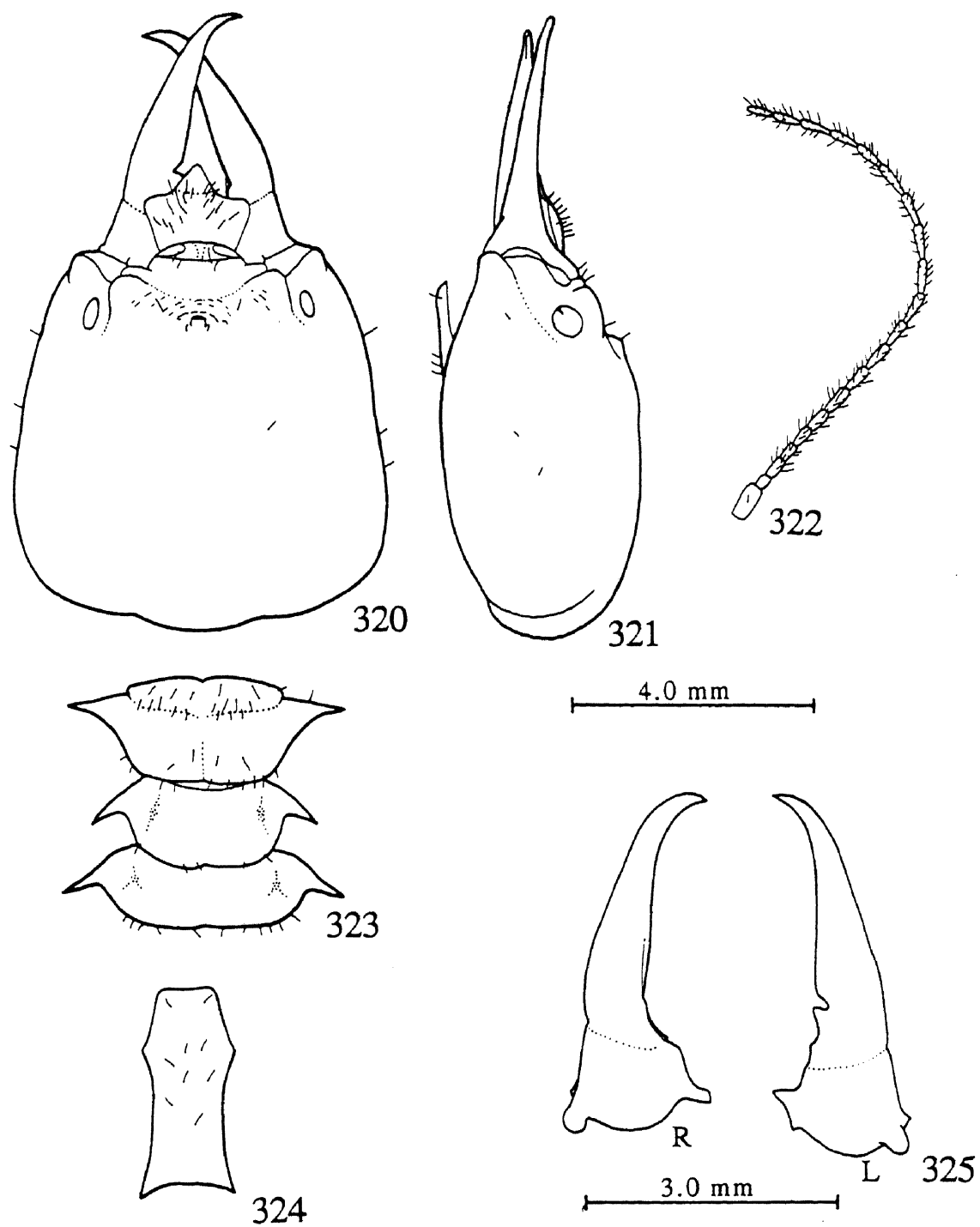
Figs. 306-310. *Syntermes spinosus*, soldier from western Amazonia, paratype of *S. chaquimayensis parvinasus*. 306. head, dorsal view; 307. head, lateral view; 308. thorax, dorsal view; 309. postmentum; 310. mandibles, ventral view.



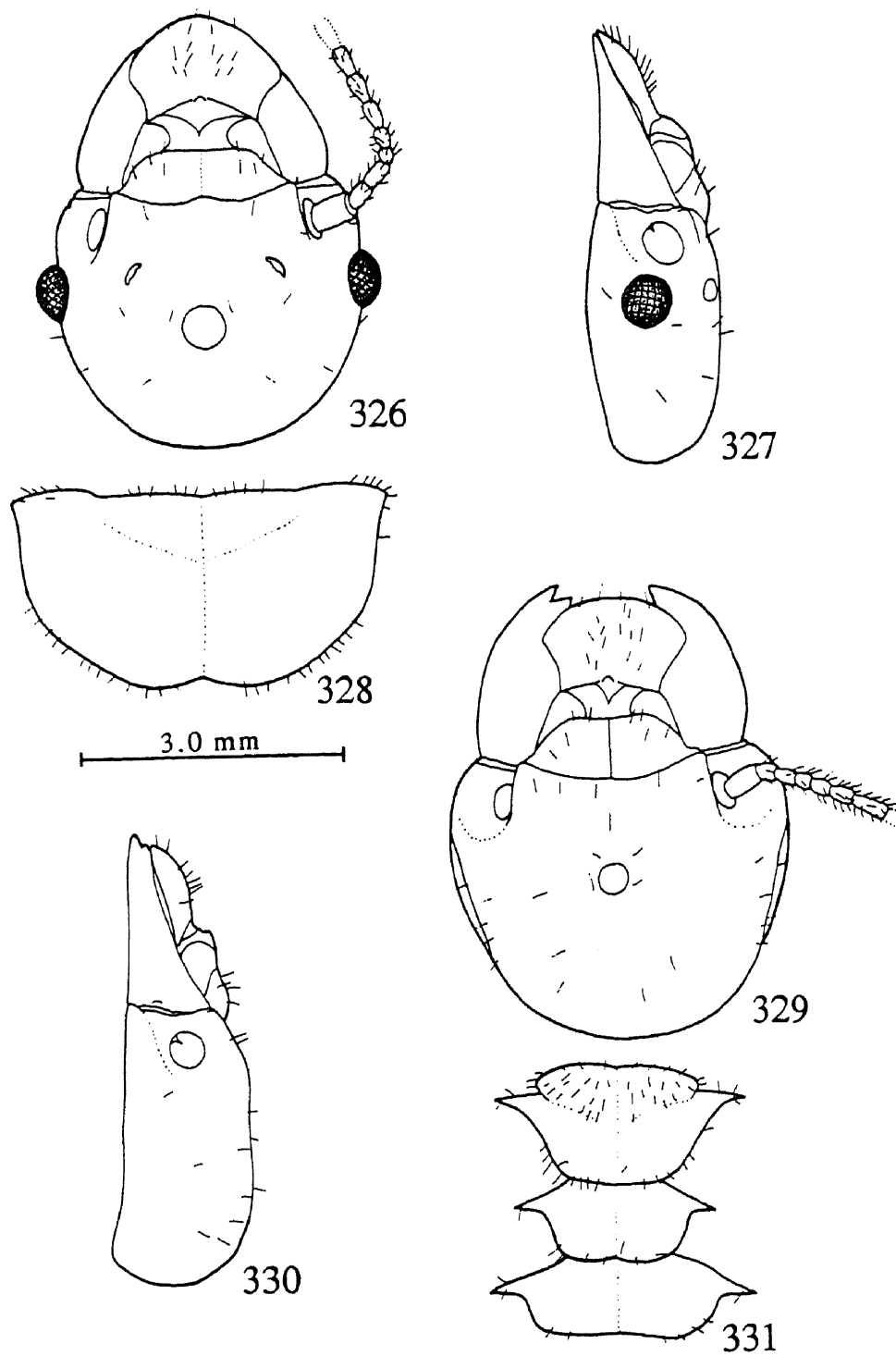
Figs. 311-313. *Syntermes spinosus*, first form soldier. 311. head, dorsal view; 312. head, lateral view; 313. pronotum.



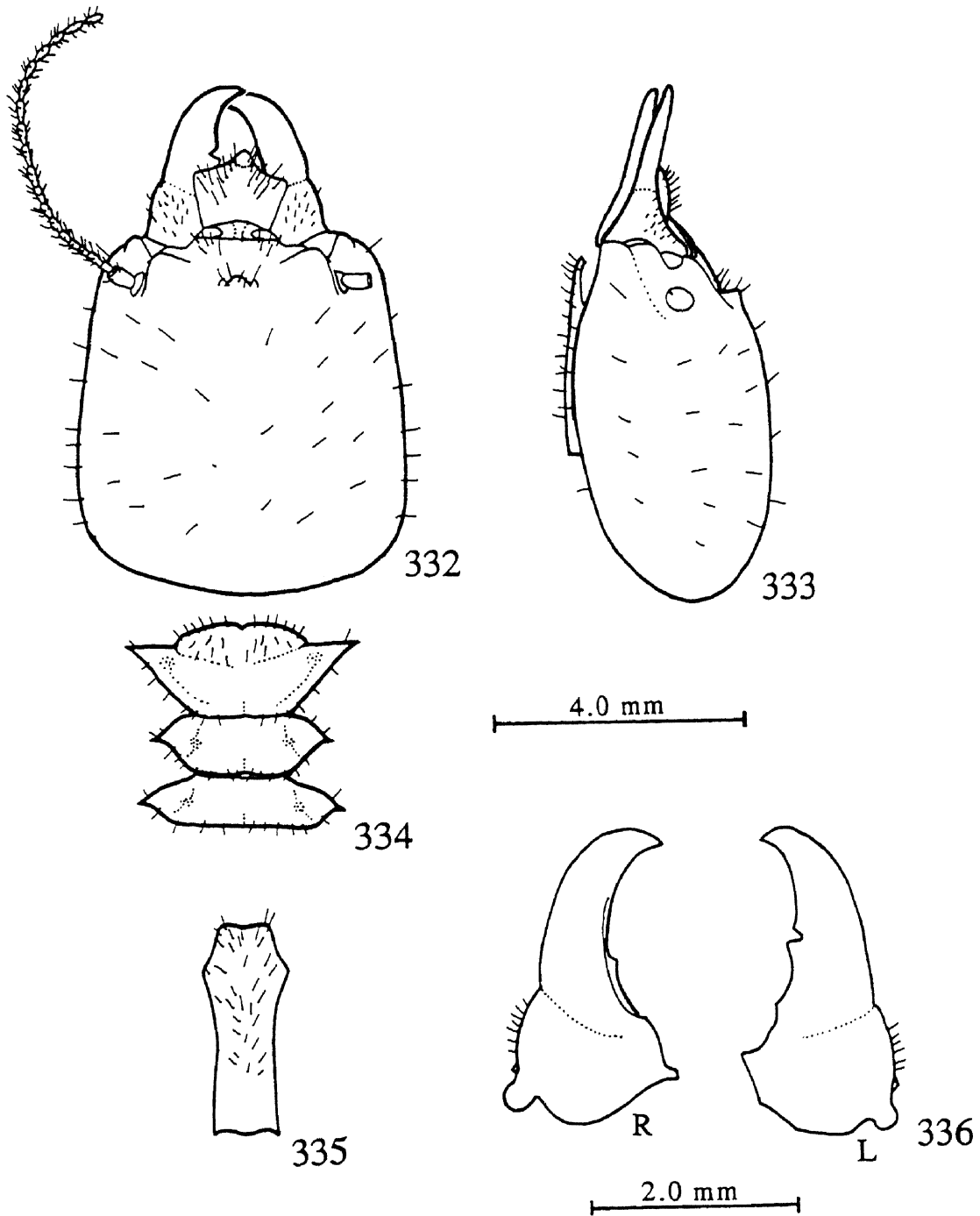
Figs. 314-319. *Syntermes spinosus*. Imago from Guyana: 314. head, dorsal view; 315. head, lateral view; 316. pronotum. Large worker: 317. head, dorsal view; 318. head, lateral view; 319. thorax.



