

# **Contributions Celebrating Kumar Krishna**

*Edited by*  
Michael S. Engel



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CONTRIBUTIONS CELEBRATING KUMAR KRISHNA

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## Kumar Krishna, in appreciation

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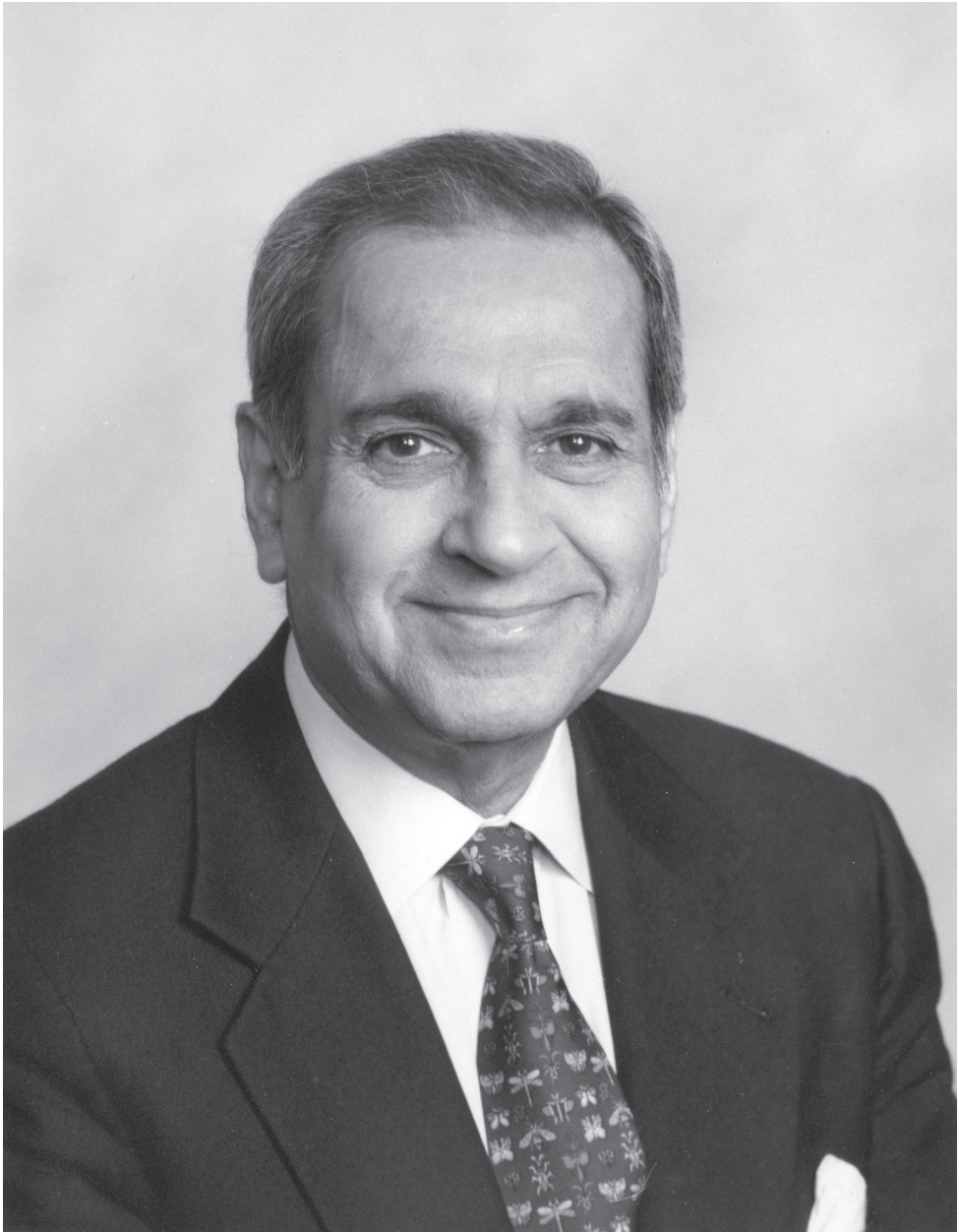
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It is with admiration and fondness that we dedicate this special issue of *ZooKeys* to Professor Kumar Krishna, dean of Isoptera research. This collection of papers is a humble testament of appreciation by the various biologists who are dedicated to studying termites, insects that are popularly maligned but actually of profound behavioral and ecological importance. Kumar's influence extends beyond the scope of isopterological studies and so several of the papers included herein are from contributors on other lineages of insects who have been similarly inspired by his indomitable spirit.

Kumar grew up in Dehra Dun in northern India, in the foothills of the Himalayas. His father was a physician, and was also one of the first Indians to be commissioned in the British army, in fact serving as a major in World War I. Kumar went to Agra University, earning a Bachelor of Science in 1950, and shortly thereafter a Master of Science degree from Lucknow University in 1952. He then served as a Research Assistant (1952–1954) to Mittan Lal Roonwal (1908–1990) at the Forest Research Institute in Dehra Dun, where he developed his interest in Isoptera. Roonwal is well known among Isoptera workers for his comprehensive papers on the systematics and general biology of termites from India and surrounding areas. Immediately thereafter, he moved to the U.S. where he was a graduate student and employed as a research assistant at the University of Minnesota from 1954–55. It was during this time that he wrote to Prof. Alfred E. Emerson (1896–1976) about graduate studies, and was soon thereafter accepted into Emerson's lab. Emerson was a professor at the University of Chicago from 1929–1962 and well known as the leading authority on the systematics and general



**Figure 1.** Prof. Dr. Kumar Krishna.

evolution of termites. He was also a coauthor of the classic *Principles of Animal Ecology* (Allee et al. 1949), and a colleague of William Morton Wheeler (1865–1937), the authority on ants at Harvard University and predecessor of E.O. Wilson. It was Emerson and Wheeler who promoted the concept of an insect colony as a superorganism, and both men built massive, global collections of their research groups. Emerson was

also a colleague of the architects of the New Synthesis in evolutionary biology – Ernst Mayr (1904–2005), George Gaylord Simpson (1902–1984), Theodosius Dobzhansky (1900–1975), and G. [George] Ledyard Stebbins (1906–2000) – as well as president of several important scientific societies, and a member of the prestigious National Academy of Science. He was hugely influential, and he had a lasting impact on Kumar.

At the University of Chicago, Kumar began a comprehensive revision of the world genera of drywood termites, still the major reference on the family Kalotermitidae (Krishna 1961). It was there that Kumar met his lifelong partner, Valerie. Valerie was studying English Literature and worked at the University of Chicago Press as an editor and proofreader, a skill that would be thoroughly utilized later on. Kumar and Valerie married in 1960. Kumar completed his doctorate in Evolutionary Biology from the University of Chicago in 1961, and was employed as a National Science Foundation postdoctoral fellow there until 1962 when he and Valerie departed for New York, and where Emerson donated his massive collection of termites to the American Museum of Natural History (AMNH). Kumar became an instructor at City College of the City University of New York (CUNY) in 1962, and a Research Associate in residence in the AMNH's Department of Entomology (now the Division of Invertebrate Zoology). He became Assistant Professor in 1964, Associate Professor in 1969, and full Professor in 1973, principally teaching Biology, Entomology, and Evolutionary Biology. Valerie herself was a Professor of English at CCNY, whose particular interest was Chaucer and *The Canterbury Tales*, and Malory's *Le Morte D'Arthur*. Though it took time away from research, Kumar held many important administrative posts at CCNY, which had significant impact on City College, CUNY, and the biological sciences. He served as Chair of the Department of Biology (1963–1968), deputy chair for the Department of Biology (1972–1975, 1978–1981), as Chair of the Graduate Program in Biology (1972–1974, 1978–1981), a member of the Faculty Research Award Program (1978–1981, 1985–1993), and as a member of the University Committee on Research (1981–1983, 1994–1996). There were some very challenging times during this period. In the 1950's, City College was a crucible of intellectualism, but was overcome by student radicalism in the 1960's. In the 1970's, New York suffered a severe financial crisis that cut deeply into the budgets of CUNY and other city organizations. But, biology prospered at CCNY, and the department even embarked on a symbiotic program with the AMNH in graduate student training in systematics.

Despite Kumar's administrative and teaching loads, perhaps the most impressive achievements are that he continued to produce influential research, funded by National Science Foundation research grants. It was during this time, for example, that Kumar Krishna and Frances M. Weesner organized and contributed to the seminal, two-volume work, *Biology of the Termites* (1969–70), synthesizing all major topics on termite biology and systematics. Interestingly, publication of *Biology of the Termites* coincided with the first major book by E.O. Wilson, *The Insect Societies* (1971). It was the heyday of social insects. Although two recent volumes on termite biology have been produced (Abe et al. 2000; Bignell et al. 2010), Krishna and Weesner remains an invaluable reference. On far more adventurous fronts, Kumar and Valerie made numerous (some-





**Figure 2.** Valerie Krishna, Kumar Krishna, Renato Araujo (1912–1978), and Alexander Sokoloff (1920–2011) at the XII International Congress of Entomology, London, 1964.

times dangerous) expeditions to collect termite specimens. Of particularly note are four weeks collecting in Myanmar (1961); a ten-month expedition across Sri Lanka, India, Thailand, and Taiwan (1968–1969); eight weeks collecting in Borneo, Malaya, and Singapore (1977–1978); four weeks in Borneo (1984–1985); four weeks in Sumatra (1988); three weeks in Malaya (1990); and seven weeks in Sulawesi and Java (1992). When Kumar retired in 1996 he was appointed Emeritus Professor at CCNY and took up residence full time on the fifth floor at the AMNH, devoting his efforts to the world's largest and most comprehensive termite collection, and to research.

It is safe to say that no one today has such comprehensive knowledge of termites globally, particularly their systematics, taxonomy, morphology, biogeography, and the fossil record. When Emerson was working, for example, there was only one Cretaceous termite known, *Cretatermes carpenteri* Emerson. Now, there are 36 species and 32 genera, nearly a quarter of which we have had the pleasure of working with Kumar to describe, but more importantly he has united a critical study of fossil termites with that of their modern counterparts. Emerson would have been immensely pleased to see how much more we now know about termite diversity, relationships, and evolution, largely as a result of Kumar's efforts. Kumar's encyclopedic knowledge makes him the ideal person to have been the principal author of the upcoming and highly anticipated magnum opus, *Treatise on the Isoptera of the World* (2012). At 2400 single-spaced manuscript pages, the work is immense, 85% of which is a taxonomic compendium of the 3138 living and fossil termite

species of the world (as of 26 March 2011) – incorporating a plethora of nomenclatural corrections made along the way, all based on direct study of over 4000 original taxonomic references and the more significant biological ones. Whereas many catalogues simply add to previous ones, propagating errors, this work was created *de novo*. Valerie applied her editorial acumen, spending months fastidiously proofing the manuscript for style and punctuation, a testament to the regard she and Kumar hold for each other.

Putting his considerable academic accomplishments aside, Kumar is one of the most positive, jovial, and generous individuals we know. Now in his eighties, his enthusiasm and energy for termite research seem tireless. When he worked on the Termitidae in Miocene Dominican amber, for example, Kumar spent hours each day hunched over his microscope, examining, sorting, comparing, and measuring hundreds of specimens and describing dozens of species. He worked like a graduate student. Indeed, there is perhaps no more enjoyable way for us to spend an afternoon than taking turns peering into a microscope alongside Kumar, discussing the details of some challenging fossil or exotic living specimen. We look forward to his residence on the fifth floor of the museum for many years to come, where we can peer through the microscope together in excited discussion.

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## **Taxa proposed by Kumar Krishna**

### **Available names as of 5 September 2011**

#### **Unranked names (2):**

Euisoptera Engel, Grimaldi, & Krishna

Neoisoptera Engel, Grimaldi, & Krishna

#### **Family-group names (6):**

†Archeorhinotermitinae Krishna & Grimaldi

Archotermopsidae Engel, Grimaldi, & Krishna

†Carinatermitinae Krishna & Grimaldi  
†Cratomastotermittidae Engel, Grimaldi, & Krishna  
Sphaerotermitinae Engel & Krishna  
Syntermitinae Engel & Krishna

**Genus-group names (19):**

†*Archeorhinotermes* Krishna & Grimaldi  
†*Baissatermes* Engel, Grimaldi, & Krishna  
*Bicornitermes* Krishna  
*Bifiditermes* Krishna  
*Ceratokalotermes* Krishna  
*Comatermes* Krishna  
†*Dharmatermes* Engel, Grimaldi, & Krishna  
*Dicuspidermes* Krishna  
†*Garmitermes* Engel, Grimaldi, & Krishna  
*Incisitermes* Krishna  
†*Kachinitermes* Engel, Grimaldi, & Krishna  
†*Khanitermes* Engel, Grimaldi, & Krishna  
*Labiocapritermes* Krishna  
*Marginitermes* Krishna  
†*Melqartitermes* Engel, Grimaldi, & Krishna  
†*Mylacrotermes* Engel, Grimaldi, & Krishna  
*Postelectrotermes* Krishna  
†*Tanytermes* Engel, Grimaldi, & Krishna  
*Tauritermes* Krishna

**Species-group names (106):**

*Aciculitermes maymyoensis* Krishna  
*Allotermes denticulatus* Krishna  
*Allotermes papillifer* Krishna  
†*Amitermes lucidus* Krishna & Grimaldi  
*Angulitermes paanensis* Krishna  
*Angulitermes resimus* Krishna  
†*Anoplotermes bobio* Krishna & Grimaldi  
†*Anoplotermes cacique* Krishna & Grimaldi  
†*Anoplotermes carib* Krishna & Grimaldi  
†*Anoplotermes maboya* Krishna & Grimaldi  
†*Anoplotermes naboria* Krishna & Grimaldi  
†*Anoplotermes nitaino* Krishna & Grimaldi  
†*Anoplotermes quisqueya* Krishna & Grimaldi  
†*Anoplotermes taino* Krishna & Grimaldi

†*Archeorhinotermes rossi* Krishna & Grimaldi  
 †*Atlantitermes antillea* Krishna & Grimaldi  
 †*Atlantitermes caribea* Krishna & Grimaldi  
 †*Atlantitermes magnoculus* Krishna & Grimaldi  
 †*Baissatermes lapideus* Engel, Grimaldi, & Krishna  
*Bicornitermes bicornis* Krishna  
*Bicornitermes emersoni* Krishna  
*Bulbitermes prabhae* Krishna  
*Calcaritermes colei* Krishna  
*Calcaritermes rioensis* Krishna  
*Calcaritermes snyderi* Krishna  
 †*Caribitermes hispaniola* Krishna & Grimaldi  
*Cavitermes rozeni* Krishna  
 †*Constrictotermes electroconstrictus* Krishna  
*Coptotermes bentongensis* Krishna  
 †*Coptotermes hirsutus* Krishna & Grimaldi  
 †*Coptotermes paleodominicanus* Krishna & Grimaldi  
*Coptotermes sepangensis* Krishna  
 †*Cryptotermes yamini* Krishna & Bacchus  
 †*Cryptotermes glaesarius* Engel & Krishna  
 †*Dharmatermes avernalis* Engel, Grimaldi, & Krishna  
*Dicuspiditermes cacuminatus* Krishna  
*Dicuspiditermes fissifex* Krishna  
*Dicuspiditermes kistneri* Krishna  
*Dicuspiditermes spinitibialis* Krishna  
 †*Dolichorhinotermes apopnus* Engel & Krishna  
*Dolichorhinotermes lanciarius* Engel & Krishna  
*Epicalotermes planifrons* Krishna  
*Foraminitermes coatoni* Krishna  
*Foraminitermes harrisi* Krishna  
 †*Garmitermes succineus* Engel, Grimaldi, & Krishna  
*Glyptotermes adamsoni* Krishna & Emerson  
*Glyptotermes concavifrons* Krishna & Emerson  
 †*Glyptotermes grimaldii* Engel & Krishna  
*Glyptotermes guamensis* Krishna & Emerson  
*Glyptotermes hendrickxi* Krishna & Emerson  
*Glyptotermes jurioni* Krishna & Emerson  
*Glyptotermes kirbyi* Krishna & Emerson  
*Glyptotermes lighti* Krishna & Emerson  
*Glyptotermes longipennis* Krishna & Emerson  
*Glyptotermes longuisculus* Krishna & Emerson

*Glyptotermes nissanensis* Krishna & Emerson  
*Glyptotermes palauensis* Krishna & Emerson  
†*Glyptotermes paleoliberatus* Engel & Krishna  
*Glyptotermes parki* Krishna & Emerson  
*Glyptotermes parvocolatus* Krishna & Emerson  
*Glyptotermes rotundifrons* Krishna & Emerson  
*Glyptotermes schmidtii* Krishna & Emerson  
*Glyptotermes seeversi* Krishna & Emerson  
*Glyptotermes sicki* Krishna & Emerson  
*Glyptotermes sinomalatus* Krishna & Emerson  
*Glyptotermes truncatus* Krishna & Emerson  
*Glyptotermes tuberifer* Krishna & Emerson  
*Homallotermes eleanorae* Krishna  
*Homallotermes exiguus* Krishna  
†*Incisitermes peritus* Engel & Krishna  
*Labritermes emersoni* Krishna & Adams  
*Labritermes kistneri* Krishna & Adams  
†*Mastotermes electrodanicus* Krishna & Grimaldi  
†*Mastotermes electromexicus* Krishna & Emerson  
†*Meiatermes araripensis* Krishna  
†*Melqartitermes myrrheus* Engel, Grimaldi, & Krishna  
†*Microcerotermes insulanus* Krishna & Grimaldi  
†*Microcerotermes setosus* Krishna & Grimaldi  
*Microcerotermes uncatus* Krishna  
*Mirocapritermes valeriae* Krishna  
†*Mylacrotermes cordatus* Engel, Grimaldi, & Krishna  
†*Nasutitermes ampliocolatus* Krishna & Grimaldi  
†*Nasutitermes electrinus* Krishna  
†*Nasutitermes electronasutus* Krishna  
*Nasutitermes fabricii* Krishna  
†*Nasutitermes incisus* Krishna & Grimaldi  
†*Nasutitermes magnocellus* Krishna & Grimaldi  
†*Nasutitermes medioculatus* Krishna & Grimaldi  
†*Nasutitermes pilosus* Krishna & Grimaldi  
†*Nasutitermes rotundicephalus* Krishna & Grimaldi  
†*Nasutitermes seminudus* Krishna & Grimaldi  
*Neocapritermes araguaia* Krishna & Araujo  
*Neocapritermes guyana* Krishna & Araujo  
*Neocapritermes talpoides* Krishna & Araujo  
*Neocapritermes taracua* Krishna & Araujo  
*Neocapritermes utiariti* Krishna & Araujo  
†*Parvitermes longinasus* Krishna & Grimaldi  
*Procapritermes parvulus* Krishna

*Procryptotermes falcifer* Krishna

† *Proelectrotermes holmgreni* Engel, Grimaldi, & Krishna

† *Subulitermes hispaniola* Krishna & Grimaldi

† *Subulitermes insularis* Krishna & Grimaldi

† *Tanytermes anawrahtai* Engel, Grimaldi, & Krishna

† *Termes primitivus* Krishna & Grimaldi

† *Termopsis ukapirmasi* Engel, Grimaldi, & Krishna

† *Velocitermes bulbosus* Krishna & Grimaldi





# Morphology and gonad development of normal soldiers and reproductive soldiers of the termite *Zootermopsis nevadensis nevadensis* (Isoptera, Archotermopsidae)

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## Abstract

Reproductive or neotenic soldiers of the Archotermopsid *Zootermopsis nevadensis nevadensis* (Hagen) are compared to sterile soldiers and primary male reproductives. Several head capsule morphometrics correlate significantly with gonad size across all forms and both sexes of soldiers. The easily observed field character of ratio of mandible length to labrum length is a consistent and reliable feature of head capsule external morphology for predicting gonad development and reproductive potential of soldier forms regardless of age, sex, or live weight.

## Keywords

evolution of soldier caste, reproductive soldier, neotenic soldier, *Zootermopsis*, morphometrics

## Introduction

Soldiers are a non-reproductive defensive caste in termites (though they may sometimes have other roles (Traniello 1981) and are not always the exclusive defensive caste in a colony (e.g. Nel 1968, Thorne 1982, Haverty and Thorne 1989, Polizzi and Forschler 1998, Delphia et al. 2003)). Compared to other colony members they generally have large, heavily sclerotized heads with enlarged mandibles, although some derived groups

(e.g. *Nasutitermes*) have vestigial mandibles and rely on chemical defense (reviewed by Weesner 1969a). A soldier caste is found in all termites except in the Termitid subfamily Apicotermitinae, in which they have been secondarily lost (reviewed in Inward et al. 2007). Primitive termites of the family Archotermopsidae (Engel et al. 2009) retain developmental plasticity which allows all castes (except normal soldiers) to become reproductive, either through development into an alate (winged dispersal form) or through molts into a non-dispersive *neotenic* (replacement) reproductive (Light and Weesner 1951, Noirot 1985, Noirot and Pasteels 1987, Thorne 1996, Roisin 2000). Although they retain the prothoracic glands necessary for molting, soldiers are the exception to the Archotermopsids' overall developmental flexibility, and are considered a terminal caste because they do not molt again (Noirot and Pasteels 1987). However, in six species of primitive termites, (Archotermopsidae: *Archotermopsis wroughtoni* Desneux, *Zootermopsis angusticollis* (Hagen), *Zootermopsis nevadensis* (Hagen), *Zootermopsis laticeps* (Banks); Stolotermitidae: *Stolotermes brunneicornis* (Hagen), *Stolotermes ruficeps* Brauer), some neotenics of both sexes have soldier-like morphological characteristics, and are called *reproductive soldiers*, or *neotenic soldiers* (reviewed by Myles 1986). These soldier-like neotenics are phylogenetically rare and have been reported only occasionally in most of the six species, but are found more commonly in *A. wroughtoni* and *Z. nevadensis* (Imms 1919, Thorne et al. 2003). Reproductive soldiers possess large mandibles similar to those of normal soldiers but have fully developed gonads upon sexual maturity (Imms 1919, Heath 1928, Castle 1934, Myles 1986). *Zootermopsis nevadensis* reproductive soldiers behave more like reproductives than soldiers (Heath 1928, Thorne et al. 2003).

Because reproductive soldiers occur only in the most socially and developmentally primitive termites, they are considered probable evolutionary relicts of an early form of soldiers: a stepping-stone toward obligatory sterility and altruistic defense (Thorne et al. 2003).

Reproductive soldiers, while possessing the generalized soldier form, typically have differences in external morphology that distinguish them from normal soldiers including a slightly rounder head shape and more curved mandibles (Heath 1928, Myles 1986). The abdomen may appear banded due to expansion of the intersegmental membrane between sternites as well as an increase in fat body and changes in its distribution (N. Breisch 2011 pers. obs.) and consistency, possibly royal fat body (Grassé 1982). However, there is often individual variation in external morphology (Light 1943, Morgan 1959, Thorne et al. 2002, Thorne et al. 2003).

Here we compare external morphology and internal gonad development in normal and neotenic soldiers of *Zootermopsis nevadensis nevadensis* (Thorne & Haverty, 1989) and in new kings and mature kings. Using measurements of several external features as well as gonad dimensions, differences are quantified between normal soldiers and reproductive soldiers (referred to collectively henceforth as "soldier morphs"). Ratios of these measurements (used to normalize the expected differences due to size and age of individuals) are analyzed for predictive value (Light 1927). Gonad size is correlated with age and live weight in male soldier morphs and primary male reproductives (kings).

## **Methods**

### **Experimental production of replacement reproductives**

Kings were removed from 64 king and queen right colonies to stimulate production of male replacement reproductives. Colonies were outbred, initiated by alate pairs that emerged from wild colonies collected near Placerville, CA (El Dorado County). At 2 wk intervals beginning 6 wks post king removal colonies were examined for replacement (neotenic) reproductive soldiers. Twelve new male reproductive soldiers were weighed live then individually preserved in Pampel's fixative (composed of 2 - 4 parts glacial acetic acid, 15 parts 95% ethyl alcohol, 30 parts distilled water, 6 parts formalin (40% formaldehyde in water): BioQuip Products). Ten mature (molted to soldier morph at least 3 months previously) male reproductive soldiers and ten mature normal/sterile (molted to soldier morph at least 3 months previously) male soldiers from similar sized colonies were also weighed live and individually preserved. After 24 h in fixative external characters (width of head capsule, length of head capsule, length of left mandible from condyle to apex, length of labrum, width of labrum) of specimens were measured using an eyepiece-mounted micrometer on a Leica MZ MPO dissecting microscope. Each termite was then pinned to a paraffin-filled Petri dish and a longitudinal incision was made on the dorsal side. The open body cavity was flooded with a solution of Nile Blue dye and water then rinsed with 70% ethanol after several seconds leaving enough ethanol to partially cover the specimen. Widest and narrowest diameter of the left testis was measured. Testis width subsequently refers to the widest measurement of the left testis for specimens of known age and weight.

### **Characterization of dealate and mature male primary reproductives**

Newly sclerotized male alates (new kings) were individually isolated with a 2 cm square of moistened paper towel until they shed their wings. After wing abscission they were weighed, preserved in Pampel's fixative and analyzed as above. A subsample of the kings removed from colonies to generate secondary reproductives were also weighed, preserved and analyzed as above. All these kings were at least two years old.

### **Characterization of archived specimens of reproductive and normal soldiers**

In addition to the production of known age reproductive soldiers, previously collected individuals were classified as "normal soldiers" ( $n = 144$ ; 84 male, 60 female) or "reproductive soldiers" ( $n = 47$ ; 38 male, 9 female) based upon external morphology and observed colony role. The majority (192) were from outcrossed laboratory colonies, which were bred from alates maturing in colonies initiated by alate pairs that emerged from wild colonies near Placerville, CA (El Dorado County). Ten individuals devel-

oped in and were collected directly from the field-collected stock colonies. Sixteen were collected directly from the field in October 2007 from Eldorado National Forest (El Dorado County, CA). The field collected individuals were preserved in ethanol without fixative, 79 were fixed in Bouin's solution (composed of 37% formaldehyde (24% by weight), picric acid (71%), and glacial acetic acid (5%); BBC Biochemical Corporation) for at least an hour before transfer to 80% ethanol, and 115 were fixed and stored in Pampel's. Eight had previously been preserved in an unidentified fixative (ethanol and/or Pampel's).

The external measurements of each soldier morph individual included: dorsal width of head capsule at widest point, dorsal length of head capsule without mandibles from the posterior margin to the base of the labrum, length of left mandible from condyle to apex, length of labrum, width of labrum, wingbud length (if present), width of postmentum at narrowest point, width of postmentum at widest point, length of postmentum, length of eye, and width of eye. Sex was recorded as well. After external measurements were completed the following measurements were taken: females—width of ovary at midpoint, width of ovary at widest point, length of ovary from tip to base of posterior ovariole, number of eggs; males—widest diameter of testis, narrowest diameter of testis. Ratios of head, labrum, and testis lengths and widths were made for each individual as a measurement of roundness. The ratio of the mandible length to the labrum length was also calculated. These morphometrics were suggested as useful differentiating characteristics for soldier morphs by laboratory experience and the published anatomical work on the reproductive system of *Z. nevadensis nevadensis* and other termites by Light (1927), Child (1934) and Weesner (1969b).

## Analysis

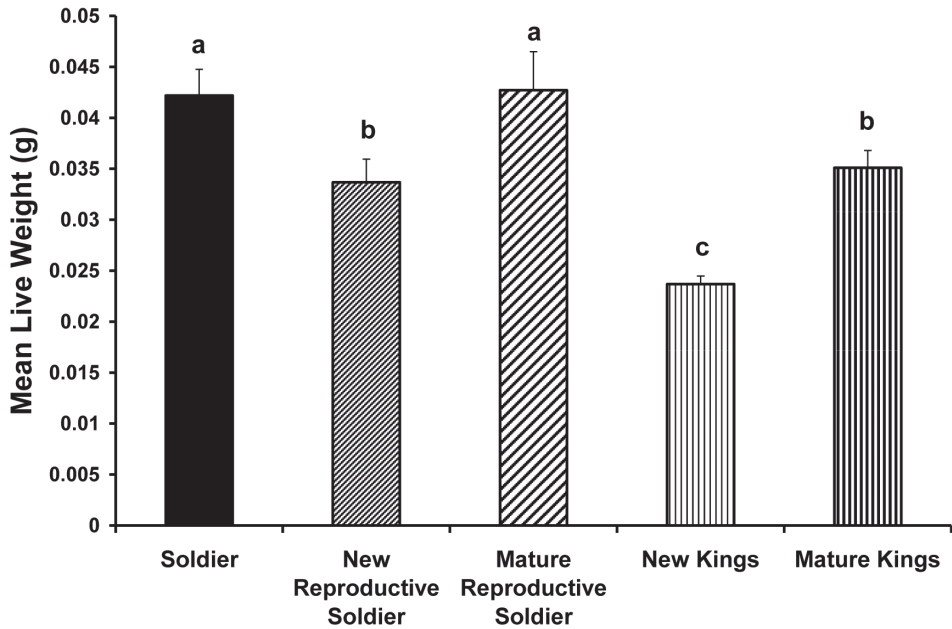
All data were analyzed using SAS 9.1 for Windows (Correlation Analysis, MANOVA, ANOVA). Results were considered significant at the 0.05 level. Correlations were univariate, and thus may result in an overall type I error rate greater than the pair-wise rate of 0.05.

## Results

### Specimens of known age and live weight

#### *Contrasting live weight of normal soldiers to reproductive soldiers and kings*

Newly differentiated male reproductive soldiers were smaller (mg live weight) than either normal sterile soldiers or mature reproductive soldiers ( $p < 0.0001$ ) but not different from mature kings. Normal sterile soldiers and mature reproductive soldiers did not differ in weight. Dealate kings were smaller than the other four morphs/castes ( $p < 0.0001$ ) (Fig. 1).



**Figure 1.** Comparison of means for live weight (g) of male soldiers, reproductive soldiers and primary reproductives (new and mature kings). Means with the same letter are not significantly different. Error bars indicate standard errors.

### *Contrasting external morphology and gonad size of normal and reproductive soldiers*

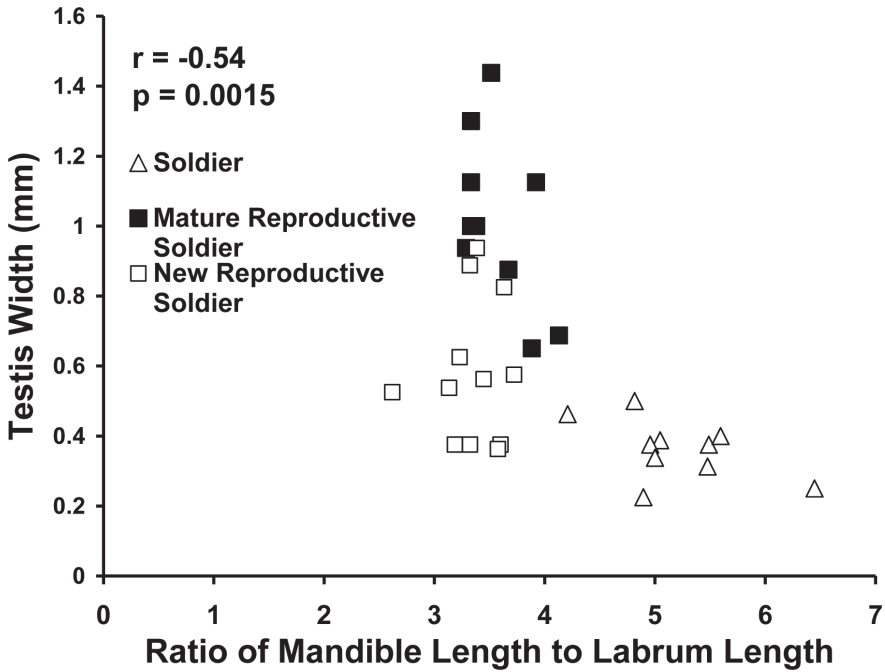
The ratio of labrum length to left mandible length distinguished sterile from reproductive soldier morphs ( $p < 0.0001$ ). Reproductive soldiers had larger testes than sterile soldiers regardless of live weight or age of reproductive soldier ( $p < 0.0001$ ). Testis width correlated with the ratio of left mandible length to labrum length ( $p = 0.0015$ ) (Fig. 2).

### *Age effects on gonad development*

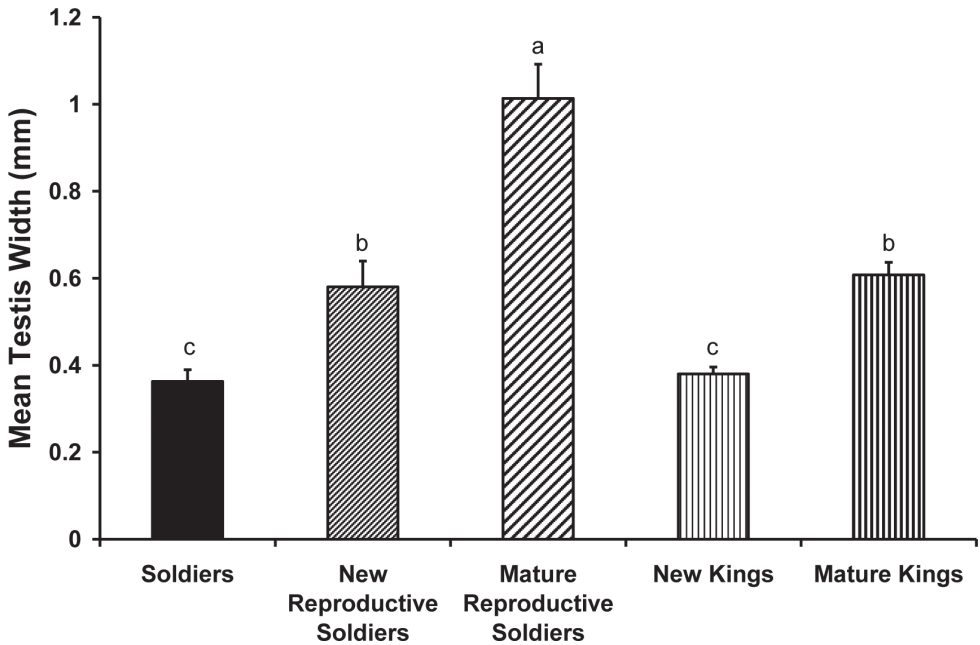
Testes (width) in recently eclosed reproductive soldiers were larger than mature sterile soldiers but smaller than mature reproductive soldiers ( $p < 0.0001$ ). Dealate kings' testes were equivalent in width to sterile soldiers', while mature kings' testes were equivalent to newly differentiated reproductive soldiers (Fig. 3).

### *Correlation of live weight and testis width*

There was no correlation between live weight and testis width in sterile soldiers ( $p = 0.2952$ ), new reproductive soldiers ( $p = 0.8225$ ), mature reproductive soldiers ( $p = 0.0639$ ) or new kings ( $p = 0.3071$ ). Mature kings ( $n = 21$ ) testis width and live weight correlated positively ( $p = 0.0448$ ).



**Figure 2.** Correlation between testis width and ratio of mandible length to labrum length in male soldiers and new and mature reproductive soldiers.



**Figure 3.** Comparison of means for testis width (mm) of male soldiers, reproductive soldiers and new and mature kings. Means with the same letter are not significantly different. Error bars indicate standard errors.

## Specimens of unknown age and live weight

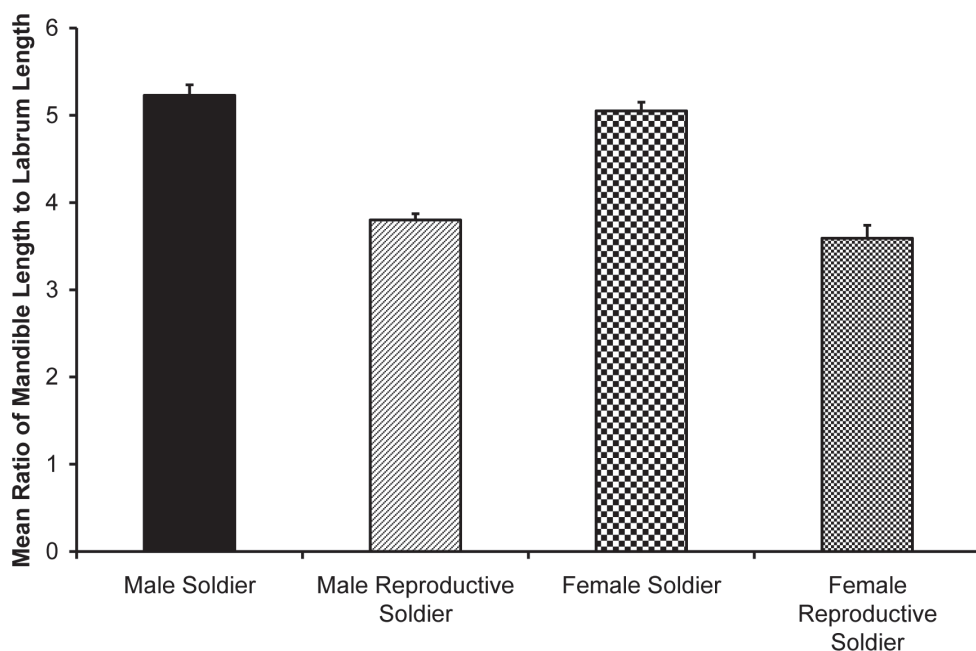
### *Morphological differences between soldiers and reproductive soldiers*

Figure 4 shows pooled means by caste, after grouping male and female data because there was no significant sex effect. Morphological differences between soldiers and reproductive soldiers by sex are listed in Table 1. Multivariate ANOVA (MANOVA) for both male and female morphology indicated no overall caste by sex interaction ( $p > 0.4$ ) and a significant overall caste effect (Wilks' Lambda statistic,  $p < 0.01$ ). (See supplementary material, Table 1, for comparison of means for significant quantitative measurements of castes using pooled male and female data with no significant sex or sex-by-caste interaction).

Four of eight female reproductive soldiers had at least one egg; none of the 50 female normal soldiers examined had eggs. There was no significant difference between possession of wingbuds by caste.

### *Correlations between external and internal morphology*

In female soldier morphs the ratio of mandible length to labrum length (Fig. 5) was correlated with ovary length. For male soldier morphs, the ratio of mandible length to labrum length (Fig. 6) was correlated with testis width. The lack of clear, discrete



**Figure 4.** Comparison of means for ratio of mandible length to labrum length of male and female soldiers and reproductive soldiers. Within sex, soldiers had statistically significantly different mean ratios than reproductive soldiers ( $p < 0.01$ ). Error bars indicate standard errors. Source data for the figure are listed in a table in the Supplementary Material.

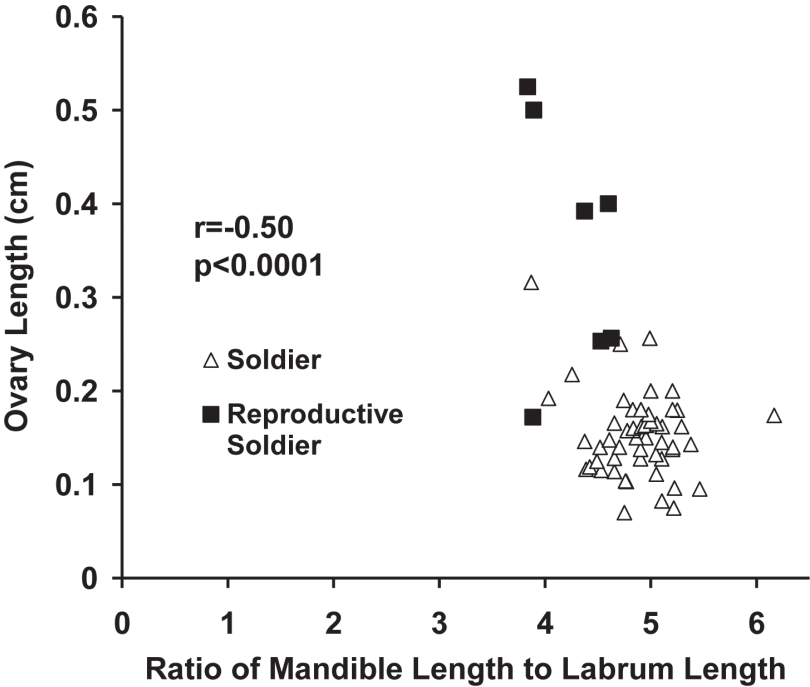
groups in Figs 5, 6 was because newly differentiated RS were intermixed with developed RS in the archived material. Ovary length and testes width would have been much greater and the groups discrete following a few weeks of development. Figure 2 shows the progression and distinct separation of known age male soldiers and reproductive soldiers. (See Appendix I for the correlation table.)

**Table 1.** Morphological differences between soldiers and reproductive soldiers by sex in *Z. n. nevadensis*

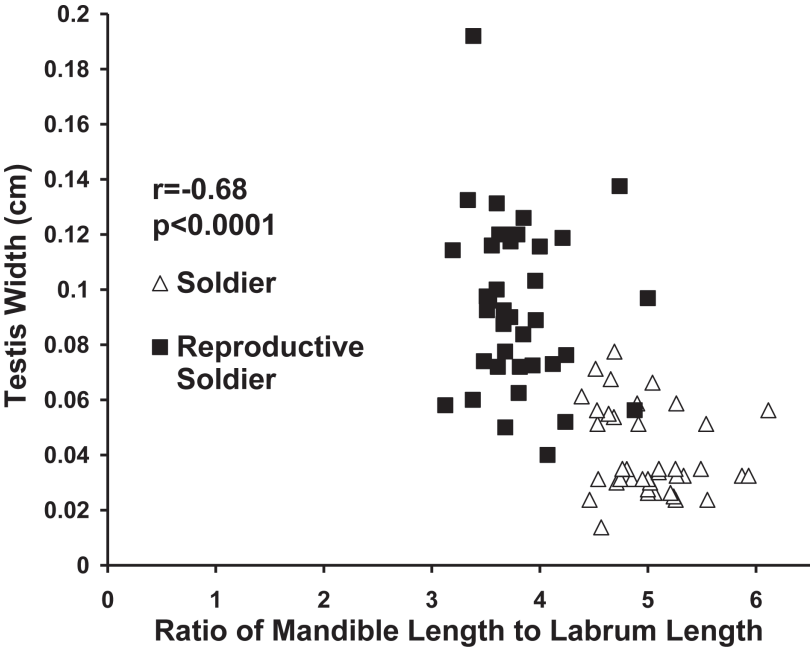
Variable	P-value of caste effect (males)		P-value of caste effect (females)	
	Mean (cm) ± SE, (n) [male soldiers]	Mean (cm) ± SE, (n) [male reproductive soldiers]	Mean (cm) ± SE, (n) [female soldiers]	Mean (cm) ± SE, (n) [female reproductive soldiers]
Eye Length	<b>0.0002</b>		0.2373	
	0.02 ± 0.0006 (84)	0.03 ± 0.0016 (38)	0.02 ± 0.0009 (60)	0.02 ± 0.002 (9)
Head Length	< <b>0.0001</b>		< <b>0.0001</b>	
	0.40 ± 0.0066 (84)	0.31 ± 0.0057 (38)	0.40 ± 0.0061 (58)	0.31 ± 0.010 (9)
Head Width	<b>0.0004</b>		<b>0.0088</b>	
	0.30 ± 0.0040 (84)	0.27 ± 0.0047 (38)	0.30 ± 0.0036 (60)	0.26 ± 0.0090 (9)
Labrum Length	0.7438		0.1484	
	0.06 ± 0.0009 (82)	0.06 ± 0.001 (38)	0.06 ± 0.0008 (60)	0.07 ± 0.002 (9)
Labrum Width	< <b>0.0001</b>		< <b>0.0001</b>	
	0.07 ± 0.0008 (82)	0.08 ± 0.001 (38)	0.07 ± 0.0008 (59)	0.08 ± 0.001 (9)
Mandible Length	< <b>0.0001</b>		< <b>0.0001</b>	
	0.32 ± 0.0047 (82)	0.24 ± 0.0044 (38)	0.32 ± 0.0040 (60)	0.24 ± 0.010 (9)
Postmentum Length	< <b>0.0001</b>		<b>0.0009</b>	
	0.28 ± 0.0055 (83)	0.20 ± 0.0053 (38)	0.28 ± 0.0062 (59)	0.21 ± 0.012 (9)
Postmentum Width (at widest point)	< <b>0.0001</b>		<b>0.0019</b>	
	0.11 ± 0.0014 (83)	0.099 ± 0.0015 (38)	0.11 ± 0.0012 (60)	0.099 ± 0.0039 (9)
Postmentum Width (at narrowest point)	<b>0.0010</b>		0.1168	
	0.064 ± 0.00066 (83)	0.069 ± 0.0014 (38)	0.065 ± 0.00094 (60)	0.067 ± 0.0024 (9)
Ratio Mandible length: labrum length	< <b>0.0001</b>		< <b>0.0001</b>	
	5.23 ± 0.12 (81)	3.80 ± 0.072 (38)	5.05 ± 0.10 (60)	3.59 ± 0.15 (9)
Testes Diameter (smallest)	< <b>0.0001</b>			
	0.033 ± 0.0012 (60)	0.074 ± 0.0036 (38)		
Testes Diameter (largest)	< <b>0.0001</b>			
	0.042 ± 0.0015 (72)	0.094 ± 0.0050 (38)		
Ovary Length			< <b>0.0001</b>	
			0.15 ± 0.0068 (53)	0.36 ± 0.051 (7)
Ovary Width (midpoint)			< <b>0.0001</b>	
			0.019 ± 0.0013 (50)	0.070 ± 0.01 (7)
Ovary Width (widest point)			< <b>0.0001</b>	
			0.025 ± 0.0013 (51)	0.087 ± 0.012 (7)

ANOVA results and descriptive statistics for each variable measured, by sex. Variables with p-values less than 0.05 were considered significant and are highlighted in bold. MANOVA indicated a significant overall caste effect for both males (p < 0.01) and females (p < 0.01) based on Wilks' Lambda statistic.





**Figure 5.** Correlation between ovary length and the ratio of mandible length to labrum length in female soldier morphs (soldiers and reproductive soldiers).



**Figure 6.** Correlation between testis diameter at the widest point and the ratio of mandible length to labrum length in male soldier morphs (soldiers and reproductive soldiers).

### ***Homogeneity of gonad size variance between soldiers and reproductive soldiers***

Variance of ovary length was 0.0182 (mm<sup>2</sup>) in female reproductive soldiers which was much greater ( $p < 0.0001$ ) than that for soldiers (0.000246). Variance in ovary width at the widest point was also greater ( $p < 0.0001$ ) in female reproductive soldiers (0.000106) than in normal soldiers (0.0000109). Variance in the widest diameter of the testis was greater ( $p < 0.0001$ ) for male reproductive soldiers (0.0000955 mm<sup>2</sup>) than that for soldiers (0.0000231).

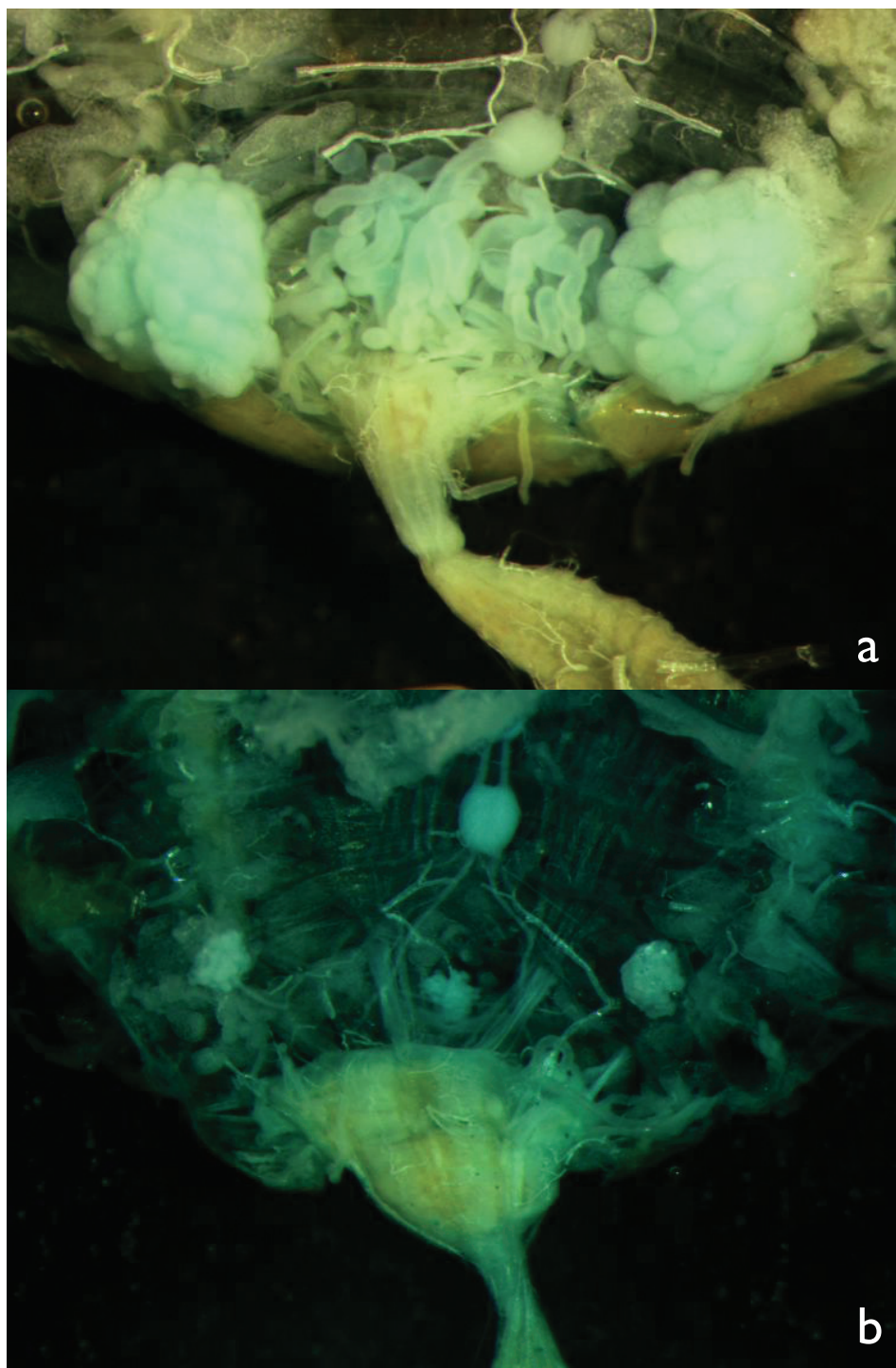
## **Discussion**

Neotenic soldiers of both sexes had smaller, rounder heads than soldiers (also observed although not formally analyzed by Heath 1928, Myles 1986), shorter (or more curved) mandibles, longer and more rectangular postmentums, wider and more oblong labrums, larger eyes, and a lower mandible-to-labrum ratio than normal/sterile soldiers. Reproductive soldiers of both sexes had larger gonads than soldiers. Male reproductive soldiers, whether newly eclosed or mature had larger testes than soldiers (Fig. 7). Unlike female reproductive soldiers, normal female soldiers never had developing eggs (Fig. 8). There was no difference between castes in terms of wingbud frequency. These results confirm the utility of these morphometrics to distinguish soldiers from reproductive soldiers. Due to age and size variance in reproductive soldiers, the morphometrics that involved ratios (head roundness, postmentum shape, labrum shape, and mandible-to-labrum ratio) are more reliable predictors of gonad development across a wide range of reproductive soldier sizes.

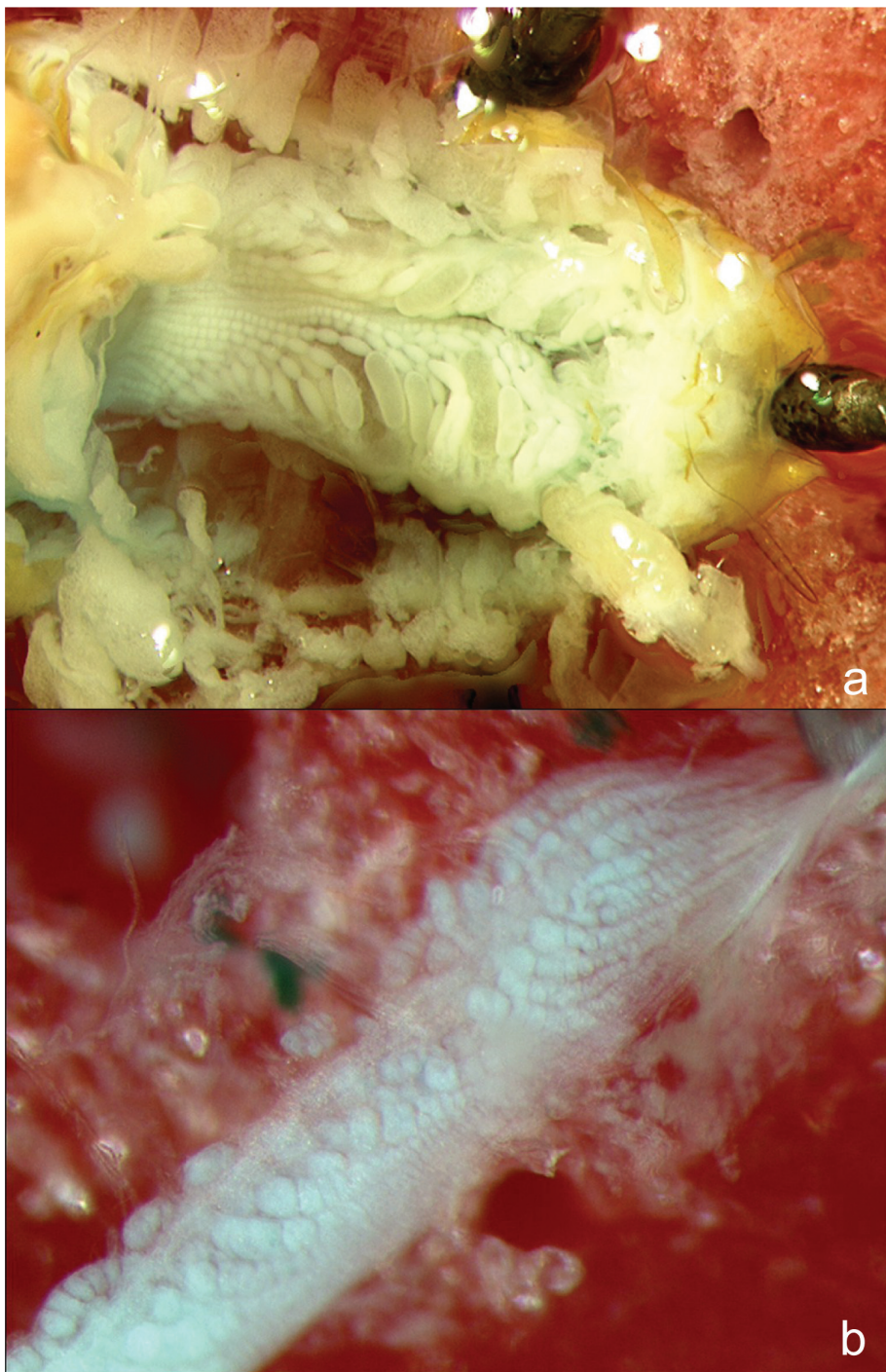
The external, ratio-based morphological measurement of mandible length to labrum length is a strong indicator of gonad size in soldier morphs of both sexes. This ratio accounts for body size and age differences and is visible before other characteristics (e.g. color and shape of abdomen) are apparent, serving as a useful, reliable correlate of gonad size in soldier morphs of a variety of ages. This ratio can easily be estimated—a labrum that extends less than a quarter of the length of the mandibles indicates a normal, sterile soldier. If the labrum is close to a third of the length of the mandible the individual is a reproductive soldier (Fig. 9).

Variation in gonad size may be due to age, as newly developed male reproductive soldiers had significantly smaller gonads than those that had been fertile for a longer period. Female reproductive soldiers had much greater variance in ovary length and ovary width at the widest point than did normal soldiers. This may be because of the inclusion of these younger, less sexually developed reproductive soldiers in the sample.

Morgan (1959) documented variation in head shape in the “emergency soldiers” of *Stolotermes ruficeps* Brauer, though he did not mention gonad development or reproductive status in these individuals. Similarly, Light (1943) noted a range of “intergrades” in *Z. nevadensis*, which he regarded as intercastes between soldiers, juveniles, nymphs, and neotemics. These observations suggest that individuals’ potential reproductive ability can be revealed without dissection or close observation of behavior. It should be noted that eggs were found only in females classified as reproductive soldiers.



**Figure 7.** Testes and accessory glands of **a** male reproductive soldier and **b** male soldier. Both preparations were photographed under the same magnification.



**Figure 8.** Ovaries of **a** a female reproductive soldier and **b** a female soldier. The female reproductive soldier ovarioles are much more developed and contain several eggs, while the female soldier ovarioles are reduced, with no evidence of egg development.





**Figure 9.** Male reproductive soldier (top) and male soldier (bottom). Note coloration of abdomen, shape of head capsule, and ratio of mandible to labrum length.

(Because sperm counts were not assessed, it is unknown whether all male “reproductive soldiers” were fertile.) The analysis of archived specimens could not distinguish between reproductive soldiers of varying sexual maturity; therefore, the continuum of morphology found in soldier morphs may in fact represent a continuum of reproductive soldier ages, as suggested by the wide variance found in reproductive soldier gonad sizes and data from known age individuals.

It is likely that modern reproductive soldiers represent an early step in soldier evolution, and that the loss of fertility in soldiers was secondary to the development of large mandibles and heavily sclerotized heads, advantageous for primitive termites in intercolony interactions (Thorne et al. 2003). The secondary loss of reproductive capacity after the evolution of soldier morphology also appears to have occurred in aphids (Stern and Foster 1997), thrips (Chapman et al. 2002) and ant soldiers (Urbani and Passera 1996), as reviewed by Thorne et al. (2003). Roisin (1999) suggested that reproductive soldiers’ distinctive morphology may merely be a non-adaptive accident of the dual roles of juvenile hormone as both a stimulus for soldier development as well as a gonadotropic hormone in reproductives. However, distinct roles and behaviors in meetings with neighboring colonies imply that this caste is not an accident (Thorne et al. 2003). Naturally occurring reproductive soldiers are distinct from artificially induced nymph/soldier intercastes. Miura et al. (2003) applied juvenile hormone analogue (JHA) to *Z. nevadensis* nymphs, causing them to molt into intercastes that share some characteristics with natural reproductive soldiers (e.g. small, round head; developed gonads; short, curved mandibles). The JHA induced

intercastes had a range of morphologies, depending on the nymphal stage at which the JHA was applied. However, all possessed wings or wingbuds. Fully formed membranous wings have never been observed in a naturally occurring soldier or reproductive soldier.

Further study is needed to elucidate the developmental pathway of reproductive soldiers and to determine whether they result from a combination of developmental or social signals, or whether they develop in response to a single stimulus. Because reproductive soldiers are considered relictual transitional forms reflecting the evolutionary history of soldiers (Thorne et al. 2003) this work suggests that soldier development may have been much more flexible in the past than in most extant termites. Studies in progress will determine whether larger gonad size in mature reproductive soldiers compared to primary reproductives confers greater fertility and more rapid increase in colony size in a species with marked intraspecific competition for nesting resources.

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## Appendix I

External morphology and gonad size: Complete means comparisons and correlations. (doi: 10.3897/zookeys.148.1672.app) File format: PDF

**Explanation note:** Table 1: "Morphological differences between soldiers and soldier neotenics of *Z. nevadensis*" and Table 2: "Correlations between external morphology and gonad size in soldier morphs of *Z. nevadensis*"

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# ***Cryptotermes* (Isoptera, Kalotermitidae) on Espiritu Santo, Vanuatu: Redescription of *Cryptotermes albipes* (Holmgren & Holmgren) and description of *Cryptotermes penaoru* sp. n.**

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**Citation:** Yves Roisin (2011) *Cryptotermes* (Isoptera, Kalotermitidae) on Espiritu Santo, Vanuatu: Redescription of *Cryptotermes albipes* (Holmgren & Holmgren) and description of *Cryptotermes penaoru*, new species. In: Engel MS (Ed) Contributions Celebrating Kumar Krishna. ZooKeys 148: 31–40. doi: 10.3897/zookeys.148.1718

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## **Abstract**

Complete series of two species of the phragmotic drywood termite genus, *Cryptotermes* (Isoptera: Kalotermitidae), were found on Espiritu Santo, Vanuatu. Here, I describe for the first time the soldier of *Cryptotermes albipes* (Holmgren & Holmgren), which resembles *C. domesticus* but presents deep depressions on the head sides and vertex. The other species, here described as *Cryptotermes penaoru* **sp. n.**, comes close to *C. tropicalis*, a species known from the tropical rainforest of northern Queensland, from which its soldier is distinguished by its more elongated head capsule.

## **Keywords**

Isoptera, *Cryptotermes*: Vanuatu, new species

## Introduction

The termite family Kalotermitidae, often called drywood termites, is present in all tropical, subtropical and warm temperate regions of the world (Emerson 1955; Eggleton 2000). Its abundance and diversity is however very variable. The major continental rainforests, albeit otherwise rich in termite species, are notoriously poor in Kalotermitidae. This family is better represented in drier biomes or in marginal or insular forest habitats, although its presence in rainforest canopies may have been overlooked (Roisin et al. 2006).

The family was revised at the genus level by Krishna (1961), whose classification is still largely accepted. The phylogeny of the family is poorly known, although some data are available for Australian lineages (Thompson et al. 2000). The genus *Cryptotermes* is remarkable for the strongly phragmotic head of its soldiers. It is widespread over the whole intertropical region. Several species are pests of furniture or structural wood and have been spread by man over extensive areas (Gay 1967; Evans 2011). The genus is one of the best known of the entire order, since it has been the subject of three important monographs in the past 30 years. Gay and Watson (1982) revised the Australian species, and Bacchus (1987) those from the rest of the world. More recently, Scheffrahn and Křeček (1999) published a revision of this genus in the West Indies, based on extensive recent sampling campaigns. However, the fauna of many Pacific islands remains poorly known. In Vanuatu, Gross (1975) mentions only one species, *C. albipes*, although Gay and Watson (1982) report the presence of *C. domesticus* as well. Collections on Espiritu Santo in 2006, under the framework of the Santo 2006 Biodiversity Survey (Bouchet et al. 2009), provided several new samples, including complete series of *C. albipes* and an undescribed species. Here, I provide the first description of the soldier of *C. albipes* and describe the new species as *Cryptotermes penaoru*.

## Methods

Collections took place between 9–26.xi.2006 in the Saratsi Range above Penaoru village, on the west coast of the Cumberland Peninsula, Espiritu Santo, Vanuatu, as part of a multiple-taxa survey of arthropods along an altitudinal gradient (Corbara 2011). Specimens were collected and preserved in 80% ethanol.

## Imaging

Series of optical images of specimens were taken with a Leica DFC290 digital camera mounted on a Leica Z6APO microscope, then combined by Helicon Focus software. SEM images were obtained with a Philips XL 30 ESEM.

## Measurements and their abbreviations

Measurements were taken to the nearest 0.005 mm with a Wild MMS 235 length-measuring set fitted to a Wild M6 stereomicroscope.

**Imagos:** **ED** – Eyes maximum diameter; **OD** – ocellus maximum diameter; **HLP** – Head length to postclypeus; **HWE** – Head width, maximum including eyes; **HWI** – Head width, interocular; **PW** – Pronotum width (not flattened); **T3L** – Hind tibia length; **FWL** – Forewing length (without scale).

**Soldiers:** **HLP** – Head length to postclypeus; **HLF** – Head length to frontal flange; **HLG** – Head length to genal horn; **HW** – Head maximum width; **PW** – Pronotum width; **LML** – Left mandible length (seen from below, from condyle to tip); **LW** – labrum width; **HD** – head depth, excluding postmentum; **PML** – Postmentum length; **MPW** – Maximum postmentum width; **T3L** – Hind tibia length.

## Collections and their abbreviations

<b>ANIC</b>	Australian National Insect Collection, Canberra, ACT, Australia
<b>MNHM</b>	Muséum National d'Histoire Naturelle, Paris, France
<b>NHMB</b>	Naturhistorisches Museum Basel, Switzerland
<b>RBINS</b>	Royal Belgian Institute for Natural Sciences, Brussels, Belgium
<b>ULB</b>	Université Libre de Bruxelles, Belgium

Most of the samples presently housed in the author's collection at the ULB will ultimately be deposited at the RBINS.

## Taxonomy

### Genus *Cryptotermes* Banks, 1906

<http://species-id.net/wiki/Cryptotermes>

*Cryptotermes* – Banks, 1906: 336. Type species, by monotypy: *Cryptotermes cavifrons* Banks, 1906.

*Cryptotermes* Banks – Krishna 1961: 379–382, Figs 77–80 (redescription).

**Stages.** Imagos of *Cryptotermes* can be recognized by the combination of the following criteria: left imago mandible with anterior margin of third marginal tooth clearly longer than posterior margin of first plus second marginals, and media vein bending forward to join radial sector in middle of wing or beyond.

Soldiers of *Cryptotermes* have a phragmotic head (like those of *Calcaritermes*) and all fore tibial spurs approximately equal.

***Cryptotermes albipes* (N. Holmgren & K. Holmgren, 1915)**

[http://species-id.net/wiki/Cryptotermes\\_albipes](http://species-id.net/wiki/Cryptotermes_albipes)

*Calotermes albipes* – Holmgren N & Holmgren K, 1915: 89–90 (imago). Type locality: Maré, Loyalty Islands (New Caledonia).

*Cryptotermes albipes* (Holmgren, N. & K.) – Snyder 1949: 38.

**Remarks.** The type series of this species only contains imagos. Bacchus (1987) redescribed this caste and announced the recent discovery of the soldier and its forthcoming description by J. Buckerfield of CSIRO, but this author, now deceased, shifted to another field and his contribution never appeared in print.

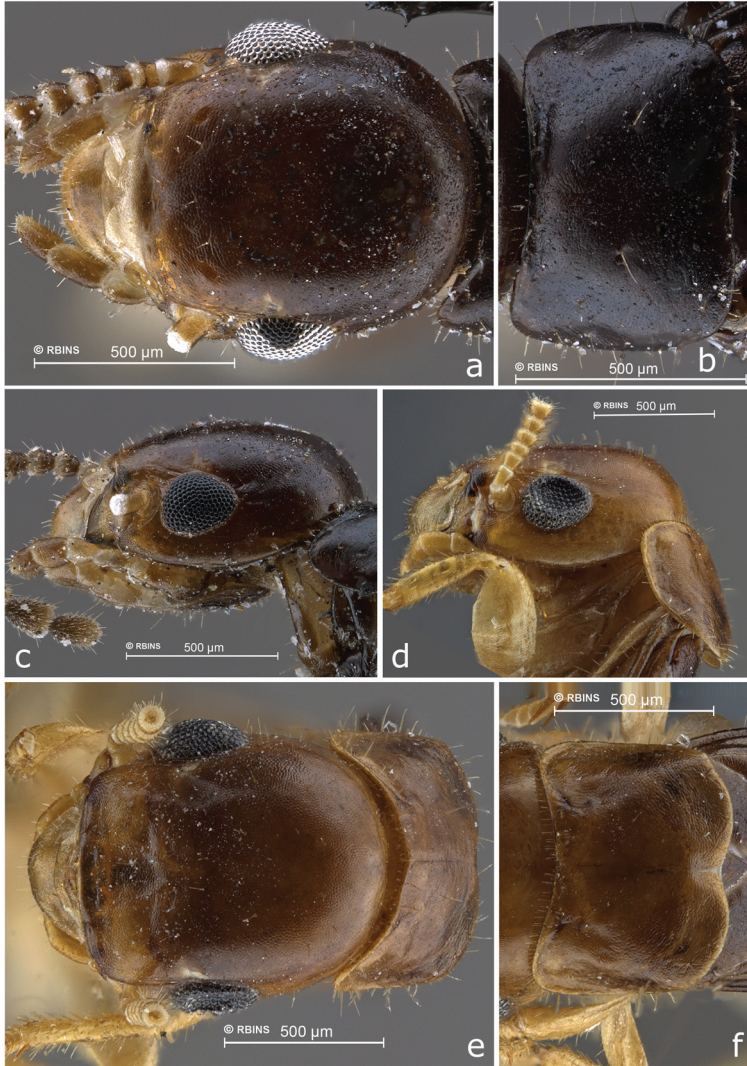
**Material examined. Paralectotypes: NEW CALEDONIA: Loyalty Islands:** Maré Island, 17.xi.1911 (coll. Sarasin & Roux), alates only (NHMB). **Other material: VANUATU: Taféa:** SW Tanna Island, 28.vii.1971 (coll. K.E. Lee, det. J. Buckerfield), alates and soldiers (ANIC#15344); **Sanma:** Espiritu Santo, 28.x.1982 (coll. R.L. Paton, det. J. Buckerfield), alates and soldiers (ANIC#18883); Espiritu Santo, 10.xi.2006 (coll. det. Y. Roisin), with 1 alate, sexuals, soldiers and immatures, on forested slope above Penaoru village, alt. 300m a.s.l. (14°57.98'S, 166°38.22'E) (ULB #Santo016); *ibidem*, 12.xi.2006 (coll. det. Y. Roisin), soldiers and immatures (RBINS #15607); *ibidem*, 16.xi.2006 (coll. det. Y. Roisin), sexuals, soldiers and immatures from dead branch about 15m above ground (RBINS #15616).

**Imago.** (Figs 1a, 1c, 1e) Redescribed by Bacchus (1987: 37, figs 6–7). Pigmented parts substantially darker than described by Bacchus, as the pigmentation of Holmgren's material faded over the years. The most remarkable feature of this species is its overall dark brown pigmentation, but with the sharp contrast between the almost white tibiae and dark brown femora.

Measurements of 6 paralectotype alates and 13 sexuals (5 alates, 8 dealates) from 4 colonies (non-type specimens between parentheses): ED: 0.270–0.310 (0.265–0.325); OD: 0.080–0.120 (0.070–0.130); HLP: 0.825–0.930 (0.835–0.885); HWE: 0.845–0.960 (0.830–0.925); HWI: 0.635–0.700 (0.620–0.665); PW: 0.755–0.885 (0.700–0.835); T3L: 0.690–0.745 (0.675–0.755); FWL: 5.06–6.11 (5.25–5.55).

Its pigmentation pattern (dark to very dark brown with pale, almost white tibiae contrasting with dark brown femora and yellow tarsi) distinguishes this species from all other *Cryptotermes* in this area.

**Soldier.** (*previously undescribed*) (Figs 2a, 2c, 2e, 3a) Head capsule very dark reddish brown to black. Head in dorsal view slightly convex on sides and on posterior margin; trapezoidal in profile, narrowing posteriorly. Frontal flange not raised, with medial notch. Frons flat, making an angle <90° with plane of mandibles. Genal horns well developed, pointing upwards; frontal horns reduced to low humps. Deep depression on vertex, delimited by broad, blunt crests running backwards from highest points of frontal flange. Sides of head capsule concave. Mandibles rather short and stout, with sharp cutting edge and small teeth. Antennae pale brown, of 10–12 articles. Pronotum widely and angularly notched, with thickened anterior margin.



**Figure 1.** Head and pronotum of imagos **a–c** *Cryptotermes albipes* **a** head from above **b** pronotum **c** head from left side **d–f** *Cryptotermes penaoru*, paratype from colony #Santo080 **d** head from left side **e** head from above **f** pronotum.

Measurements of 6 soldiers from 5 colonies: HLP: 0.975–1.230; HLF: 0.955–1.215; HLG: 0.975–1.230; HW: 0.920–1.085; PW: 0.795–1.075; LML: 0.495–0.615; LW: 0.185–0.225; HD: 0.730–0.890; T3L: 0.525–0.625.

Vertical to overhanging frons distinguishes *C. albipes* from all other species from the area except *C. domesticus*. Depression in middle of vertex with conspicuous anteroposterior ridges on both sides is characteristic of *C. albipes*.

**Distribution and biology.** *Cryptotermes albipes* is known from the Loyalty Islands (east of New Caledonia) and Vanuatu (Espiritu Santo and Tanna). It also occurs in



New Guinea (unpublished data). Its biology is poorly known. On Santo, this species was found at 300m a.s.l. in dead tree trunks on the ground, as well as in a dead branch on a living tree at a height of 15m. Colony boundaries seem rather diffuse. Several reproductive pairs can be found in the same log, and may possibly reside in the same network of interconnecting tunnels.

***Cryptotermes penaoru* sp. n.**

urn:lsid:zoobank.org:act:B0BB619F-6C57-4E5E-A30C-4B07B306C723

[http://species-id.net/wiki/Cryptotermes\\_penaoru](http://species-id.net/wiki/Cryptotermes_penaoru)

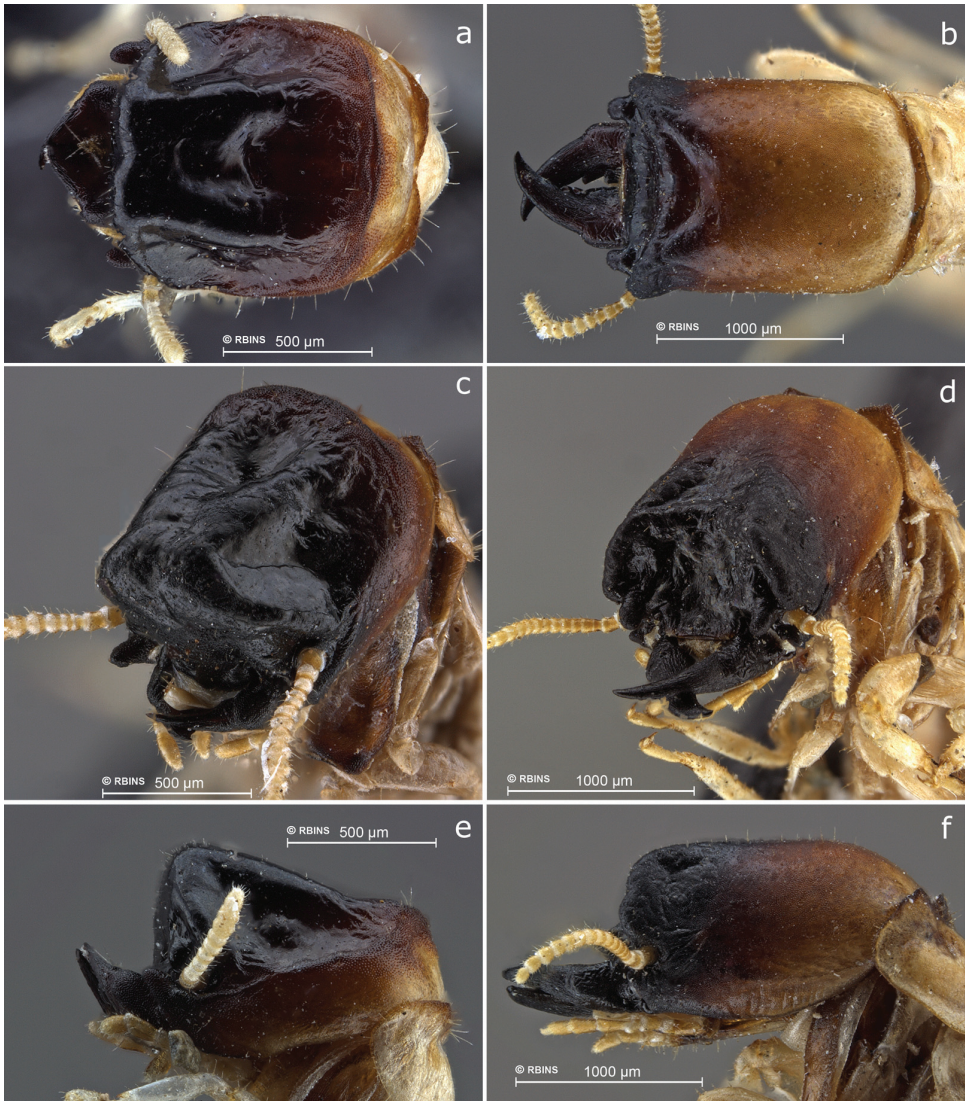
**Remarks.** Samples of this species were previously identified as *Cryptotermes tropicalis* Gay & Watson (Roisin et al. 2011), but further examination revealed them to belong in an undescribed species.

**Material examined. Holotype, soldier: VANUATU: Sanma:** Espiritu Santo, 09.xi.2006 (coll. det. Y. Roisin), in standing dead wood, on forested slope above Penaoru village, alt. 100m a.s.l. (14°57.69'S, 166°37.90'E) (ULB #Santo003; RBINS #15589: type colony). **Paratypes:** alates, 1 soldier and immatures from type colony (same data as holotype); *ibidem*, 18.xi.2006 (coll. det. Y. Roisin), 1 male (dealate), 3 soldiers, immatures (ULB #Santo080).

**Imago.** (Figs 1b, 1d, 1f) Overall colour medium brown; head, pronotum and wing scales darker; legs paler, with femora paler than tibiae; abdominal sternites palest. Wings brown, paler than tergite colour, with pimple-like nodules. Head parallel-sided, almost circular behind. Eyes large; ocelli large, oval, contiguous to eyes. Antennae of 14–16 segments in alates, broken down to 7 segments in dealate of colony #Santo080. Pronotum almost as wide as head, widely concave anteriorly, with convex sides narrowing posteriorly, posterior margin biconvex. Pilosity of head and pronotum sparse and short. Wings with subcosta, radius and radial sector sclerotized, and slight sclerotization of cubital branches. Media unsclerotized, except at junction with radial sector, beyond half length of wing. Arolium present.

Measurements of paratypes: 4 alates from type colony (#Santo003) and 1 dealate from colony #Santo080 (parentheses): ED: 0.265–0.295 (0.275); OD: 0.100–0.115 (0.090); HLP: 0.950–1.000 (0.950); HWE: n.a. (0.935); HWI: 0.695–0.730 (0.705); PW: 0.810–0.910 (0.865); T3L: 0.745–0.870 (0.825); FWL: 6.82–7.15 (n.a.).

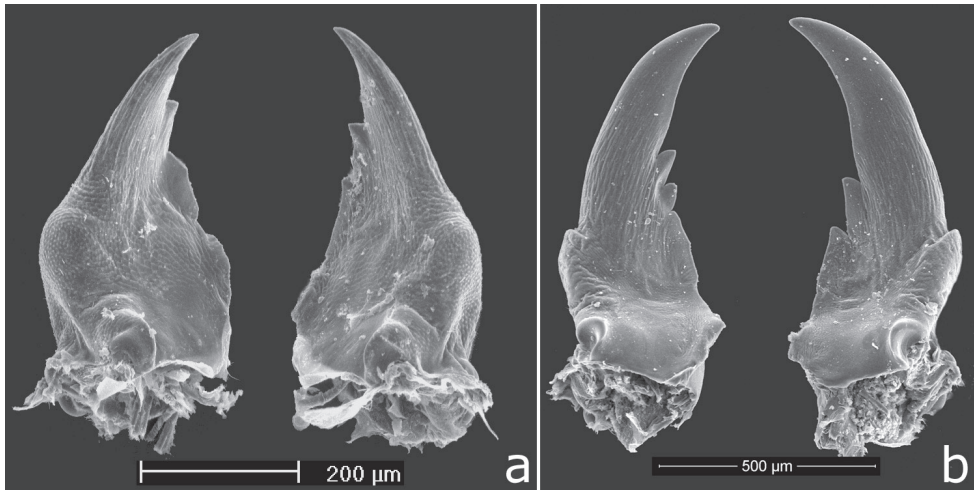
**Soldier.** (Figs 2b, 2d, 2f, 3b) Head capsule from ferruginous posteriorly to black in frontal area. Mandibles almost black, antennae and labrum dark orange. Head quadrangular, distinctly longer than wide, with straight parallel sides and convex posterior margin. Frontal flange prominent only on sides, extending as low ridges backwards at an angle of ~45° with sagittal plane. Frons-vertex ridge concave, delimiting with posterior extensions of frontal flange a triangular depression anteriorly on vertex. Frons falling steeply on postclypeus. Frontal horns stout, prominent, blunt. Genal horns very small, blunt. Slight lateral depression and rugosity posterior to frontal flange. Eyes



**Figure 2.** Heads of soldiers **a, c, e** *Cryptotermes albipes* **a** from above **c** oblique view from upper left front side **e** lateral view **b, d, f** *Cryptotermes penatoru*, paratype from type colony **b** from above **d** oblique view from upper left front side **f** lateral view.

visible as distinct pale spots. Mandibles long, with prominent external hump at basal third. Marginal teeth small but distinct. Antennae of 10–15 articles. Pronotum widely and angularly notched, with thickened anterior margin.

Measurements of holotype, paratype from type colony [brackets] and 3 paratypes from colony #Santo080 (parentheses). HLP: 1.755 [1.675] (1.610–1.650); HLG: 1.615 [1.645] (1.560–1.580); HW: 1.250 [1.165] (1.135–1.175); PW: 1.175 [1.055]



**Figure 3.** SEM pictures of soldier mandibles, from above **a** *Cryptotermes albipes* **b** *Cryptotermes penaoru* (paratype from colony #Santo080).

(1.035–1.095); LML: 1.025 [0.950] (0.955–0.995); LW: 0.320 [0.270] (0.260–0.325); HD: 1.025 [0.920] (0.925–0.950); T3L: 0.920 [0.875] (0.775–0.815).

This species comes clearly close to *C. tropicalis*, from Queensland, but can be distinguished by its more elongated head.

**Distribution, etymology and biology.** *Cryptotermes penaoru* was found in a single site in lowland forest near Penaoru village, hence its name. The type colony was collected from a small standing dead tree.

## Discussion

*Cryptotermes penaoru* clearly belongs in a group of moderately phragmotic species with low or medially indistinct frontal flange, weak to moderate lateral rugosity behind frontal flange, and relatively long mandibles with distinctive marginal teeth. This group includes the Australian species *C. tropicalis*, *C. primus*, *C. austrinus*, *C. queenslandis* and *C. simulatus*, which form a monophyletic lineage (Thompson et al. 2000). As *Cryptotermes* species readily colonize islands and often speciate locally (Scheffrahn and Křeček 1999), the discovery of new species related to this Australian lineage in the south Pacific could be expected. The affinities of *C. albipes* are much less obvious, as this species does not closely resemble any other one. In view of the head shape of its soldiers, *C. domesticus* might be the best candidate to be the closest relative of *C. albipes*. *Cryptotermes domesticus* has been widely disseminated by man, but its region of origin probably lies within southeast Asia (Evans 2011), and how far its indigenous distribution extends through Sundaland into the Papuan region and south Pacific islands is uncertain. Molecular data are badly needed to further resolve the phylogeny and phylogeography of this group.



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# Distribution, diversity, mesonotal morphology, gallery architecture, and queen physogastry of the termite genus *Calcaritermes* (Isoptera, Kalotermitidae)

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## Abstract

An updated New World distribution of the genus *Calcaritermes* is given along with photographs and a key to the New World species outside Mexico. *Calcaritermes recessifrons* is found to be a junior synonym of *C. nigriceps*. Except for *C. temnocephalus*, pseudergates of the other seven studied *Calcaritermes* species possess a mesonotal rasp. The rasps suggest a role in propagation of microbes on gallery surfaces and microbial infusion below the wood surface. *Calcaritermes temnocephalus* is shown to have an unusually large physogastric queens for a kalotermitid and several species produce large eggs.

## Keywords

Neotropical distribution, species synonymy, field photography, taxonomic soldier key, mesonotal rasp, microbial symbiosis, queen physogastry, eggs

## Introduction

In his monumental revision of the family Kalotermitidae, Krishna (1961) formed the current taxonomic definition of the termite genus *Calcaritermes* (Snyder 1925). Krishna (1961) separated *Calcaritermes* from all other genera by the diagnostic enlargement of the outer spine (“spur” *sensu* Snyder 1925b) of the fore tibia relative to the other two tibial spines. Soldiers also possess a dark, rather smooth, and cylindrical head cap-

sule. *Calcaritermes* is a basal group within the Kalotermitidae (Legendre et al. 2008) and is not closely related to the sympatric *Cryptotermes* which also possess phragmotic dark-headed soldiers. Krishna 1961, however, could not morphologically distinguish *Calcaritermes* alates from those of the genus *Glyptotermes*. Even so, Emerson (1969) described *C. vetus* from a fossilized alate in amber collected in the Simojovel region of Chiapas, Mexico. Emerson based his generic assignment on the similarity of the fossil to that of *C. temnocephalus* and its range in southeastern Mexico. The most recent review of *Calcaritermes* distribution was also provided by Emerson (1969).

As with most non-pest termite genera, details of the ecology and bionomics of the *Calcaritermes* are completely unknown. Almost all that is published about *Calcaritermes* relates to identification of preserved specimens for faunal surveys (e.g. Scheffrahn et al. 2005 and part of this paper). The only research involving *Calcaritermes* biology stems from two studies: one of their protist gut fauna (Gile et al. 2010) and the other of alate flight in forest canopy (Bourguignon et al. 2009).

In the current paper, the New World distribution and diversity of *Calcaritermes* is revised based on material in the University of Florida collection. I use field photography to show the live habitus of castes of seven *Calcaritermes* species and depict eight soldiers using montage photography of preserved material. I also reassess the mesonotal “rasp” of pseudergate castes of *Calcaritermes* and provide an example of extreme queen physogastry in the Kalotermitidae. Finally, I describe the atypical feeding galleries of this genus and hypothesize a relationship between gallery architecture and the mesonotal rasp in terms of microbial symbiosis.

## Material and methods

A total of 214 colony samples of *Calcaritermes* from 122 localities (Fig. 1) were collected between 1996 and 2010 and identified by the author from original descriptions and comparisons. These samples are included in the University of Florida (UF) Termite Collection, Fort Lauderdale Research and Education Center, Davie, Florida. This collection houses over 34,000 samples, mostly from the Caribbean Basin, which the author and his colleagues have amassed since 1986. The findings herein are a direct result of field observations made while collecting *Calcaritermes* during various survey expeditions.

Field photographs (Figs 2, 4E, 4F, and 5) were taken with a Nikon Coolpix S7c digital camera set to macro and flash mode. Specimens were usually photographed in a 5.5 cm dia. plastic Petri dish bottom lined with manila folder cardboard although natural substrate (Figs 3D and 3I) was sometimes suitable. Figures 3 and 4C were taken as multilayer montages using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software. Montage specimens were taken from 85% ethanol and suspended in a pool of Purell® Hand Sanitizer to position the specimens in a transparent plastic Petri dish. Mesonotal rasps (Figs 4A and B) were slide-mounted with PVA mounting medium (BioQuip Products, Inc) and photographed with an Olympus BH-2 compound microscope fitted with phase contrast optics. Figure 3D

was taken of a pseudergate that was freshly killed by desiccation and photographed with a Hitachi 4700 FESEM scanning electron microscope at 3–5 kV.

## Results and discussion

### Distribution

*Calcaritermes* is primarily a neotropical genus with the exceptions of a relic nearctic species, *C. nearcticus* Snyder, 1933, found from central and northeastern Florida to southeastern Georgia (Scheffrahn et al. 2001) and an anomalous indomalaysian congener, *C. krishnai* (Maiti and Chakraborty) known from Great Nicobar Island (Roonwal and Chhotani 1989) and Papua New Guinea (Y. Roisin, unpublished data). The current New World distribution of *Calcaritermes* is given in Fig. 1. Literature localities in Fig. 1 include *C. colei* Krishna from San Luis Potosi, Mexico and *C. snyderi* Krishna from El Salvador (Krishna 1962), *C. imminens* from Colombia (Snyder 1925b), *C. parvinitus* Light from Colima, Mexico (Light 1933) and from Chamela, Mexico (Nickle and Collins 1988) and *C. rioensis* from Brazil (Krishna 1962, Reis and Cancellato 2007). Emerson's 1969 localities for *C. guatemalae* (Tabasco region of Mexico) and *C. nigriceps* (central Colombia) not mapped in Fig. 1 because they were deemed too vague.

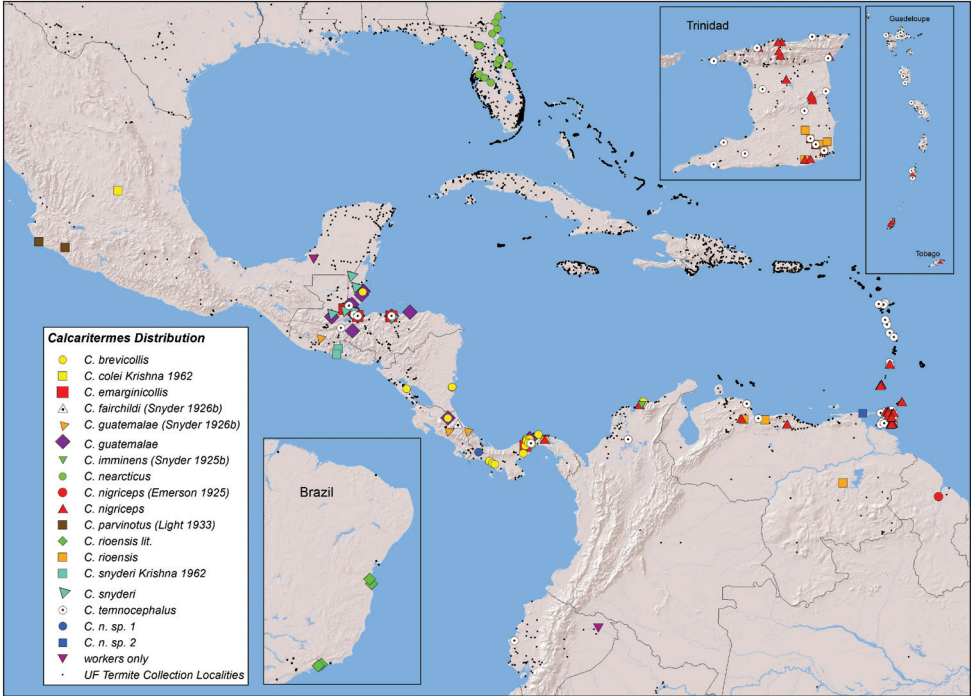
### Nomenclatural revisions

Krishna (1962) redescribed *C. temnocephalus* (Silvestri 1901) from types collected in Venezuela (Silvestri 1903) and additional material from Trinidad. The type locality, Las Trincheras (10.31, -68.09), Carabobo State, is in the vicinity of Caracas where Frederik Vilhelm August Meinert collected insects in 1891 (Reuter 1904) of which the termites were studied by Silvestri (1901, 1903). In 2008, we collected all castes of a *Calcaritermes* sp. at P.N. San Sebastián, Carabobo, Venezuela (10.402, -68.000, elev. 105 m). Our material matched Krishna's 1962 redescription of *C. temnocephalus* and substantiates our earlier synonymy that *C. fairchildi* is a junior synonym of *C. temnocephalus* (Scheffrahn et al. in press). Specifically, the description of *C. fairchildi* (= *thompsonae*) (Snyder 1926b, 1926c) from Costa Rica (Fig. 1) also compares favorably with our Venezuela sample. I have compared 50 colony series of *C. temnocephalus* from Guadeloupe to Ecuador and Belize. *C. temnocephalus* is unique among congeners in the UF collection (species shown in Fig. 3) because pseudergate castes do not have a mesonotal rasp and also lack the concavity of the posterior margin of the pronotum (Figs 4E, 5C). Imagos of *C. temnocephalus* are unique among those described in the genus in that they are orange-brown in body coloration and have hyaline wings (Fig. 2B, 5C). The next lightest imago is *C. brevicollis* with a medium brown dorsal coloration and lightly pigmented wings. All eight other described *Calcaritermes* imagos are dark brown to blackish and have smoky wings (e.g., Fig. 2D, 2I).

Snyder (1925b) described *C. recessifrons* from one soldier and a series of alates (type locality Cincinnati, 11.10, -74.08, Fig. 1) collected by W. M. Mann during his expedition to Colombia. In 2009, we surveyed termites near the type locality for *C. recessifrons* (“above” Minca 11.126, -74.120, elev. 712 m) and collected several colony samples of *Calcaritermes* there. Our material matched Snyder’s description of *C. ressesifrons*. The description of *C. nigriceps* (Emerson 1925) from British Guiana (Fig. 1, now Guyana) also compared favorably with our sample. Further comparison of *Calcaritermes* specimens collected from Grenada to Panama (Fig. 1) confirmed that *C. recessifrons* is a junior synonym of *C. nigriceps* as previously reported by Scheffrahn et al. (in press). *C. nigriceps* soldiers are unique among congeners in the UF collection as the frontal furrow is shallow and unsculptured (Fig. 3C). Cincinnati, Colombia, is also the type locality of *C. imminens* (Snyder 1925b); however, we were unable to collect this distinctive medium-sized species in which the soldier has an overhanging frons. Table 1 lists the current New World species of *Calcaritermes* and their type localities.

### Key to *Calcaritermes* in the UF collection based on the soldier or pseudergate caste

- 1 Pseudergates (pseudergates without large wing buds) lack mesonotal rasp or concave posterior margin of pronotum; soldier with frontal furrow rather even in depth extending length of frons at a shallow angle, frontal lobes with distinct elongate rugosity (Fig. 3G) ..... ***C. temnocephalus***
- Pseudergates with mesonotal rasp and concave posterior margin of pronotum (Fig. 4C), soldier unlike above ..... **2**
- 2 Soldier maximum head width 1.4 mm or more, head capsule elongate; furrow rugose; frontal lobes clearly not overhanging frons (Fig. 3A) ..... ***C. guatemalae***
- Soldier maximum head width less, or much less than 1.4 mm, head variable.... **3**
- 3 Head capsule somewhat to clearly elongate (Figs 3C, 3D, 3E, 3H) ..... **4**
- Head capsule truncate, mandibles short (Figs 3B, 3F) ..... **7**
- 4 Frontal furrow unsculptured; frontal lobes smooth; lobes obtuse in angle ca. 145° (Fig. 3C) ..... ***C. nigriceps***
- Frontal furrow and lobes with sculpturing; lobes form angle ca. 90–100° (Figs 3D, 3E, 3H) ..... **5**
- 5 Frontal lobes rounded, ovoid depression near center of lobes (Fig. 3H) ..... ***C. snyderi***
- Frontal lobes more acutely pointed, no ovoid depression near center of lobes (Figs 3D, 3E) ..... **6**
- 6 Larger species, maximum head width 1.2–1.3 mm, frontal lobes with slightly overhanging tips, neotropical distribution (Fig. 3E) ..... ***C. emarginicollis***
- Smaller species, maximum head width 1.1 mm, frontal lobes evenly angled, Nearctic distribution only (Fig. 3D) ..... ***C. nearcticus***



**Figure 1.** *Calcaritermes* distribution in the New World. Species and junior synonym names followed by citations or by “lit” are mapped from citation data only. All other species localities are mapped from records of the University of Florida Termite Collection.

**Table 1.** Revised New World list of *Calcaritermes* Snyder, 1925 and type localities.

<i>C. brevicollis</i> (Banks 1918)	Panama*
<i>C. colei</i> Krishna 1962	San Luis Potosi
<i>C. emarginicollis</i> (Snyder 1926a)	Rio Chinilla, Canal Zone, Panama*
<i>C. guatemalae</i> (Snyder 1926b)	Mixco, Guatemala*
<i>C. imminens</i> (Snyder 1925b)	Cincinnati, Colombia
<i>C. nearcticus</i> (Snyder 1933)	Clay County, Florida*
<i>C. nigriceps</i> (Emerson 1925)	Kartabo, Guyana*
<i>C. parvinotus</i> (Light 1933)	Colima, Mexico
<i>C. rioensis</i> Krishna 1962	Ihla Grande, Rio de Janeiro, Brazil*
<i>C. snyderi</i> Krishna 1962	Volcan de Santa Ana, El Salvador*
<i>C. temnocephalus</i> (Silvestri 1901)	Las Trincheras, Venezuela (see text)*
Undescribed sp. 1	Boquette, Panama*
Undescribed sp. 2	Paria Pennisula, Venezuela*

\* Specimens housed in UF collection.



- 7 Frontal lobes nearly overhanging frons; raised well above vertex; distinct ovoid depression in center of lobes (Fig. 3F) ..... *C. brevicollis*  
 – Frontal lobes not overhanging frons; almost even with vertex; lacking ovoid depression in center of lobes (Fig. 3B)..... *C. rioensis*

### Mesonotum morphology

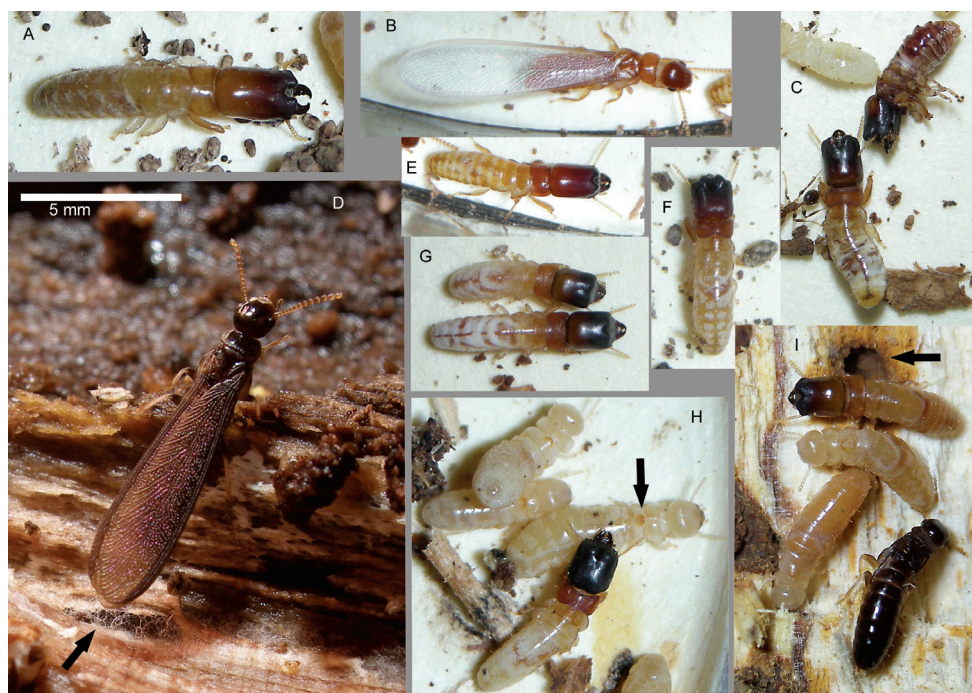
Mandible dentition of pseudergate or nymphal castes has been used for generic grouping of some Kalotermitidae (Krishna 1961), but for most genera, these weak and often overlapping characters by themselves lead to tenuous or uncertain identifications. In describing the imago and immature forms of *C. emarginicollis* from Costa Rica, Snyder (1925a) was first to observe and depict (Snyder's Figs 2, 4) that the mesonotum of the brachypterous nymph had an "aspirate or rugose area" while in the presoldier caste, he noted that the aspirate area of the mesonotum was elevated. Snyder (1925b, 1926ab), Light (1933), and Krishna (1962) described eight more *Calcaritermes* species, but the mesonotal rugosity was not mentioned again for any caste until Miller (1943) reported that nymphs of *C. nearcticus* had a "slightly raised median mesonotal area upon which appear numerous aspirities". In Krishna's 1961 revision of the Kalotermitidae, the mesonotal character was not mentioned.