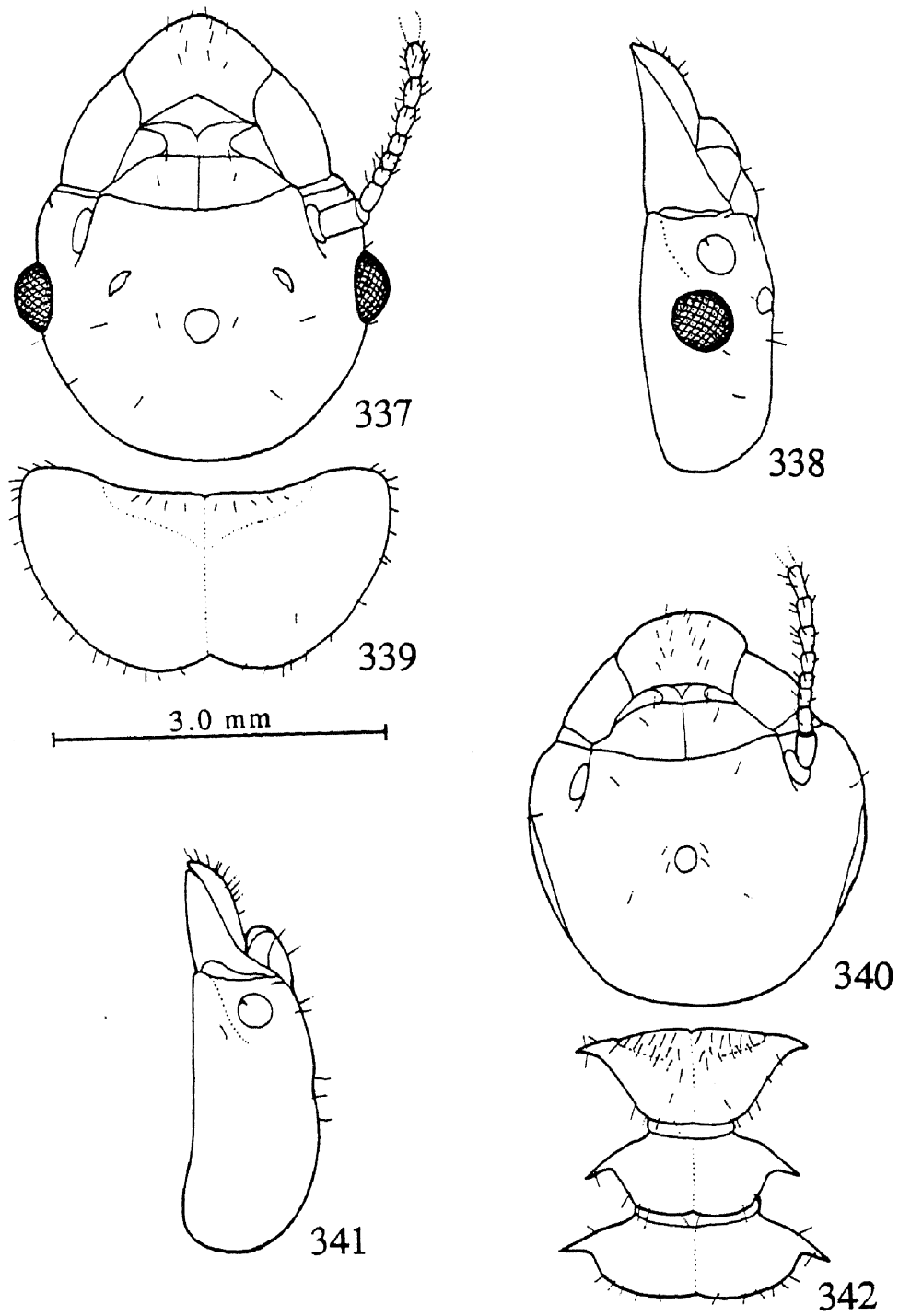
Figs. 320-325. *Syntermes tanygnathus*, new species, soldier. 320. head, dorsal view; 321. head, lateral view; 322. antenna; 323. thorax, dorsal view; 324. postmentum; 325. mandibles, ventral view.



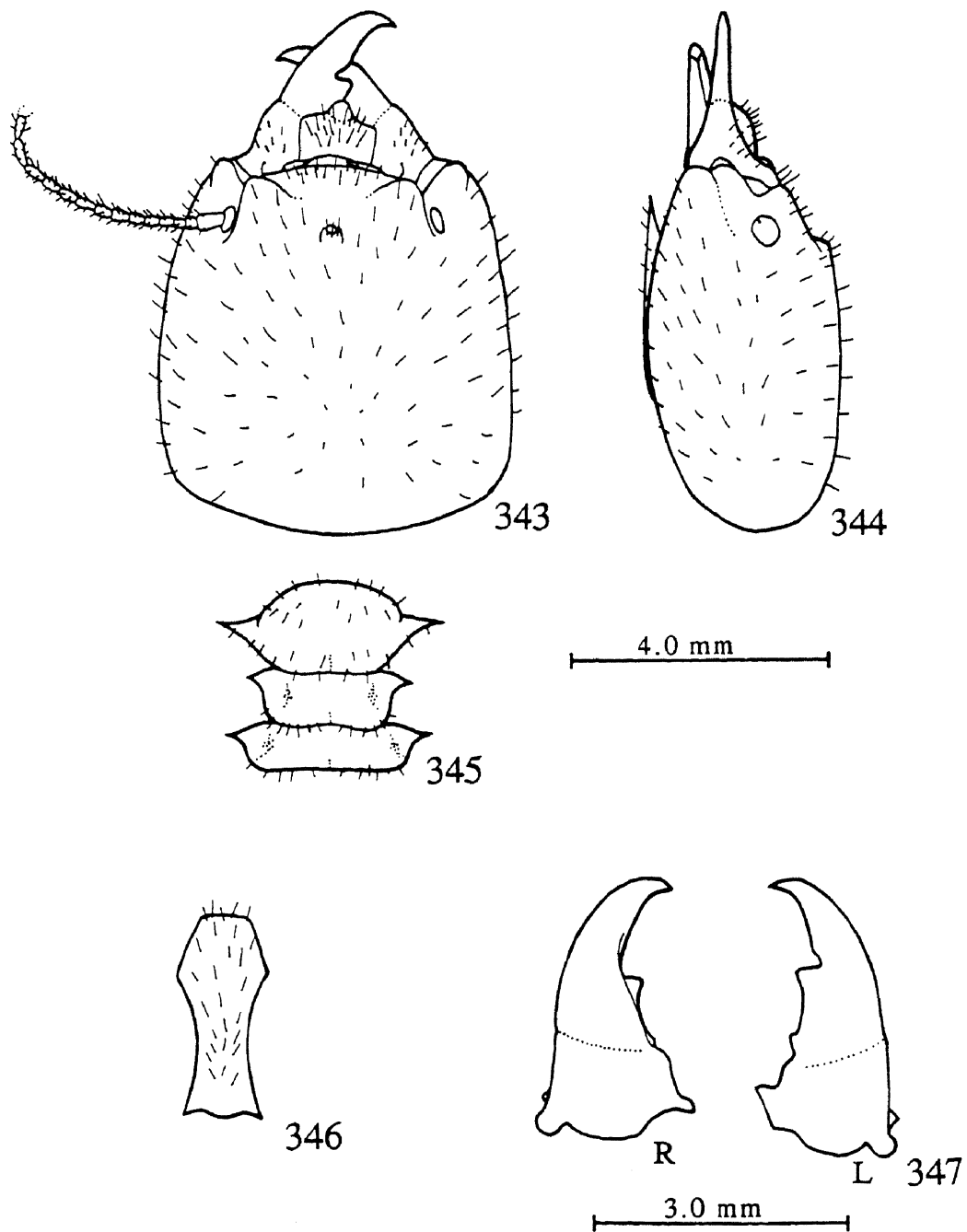
Figs. 326-331. *Syntermes tanygnathus*, new species. Imago: 326. head, dorsal view; 327. head, lateral view; 328. pronotum. Large worker: 329. head, dorsal view; 330. head, lateral view; 331. thorax.



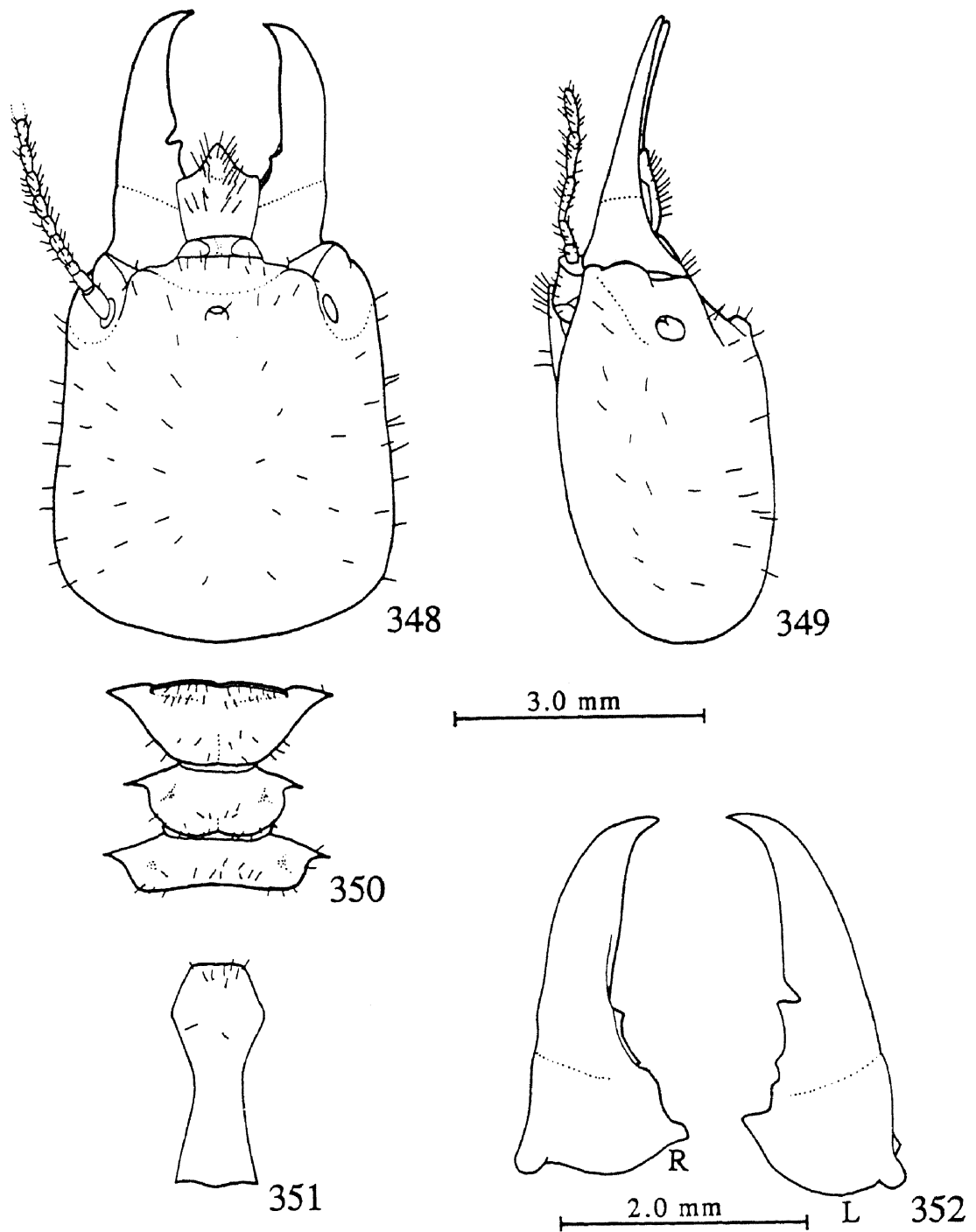
Figs. 332-336. *Syntermes territus*, soldier. 332. head, dorsal view; 333. head, lateral view; 334. thorax, dorsal view; 335. postmentum; 336. mandibles, ventral view.



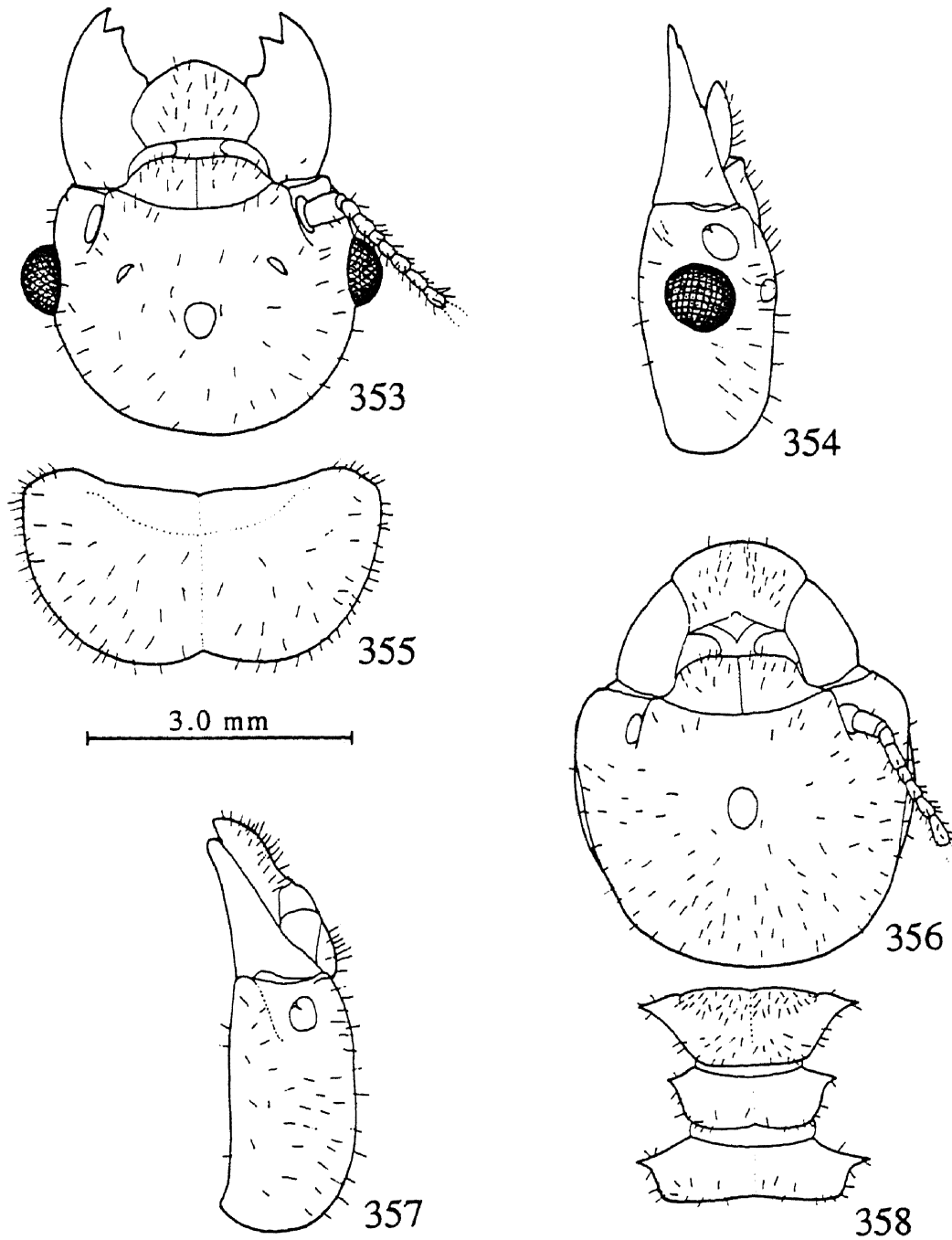
Figs. 337-342. *Syntermes territus*. Imago: 337. head, dorsal view; 338. head, lateral view; 339. pronotum. Large worker: 340. head, dorsal view; 341. head, lateral view; 342. thorax.