These mesonotal "rasps" were found on all apterous pseudergates, early stage brachypterous nymphs, and most soldiers of *Calcaritermes* for species in the UF Collection (Table 1) with the exception of *C. temnocephalus* in which the rasp is absent. Under magnification, it was observed that each of these rasps actually consist of a single layer of slightly overlapping spatulate scales with basal attachments at their anterior ends (Figs 4A, 4B, 4D). The mesonotal rasps have a midline divide and form an elevated mound raised above the remainder of the dorsum (Fig. 4C, right). The posterior margin of the pronotum of all eragroid/nymphoid castes, except again *C. temnocephalus*, has a posterior marginal concavity that partially surrounds the anterior of the rasp (Fig. 4C, arrow). The pronotum is steeply angled toward the head anterior to the rasp (Fig. 4C, right). The scale patterns and lateral profile of the rasps vary somewhat among species (e.g., Figs 4A, 4B) but no species-specific morphology was investigated in this study. No rasp was found on any mature reproductive and the robustness of the rasp was inversely proportional to wing bud size disappearing when the nymphs were one molt from adulthood. The mesonotal rasp is the first external character to provide a diagnostic, generic identification of an immature kalotermitid.

Microscopic examination of the mesonotal rasps from ethanol-preserved specimens did not reveal microbial material around the scales. However, when live specimens of *C. nearcticus* were prepared for SEM without cleaning or rinsing, an organic (microbial?) paste was observed between the scales (Fig 4D).

**Queen physogastry.** Over the years, I have observed hundreds of mature queens in kalotermitid nests but was struck by the extreme queen physogastry in *C. temnocephalus*. On 26 May 2008, two colonies of *C. temnocephalus* were collected by the UF

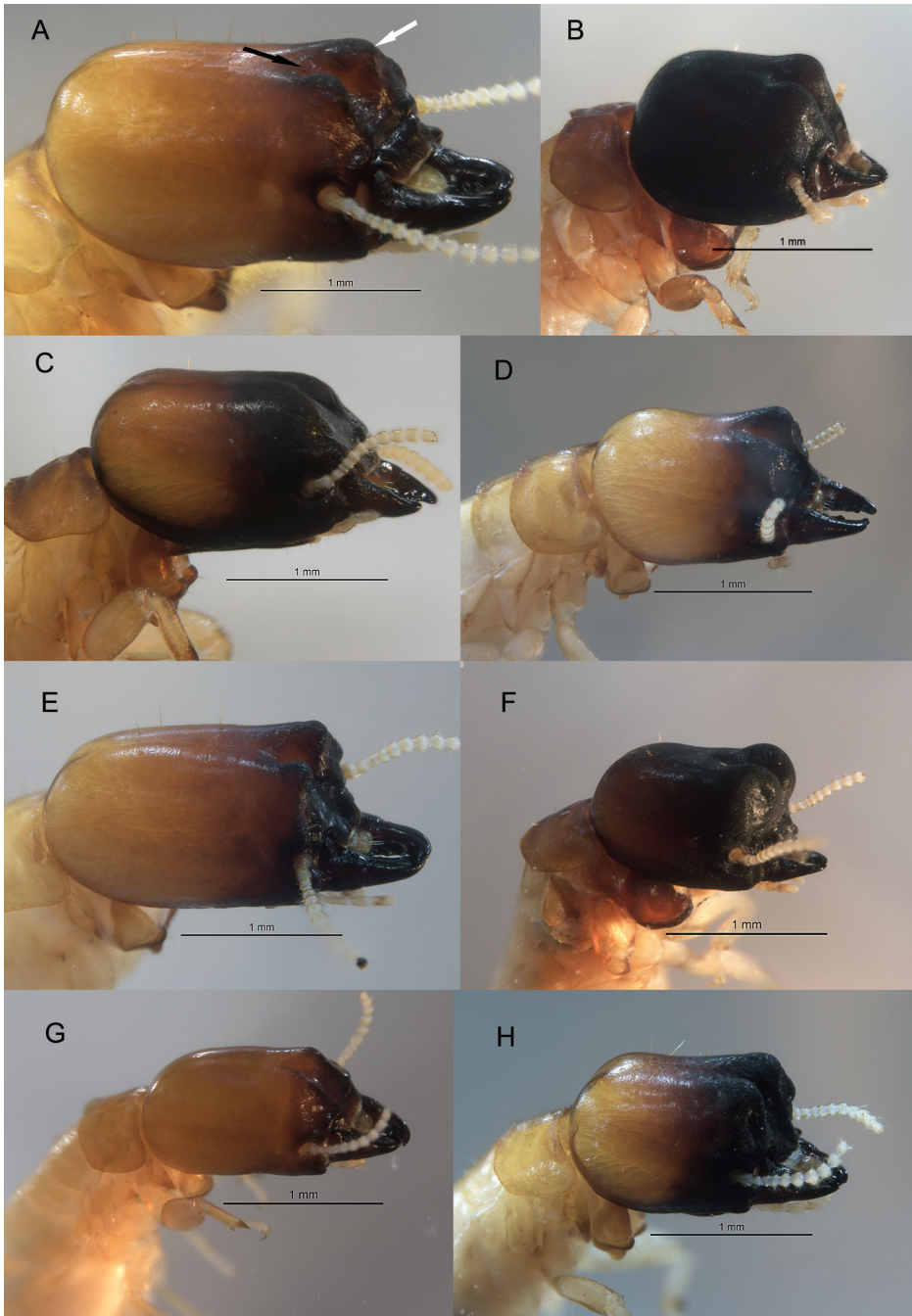




**Figure 2.** Photographs of live *Calcaritermes* specimens taken during collection. **A** Soldier of *C. guatemalae*, Honduras **B** Alate of *C. temnocephalus*, Venezuela **C** Soldiers of *C. snyderi* Honduras **D** Alate of *C. guatemalae*, Belize (arrow denotes fungal hyphae growing in gallery) **E** Soldier of *C. temnocephalus*, Venezuela **F** Soldier of *C. brevicollis*, Colombia **G** Two soldiers from the same colony of *C. nigriceps*, Colombia **H** Soldier and pseudergates of *C. rioensis*, Venezuela (arrow denotes mesonotal rasp of pseudergate) **I** Soldier, dealate, and pseudergates of *C. nearcticus*, Florida (arrow denotes fungal staining around gallery). All images to same scale.

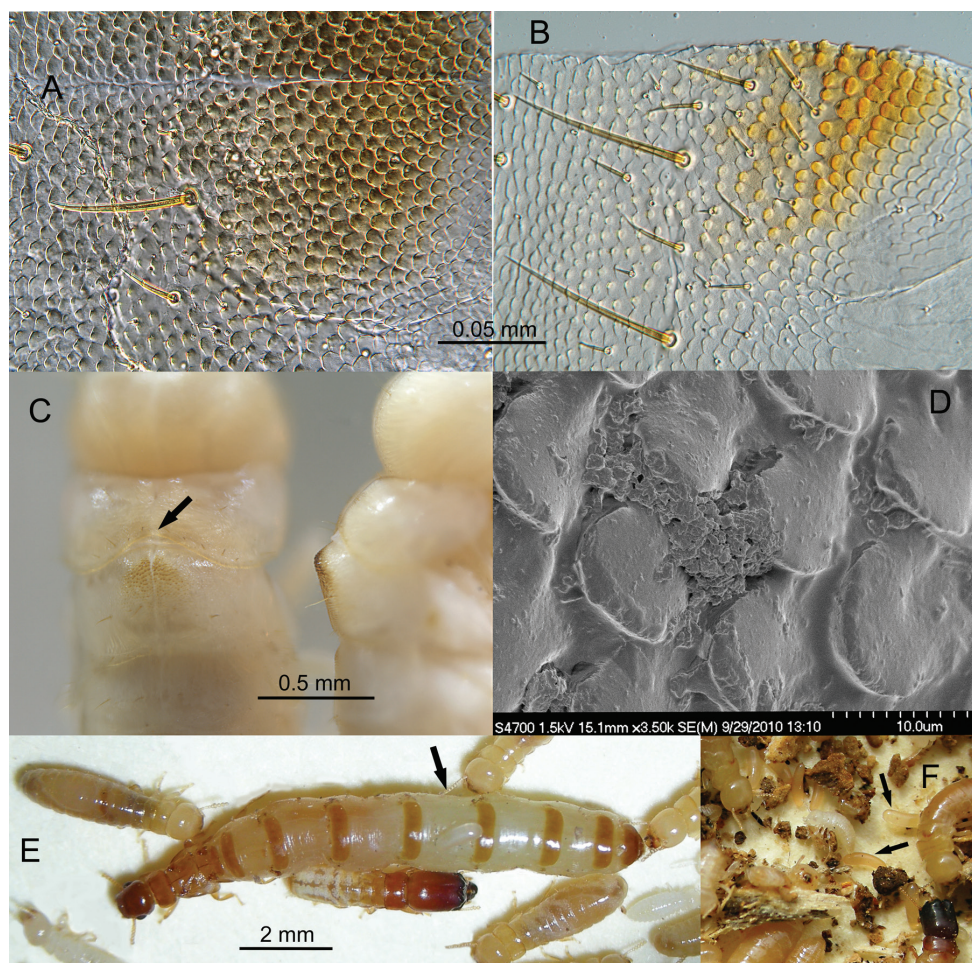
survey team at Silva Seco de Capadare, Guiermo, Venezuela (11.154, -68.590, elev. 58m). Both colonies were large and occupied rather sound wood from which a mature primary queen was removed (Fig. 4E). The extent of physogastry of these queens is what is typically observed in the Rhinotermitidae or Termitidae in which the intersegmental membrane stretches well beyond the width of the tergites or sternites. Typically the extended intersegmental membrane in primary queens of the Kalotermitidae is narrower than the width of adjacent abdominal sclerites, but in the *C. temnocephalus* queens, the membrane is much wider than the sclerites. Eggs from one of the *C. temnocephalus* colonies (Fig. 4E, arrow) and from a *C. brevicollis* colony in Panama (Fig. 4F, arrows) also appeared disproportionately large compared to other kalotermitids.

**Nests.** *Calcaritermes* colonies infest damp or wet wood, usually in the shade of forest canopy. At ground level, populations are never plentiful in a given area. However, Roisin et al. (2006) found that the preponderance of *C. brevicollis* colonies in a Panamanian rain forest were occupying dead branches 10 m or higher above the ground.



**Figure 3.** Oblique view of *Calcaritermes* soldiers from the University of Florida collection. **A** *C. guatemalae*, Honduras (black arrow shows orientation of frontal furrow, white arrow points to frontal lobe) **B** *C. rioensis*, Trinidad. **C** *C. nigriceps*, Trinidad **D** *C. nearcticus*, Florida **E** *C. emarginicollis* Honduras **F** *C. brevicollis*, Nicaragua **G** *C. temnocephalus*, Guatemala **H** *C. snyderi*, Guatemala. Enlarge outer tibial spines visible in B and G. Photos to same scale.





**Figure 4.** **A** Light micrograph of partial mesonotal rasp of *C. nearcticus* pseudergate from an ethanol-preserved specimen. Mid-line is horizontal near top of figure **B** Micrograph of half of mesonotal rasp of *C. brevicollis* pseudergate. Rasp is separated at the mid-line **C** Dorsal and lateral view of rasps on *C. brevicollis* pseudergates (arrow denotes concavity of posterior margin of pronotum to accommodate elevation of the rasp) **D** SEM of rasp of *C. nearcticus* from an unrinsed, freshly prepared specimen **E** Physogastric queen and other castes of *C. temnocephalus* (arrow denotes egg on queen dorsum) **F** Eggs (arrows amongst nest debris) of *C. brevicollis*, Colombia.

Workers and soldiers move rather slowly compared to most other kalotermitids, but in contrast, the alates flutter in hyperkinetic fashion as soon as their galleries are opened. Bourguignon et al. (2009) collected all dispersing *C. brevicollis* alates during March to June in flight intercept traps. No alates were attracted to light traps indicating that *C. brevicollis*, and probably the other dark-colored species, are daytime flyers.

The gallery system of *Calcaritermes* differs from other kalotermitids in several distinct ways. First, the galleries are narrow and tubular, maybe allowing only two termites to pass at one time. The galleries are spaced rather far apart in the wood matrix, thus





**Figure 5.** **A** *C. nigriceps* galleries exposed in Colombia **B** *C. nearcticus* galleries in oak wood, Florida **C** *C. temnocephalus* galleries in Venezuela. Images not to same scale.

occupying a relative small volume of the colonized member (Figs 5A, 5B). Secondly, the galleries contain very few loose fecal pellets, but gallery surfaces are generously lined with what appears to be a moist fecal/microbial? paste (Figs 5A, 5B, 5C). Miller (1949) noted that *C. nearcticus* “lines some of its galleries with a coating of brownish material”. Thirdly, the peripheries of the galleries are stained or exhibit halos suggesting fungal infection emanating from the gallery surfaces into the wood at varying depths (Figs 5A, 5B). Again, the exception is *C. temnocephalus* which infests wood in open, often dryer conditions, had less fecal coating and microbial growth (Fig. 5C) in their galleries.

Given the mesonotal rasp, the low volume of wood excavated, gallery coating, and peripheral gallery staining, one can hypothesize that *Calcaritermes* derives some nutrition via a symbiotic relationship with microbes growing on the surface of their galleries. The rasp may be used by foragers to inoculate gallery surfaces with fungal or bacterial spores analogous to the mycangium (Stone et al. 2007) found in bark beetles (Scolytinae). Unlike the mycangia of adult beetles, *Calcaritermes* adults (alates) show no obvious external structure for horizontal transfer of spores to new nesting sites although alimentary storage is a possibility. So whether *Calcaritermes*, like bark beetles, have some form of external association with microorganism (Gilbertson 1984) or actually rely on symbiotic mycophagy (Harrington 2005) remains to be studied.

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# Revision of the termite family Rhinotermitidae (Isoptera) in New Guinea

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## Abstract

Recently, we completed a revision of the Termitidae from New Guinea and neighboring islands, recording a total of 45 species. Here, we revise a second family, the Rhinotermitidae, to progress towards a full picture of the termite diversity in New Guinea. Altogether, 6 genera and 15 species are recorded, among which two species, *Coptotermes gambrinus* and *Parrhinotermes barbatus*, are new to science. The genus *Heterotermes* is reported from New Guinea for the first time, with two species restricted to the southern part of the island. We also provide the first New Guinea records for six species of the genera *Coptotermes* and *Schedorhinotermes*. We briefly describe soldiers and imagoes of each species and provide a key based on soldier characters. Finally, we discuss the taxonomic and biogeographical implication of our results. A replacement name, *Schedolimulus minutides* Bourguignon, is proposed for the termitophilous staphylinid *Schedolimulus minutus* Bourguignon, to solve a question of secondary homonymy.

## Keywords

termites, Papua New Guinea, Indonesia, new species

## Introduction

The Rhinotermitidae constitute one of the most widespread termite families, including numerous pest species. First established under the invalid name Mesotermitidae (Holmgren 1910a, b), then reestablished as Rhinotermitidae by Light (1921), the family originally included all termites possessing a fontanelle and a frontal gland in the imago and soldier castes, 8 malpighian tubules and hindgut with short anterior (pre-paunch) sections. Later on, the Stylotermitidae and Serritermitidae were separated as distinct families (Chatterjee and Thakur 1964, Emerson 1965), a position recently endorsed by Engel et al. (2009). The Rhinotermitidae now comprise several genera of uncertain affinities, such as *Prorhinotermes*, *Termitogeton* and *Psammotermes*, and two well-supported clades: (i) the Rhinotermitinae, including *Parrhinotermes*, *Schedorhinotermes* and the neotropical *Rhinotermes*-group; (ii) the Heterotermitinae + Coptotermitinae, comprising *Reticulitermes*, *Heterotermes* and *Coptotermes*. As presently defined, the Rhinotermitidae might still be paraphyletic with respect to the Serritermitidae or Termitidae, but the actual phylogeny of this group remains uncertain (Lo et al. 2004, Ohkuma et al. 2004, Inward et al. 2007).

The Rhinotermitidae are widely distributed across tropical, subtropical and temperate regions (Eggleton 2000). Whereas the genus *Prorhinotermes* is notable for its pantropical insular distribution (Emerson 1952), other genera are either pantropical (e.g. *Coptotermes*) or limited to one (e.g. *Termitogeton*) or a few zoogeographic areas (e.g. *Schedorhinotermes*). In southeast Asia, the Rhinotermitidae are represented by six genera: *Parrhinotermes*, *Schedorhinotermes*, *Coptotermes*, *Heterotermes*, *Prorhinotermes* and *Termitogeton*. All but the last one are also present in Australia. The former two belong to the subfamily Rhinotermitinae, whose soldiers are equipped to bite and smear a poisonous liquid with their elongated brush-like labrum (Quennedey and Deligne 1975). In the other genera, soldiers can simultaneously bite and emit a toxic or sticky chemical secretion from their frontal gland (Prestwich 1979, Šobotník et al. 2010a). Alates are also equipped with a frontal gland, variously developed according to the genus (Šobotník et al. 2010b).

Some recent revisions or compilations of distributional data are available for Rhinotermitidae in Southeast Asia and Australia. Faunal lists mention 21 species from Sundaland (Peninsular Malaysia to Borneo: Gathorne-Hardy 2004), 12 from Sulawesi (Gathorne-Hardy et al. 2000), 24 from Australia (Watson et al. 1998). However, prior to the beginning of our survey in 1978, only five species in two genera were known from New Guinea: *Coptotermes elisae* (Desneux, 1905), *Coptotermes obiratus* Hill, 1927, *Schedorhinotermes dimorphus* (Desneux, 1905), *Schedorhinotermes translucens* (Haviland, 1898), and *Schedorhinotermes celebensis* (Holmgren, 1911a). *Prorhinotermes inopinatus* Silvestri, 1909, was reported more recently (Gay and Barrett 1983). Findings of *Prorhinotermes* (identified as *P. inopinatus*), *Parrhinotermes* (as *P. browni* (Harris, 1958)) and *Termitogeton* (as *T. nr. planus* (Haviland, 1898)) were mentioned in studies focused on caste patterns (Roisin 1988a, b, Parmentier and Roisin 2003), bringing the

total number of New Guinean species to 8 in 5 genera. The present revision is primarily based on extensive collections carried out in New Guinea between 1978 and 1995. We recorded 15 species in 6 genera, among which 2 species are new to science. The present work complements our series of monographic revisions on New Guinean Termitidae, in which we recorded a total of 45 species in 13 genera (Roisin 1990, Roisin and Pasteels 1996, 2000, Bourguignon et al. 2008).

## Materials and methods

### Biological material

Extensive termite collecting was carried out by J. M. Pasteels (in collection records: **JMP**), Y. Roisin (**YR**) and M. Leponce (**ML**) in New Guinea and some neighboring islands between 1978 and 1995 although records from Indonesian Papua are almost exclusively limited to the “bird’s neck” area, around Nabire and Kaimana (Figs 30, 82). Termite specimens were collected with tweezers and preserved in 80% alcohol or fixed in Bouin’s fluid or in a formol-alcohol-acetic acid (20:75:5) mixture. We also had the opportunity to examine samples collected in alcohol by Alfred E. and Eleanor Emerson in 1962–1963 (**AE**), as well as a few samples from other sources. Localities where specimens were collected are given as well as their approximate geographic coordinates (Appendix 1), obtained by cross-checking maps, Google<sup>TM</sup> Earth positioning and the National Geospatial Agency GEOnet Names Server (<http://geonames.nga.mil/ggmagaz/>).

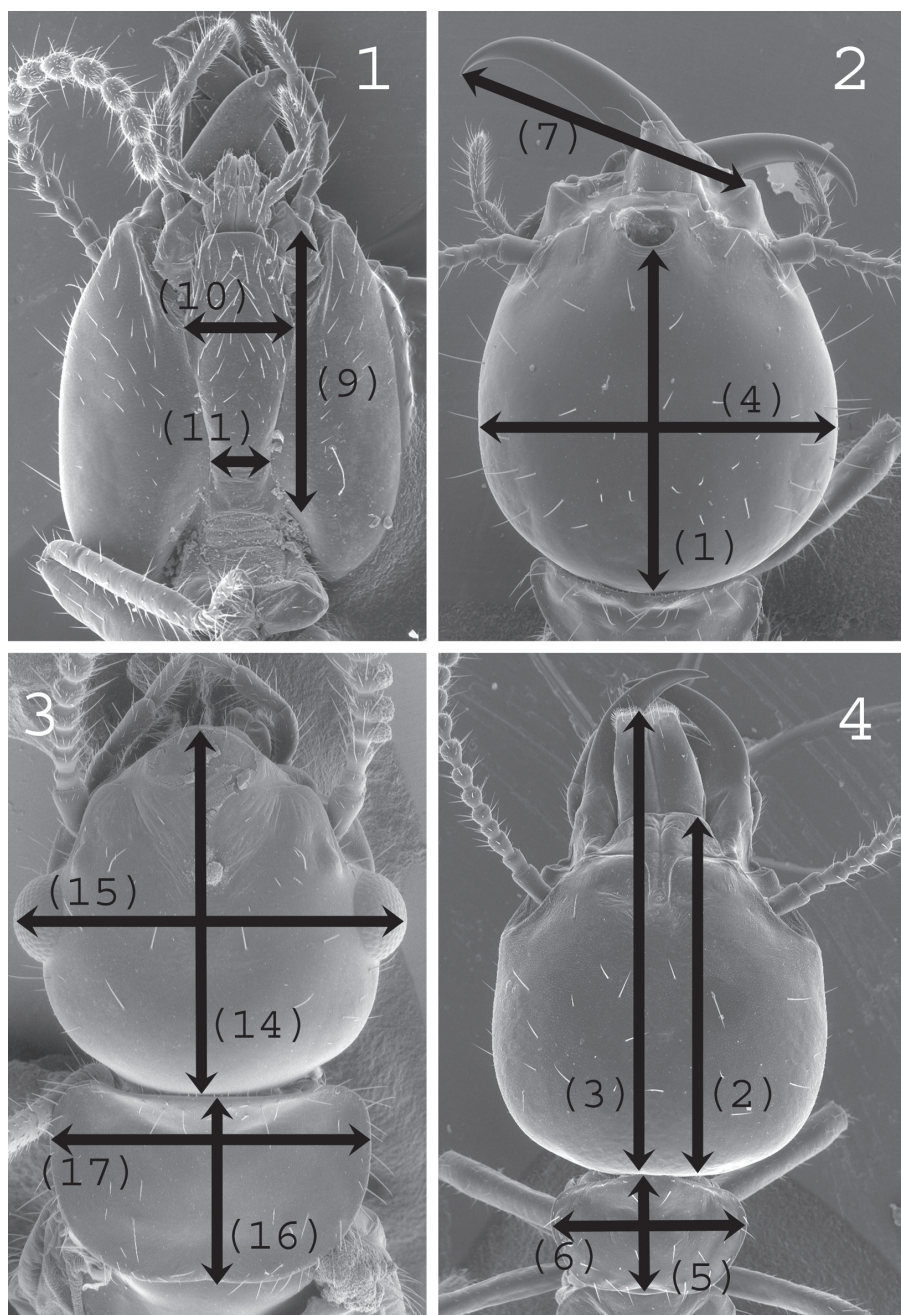
### Systematic characters

This study is based on the morphology of soldier and alate castes. Soldiers supply most of the important taxonomic information at the species level. The following characters are of major interest: size, general shape of the head, shape of mandibles, shape of postmentum, pilosity of head and number of antennal articles. Alates, when available, may give taxonomic information at the species level by the general shape of their head and pronotum.

### Measurements and their abbreviations

The measurements used, detailed below, follow the guidelines of Roonwal (1970).

**Soldiers.** (Figs 1, 2, 4): **HLF** – Head length to fontanelle; **HLC** – Head length to apex of the clypeus; **HLL** – Head length to apex of the labrum; **HW** – Head maximum width; **PL** – Pronotum length; **PW** – Pronotum width; **RML** – Right mandible



**Figures 1–4.** Measurements. **A–B, D** soldier: (1), HLE, head length to fontanelle; (2), HLC, head length to apex of the clypeus; (3), HLL, head length to apex of the labrum; (4), HW, head maximum width; (5), PL, pronotum length; (6), PW, pronotum width; (7), RML, right mandible length; (9), PML, postmentum length; (10), MPW, maximum postmentum width; (11), mPW, minimum postmentum width. **C** imago: (14), HLC, head length to apex of the clypeus; (15), HWE, head width with eyes; (16), PL, pronotum length; (17), PW, pronotum width.

length; **LML** – Left mandible length; **PML** – Postmentum length; **MPW** – Maximum postmentum width; **mPW** – Minimum postmentum width; **T3L** – Hind tibia length.

**Imagoes.** (Fig. 3): **TBL** – Total body length (without wings); **HLC** – Head length to apex of the clypeus; **HWE** – Head width with eyes; **PL** – Pronotum length; **PW** – Pronotum width; **FWL** – Forewing length (with scale); **ED** – Eyes maximum diameter

## Microscopy

For scanning electron microscopy, specimens were dehydrated in a conventional ethanol series, impregnated for 24 h in hexamethyldisilazane, air dried and gold coated. Digital images were taken with a Philips XL 30 ESEM.

## Collections and their abbreviations

Species determinations were carried out after comparison with type series or identified specimens kept in the following museums

<b>AMNH</b>	American Museum of Natural History, New York, USA
<b>BMNH</b>	Natural History Museum, London, UK
<b>CUMZ</b>	Cambridge University Museum of Zoology, Cambridge, UK
<b>IRSNB</b>	Institut Royal des Sciences Naturelles, Brussels, Belgium
<b>MVMA</b>	Museum of Victoria, Abbotsford, Victoria, Australia
<b>NHRS</b>	Naturhistoriska Riksmuseet, Stockholm, Sweden

Samples numbered **#PNGT\*\*\*** (Papua New Guinea Termites) or **#IRJT\*\*\*** (Iranian Jaya Termites) are in the authors' laboratory collection at the Université Libre de Bruxelles. The major part of this collection will ultimately be deposited at the IRSNB.

## Systematics

### Genus *Coptotermes* Wasmann, 1896

<http://species-id.net/wiki/Coptotermes>

*Termes* (*Coptotermes*) Wasmann 1896: 629.

**Type species.** *Termes gestroi* Wasmann, 1896, by monotypy.

**Diagnosis.** Imago head circular, covered by many setae. Fontanelle indistinct and appearing as a small spot in the middle of the head. Large ocelli located above the eyes. Pronotum and abdomen densely hairy. Soldiers with pyriform head capsule, slightly



hairy. Fontanelle very large, directed forward, through which the latex-like secretion of the frontal gland is discharged. Labrum short, triangular-shaped. Mandibles narrow and elongated, curved at tip; right mandible without subsidiary teeth and serrations; left one with a basal tooth and serrations. Antennae with 12 to 16 articles.

**Distribution.** The genus *Coptotermes* is broadly distributed, occurring in all tropical and subtropical regions. It comprises species adapted to all major biomes, from tropical rainforest to arid steppes and deserts. Nests are generally found in logs, in the heartwood of living trees, or underground (Emerson 1971). Several species, such as *Coptotermes formosanus*, are major pests of buildings (Su and Scheffrahn 2000).

***Coptotermes elisae* (Desneux, 1905)**

[http://species-id.net/wiki/Coptotermes\\_elisae](http://species-id.net/wiki/Coptotermes_elisae)

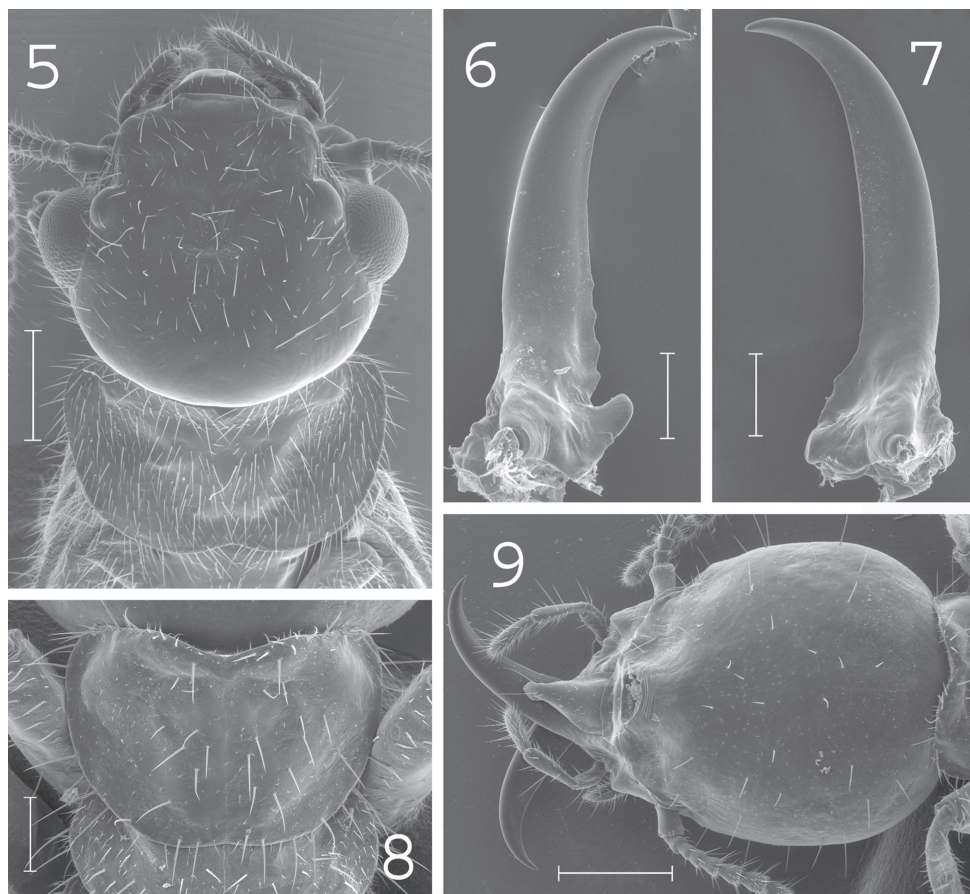
Figs 5–9, 30

*Termes* (*Coptotermes*) *Elisae* Desneux 1905: 368.

*Coptotermes Elisae* Desneux. Holmgren 1911a: 456.

*Coptotermes hyaloapex* Holmgren 1911a: 457 (synonymized by Gay 1963: 421–423).

**Material examined. Syntypes:** PAPUA NEW GUINEA: **Morobe:** Simbang, 12.ix.1898 (L. Biró), alates only (IRSNB). **Other material. PAPUA NEW GUINEA: Madang:** Laing Island, 28.xi.1978 (JMP), with queen and alate (#PNGT22); Laing Island, 11.vi.1987 (YR), with alates (#PNGT1101); Laing Island, 24.viii.1988 (YR), nest within fallen *Erythrina* tree (#PNGT1260); Manam Island, 23.vi.1981 (JMP), feeding on live tree (#PNGT101); Bogia–Josephstaal road, 10 km S Guam bridge, 26.vi.1984 (YR) (#PNGT711); Hansa Point, 22.viii.1984 (YR) (#PNGT785); Awar, 16.ix.1984 (YR) (#PNGT831); Tabele (Manam Island), 19.ix.1984 (YR), in decaying palm (#PNGT839); Sepen No.1, 01.iii.1988 (YR) (#PNGT1164); Baitabag, v.1999 and 17.x.1999 (L. Čížek) (#7, #15, J. Šobotník's collection). **Morobe:** Sirasira, 14.v.1988 (YR) (#PNGT1213); Bulolo, 22.v.1987 (YR), in dead hoop pine (*Araucaria cunninghamii*) trunk on the ground (#PNGT1080); **Central:** Brown River forest, 15.xi.1962 (AE), from dead branch on forest floor (AMNH); Brown River, 21.xi.1962 (AE), from standing dead stump in forest (AMNH); 24 km NE Port Moresby, 23.xi.1962 (AE), covered galleries over large surface of live tree, with hole to heart wood (AMNH); Subitana plantation, 24.xi.1962 (AE), from standing dead rubber tree in mature grove (AMNH); Sogeri, 15.vii.1984 (YR), in dead liana along tree trunk in small patch of forest (#PNGT740); Sogeri, 23.iii.1985 (JMP & YR) (#PNGT1005); **Oro:** Kokoda, 13.iii.1985 (JMP & YR) (#PNGT952); Kokoda, 17.iii.1985 (JMP & YR) (#PNGT981); Koiiasi, 14.iii.1985 (JMP & YR) (#PNGT959); **New Ireland:** Konos, 29.v.1984 (JMP & YR) (#PNGT624); **Sandaun:** Yapsiei, 10.iii.1994 (YR & ML) (#PNGT1733 & 1734); **Fly:** Morehead, 25.iii.1989 (YR & ML) (#PNGT1447); Wipim, 01.iv.1989 (YR & ML) (#PNGT1509); Tabubil, 20.v.1990 (YR & ML) (#PNGT1541); Lake Murray, 24.v.1990 (YR & ML) (#PNGT1582); Lake Murray,



**Figures 5–9.** *Coptotermes elisae*. Imago: **5** head and pronotum. Soldier: **6** left mandible; **7** right mandible; **8** pronotum; **9** head. Scale bars: **5**, **9**: 0.5mm; **6**, **7**, **8**: 0.2mm.

25.v.1990 (YR & ML), with queen (#PNGT1589); Nomad, 29.v.1990 (YR & ML) (#PNGT1609); Nomad, 31.v.1990 (YR & ML) (#PNGT1624); Nomad, 01.vi.1990 (YR & ML) (#PNGT1637); **Southern Highlands:** Pimaga, alt. 950m, 18.x.1988 (YR) (#PNGT1316); **INDONESIA: Papua:** Road Nabire-Mapia km 43, 26.xi.1995 (YR) (#IRJT171); Road Nabire-Mapia km 62, 18.xi.1995 (YR) (#IRJT72, 73); Coa, 22.xi.1995 (YR) (#IRJT123); Kaimana, 23.xi.1995 (YR) (#IRJT140).

**Imago.** (Fig. 5). Head rounded and densely hairy. Large eyes. Pronotum wide and elongated, covered by numerous setae of medium and large size. Antennae with 20 to 22 articles. Measurements (mm) of 8 imagoes from the type colony and 4 imagoes from one other colony (between parentheses): TBL: 8.27–8.99 (7.81–8.12); HLC: 1.53–1.87 (1.48–1.62); HWE: 1.84–1.96 (1.79–1.81); PL: 1.04–1.12 (1.02–1.07); PW: 1.63–1.70 (1.59–1.61); FWL: n.a. (13–13.2); ED: 0.45–0.50 (0.45–0.5).

**Soldier.** (Figs 6–9). Soldiers of large size. Head rounded, covered by about 40 setae. Fontanelle large, with opening well visible from above. Antennae generally with



16 articles. Pronotum elongated, covered by about 70 setae mainly located on the edges. Mesonotum, metanotum and abdomen bearing plenty of setae. Mandibles with tips extremely curved. Measurements (mm) of 99 soldiers from 33 colonies: HLF: 1.11–1.47; HLL: 1.70–2.20; HW: 1.21–1.54; PL: 0.38–0.64; PW: 0.77–1.03; RML: 0.97–1.20; MPW: 0.30–0.49; T3L: 1.05–1.34.

**Comparisons.** *C. elisae* can be distinguished from other New Guinean species by its large rounded head with fontanelle opening well visible from above, its strongly curved mandibles and elongated pronotum in the soldier caste.

**Distribution.** (Fig. 30). This species is widespread in New Guinean forests. It also occurs in New Ireland. It has also been reported from the following localities, but the relevant material was not examined: Bukaua (as *C. hyaloapex*: Holmgren 1911a), Popondetta (Gay 1963). According to Gathorne-Hardy (2004), it is present from Peninsular Malaysia throughout Sundaland.

**Termitophiles.** *Coptophysa obesa* (Coleoptera: Staphylinidae) was found in colony #PNGT740 of this species in Sogeri (Roisin and Pasteels 1990).

### *Coptotermes remotus* Hill, 1927

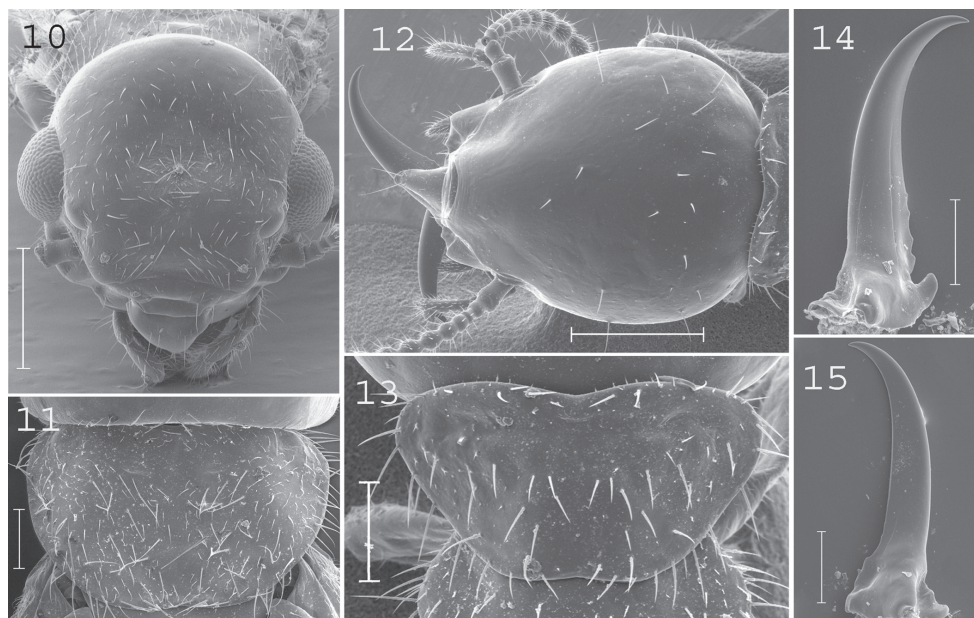
[http://species-id.net/wiki/Coptotermes\\_remotus](http://species-id.net/wiki/Coptotermes_remotus)

Figs 10–15, 31

*Coptotermes remotus* Hill 1927: 16.

**Material examined. Syntypes: PAPUA NEW GUINEA: New Ireland:** Kavieng (as Kaewieng), 4.x.1923 (H.G. Wallace) (NMVA T-18703, T-18704). **Other material: PAPUA NEW GUINEA: Madang:** Hansa Point, 08.vii.1984 (YR) (#PNGT719); Awar, 11.ix.1984 (YR) (#PNGT828); Nubia, 17.ii.1988 (YR) (#PNGT1154); Potsdam plantation, 22.xi.1988 (YR) (#PNGT1333); Hatzfeldhafen, 25.viii.1984 (YR) (#PNGT795); Baitabag, 17.x.1999 (L. Čížek) (#1, J. Šobotník's collection); **Sandaun:** Yapsiei, 10–11.iii.1994 (YR & ML) (#PNGT1735, 1744). **Central:** Sirinumu Dam, 7.iii.1985 (JMP & YR) (#PNGT923); **Fly:** Lake Murray, 23.v.1990 (YR & ML) (#PNGT1569). **INDONESIA: Papua:** Pusppenssat-IrJa, 13.xi.1995 (YR) (#IRJT6, 10, 12); Pusppenssat-IrJa, 19.xi.1995 (YR) (#IRJT84, 85); Pusppenssat-IrJa, 30.xi.1995 (YR) (#IRJT207); Road Nabire-Mapia km 43, 15.xi.1995 (YR) (#IRJT40, 41); Road Nabire-Mapia km 43, 26.xi.1995 (YR) (#IRJT169, 170); Road Nabire-Mapia km 62, 18.xi.1995 (YR) (#IRJT74, 75); Topo, 28.xi.1995 (YR) (#IRJT189); Sanoba, 29.xi.1995 (YR) (#IRJT195); Coa, 22.xi.1995 (YR) (#IRJT131); Kaimana, 23.xi.1995 (YR) (#IRJT141). **Samples included with doubt: PAPUA NEW GUINEA: East Sepik:** Koil Island, 17.vi.1981 (JMP) (#PNGT75); **Madang:** Hansa Point, 23.ix.1988 (YR) (#PNGT1281).

**Imago.** (Figs 10–11). Head densely hairy. Pronotum with many medium and large setae. Antennae with 17 articles. Measurements (mm) of 6 imagoes from 1 colony:



**Figures 10–15.** *Coptotermes remotus*. Imago: **10** head; **11** pronotum. Soldier: **12** head; **13** pronotum; **14** left mandible; **15** right mandible. Scale bars: **10, 12:** 0.5mm; **11, 13, 14, 15:** 0.2mm.

TBL: 5.75–6.39; HLC: 1.09–1.18; HWE: 1.30–1.38; PL: 0.57–0.73; PW: 0.97–1.08; FWL: 9.92–11.09; ED: 0.33–0.44.

**Soldier.** (Figs 12–15). Soldiers of small size. Head slightly longer than broad, covered by about 20 setae. Fontanelle with opening directed forward, not visible from above. Antennae generally with 14 articles, but occasionally with only 13 articles. Pronotum larger anteriorly than posteriorly, trapezoid-shaped, covered by about 50 setae. Mandibles with tips extremely curved. Right mandible with four serrations. Measurements (mm) of 5 soldiers from the type colony and 72 soldiers from 24 colonies (parentheses): HLF: 1.11–1.19 (1.01–1.29); HLL: 1.45–1.56 (1.23–1.63); HW: 1.00–1.04 (0.83–1.11); PL: 0.36–0.39 (0.29–0.46); PW: 0.67–0.70 (0.59–0.78); RML: 0.78–0.83 (0.69–0.85); MPW: 0.28–0.31 (0.26–0.38); T3L: 0.83–0.89 (0.68–0.99).

**Comparisons.** This species shows variation in size along its distribution range although no consistent characters allowed us to split it up. *Coptotermes remotus* most resembles the Australian species *C. lacteus* and the Malayan ones *C. bentongensis* and *C. sepangensis*. These last two species occur in sympatry and are morphologically undistinguishable, making them probable synonyms. Soldiers of *C. remotus* can be distinguished from other New Guinean species by their small size and mandibles curved at the tip.

**Distribution.** This species, originally described from Kavieng, New Ireland, is widespread throughout New Guinean forests. It is abundant in the bird's neck area of Indonesian Papua, but only a few specimens were collected from Papua New Guinea (Fig. 31).

**Termitophiles.** *Coptophysella pulposa* (Coleoptera: Staphylinidae) was found in colony #PNGT795 of this species in Hatzfeldhafen (Roisin and Pasteels 1990). A possibly new species of *Coptophysella* was also found in colony #IRJT12 in Pusppenssat–IrJa (new record).

***Coptotermes grandiceps* Snyder, 1925**

[http://species-id.net/wiki/Coptotermes\\_grandiceps](http://species-id.net/wiki/Coptotermes_grandiceps)

Figs 16–21, 30

*Coptotermes grandiceps* Snyder 1925: 401.

*Coptotermes solomonensis* Snyder 1925: 403 (synonymised by Hill 1942: 153).

*Coptotermes obiratus* Hill 1927: 17, **new synonymy**.

*Coptotermes solomonensis* Hill 1927: 19 (junior primary homonym of *Coptotermes solomonensis* Snyder; synonymised by Hill 1942: 153).

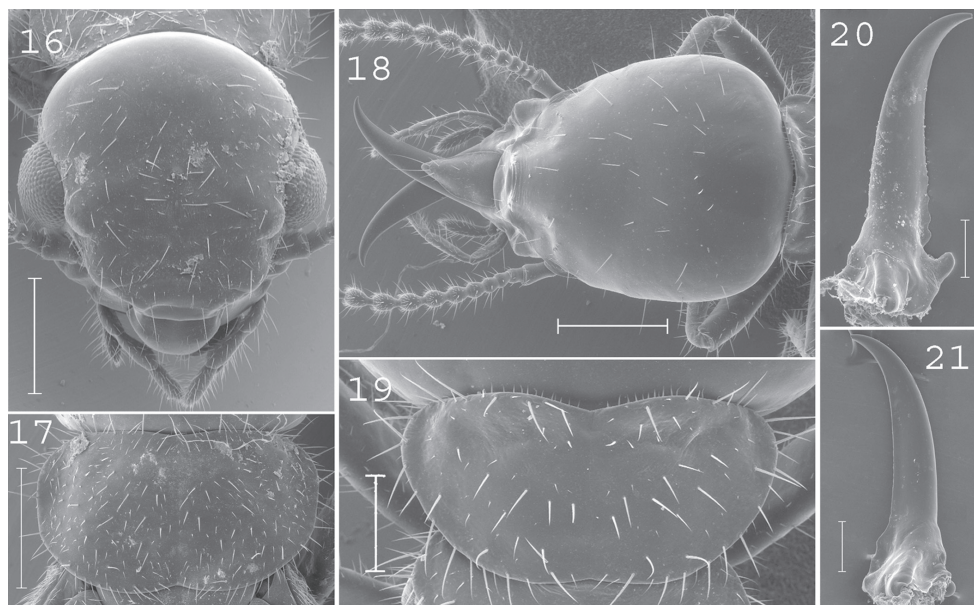
*Coptotermes froggatti* Light and Davis 1929: 62 (synonymised by Hill 1942: 153).

**Material examined. Topotype: SOLOMON ISLANDS:** Tulaghi (as Tulagi), iii.1933 (R.A. Lever) (AMNH). **Holotype of *C. obiratus*: PAPUA NEW GUINEA: Central:** Waima, vii.1922 (G.F. Hill) (NMVA).

**Other materials. PAPUA NEW GUINEA: Oro:** Mambare River, 27.iv.1922 (G.F. Hill) (NMVA). **Fly:** Morehead, 25.iii.1989 (YR & ML) (#PNGT1447); Wipim, 30.iii.1989 (YR & ML) (#PNGT1488); Lake Murray, 22.v.1990 (YR & ML) (#PNGT1561); Lake Murray, 25.v.1990 (YR & ML) (#PNGT1594); Nomad, 31.v.1990 (YR & ML) (#PNGT1627); Nomad, 02.vi.1990 (YR & ML) (#PNGT1651); **Central:** Subitana plantation, 24.xi.1962 (AE), in stump of rubber tree (AMNH); Sirinumu Dam, 06.iii.1985 (JMP & YR) (#PNGT916); Sirinumu Dam, 08.iii.1985 (JMP & YR) (#PNGT929); Varirata National Park, 06.xii.1988 (YR & Phille P. Daur) (#PNGT1346); **National Capital:** 2 km E Port Moresby, 18.xi.1962 (AE), from log in dry eucalypt savanna (AMNH); 8 km E Port Moresby, 16.xi.1962 (AE), under log in eucalypt savanna (AMNH); 8 km E Port Moresby, 18.xi.1962 (AE), from dead log in ravine woods in savanna (AMNH); 10 km NW Port Moresby, 20.xi.1962 (AE), from log on ground in eucalypt savanna (AMNH); 19 km NW Port Moresby, 22.xi.1962 (AE), from fallen log in savanna (AMNH); **INDONESIA: Papua:** Pusppenssat–IrJa, 13.xi.1995 (YR) (#IRJT17).

**New synonymy.** In his revision of termites from Australia, Hill (1942) mentioned that soldiers of *C. grandiceps* and *C. obiratus* are morphologically indistinguishable, the two species being potential synonyms. After examining material of the two species, we reached the same conclusion and therefore consider *C. obiratus* as a junior synonym of *C. grandiceps*.

**Imago.** (Figs 16–17). Head moderately hairy. Pronotum covered by many setae of medium size. Antennae with 20 articles. Measurements (mm) of 6 imagoes from one



**Figures 16–21.** *Coptotermes grandiceps*. Imago: **16** head; **17** pronotum. Soldier: **18** head; **19** pronotum; **20** left mandible; **21** right mandible. Scale bars: **16**, **17**, **18**: 0.5mm; **19**, **20**, **21**: 0.2mm.

colony: TBL: 6.08–7.55; HLC: 1.19–1.27; HWE: 1.33–1.41; PL: 0.73–0.82; PW: 1.23–1.29; FWL: 9.97–10.61; ED: 0.31–0.42.