Figs. 343-347. *Syntermes wheeleri*, holotype soldier (except mandibles). 343. head, dorsal view; 344. head, lateral view; 345. thorax, dorsal view; 346. postmentum; 347. mandibles, ventral view.



Figs. 348-352. *Syntermes wheeleri*, first form soldier. 348. head, dorsal view; 349. head, lateral view; 350. thorax, dorsal view; 351. postmentum; 352. mandibles, ventral view.



Figs. 353-358. *Syntermes wheeleri*. Imago: 353. head, dorsal view; 354. head, lateral view; 355. pronotum. Large worker: 356. head, dorsal view; 357. head, lateral view; 358. thorax.



Fig. 359. Known geographical distribution of *Syntermes aculeosus*, *S. cearensis*, new species, and *S. dirus*. The dotted line indicates the limits of distribution for the genus.



Fig. 360. Known geographical distribution of *Syntermes calvus*, *S. magnoculus* and *S. tanygnathus*, new species. The dotted line indicates the limits of distribution for the genus.

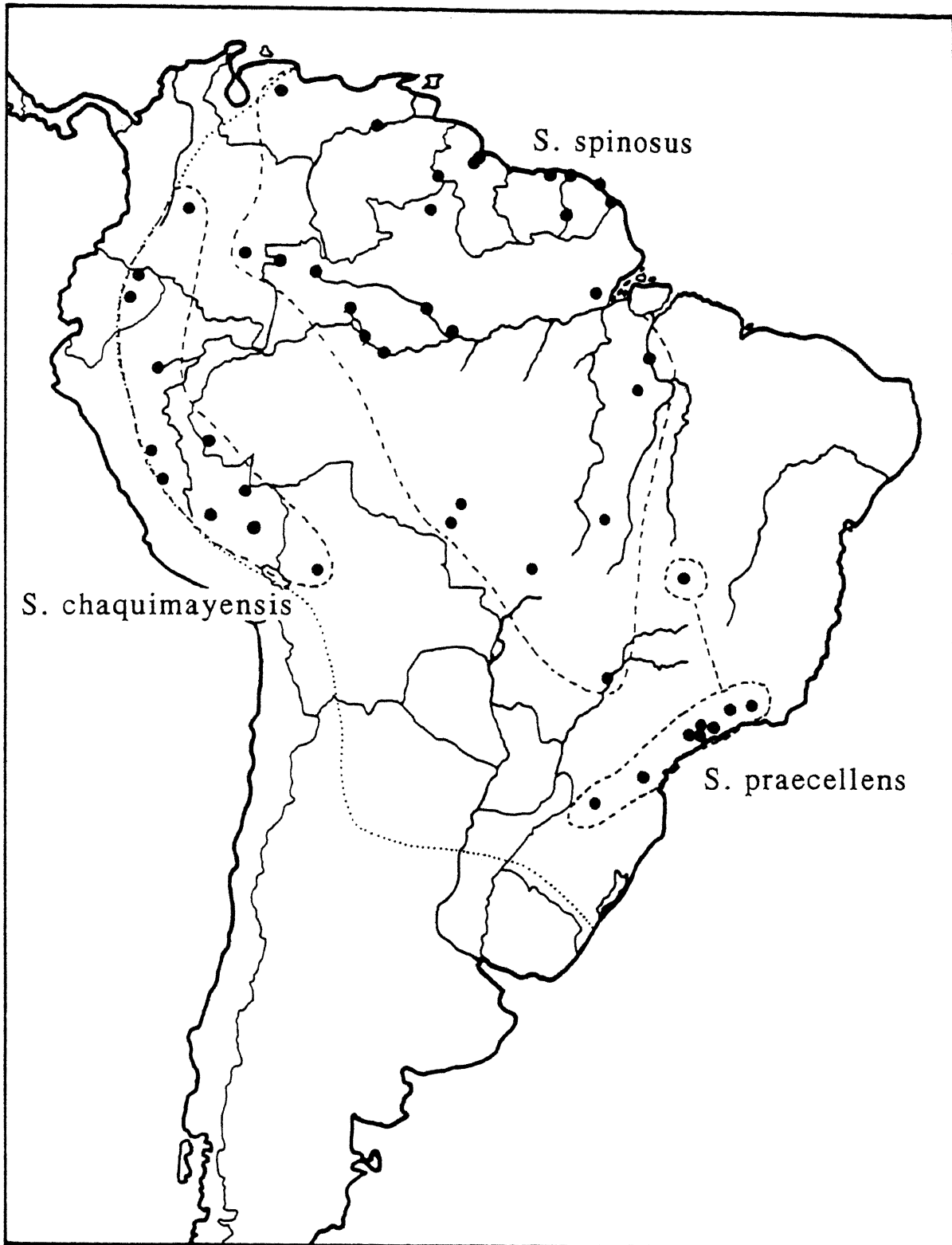


Fig. 361. Known geographical distribution of *Syntermes chaquimayensis*, *S. praecellens* and *S. spinosus*. The dotted line indicates the limits of distribution for the genus.

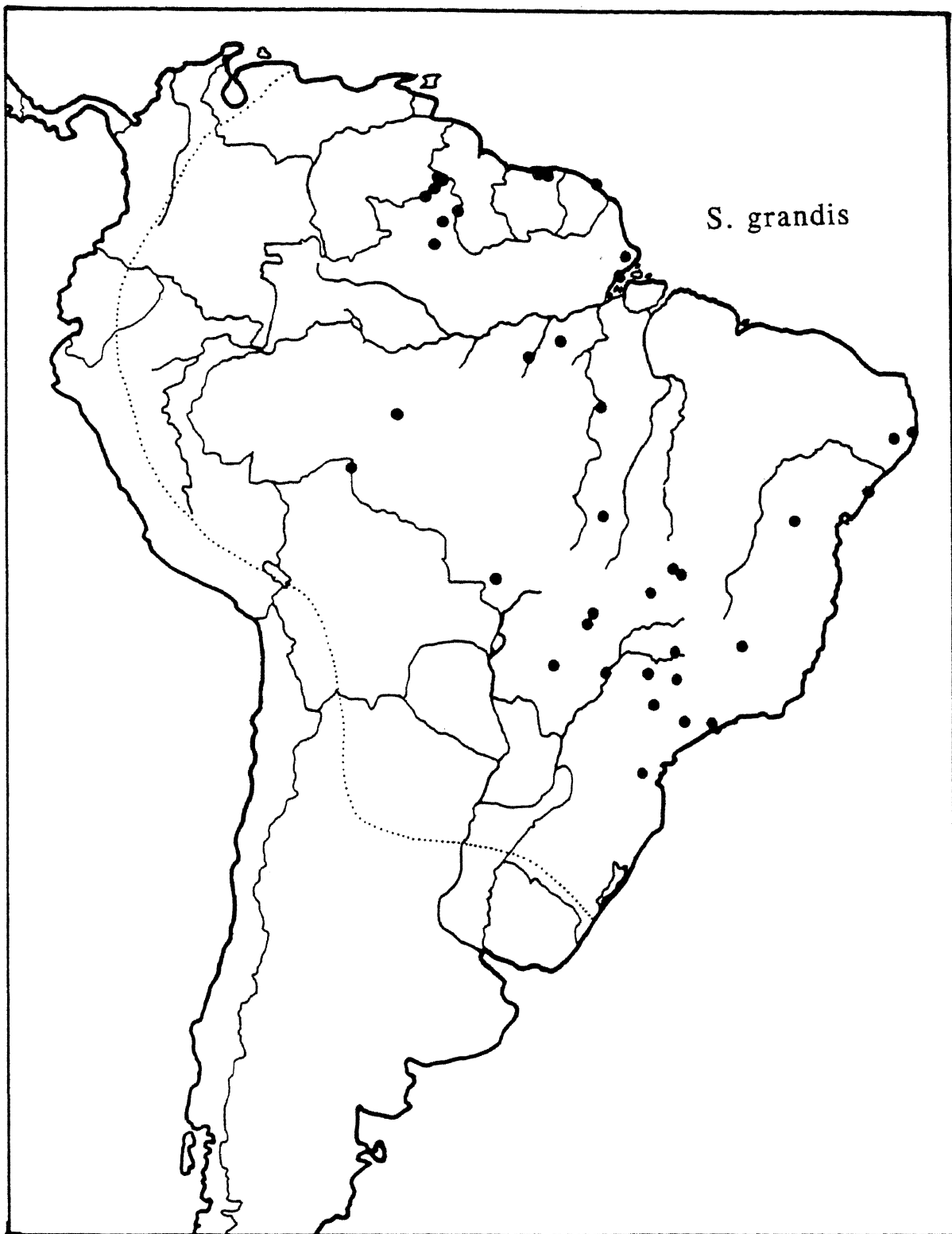


Fig. 362. Known geographical distribution of *Syntermes grandis*. The dotted line indicates the limits of distribution for the genus.

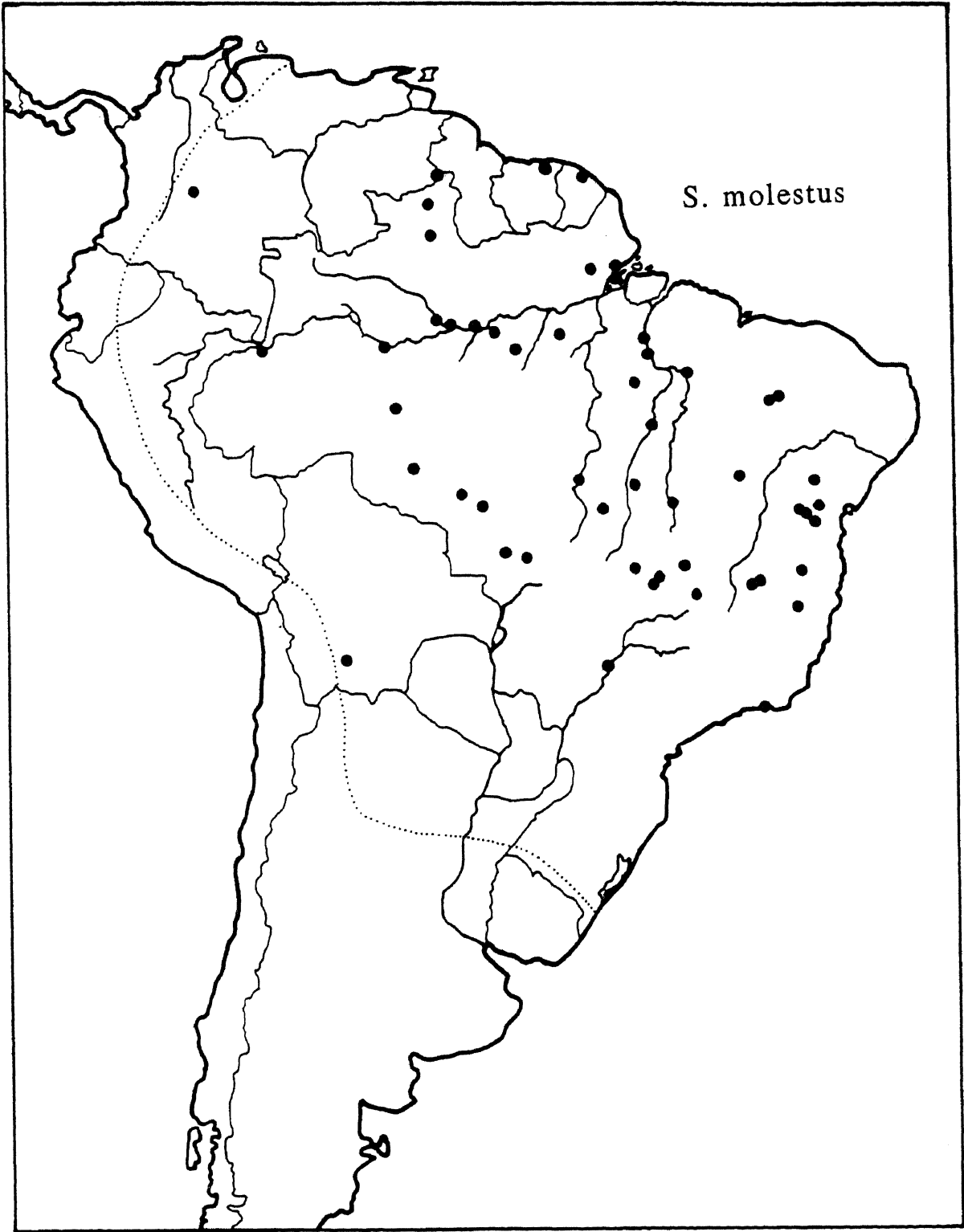


Fig. 363. Known geographical distribution of *Syntermes molestus*. The dotted line indicates the limits of distribution for the genus.

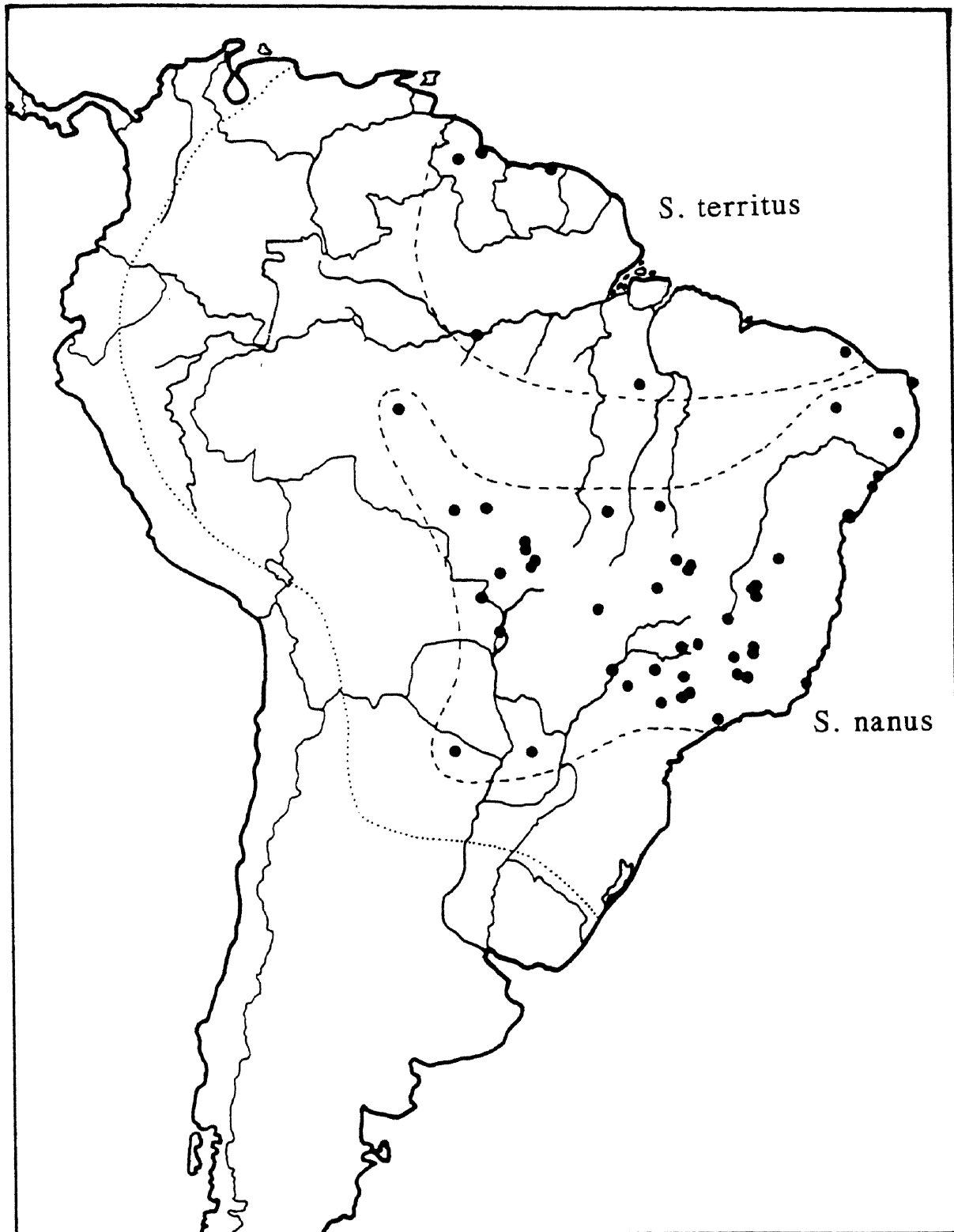


Fig. 364. Known geographical distribution of *Syntermes nanus*, new species, and *S. territus*. The dotted line indicates the limits of distribution for the genus.

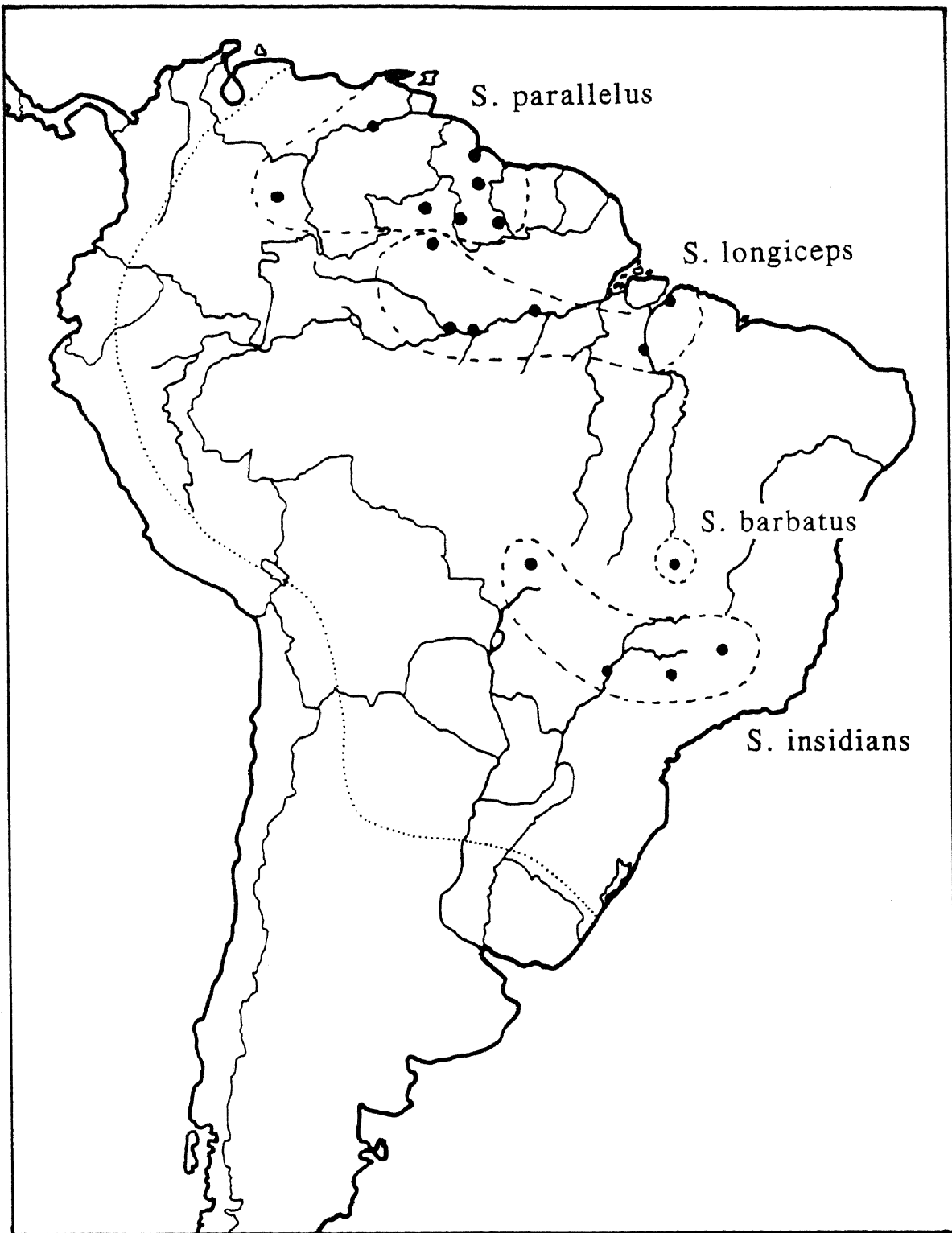


Fig. 365. Known geographical distribution of *Syntermes barbatus*, *S. insidians*, *S. longiceps*, and *S. parallelus*. The dotted line indicates the limits of distribution for the genus.

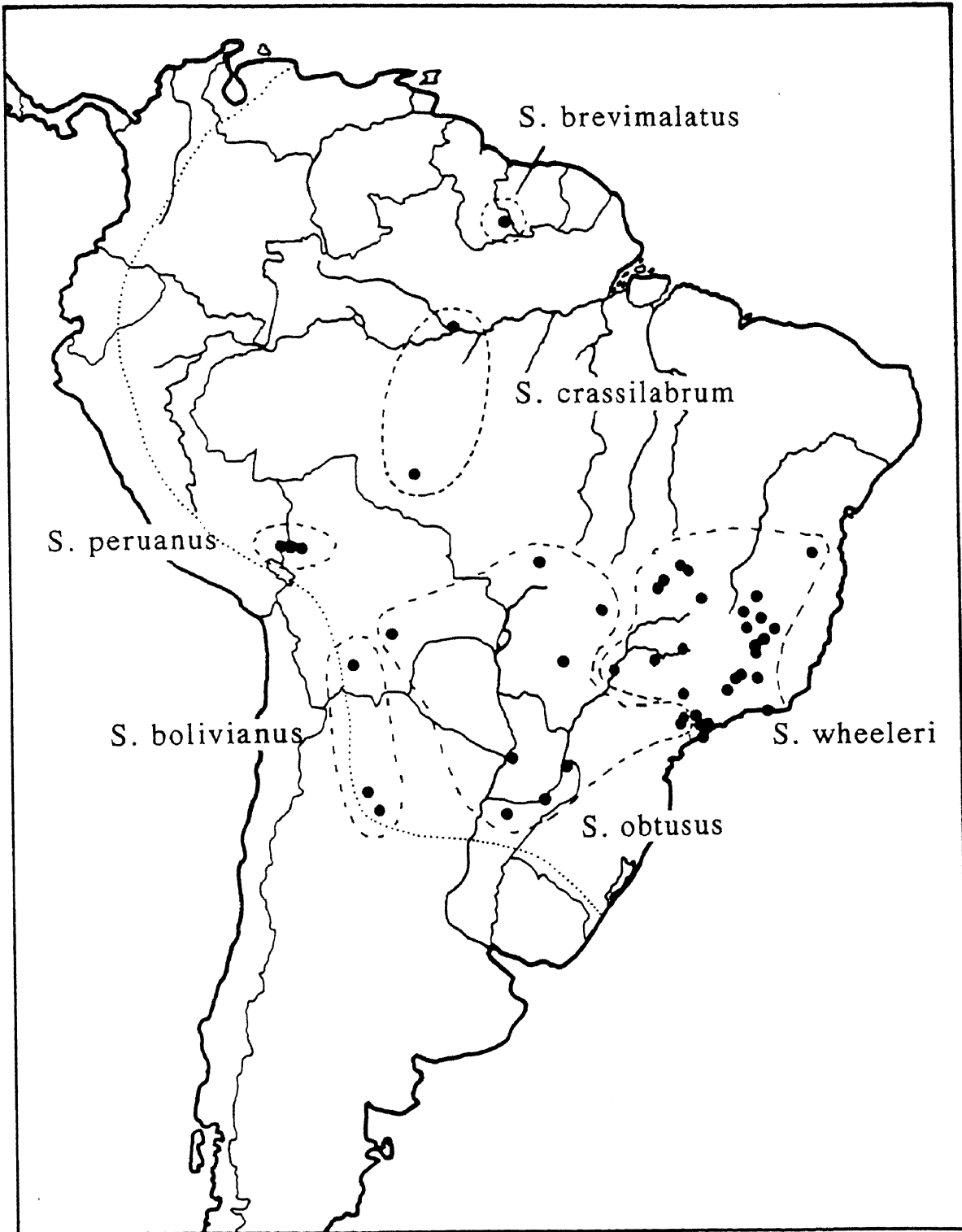


Fig. 366. Known geographical distribution of *Syntermes bolivianus*, *S. brevimalatus*, *S. crassilabrum*, *S. obtusus*, *S. peruanus* and *S. wheeleri*. The dotted line indicates the limits of distribution for the genus.