**Soldier.** (Figs 18–21). Soldiers of large size. Head elongated, larger posteriorly than anteriorly, covered by about 30 setae. Fontanelle narrow, with opening directed frontally, not visible from above. Antennae generally with 15 articles, sometimes with 14 articles. Pronotum wide, moderately long, covered by about 60 setae. Mandibles elongated, curved at tip. Measurements (mm) of holotype of *Coptotermes obiratus*, 1 soldier from the type colony of *C. grandiceps* [brackets], and 27 soldiers from 9 colonies (parentheses): HLF: 1.53 [1.52] (1.21–1.44); HLL: 2.17 [2.19] (1.89–2.20); HW: 1.38 [1.31] (1.17–1.33); PL: 0.51 [0.50] (0.40–0.56); PW: 0.97 [0.95] (0.79–1.00); RML: 1.17 [1.24] (1.03–1.15); MPW: 0.48 [0.42] (0.31–0.46); T3L: 1.22 [n.a.] (1.07–1.21).

**Comparisons.** This species is closely allied to *C. pamuae* from which it can be distinguished by its larger soldiers with more curved mandibles.

**Distribution.** (Fig. 30). *C. grandiceps*, originally described from the Solomon Islands, occurs in southern New Guinea and the Papuan peninsula.

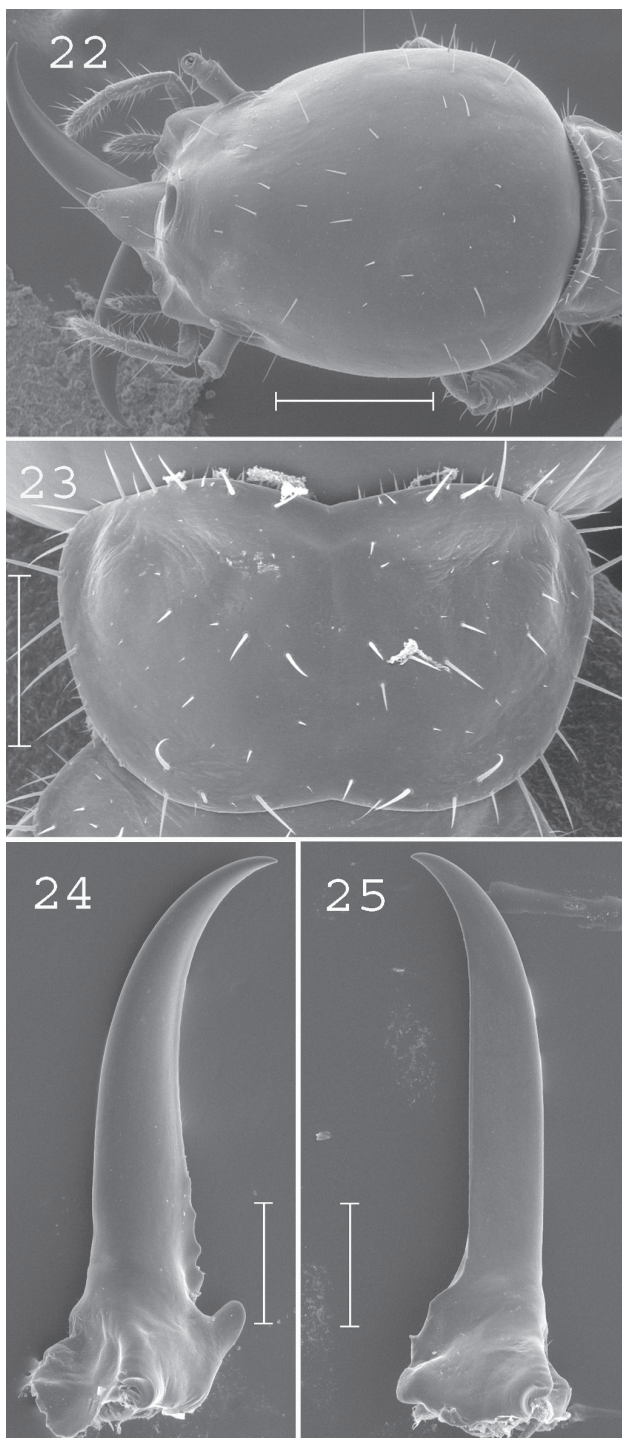
### *Coptotermes pamuae* Snyder, 1925

[http://species-id.net/wiki/Coptotermes\\_pamuae](http://species-id.net/wiki/Coptotermes_pamuae)

Figs 22–25, 31

*Coptotermes pamuae* Snyder, 1925: 402.





**Figures 22–25.** *Coptotermes pamuae*. Soldier: **22** head; **23** pronotum; **24** left mandible; **25** right mandible. Scale bars: **2**:**2** 0.5mm; **23**, **24**, **25**: 0.2mm.

**Material examined. Paratype soldier from type colony: SOLOMON ISLANDS: San Cristobal:** Pamua, viii.1916 (W.M. Mann) (AMNH). **PAPUA NEW GUINEA: National Capital:** UPNG campus, 04.xii.1988 (YR) (#PNGT1338); **Central:** Varirata National Park, 06.xii.1988 (YR & Phille P. Daur) (#PNGT1348); **Fly:** Morehead, 27.iii.1989 (YR & ML) (#PNGT1466); Wipim, 30.iii.1989 (YR & ML) (#PNGT1486).

**Imago.** Unknown.

**Soldier.** (Figs 22–25). Soldiers of medium size. Head elongated, egg-shaped, slightly larger posteriorly than anteriorly, covered by about 30 setae. Fontanelle narrow, with opening directed forward. Antennae generally with 13 articles, sometimes with 14 articles. Pronotum short and narrow, covered by about 40 setae. Mandibles elongated, slightly curved at tip. Measurements (mm) of 1 paratype and 12 soldiers from 4 colonies (parentheses): HLF: 1.28 (1.11–1.27); HLL: 1.70 (1.58–1.79); HW: 1.12 (1.00–1.10); PL: 0.41 (0.31–0.44); PW: 0.79 (0.63–0.74); RML: 0.77 (0.89–0.98); MPW: 0.37 (0.28–0.32); T3L: 0.82 (0.92–1.08).

**Comparisons.** This species is closely related and imperfectly separated from *Coptotermes grandiceps*. However, the size and morphological differences between the two species are high enough to retain them as distinct taxa, even though some individuals cannot be unambiguously assigned. The same was already observed in the related Australian species *Coptotermes acinaciformis* Froggatt, which is believed to form a species complex (Brown et al. 1990). The main criteria differentiating *C. pamuae* from *C. grandiceps* are its smaller soldiers with less hairy pronotum and less curved mandibles.

**Distribution.** (Fig. 31). This species, originally described from the Solomon Islands, was only collected in southern Papua New Guinea (Fly savannas and the Port Moresby region).

***Coptotermes gambrinus* sp. n.**

urn:lsid:zoobank.org:act:8E27AAD1-29A7-471B-BD03-58F21AC53514

[http://species-id.net/wiki/Coptotermes\\_gambrinus](http://species-id.net/wiki/Coptotermes_gambrinus)

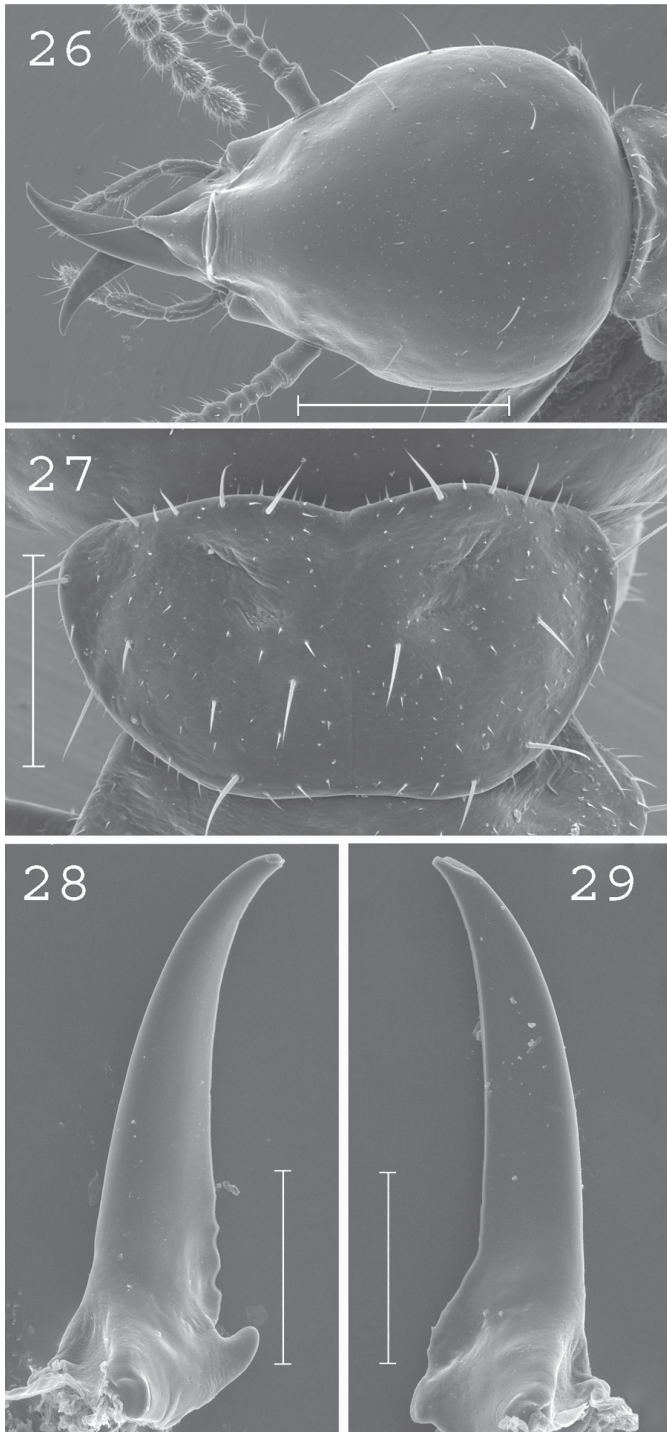
Figs 26–29, 31

**Holotype. Soldier: PAPUA NEW GUINEA: Morobe:** Bulolo, 22.v.1987 (YR), from stump of klinkii pine (*Araucaria hunsteinii*) (#PNGT1077). **Paratypes: PAPUA NEW GUINEA: Morobe:** Soldiers and workers from same colony as holotype, same data (#PNGT1077); Mount Susu, 19.v.1988 (YR), in dead branch of klinkii pine on the ground (#PNGT1232); McAdam National Park, 20.v.1988 (YR) (#PNGT1238). **Madang:** Hatzfeldhafen, 23.ix.1984 (YR) (#PNGT847); **Oro:** Kokoda, 13.iii.1985 (JMP & YR) (#PNGT950); Popondetta, 18.iii.1985 (JMP & YR) (#PNGT986). **Central:** Sirinumu dam, 07.iii.1985 (JMP & YR) (#PNGT918); Brown River, 21.iii.1985 (JMP & YR) (#PNGT996); **East New Britain:** Warengoi, 19.v.1984 (JMP & YR) (#PNGT562, 567).

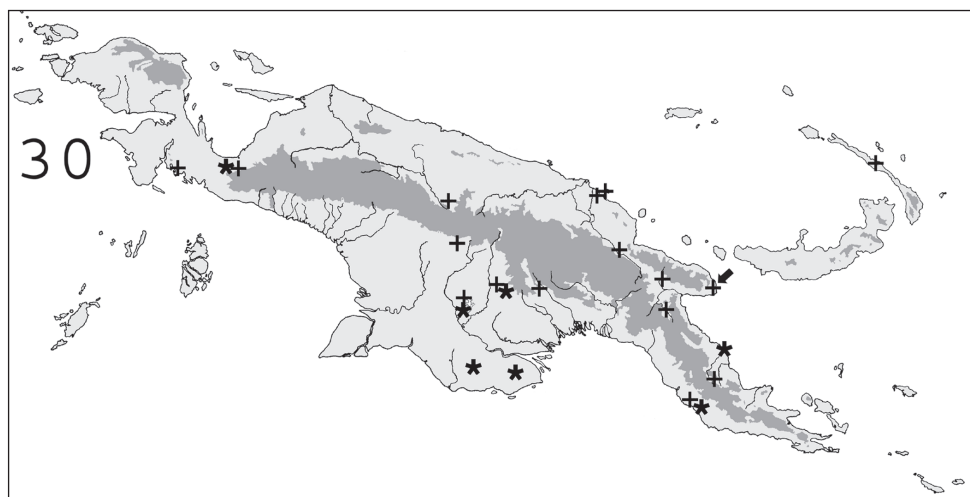
**Imago.** unknown.

**Soldier.** (Figs 26–29). Soldiers of small size. Head twice broader posteriorly than anteriorly (at the level of mandibles), covered by about 10 setae. Antennae generally

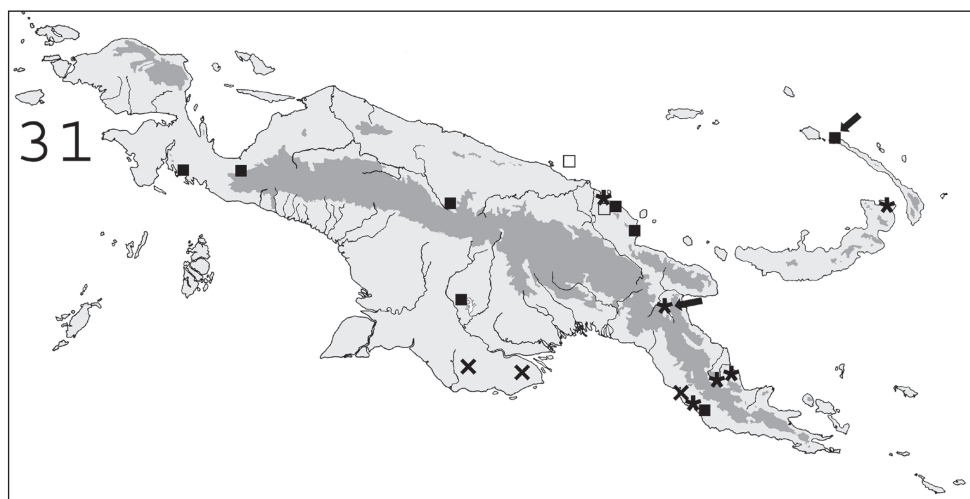




**Figures 26–29.** *Coptotermes gambrinus*. Soldier: **26** head; **27** pronotum; **28** left mandible; **29** right mandible. Scale bars: **26**: 0.5mm **27**, **28**, **29**: 0.2mm.



**Figure 30.** Known distribution in New Guinea of: + *Coptotermes elisae*; \* *Coptotermes grandiceps*. Arrow points to type locality.



**Figure 31.** Known distribution in New Guinea of: \* *Coptotermes gambrinus*; x *Coptotermes pamuae*; ■ *Coptotermes remotus*; □ doubtful samples of *Coptotermes remotus*. Arrows point to type localities.

with 15 articles. Pronotum covered by about 15 setae, slightly larger anteriorly than posteriorly. Mandibles very short, with apex almost not curved. Measurements (mm) of 30 soldiers from 10 colonies: HLF: 0.92–1.07; HLL: 1.22–1.48; HW: 0.82–0.98; PL: 0.27–0.41; PW: 0.50–0.70; RML: 0.56–0.74; MPW: 0.23–0.36; T3L: 0.75–0.88.

**Comparisons.** This species is allied to *Coptotermes remotus* from which it is easily recognisable by its shorter and less curved soldier mandible tips.

**Distribution.** (Fig. 31). This species occurs in Eastern New Guinea and in New Britain.

**Etymology.** We named this species in honor of *Gambrinus*, a legendary character from Flanders, famous for enjoying life.

**Genus *Heterotermes* Froggatt, 1897**

[http://species-id.net/wiki/Genus\\_Heterotermes](http://species-id.net/wiki/Genus_Heterotermes)

*Heterotermes* Froggatt 1897: 518.

**Type species.** *Heterotermes platycephalus* Froggatt, 1897, by monotypy.

**Diagnosis.** Imago head roughly oval, narrower anteriorly than posteriorly. Fontanelle small, located in the middle of the head. Eyes small and flat. Ocelli situated in front of the head, before eyes. Antennae generally with 15 to 19 articles. Pronotum elongated, narrower than head. Soldier head long and narrow, rectangular-shaped. Fontanelle small, circular, situated forward. Labrum short to medium-sized, about half as long as mandibles. Mandibles sabre-shaped, slightly curved at tips. Left mandible with a tooth and some serrations at the base. Right mandible without basal tooth and serrations. Antennae with 13 to 18 articles.

**Distribution.** Most species of *Heterotermes* are tropical (Emerson 1971). This genus was known from the Neotropics, northern Africa, Asia (from the Arabic peninsula to Indonesia), and Australia, occurring from humid forests to desert edges. Here, we extend its known distribution to southern New Guinea.

***Heterotermes vagus* (Hill, 1927)**

[http://species-id.net/wiki/Heterotermes\\_vagus](http://species-id.net/wiki/Heterotermes_vagus)

Figs 32–36, 44

*Leucotermes vagus* Hill 1927: 53–55.

*Heterotermes vagus* (Hill). Hill 1942: 134–136.

*Leucotermes venustus* Hill 1927: 55. **New synonymy.**

*Heterotermes venustus* (Hill). Hill 1942: 131–134.

**Material examined. Lectotype and paralectotype soldier: AUSTRALIA: Northern Territory:** Darwin, 01.viii.1914 (G.F. Hill) (NMVA #T-10848, #T-18705) **Lectotype of *H. venustus*: AUSTRALIA: Northern Territory:** Stapleton, 4.xi.1914 (G.F. Hill) (NMVA #T-10850). **Other material: PAPUA NEW GUINEA: Fly:** Morehead, 23.iii.1989 (YR & ML) (#PNGT1419, 1420, 1422); Morehead, 25.iii.1989 (YR & ML) (#PNGT1441); Lake Murray, 25.v.1990 (YR & ML) (#PNGT1588, 1597).

**New synonymy.** Hill (1942) pointed out the similarity of *H. venustus* and *H. vagus*, but maintained both names arguing that *H. venustus* has a larger labrum and antennae with more articles. However, after comparing the type series of both species, we did not notice any difference in these characters, nor in any other morphological feature. For this reason, we consider these two species as synonyms and hereby give precedence to *Heterotermes vagus*.

**Imago.** Unknown from New Guinea (see Hill 1942 for further details).



**Figures 32–36.** *Heterotermes vagus*. Soldier: **32** head in dorsal view; **33** head in lateral view; **34** pronotum; **35** left mandible; **36** right mandible. Scale bars: **32**, **33**: 0.5mm; **34**, **35**, **36**: 0.2mm.

**Soldier.** (Figs 32–36). Soldiers of small size. Head elongated, with a prominent hump at front, covered by plenty of short setae. Labrum elongated with sharp tip. Antennae generally with 13 articles. Pronotum short and narrow, covered by about 50 setae. Postmentum slightly narrow, without setae. Mandibles slightly curved at tips. Measurements (mm) of lectotype of *Heterotermes vagus*, lectotype of *H. venustus* [brackets] and 18 soldiers from 6 colonies (parentheses): HLC: 1.32 [1.43] (1.12–1.37); HLL: 1.75 [1.83] (1.48–1.76); HW: 0.80 [0.82] (0.74–0.83); PL: 0.40 [0.41] (0.32–0.50); PW: 0.55 [0.62] (0.49–0.60); RML: 0.92 [0.89] (0.80–0.93); MPW: 0.34 [0.31] (0.29–0.33); T3L: 0.65 [0.66] (0.54–0.66).

**Distribution.** (Fig. 44). This species was collected in Southern Papua New Guinea. It is also known from northernmost Queensland and Northern Territory (Australia) (Watson & Abbey 1993).

***Heterotermes paradoxus* (Froggatt, 1898)**

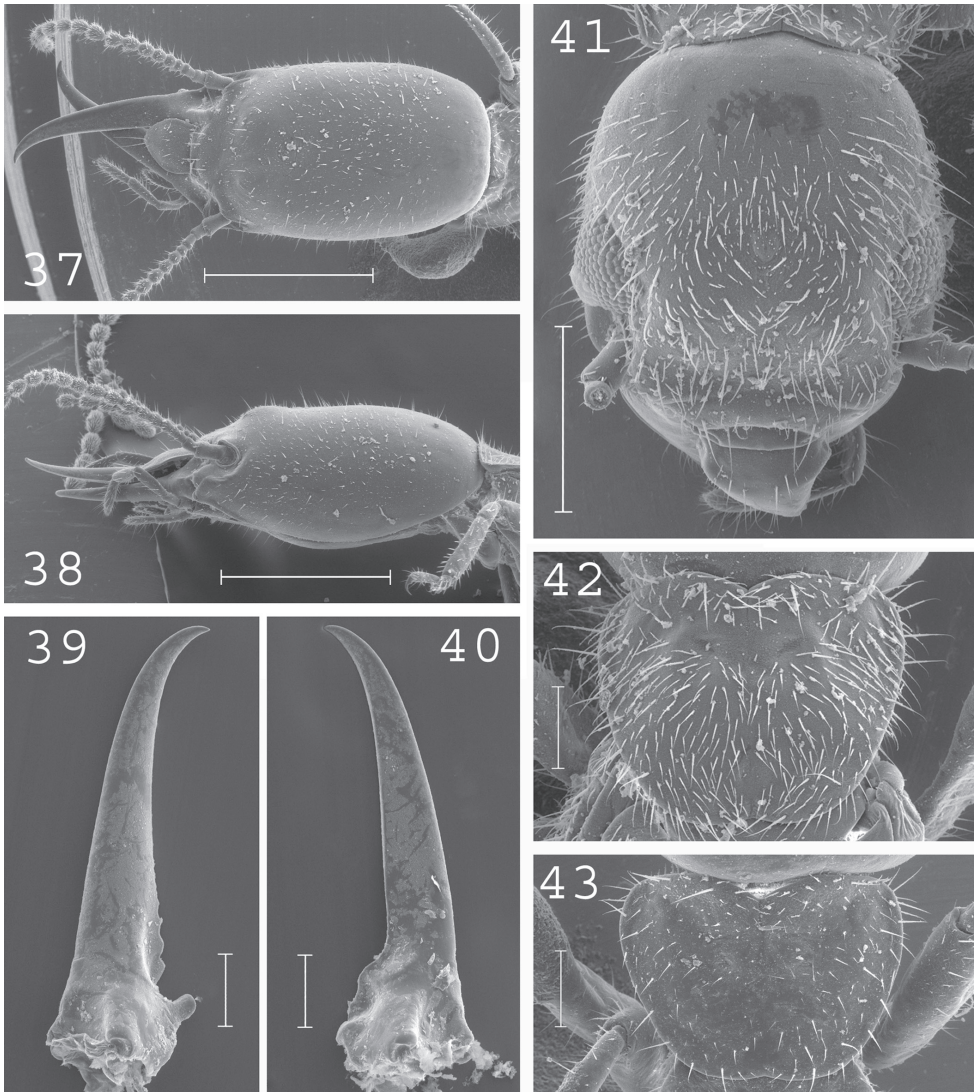
[http://species-id.net/wiki/Heterotermes\\_paradoxus](http://species-id.net/wiki/Heterotermes_paradoxus)

Figs 37–44

*Termes paradoxus* Froggatt, 1898: 728.

*Heterotermes paradoxus* (Froggatt). Hill 1932: 146.





**Figures 37–43.** *Heterotermes paradoxus*. Soldier: **37** head in dorsal view; **38** head in lateral view; **39** left mandible; **40** right mandible; **43** pronotum. Imago: **41** head; **42** pronotum. Scale bars: **37**, **38**: 1mm; **41**: 0.5mm; **39**, **40**, **42**, **43**: 0.2mm.

**Material examined.** **AUSTRALIA: Northern Territory:** 37 km SE Newcastle Waters, 16.vi.1936 (coll. det. G.F. Hill) (ANIC #10–2186); **Queensland:** Weipa mission, 05.x.1957 (F.J. Gay & J.H. Calaby) (ANIC #10–8659); **PAPUA NEW GUINEA: Central:** Sogeri, 14.vii.1984 (YR) (#PNGT731); Sogeri, 4.ii.1985 (YR) (#PNGT855); Sirinumu Dam, 6.iii.1985 (JMP & YR) (#PNGT912); **Fly:** Morehead, 24.iii.1989 (YR & ML) (#PNGT1431); Wipim, 29.iii.1989 (YR & ML) (#PNGT1471); Wipim, 2.iv.1989 (YR & ML) (#PNGT1517); Lake Murray, 22.v.1990 (YR & ML)

(#PNGT1562); Lake Murray, 24.v.1990 (YR & ML) (#PNGT1577); Lake Murray, 25.v.1990 (YR & ML) (#PNGT1590a,); Lake Murray, 27.v.1990 (YR & ML) (#PNGT1598, 1606). **INDONESIA: Papua:** Kaimana, 21.xi.1995 (YR) (#IRJT104, 111, 112); Kaimana, 23.xi.1995 (YR) (#IRJT142), two samples with alates (#IRJT143, 144); Puspenssat-Irja, 26.xi.1995 (YR) (#IRJT166).

**Imago.** (Figs 41–42). Head slightly elongated covered by several hundreds of setae. Pronotum elongated and moderately wide, covered by several hundreds of setae. Antennae generally with 18 articles, rarely with 17 articles. Eyes flat. Small ocelli in front of the eyes. Measurements (mm) of 12 imagoes from 1 colony: TBL: 5.16–6.31; HLC: 1.13–1.29; HWE: 0.98–1.14; PL: 0.59–0.64; PW: 0.76–0.85; FWL: 8.79–9.92; ED: 0.25–0.33.

**Soldier.** (Figs 37–40, 43) Soldiers of large size. Head elongated, slightly rounded in the corners, with a well developed hump at front. Labrum with rounded apex. Antennae with 16 or 17 articles. Pronotum elongated, covered by numerous setae. Mandibles elongated, slightly curved at tip. Measurements (mm) of 55 soldiers from 19 colonies: HLC: 1.34–1.98; HLL: 1.63–2.40; HW: 0.86–1.16; PL: 0.39–0.60; PW: 0.62–0.87; RML: 1.03–1.34; MPW: 0.35–0.48; T3L: 0.70–0.93.

**Comparisons.** Morphological variation occurs along the distribution range of *H. paradoxus*, though it appears insufficient to recognize distinct species. *H. paradoxus* differs from *H. vagus* by the larger size of its soldiers, its less elongated labrum with rounded end and its antennae with 16 or 17 articles.

**Distribution.** (Fig. 44). This species is widespread in southern Papua New Guinea, and was found on both coasts of the “bird’s neck” in Indonesian Papua. It is also known from northern Australia, especially Queensland (Watson & Abbey 1993). It occurs in savanna as well as in forest.

### Genus *Parrhinotermes* Holmgren, 1910

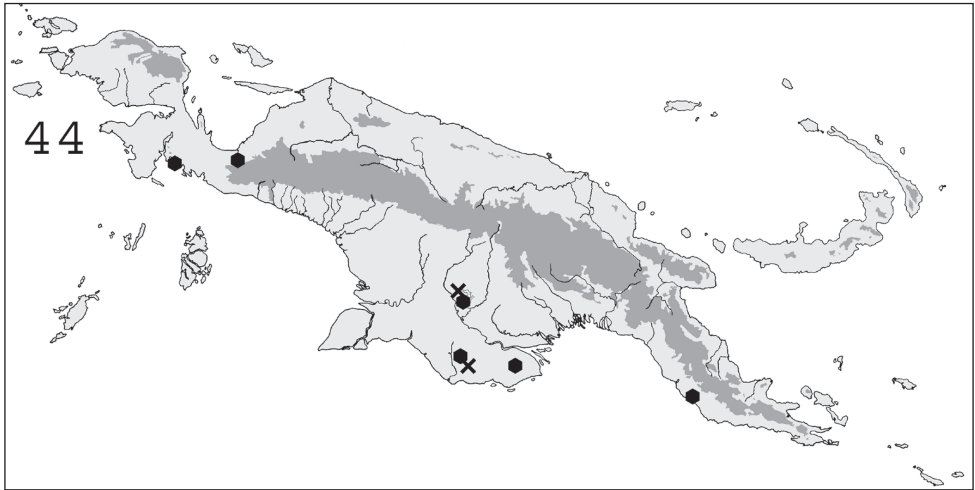
<http://species-id.net/wiki/Parrhinotermes>

*Parrhinotermes* Holmgren 1910a: 285.

**Type species.** *Termes aequalis* Haviland, 1898, by monotypy (as *T. aqualis*, incorrect spelling).

**Diagnosis.** Imago head approximately circular, with fontanelle situated between eyes. Frons with a slightly visible groove. Labrum short, inclined downward, without groove. Antennae with 16 or 17 articles. Pronotum relatively short, generally of the same width or slightly narrower than head. Soldier head rectangular to ovoid. Frons and clypeus with a groove, from the narrow fontanelle to the beginning of the labrum. Labrum elongated, crossed by a groove in the middle, and garnished with an apical brush. Base of mandibles serrated. Left mandible with two subsidiary teeth. Right mandible with one subsidiary tooth. Antennae with 13 articles.





**Figure 44.** Known distribution in New Guinea of: ✕ *Heterotermes vagus*; ● *Heterotermes paradoxus*.

**Distribution.** This genus is known from the Oriental region, northeastern India, the Papuan region and northern Australia (in northern Queensland) (Emerson 1955, Tho 1992). It occurs in tropical rainforest where it nests in dead logs.

***Parrhinotermes browni* (Harris, 1958)**

[http://species-id.net/wiki/Parrhinotermes\\_browni](http://species-id.net/wiki/Parrhinotermes_browni)

Figs 45–49, 55

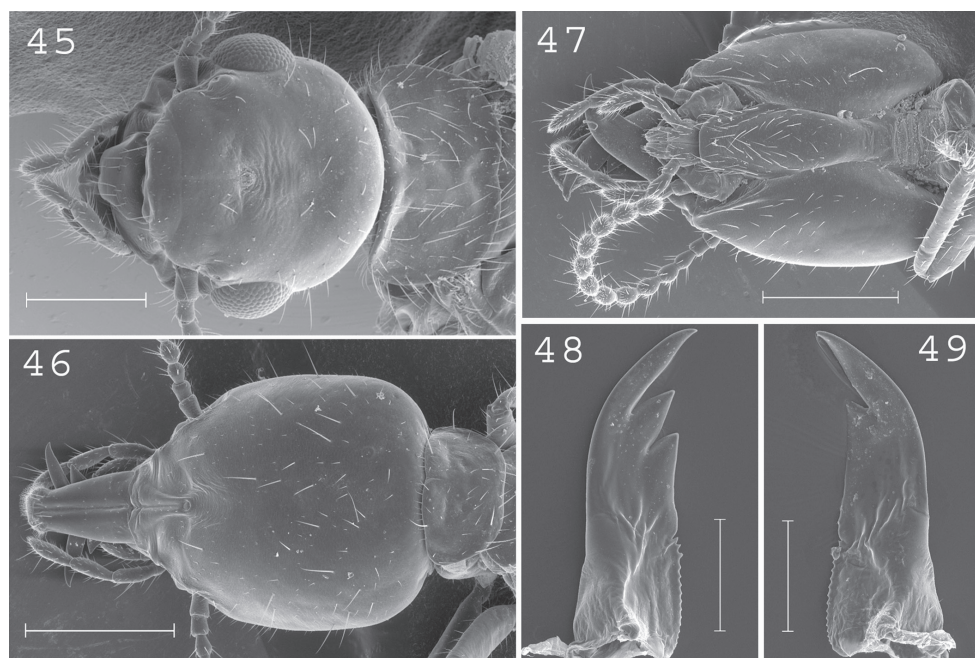
*Schedorhinotermes browni* Harris 1958: 59.

*Parrhinotermes browni* (Harris): Roisin 1988a: 22.

**Material examined. Paratypes, soldiers and workers: SOLOMON ISLANDS:**

**Guadalcanal:** Gold Ridge, 22.iii.1955 (E.S. Brown) (Brit. Mus. 1957–137, BMNH).

**Other material: PAPUA NEW GUINEA: East Sepik:** Tsenap, 18.v.1929 (K.P. Schmidt), from log on ground (AMNH); **Madang:** Yagaum Hospital, 07.iv.1983 (YR) (#PNGT303, 306); Yagaum Hospital, 13.v.1983 (YR) (#PNGT340, 341); Bunapae, 18.ii.1984 (YR) (#PNGT546); Bunapae, 12.vi.1984 (YR) (#PNGT681); Guam bridge, 09.viii.1984 (YR), with royal pair (#PNGT782); Guam bridge, 12.ii.1985 (JMP & YR), with royal pair (#PNGT867); Guam bridge, 9.vi.1986 (YR), large colony with royal pair in rotten wood (#PNGT1023), and small sample (#PNGT1024); Sepen No.1, 29.vi.1986 (YR) (#PNGT1031); Hatzfeldthafen, 22.viii.1987 (YR), with primary king and ergatoid queen (#PNGT1130); Braham mission, 06.v.1988 (YR) (#PNGT1204); Wanuma, 05.viii.1969 (R. Zweifel) (AMNH); **Morobe:** Busu River, 17.xii.1962 (AE) (AMNH); 18 mi W Lae, 28.xi.1962 (AE), nest with royal pair in



**Figures 45–49.** *Parrhinotermes browni*. Imago: **45** head. Soldier: **46** head in dorsal view; **47** head in ventral view; **48** left mandible; **49** right mandible. Scale bars: **45, 46, 47:** 0.5mm **48, 49:** 0.2mm.

large log on forest floor (AMNH); Bulolo, 22.v.1987 (YR), in hoop pine (*Araucaria cunninghamii*) plantation (#PNGT1081); McAdam National Park, 20.v.1988 (YR) (#PNGT1236); **Sandaun:** Yapsiei, 11.iii.1994 (YR & ML) (#PNGT1742); Yapsiei, 12.iii.1994 (YR & ML), in standing dead wood, with alates (#PNGT1751); **Central:** Subitana plantation, xi.1962 (AE) (AMNH). **INDONESIA: Papua:** Pusppenssat-IrJa, 13.xi.1995 (YR) (#IRJT7, 9); Pusppenssat-IrJa, 14.xi.1995 (YR) (#IRJT28); Pusppenssat-IrJa, 15.xi.1995 (YR) (#IRJT39); Pusppenssat-IrJa, 29.xi.1995 (YR) (#IRJT203); road Nabire-Mapia km 43, 26.xi.1995 (YR) (#IRJT167).

**Imago.** (Fig. 45). Head covered by about 15 setae with posterior edges strongly rounded, frons and clypeus short. Pronotum covered by about 100 setae. Antennae with 17 articles. Measurements (mm) of 6 imagoes from 1 colony: TBL: 5.76–6.34; HLC: 1.04–1.18; HWE: 1.19–1.26; PL: 0.47–0.65; PW: 0.90–0.95; FWL: 8.34–8.93; ED: 0.27–0.36.

**Soldier.** (Figs 46–49) Head rectangular-shaped with edges slightly rounded, covered by about 50 small setae and 10 large ones. Labrum elongated, reaching the tip of mandibles, with a rounded apical brush. Postmentum covered by setae only on its upper part. Antennae with 13 articles. Mandibles straight, slightly curved at tip, slightly serrated at base. Measurements (mm) of 6 soldiers of the type colony and 39 soldiers from 13 colonies (parentheses): HLC: 1.13–1.19 (1.01–1.33); HLL: 1.56–1.64 (1.40–1.79); HW: 0.90–0.94 (0.86–1.05); PW: 0.52–0.56 (0.51–0.68); RML: 0.69–

0.73 (0.64–0.78); MPW: 0.27–0.31 (0.27–0.34); mPW: 0.16–0.18 (0.16–0.22); T3L: 0.75–0.81 (0.70–0.89).

**Distribution.** (Fig. 55). This species, originally described from the Solomon Islands, is common in Northern New Guinea and in the bird's neck area.

**Termitophiles.** Several species of Trichopseniini (Coleptera, Staphylinidae) were reported from this species (Bourguignon et al. 2007): *Parrhinopsenius brevipilosus*, *P. longipilosus*, *P. hirsutus*, *P. parvus*, and one specimen of *Schedolimulus latus*.

***Parrhinotermes barbatus* sp. n.**

urn:lsid:zoobank.org:act:10EADBE0-140F-46D1-BEED-EFD6E6FA8C01

[http://species-id.net/wiki/Parrhinotermes\\_barbatus](http://species-id.net/wiki/Parrhinotermes_barbatus)

Figs 50–55

**Holotype. Soldier: PAPUA NEW GUINEA: Southern Highlands:** Lake Kutubu, 11.x.1988 (YR) (#PNGT1285). **Paratypes: PAPUA NEW GUINEA: Southern Highlands:** Lake Kutubu, 11.x.1988 (YR), two colonies, one with alates, the other one with late nymphs (#PNGT1285, 1286); Lake Kutubu, 12.x.1988 (YR), with late nymphs (#PNGT1292); Lake Kutubu, 13.x.1988 (YR), with late nymphs (#PNGT1296); Pimaga, 16.x.1988 (YR) (#PNGT1306); Pimaga, 17.x.1988 (YR), with late nymphs (#PNGT1315); **Fly:** Nomad, 31.v.1990 (YR & ML), two colonies in dead wood, with queen (#PNGT1628, 1630); Nomad, 31.v.1990 (YR & ML) (#PNGT1650). **INDONESIA: Papua:** Road Nabire-Mapia km 62, 18.xi.1995 (YR) (#IRJT71).

**Imago.** (Fig. 50). Head covered by about 15 setae with posterior margin strongly rounded, frons and clypeus of medium size. Pronotum covered by about 100 setae (Fig. 52). Antennae with 17 articles. Measurements (mm) of 6 imagoes from 1 colony: TBL: 5.23–6.02; HLC: 1.06–1.10; HWE: 1.24–1.27; PL: 0.44–0.65; PW: 0.85–0.98; FWL: 8.02–8.84; ED: 0.27–0.39.

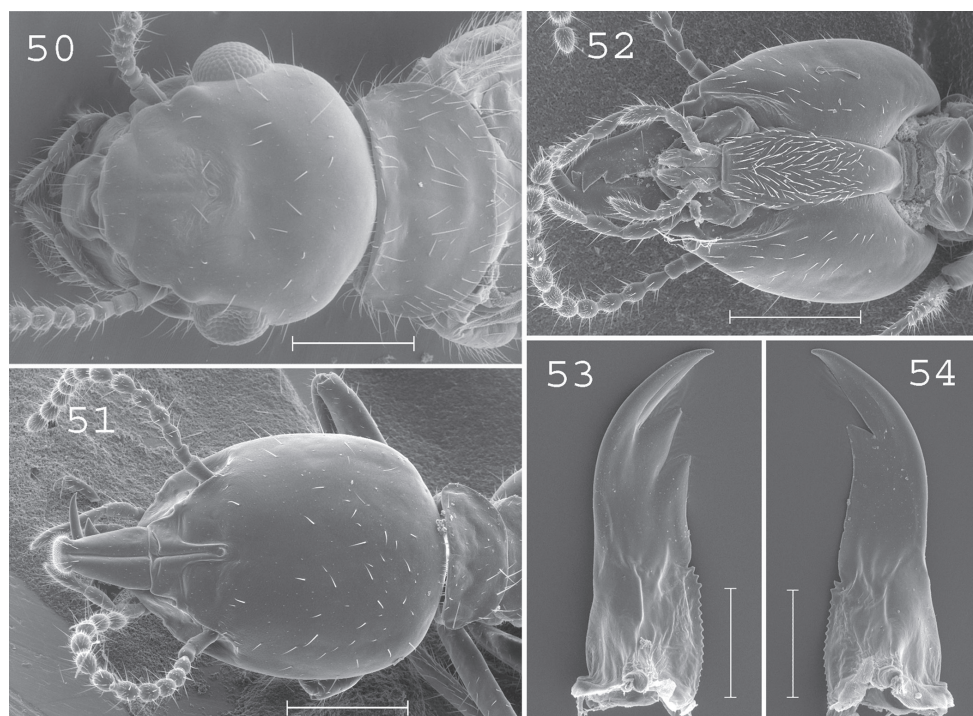
**Soldier.** (Figs 51–54). Head ellipsoid, covered by about 50 small setae. Labrum elongated, reaching the tip of mandibles, ending in a rounded brush. Postmentum covered by setae from the base to the upper part. Antennae with 13 articles. Mandibles straight, slightly curved at tip, slightly serrated at base. Measurements (mm) of 30 soldiers from 10 colonies: HLC: 1.11–1.33; HLL: 1.51–1.75; HW: 0.95–1.12; PW: 0.53–0.65; RML: 0.66–0.79; MPW: 0.25–0.34; mPW: 0.16–0.22; T3L: 0.74–0.90.

**Comparisons.** This species is distinguishable from *P. browni* and *P. queenslandicus* Mjöberg, 1920 by the postmentum of soldiers, completely covered by setae.

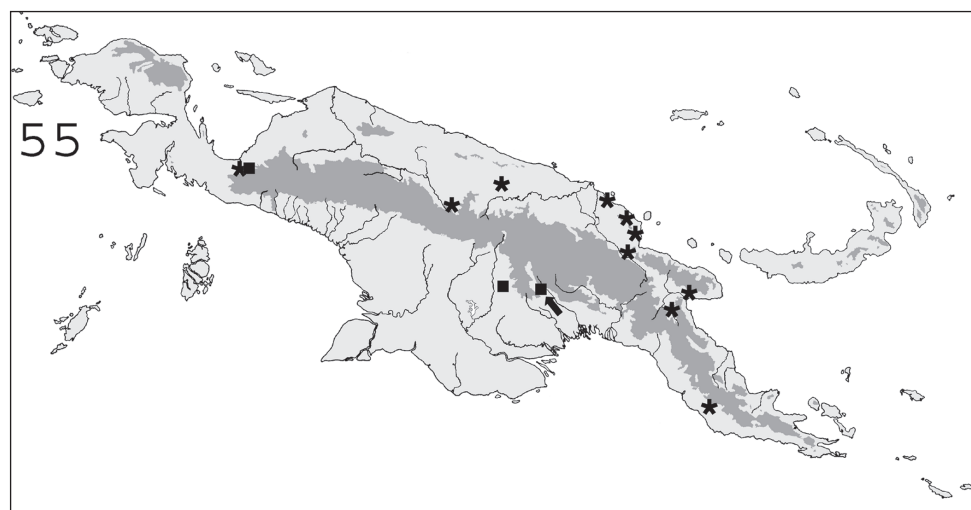
**Distribution.** (Fig. 55). This species is common in southern New Guinean forests, and was also collected once in Indonesian Papua.

**Termitophiles.** The four species of *Parrhinopsenius* found with *Parrhinotermes browni* were also found with this species, previously referred to as *Parrhinotermes* nr. *queenslandicus* (Bourguignon et al. 2007).

**Etymology.** We named this species after the latin “*barba*”, referring to the postmentum of its soldiers fully covered by setae.



**Figures 50–54.** *Parrhinotermes barbatus*. Imago: **50** head. Soldier: **51** head in dorsal view; **52** head in ventral view; **53** left mandible; **54** right mandible. Scale bars: **50, 51, 52:** 0.5mm; **53, 54:** 0.2mm.



**Figure 55.** Known distribution in New Guinea of: ★ *Parrhinotermes browni*; ■ *Parrhinotermes barbatus*. Arrow points to type locality.



**Genus *Schedorhinotermes* Silvestri, 1909**

<http://species-id.net/wiki/Schedorhinotermes>

*Rhinotermes* (*Schedorhinotermes*) Silvestri 1909: 289.

*Schedorhinotermes* Silvestri. Snyder, 1949: 89.

**Type species.** *Rhinotermes intermedius* Brauer, 1865, by original designation.

**Diagnosis.** Imagoes very similar to those of *Parrhinotermes*. Head approximately circular in shape. Fontanelle situated in the middle of the head. Frons with a slightly visible groove. Labrum short, inclined downward, without groove. Soldiers generally dimorphic and sometimes trimorphic. All species described here have dimorphic soldiers, excepted *S. seclusus* in which the minor soldiers can sometimes be further separated into two morphs (Miller 1987). Minor soldiers with elongated head. Frons and clypeus with a groove in the middle that joins the opening of the fontanelle to the labrum. Labrum elongated, crossed by a groove in the middle, ending in a brush. Mandibles long and slender. Left mandible with two short subsidiary teeth. Right mandible with one short subsidiary tooth. Major soldiers with labrum proportionally shorter than in minor soldiers. Frons and clypeus with a groove in the middle, from the fontanelle to the labrum. Labrum short and large, with a groove in the middle and an apical brush. Mandibles stout and strongly curved. Left mandible with two large subsidiary teeth. Right mandible with one large subsidiary tooth, as well as a hump at the base. Major soldiers supply more relevant systematic information to distinguish species.

**Distribution.** This genus is known from Africa, Southeast Asia, the Papuan region and Australia (Emerson 1955, Harris 1968). It feeds on dead wood.

***Schedorhinotermes seclusus* (Hill, 1933)**

[http://species-id.net/wiki/Schedorhinotermes\\_seclusus](http://species-id.net/wiki/Schedorhinotermes_seclusus)

Figs 56–61, 82

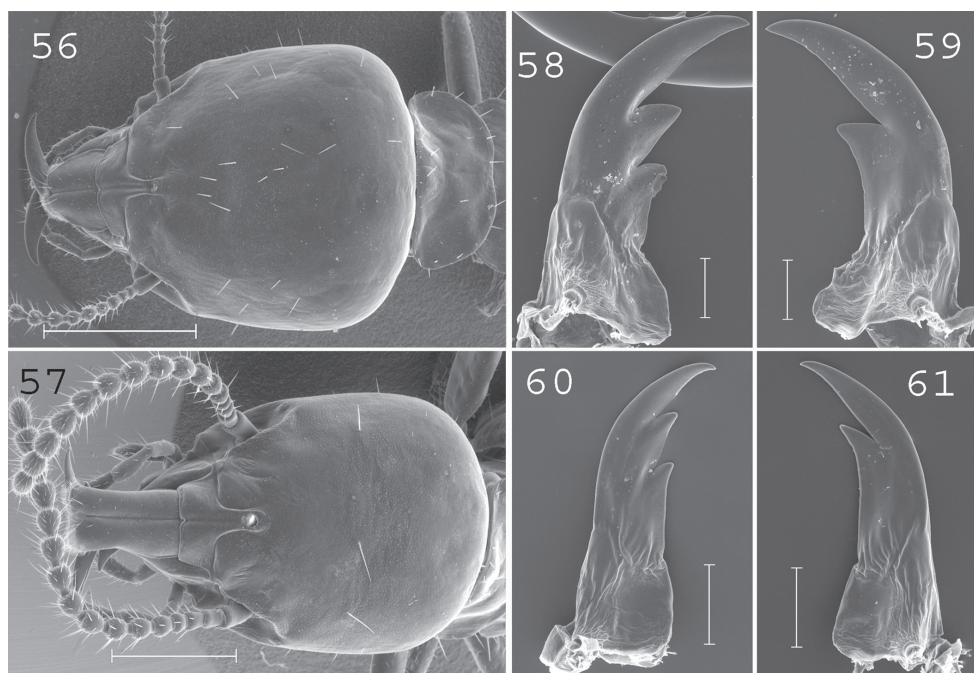
*Rhinotermes* (*Schedorhinotermes*) *intermedius seclusus* Hill 1933: 5.

*Schedorhinotermes intermedius seclusus* (Hill). Snyder 1949: 92.

*Schedorhinotermes seclusus* (Hill). Watson et al. 1998: 197.

**Material examined. Lectotype:** AUSTRALIA: Queensland: Babinda, 06.i.1925 (G.F. Hill) (NMVA #T-10854). **Other material:** PAPUA NEW GUINEA: **Southern Highlands:** Lake Kutubu, 13.x.1988 (YR) (#PNGT1295); **Fly:** Morehead, 25.iii.1989 (YR & ML) (#PNGT1438); Morehead, 26.iii.1989 (YR & ML) (#PNGT1453); Wipim, 15.viii.1962 (R. Zweifel), with nymphs (AMNH); Wipim, 30.iii.1989 (YR & ML) (#PNGT1480, 1482); Wipim, 31.iii.1989 (YR & ML) (#PNGT1495); Wipim, 01.iv.1989 (YR & ML) (#PNGT1504); Lake Murray, 22.v.1990 (YR & ML) (#PNGT1558, 1559, 1560); Lake Murray, 23.v.1990 (YR & ML) (#PNGT1573,





**Figures 56–61.** *Schedorhinotermes seclusus*. Major soldier: **56** head; **58** left mandible; **59** right mandible. Minor soldier: **57** head; **60** left mandible; **61** right mandible. Scale bars: **56**, **57**: 0.5mm; **58**, **59**, **60**, **61**: 0.2mm.

1576); Lake Murray, 24.v.1990 (YR & ML) (#PNGT1579); Lake Murray, 25.v.1990 (YR & ML) (#PNGT1596); Lake Murray, 27.v.1990 (YR & ML) (#PNGT1604); Nomad, 31.v.1990 (YR & ML) (#PNGT1633).

**Imago.** Unknown.

**Major soldier.** (Figs 56, 58–59) Soldiers of large size. Head covered by about 30 setae. Labrum short and large, not reaching the tip of mandibles. Antennae generally with 17 articles, sometimes with 16 or 18 articles. Pronotum large, covered by about 15 setae principally situated on the edges. Abdomen densely hairy, with 20 to 40 setae per segment. Mandibles moderately curved. Left mandible with the first subsidiary tooth shorter than the second and with a small hump at the base. Right mandible with a slight hump at the base. Measurements (mm) of 1 major soldier from the type colony and 30 major soldiers from 10 colonies (parentheses): HLC: 2.07 (1.82–2.33); HLL: 2.52 (2.24–2.74); HW: 1.96 (1.69–2.05); PW: 1.27 (1.08–1.42); RML: 1.27 (1.00–1.36); mPW: 0.36 (0.22–0.38); T3L: 1.76 (1.43–1.73).