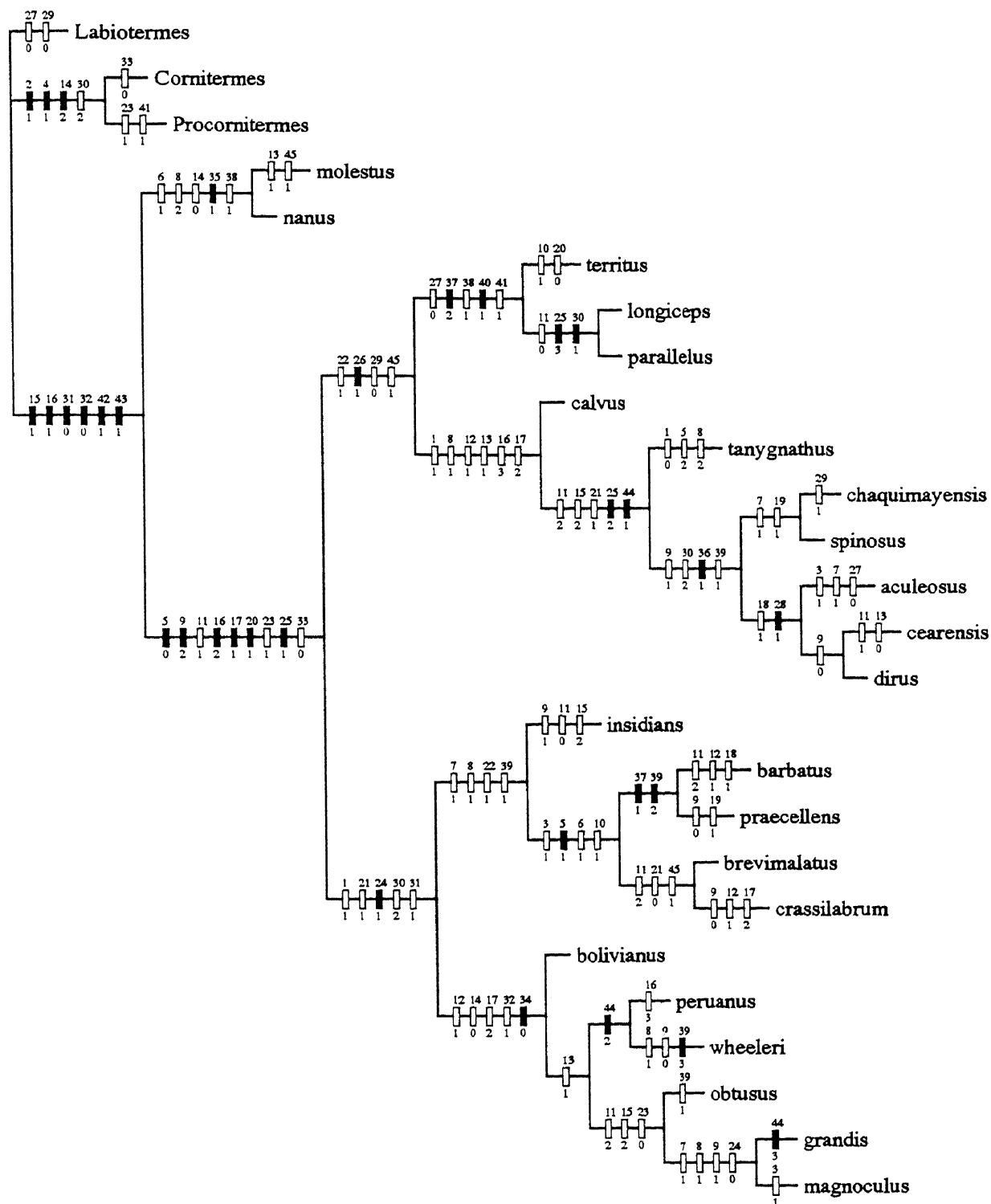


Fig. 367. Tree from analysis 3A. All species included; equal weights for all characters. Length=124, $ci=0.50$, $ri=0.76$. Numbers above each branch refer to characters as defined in text; numbers below each branch refer to character states. Black bars indicate character states that are unique and unreversed within the clade subtended by the branch; white bars indicate characters that originate more than once on the tree or undergo reversal within the clade subtended by the branch.

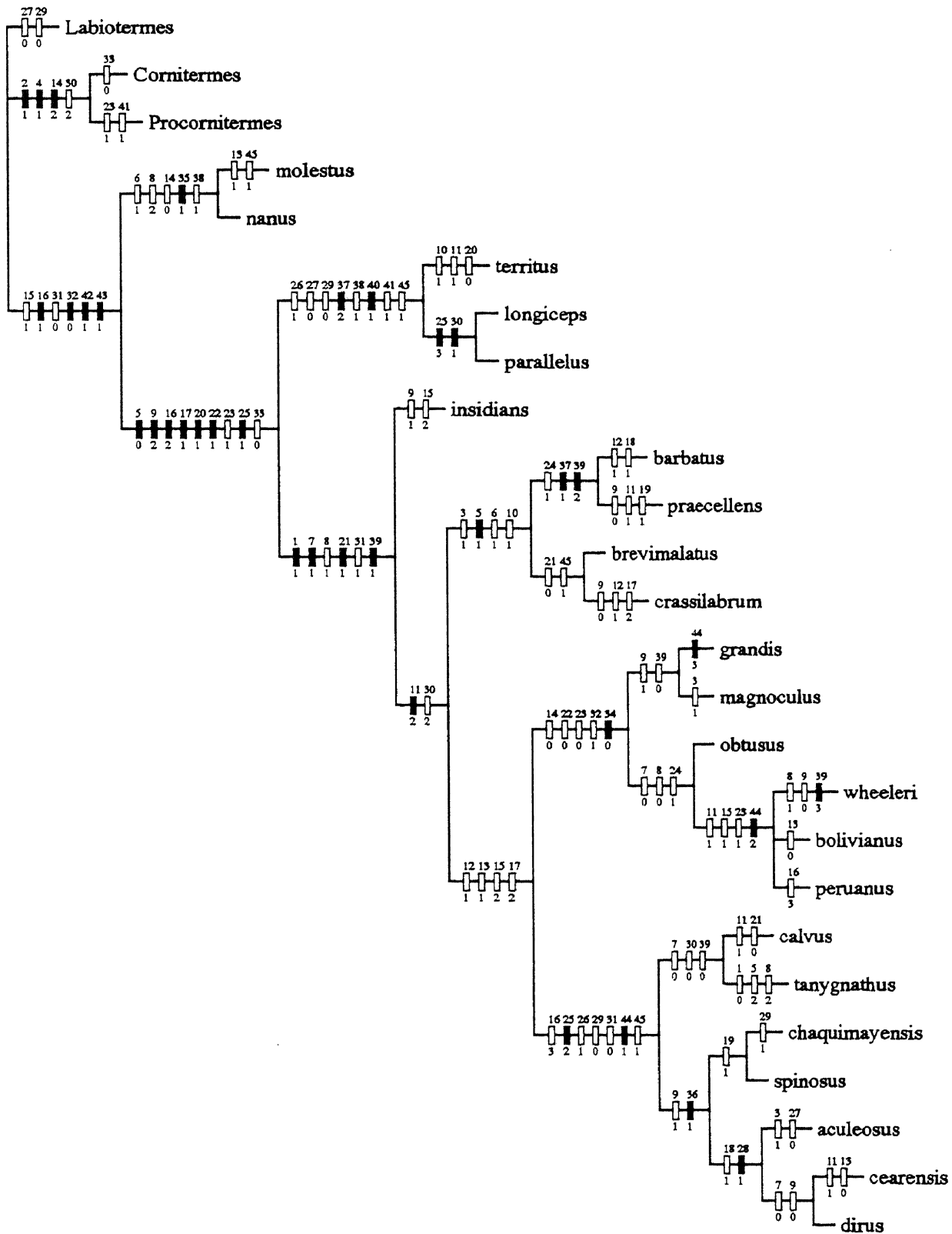


Fig. 368. Another tree from analysis 3A. All species included; equal weights for all characters. Length= 124, ci= 0.50, ri= 0.76. Symbols for characters and their states as in Fig. 367.

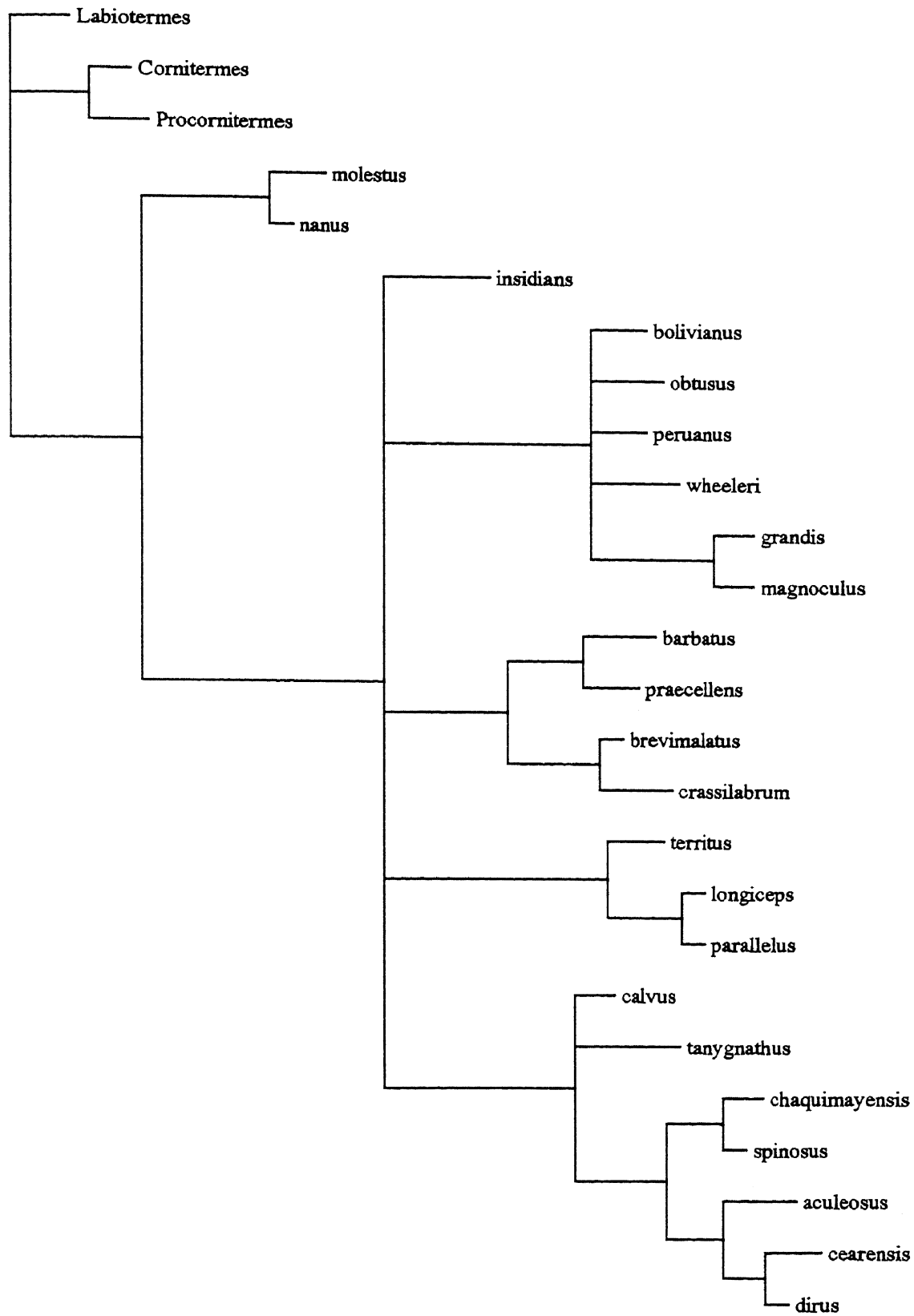


Fig. 369. Strict consensus tree from analysis 3A. All species included, equal weights for all characters.

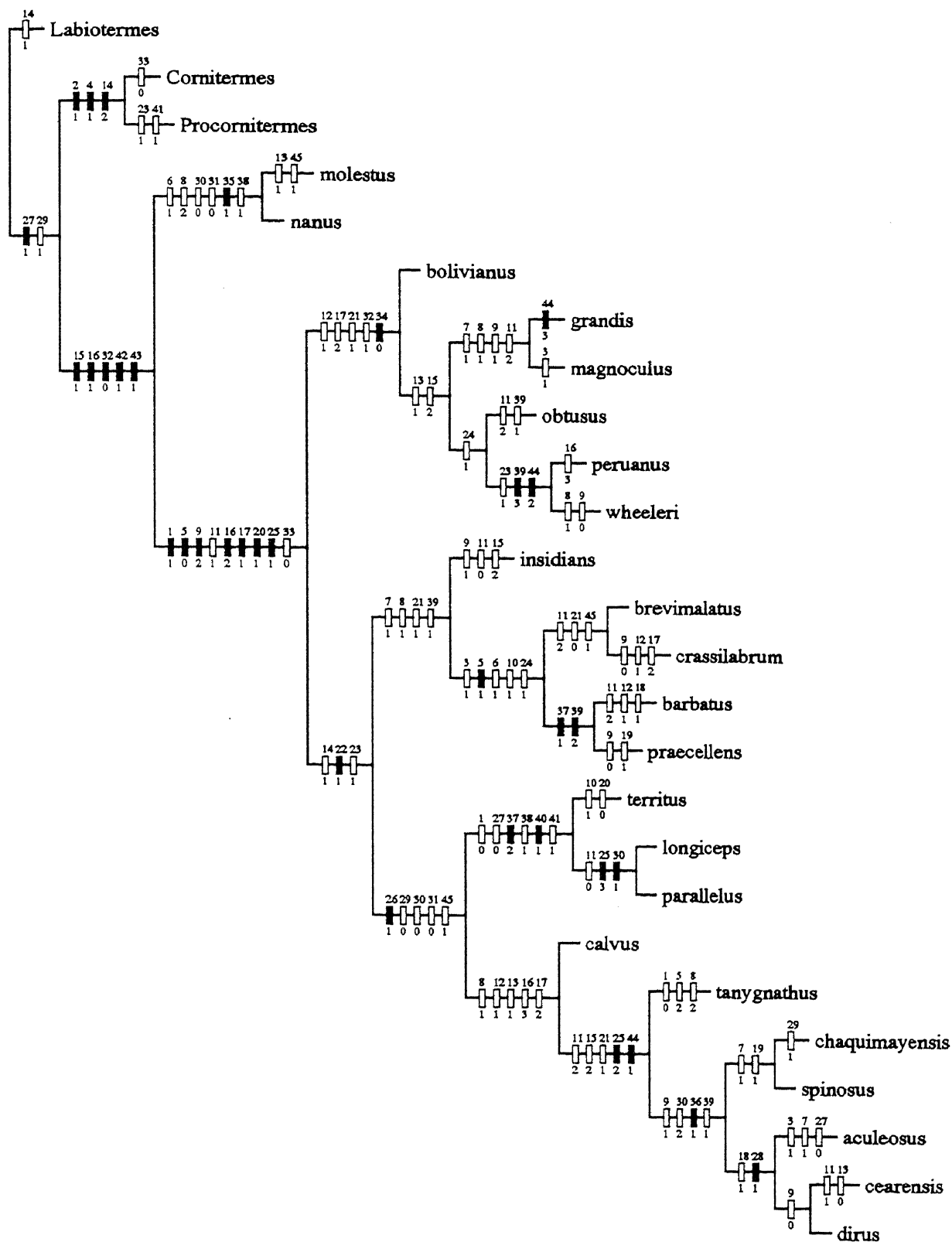


Fig. 370. Single tree from analysis 3C. All species included; implied weights using Pee-Wee. Fit= 335.5. Symbols for characters as in Fig. 367.

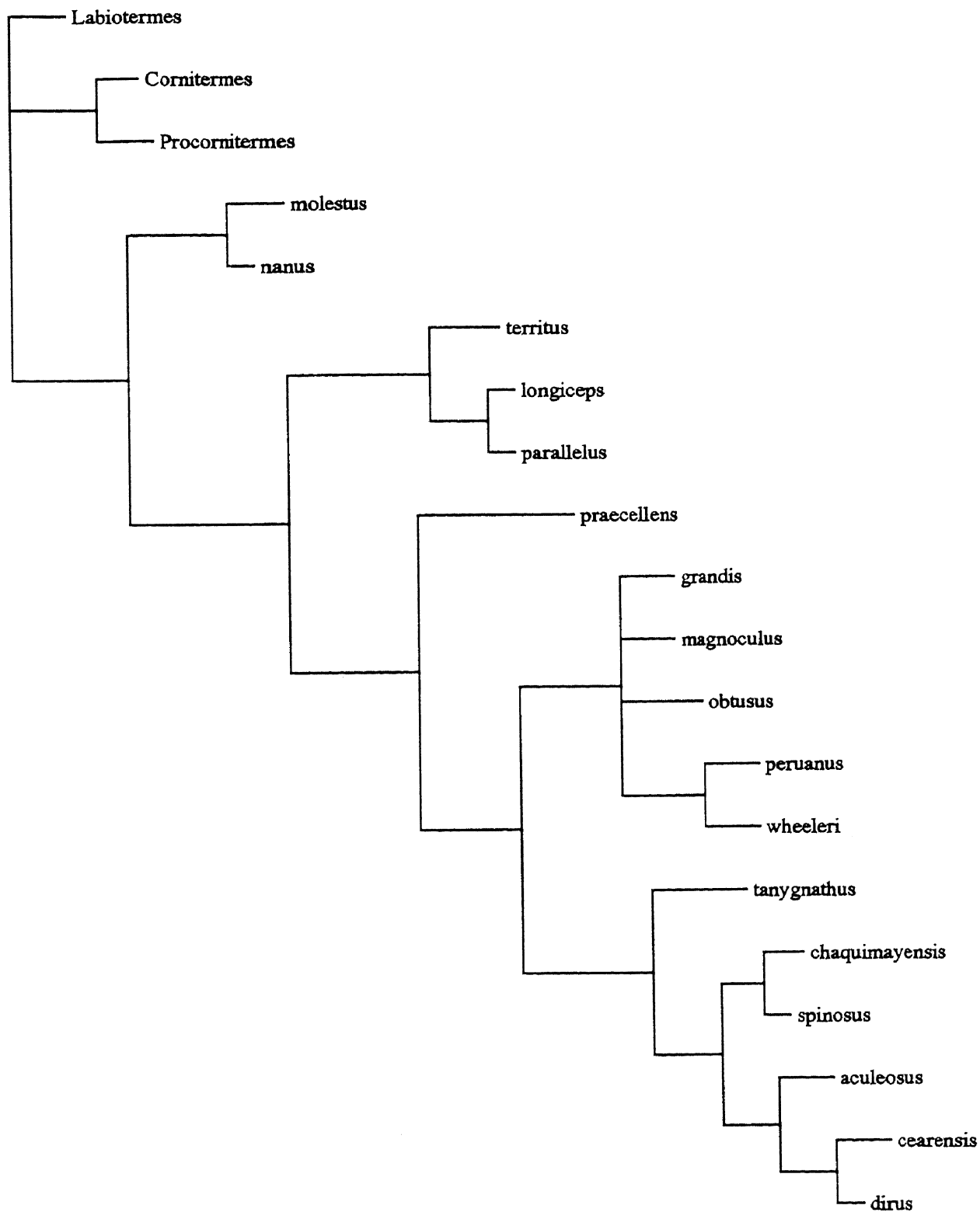


Fig. 371. Strict consensus tree from analysis 4A. Only species with known imagoes included; equal weights for all characters. From three different trees of length 109, $ci = 0.56$, $ri = 0.78$.

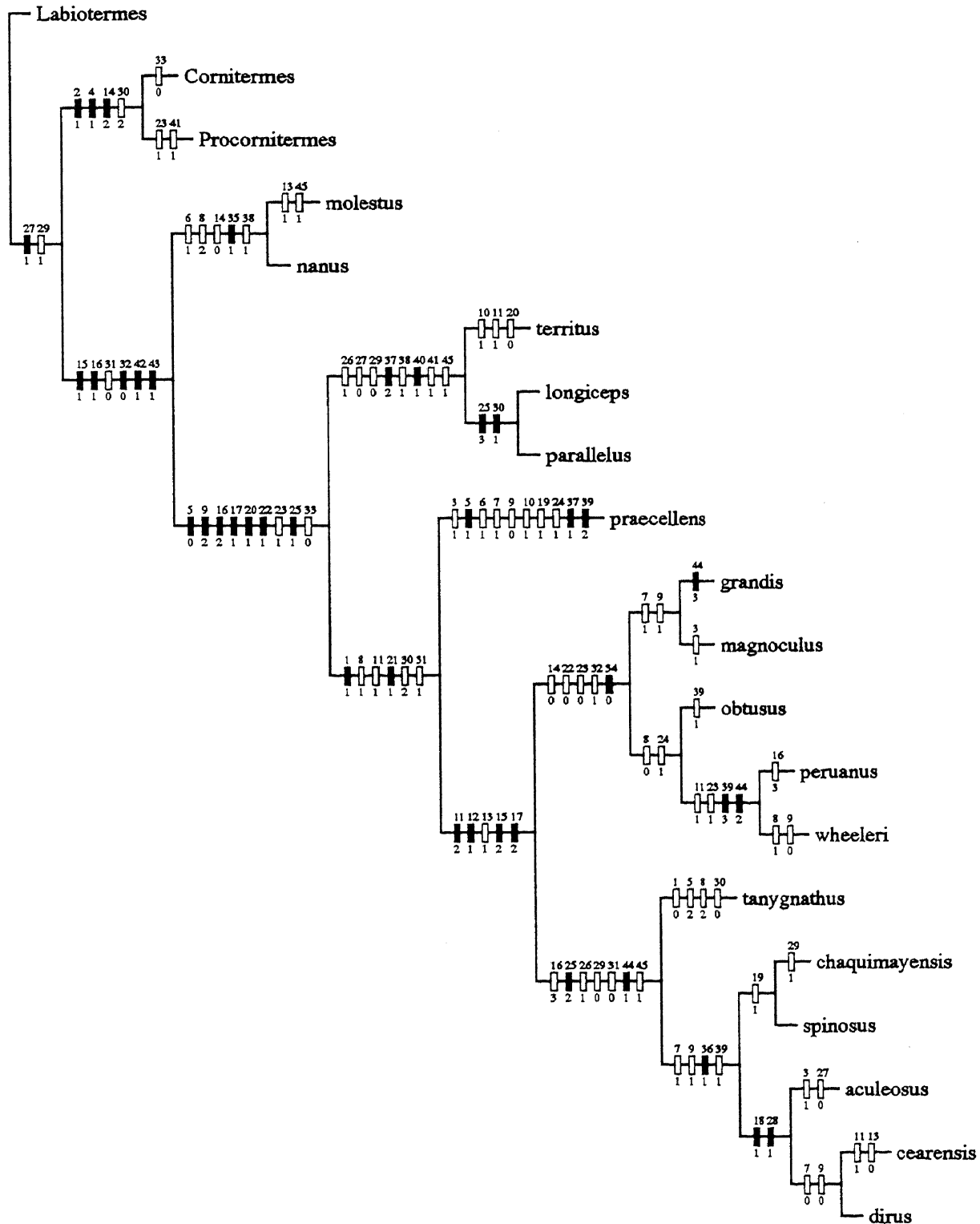


Fig. 372. Tree from analyses 4B (successive weighting) and 4C (implied weights), which both selected the same tree. Only species with known imagoes included. Tree from 4B with length 450, $ci = 0.78$, and $ri = 0.91$. Tree from 4C with $fit = 355.2$. Symbols for characters and their states as in Fig. 367.

CHAPTER III

A NEW GENUS OF NASUTITERMITINAE WITH MANDIBULATE SOLDIERS FROM
TROPICAL NORTH AMERICA (ISOPTERA: TERMITIDAE)

INTRODUCTION

Within the subfamily Nasutitermitinae there is an exclusively neotropical group of genera with mandibulate soldiers. This group presently includes 12 genera, eight of them restricted to South America. The occurrence of four genera of this group, *Armitermes*, *Cornitermes*, *Embiratermes* and *Rhynchotermes*, in Panama and Costa Rica seems to be the result of recent invasions. A single species of *Armitermes*, *A. intermedius*, has been recorded from Honduras (Snyder, 1922).

Armitermes was originally described by Wasmann (1897) and initially included all species whose soldiers had functional mandibles and a long frontal tube. Holmgren (1912) divided *Armitermes* into three subgenera, *Armitermes* s. str., *Curvitermes* and *Rhynchotermes*, which received generic status in Snyder's (1949) catalog. Later, Fontes (1985) subdivided *Armitermes*, transferring half of its species to genus *Embiratermes*, and also described the genera *Ibitermes* (closely related to *Embiratermes*) and *Cyrilliotermes* (closely related to *Curvitermes*). More recently, Canello & Bandeira (1992) described the genus *Macuxitermes*, with one species from the Brazilian Amazon, the only one in this group with dimorphic soldiers.

Based on the cladistic analysis presented in Chapter I, it became clear that the inclusion of *A. intermedius* and of a closely related undescribed species from Mexico in *Armitermes* would cause this genus to be polyphyletic. The superficial similarity of their soldiers with those of *Armitermes* seems to be the result of convergence.

In this Chapter I describe a new genus, *Cahuallitermes*, for the two aberrant species that do not form a clade with other species of *Armitermes*. A new species from southern Mexico, *C. aduncus*, is described; and *C. intermedius*, new combination, is redescribed.

METHODS

Drawings were prepared using a camera lucida coupled with a dissection microscope. Measurements were taken with a micrometric reticle on the eyepiece of the dissection microscope.

Measurements presented in the descriptions correspond to the following numbers in Roonwal's (1970) system: length of head to side base of mandibles = no. 5; length of frontal tube = no. 13; width of head = no. 17; height of head excluding postmentum = no. 21; length of left mandible = no. 37; width of pronotum = no. 68; length of hind tibia = no. 85. Terms used for hair-like structures are comparative. Bristles are long, with well-marked bases, and found on top of head, posterior margins of tergites and sternites and legs. Hairs are shorter and less conspicuous.

The material examined belongs to the entomological collections of the American Museum of Natural History (AMNH), New York, and of the U.S. National Museum of Natural History (USNM), Washington, D.C.

Cahuallitermes, new genus

Type-species: *Cahuallitermes aduncus*, new species.

Etymology: From the Nahuatl *Cahualli*, an abandoned one.

Imago. Unknown.

Soldier (Figs. 373-376, 379-383). Head capsule moderately elongate with convex sides; height of head approximately equal to its width. Frontal tube conical with broad tip, shorter than mandibles in dorsal view; its length equal to 50-60% width of head. Labrum weakly to conspicuously tri-lobed, strongly inflated, with a large, white median tip (probably a well-developed labral gland). Postmentum (Figs. 376, 383) strongly inflated, with convex sides, wider in the middle; surface finely and densely rugose. Anterior margin of pronotum strongly elevated in profile. Mandibles well-developed, curved, with sharp points; each with a distinct marginal tooth near the middle, with a notch anterior to it, and a much smaller tooth near base; apical cutting edge sigmoid. Antenna with 15-16 articles. Coxa without projection on its outer margin. Tibial spurs 2:2:2.

Worker (Figs. 377-378, 384-385). Head rounded with a strongly inflated post-clypeus. Fontanelle dome-shaped and very conspicuous. Antenna with 15 articles. Anterior femur with two rows of long and thick bristles on inner margin. Foretibia with an irregular row of five to six long and thick bristles on inner margin. Both mandibles with short apical teeth. Index of left mandible about 0.5. Cutting edge of 1st plus 2nd marginal tooth of left mandible straight. Molar plate concave, elongate,

with well-developed ridges and a very conspicuous basal notch. Third marginal tooth of left mandible and 2nd marginal of right mandible weakly developed. Molar tooth completely covered by molar prominence in dorsal view.

Digestive tube. Crop small. Insertion of the foregut into midgut subapical. Mixed segment very long and dilated. Origin of mesenteric prolongation orientated ventrally. First segment of hindgut dilated. Malpighian tubules inserted in two separate pairs at junction of midgut and hindgut. Enteric valve wide and weakly armed, with single, small swelling bearing short spines. Paunch well-developed.

Comparisons. The soldier of *Cahuallitermes* superficially resembles that of *Armitermes* and related genera, but can be easily distinguished by its mandibles with two marginal teeth each and the notch anterior to the first marginal tooth, the enormous labral gland and the microsculpture on the postmentum. The soldier of *Rhynchotermes* has a much more elongate frontal tube and much more curved mandibles. The mandibles of the soldier of *Cahuallitermes* resemble those of *Syntermes*, *Cornitermes*, *Labiotermes* and *Procornitermes*, except that they are less curved in the latter.

Cahuallitermes aduncus, new species

Holotype: Soldier, *Mexico*: Chiapas, 5 miles NE Chiapa, 22.viii.1966; Coll. J. and W. Ivie [AMNH].

Paratypes: soldiers (six) and workers (three), same data as holotype [AMNH].