**Minor soldier.** (Figs 57, 60–61). Soldiers of large size. Head covered by about 15 setae. Labrum 1.5 times longer than wide, reaching the tip of mandibles. Antennae with 16 articles. Pronotum of large size with about 10 setae on the edges. Abdomen abundantly hairy, with 10 to 15 setae per segment. Large mandibles strongly curved. Measurements (mm) of 1 minor soldier from the type colony and 10 minor soldiers from 10 colonies (parentheses): HLC: 1.11 (1.10–1.41); HLL: 1.52 (1.59–1.97);

HW: 0.86 (0.95–1.19); PL: 0.44 (0.38–0.48); PW: 0.66 (0.68–0.86); RML: 0.75 (0.79–0.97); MPW: 0.35 (0.34–0.39); T3L: 1.09 (1.01–1.32).

**Comparisons.** This species is easily distinguishable from others by its large size and its densely hairy abdomen in the minor and major soldier castes. Minor soldiers are highly variable in size, indicating the likely presence of two developmental subcategories (Miller 1987).

**Distribution.** (Fig. 82). This species is widespread throughout southern Papua New Guinea. It is also known from Queensland, Australia.

**Termitophiles.** Three species of Trichopseniini (Coleoptera, Staphylinidae, Aleocharinae) were reported by Bourguignon et al. (2007): *Schedolimus seclusi*, *S. planus* and *Papuapsenius magnus*.

### ***Schedorhinotermes malaccensis* (Holmgren, 1913)**

[http://species-id.net/wiki/Schedorhinotermes\\_malaccensis](http://species-id.net/wiki/Schedorhinotermes_malaccensis)

Figs 62–67, 82

*Rhinotermes* (*Schedorhinotermes*) *malaccensis* Holmgren 1913: 86.

*Schedorhinotermes malaccensis* (Holmgren). Snyder 1949: 93.

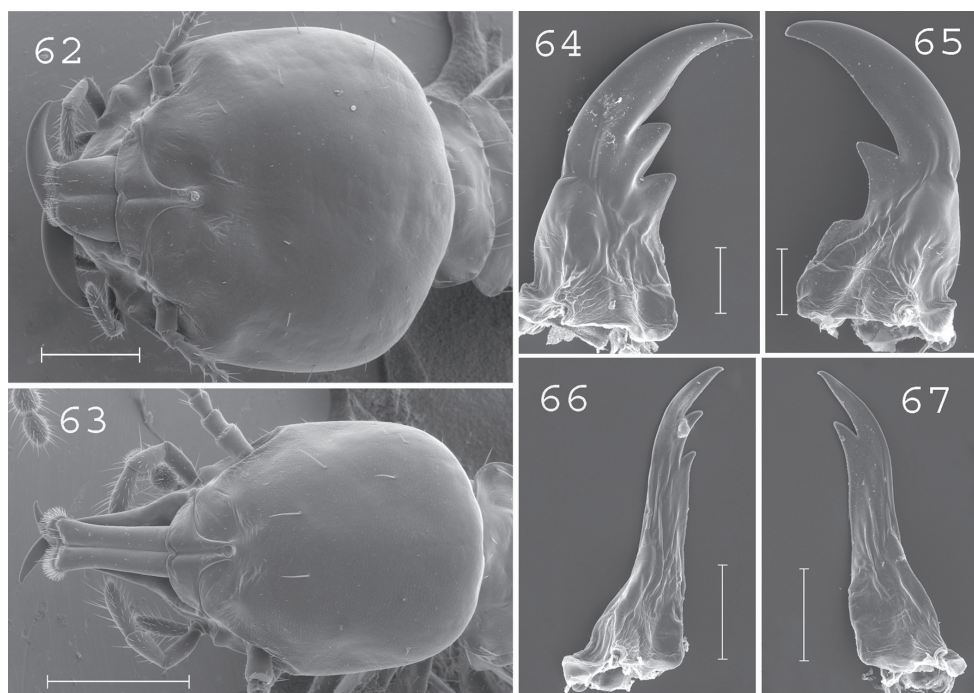
**Material examined. Paratype:** NHRS collections. **Other material: INDONESIA: Papua:** Pusppenssat-IrJa, 13.xi.1995 (YR) (#IRJT15); Road Nabire-Mapia km 48, 15.xi.1995 (YR) (#IRJT43).

**Imago.** Unknown.

**Major soldier.** (Figs 62, 64–65). Soldiers of large size. Head rounded, as long as large, covered by about 20 setae. Labrum short and large. Antennae generally with 16 articles. Pronotum large, covered by about 15 setae situated on the edges. Mesonotum and metanotum covered by about 10 setae on posterior margin. Abdomen covered by about 10 setae per segment. Mandibles very large. Right mandible with large hump at the basis. Measurements (mm) of 6 major soldiers from 2 colonies: HLC: 1.70–2.09; HLL: 2.03–2.43; HW: 1.95–2.04; PW: 1.17–1.25; RML: 1.07–1.15; mPW: 0.26–0.34; T3L: 1.54–1.64.

**Minor soldier.** (Figs 63, 66–67). Head covered by 5 to 10 setae. Labrum moderately elongated, almost reaching the tip of mandibles. Fronto-clypeus short and wide. Antennae with 15 or 16 articles. Pronotum with about 10 setae placed on the edges. Mesonotum and metanotum with about 8 setae on the posterior edge. Mandibles elongated, slender, with short subsidiary teeth. Measurements (mm) of 1 minor soldier from the type colony and 6 minor soldiers from 2 colonies (parentheses): HLC: 1.28 (1.01–1.22); HLL: 1.77 (1.52–1.78); HW: 1.00 (0.81–0.95); PL: 0.50 (0.37–0.49); PW: 0.70 (0.59–0.73); RML: 0.85 (0.72–0.87); MPW: 0.36 (0.30–0.35); T3L: 1.18 (1.03–1.14).

**Comparisons.** This species is easily distinguished from other New Guinean species by the large rounded head and stout mandibles of its major soldiers.



**Figures 62–67.** *Schedorhinotermes malaccensis*. Major soldier: **62** head; **64** left mandible; **65** right mandible. Minor soldier: **63** head; **66** left mandible; **67** right mandible. Scale bars: **62, 63:** 0.5mm; **64, 65, 66, 67:** 0.2mm.

**Distribution.** (Fig. 82). This species is widespread throughout Sundaland (Gathorne-Hardy 2004). In New Guinea, it was only collected twice in northwestern Papua.

***Schedorhinotermes longirostris* (Brauer, 1866)**

[http://species-id.net/wiki/Schedorhinotermes\\_longirostris](http://species-id.net/wiki/Schedorhinotermes_longirostris)

Figs 68–74, 82

*Termes longirostris* Brauer 1866: 47.

*Rhinotermes* (*Schedorhinotermes*) *longirostris* (Brauer). Holmgren 1913: 86.

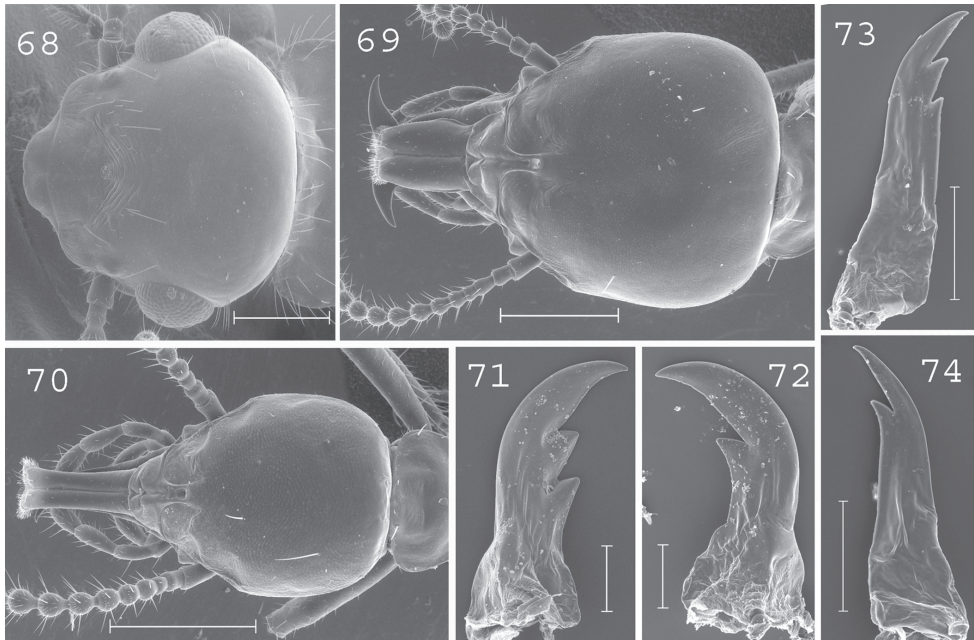
*Schedorhinotermes longirostris* (Brauer). Snyder 1949: 93.

*Rhinotermes dimorphus* Desneux 1905: 368. syn. n.

*Rhinotermes* (*Schedorhinotermes*) *dimorphus* Desneux. Holmgren 1911a: 458.

*Schedorhinotermes dimorphus* (Desneux). Snyder 1949: 90.

**Material examined. Syntypes, minor soldier and workers: INDIA: Nicobar Islands:** Kondul Island (NHRS). **Syntypes of *S. dimorphus*, major soldiers, minor soldiers and workers: PAPUA NEW GUINEA: Madang:** Madang (as Friedrich-Wilhelmshafen),



**Figures 68–74.** *Schedorhinotermes longirostris*. Imago: **68** head. Major soldier: **69** head; **71** left mandible; **72** right mandible. Minor soldier: **70** head; **73** left mandible; **74** right mandible. Scale bars: **68, 69, 70:** 0.5mm; **71, 72, 73, 74:** 0.2mm.

8.i.1901 (L. Biró) (IRSNB). **Other material: PAPUA NEW GUINEA: Sandaun:** Vani-mo, 08.iii.1994 (YR & ML) (#PNGT1718); **East Sepik:** Marangis, 07.iii.1983 (JMP & YR) (#PNGT253); **Madang:** Road Madang-Lae km 30, 04.vii.1981 (JMP) (#PNGT120, 121); Bunapas road, 07.vii.1981 (JMP) (#PNGT132, 141); Potsdam plantation, 23.iii.1983 (YR) (#PNGT275); Nubia, 18.v.1983 (YR) (#PNGT353), Potsdam plan-tation, 20.vi.1983 (YR) (#PNGT386); Bunapae, 25.x.1983 (YR) (#PNGT415); Sepen No.1, 29.x.1983 (YR) (#PNGT425); Potsdam plantation, 25.xi.1983 (YR), with nymphs (#PNGT479); Bunapae, 12.vi.1984 (YR) (#PNGT680); Potsdam plantation, 20.vii.1984 (YR) (#PNGT743); Bunapae, 23.vii.1984 (YR) (#PNGT748); Potsdam plantation, 24.vii.1984 (YR) (#PNGT753); Hansa point, 22.viii.1984 (YR) (#PNGT786); Hansa point, 08.ix.1984 (YR) (#PNGT823); Sepen No.1, 16.ii.1985 (JMP & YR), with alates (#PNGT876); Sepen No.1, 01.iii.1988 (YR) (#PNGT1165, 1166); Yagaum hospital, 10.iv.1983 (YR) (#PNGT304); Gilagil River bridge, 12.iii.1988 (YR) (#PNGT1170); Baitabag, 15.v.1999 (L. Čížek) (#2, J. Šobotník's collection); Tabobo, 07.i.1989 (ML) (#PNGT1383); Road Kausi-Bundi, 07.v.1988 (YR) (#PNGT1207); Bundi, 10.v.1988 (YR) (#PNGT1210); **Morobe:** Wampit, 06.ii.1983 (JMP & YR) (#PNGT178); Kaia-pit, 19.ii.1983 (JMP & YR) (#PNGT192); Sirasira, 15.v.1988 (YR) (#PNGT1219, 1220). Bulolo, 14.ii.1983 (JMP & YR) (#PNGT168); Mount Susu, 23.v.1987 (YR), in branch of klinkii pine on the ground (#PNGT1085); Mount Susu, 19.v.1988 (YR), in branch of klinkii pine on the ground (#PNGT1233); **Oro:** Kokoda, 13.iii.1985 (JMP & YR), in tree stump in cocoa plantation (#PNGT949); Koiasi, 14.iii.1985 (JMP & YR)



(#PNGT957); Kokoda, 19.iii.1985 (JMP & YR), in dead wood in rubber plantation (#PNGT987); **East New Britain:** Warengoi, 19.v.1984 (JMP & YR) (#PNGT561); Ataliklikun Bay, 30 km W of Keravat, 23.v.1984 (JMP & YR) (#PNGT595); **New Ireland:** Lelet plateau, 27.v.1984 (JMP & YR) (#PNGT609, 610); Konos, 29.v.1984 (JMP & YR) (#PNGT623); **Manus:** Road Lorengau-Yiringo km 32, 04.vi.1984 (JMP & YR) (#PNGT659); **Central:** Sogeri area, 23.xi.1962 (AE), 2 samples with alates, from logs in rubber grove (AMNH); Sirinumu Dam, 06.iii.1985 (JMP & YR) (#PNGT913); Sirinumu Dam, 08.iii.1985 (JMP & YR) (#PNGT926, 931); **Southern Highlands:** Lake Kutubu, 11.x.1988 (YR) (#PNGT1287, 1288); Pimaga, 16.x.1988 (YR) (#PNGT1304); **Fly:** Tabubil, 20.v.1990 (YR & ML) (#PNGT1548); Lake Murray, 22.v.1990 (YR & ML) (#PNGT1557); Lake Murray, 24.v.1990 (YR & ML) (#PNGT1583); Nomad, 31.v.1990 (YR & ML) (#PNGT1626). **INDONESIA: Papua:** Road Nabire-Mapia km 43, 26.xi.1995 (YR) (#IRJT168); Kaimana, 21.xi.1995 (YR), three samples, the last one with large nymphs (#IRJT103, 109, 113); Kaimana, 23.xi.1995 (YR) (#IRJT142).

**New synonymy.** We compared the type material of *S. longirostris* and *S. dimorphus* with our material and were not able to find any relevant morphological characters to distinguish the two species. Therefore, we consider *S. dimorphus* as a junior synonym of *S. longirostris*.

**Imago.** (Fig. 68). Head covered by 10–15 setae. Eyes of medium size. Pronotum covered by about 50 setae mainly located on the edges. Antennae with 20 articles. Measurements (mm) of 6 imagoes from 1 colony: TBL: 7.39–8.79; HLC: 1.37–1.58; HWE: 1.51–1.62; PL: 0.73–0.79; PW: 1.23–1.36; FWL: 8.70–9.80; ED: 0.31–0.33.

**Major soldier.** (Figs 69, 71–72). Soldiers of small size. Head, excluding labrum, square-shaped, slightly longer than wide, covered by about 10 setae. Labrum slightly longer than wide, reaching the tip of mandibles. Antennae with 15 or 16 articles. Pronotum covered by 6 long setae disposed in each corners. Mesonotum and metanotum with 4 long setae. Abdomen with 6 long setae per segment, plus sometimes 1 or 2 smaller ones. Mandibles strongly curved at tip with short subsidiary teeth. Left mandible with 2 subsidiary teeth of the same length. Right mandible without hump at the basis. Measurements (mm) of 1 major soldier from the type colony of *S. longirostris*, 2 major soldiers from the type colony of *S. dimorphus* [brackets], and 77 major soldiers from 29 colonies (parentheses): HLC: 1.56 [1.50–1.56] (1.35–1.95); HLL: 2.05 [1.92–1.99] (1.65–2.21); HW: 1.32 [1.31–1.35] (1.17–1.51); PW: 0.74 [0.73–0.75] (0.65–0.86); RML: 0.98 [0.89–0.97] (0.75–1.06); mPW: 0.25 [0.24] (0.19–0.30); T3L: 1.19 [1.09–1.16] (1.11–1.36).

**Minor soldier.** (Figs 70, 73–74). Soldiers of small size. Head elongated, covered by 5–10 setae. Labrum very elongated, 3 times longer than wide, reaching beyond mandibles. Fronto-clypeus of medium size. Antennae with 15 or 16 articles. Pronotum covered by 6 large setae disposed in each corner. Mesonotum and metanotum with 4 long setae. Abdomen with 6 long setae per segment, plus sometimes 1 or 2 smaller ones. Mandibles elongated, hardly curved, with short subsidiary teeth. Measurements (mm) of 10 minor soldiers from 10 colonies of *S. longirostris*, plus 6 minor soldiers of the type colony of *S. dimorphus* [brackets]: HLC: 0.82–1.05 [0.90–0.94]; HLL:



1.18–1.54 [1.30–1.37]; HW: 0.60–0.77 [0.66–0.69]; PL: 0.28–0.36 [0.30–0.33]; PW: 0.40–0.53 [0.44–0.51]; RML: 0.52–0.70 [0.51–0.64]; MPW: 0.25–0.31 [0.24–0.28]; T3L: 0.74–0.94 [0.71–0.87].

**Comparisons.** This species can be distinguished from other New Guinean species by the number of setae on the pronotum (6 per segment), mesonotum (4), metanotum (4) and abdomen (6) in the major soldier caste.

**Distribution.** (Fig. 82). This species is common in forested areas throughout New Guinea. It probably also occurs in Indonesia, since it was described from the Nicobar islands.

**Termitophiles.** Several Aleocharinae (Coleoptera, Staphylinidae) were found with this species. *Schedotermoeicia kaimanensis* (Coptotermoeiciina) was described from colony #IRJT142, and its congener *S. papuana* from #PNGT1165 (Bourguignon & Roisin 2006). The following Trichopseniini also occur with this species: *Schedolimulus elongatus*, *S. planus* and *S. minutides* Bourguignon, *nomen novum* (here proposed as replacement name for *S. minutus* Bourguignon, 2007, to remove secondary homonymy with *Phorilimulus minutus* Pasteels & Kistner, 1971, transferred to *Schedolimulus* by Kanao et al. 2011).

### ***Schedorhinotermes translucens* (Haviland, 1898)**

[http://species-id.net/wiki/Schedorhinotermes\\_translucens](http://species-id.net/wiki/Schedorhinotermes_translucens)

Figs 75–81, 83

*Termes translucens* Haviland 1898: 394.

*Rhinotermes translucens* (Haviland). Desneux 1904b: 28.

*Rhinotermes* (*Schedorhinotermes*) *translucens* (Haviland). Holmgren 1911a: 458.

*Rhinotermes* (*Schedorhinotermes*) *celebensis* Holmgren 1911a: 458. **New synonymy.**

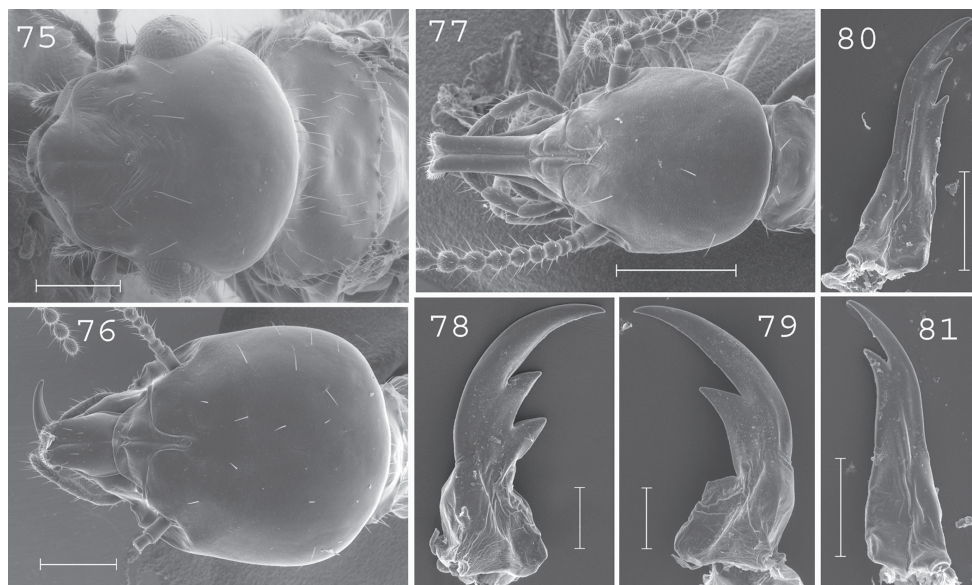
*Rhinotermes* (*Schedorhinotermes*) *marjoriae* Snyder 1925: 404–405. **New synonymy.**

*Schedorhinotermes marjoriae* (Snyder). Snyder 1949: 94.

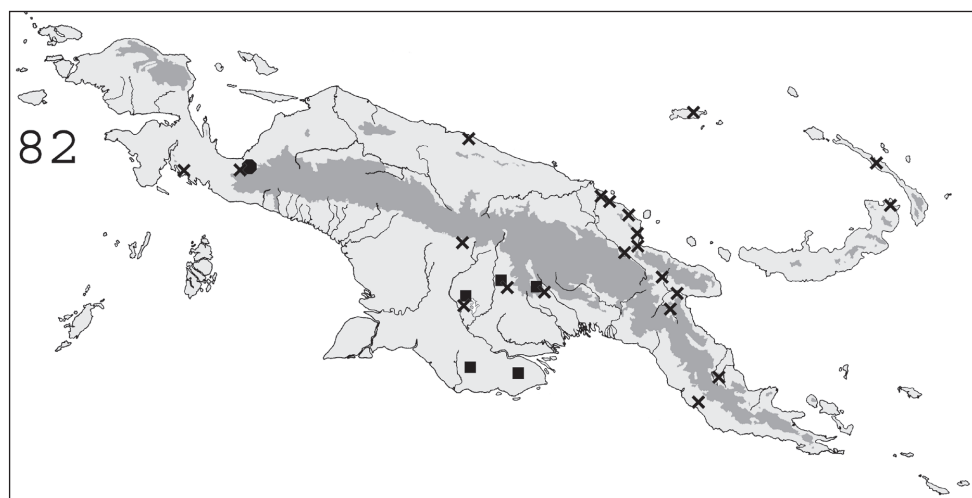
*Schedorhinotermes celebensis* (Holmgren). Snyder 1949: 90.

*Schedorhinotermes translucens* (Haviland). Snyder 1949: 96.

**Material examined. Syntypes, all castes: MALAYSIA: Sarawak:** Kuching, xi.1894 (G.D. Haviland) (type No. 299, B.M.1899–41, BMNH, collection data from Harris 1966). **Syntype of *S. celebensis*, alate:** Celebes, Hickson (BMNH). **Other material: SOLOMON ISLANDS:** Guadalcanal, 24.xi.1954 (E.S. Brown), labelled *S. marjoriae* (BMNH). **PAPUA NEW GUINEA: Madang:** Bunapas road, 26.vi.1981 (JMP) (#PNGT104); Nubia, 18.v.1983 (YR) (#PNGT352); Hatzfeldthafen, 20.v.1983 (YR), in bamboo thicket (#PNGT363); Potsdam, 10.xii.1983 (YR) (#PNGT495); Boisa Island, 06.ix.1984 (YR) (#PNGT819); Tabele (Manam Is.), 19.ix.1984 (YR) (#PNGT841); Guam bridge, 12.ii.1985 (JMP & YR) (#PNGT872); Bunapas road, 16.ii.1985 (JMP & YR) (#PNGT877); Hatzfeldthafen, 22.ii.1985 (JMP & YR), with royal pair, 1 alate in log on the ground (#PNGT893); Bogia-Tangu road km 10, 28.vii.1987 (YR) (#PNGT1125 ?1124?); Nubia, 17.ii.1988 (YR), with 3 alates



**Figures 75–81.** *Schedorhinotermes translucens*. Imago: **75** head. Major soldier: **76** head; **78** left mandible; **79** right mandible. Minor soldier: **77** head; **80** left mandible; **81** right mandible. Scale bars: **75, 76, 77:** 0.5mm; **78, 79, 80, 81:** 0.2mm.



**Figure 82.** Known distribution in New Guinea of: ■ *Schedorhinotermes seclusus*; ● *Schedorhinotermes malaccensis*; × *Schedorhinotermes longirostris*.

(#PNGT1155); Baitabag, 15.v.1999 (L. Čížek) (#11, J. Šobotník's collection); Tabobo, 07.i.1989 (ML), with alates (#PNGT1385); Braham mission, 05.v.1988 (YR) (#PNGT1199); **Morobe:** Kaiapit, 18–19.ii.1983 (JMP & YR) (#PNGT185, 190); 19 km W Lae, 28.xi.1962 (AE) (AMNH); 40 km S Lae on Bulolo road, 15.xii.1962 (AE) (AMNH); 21 km ENE Lae, 20.xii.1962 (AE) (AMNH); Markham River (21

km NW Lae), 08.xii.1962 (AE), with nymphoid queen, in standing tree besides stream (AMNH); Oomsis, 25.v.1987 (YR) (#PNGT1089); Bulolo, 14.ii.1983 (JMP & YR) (#PNGT166, 167); Bulolo, 22.v.1987 (YR) (#PNGT1078); 8 km S Bulolo, alt. 900m, 14.xii.1962 (AE) (AMNH); Manki ridge, 18.v.1988 (YR), in *Castanopsis* forest (#PNGT1227); Mount Susu, 19.v.1988 (YR), in hoop pine log (#PNGT1234); Wau-Edie Creek road, 10.ii.1983 (JMP & YR) (#PNGT157, 158); Mount Missim, 12.ii.1983 (JMP & YR) (#PNGT163); Kaulz Creek, 13.xii.1962 (AE), 2 samples from wood stump in mid-montane forest (AMNH); **Eastern Highlands:** Aiyura, 03.i.1963 (AE), 2 samples from stumps, one in *Castanopsis acuminata* forest, one in garden (AMNH); **Sandaun:** Yapsiei, 10.iii.1994 (YR & ML) (#PNGT1731, 1732); Yapsiei, 11.iii.1994 (YR & ML) (#PNGT1743); Yapsiei, 12.iii.1994 (YR & ML), with 1 alate (#PNGT1752); **Manus:** Lorengau-Yiringo road km 32, 04.vi.1984 (JMP & YR) (#PNGT655); Lorengau-Yiringo road km 32, 06.vi.1984 (JMP & YR) (#PNGT674); **East New Britain:** Ataliklikun Bay, 30 km W of Keravat, 23.v.1984 (JMP & YR) (#PNGT596); **Oro:** Kokoda, 13.iii.1985 (JMP & YR) (#PNGT951); Kokoda, 17.iii.1985 (JMP & YR) (#PNGT978, 979); Kokoda, 17.iii.1985 (JMP & YR), in rubber plantation (#PNGT991, 992); **Central:** Sirinumu Dam, 09.iii.1985 (JMP & YR) (#PNGT941); Brown River, 21.iii.1985 (JMP & YR) (#PNGT995); **Southern Highlands:** Bosavi mission, 25.vi.1999 (L. Čížek) (#19, J. Šobotník's collection); Lake Kutubu, 13.x.1988 (YR) (#PNGT1294); Pimaga, 16–17.x.1988 (YR) (#PNGT1303, 1305, 1311); Pimaga, 19.x.1988 (YR) (#PNGT1320); **Fly:** Morehead, 23.iii.1989 (YR & ML) (#PNGT1417); Wipim, 29.iii.1989 (YR & ML) (#PNGT1474); Tabubil, 19.v.1990 (YR & ML) (#PNGT1538); Lake Murray, 23.v.1990 (YR & ML) (#PNGT1568); Nomad, 29.v.1990 (YR & ML) (#PNGT1615); Nomad, 31.v.1990 (YR & ML) (#PNGT1629); Nomad, 01.vi.1990 (YR & ML) (#PNGT1638, 1641, 1646); Nomad, 02.vi.1990 (YR & ML) (#PNGT1666). **INDONESIA:** **Papua:** Pusppenssat-IrJa, 14.xi.1995 (YR) (#IRJT25); Road Nabire-Mapia km 48, 15.xi.1995 (YR) (#IRJT42); Road Nabire-Mapia km 62, 18.xi.1995 (YR) (#IRJT69, 70); Pusppenssat-IrJa, 19.xi.1995 (YR) (#IRJT83, 93); Topo, 28.xi.1995 (YR) (#IRJT191); Sanoba, 29.xi.1995 (YR) (#IRJT196); Pusppenssat-IrJa, 01.xii.1995 (YR) (#IRJT212). **Samples included with doubt: PAPUA NEW GUINEA:** **Madang:** Usino, 22.ii.1983 (JMP & YR) (#PNGT215); Nubia, 18.v.1983 (YR) (#PNGT352); Guam bridge, 12.ii.1985 (JMP & YR) (#PNGT868); Hatzfeldthafen, 22.ii.1985 (JMP & YR) (#PNGT892); **East New Britain:** Warengoi, 19.v.1984 (JMP & YR) (#PNGT571).

**New synonymy.** *S. celebensis* was described by Holmgren (1911a) based on the alate caste. The distinction of rhinotermitid species based only on alates is uncertain, as only few characters give relevant taxonomic information. After comparison of the type series of *S. celebensis* and *S. translucens* it appears that alates of the two species are morphologically identical and could be considered as the same species. Moreover, *S. celebensis* was mentioned in New Guinea and was therefore expected to occur in our samples. Thus, even though the soldiers could not be compared, we consider *S. celebensis* as a junior synonym of *S. translucens*.

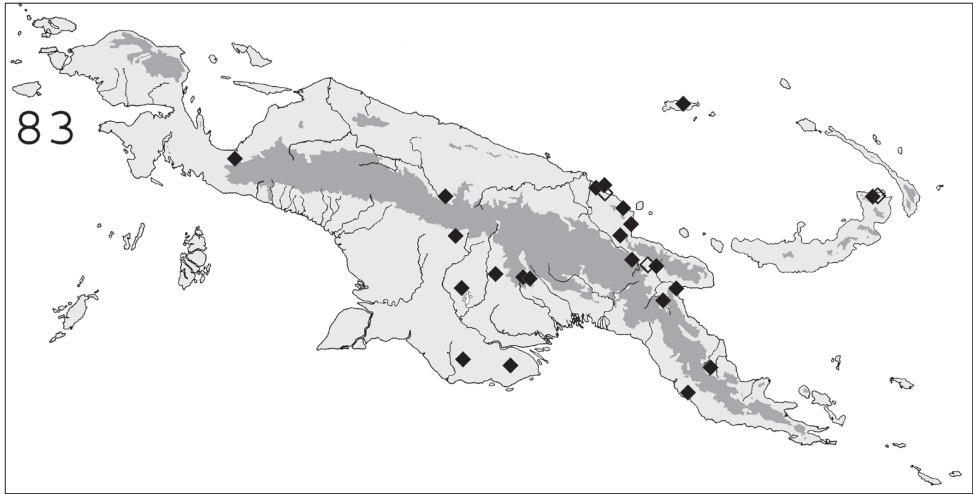
*S. marjoriae* was described by Snyder (1925) based on specimens collected in the Solomon Islands. He pointed out its resemblance with *S. translucens* and gave as sole character to distinguish these species the morphology of major soldier mandibles. After examination of samples of *S. marjoriae* and *S. translucens*, we found that differences between soldier mandibles of the two alleged species are by far smaller than variation observed among New Guinean specimens. For this reason, we also consider *S. marjoriae* as a junior synonym of *S. translucens*.

**Imago.** (Fig. 75). Head slightly rounded posteriorly, covered by about 15 setae. Eyes relatively large. Pronotum bearing about 50 setae, principally located on edges. Antennae with 20 articles. Measurements (mm) of 3 imagoes from the type colony of *S. translucens*, 1 imago from the type colony of *S. celebensis* [brackets], and 26 imagoes from 5 colonies (parentheses): TBL: 7.31–8.95 [7.18] (7.02–8.95); HLC: 1.62–1.68 [1.54] (1.36–1.67); HWE: 1.72–1.76 [1.66] (1.63–1.84); PL: 0.88–0.98 [0.80] (0.74–0.89); PW: 1.48–1.55 [1.39] (1.30–1.56); FWL: 10.21–10.70 [n.a.] (9.60–11.40); ED: 0.51–0.54 [0.41] (0.31–0.48).

**Major soldier.** (Figs 76, 78–79). Soldiers of medium size. Head slightly longer than wide, covered by about 30 setae. Labrum not reaching the tip of mandibles. Antennae with 16 articles. Pronotum large, covered by about 15 setae. Mesonotum and metanotum covered by about 10 setae on the posterior margin. Abdomen with 15 to 20 setae per segment. Left mandible with the first subsidiary tooth slightly longer than the second. Right mandible with well developed outgrowth on interior side of base. Measurements (mm) of 3 major soldiers from the type colony of *S. translucens*, 6 major soldiers from one determined sample of *S. marjoriae* [brackets], and 87 major soldiers from 29 colonies (parentheses): HLC: 1.91–1.97 [1.95–2.06] (1.45–2.10); HLL: 2.38–2.42 [2.40–2.58] (1.82–2.62); HW: 1.67–1.79 [1.75–1.89] (1.32–1.84); PW: 1.02–1.08 [1.04–1.12] (0.74–1.17); RML: 1.11–1.14 [1.12–1.19] (0.88–1.23); MPW: 0.27–0.30 [0.29–0.34] (0.20–0.34); T3L: 1.54–1.57 [1.42–1.53] (1.15–1.63).

**Minor soldier.** (Figs 77, 80–81). Head elongated, rounded posteriorly, covered by about 10 setae. Labrum 2.5 times longer than wide, reaching the tip of mandibles. Fronto-clypeus elongated. Antennae with 15 articles. Pronotum with about 10 setae on the edges. Mesonotum and metanotum with about 10 setae on the posterior edge. Abdomen with about 8 to 10 setae per segment. Mandibles slender. Measurements (mm) of 5 minor soldiers from the type colony of *S. translucens*, 6 minor soldiers of one determined sample of *S. marjoriae* [brackets] and 10 minor soldiers from 10 colonies (parentheses): HLC: 0.99–1.19 [0.98–1.20] (0.90–1.11); HLL: 1.44–1.72 [1.49–1.67] (1.34–1.68); HW: 0.78–0.93 [0.78–0.87] (0.71–0.90); PL: 0.40–0.48 [0.35–0.46] (0.28–0.43); PW: 0.59–0.69 [0.52–0.63] (0.45–0.65); RML: 0.65–0.78 [0.60–0.72] (0.55–0.77); MPW: 0.30–0.35 [0.28–0.32] (0.24–0.34); T3L: 1.04–1.24 [0.89–1.02] (0.87–1.04).

**Comparisons.** This species is related to *Schedorhinotermes longirostris*, from which it can be distinguished by its more hairy pronotum, mesonotum, metanotum and abdomen of major soldiers.



**Figure 83.** ◆ Known distribution in New Guinea of *Schedorhinotermes translucens*; ◇ dubious samples.

**Distribution.** (Fig. 83). *S. translucens* is widespread throughout New Guinea, both in savannas and forests. The following additional records are from the literature (samples not examined): Holmgren (1911a): Sattelberg, Kola; as *S. celebensis*: Aitape (as Eitape (Berlinerhafen)); Roonwal & Maiti (1966): Meervlakte.

**Termitophiles.** *Myrmedonota termitophila* (Coleoptera, Staphylinidae, Aleocharinae, Lomechusini) was discovered in colony #PNGT163 (Bourguignon & Roisin 2006). The following Trichopseniini (also Aleocharinae), were reported as guests of this species (Bourguignon et al. 2007): *Schedolimulus elongatus*, *S. latus*, *S. planus*, and *Schizelythron papuanum*.

### Genus *Prorhinotermes* Silvestri, 1909

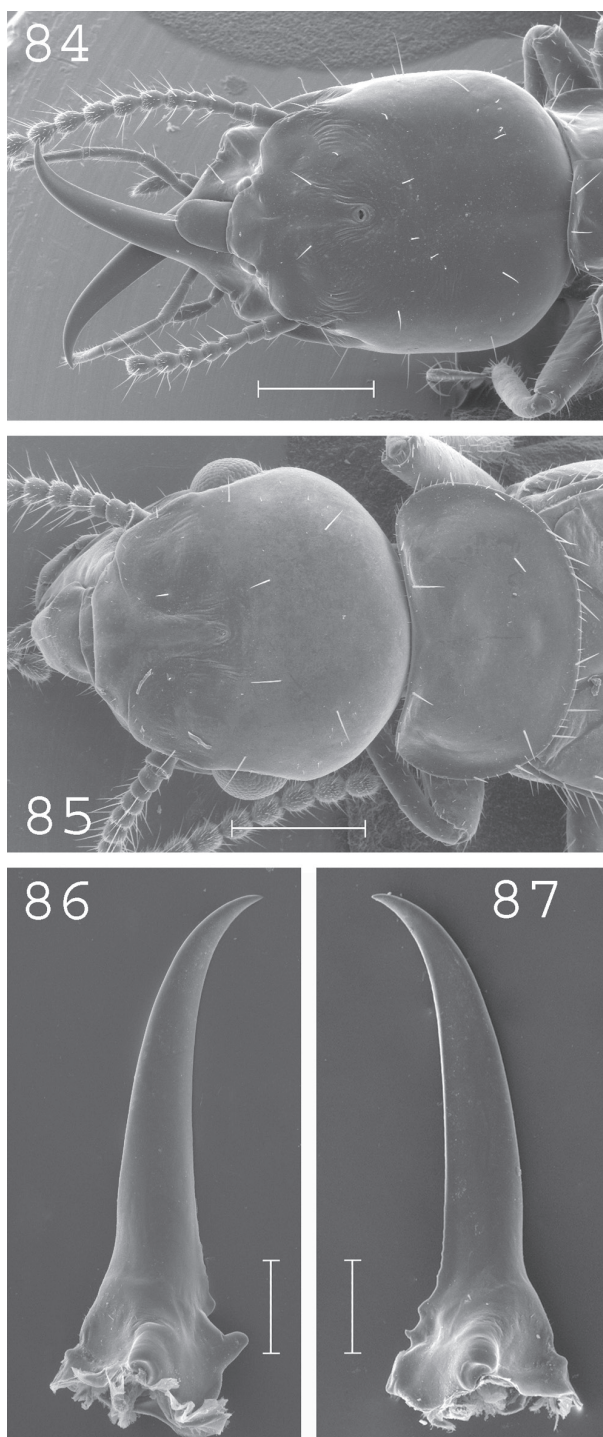
<http://species-id.net/wiki/Prorhinotermes>

*Prorhinotermes* Silvestri 1909: 286.

**Type species.** *Prorhinotermes inopinatus* Silvestri, 1909, by original designation.

**Diagnosis.** Imago head oval to circular-shaped, with ocelli located before the well developed eyes. Fontanelle situated in the middle of the head. Antenna with 19 to 22 articles. Pronotum narrower than head. Soldier head variable in shape, often larger posteriorly than anteriorly. Fontanelle narrow, placed at anterior third of the head. Frons with a groove in the middle from opening of fontanelle to clypeus. Eyes present as hyaline spots, more or less developed. Antennae with 13 to 20 articles. Pronotum generally wide. Mandibles elongated, left one with a short marginal tooth at the basis, right one without marginal teeth. Soldiers and workers very variable in size (Tho 1992).





**Figures 84–87.** *Prorhinotermes inopinatus*. Soldier: **84** head; **86** left mandible; **87** right mandible. Imago: **85** head and pronotum. Scale bars: **84**, **85**: 0.5mm; **86**, **87**: 0.2mm.

**Distribution.** *Prorhinotermes* has an insular distribution. It is found in the West Indies, Pacific islands, East Indies and islands of the Indian Ocean including Madagascar. It is not reported from continents excepted in Central America, Southern Florida and Northern Australia (Emerson 1952, Gay and Barrett 1983, Roisin et al. 2006).

***Prorhinotermes inopinatus* Silvestri, 1909**

[http://species-id.net/wiki/Prorhinotermes\\_inopinatus](http://species-id.net/wiki/Prorhinotermes_inopinatus)

Figs 84–87, 93

*Prorhinotermes inopinatus* Silvestri 1909: 287–288.

*Prorhinotermes manni* Snyder 1925: 399 (synonymized by Snyder 1949: 86).

*Prorhinotermes solomonensis* Snyder 1925: 400 (synonymized by Snyder 1949: 86).

**Material examined. Syntype: TONGA:** Niua Fo'ou (as Insulae Samoa, Ninafoon) (B. Friedländer) (AMNH). **Other material: PAPUA NEW GUINEA: Madang:** Bunapas road, 26.vi.1981 (JMP), with neotenic reproductives (#PNGT111); Road Bogia-Tangu km 10, 07.vii.1981 (JMP) (#PNGT129); Potsdam, 18.iv.1983 (YR) (#PNGT325); Nubia, 18.v.1983 (YR) (#PNGT354); Sepen No.1, 29.x.1983 (YR), with nymphs and neotenics (#PNGT426); Bunapae, 12.vi.1984 (YR) (#PNGT687); Bunapae, 23.vii.1984 (YR), with queen in dead wood (#PNGT749); Potsdam, 24.vii.1984 (YR), with neotenics (#PNGT754); Hansa point, 05.ix.1984 (YR) (#PNGT808); Tabele (Manam Is.), 19.ix.1984 (YR) (#PNGT840); Laing Island, 06.ii.1985 (JMP & YR), with alates and neotenics (#PNGT857); Nubia, 25.v.1986 (YR), two colonies, the former dissected completely, with two primary queens and one neotenic male, and nymphs (#PNGT1012, 1013); Potsdam, 03.vi.1986 (YR), two colonies, the latter with many alates (#PNGT1019, 1020); Sepen No.1, 06.vii.1986 (YR) (#PNGT1035); Nubia, 12.vii.1986 (YR), two small colonies (#PNGT1039, 1040); Road Potsdam-Makarup km?, 30.viii.1987 (YR) (#PNGT1137); Sepen No.1, 26.iv.1988 (YR), with two neotenic females (#PNGT1192); Laing Island, 12.iii.1989 (ML), in log on sea shore, with alates (#PNGT1405); Hatzfeldthafen, 20.v.1983 (YR) (#PNGT362); Tabobo, 23.ii.1983 (JMP & YR), with royal pair (#PNGT219); Yagaum Hospital, 07.ii.1983 (JMP & YR), with neotenics (#PNGT149); Yagaum Hospital, 12.iv.1983 (YR), two colonies, the former with alates (#PNGT310, 311); Yagaum Hospital, 13.v.1983 (YR) (#PNGT346); Baitabag, xi.1999 (L. Čížek) (#12, J. Šobotník's collection). **Morobe:** 21 km NW Lae, 08.xii.1962 (AE), from log on ground in lowland forest (AMNH); Lae, 11.xii.1962 (P. Aloma & AE), rather wet log on forest floor in Botanic Garden (AMNH); 5 km S Lae, 21.xii.1962 (P. Aloma), 2 samples in mangrove branches and stump in water (AMNH); 8 km NW Lae, 27.xii.1962 (AE) (AMNH); 32 km NW Lae (Markham road), 27.xii.1962 (AE), in standing dead tree on edge of *Pandanus* forest (AMNH); 32 km SW Lae, 29.xii.1962 (AE), in sago forest (AMNH); Oomsis, 24.v.1988 (YR) (#PNGT1241); **Sandaun:** Yap-

siei, 12.iii.1994 (YR & ML) (#PNGT1753); **Fly:** Tabubil, 20.v.1990 (YR & ML) (#PNGT1539); Nomad, 29.v.1990 (YR & ML), two colonies, the former with neotenics (#PNGT1608, 1612); Nomad, 01.vi.1990 (YR & ML), (#PNGT1635). **INDONESIA: Papua:** Pusppenssat-IrJa, 13–15.xi.1995 (YR), three colonies, the first two with neotenics (#IRJT16, 27, 44); Pusppenssat-IrJa, 18.xi.1995 (YR) (#IRJT76); road Nabire-Mapia km 43, 26.xi.1995 (YR) (#IRJT172); Pusppenssat-IrJa, 01.xii.1995 (YR) (#IRJT213). Kaimana, 23.xi.1995 (YR), in dead log on limestone hill (#IRJT145).

**Imago.** (Fig. 85). Head slightly rounded, covered by about 10 setae. Eyes variable in size. Pronotum with large setae mainly situated on the edges. Measurements (mm) of 12 imagoes from 2 colonies: TBL: 4.38–6.72; HLC: 1.09–1.33; HWE: 1.20–1.47; PL: 0.65–0.81; PW: 1.09–1.27; FWL: 6.67–8.42; ED: 0.24–0.37.

**Soldier.** (Figs 84, 86–87). Head slightly elongated, covered by about 15 setae. Eyes of medium size. Pronotum, mesonotum and metanotum long and wide. Abdomen covered by 6 to 12 long setae per segment. Large mandibles, slightly curved at tip. Measurements (mm) of syntype and 94 soldiers from 32 colonies (parentheses): HLC: 1.79 (1.39–1.85); HLL: 2.02 (1.65–2.16); HW: 1.10 (1.13–1.53); PL: 0.56 (0.45–0.69); PW: 1.17 (0.86–1.24); RML: 1.22 (0.95–1.40); MPW: 0.51 (0.37–0.57); T3L: 1.35 (1.02–1.48).

**Distribution.** (Fig. 93). This species occurs throughout New Guinean forests, or forested swamps (Roisin 1988b). It also occurs in Northern Australia (Gay and Barrett 1983), the Solomons, Santa Cruz, Fiji, Samoa, Ellice and Mariana Islands (Hill 1942) and Vanuatu (Roisin et al. 2011).

### Genus *Termitogeton* Desneux, 1904

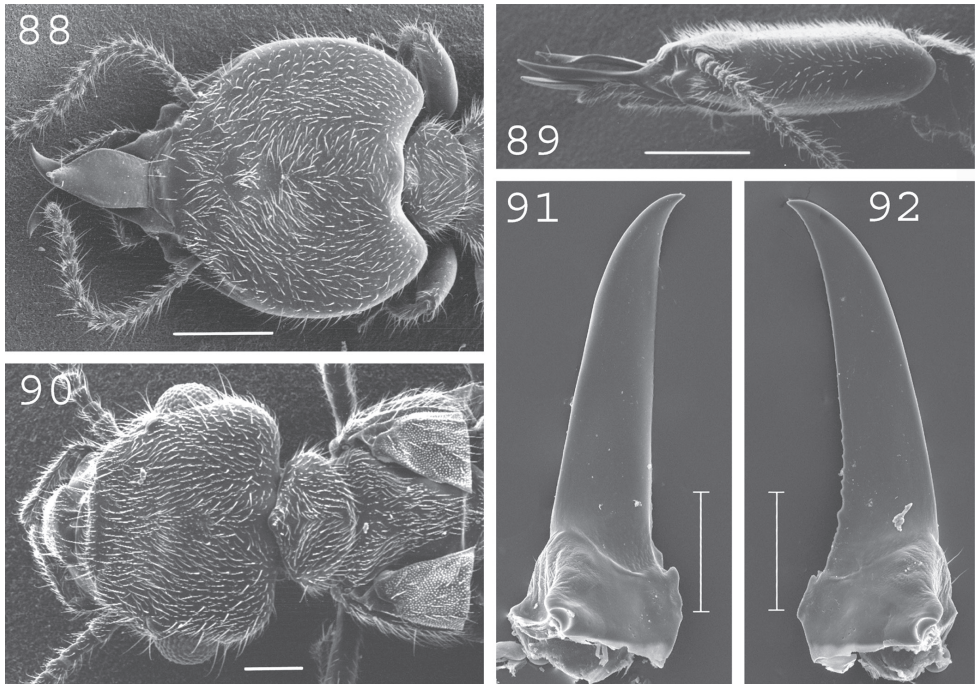
<http://species-id.net/wiki/Termitogeton>

*Termes* (*Termitogeton*) Desneux 1904a: 373–374.

*Termitogeton* Desneux. Holmgren 1911b: 75.

**Type species.** *Termes planus* Haviland, 1898, by monotypy.

**Note on type species designation.** Snyder (1949) mentioned *Termes umbilicatus* Hagen, 1858, as type species of *Termitogeton*. However, Desneux (1904a) explicitly based the original description of the subgenus *Termitogeton* on *Termes planus*. In this paper, he mentions *T. umbilicatus* only once, stating that *T. planus* “est probablement synonyme de *T. umbilicatus* Hagen”. That two species are considered probable synonyms by an author does not automatically imply that this author has no doubt about their subgeneric assignment. Consequently, *T. umbilicatus* should be considered as doubtfully included in *Termitogeton*, and ineligible for type species fixation (Art. 67.2.5 of the Code). *Termitogeton* Desneux should therefore be considered as monotypic when established, *Termes planus* becoming automatically the type species. The fact that Desneux (1904b) subsequently mentioned *T. umbilicatus* as single valid



**Figures 88–92.** *Termitogeton planus*. Soldier: **88** head and pronotum in dorsal view; **89** head in lateral view; **91** left mandible; **92** right mandible. Imago: **90** head, pro- and mesonotum. Scale bars: **88, 89:** 0.5mm; **90, 91, 92:** 0.2mm.

species of *Termes* (*Termitogeton*), with *T. planus* as a ?-marked junior synonym, is irrelevant.