Imago. Unknown.

Soldier (Figs. 373-376). Head capsule rounded; top straight in profile. Frontal tube long and down-turned. Labrum weakly tri-lobed. Marginal teeth of both mandibles relatively small. Antenna with 15 articles; 1st longer than 2nd; 3rd the shortest; 2nd longer than 4th; 4th and 5th subequal. Anterior margin of pronotum rounded. Head capsule with 3-4 bristles on top and sides. Frontal tube with numerous short hairs around the fontanelle. Labrum with many bristles. Clypeus with four bristles. Postmentum with two bristles on anterior margin. Pronotum with a row of bristles on anterior margin. Meso and metanotum with one or two bristles each, on lateral margins. Fore femur with two rows of thick bristles on inner margin. Fore tibia with irregular row of short, thick bristles on inner margin. Tergites with irregular row of long bristles on posterior margin and scattered shorter ones on surface. Sternites with row of bristles on posterior margin and many shorter ones on surface.

Head capsule and frontal tube yellow-orange; pronotum yellow; legs yellowish-white; abdomen transparent.

Measurements (in millimeters) of four soldiers from the type series: length of head to side base of mandibles 1.36-1.50; length of frontal tube 0.61-0.75; width of head 1.36-1.47; height of head without postmentum 1.06-1.13; width of pronotum 0.75-0.82; length of left mandible 0.75-0.78; length of hind tibia 1.43-1.57.

Worker (Figs. 377-378). Head capsule with about 12 bristles on top and sides. Clypeus with two bristles on anterior margin and two longer ones near the middle. Labrum with two longitudinal rows of four to five bristles. Pronotum with a row of long bristles on anterior margin and a few short ones on lateral and posterior margins. Meso and metanotum with two bristles on lateral margins, one on each side. Chaetotaxy of abdomen and legs similar to that of soldiers. Head capsule pale-yellow; thorax and legs yellowish-white; abdomen transparent.

Comparisons. Compared to *C. intermedius*, the soldier of *C. aduncus* is smaller, has a proportionally longer, down-turned frontal tube, less developed lateral angles of the labrum, and smaller marginal teeth on both mandibles. The worker of *C. aduncus* has a longer clypeus and a smaller fontanelle than that of *C. intermedius*.

Cahuallitermes intermedius (Snyder), new combination

Armitermes intermedius Snyder 1922: 23; fig. 3. Holotype soldier, *Honduras*: Ceiba, February 1920, Coll. W.M. Mann [USNM].

Material Examined. *Honduras*: Ceiba, no data, two soldiers and five workers (probably part of the original series studied by Snyder, but not labelled as paratypes) [USNM]. Lombardia, no data; one soldier and four workers [USNM]. *Belize*: Label data: "British Honduras, tinamou feeding on", four soldiers and five workers [USNM]. Blue Creek, 17.vi.1981, Coll. M. Collins, rotten log, four soldiers and four workers. 9.vi.1981, Coll. M. Collins, six soldiers and five workers. Columbia Woods. 11.vi.1981, Coll. W. Steiner Jr., eight soldiers and many workers [from Dr. M.S. Collins' personal collection].

Imago. Unknown.

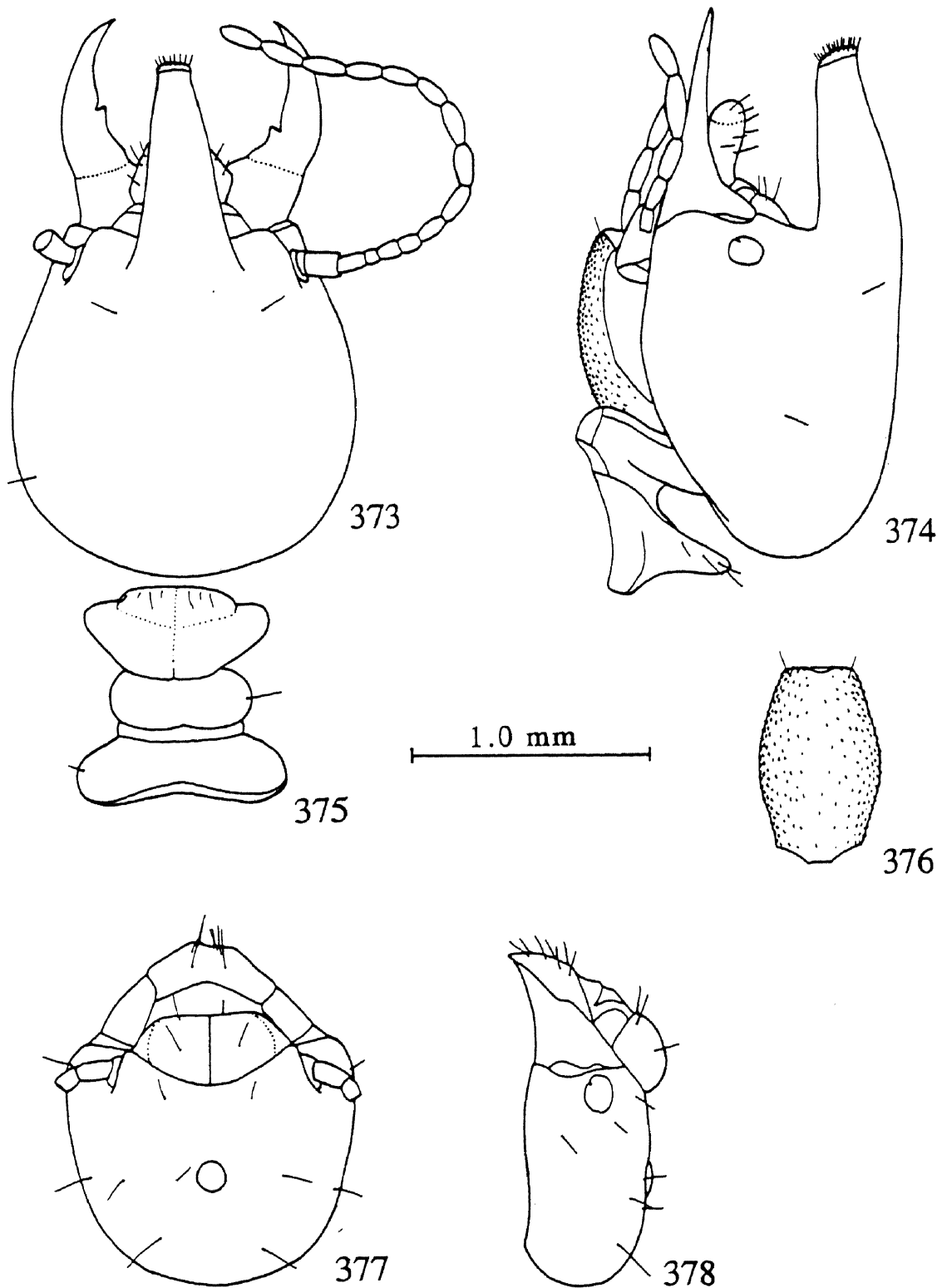
Soldier (Figs. 379-383). Head capsule rounded, moderately elongate; top straight in profile. Frontal tube relatively short and upturned. Labrum strongly tri-lobed. Marginal teeth well-developed on both mandibles. Antenna with 15-16 articles. If with 15 articles, second article is the shortest; 1st longer than 3rd; 3rd, 4th and 5th subequal. If with 16 articles, the shortest is the 3rd one. Anterior margin of pronotum slightly emarginate. Head capsule with five to six bristles on top and sides. Frontal tube with numerous short hairs around the fontanelle. Labrum with many bristles. Clypeus with four bristles. Postmentum with two bristles on anterior margin. Pronotum with a row of long bristles on anterior margin and one or two on lateral margins. Fore femur with two rows of thick bristles on inner margin. Fore tibia with irregular row of short, thick bristles on inner margin. Tergites with row of long bristles on posterior margin and many long and short ones on surface. Sternites with row of long, anteriorly directed bristles on posterior margin, and numerous shorter, posteriorly directed ones on surface. Head and frontal tube orange; pronotum orange-yellow; legs yellow; abdomen transparent.

Measurements (in millimeters) of 11 soldiers from all localities listed (three from Honduras and eight from Belize): length of head to side base of mandibles 1.8-2.05; length of frontal tube 0.65-0.88; width of head 1.74-1.95; height of head without postmentum 1.33-1.58; width of pronotum 1.0-1.1; length of left mandible 0.97-1.05; length of hind tibia 1.91-2.01.

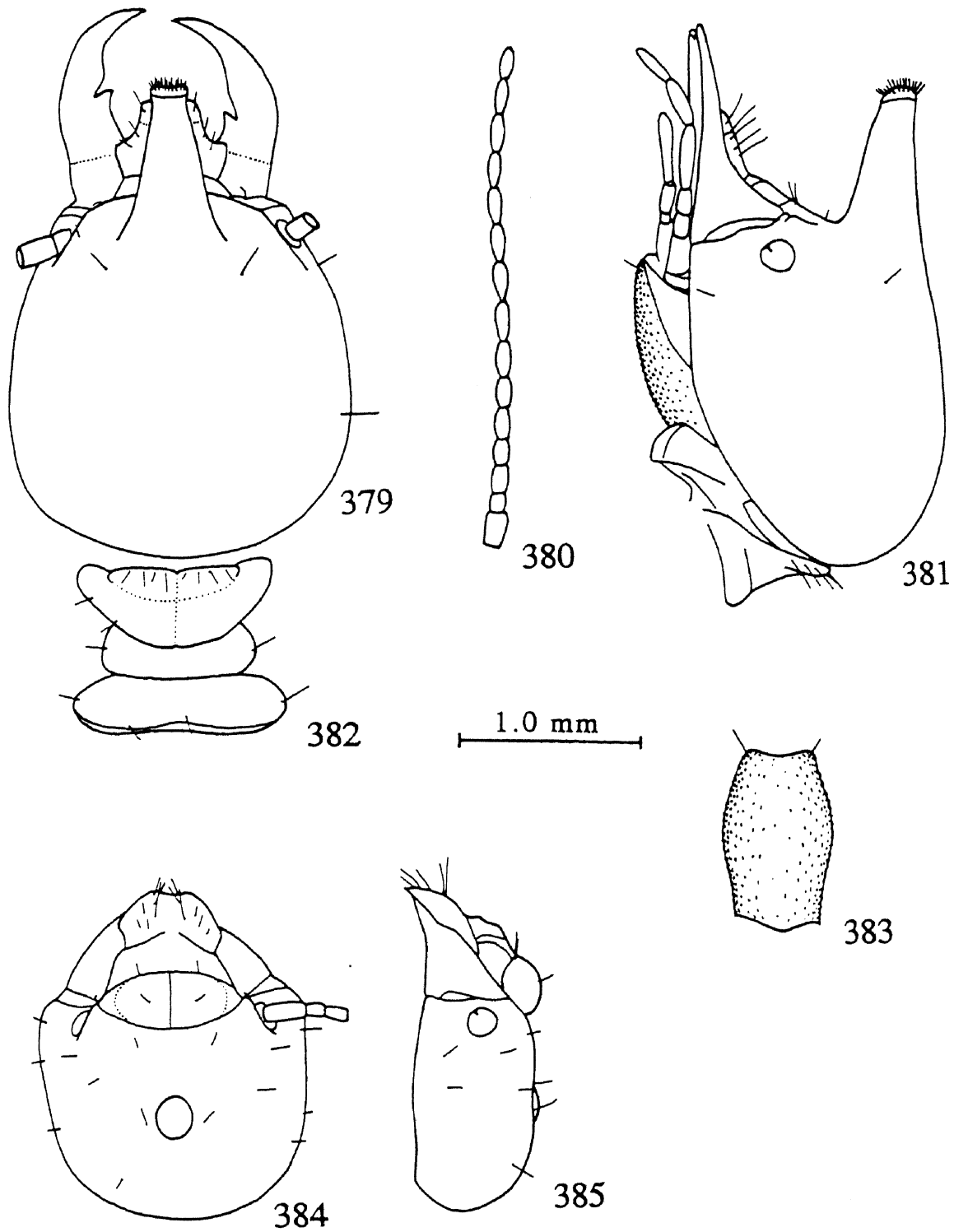
Worker (Figs. 384-394). Head capsule with about 16 bristles on top and sides. Clypeus with two bristles on anterior margin and two near the middle. Labrum with two longitudinal rows of six to seven bristles. Pronotum with a row of long bristles on anterior margin and a few bristles on posterior margin. Meso and metanotum with a few bristles on posterior and lateral margins. Chaetotaxy of legs and abdomen similar to that of soldiers. Head capsule yellow; thorax and legs yellowish white; abdomen transparent.

Remarks. Snyder's (1922: 23, Fig. 3) description of *Armitermes intermedius* is inaccurate in several respects. The drawing of the soldier was clearly made with the specimen inclined anteriorly, creating the impression that its frontal tube is much longer than it really is. He does not mention how the measurements were taken and which and how many soldiers were measured, but all his measurements are larger than mine, and I believe they are incorrect. Although I did not measure the holotype, I compared it with other soldiers from other localities and it seemed to be in the same size range.