**Diagnosis.** Imagoes densely hairy. Head larger posteriorly than anteriorly. Fontanelle very narrow, placed in the middle of the head. Eyes small. Antennae with 10 to 15 articles. Pronotum very small, half as broad as head. Wings without median and radial vein (Krishna 1970). Soldiers densely hairy, with characteristic heart-shaped, dorso-ventrally flattened head. Antennae generally with 13 to 15 articles. Labrum roughly triangular-shaped. Mandibles elongated, without marginal teeth. Pronotum half as broad as head.

**Distribution.** *Termitogeton* is a rainforest-dwelling wood feeder known from Sri Lanka, Borneo, Peninsular Malaysia (Tho 1992) and western New Guinea (Parmentier and Roisin 2003).

***Termitogeton planus* (Haviland, 1898)**

[http://species-id.net/wiki/Termitogeton\\_planus](http://species-id.net/wiki/Termitogeton_planus)

Figs 88–93

*Termes planus* Haviland 1898: 397.



*Termes* (*Termitogeton*) *planus* Haviland. Desneux 1904a: 373–374.

*Termitogeton planus* (Haviland). Holmgren 1911b: 75.

**Material examined. Syntypes: MALAYSIA: Sarawak:** Santubong, 16.ix.1894 (G.D. Haviland) (type No. 164, CUMZ, collection data from Harris 1966). **Other material: INDONESIA: Papua:** Puspenssat-IrJa (YR): 13.xi.1995 (#IRJT23, in large log on the ground, with alates); 14.xi.1995 (#IRJT26, in large rotten red wood log, with nymphs; #IRJT29); 16.xi.1995 (#IRJT60, small colony with queen); 25.xi.1995 (#IRJT155, 156, 157); 30.xi.1995 (#IRJT202, large colony with alates, nymphs, one neotenic reproductive, in standing dead tree, hard red wood); 01.xii.1995 (#IRJT214, with queen and neotenic reproductives; #IRJT215, 216); Road Nabire-Mapia km 43, 26.xi.1995 (YR) (#IRJT173, 174, in hard red wood). Several of the Indonesian samples mentioned above, then identified as *Termitogeton* nr. *planus*, were previously used in a study of caste patterns (Parmentier & Roisin 2003).

**Imago.** (Fig. 90). Very small. Overall body covered by many small setae. Head narrower anteriorly than posteriorly, heart-shaped. Large eyes. Ocelli in front of eyes. Antennae generally with 9 to 15 articles. Pronotum approximately half as broad as head, with a small projection forward. Measurements (mm) of 4 imagoes from the type colony and 10 imagoes from 2 colonies (parentheses): TBL: 3.23–3.94 (3.19–3.94); HLC: 0.59–0.63 (0.59–0.70); HWE: 0.82–0.85 (0.85–0.93); PL: 0.27–0.28 (0.28–0.30); PW: 0.39–0.45 (0.43–0.51); FWL: n.a. (4.93–5.23); ED: 0.14–0.18 (0.18–0.23).

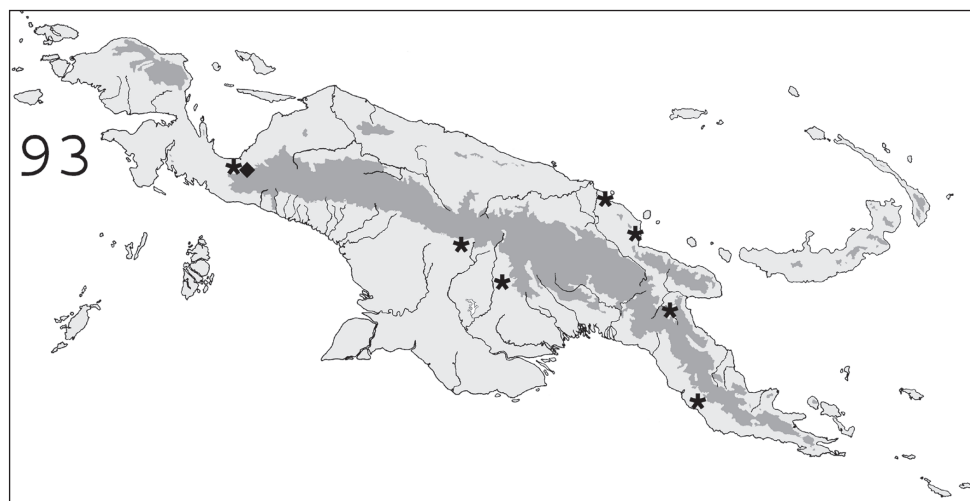
**Soldier.** (Figs 88–89, 91–92). Overall body covered by many small setae. Head heart-shaped. Labrum elongated, pointed at the tip, narrow at the basis, broadest apical one-third. Antennae with 11 to 15 articles. Pronotum half as broad as head, elongated anteriorly in the middle. Mandibles short, without marginal teeth, slightly curved at tip. Measurements (mm) 4 soldiers from the type colony and 32 soldiers from 8 colonies (parentheses): HLC: 1.16–1.27 (1.10–1.37); HW: 1.21–1.31 (1.12–1.48); PW: 0.51–0.55 (0.45–0.58); LML: 0.71–0.73 (0.75–0.86); PML: 0.87–0.94 (0.77–0.97); mPW: 0.10–0.13 (0.11–0.15); T3L: 0.58–0.62 (0.51–0.65).

**Distribution.** (Fig. 93). In New Guinea, this species was only collected in the bird's neck area (western Indonesian Papua). Originally described from from Sarawak (Haviland 1898), it is also known from Sabah (Thapa 1982) and Peninsular Malaysia (Tho 1992).

### Key to New Guinean Rhinotermitidae species, based on the soldier caste

- 1 Mandibles sabre-like, without subsidiary teeth (Figs 14–15) ..... 2
- Left and right mandibles with 2 and 1 subsidiary teeth respectively (Figs 53–54) ..... 10
- 2 Head rounded to ovoid, with broad fontanelle opening in front (Fig. 12) ..... *Coptotermes* 3





**Figure 93.** Known distribution in New Guinea of: ★ *Prorhinotermes inopinatus*; ◆ *Termitogeton planus*.

- Head of different shape, with dot-like fontanelle distant from clypeal border ..... 7
- 3 Head rounded, fontanelle well visible from above, mandibles strongly curved at tip (Figs 6, 7, 9) ..... *C. elisae*
- Soldier head of different shape, fontanelle directed forwards ..... 4
- 4 Head distinctly narrowing anteriorly (Figs 18, 22) ..... 5
- Head ovoid (Figs 12, 26) ..... 6
- 5 Small-sized soldier (HW < 1.10 mm), mandibles slightly curved (Figs 22–25) ..... *C. pamuae*
- Large-sized soldier (HW > 1.15) mm, mandibles distinctly curved (Figs 18–21) ..... *C. grandiceps*
- 6 Mandibles curved at tips (Figs 14, 15) ..... *C. remotus*
- Mandibles almost not curved at tips (Figs 28, 29) ..... *C. gambrinus*
- 7 Soldier flattened with heart-shaped head (Fig. 88) ..... *Termitogeton planus*
- Soldier not flattened, head ovoid or with parallel sides, with posterior margin not indented (Figs 32, 37, 84) ..... 8
- 8 Soldier head with sparse setae (Fig. 84) ..... *Prorhinotermes inopinatus*
- Soldier head covered by hundreds of setae (Figs 32, 37) ..... *Heterotermes* 9
- 9 Head with a small hump anteriorly (Fig. 33); labrum long and pointed, reaching well beyond half length of mandibles ..... *H. vagus*
- Head with a large hump anteriorly (Fig. 38); labrum rounded and short, ending well before half length of mandibles ..... *H. paradoxus*
- 10 Monomorphic soldiers with serrated mandible base (Figs 48, 49) ..... *Parrhinotermes* 11
- Polymorphic soldiers, mandible base not serrated ..... *Schedorhinotermes* 12
- 11 Postmentum completely covered by setae (Fig. 52) ..... *P. barbatus*

- Postmentum covered by setae only in the anterior part (Fig. 47) .... *P. browni*
- 12 Pronotum and abdomen of major soldiers with 6 setae per segment ..... *S. longirostris*
- Pronotum and abdomen of major soldiers with 10 or more setae per segment ..... 13
- 13 Major soldier head rounded, with stout mandibles (Fig. 62) .. *S. malaccensis*
- Major soldier head somewhat flattened on sides and posterior margin (Figs 56, 76)..... 14
- 14 Abdomen of major soldier with more than 20 setae per segment .. *S. seclusus*
- Abdomen of major soldier with less than 20 setae per segment... *S. translucens*

## Discussion

This study reveals that the richness of Rhinotermitidae in New Guinea is much higher than the 8 species previously recognized. Overall, we found 6 genera and 15 species, a diversity which appears slightly lower than that of neighboring areas such as Peninsular Malaysia (6 genera, 24 species (Tho 1992)), Sabah (6 genera, 19 species (Thapa 1982)) and Australia (5 genera, 23 species (Watson and Abbey 1998)). However, these richness figures deserve closer scrutiny, because several species are known only from their original description. Furthermore, the Rhinotermitidae display several characteristics predisposing them to synonymy. (i) In several genera, soldiers may be derived from a series of larval or worker instars, producing a substantial variation in size and number of antennal articles (Hanus et al. 2006). Differences are especially conspicuous between incipient and mature colonies. Therefore, these criteria, though frequently used, are of limited value for species discrimination. (ii) Wood feeders are generally good dispersers and can easily cross salt water gaps by rafting (Eggleton and Tayasu 2001). Extensive colonization of islands and large intercolonial variability favored multiple descriptions of single species under different names along their distribution range. Some pruning, as initiated by Gathorne-Hardy (2004) who placed 11 species of Rhinotermitidae from Sundaland and the western Pacific into synonymy, is clearly needed. On the other hand, the existence of cryptic species has been documented in several Rhinotermitidae (*Heterotermes*, Watson et al. 1989; *Coptotermes*, Brown et al. 1990; *Reticulitermes*, Copren et al. 2005) and Termitidae (*Macrotermes*, Bagine et al. 1994; *Cubitermes*, Roy et al. 2006), so that morphologically homogenous taxa might have to be split when submitted to detailed chemical or molecular analyses.

The distribution patterns of rhinotermitid species match those found in termitids (Roisin 1990, Roisin and Pasteels 1996, 2000, Bourguignon et al. 2008). The central mountain range constitutes a barrier for several species, as in the genus *Parrhinotermes* where *P. browni* occurs almost exclusively on the north slope, while *P. barbatus* occurs in the south. In a similar way, *Heterotermes* is completely missing in the northern part of New Guinea but is represented by two species, also present in Australia, in the south, like the nasute genus *Niuginitermes* (Roisin and Pasteels 1996). Interestingly, northern

and southern species meet in the bird's neck area, where several low valleys connect the two coasts. A second barrier shaping termite species distribution in New Guinea is the ecotone between southern Papuan savannas and the forest-covered areas to the north. Typically, the invertebrate fauna of Papuan savannas shows close affinities with that of northern Australia, whereas forested areas of New Guinea mainly harbor species with Oriental affinities (Gressitt 1982). This situation is illustrated by *Heterotermes vagus* and *Coptotermes pamuae*, which were only found in southern Papuan savannas but also occur in Australia (Hill 1942). Among the Termitidae, at least 11 species (e.g., *Amitermes arboreus*, *Nasutitermes triodiae*, *Microcerotermes taylori*, *Lophotermes aduncus*) are in this case (Roisin 1990, Miller 1994, Roisin and Pasteels 1996, 2000, Bourguignon et al. 2008). Fewer species inhabiting Papuan and northern Australian savannas penetrate deep into southern forests, but *Schedorhinotermes seclusus* and the termitid *Ephelotermes cheeli* do (Bourguignon et al 2008). *Heterotermes paradoxus* was also found in forests in the bird's neck area. East-west patterns are less conspicuous than north-south ones, but some termitid species show a longitude-restricted range: the genus *Hospitalitermes*, of clear oriental origin, was not found east of Nomad (Roisin and Pasteels 1996), whereas *Microcerotermes piliceps* is restricted to eastern Papua New Guinea and islands further east (Roisin and Pasteels 2000). Here, two species known from as far west as the Malay peninsula, *Schedorhinotermes malaccensis* and *Termitogeton planus*, were recorded only from the bird's neck area, but their eastern limits are unknown due to the near absence of termite samples from the huge area between the bird's neck region and the Papua New Guinean border (141° E meridian).

We expect the rhinotermitid diversity found in this study to reflect the overall richness of the island, although it is inevitable that some rare or locally distributed taxa escaped detection. Two regions are particularly likely to host undiscovered taxa: (i) southern Papuan savannas, in which our collecting effort was limited, possibly host additional taxa of Australian affinities; (ii) as stated above, the western half of New Guinea (Indonesian Papua) was also poorly explored and is therefore likely to conceal further taxa of Oriental origin, in the vein of *Termitogeton planus* and *Schedorhinotermes malaccensis*.

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## Appendix I

**Table I.** Situation of collecting localities in Papua New Guinea and Indonesian Papua

Locality	S	E	Altitude (m a.s.l.)
Aitape	03°08'	142°21'	
Aiyura	06°20'	145°54'	1700
Ataliklikun Bay	04°20'	151°55'	
Awar	04°08'	144°51'	
Baitabag	05°08'	145°46'	
Bogia-Tangu road km 3-5	04°17'	144°57'	
Bogia-Tangu road km 10	04°19'	144°57'	
Boisa Island	04°00'	144°58'	
Bosavi (mission)	06°25'	142°50'	600
Braham mission	05°45'	145°22'	
Brown River (bridge)	09°14'	147°12'	
Bukaua	06°44'	147°22'	
Bulolo	07°12'	146°39'	800
Bunapae	04°12'	144°41'	
Bunapas road	04°11'	144°43'-50'	
Bundi	05°44'	145°14'	1000
Busu River	06°38'	147°01'	
Coa (Kaimana airfield)	03°39'	133°41'	

Locality	S	E	Altitude (m a.s.l.)
Gilagil bridge	04°43'	145°39'	
Guam bridge	04°33'	144°58'	
Hansa Point	04°12'	144°55'	
Hatzfeldthafen (Yoro road)	04°25'	145°14'	
Kaiapit	06°16'	146°16'	
Kaimana	03°39'	133°45'	
Kaulz Creek	07°21'	146°46'	1300
Kausi-Bundi road	05°44'	145°18'	650
Kavieng	02°34'	150°48'	
Koiasi	08°54'	147°43'	
Koil Island	03°21'	144°08'	
Kokoda	08°53'	147°44'	
Kola	05°14'	151°25'	
Konos	03°07'	151°43'	
Lae	06°44'	147°00'	
Laing Island	04°10'	144°52'	
Lake Kutubu (Geseg)	06°27'	143°25'	
Lake Murray	07°02'	141°28'	
Lelet plateau	03°19'	151°55'	950
Lorengau-Yiringo road km 32	02°05'	147°09'	
Madang-Lae road km 30	05°24'	145°38'	
Mambare River	08°03'	148°02'	
Manam Island	04°02'-07'	145°00'-05'	
Manki range	07°15'	146°36'	1350
Marangis	04°01'	144°36'	
Markham River	06°36'	146°47'	
McAdam National Park	07°16'	146°38'	850
Meervlakte	03°20'	139°	
Morehead	08°33'	141°39'	
Mount Missim	07°17'	146°49'	1700
Mount Susu	07°14'	146°37'	950
Nabire-Mapia road km 43	03°29'	135°40'	250
Nabire-Mapia road km 48	03°29'	135°42'	350
Nabire-Mapia road km 62	03°31'	135°44'	300
Nomad	06°18'	142°14'	
Nubia	04°11'	144°51'	
Oomsis	06°41'	146°48'	
Pimaga	06°30'	143°31'	800
Popondetta	08°46'	148°14'	
Port Moresby	09°28'	147°12'	
Potsdam (plantation)	04°13'	144°56'	
Pusppenssat-IrJa	03°29'	135°43'	750
Sanoba	03°18'	135°34'	
Sattelberg	06°29'	149°49'	
Sepen No.1	04°11'	144°45'	
Simbang	06°35'	147°50'	
Sirasira	06°19'	146°29'	600

Locality	S	E	Altitude (m a.s.l.)
Sirinumu Dam	09°29'	147°27'	
Sogeri	09°25'	147°24'	
Subitana plantation	09°25'	147°32'	
Tabele	04°07'	145°00'	
Tabobo	05°36'	145°40'	
Tabubil	05°17'	141°14'	500
Topo	03°28'	135°35'	
Tsenap	04°16'	142°19'	
UPNG campus	09°25'	147°10'	
Usino	05°34'	145°25'	
Vanimo	02°41'	141°18'	
Varirata National Park	09°26'	147°22'	
Waima	08°38'	146°27'	
Wampit	06°44'	146°40'	
Wanuma	04°54'	145°19'	650
Warengoi	04°31'	152°21'	
Wau-Edie Creek road	07°20'	146°40'	2100
Wipim	08°47'	142°52'	
Yagaum Hospital	05°18'	145°45'	
Yapsiei	04°38'	141°06'	





# The termites of Early Eocene Cambay amber, with the earliest record of the Termitidae (Isoptera)

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**Citation:** Engel MS, Grimaldi DA, Nascimbene PC, Singh H (2011) The termites of early Eocene Cambay amber, with the earliest record of the Termitidae (Isoptera). In: Engel MS (Ed) Contributions Celebrating Kumar Krishna. ZooKeys 148: 105–123. doi: 10.3897/zookeys.148.1797

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## Abstract

The fauna of termites (Isoptera) preserved in Early Eocene amber from the Cambay Basin (Gujarat, India) are described and figured. Three new genera and four new species are recognized, all of them Neoisoptera – *Parastylotermes krishnai* Engel & Grimaldi, **sp. n.** (Stylotermitidae); *Prostylotermes kamboja* Engel & Grimaldi, **gen. et sp. n.** (Stylotermitidae?); *Zophotermes* Engel, **gen. n.**, with *Zophotermes ashoki* Engel & Singh, **sp. n.** (Rhinotermitidae: Prorhinotermitinae); and *Nanotermes isaacae* Engel & Grimaldi, **gen. et sp. n.** (Termitidae: Termitinae?). Together these species represent the earliest Tertiary records of the Neoisoptera and the oldest definitive record of Termitidae, a family that comprises >75% of the living species of Isoptera. Interestingly, the affinities of the Cambay amber termites are with largely Laurasian lineages, in this regard paralleling relationships seen between the fauna of bees and some flies. Diversity of Neoisoptera in Indian amber may reflect origin of the amber deposit in Dipterocarpaceae forests formed at or near the paleoequator.

**Keywords**

India, Tertiary, Eocene, termites, Termitidae, Rhinotermitidae, Stylotermitidae, Neoisoptera

**Dedication**

It is with great admiration that we dedicate this paper to our dear friend and colleague, Prof. Kumar Krishna, the authority on living and fossil termites. We have had the pleasure of working alongside Kumar for many years now and on numerous projects, none of which would have seen successful completion had it not been for his keen insight and global and encyclopedic knowledge of the Isoptera. Now 83, Kumar continues to be our guide through the wonders and subtle nuances of termite systematics and biology. We look forward to many more years of such pleasurable mentorship and amity.

**Introduction**

The fossil record of termites has expanded greatly during the last 10–15 years, with numerous new taxa uncovered from deposits throughout the world. Of particular importance are the plethora of new specimens in amber which, with their exceptionally high fidelity of preservation, have permitted dramatic new insights into the history of the order and its paleobiology (e.g., Engel et al. 2009). As revealed in these studies, while termites diversified in the latest Jurassic or earliest Cretaceous into numerous lineages today recognized as the various families and subfamilies (Engel et al. 2009; Ware et al. 2010), as well as several extinct stem groups, they apparently did not rise in abundance or specific diversity until the Tertiary (Engel et al. 2009). Accordingly, the Paleogene record of Isoptera has a special significance, since it provides a window into a major shift in termite evolution, specifically the origin and proliferation of the higher termites in the family Termitidae. Previously the critical windows into these epochs were the Eocene deposits of amber in the Baltic region and Paris Basin (Nel and Bourget 2006; Engel et al. 2007a; Engel 2008). The recent discovery and documentation of abundant amber from western India of Paleogene age is therefore of considerable interest, particularly as termites have been revealed as inclusions (Rust et al. 2010). Herein we provide an overview of the isopteran fauna presently known from the Early Eocene of India (Figs 1, 2), a fauna similar to that of the slightly younger Baltic amber but which most surprisingly harbors the earliest record of Termitidae (Fig. 1A). As excavations and screening of the Indian amber continue, this termite paleofauna will surely grow.

**Material and methods**

The Cambay amber deposits, their biotic diversity, and biogeographical significance were reviewed by Rust et al. (2010). Amber was collected by the authors from large

lignite mines in Gujarat State, India, during January of 2009, 2010, and 2011. Preparation of pieces followed the methods outlined in Nascimbene and Silverstein (2000). Morphological terminology and the format for the descriptions generally follows that used elsewhere for fossil termites (e.g., Krishna and Grimaldi 2000, 2003, 2009; Wappler and Engel 2003; Engel and Krishna 2007a, 2007b; Engel et al. 2007a, 2007b; Grimaldi et al. 2008; Engel and Gross 2009; Engel and Delclòs 2010). The higher classification adopted herein follows that of Engel et al. (2009). Institutional acronyms are **BSIPL**, Birbal Sahni Institute of Palaeobotany, Lucknow, India; **AMNH**, American Museum of Natural History, New York, and **SEMC**, Snow Entomological Collections, Division of Entomology, University of Kansas Natural History Museum, Lawrence.

## Systematic paleontology

### Family Stylotermitidae Holmgren & Holmgren

#### Genus *Parastylotermes* Snyder & Emerson

<http://species-id.net/wiki/Parastylotermes>

*Parastylotermes* Snyder & Emerson in Snyder 1949: 378. Type species: *Stylotermes washingtonensis* Snyder, 1931, by original designation.

**Comments.** The genus *Parastylotermes* was erected by Snyder and Emerson (*in* Snyder 1949) to accommodate two Tertiary species of Laurasian termites allied to the Recent genus *Stylotermes* Holmgren and Holmgren, from India, Bangladesh, Malaysia, and southern China (Emerson 1971; Krishna et al. *in press*). Two further species of *Parastylotermes* were subsequently added by Snyder (1955) and Pierce (1958) from Miocene deposits in southern California. Like *Stylotermes*, *Parastylotermes* has trimerous tarsi (a rare condition among the Isoptera) and similar wing pilosity (membrane largely without setae except on scale, where they are numerous and relatively long), in addition to other stylotermitid features (Emerson 1971). *Parastylotermes* differs from *Stylotermes* in the 2-2-2 tibial spur formula (vs. 3-2-2 in *Stylotermes*), M closer to CuA, and more numerous-branching CuA. The hitherto known species were *Parastylotermes robustus* (Rosen) in mid-Eocene Baltic amber (Rosen 1913; Weidner 1955; Emerson 1971; Engel et al. 2007a), *P. washingtonensis* (Snyder) from the Miocene Latah Formation of Washington (Snyder 1931), *P. frazieri* Snyder from the Miocene of Frazier Mountain, California (Snyder 1955; Emerson 1971), and *P. calico* Pierce from the Miocene nodules of the Calico Mountains, California (Pierce 1958; Emerson 1971). Remarkably, a fifth species now has been identified in the Early Eocene Cambay amber, significantly expanding the known distribution of the genus and well into the area today occupied by *Stylotermes*.

***Parastylotermes krishnai* Engel & Grimaldi, sp. n.**

urn:lsid:zoobank.org:act:9B0E707D-8F26-4FCE-A806-F708CAFD518D

[http://species-id.net/wiki/Parastylotermes\\_krishnai](http://species-id.net/wiki/Parastylotermes_krishnai)

Figs 1B, 3

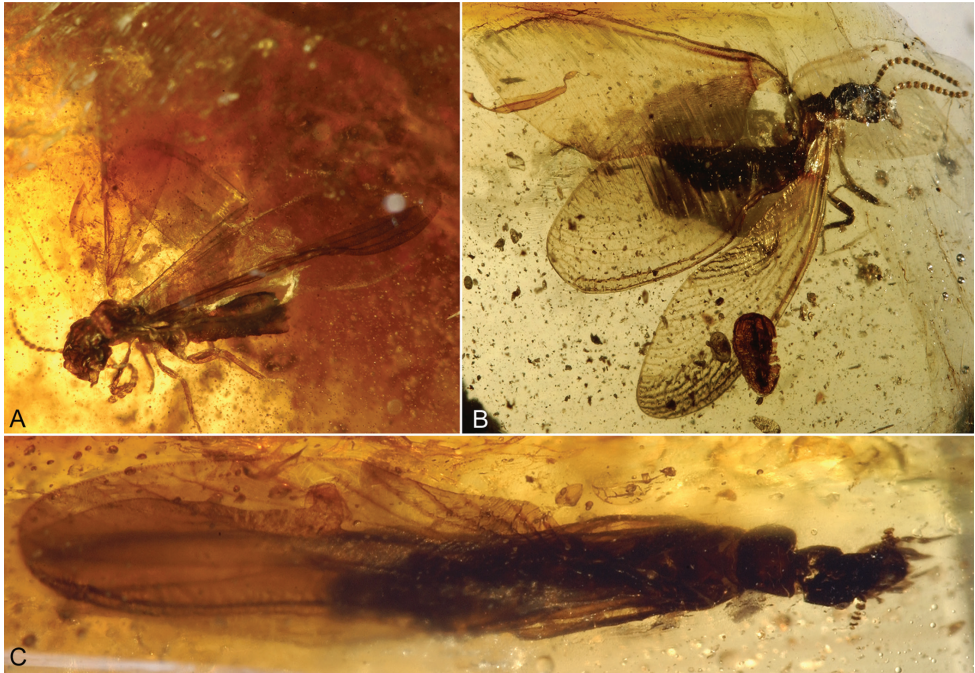
**Holotype.** Imago (sex unknown); Tad-277 (Fig. 1B), India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 17–22 January 2010 (BSIPL).

**Additional material.** Imago; Tad-96, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 7–12 January 2009 (AMNH). This specimen is a poorly preserved alate, with much of the specimen crushed and large portions of the upper body, wings, &c. missing. However, the front of the head is not deformed, with a good frontal view of the clypeus (Fig. 3B). The existing wing fragments show a venation very similar to that of the holotype, and the antenna has 14 antennomeres, as in the holotype. These features, along with the trimerous tarsi, strongly suggest that this is an additional individual of this species.

**Diagnosis.** The new species can be distinguished from all other *Parastylotermes* by the apical branching of the medial vein in the forewing (branching in the apical quarter rather than being unbranched or branched only at the extreme wing apex), less reticulation, more CuA branches (10, versus 7–8 in *P. robustus*) and by the smaller number of antennal articles (14 in the new species, 16–17 in *P. robustus*, unknown for *P. frazieri*, *P. washingtonensis*, and *P. calico*, which are just forewings preserved as compressions). In all other respects, *P. krishnai* matches the description and lectotype (*visum*) for *P. robustus* in Baltic amber except for in general metrics and some aspects of coloration (Weidner 1955; Emerson 1971; Engel et al. 2007a).

**Description.** *Imago*: Total length without wings (as preserved) ~4.0 mm; forewing length 5.7 mm, width 1.7 mm; length of forewing scale 0.8 mm; three maxillary and labial palpomeres. Integument finely imbricate throughout; head dark brown with scattered long, erect, light brown setae, short setae exceptionally sparse; antenna brown, with 14 articles, each with scattered short setae and a few long setae apically; compound eyes round, of moderate size; ocelli not visible owing to preservation of head cuticle; Y-shaped ecdysial cleavage lines and fontanelle not evident (obscured by folding of head cuticle; however, in living *Stylotermitidae* the fontanelle is exceptionally small and often not visible). Pronotum brown, with scattered, long, fine, erect setae; anterolateral angle acutely rounded, posterior lateral angles broadly rounded, with small medial emargination along anterior border. Legs brown with sparse, short setae except more numerous and stout on tibiae and tarsi; tibial spur formula 2-2-2, perhaps with a single outer spine present on protibia (difficult to discern in holotype), articulating bases of spurs oblique; tarsi trimerous, apical tarsomere longer than combined lengths of basitarsus and second tarsomere, second tarsomere projecting apically beneath base of apical tarsomere; pretarsal claws simple, arolium absent. Forewing scale large, overlapping hind wing





**Figure 1.** Photomicrographs of Cambay amber (Early Eocene) termites. **A** *Nanotermes isaacae* Engel & Grimaldi, gen. et sp. n., holotype (Termitidae: Tad-262) **B** *Parastylotermes krishnai* Engel & Grimaldi, sp. n., holotype (Stylotermitidae: Tad-277) **C** *Zophotermes ashoki* Engel & Singh, sp. n., holotype (Rhinoitermitidae: Tad-42). Not to the same scale.

scale, humeral margin faintly convex, apical margin straight, CuP (claval fissure) gently arched, meeting posterior margin of scale well before suture, scale with numerous long, erect setae, particularly along humeral margin, without short setae; C and R more darkly pigmented than remaining veins; Sc apparently short, terminating within scale; veins more separated apically than proximally; Rs unbranched, running close and parallel to costal margin, slightly more widely separated from margin apically than proximally; M about midway between R and CuA, branching twice in apical quarter of wing, reaching to wing apex, apical branches of M strongly arched posteriad, such that apices meet wing margin posterior to wing apex; CuA with 10 primary branches reaching to posterior wing margin, apical-most termination of CuA just posterior to wing apex; veins with sparse, minute setulae; membrane completely bare, between major veins reticulate and with strong, apically-slanting veinlets, particularly midway between R, M, and CuA. Hind wing scale with straight apical margin (suture). Abdomen brown to dark brown; largely crushed and obscured in holotype.

**Etymology.** The specific epithet is a patronym honoring Prof. Kumar Krishna, world authority on living and fossil termites, in recognition of his many contributions to the subject.

***Prostylotermes* Engel & Grimaldi, gen. n.**

urn:lsid:zoobank.org:act:0B6B19C4-F041-4589-A363-8E5D605C6003

<http://species-id.net/wiki/Prostylotermes>**Type species.** *Prostylotermes kamboja* Engel & Grimaldi, sp. n.

**Diagnosis.** *Imago*: Head subcircular (Figs 2A, 2B, 4A); compound eyes small, circular; ocelli apparently present, separated from compound eye by more than ocellar diameter (Fig. 4A); postclypeus short, weakly arched (Fig. 4A); antenna with 17 articles. Pronotum flat, narrower than head; tibial spurs 2-2-2; tarsi trimerous, with second tarsomere distinctly projected ventroapically, extension longer than dorsal length of second tarsomere (Fig. 4D). Forewing with scale overlapping base of hind wing scale, slightly larger than hind wing scale (Fig. 4C), scale without numerous setae over surface, with long setae along humeral margin (Fig. 4C) (other stylotermitids have numerous and relatively long setae over the entire scale surface). Cerci short, with two cercomeres (Figs 4E, 4F); styli present in male only, not extending to abdominal apex (Fig. 4F).

**Etymology.** The new genus-group name is a combination of *pro* (Greek, meaning “before”) and *Stylotermes*, type genus of the family. The name is masculine.

***Prostylotermes kamboja* Engel & Grimaldi, sp. n.**

urn:lsid:zoobank.org:act:973DA7E6-C12C-4CB2-8FBB-A61E3CFCEFB9

[http://species-id.net/wiki/Prostylotermes\\_kamboja](http://species-id.net/wiki/Prostylotermes_kamboja)

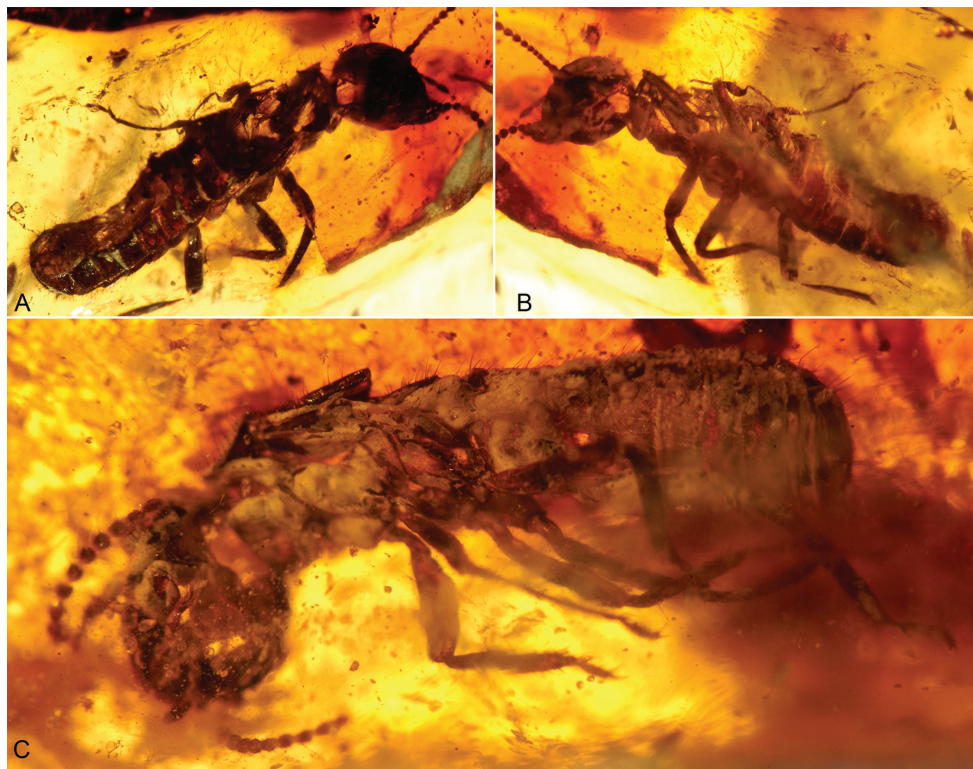
Figs 2, 4

**Holotype.** *Imago* ♀ (dealate) (Figs 2A, 2B); Tad-321C, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 17–22 January 2010 (BSIPL).

**Paratype.** *Imago* ♂ (dealate) (Fig. 2C); Tad-321C, same piece and repository as holotype.

**Diagnosis.** As for the genus (*vide supra*).

**Description.** *Imago (dealate)*: Total length of female 5.0 mm, of male 3.8 mm; body entirely dark brown, including wing scales and legs, pleural areas lighter. Head of female with length 1.10 mm; compound eye virtually round, diameter 0.25–0.28 mm; fine short pilosity on vertex; postclypeus weakly bulging, length ~0.20 mm, clypeal length ~0.30 mm; fontanelle and coronal ecdysial cleavage line (= Y-shaped suture) not observable as preserved; four maxillary palpomeres, three labial palpomeres; apex of lacinia bifid (Fig. 4B); antenna with 17 articles; flagellomeres slightly and gradually increasing in width distad, basal flagellomere ~0.65x width of apicalmost flagellomere. Pronotum not entirely observable, mostly lost in female and dorsal view obscured in male, portions preserved for female indicate it is narrower than head width. Only wing scales present (wings shed); forewing scale briefly overlapping hind wing scale (by nearly 0.3x length of hind wing scale); both scales with CuP fracture basally very broad, tapered to a point just before or at scale margin; fine setae on costal margin of forewing scale, none on broad

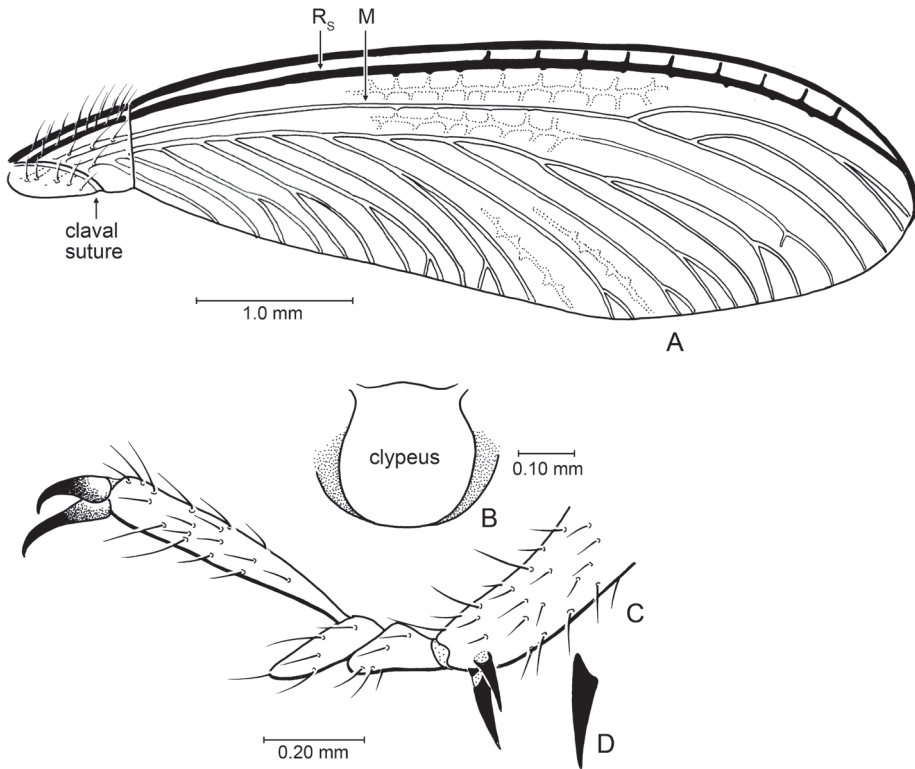


**Figure 2.** Photomicrographs of dealate male and female of *Prostylotermes kamboja* Engel & Grimaldi, gen. *et* sp. n. (Stylotermitidae: Tad-321C). **A** Dorsal view of female **B** Ventral view of female **C** Ventral view of male. Not to the same scale.

surface; some fine setae on broad surface of hind wing scale. Legs with sparse, fine setae on femora and tibiae; tibial spurs 2-2-2, without preapical dorsal spines on tibiae; tarsi trimerous, basitarsomere smallest, second tarsomere with ventroapical extension; distitarsomere 2.5x length of other tarsomeres (excluding second tarsomere extension and pretarsal claws); pretarsal claws simple, arolium absent; meso- and meta- epicoxal regions bulging, slightly explanate. Abdominal tergites and sternites well developed (meeting laterally); abdomen mildly dorsoventrally flattened; apex of abdomen (terminal sternites and tergites) broad, apical margins flattened; cerci short, with two cercomeres (apicalmost cercomere minute, sometimes separated by distinctive membrane from basal cercomeres [in female]); male with small styli; female without styli.

**Eggs:** Oocytes elliptical, with fine, microscopic chorionic structure; longer one with fine papillae over most of chorion (Fig. 4E). First oocyte length 0.75 mm, width 0.20 mm; second oocyte length 0.53 mm, width 0.20 mm.

**Etymology.** The specific epithet is treated as a noun in apposition. The name Kamboja (perhaps of Scythian origin) refers to the Indo-Iranian Kshatriya tribe (Hindu warrior elites) who appear in various ancient Indian texts such as the *Vamsa Brahmana* and the *Mahabharata*. In the second century B.C. the Kambojas invaded northern



**Figure 3.** Details of *Parastylotermes krishnai* Engel & Grimaldi, sp. n., holotype (Tad-277). **A** Forewing venation **B** Clypeus (from Tad-96) **C** Pretarsus, tarsus, and extreme apex of tibia **D** Detail of spur.

India and took control of various Indo-Aryan territories such as Gujarat, eventually settling the area and lending their name to Khambat (Cambay) and the area in which the amber harboring this species was recovered.

**Comments.** This piece preserves together two virtually complete dealate adults – one a female, the other a male – though dorsal portions of the female have been lost at the amber surface. Interestingly, two eggs are preserved at the abdominal apex of the female (Fig. 4E).

### Family Rhinotermitidae Froggatt

#### Subfamily Prorhinotermitinae Quennedey & Deligne

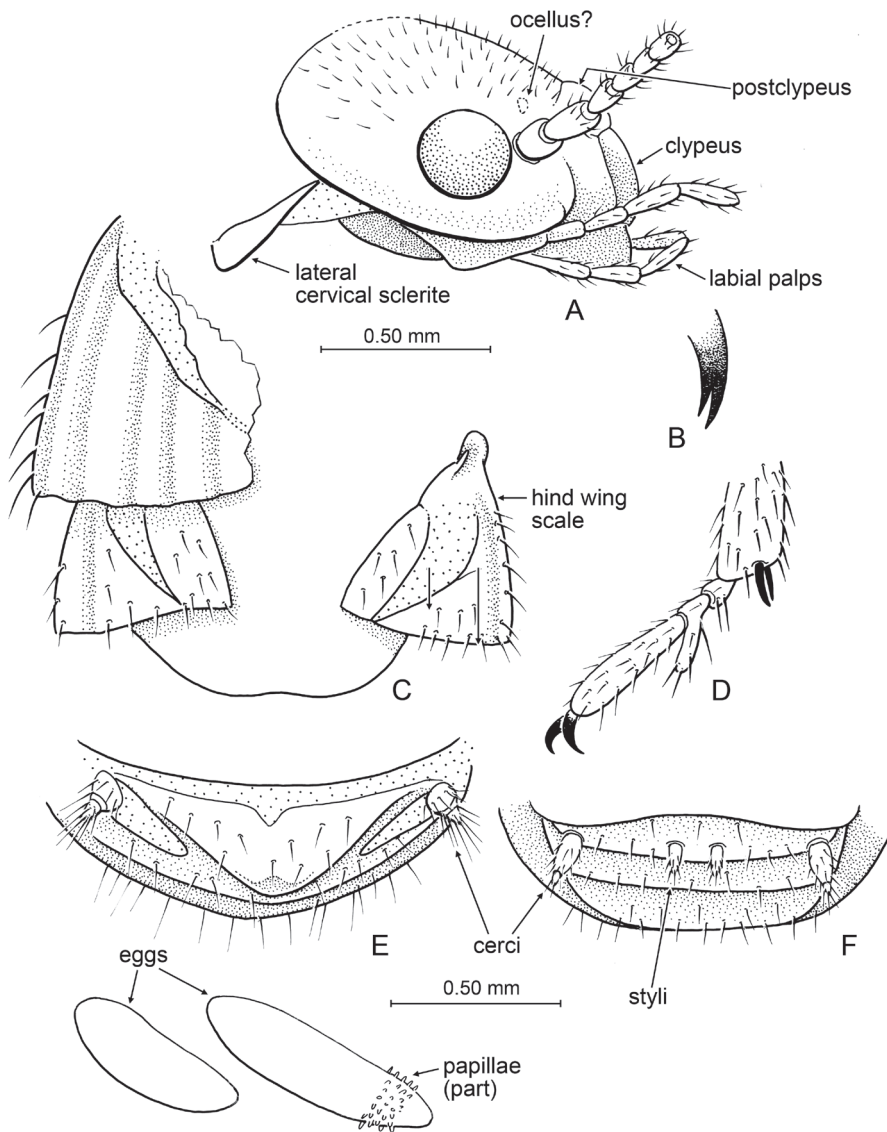
#### *Zophotermes* Engel, gen. n.

urn:lsid:zoobank.org:act:07D6FDAC-35C5-4DF8-9BD0-0939B19155C7

<http://species-id.net/wiki/Zophotermes>

**Type species.** *Zophotermes ashoki* Engel & Singh, sp. n.





**Figure 4.** Detail of *Prostylotermes kamboja* Engel & Grimaldi, gen. et sp. n. (Tad-321C). **A** Head in lateral aspect **B** Tip of lacinia **C** Dorsal view of wing scales (female specimen) **D** Meso-pretarsus, mesotarsus, and extreme apex of mesotibia (female specimen) **E** Apex of female abdomen, ventral view, with detail of eggs preserved at abdominal apex **F** Apex of male abdomen, ventral view. Scale bars are identical and apply to all figures except the detail enlargements of **B** and **D**.

**Diagnosis.** *Imago*: Head not flattened, narrow oval in shape, with sides somewhat parallel (appears similar to condition in Heterotermitinae but there is some compression which may be obscuring slightly roundish borders), posterior margin even; postclypeus without nose-like projection, without groove from fontanelle to apex of labrum, short



relative to width, somewhat arched (as in *Prorhinotermitinae*); compound eyes small; ocelli present. Pronotum flat, narrower than head, anterior margin with medial emargination (Fig. 5); tibial spurs 2-2-2 (3-2-2 in *Prorhinotermes* Silvestri, *Psammotermitinae*, and *Heterotermitinae*); tarsi tetramerous. Forewing with scale overlapping hind wing scale; M branching from CuA outside of scale (Fig. 5) (as in *Prorhinotermitinae* and *Psammotermitinae*); wing membrane with relatively few setae (as in *Prorhinotermitinae*).

**Etymology.** The new genus-group name is a combination of *zophos* (Greek, meaning, “nether world” or “gloom”), and *Termes*, type genus of the Termitidae. The name is masculine.

***Zophotermes ashoki* Engel & Singh, sp. n.**

urn:lsid:zoobank.org:act:CA5E2EBA-B8CB-4C11-83E4-B6A5B7E5C1D9

[http://species-id.net/wiki/Zophotermes\\_ashoki](http://species-id.net/wiki/Zophotermes_ashoki)

Figs 1C, 5, 6A

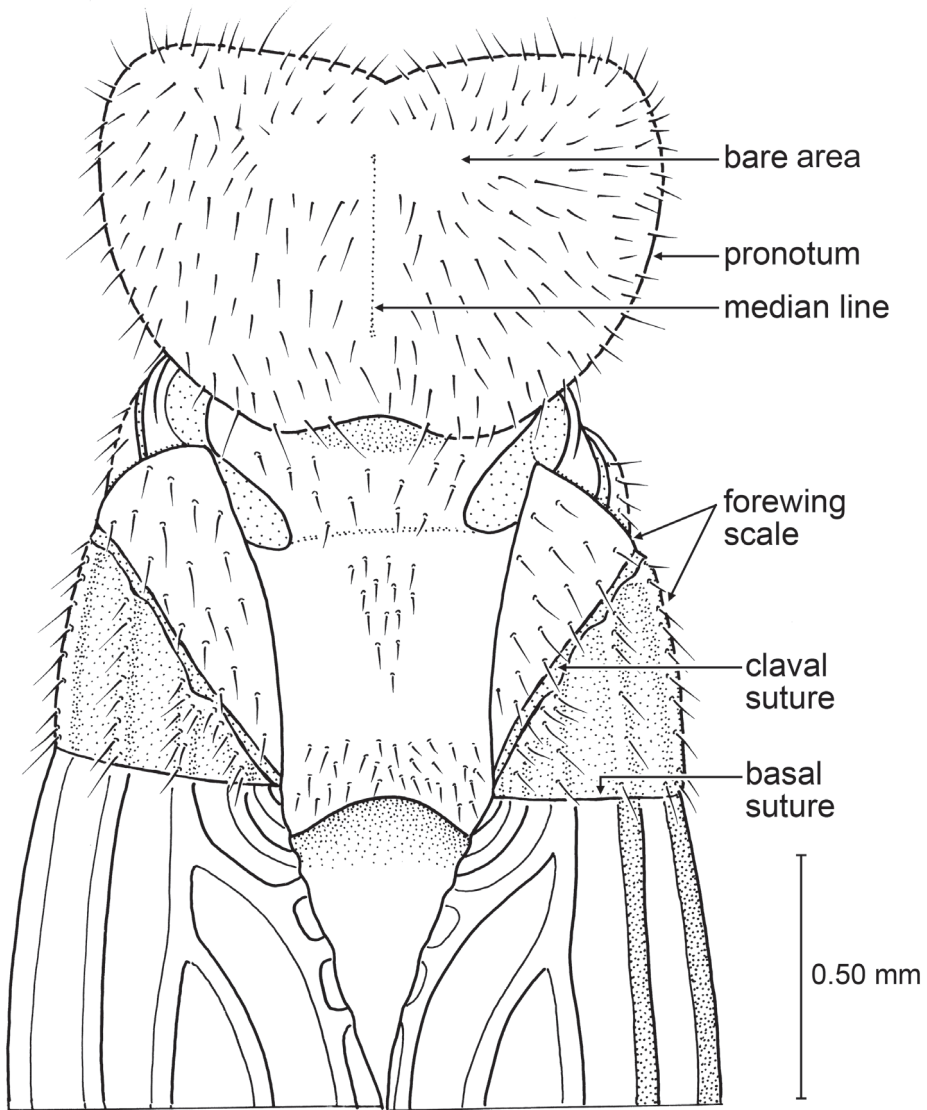
Rhinotermitidae sp.; Rust et al. 2010: 18362–18364, fig. 2G.

**Holotype.** Imago (sex unknown); Tad-42 (Fig. 1C), India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400'N, 73°4.532'E, 7–12 January 2009 (BSIPL).

**Additional material.** Imago (wings only); Tad-97, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400'N, 73°4.532'E, 7–12 January 2009 (AMNH).

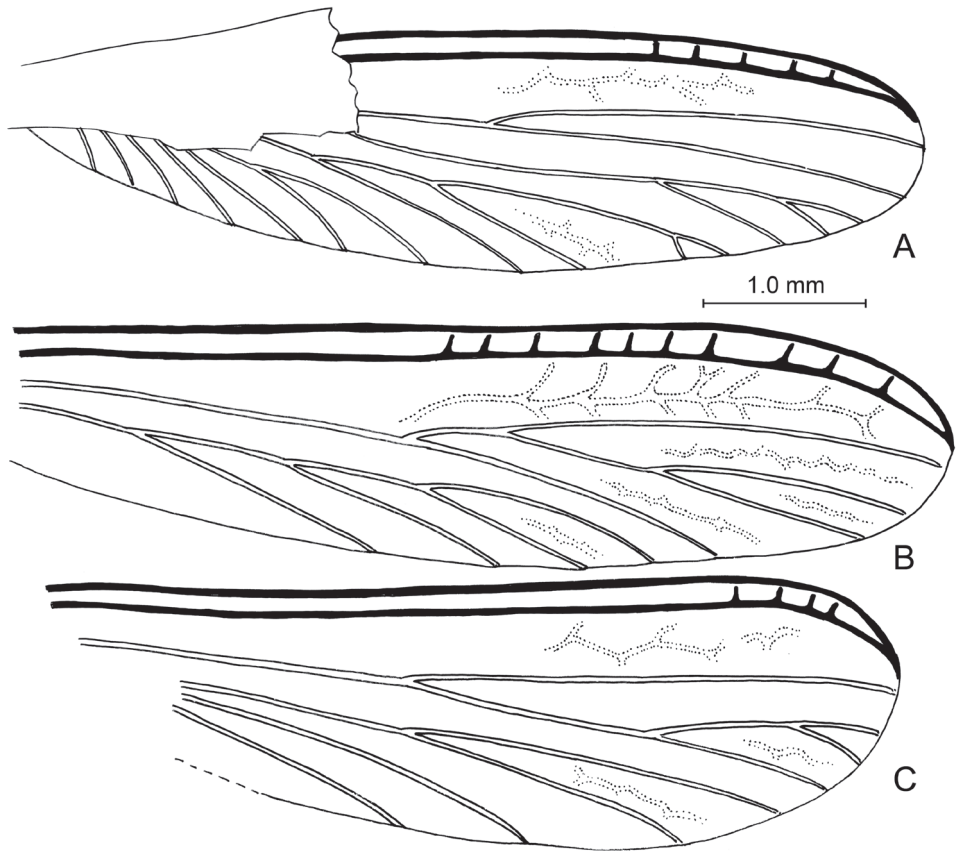
**Diagnosis.** As for the genus (*vide supra*).

**Description.** *Imago*: Total length without wings (as preserved) 4.9 mm; forewing length 6.0 mm; pronotal length (medial) 0.75 mm, width 1.20 mm; length of forewing scale 0.80 mm. Integument of head dark brown, nearly black, except antenna and mouthparts brown; pronotum and remainder of thorax dark reddish brown, legs brown; abdomen dark brown. Integument apparently finely imbricate (where evident). Head relatively large (although left side and much of vertex distorted by compression), length greater than width, lateral borders slightly convex and parallel, with scattered, erect, stout setae, such setae sparse on lateral surface behind compound eye. Compound eyes relatively small, circular, weakly exophthalmic, positioned well anterior on head, separated from posterior border of head by more than compound eye diameter. Fontanelle present, circular, located midway along tangent between middle of compound eyes. Ocelli small, semicircular, positioned anterodorsal to compound eye, separated from compound 2.5–3.0x ocellar diameter. Antenna moniliform, number of articles indeterminate owing to preservation, visible articles with moderately numerous, minute, apically-directed setae and microtrichia. Pronotum slightly wider than long, slightly broader than head, anterior margins slightly convergent mediad, apicolateral corners acutely rounded, lateral margins initially parallel in apical quarter then slightly tapering posteriorly with broadly-rounded posterior corners, medial posterior margin relatively straight; surface with numerous stout, short, suberect,



**Figure 5.** Detail of *Zophotermes ashoki* Engel and Singh, sp. n. (Tad-42), dorsal view of thorax and anterior portion of forewings (slightly reconstructed).

posteriorly-directed setae except those along anterior margins slightly more dense and directed antiad. Legs with numerous short to moderate-length setae; tibiae without distinct spines; tibial spur formula 2-2-2; tarsi tetramerous; pretarsal ungues simple; arolium absent. Forewing scale large, slightly overlapping hind wing scale; hind wing scale smaller than forewing scale; both fore and hind wing scales covered with numerous, stout, short, erect to suberect setae, such setae intermingled with longer setae, particularly apically along veins; hind wing with C+Sc+R and Rs thick, sclerotized, with ~5 short, perpendicular



**Figure 6.** Wing venation of Cambay amber species of *Zophoterme* Engel, gen. n. **A** Hind wing of *Zophoterme ashoki* Engel & Singh, sp. n. (Tad-42) **B** Forewing of *Zophoterme?* sp. (Tad-95) **C** Hind wing of *Zophoterme?* sp. (Tad-278). Scale bar applies to all figures.

crossveins connecting them in apical third; M bifurcate in apical half, originating from CuA outside of wing scale; Cu with at least five main branches, two branches with short bifurcate branches at apex; apex of Cu reaches to 0.92x length of wing; no reticulate crossveins present; membrane very finely and densely pimplate. Abdomen apparently with scattered setae similar to those on wing scales.

**Etymology.** The specific epithet is a patronym honoring Dr. Ashok Sahni, sage of Indian paleontology and wonderful colleague.

### *Zophoterme?* indeterminate

Figs 6B, 6C

**Material.** Imago (wing and fragments only); Tad-95, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 7–12

January 2009 (AMNH). Imago (wing fragment only); Tad-278, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 17–22 January 2010 (AMNH). Imago (very badly crushed and obscured); SEMC-F000157, India: Gujarat: Tadkeshwar mine, Surat District, Cambay Basin, 21°19'26"N, 73°4'32"E, 7–12 January 2009 (SEMC). Imago (head, anterior thorax, and wing bases only); Tad-304, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 17–22 January 2010 (AMNH).

**Comments.** The above four specimens are too poorly preserved to permit conclusive assignment to any particular species but for each the observable details are indicative of a prorhinotermitine and they are apparently of the genus *Zophotermes*. Most, if not all, could be conspecific with *Z. ashoki* described herein but we have hesitated to make a formal assignment as the condition of each is inadequate.

### **Rhinotermitidae indet.**

**Material.** Imago (largely crushed dealate, sex unknown); Tad-155, India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400' N, 73°4.532' E, 7–12 January 2009 (AMNH).

**Comments.** This specimen is badly damaged and while it certainly has the appearance of a *Heterotermes*, assignment as to genus, or even subfamily, cannot be made with confidence.

## **Family Termitidae Latreille**

### **Subfamily Termitinae? Latreille**

#### ***Nanotermes* Engel & Grimaldi, gen. n.**

urn:lsid:zoobank.org:act:2D8541FC-A9DD-4593-81B3-405EAE33FBDD

<http://species-id.net/wiki/Nanotermes>

**Type species.** *Nanotermes isaacae* Engel & Grimaldi, sp. n.

**Diagnosis.** *Imago*: Minute termites (ca. 2.0 mm in length excluding wings, forewing ca. 2.6 mm), with head longer than wide and sparsely setose. Labrum possibly without dark, sclerotized transverse band, relatively long; postclypeus prominent and large; fontanelle apparently obscure or obscured (owing to folding of the cuticle); antenna moniliform, with 12 articles, increasing in size apicad (apical flagellomere 2x width of basal flagellomere). Forewing scale small, not overlapping hind wing scale, with basal suture relatively straight, humeral margin straight, all veins originating within scale, CuP relatively straight and terminating before basal suture; wing membrane microtrichose, not reticulate, not infusate; Sc and R pigmented, remainder of veins faint; M and CuA become nebulous to spectral by about one-third wing length (CuA can be discerned by tilting specimen; apical two-thirds of M cannot be detected). Tibial spur formula 2-2-2; tibiae without outer spines; tarsi trimerous (similar in this

respect to *Indotermes* Roonwal and Sen-Sarma of the Apicotermatinae: *Speculitermes* Group); pretarsal claws simple, arolium absent. Pronotum wider than long, slightly narrower than head; anterior margin straight, with very faint medial notch, apico-lateral corners acutely rounded; lateral borders parallel-sided, with broadly-rounded posterior corners; posterior border relatively straight; setae nearly absent except a few along margins.

**Etymology.** The new genus-group name is a combination of *nanos* (Gr., meaning, “small”), as this is probably the smallest known alate termite, and *Termes*, type genus of the Termitidae. The name is masculine.

***Nanotermes isaacae* Engel & Grimaldi, sp. n.**

urn:lsid:zoobank.org:act:8A3AF869-D486-4A22-94A5-C8F2DDC66D5D

[http://species-id.net/wiki/Nanotermes\\_isaacae](http://species-id.net/wiki/Nanotermes_isaacae)

Figs 1A, 7

**Holotype.** Imago; Tad-262 (Fig. 1A), India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400'N, 73°4.532'E, 17–22 January 2010 (BSIPL).

**Diagnosis.** As for the genus (*vide supra*).

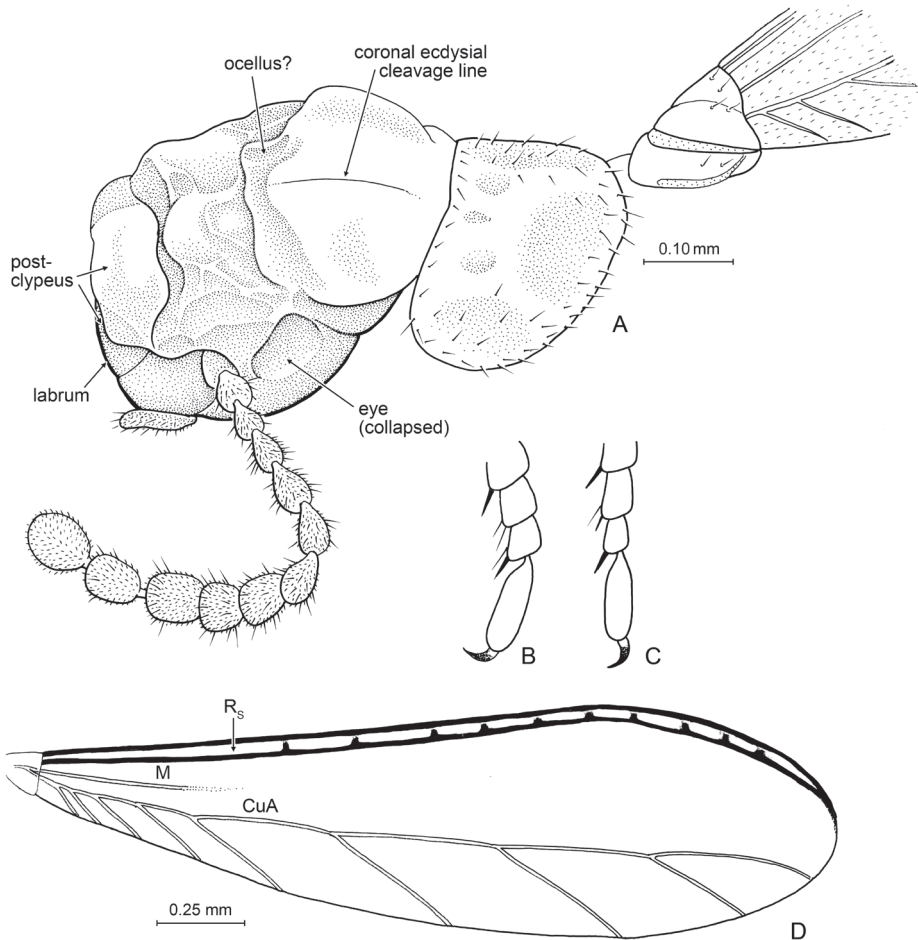
**Description.** As described for the genus with the following details: *Imago*: Total length without wings (as preserved) 2.0 mm; forewing length 2.60 mm; head length ~0.40 mm; length of head to base of clypeus 0.30 mm; clypeal medial length 0.06 mm; pronotal length (medial) 0.18 mm, width ~0.275 mm; length of forewing scale 0.15 mm. Integument of head and abdomen generally dark brown except labrum, postclypeus, and pronotum brown, antennae and legs light brown, labrum with apical margin white (as in some Nasutitermitinae). Integument (where evident) faintly imbricate to smooth. Head largely without setae except for a few laterally; forewing scale with only some sparse short setae.

**Etymology.** The specific epithet is a matronym for Ms. Charlotte Isaac, who diligently processed and screened amber, and who discovered the holotype among many other interesting inclusions.

## Discussion

Although exploration of Cambay amber remains in its initial stages it is remarkable that such an interesting diversity of termites has already been recovered, with representatives of three different families, including the earliest evidence of the Termitidae. This relative diversity of Neoisoptera may reflect the origin of the amber deposit in dipterocarp forests formed at or near the paleoequator. The species here documented show largely Laurasian connections, particularly with the mid-Eocene fauna of Baltic amber, a pattern mirrored for many other insect lineages (e.g., bees, *Pareuthychaeta* [Diptera, Diastatidae]: Engel unpubl. data; Grimaldi and Singh in press). For example,





**Figure 7.** Details of *Nanotermes isaacae* Engel & Grimaldi, gen. et sp. n. (Tad-262). **A** Head (as preserved, showing preservational distortion), pronotum, and base of right forewing **B** Protarsus, propretarsus, and extreme apex of protibia **C** Metatarsus, meta-pretarsus, and extreme apex of metatibia **D** Forewing (reconstructed from both wings). Detail enlargements in **B** and **C** not to same scale.

*Parastylotermes* is largely distributed in western North America and northern Europe. Another interesting connection is highlighted by *Zophotermes*, which has affinities to *Prorhinotermes*. The 11 species of *Prorhinotermes* are largely insular, occurring widely on tropical islands in the Old and New World except for the coasts of Central America, southern Florida, and the Cape York Peninsula (Emerson 1952; Gay and Barrett 1983). It is fascinating to note that a prorhinotermitine-like lineage would be found on the Indian subcontinent just prior to complete suturing with Asia.

*Parastylotermes krishnai* can be readily distinguished from the other species of the genus owing to the more deeply branched medial vein in the forewing and the smaller number of antennal articles. A new genus could have been established for the species but

this is presently unwarranted as the observed differences are relatively minor and, while putatively apomorphic, might render *Parastylotermes* paraphyletic. It could of course also be asked whether *Parastylotermes* is simply a stem group to *Stylotermes* and already paraphyletic with respect to the latter. While no phylogenetic analysis yet exists for the species of Stylotermitidae it would appear on the surface that *Parastylotermes* is monophyletic, or more precisely that at least *P. robustus* and *P. krishnai* are related. The fossil species from western North America are fragmentary, and their relationships are obscure. Most basal Neoisoptera have a 3-2-2 tibial spur formula and this is likely the plesiomorphic condition for this group, suggesting that the more reduced condition observed in *Parastylotermes*, i.e., 2-2-2 (loss of one of the protibial spurs), is synapomorphic for the genus, or perhaps between *Parastylotermes* and *Prostylotermes*, the latter discussed below.

*Prostylotermes kamboja* is a fascinating discovery in that it exhibits many putative plesiomorphic traits for the entire Neoisoptera clade, symplesiomorphies such as the presence of two cercomeres, styli in the male (absent in *Parastylotermes* and *Stylotermes*: Emerson 1971), and a forewing scale that briefly overlaps the hind wing scale (also present in *Parastylotermes*, forewing scale just meets hind wing scale in *Stylotermes*). However, the species simultaneously has the trimerous tarsal condition of stylotermitids, a feature so distinctive among these primitive neoisopterans. Between the two genera of Stylotermitidae, *Prostylotermes* shares the 2-2-2 tibial spur formula with *Parastylotermes* and, if this is derived within the family as discussed above, could represent a synapomorphy for these two genera. Alternatively, the 2-2-2 condition is primitive for Stylotermitidae, with modern *Stylotermes* exhibiting a reversal to the putatively primitive condition (3-2-2) for Neoisoptera. *Prostylotermes* is remarkable in that it partially “deconstructs” the stylotermitid diagnosis, in plesiomorphic features only, relative to basal Neoisoptera.

*Zophotermes ashoki* is particularly fascinating in that it agrees with *Prorhinotermitinae* in all traits except for the 2-2-2 tibial spur formula. It shares with *Prorhinotermitinae* and *Psammotermitinae* the unique branching of the forewing M from CuA outside of the scale (Fig. 5), otherwise unknown among the *Rhinotermitidae*. It lacks the flattened head or other distinctive traits of *Psammotermitinae* (*vide supra*). As noted above, the distribution of the 3-2-2 tibial spur formula across *Rhinotermitidae*, and even Neoisoptera as a whole, suggests that it is a plesiomorphic condition for these subfamilies, in which case the 2-2-2 tibial formula in *Zophotermes* is apomorphic. It is tantalizing to speculate that *Z. ashoki* lacked a true worker caste as is unique to *Prorhinotermitinae* among modern *Rhinotermitidae*.

While it is difficult to identify phylogenetic affinities of *Nanotermes* given the challenge of working solely from alates, the significance of this fossil is that it is the oldest definitive representative of the Termitidae. All previous records of Termitidae are from the Late Oligocene or younger (Nel and Paicheler 1993; Martins-Neto and Pesenti 2006; Krishna and Grimaldi 2009). *Nanotermes* thereby extends the age of this family by a further 20 million years. Given that Termitidae comprise today more than 75% of all termite species and that the family as a whole likely originated in the Paleocene, it is remarkable that this overwhelming diversity came about during the mid-Tertiary, such that relatively modern faunas were established by the earliest Miocene (Krishna

and Grimaldi 2009). Termitids apparently were rare in the Paleogene and their rise in abundance and ecological dominance likely was rapid sometime after the Early Oligocene (Engel et al. 2009). Accordingly, it would not be surprising to find Eocene or Early Oligocene termitids which cannot be confidently assigned to any particular subfamily. Indeed, subfamilial placement of *Nanotermes* is challenging and it could represent a stem-group termitid. However, given the paucity of observable features its enigmatic nature may reflect absence of data rather than truly plesiomorphic or mosaic combinations of characters removing it from modern subfamilial lineages. Regardless, *Nanotermes* can be excluded from the Macrotermitinae owing to the absence of a dark, sclerotized transverse band on the labrum and from the Termitinae owing to the 2-2-2 tibial spur formula. The dorsal surface of the head is not ideally preserved but there does not appear to be a slit-like fontanelle, and the structure may be somewhat obscured. If this is the case, then the condition would be reminiscent of Apicotermitinae. The 2-2-2 tibial spur formula is found among the Apicotermitinae, Termitinae, Syntermitinae (other taxa in these subfamilies have the plesiomorphic condition of 3-2-2 which is universal in Macrotermitinae, Foraminitermitinae, Sphaerotermitinae, and Cubitermitinae), and universally in the Nasutitermitinae. Among the subfamilies in which the 2-2-2 condition may be found only the *Amitermes* Group (Termitinae, formerly Amitermitinae) and Nasutitermitinae have the reduced number of antennal articles as low as that observed for *Nanotermes*, although some Syntermitinae come close with 13 antennal articles. Syntermitinae have a relatively large fontanelle which, despite the distortion to the head, would presumably be apparent. Similarly, there does not appear to be a slit-like fontanelle present on *Nanotermes* either, which would, in combination with a postclypeus that is arched and relatively long (length about one-half width) seems to exclude an assignment to Nasutitermitinae. It seems most likely that *Nanotermes* is a termitine and perhaps allied to the *Amitermes* group of genera, although definitive attribution must remain for the time being uncertain. Certainly the trimerous tarsi are unique among all of these lineages but are perhaps not surprising for such a diminutive species.

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# A new genus and species of mandibulate nasute termite (Isoptera, Termitidae, Syntermitinae) from Brazil

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## Abstract

*Acangaobitermes krishnai* **gen. et sp. n.**, is described here, based on soldiers and workers collected in Brazil. Some characteristics suggest a close kinship with *Noirotitermes* Cancelló & Myles, and both genera share the following traits absent in all other Syntermitinae: the microsculpturing on the soldier head capsule surface with internal granulations; the piercing mandibles with a single very reduced marginal tooth and the worker very similar in both genera. The most conspicuous differences between *Acangaobitermes* and *Noirotitermes* are the shape of the soldier head, the frontal tube and pronotum. The shape of the soldier head in *Noirotitermes* is unusual, with a very broad and short frontal tube, four conspicuous protuberances like sharp corners at the rear, while in the new genus the posterior contour of the head is devoid of these protuberances. The frontal tube of *Acangaobitermes* is elongate and conical, while in *Noirotitermes* it is short and very broad. The pronotum of *Acangaobitermes* is saddle-shaped as is usual in other Syntermitinae, while it is aberrant in *Noirotitermes*.

## Keywords

Termite, *Acangaobitermes*, Syntermitinae, taxonomy

## Introduction

The “mandibulate nasutes” comprise a group of termite genera endemic to the Neotropical region. Fourteen genera are recognized within this group (*Armitermes* Wasmann, *Cahuallitermes* Constantino, *Cornitermes* Wasmann, *Curvitermes* Holmgren, *Cyrtillitermes* Fontes, *Embiratermes* Fontes, *Ibitermes* Fontes, *Labiatermes* Holmgren, *Macuxitermes* Cancellato and Bandeira, *Noirotitermes* Cancellato and Myles, *Paracurvitermes* Constantino and Carvalho, *Procornitermes* Emerson, *Rhynchotermes* Holmgren and *Syntermes* Holmgren), ranging from south of Mexico (*Cahuallitermes*) to northern Argentina (*Procornitermes*, *Syntermes*). The group is morphologically characterized by having soldiers with a large frontal gland opening, situated at the frontal tube apex, and functional mandibles.

In the past, the mandibulate nasutes were considered an ancestral group of Nasutitermitinae but recent studies highlighted an evolutionary history independent of true nasutes (Noirot 2001, Ohkuma et al. 2004, Inward et al. 2007). Engel and Krishna (2004) proposed Syntermitinae as a subfamily of Termitidae including four of the thirteen genera of mandibulate nasutes, and they affirm that the other mandibulate genera of Nasutitermitinae “may eventually be included” in the subfamily.

In this work we describe a new monotypic termite genus that seems to be closely related to *Noirotitermes*. Both genera share traits absent in all other Syntermitinae: the microsculpturing on the soldier head capsule surface with internal granulations; the piercing mandibles upturned, with a single reduced marginal tooth; and the worker almost identical in both genera.

## Materials and methods

The studied samples, including the holotype and paratypes, are in the Museum of Zoology of the University of São Paulo, São Paulo, Brazil (MZUSP). All comparisons with other syntermitine genera were based on data from taxonomic reviews or original descriptions [*Armitermes* (Rocha 2011), *Cahuallitermes* (Constantino 1994), *Labiatermes* (Constantino et al., 2006), *Macuxitermes* (Cancellato and Bandeira 1992, Constantino 1997), *Noirotitermes* (Cancellato and Myles 2000), *Paracurvitermes* (Constantino and Carvalho 2011) and *Syntermes* (Constantino 1995)] and examination of material in the MZUSP collection, that has specimens of all type species of syntermitine genera.

Terms used for pilosity are comparative: bristles are long erect setae with well-marked bases; hairs are shorter than bristles, less rigid and with inconspicuous bases; microscopic hairs are very short and visible only under at least 50 × magnification (not illustrated in the figures). Gut terminology follows Noirot (2001).

The morphometric characters used here and their correspondence with Roonwal's system (Roonwal 1970) are indicated in parentheses as follows: length of head capsule, LH (9); width of head capsule, WH (18); length of frontal tube, LFT (28); length of left hind tibia, LT (85). All measurements were taken with a micrometric reticle.

Line drawings were made with a camera lucida, soldier photographs were obtained with a digital camera coupled to a stereomicroscope Leica M205C, and images of different depth of focus were further processed and merged with software. Worker mandibles were dissected and prepared for scanning electron microscopy. The worker enteric valve was mounted on Entellan (Merck) and photographed under an optic microscope. Scales are indicated in each illustration.

## Taxonomic treatment

### *Acangaobitermes* gen. n.

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<http://species-id.net/wiki/Acangaobitermes>

**Type species.** *Acangaobitermes krishnai* sp. n.

**Etymology.** From Tupi, indigenous South American language, *acangaobi* meaning funneled head and the Latin *termes* meaning termite, in reference to soldier head capsule shape in profile. The name is masculine.

**Description. Imago.** Unknown.

**Soldier.** Monomorphic. Head capsule sub-quadrangular with almost parallel lateral margins and two very discrete saliencies on the latero-posterior corners (Fig. 7, arrows). Surface of head capsule covered with numerous minute and closely set points of about equal diameter, forming a conspicuous and characteristic microsculpture (Figs 7–8). Frontal tube conical and upturned, in profile, apex with a relatively wide aperture surrounded by a white membrane. Antennae with 14 articles. Piercing slender mandibles; blade strongly curved inwards and upturned; a very small tooth at the base of the blade and a molar plate/prominence fully developed with no ridges. Clypeus very reduced. Labrum with a rounded and flat hyaline tip. Posmentum sub-rectangular with antero-lateral margins slightly concave. Coxae with a keel shape projection, pointing outwards and situated at distal antero-lateral margins (Fig. 2, arrow). Tibial spurs 2:2:2.

**Worker.** Monomorphic. Head capsule rounded. Postclypeus inflated. Antennae with 14 articles. Left mandible (Fig. 3): apical tooth larger than M1+2, margin between M1+2 and M3 sinuate, M3 distinct and smaller than M1+2, molar tooth conspicuous, partially hidden by molar prominence; molar prominence concave without ridges. Right mandible (Figs 3, 5): apical tooth larger than marginal teeth, M1 and M2 clearly distinct, molar plate concave without ridges (Fig. 5). Coxae smooth without projections. Body slender and elongated, digestive tube visible through abdominal sclerites. Tibial spurs 2:2:2.

Worker digestive tube. Crop asymmetrical, without any constriction separating it from gizzard. Cuticular armature of gizzard with 24 visible folds, six of first order, six of second and 12 of third; ratio between columnar and pulvillar belt approximately equal to one; pulvilli without armature or ornamentation. Mesenteron tubular. Short mixed seg-

ment present. Mesenteric tongue on the external side of the mesenteric arch, slightly strangled proximally. Two pairs of Malpighian tubules attached at the mesenteron-proctodeum junction, one internal side to the mesenteric arch and the other external. First proctodeal segment (P1), diagonal to body axis, more enlarged than mesenteron with about same size of proximal portion of paunch (P3a); distal end of P1 narrowed, forming a short neck prior to the attachment to P3. Enteric valve (P2) at the left side of the body. P3 slightly constricted between P3a and P3b. Dorsal torsion well-developed. P3 joined to colon (P4) on left side, isthmus short and parallel to body length. P4a dilated, U-Turn and P4b tubular.

### Comparisons with other genera of Syntermitinae

Soldiers of *Syntermes*, *Cornitermes*, *Labiatermes*, and *Procornitermes* have a short frontal tube, not exceeding the labrum; a well-developed hyaline tip to the labrum; straighter cutting mandibles, with well-developed marginal teeth; and a larger body size. Soldiers of *Cahuallitermes* have straighter cutting mandibles, with well-developed marginal teeth; a well-developed hyaline tip to the labrum; and a larger body size. Soldiers of *Embiratermes* and *Ibitermes* have a larger body size, straighter and large mandibles, with well-developed marginal teeth in *Embiratermes* or totally absent in *Ibitermes*. Soldiers of *Cyrelliatermes* and *Curvitermes* have aberrant mandibles, with a molar plate, molar prominence and marginal teeth very similar to their corresponding worker mandibles; apical tooth fish-hooked in *Curvitermes*, reduced in *Cyrelliatermes*; and the frontal tube cylindrical and elongate in *Cyrelliatermes* (see more details of these two genera, including the dissected soldier mandibles, in Mathews 1997, page 226). *Paracurvitermes* has a broader head capsule with well developed conical and shorter frontal tube than *Acangaobitermes*; the mandibles are much longer, less curved with triangular teeth, very different from the new genus. The soldiers of *Rynchotermes* have strongly curved mandibles; a very long frontal tube; procoxae with a spine-like lateral projection; and a much larger body size. Soldiers of *Armitermes* have the pronotum, mesonotum, and metanotum with serrate lateral margins; mandibles with well-developed marginal teeth; and a larger body size (see Rocha, 2011, for a redescription and new illustrations of the genus). Lastly, the genus *Macuxitermes* has dimorphic soldiers, with an aberrant head shape; pronotum, mesonotum and metanotum with serrate lateral margins; and mandibles with well-developed marginal teeth.

Despite differences in the shape of the soldier head, *Acangaobitermes* shares many exclusive traits with *Noirotitermes*. The worker of *Acangaobitermes* is very similar to that of *Noirotitermes*, with same mandibular pattern, body size and shape (elongate), labrum and digestive tract, including the enteric valve armature. The worker differences between both genera are: the inner margin of apical teeth in left and right mandibles are much more concave in *Noirotitermes* than in the new genus; the M3 in left mandible and M2 in right mandible both are larger in *Acangaobitermes* than in *Noirotitermes*; and the insertion of the enteric valve is in the body axis, while in *Noirotitermes* it is perpendicular to the body axis.



The soldiers of both species have the same microsculpturing on the head capsule surface and the internal granulations (Fig. 8), that are otherwise absent in all other species of Syntermitinae. The piercing, upturned mandibles, with a single marginal tooth reduced are nearly identical in both genera, while in all other Syntermitinae the marginal teeth are well-developed (or completely absent in *Ibitermes*). The two occipital salencies are present in both genera and in *Macuxitermes*, but are much more discrete in *Acangaobitermes* (Fig. 7, arrows).

The most conspicuous differences between the new genus and *Noirotitermes* are the shapes of the soldier head and pronotum. The pronotum is aberrant in *Noirotitermes* and saddle-shaped in *Acangaobitermes*, as is usual for other Syntermitinae. The shape of the soldier head in *Noirotitermes* is unusual, with a very broad frontal tube and two protuberances like sharp corners at the rear, while in the new genus the frontal tube is elongate and conical, similar to *Armitermes*, and the posterior rear part of the head is devoid of conspicuous projections.

***Acangaobitermes krishnai* sp. n.**

urn:lsid:zoobank.org:act:D82B4A68-0687-45E3-8275-AA24B9D4BFF3

[http://species-id.net/wiki/Acangaobitermes\\_krishnai](http://species-id.net/wiki/Acangaobitermes_krishnai)

Figs 1–9

**Holotype.** Soldier. Part of the lot MZUSP 13167, labeled “Parque Nac. Emas, GO, 22.iv.2004. Ninho 212, D. Costa col.” Kept separately in the same vial with paratypes.

**Type-locality.** BRAZIL. Goiás: Parque Nacional das Emas (18°01.49'S; 52°57.87'W, 850 m).

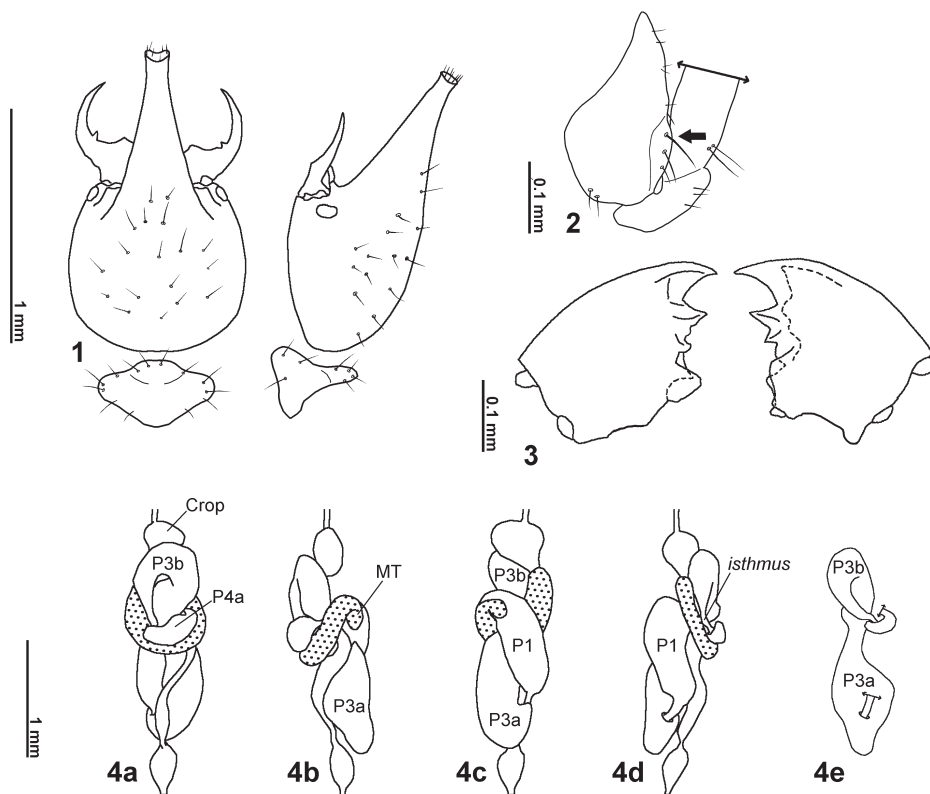
**Paratypes.** Soldiers and workers of MZUSP 13167 with same data as holotype. Goiás: Parque Estadual da Serra de Caldas Novas (17°44.7'S; 48°37.5'W, 1000 m), 23.iii.2008, D. E. Oliveira coll. (MZUSP 13168). Minas Gerais: Serra de São José (21°4.98'S; 44°10.02'W, 1250m), 11.iv.2007, E.M. Cancelló coll. (MZUSP 11956). Rondônia: UHE Santo Antônio (8°50.63'S; 64°3.75'W, 100 m), 22.ix.2010, T. Carrijo & R. Santos coll. (MZUSP 13670).

**Diagnosis.** As for the genus (*vide supra*).

**Etymology.** Named in honor of Dr Kumar Krishna, for his important contributions to termite taxonomy.

**Description. Imago.** Unknown.

**Soldier.** Shape of head, frontal tube, labrum, mandibles, pronotum under generic description. Antennae with 14 articles, 2nd half size of 1st, 3rd half of 2nd, 4th half of 3rd, 5th twice the size of 4th, subsequent articles sub-equal and similar to third. Scattered bristles, short hairs and microscopic hairs on top and lateral sides of head capsule, few bristles at rear portion. Frontal tube with microscopic hairs along its length and hairs around aperture of frontal tube. Pronotum with bristles on margins, plus two pairs of bristles at middle of anterior lobe. Mesonotum and metanotum with a row of bristles on posterior margins. Abdominal tergites and sternites with short hairs over

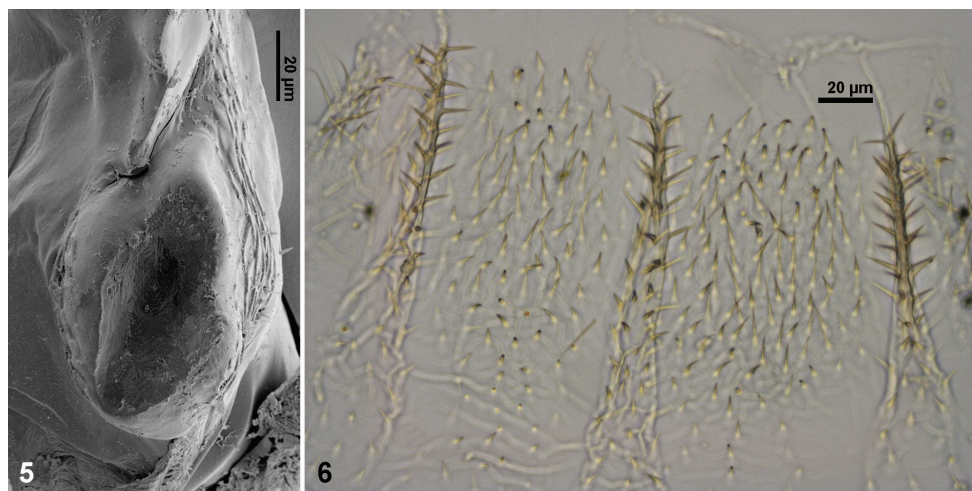


**Figures 1–4.** *Acangaobitermes krishnai* gen. et sp. n. **1** soldier head and pronotum in dorsal and profile view **2** soldier coxa in frontal view (arrow: keel shape projection) **3** worker mandibles **4** worker digestive tube *in situ*, a: dorsal view, b: right view, c: ventral view, d: left view and e: paunch in left view. MT= Mesenteric tongue; P1= first proctodeal segment (ileum); P3a and b = third proctodeal segment (paunch); P4a= first part of fourth proctodeal segment (colon).

surfaces and bristles on posterior margins. Head orange, mandibles ferruginous, body pale-yellow. Measurements, in millimeters, of four soldiers including the holotype: LH: 1.26–1.52; WH: 0.62–0.70; LFT: 0.56–0.74; LT: 0.64–0.66.

**Worker.** External morphology under generic description. Head capsule with scattered bristles, antennae with some short hairs and sparse bristles, pronotum with bristles on margins and over surface of anterior lobe, mesonotum and metanotum with bristles on posterior margins. Abdominal tergites and sternites with short hairs over surfaces and bristles on posterior margins.

Digestive tube (Figs 4a–4e, 6). Coiling gut pattern and gizzard armature under generic description (Fig. 6) with three longitudinal equidistant cushions covered with strong and erect spines oriented perpendicular to gut contents flow,



**Figures 5–6.** *Acangaobitermes krishnai* gen. et sp. n. **5** worker molar plate **6** enteric valve armature.

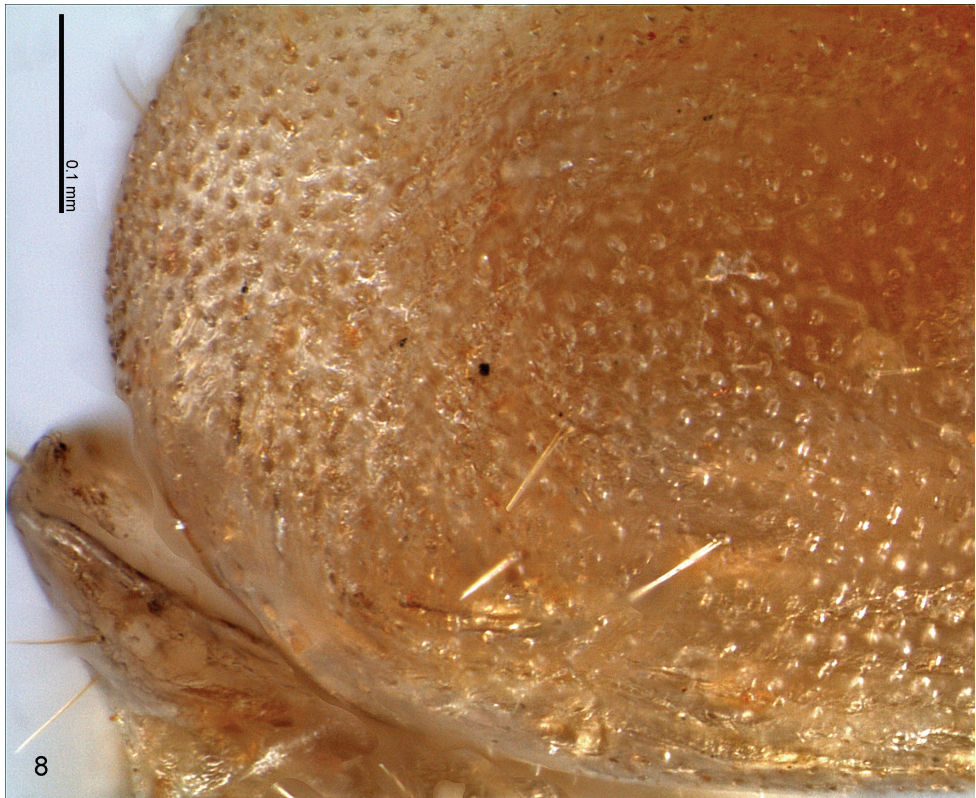


**Figure 7.** *Acangaobitermes krishnai* gen. et sp. n. Soldier head in dorsal view (Arrows: saliencies on latero-posterior margins).

among the cushions minor spines settled at different orientations. P3 internally ornamented with long cuticular filaments (as described in Noirot 2001).

**Biology.** All the samples were collected in the soil or in nests of *Cornitermes cumulans* (Kollar) and *Armitermes euamignathus* Silvestri, in areas of openformation. The



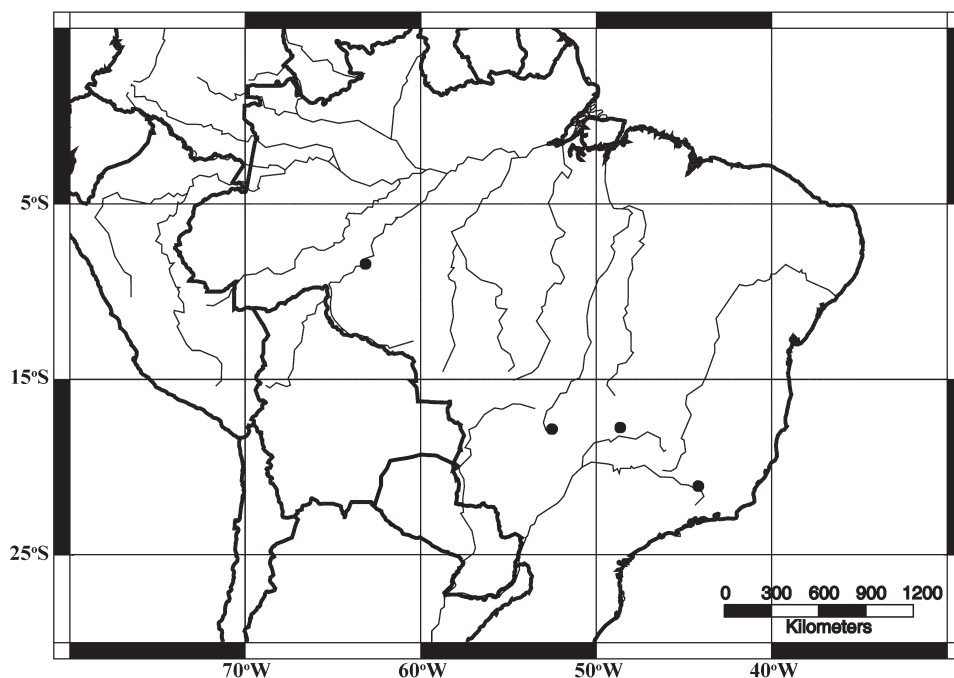


**Figure 8.** *Acangaobitermes krishnai* gen. et sp. n. Detail of the microsculpture of the soldier head capsule.

specimens from state of Goiás are collected in a Cerrado formation. From the state of Rondônia in a border line between primary forest and pasture. From Minas Gerais state in a “Campo rupestre”, a characteristic altitudinal field, with granitic outcrops and composed by xeric vegetation.

## Discussion

Relationships among the mandibulate nasute genera are not yet clear, despite considerable evidence that they are a monophyletic group (e.g., Inward et al., 2007). Rocha (2011) conducted a taxonomic revision and a phylogenetic analysis of the genus *Armitermes*, including all type species of the genera of Syntermitinae. This analysis supports the hypothesis that *Macuxitermes*, *Acangaobitermes*, and *Noirotitermes* form a monophyletic group and that the last two are most closely related, with the occipital salencies and the type of folds and their arrangement on the enteric valve as synapomorphies for the three genera.



**Figure 9.** Geographic distribution of *Acangaobitermes krishnai*, gen. et sp. n.

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# Taxonomic Notes on *Nasutitermes* and *Bulbitermes* (Termitidae, Nasutitermitinae) from the Sunda region of Southeast Asia based on morphological and molecular characters

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## Abstract

The Sunda region of Southeastern Asia is rich in termite fauna, but termites from this region have been poorly described. In this study, we described eight species from two diverse genera from this region, and from the family Termitidae. We describe *Bulbitermes* 4 spp. and *Nasutitermes* 4 spp. from new field collections. Where possible we examine original holotype specimens, and describe the essential morphological characters for soldier and worker castes. We devise two new bifurcating keys to guide the field identification of each species. In addition, we develop a nucleotide sequence profile for the COI gene. From this molecular character matrix, we use Neighbour-Joining analysis to test the monophyly of each morphospecies and genus. We find that the morphological and molecular characters are highly concordant, whereby all taxa appear to represent distinct molecular clades. For termites, there is therefore agreement between the morphological taxonomic characters used to sort species from a bifurcating key and the molecular taxonomic characters used to sort species on a bifurcating tree. This joint analysis suggests that DNA barcoding holds considerable promise for termite taxonomy, especially for diverse clades like *Bulbitermes* and *Nasutitermes* for which a global morphological key would be intractable.

## Keywords

Isoptera, Southeast Asia, morphological key, DNA barcodes, barcode gap

## Introduction

As the largest subfamily among the higher termites (Family Termitidae), the Nasutitermitinae include more than 650 species from over 80 genera (Kambhampati and Eggleton 2000). This diversity within a single subfamily creates some taxonomic challenges for delineating between species and among genera, and there are presumably additional taxa not yet described. In this study we describe representative taxa from two of the largest genera within Nasutitermitinae, *Nasutitermes* (4 spp.) and *Bulbitermes* (4 spp.), as represented from newly collected material from the Sunda region of Southeast Asia.

Globally, the Nasutitermitinae have a broad dispersion. Genera from this subfamily are present in all biogeographical regions except the palearctic (Pearce and Waite 1994), and include at least 16 genera that are endemic to Southeast Asia (Tho 1992). Relative to other biogeographic regions, the taxonomy of Nasutitermitinae in Southeast Asia remains poorly understood (Chhotani 1987, 1997; Gathorne-Hardy 2001). This may stem in part from the historically poor taxon sampling from within this region (Eggleton 1999), but may also stem from a lack of diagnostic characters that clearly distinguish some of the genera.

This lack of morphological variation also hinders phylogeny. One outstanding question is the affinity between *Nasutitermes* and *Bulbitermes* (Collins 1989; Jones and Brendell 1998; Tho 1992; Gathorne-Hardy 2001). Are these genera phylogenetically distinct, or do they represent a synonymy that should be re-classified? *Bulbitermes* was separated from *Nasutitermes* by Emerson (in Snyder 1949). However, this distinction is based mostly on negative criteria – for example, *Bulbitermes* is a wood-feeding nasute genus that has constrictions behind the antennal sockets on the soldiers and that is not *Longipeditermes*, *Lacessitermes*, *Hospitalitermes* or *Ceylonitermes* (Gathorne-Hardy 2001). For this reason, *Nasutitermes* and *Bulbitermes* remain poorly distinguished based on morphology, and these genera may even be paraphyletic.

In this report we present the taxonomic notes for representative *Bulbitermes* and *Nasutitermes* species collected from Sumatra and Malay Peninsula (i.e., the Sunda region) within Southeast Asia. Specifically, we use morphological characters to describe eight species, and devise a key for their field identification. Further, we use molecular sequence information from the mitochondrial gene ‘barcode’ region to test the idea that *Bulbitermes* and *Nasutitermes* each form monophyletic and evolutionarily distinct genera.

## Materials and methods

### Collection procedure

All specimens were collected from the field using a mix of random and systematic transect searches. For transect sampling we adopted a standardized protocol (Jones and Eggleton 2000). We laid straight belt-transects (100 × 2 m) at random through the forest. Each transect was divided into 20 five-meter sections, and each section was searched

by one person for one hour. For each section, 12 samples of surface soil with associated leaf litter and woody debris were scraped up and carefully examined for termites (approximate size of surface sample,  $50\text{ cm}^2 \times 5\text{ cm}$  deep). Finally, tree trunks and buttress roots were also examined for the presence of termites. Particular attention was paid to the deep accumulations of litter and organic-rich soil between buttresses. Also, any carton sheeting or runways suggesting the presence of live termites were examined, up to a height of two meters. For random sampling, we simply used our best judgment to search for termites within the above types of habitat, but without the use of transects. Wherever possible, all castes and both sexes were sampled. In total, termites included in this study were sampled from multiple regions in Sunda region from 1999–2010.

### **Morphological analysis**

Morphological character terminology used for describing soldiers and workers follows the convention of Roonwal and Chhotani (1989) and Sands (1998). For all species, we photographed the heads, bodies (in profile) and pronota of the soldier caste using a high-quality digital microscope (HFVH-8000, KEYENCE, Osaka). Further, from select samples we removed the antennae from the soldier caste and the mandibles of the worker caste. We then examined these diagnostic characters on glass slides mounted with Euparal 3C 239 (Waldeck GmbH & Co. KG, Muenster Germany). We photographed the mounts using a conventional digital camera (Coolpix 3340, Nikon, Tokyo) attached to a Nikon Eclipse E600 lens. From these images, we constructed a multi-focused montage using Helicon Focus 4.03 Pro software (Helicon Soft Ltd. Kharkov).

### **Molecular barcode analysis**

To aid with taxonomic analysis, we developed a cytochrome c oxidase I gene (COI) profile. The profile consists of nucleotide sequence from the 'barcode' region of the mitochondrial genome (Herbert et al. 2003). First, we removed single legs from representative specimens and used in-house protocols at the Canadian Center for DNA Barcoding (Guelph, Ontario) to extract DNA (Ivanova et al. 2006) and PCR-amplify (Ivanova and Grainer 2007) the barcode region using the LCO1490t1 / HCO2198t1 primer combination. Finally, we sequenced the resultant 658 base pair (bp) fragment in both directions using the M13R/M13F primer pair. For sequencing, we used an ABI 3730XL automated sequencer and associated software (Applied Biosystems). From forward and reverse sequences, we generated a single consensus sequence using CodonCode Aligner v. 3.0.2 (CodonCode Corporation). We have deposited all sequence trace files and detailed specimen records, including precise sampling localities and GenBank accession numbers, onto the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007) under the Project name 'Termites of Indonesia' with Project code TINDS.