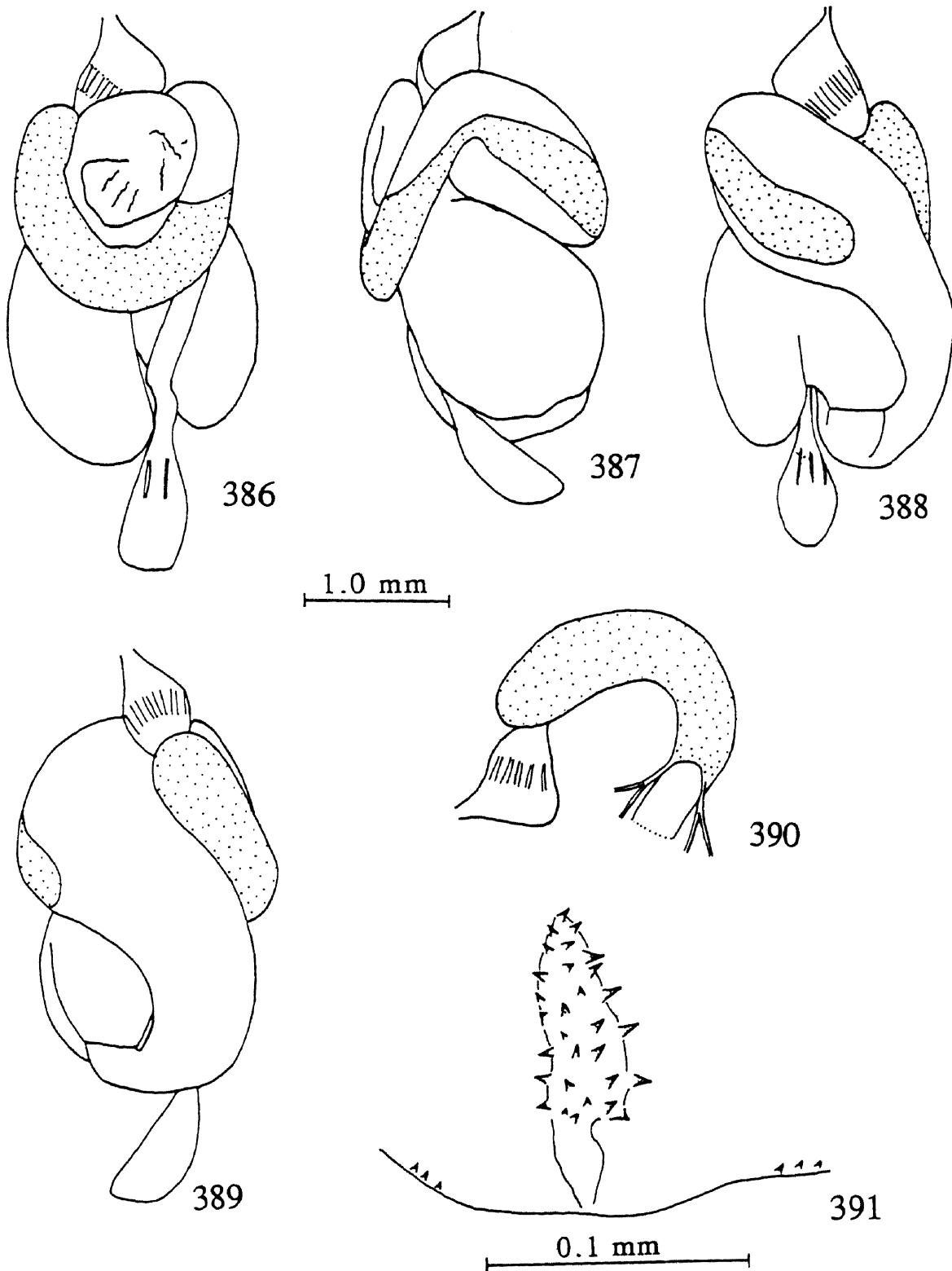
Geographical Variation. In the material examined, specimens from Belize (four samples from three localities) are a little smaller and have a proportionally shorter frontal tube compared to those from Honduras (two samples from two localities). Since there is no other difference and the variation seems to be continuous, I believe they belong to a single species.



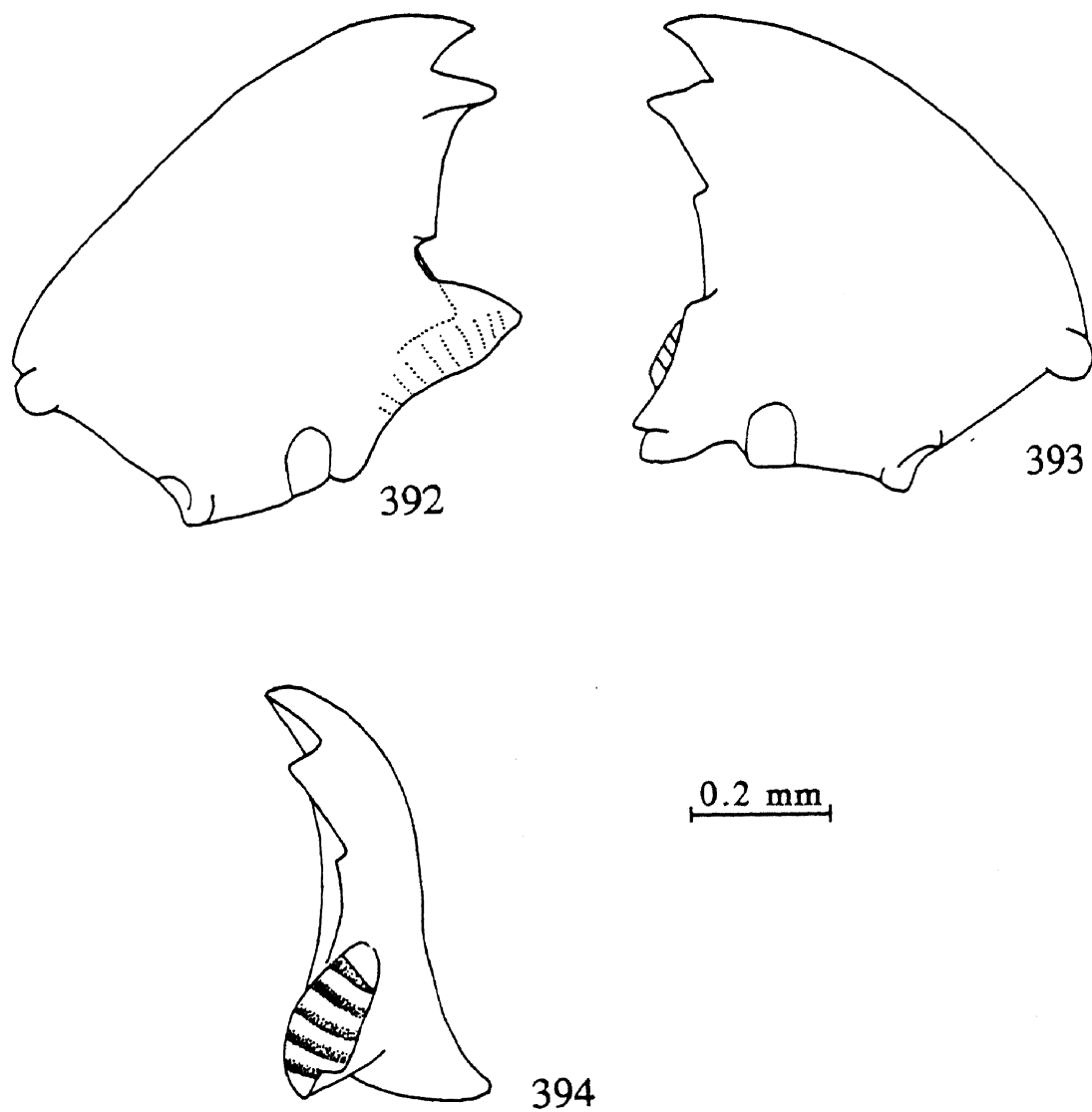
Figs. 373-378. *Cahuallitermes aduncus*, new species (from Chiapas, Mexico). Soldier: 373. head, dorsal view; 374. head, lateral view; 375. thorax, dorsal view; 376. postmentum, ventral view. Worker head: 377. lateral view; 378. dorsal view.



Figs. 379-385. *Cahuallitermes intermedius*, new combination (from Belize). Soldier: 379. head, dorsal view; 380. antenna; 381. head, lateral view; 382. thorax, dorsal view; 383. postmentum, ventral view. Worker head: 384. lateral view; 385. dorsal view.



Figs. 386-391. *Cahuallitermes intermedius*, new combination. Digestive tube of worker: 386. dorsal; 387. right; 388. ventral; 389. left; 390. insertion of Malpighian tubules; 391. enteric valve armature (a single swelling with short spines).



Figs. 392-394. *Cahuallitermes intermedius*, new combination. Worker: 392. left mandible, dorsal view; 393. right mandible, dorsal view; 394. right mandible, view of mesal face.

APPENDIX

The Digestive Tube of *Macuxitermes triceratops*

The motypic genus *Macuxitermes* was described from a single series collected in the Brazilian Amazon (Canello & Bandeira, 1992). The original description did not include any information about the digestive tube, which is known to provide good evidence for the relationship among genera. In order to study the gut morphology of this genus, I dissected two paratype workers (with authorization from the curator).

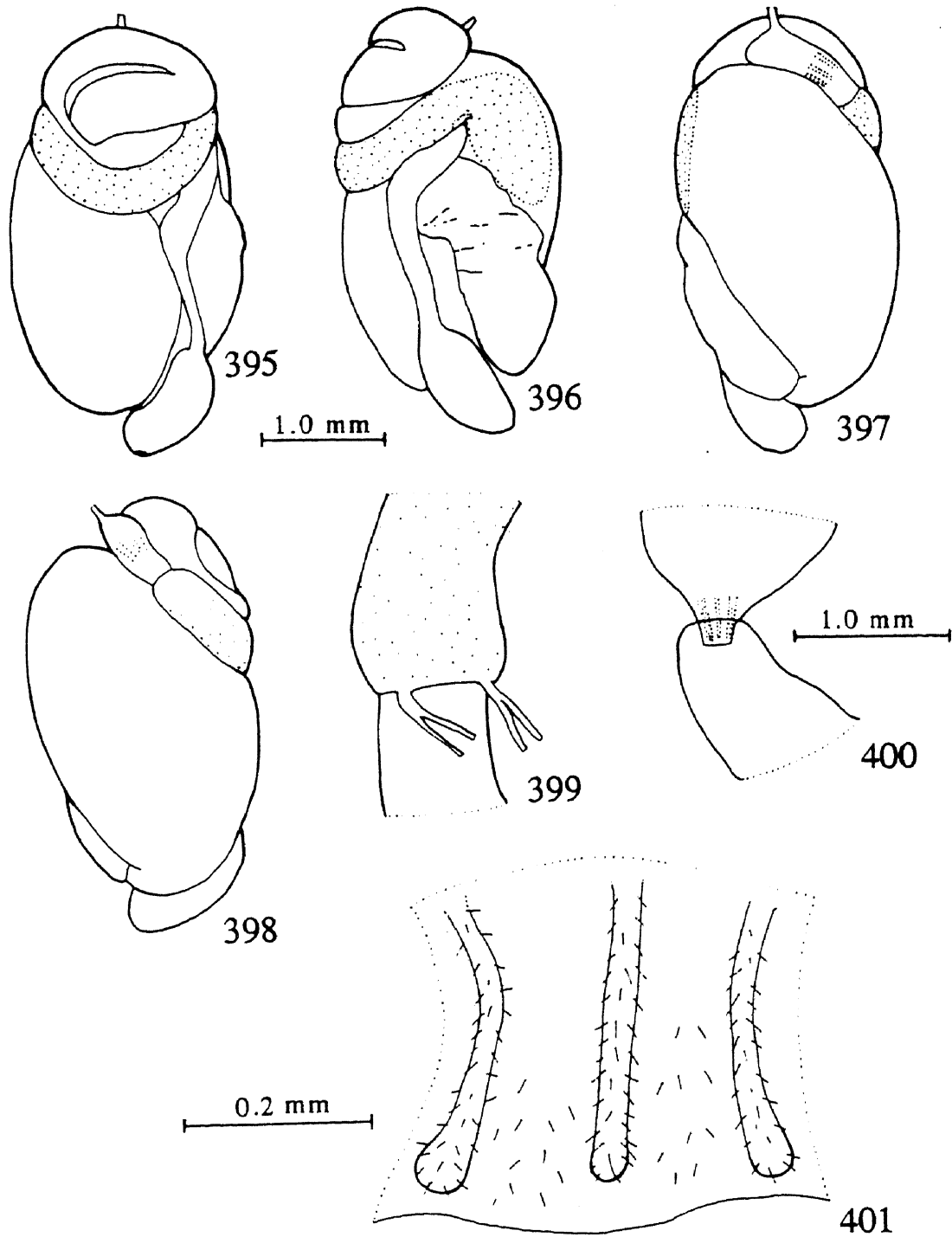
Macuxitermes Canello & Bandeira

Type species: *Macuxitermes triceratops*, by original designation.

Macuxitermes Canello & Bandeira 1992: 2 [major and minor soldiers, worker].

Digestive tube of worker (Figs. 395-401). Crop very small. Mixed segment very long and dilated. Origin of mesenteric prolongation oriented dorsally. Mesenteric prolongation tongue-shaped and broad. First segment of hindgut very large and strongly dilated. Malpighian tubules inseted in two separate pairs at junction of midgut and hindgut (Fig. 366). Enteric valve narrow, with three finger-like swellings convered with long, slender, and straight spines (Figs. 367-368). Paunch considerably smaller than first proctodeal segment.

Comparisons. The digestive tube of *Macuxitermes* is similar to those of *Embiratermes* and *Ibitermes*, except that the first proctodeal segment is conspicuously larger in *Macuxitermes*, and the mesenteric prolongation of the mixed segment is wider. The enteric valve armature is almost identical to those genera.



Figs. 395-401. Digestive tube of *Macrocitermes triceratops*. 395. dorsal; 396. right; 397. ventral; 398. left; 399. insertion of Malpighian tubules; 400. enteric valve; 401. internal armature of enteric valve.

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