Using the BOLD on-line workbench, we aligned nucleotide sequences and calculated a pairwise Kimura-2-parameter (K2P) distance matrix. For each species in the matrix, we calculated the minimum, mean and maximum genetic distance. We also calculated the mean nearest neighbour distance (average distance to the most closely related species). From these data, we tested for the presence of a ‘barcode gap’ - a disjunction between levels of intraspecific and interspecific variability—by plotting maximum intraspecific distance against mean distance to nearest neighbour (NN). A gap is evident from this plot when the NN distance consistently exceeds the intraspecific distance. Finally, we used the K2P distance matrix to build a Neighbour-Joining (NJ) Taxon ID tree.

## Results

### Species descriptions

For all species described below, we provide comparative images of key morphological traits. For *Bulbitermes*, soldiers are profiled in Figures 1–4 and workers (mandibles) are profiled in Figures 9–16. For *Nasutitermes*, soldiers are profiled in Figures 5–8, and workers (mandibles) are profiled in Figures 17–24.

#### *Bulbitermes flavicans* (Holmgren)

[http://species-id.net/wiki/Bulbitermes\\_flavicans](http://species-id.net/wiki/Bulbitermes_flavicans)

*Euternes (Euternes) flavicans* Holmgren, 1913, pp. 173–174.

*Euternes (Euternes) flavicans*: John, 1925, p. 394.

*Bulbitermes flavicans*: Snyder, 1949, p. 308.

*Bulbitermes flavicans*: Ahmad, 1958, p. 132 (key).

*Bulbitermes flavicans*: Thapa, 1981, pp. 335–337.

*Bulbitermes flavicans*: Tho, 1992, p.159.

**Material examined.** Syntype: soldier, West Sumatra, Harau, Pajacombo, 17.iii.1913, Oscar John Coll. B.M. 1926–242 BMNH103898. Other material: SYK1999&2001-L-0146, 1453–56, 1463, 1465, 1467. Soldiers and workers from undisturbed forests, 1,000–1,400 m altitude, Kemiri Mountain, Southeast Aceh; SYK1999&2001-L-1457–60, 1462. Soldiers and workers from undisturbed forests, 150–350 m altitude, Bukit Lawang, Langkat, North Sumatra; SYK2000-L-1466. Soldiers and workers from undisturbed forest, 500 m altitude, Ketambe, Southeast Aceh; SYK2006-AL-0001, 0777, 1613. Soldiers and workers from disturbed. SYK2010-KTB-011, 027, 051, 098. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra.

**Description.** Imago: Unknown.



Soldiers. Head: in dorsal view the anterior part darker than posterior part in coloration; rostrum dark brown with the apex paler; antenna much paler than anterior part of head capsule, uniformly coloured. Head with five or six scattered bristles, tip of nasus with four bristles, pronotum and abdominal tergites with microscopic hairs. Head capsule somewhat round, weakly constricted behind antennal sockets; posterior margin roundly convex; dorsal outline (including rostrum) in profile nearly straight with two shallow indentations near base of rostrum, and up-curved apically. Mandible with weak apical processes. Antenna with 12 articles; second clearly shorter than third and fourth; third clearly longer than fourth; fourth and fifth almost equal in length. Thorax: pronotum seen from above paler than anterior part of head capsule; its periphery paler than central area. Coxae pale brown; femora yellowish; tibiae whitish yellow. Anterior margin of pronotum nearly straight; posterior margin roundly convex. Abdomen: tergites pale brown.

Soldiers (n = 10; (size range) in mm): head length including nasus (HLN) (1.22–1.40); head length measured to base of mandible (HL) (0.97–1.00); nasus length (NL) (0.30–0.42); nasus index = NL/HL (0.30–0.42); maximum head width at posterior part (HWP) (0.75–0.84); maximum height of head excluding postmentum (HH) (0.57–0.65); pronotum length (PL) (0.15–0.17); pronotum width (PW) (0.37–0.45).

Workers. Antenna: whitish yellow to yellow; 13 articles; second shorter than third; third clearly longer than fourth; fourth wider than fifth. Left mandible: apical tooth and first marginal tooth almost equal in length; third marginal moderately protruding from cutting edge; fourth almost completely hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar plate undeveloped and notch at proximal end of molar plate obsolete.

**Geographical distribution.** Sumatra, Peninsular Malaysia and Borneo.

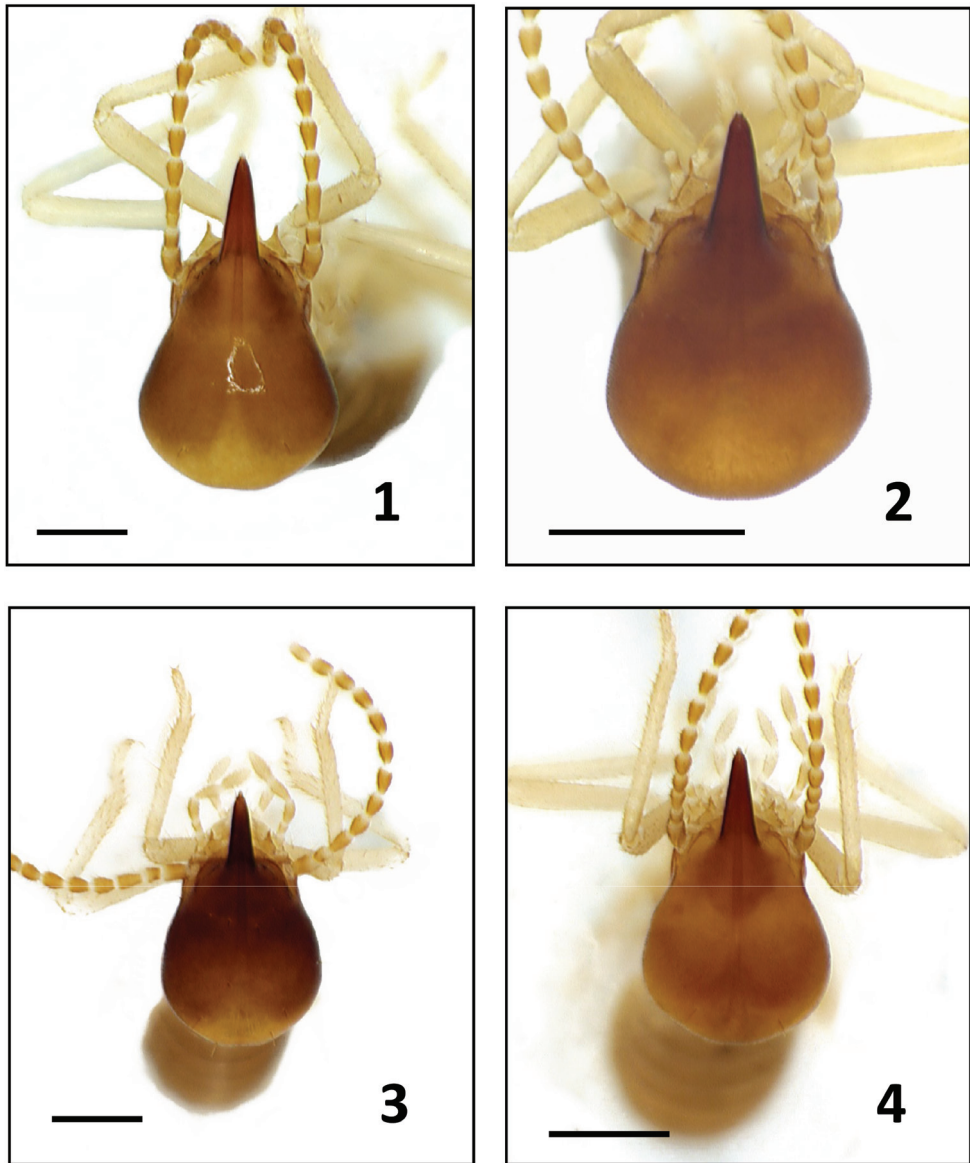
### ***Bulbitermes neopusillus* Snyder & Emerson**

[http://species-id.net/wiki/Bulbitermes\\_neopusillus](http://species-id.net/wiki/Bulbitermes_neopusillus)

*Bulbitermes neopusillus* Snyder & Emerson, 1949, p. 309.

*Bulbitermes neopusillus*: Ahmad, 1958, p.133 (key).

**Material examined.** Soldiers, Sumatra, Siak, 9.ii.1913, Oscar John Coll. B.M. 1926-242 BMNH103902. SYK2006-KSNP-0032, 0034, 0047. Soldiers and workers from disturbed forest, 500 m altitude, Air Hangat, Kerinci, Jambi; SYK1999-L-1409. Soldiers and workers from undisturbed forest, 1,250 m altitude, Kemiri Mountain, Southeast Aceh; SYK1999-L-1418, 1632, 1646, 1651, 1682. Soldiers and workers from undisturbed forest, 200–400 m altitude, Bengkung, Southeast Aceh; SYK1999&2000-L-1412, 1420, 1426, 1434, 1437, 1441, 1444, 1604, 1608, 1636, 1639, 1645, 1654, 1657, 1659, 1668, 1669. Soldiers and workers from undisturbed forest, 150–350 m altitude, Bukit Lawang, Langkat, North Sumatra; SYK1999-L-1405, 1442, 1448,



**Figures 1–4.** Soldiers of *Bulbitermes* from Sunda region in dorsal view. *B. constrictus* **1** *B. singaporiensis* **2** *B. flavicans* **3** *B. neopusillus* **4**

1612. Soldiers and workers from disturbed forest, 50 m altitude, Sekundur, Langkat, North Sumatra; SYK2000-L-1398, 1849. Soldiers and workers from disturbed forest, 80 m altitude, Soraya, Singkil, Aceh; SYK2000&2001-L-1394, 1395, 1415. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe, Southeast Aceh; SYK2006-AL-0778, 0779, 0780. Soldiers and workers from disturbed forest, 30 m altitude, Maestong, Sungai Batang Hari, Jambi; SYK2007-SPR-0038. Soldiers and workers from disturbed forest, <100 m altitude, Tua Pejat, Sipora Island, Mentawai, West

Sumatra. SYK2010-KTB-003, 004, 005, 018, 035, 044, 045, 047, 048, 054, 055, 056, 057, 059, 060, 065, 066, 067, 068, 071, 075. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra.

**Description.** Imago: Unknown.

Soldiers. Head: in dorsal view anterior and posterior parts almost similar in coloration; rostrum paler than anterior part of head capsule. Antenna paler than anterior part of head capsule in coloration, with the first segment darkest. Head with two scattered bristles, tip of nasus with four bristles, pronotum and abdominal tergites with microscopic hairs. In dorsal view head capsule somewhat pear-shaped, strongly constricted behind antennal sockets; its posterior margin weakly indented in middle; dorsal outline (including rostrum) in profile nearly straight. Mandible with short apical processes. Antenna with 13 articles; second shorter than third; third twice as long as fourth; fourth shorter than fifth. Thorax: pronotum seen from above similar to the posterior part of head capsule in coloration; its periphery darker than central area. Coxae and femora pale brown; tibiae pale yellow. Anterior and posterior margins of pronotum nearly straight. Abdomen: tergites pale brown to brown.

Soldiers (n = 10; (size range) in mm): head length including nasus (HLN) (1.45–1.60); head length measured to base of mandible (HL) (0.90–0.93); nasus length (NL) (0.55–0.62); nasus index = NL/HL (0.62–0.67); maximum head width at posterior part (HWP) (0.85–0.87); maximum height of head excluding postmentum (HH) (0.60–0.63); pronotum length (PL) (0.15–0.18); pronotum width (PW) (0.50–0.55).

Workers. Antenna: whitish yellow; 14 articles; second longer than third and fourth; third clearly longer than fourth; fourth the shortest; fifth shorter than sixth. Left mandible: apical tooth shorter than first marginal tooth; third marginal tooth moderately protruding from cutting edge; fourth marginal tooth hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar undeveloped and notch at proximal end of molar plate weakly developed.

**Geographical distribution.** Sumatra, Mentawai Islands, Peninsular Malaysia, Java and Borneo.

### ***Bulbitermes constrictus* (Haviland)**

[http://species-id.net/wiki/Bulbitermes\\_constrictus](http://species-id.net/wiki/Bulbitermes_constrictus)

*Termes constrictus* Haviland, 1898, pp. 420–421.

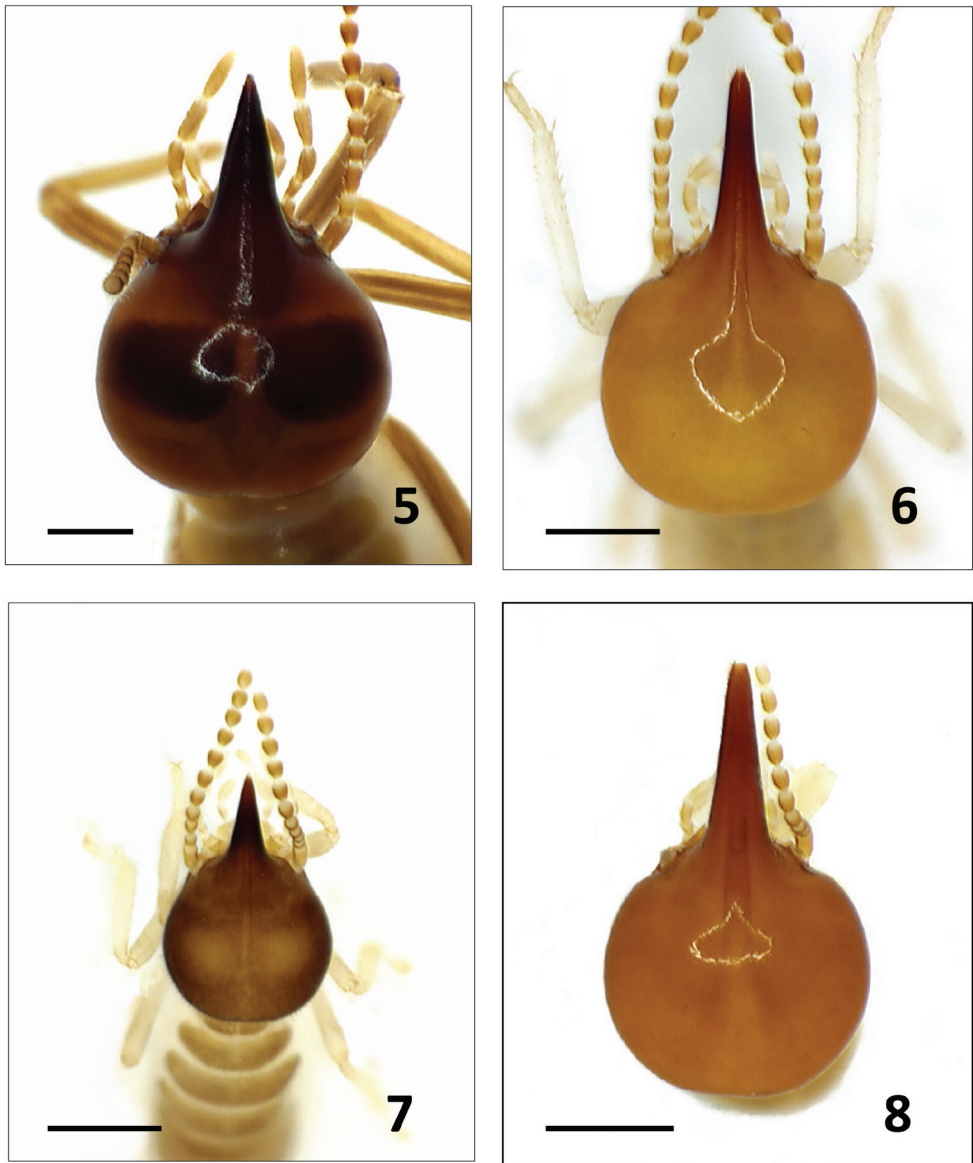
*Eutermes (Eutermes) constrictus*: Holmgren 1913, p. 172.

*Bulbitermes constrictus*: Snyder, 1949, p. 308.

*Bulbitermes constrictus*: Ahmad, 1958, p.p. 129, 133–134 (key).

*Bulbitermes constrictus*: Thapa, 1981, pp. 332–335.

**Material examined.** Syntype: Soldiers, Sarawak, Coll. & Det. G.D. Haviland, No. 292, (Ex. Dundee) (*Bulbitermes*) MNH103897. Other material: SYK2006-KSNP-0006,



**Figures 5–8.** Soldiers of *Nasutitermes* from Sunda region in dorsal view. *N. matangensis* **5** *N. longinasoides* **6** *N. neoparvus* **7** *N. longinasus* (largest soldier) **8** Scale bar: 0.5 mm. Scale bar: 0.6 mm.

0083. Soldiers and workers from undisturbed forest, 300 m altitude, Sungai Manau, Merangin, Jambi; SYK2006-KSNP-0081, 0090. Soldiers and workers from disturbed forest, 500 m altitude, Air Hangat, Kerinci, Jambi; SYK2000-L-1507, 1522. Soldiers and workers from undisturbed forest, 250–350 m altitude, Bukit Lawang, Langkat, North Sumatra; SYK2000&2001-L-1496, 1497, 1498. Soldiers and workers from disturbed forest, 50 m altitude, Sekundur, Langkat, North Sumatra. SYK2010-KTB-013,

014, 015, 137, 038, 046, 049, 050, 100. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra.

**Description.** Imago: Unknown.

Soldiers. Head: in dorsal view anterior and posterior parts almost similar in coloration; except around posterior margin, much paler in coloration; rostrum darker than anterior part of head capsule; antenna paler than anterior part of head capsule in coloration. Head with two bristles, tip of nasus with four bristles, pronotum with bristles, abdominal tergites with hairs and bristles.

In dorsal view head capsule somewhat pear-shaped, strongly constricted behind antennal sockets; its posterior margin weakly indented; dorsal outline (including rostrum) in profile nearly straight. Mandible with moderately developed apical processes. Antenna with 14 articles; second longer than third; third the shortest; fourth and fifth almost equal in length. Thorax: pronotum seen from above paler than anterior part of head capsule; its periphery darker than central area. Coxae and femora yellow; tibiae pale yellow. Anterior margin of pronotum weakly indented in the middle, while posterior margin roundly convex. Abdomen: tergites yellowish to pale brown.

Soldiers ( $n = 10$ ; (size range) in mm): head length including nasus (HLN) (1.55–1.65); head length measured to base of mandible (HL) (1.05–1.13); nasus length (NL) (0.50–0.60); nasus index = NL/HL (0.47–0.53); maximum head width at posterior part (HWP) (0.95–0.10); maximum height of head excluding postmentum (HH) (0.60–0.65); pronotum length (PL) (0.22–0.25); pronotum width (PW) (0.52–0.55).

Workers. Antenna: whitish yellow to yellow; 15 articles; second clearly longer than third; third the shortest; fourth and fifth almost equal in length. Left mandible: apical and first marginal teeth almost equal in length; third marginal moderately protruding from cutting edge; fourth almost completely hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar not developed; notch at proximal end of molar plate weakly developed.

**Geographical distribution.** Sumatra and Borneo.

### *Bulbitermes singaporiensis* (Haviland)

[http://species-id.net/wiki/Bulbitermes\\_singaporiensis](http://species-id.net/wiki/Bulbitermes_singaporiensis)

*Termes singaporiensis* Haviland, 1898, pp. 429.

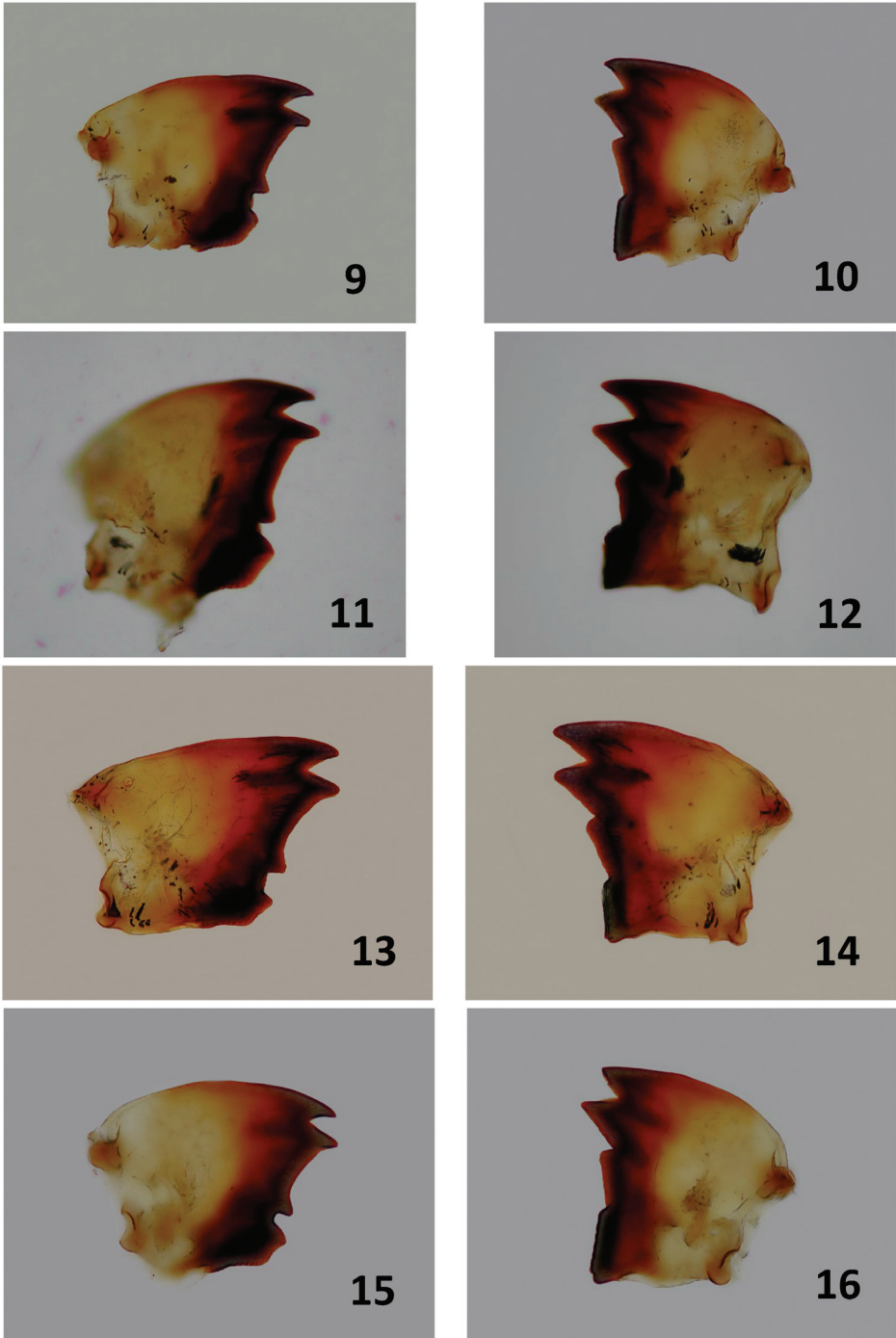
*Eutermes* (*Eutermes*) *singaporiensis*: Holmgren, 1913, p. 179.

*Bulbitermes singaporiensis*: Snyder, 1949, p. 309.

*Bulbitermes singaporiensis*: Tho, 1992, pp. 158–159.

**Material examined.** Syntype: soldiers, *Termes singaporiensis*, Singapore, 1893, Coll. & Det. G. D. Haviland, No. 16 (Ex. Dundee) (*Bulbitermes*) BMNH103923. Other material: SYK(1998–2001)-L-0205, 0212, 0219, 1802, 1812, 1817, 1821–23, 1825–29, 1831, 1832, 1834, 1835, 1839, 1840, 1843, 1846–48, 1851, 1853–55,





**Figures 9–16.** Workers of *Bulbitermes* from Sunda region. Left **9, 11, 13, 15** and right **10, 12, 14, 16** mandibles. *B. constrictus* **9, 10** *B. singaporiensis* **11, 12** *B. flavicans* **13, 14** *B. neopusillus* **15, 16**. Scale bar: 0.1 mm.

1859, 1860, 1865, 1867, 1868, 1870, 1877, 1883, 1884, 1850, 1877, 1879, 1880, 1975, 1978. Soldiers and workers from undisturbed forest, 150–350 m altitude, Bukit Lawang, Langkat, North Sumatra.; SYK2006-AL-0004, 0801, 0802, 1886. Soldiers and workers from disturbed forest, 30 m altitude, Maestong, Sungai Batang Hari, Jambi; SYK2006-L1852. Soldiers and workers from undisturbed forest, 50 m altitude, Sekundur, Langkat, North Sumatra; SYK1999-L-1882. Soldiers and workers from undisturbed forest, 400 m altitude, Bengkung, Southeast Aceh. SYK&FAZLY2009-ER-020, 022, 024, 039, 043, 044, 047, 051, 057, 058, 062, 063, 087. Soldiers and workers from undisturbed forest, >100 m altitude, Endau Rompin National Park, Johor, Peninsular Malaysia.

**Description.** Imago: Unknown.

Soldiers. Head: in dorsal view anterior part of head capsule darker than the posterior part in coloration; rostrum slightly darker than anterior part of head capsule; antenna paler than anterior part of head capsule. Head with two bristles, tip of nasus with four bristles, pronotum with microscopic hairs, abdominal tergites with hairs and bristles. In dorsal view head capsule somewhat pear-shaped and weakly constricted behind antennal sockets; its posterior margin nearly straight in the middle; dorsal outline (including rostrum) in profile nearly straight; mandible with moderately developed apical processes. Antenna with 12 articles; second and third almost equal in length, the former wider than the latter in width; third the shortest; fourth and fifth almost equal in length. Thorax: pronotum seen from above paler than anterior part of head capsule; its anterior part slightly darker than posterior part. Coxae pale brown; femora yellowish; tibiae pale yellow. Anterior margin of pronotum moderately indented in the middle, while posterior margin nearly straight in the middle. Abdomen: tergites dark brown to very dark sepia brown.

Soldiers (n = 10; (size range) in mm): head length including nasus (HLN) (1.24–1.35); head length measured to base of mandible (HL) (0.98–1.12); nasus length (NL) (0.32–0.37); nasus index = NL/HL (0.31–0.35); maximum head width at posterior part (HWP) (0.80–0.84); maximum height of head excluding postmentum (HH) (0.57–0.61); pronotum length (PL) (0.16–0.18); pronotum width (PW) (0.37–0.44).

Workers. Antenna: whitish yellow to yellow with first article darker than the subsequent; 14 articles; second much longer than third and fourth; third longer than fourth; fourth the shortest. Left mandible: apical tooth shorter than first marginal tooth; third marginal moderately protruding from cutting edge; fourth almost completely hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth weakly concave; inner layer of molar plate and notch at proximal end of molar plate obtuse.

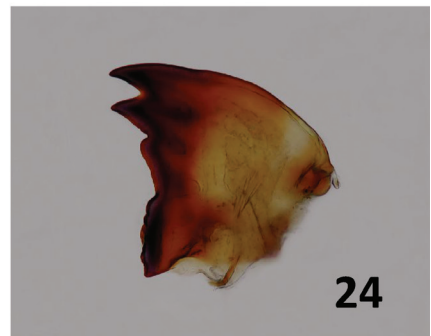
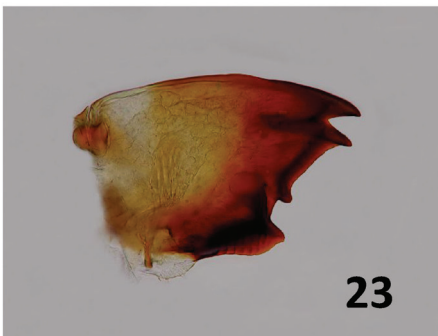
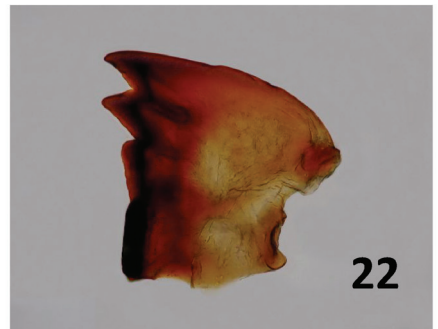
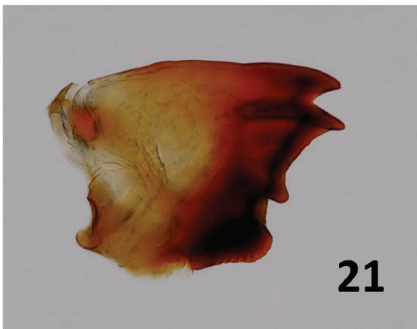
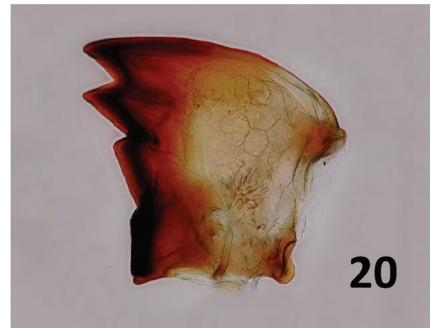
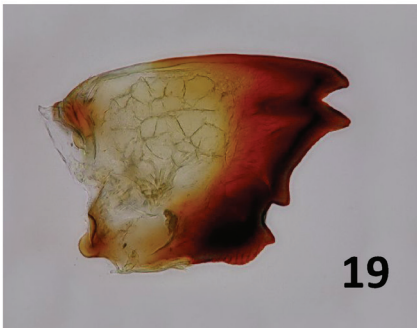
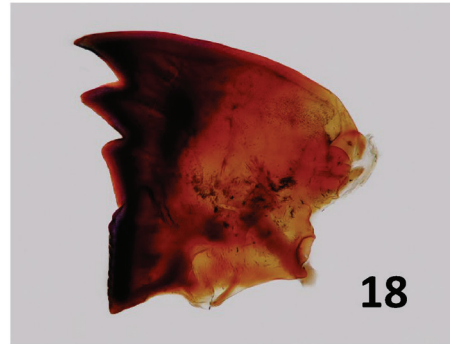
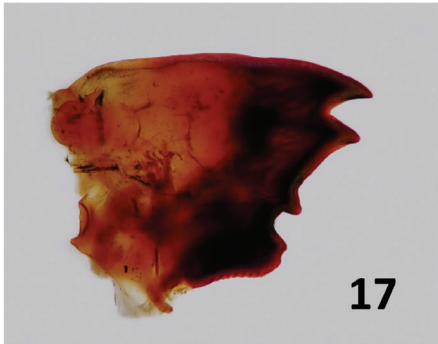
**Biogeographical distribution.** Sumatra, Peninsular Malaysia, Java and Borneo.

***Nasutitermes matangensis* (Haviland)**

[http://species-id.net/wiki/Nasutitermes\\_matangensis](http://species-id.net/wiki/Nasutitermes_matangensis)

*Termes matangensis* Haviland, 1898, pp. 427–428.

*Eutermes (Eutermes) matangensisformis*: Holmgren, 1913, p. 185.



**Figures 17–24.** Workers of *Nasutitermes* from Sunda region. Left **17, 19, 21, 23** and right **18, 20, 22, 24** mandibles. *N. matangensis* **17, 18** *N. longinasoides* **19, 20** *N. neoparvus* **21, 22** *N. longinasus* **23, 24**. Scale bar: 0.1 mm.

*Eutermes (Eutermes) matangensis*: Holmgren, 1913-14, pp. 26-265.

*Eutermes (Eutermes) matangensis*: John, 1925, p. 398.

*Nasutitermes matangensis*: Snyder, 1949, p. 287.

*Nasutitermes matangensis*: Ahmad, 1958, p. 147(key).

*Nasutitermes matangensis*: Thapa, 1981, pp. 312-315.

*Nasutitermes matangensis*: Tho, 1992, p. 159.

**Material examined.** Syntype: Soldiers, *Termes matangensis*, Sarawak, Coll. G. D. Haviland. BMNM No. 358. (Ex. Dundee) (*Nasutitermes*). Other material: SYK2006-KSNP-0017, 0023, 0025, 0041. Soldiers and workers from undisturbed forest, 300 m altitude, Sungai Manau, Merangin, Jambi; SYK1999&2001-L-1039, 1040, 1042, 1043, 1045, 3080. Soldiers and workers from undisturbed forest, 1,000-1,400 m altitude, Kemiri Mountain, Southeast Aceh; SYK2007-UGDT-0010, 0063-70. Soldiers and workers from disturbed forest, 900 m altitude, Ulu Gadut, Padang, West Sumatra; SYK2007-SRSR-0005, 0040, 0063, 0066, 0632. Soldiers and workers from disturbed forest, <100 m altitude, Siberut Tengah, Mentawai, West Sumatra; SYK2007-SBRT-0016, 0034, 0039, 0046, 0047, 0060, 0070, 0080. Soldiers and workers from undisturbed forest, <100 m altitude, Simabuggei, Siberut Island, Mentawai, West Sumatra; SYK2001-S-0128, 0030. Soldiers and workers from disturbed forest, 200 m altitude, Aceh Besar; SYK2006-SB-0001-04, 0044, 0045, 0050, 0051. Soldiers and workers from disturbed forest, <100 m altitude, Sabang, Weh Island, Aceh; SYK1999-L-1062. Soldiers and workers from undisturbed forest, 300 m altitude, Ketambe, Southeast Aceh; SYK2006-AL-0901. Soldiers and workers from disturbed forest, 30 m altitude, Maestong, Sungai Batang Hari, Jambi; SYK2002-NIAS-0111. Soldiers and workers from disturbed forest, <100 m altitude, Gunung Sitoli, Nias Island, North Sumatra; SYK2002-PRP-0100. Soldiers and workers from disturbed forest, 900 m altitude, Toba Lake, Parapat, North Sumatra; SYK2007-LP-0093. Soldiers and workers from disturbed forest, 1100 m altitude, Sumber Jaya, Kota Bumi, Lampung; SYK2007-LBAN-0004, 0012. Soldiers and workers from disturbed forest, 600 m altitude, Lembah Anai, Tanah Datar, West Sumatra; SYK2005&2006-RKT-0002, 0004, 0006, 0007, 0009-0021, 0033-40, 0042-48, 0050, 0055, 0056, 0058, 0059, 0061-0063, 0065, 0066, 0072. Soldiers and workers, <10-300 m altitude, Rakata island, the Krakataus, Lampung; SYK2005&2006-ANK-0040, 0041, 0043, 0139, 0144-46, 0148, 0149, 0151, 0154, 0155, 0277-79, 0301, 0302. Soldiers and workers, <100 m altitude, Anak Krakatau, the Krakataus, Lampung; SYK2005&2006-PJG-0073-0083, 0092-0095, 0137, 0138, 0141, 0142, 0147, 0150-0153, 0156, 0157. Soldiers and workers, <100 m altitude, Panjang island, the Krakataus, Lampung; SYK2005&2006-SRTG-0006, 0120, 0126-30, 0041-44, 0173-90, 0192-95, 0197-200, 0216, 0227-30, 0238. Soldiers and workers, <100 m altitude, Sertung island, the Krakataus, Lampung; SYK2005-SBK-0235, 0237-42, 0246, 0263. Soldiers and workers, <100 m altitude, Sebuk island, the Krakataus, Lampung; SYK2005-SBS- 0064, 0067, 0069-71, 0073-75, 0077-88, 0090. Soldiers and workers, <100 m altitude, Sebesi island, the Krakataus, Lampung; SYK2007-LGD-0031, 0050-52,

0058, 0059. Soldiers and workers, <100 m altitude, Legundi island, the Krakataus, Lampung; SYK2007-LP-0002, 0006. Soldiers and workers, from disturbed forest, <100 m altitude, Pantai Mutun, Lampung. SYK2010-KTB-002, 006, 019, 041, 095. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra; SYK2010-PK-005, 006. Soldiers and workers from disturbed forest, 150 m altitude, Peukan Biluy, Darul Kamal, Aceh Besar, Sumatra; SYK&FAZLY2009-ER-038, 050, 073. Soldiers and workers from undisturbed forest, >100 m altitude, Endau Rompin National Park, Johor, Peninsular Malaysia.

**Description.** Imago: Unknown.

**Soldiers.** Head: in dorsal view head capsule excluding rostrum brown to dark sepia brown; rostrum darker than head capsule; entire rostrum almost uniformly coloured; antenna paler than head capsule in coloration. Head with a few number of scattered bristles, tip of nasus with four bristles, pronotum hairs, abdominal tergites with hairs and bristles. In dorsal view head capsule round; its posterior margin nearly straight in the middle; dorsal outline (including rostrum) in profile nearly straight, down-curved apically. Antenna with 13 articles; second slightly longer than fourth; third the longest; fourth shorter than fifth. Thorax: pronotum seen from above paler than head capsule in coloration; its anterior part darker than posterior part. Coxae and femora sepia brown; tibiae yellowish. Anterior margin of pronotum moderately indented in the middle; posterior margin nearly straight in the middle. Abdomen: tergites yellowish to pale brown.

Soldiers ( $n = 10$ ; (size range) in mm): head length including nasus (HLN) (2.05–2.18); head length measured to base of mandible (HL) (1.20–1.25); nasus length (NL) (0.82–0.95); nasus index = NL/HL (0.68–0.76); maximum head width (HW) (1.37–1.50); maximum height of head excluding postmentum (HH) (0.90–0.95); pronotum length (PL) (0.25–0.30); pronotum width (PW) (0.60–0.70).

**Workers.** Antenna: pale yellow to yellow; 14 articles; second clearly longer than third and fourth; third longer than fourth. Left mandible: apical tooth longer than first marginal tooth; third marginal moderately protruding from cutting edge; fourth almost completely hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar plate undeveloped; notch at proximal end of molar plate absent.

**Geographical distribution.** Sumatra, Mentawai islands, Malay Peninsula, Java and Borneo.

***Nasutitermes neoparvus* Thapa**

[http://species-id.net/wiki/Nasutitermes\\_neoparvus](http://species-id.net/wiki/Nasutitermes_neoparvus)

*Nasutitermes neoparvus* Thapa, 1981, pp. 329–332.

**Material examined.** SYK2006-KSNP-0007, 0053. Soldiers and workers from undisturbed forest, 300 m altitude, Sungai Manau, Merangin, Jambi; SYK2006-



KSNP-0054, 0076, 0085. Soldiers and workers from disturbed forest, 500m altitude, Air Hangat, Kerinci, Jambi; SYK2007-SRSR-0006, 0011. Soldiers and workers from disturbed forest, <100 m altitude, Surisura, Siberut Tengah, Mentawai, West Sumatra; SYK2006-SBRT-0006, 0028, 0077, 0084, 0103. Soldiers and workers from undisturbed forest, <100 m altitude, Simabuggei, Siberut island, Mentawai, West Sumatra; SYK1999&2000-L-0916, 0923, 0931, 0932, 0935, 0937, 0940, 0943. Soldiers and workers from undisturbed forest, 150–350 m altitude, Bukit Lawang, Langkat, North Sumatra; SYK2000&2001-L- 0214, 0913, 0918, 0922, 0926, 0928, 0933, 0934, 0941, 0942. Soldiers and workers from disturbed forest, 50 m altitude, Sekundur, Langkat, North Sumatra; SYK1999-L-0208, 0235, 0241, 0930, 0917, 0921, 0924, 0936, 0939. Soldiers and workers from undisturbed forest, 200–400 m altitude, Bengkung, Southeast Aceh; SYK1999-L-0211, 0225, 0911, 0914, 0915, 0919, 0920, 0925, 0927, 0929, 0938, 1171. Soldiers and workers from disturbed forest, 80 m altitude, Soraya, Singkil, Aceh; SYK1999-L- 0912, 0215, 0237, 0244, 0245. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe, Southeast Aceh; SYK2007-LP-0081. Soldiers and workers from disturbed forest, <100 m altitude, Pantai Mutun, Lampung. SYK2010-KTB-029, 053, 058, 061. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra; SYK&FAZLY2009-ER-034. Soldiers and workers from undisturbed forest, >100 m altitude, Endau Rompin National Park, Johor, Peninsular Malaysia.

**Description.** Imago: Unknown.

**Soldiers.** Head: in dorsal view head capsule excluding rostrum dark brown to sepia brown; rostrum darker than head capsule; antenna much paler than head capsule. Head with combination long and short bristles, tip of nasus with short hairs and four long bristles, pronotum with short and long bristles, abdominal tergites densely with short hairs and long bristles. In dorsal view head capsule somewhat round; its posterior margin roundly convex in the middle; dorsal outline of head capsule (excluding rostrum) in profile nearly straight. Antenna with 11 articles; second shorter than fourth; third longer than fourth; fourth and fifth almost equal in length. Thorax: pronotum seen from above paler than head capsule in coloration; its periphery darker than central area. Coxae and femora yellow; tibiae whitish yellow. Anterior margin of pronotum nearly straight in the middle; posterior margin strongly indented in the middle. Abdomen: tergites dark yellow to brown.

Soldiers (n = 10; (size range) in mm): head length including nasus (HLN) (1.25–1.37); head length measured to base of mandible (HL) (0.62–0.77); nasus length (NL) (0.57–0.62); nasus index = NL/HL (0.79–0.80); maximum head width (HW) (0.77–0.80); maximum height of head excluding postmentum (HH) (0.50–0.60); pronotum length (PL) (0.12–0.15); pronotum width (PW) (0.37–0.42).

**Workers.** Antenna: pale yellow to yellow; 12 articles; second clearly longer than fourth; third longer than fourth; fourth shorter than fifth. Left mandible: apical tooth clearly shorter than first marginal tooth; third marginal moderately protruding from cutting edge; fourth visible in the gap between third marginal and mo-

lar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar plate undeveloped, and notch at proximal end of molar plate obtuse.

**Geographical distribution.** Sumatra and Borneo.

***Nasutitermes longinasus* (Holmgren)**

[http://species-id.net/wiki/Nasutitermes\\_longinasus](http://species-id.net/wiki/Nasutitermes_longinasus)

*Eutermes (Eutermes) longinasus* Holmgren, 1913, p. 171.

*Eutermes longinasus*: John, 1925, p. 392.

*Nasutitermes longinasus*: Snyder, 1949, p. 284.

*Nasutitermes longinasus*: Ahmad, 1958, p. 54 (key).

*Nasutitermes longinasus*: Thapa, 1981, pp. 323–326.

*Nasutitermes longinasus*: Tho, 1992, p. 150.

**Material examined.** SYK2006-KSNP-0040, 0049, 0052. Soldiers and workers from undisturbed forest, 300 m altitude, Sungai Manau, Merangin, Jambi; SYK(1998–2001)-L-0012, 0025, 0027, 0234, 0036, 0167, 0218, 0231, 0851, 0856, 1034, 1070, 1071, 1080, 1085, 1095. Soldiers and workers from disturbed forest, 80 m altitude, Soraya, Singkil, Aceh; SYK1999-L-0010, 0020, 0029, 0030, 0035, 0039, 0044, 0047–49, 0055, 0056, 0061, 0065, 0066, 0071, 0110, 0222, 0226, 0235, 0240, 0246, 0249, 0277, 0825, 0826, 0848–50, 0853–55, 0857, 0859–61, 1044, 1048, 1068, 1069, 1073, 1074, 1076, 1078, 1079, 1081–83, 1086, 1089–92, 1096, 1097. Soldiers and workers from undisturbed forest, 200–400 m altitude, Bengkung, Southeast Aceh; SYK1999&2000-L-0069, 0210, 0233, 0858, 1072, 1075, 1077, 1087. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe, Southeast Aceh; SYK(1999–2001)-L-0018, 0406, 1087, 1088, 1093. Soldiers and workers from undisturbed forest, 150–350 m altitude, Bukit Lawang, Langkat, North Sumatra. SYK2010-KTB-026, 028, 031, 032, 033, 034, 076, 077, 079, 082, 083, 084, 085, 086, 088, 091, 092, 093, 094, 096, 097. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra.

**Description.** Imago: Unknown.

Major soldiers. Head: in dorsal view head capsule excluding rostrum pale brown to brown; rostrum darker than head capsule; antenna much paler than head capsule in coloration. Head with hairs and two long bristles, tip of nasus with hairs and four bristles, pronotum with short and long bristles, pronotum and abdominal tergites with hairs and bristles. In dorsal view head capsule round; its posterior margin nearly straight in the middle; dorsal outline of head capsule (including rostrum) in profile nearly straight. Antenna with 13 articles; second longer than fourth; third clearly longer than fourth; fourth the shortest. Thorax: pronotum seen from above paler than head capsule in coloration; its periphery darker than central area. Coxae

and femora yellow; tibiae whitish yellow. Anterior margin of pronotum moderately indented in the middle, while posterior margin roundly convex in the middle. Abdomen: tergites yellow to brown.

Major soldiers ( $n = 10$ ; (size range) in mm): head length including nasus (HLN) (2.00–2.20); head length measured to base of mandible (HL) (1.07–1.15); nasus length (NL) (0.95–1.12); nasus index =  $NL/HL$  (0.88–0.97); maximum head width (HW) (1.15–1.30); maximum height of head excluding postmentum (HH) (0.80–0.85); pronotum length (PL) (0.25–0.30); pronotum width (PW) (0.52–0.58).

Minor soldiers: in dorsal view head capsule excluding rostrum deep reddish brown; rostrum same color as head capsule; antenna paler than head capsule in coloration. Head with hairs and two long bristles, tip of nasus with hairs and four bristles, pronotum with short and long bristles, pronotum and abdominal tergites with hairs and bristles. In dorsal view head capsule round; its posterior margin weakly constricted in the middle; dorsal outline of head capsule (including rostrum) in profile nearly straight. Antenna with 13 articles; second longer than fourth; third clearly longer than fourth; fourth the shortest. Thorax: pronotum seen from above slightly paler than head capsule in coloration; its periphery darker than central area. Coxae and femora brownish yellow; tibiae yellow. Anterior margin of pronotum weakly to moderately indented in the middle, while posterior margin roundly convex in the middle. Abdomen: tergites brown.

Minor soldiers ( $n = 10$ ; (size range) in mm): head length including nasus (HLN) (1.72–1.82); head length measured to base of mandible (HL) (0.82–0.86); nasus length (NL) (0.71–0.77); nasus index =  $NL/HL$  (0.86–0.89); maximum head width (HW) (0.86–0.94); maximum height of head excluding postmentum (HH) (0.59–0.67); pronotum length (PL) (0.20–0.23); pronotum width (PW) (0.49–0.51).

Workers. Antenna: pale yellow to yellow, with the first article darker than the subsequent; 14 articles; second and third clearly longer than fourth; fourth the shortest. Left mandible: apical tooth longer than first marginal tooth; third marginal weakly protruding from cutting edge; fourth hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar plate weakly developed; notch at proximal end of molar plate obtuse.

**Geographical distribution.** Sumatra, Peninsular Malaysia and Borneo.

### *Nasutitermes longinasoides* Thapa

[http://species-id.net/wiki/Nasutitermes\\_longinasoides](http://species-id.net/wiki/Nasutitermes_longinasoides)

*Nasutitermes longinasoides* Thapa, 1981, pp. 301–303.

**Material examined.** SYK2006-KSNP-0028, 0031, 0037, 0039, 0050, 0058. Soldiers and workers from undisturbed forest, 300 m altitude, Sungai Manau, Merangin, Jambi; SYK2006-AL-0016, 0021, 0106, 0950-0952. Soldiers and workers from disturbed forest, 30 m altitude, Maestong, Sungai batang hari, Jambi; SYK1999&2000-

L- 1063–1066. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe, Southeast Aceh; SYK2002-PRP-0101, 0102. Soldiers and workers from disturbed forest, 900 m altitude, Parapat, North Sumatra. SYK2010-KTB-012, 022, 030, 042, 043, 063, 069, 090. Soldiers and workers from undisturbed forest, 300–500 m altitude, Ketambe Research Station, Ecosystem Leuser, Sumatra.

**Description.** Imago: Unknown.

Soldiers. Head: in dorsal view head capsule excluding rostrum pale yellow to yellow; rostrum darker than head capsule; antenna slightly paler than head capsule in coloration. Head with three or four scattered bristles, tip of nasus a hairs and four bristles, pronotum and abdominal tergites with hairs and bristles. In dorsal view head capsule round; its posterior margin roundly convex in the middle; dorsal outline of head capsule (including rostrum) in profile nearly straight. Antenna with 13 articles; second and fourth almost equal in length; third clearly longer than fourth; fourth shorter than fifth. Thorax: pronotum seen from above paler than head capsule in coloration; its periphery darker than central area. Coxae and femora pale yellow; tibiae whitish. Anterior and posterior margins of pronotum nearly straight in the middle. Abdomen: tergites yellow to pale brown.

Soldiers (n = 10; (size range) in mm): head length including nasus (HLN) (2.10–2.20); head length measured to base of mandible (HL) (1.07–1.25); nasus length (NL) (0.92–1.07); nasus index = NL/HL (0.85–0.86); maximum head width (HW) (1.23–1.32); maximum height of head excluding postmentum (HH) (0.80–0.83); pronotum length (PL) (0.20–0.23); pronotum width (PW) (0.56–0.60).

Workers. Antenna: pale yellow to yellow; 14 articles; second much longer than fourth; third longer than fourth; fourth the shortest. Left mandible: apical tooth shorter than first marginal tooth; third marginal moderately protruding from cutting edge; fourth completely hidden behind molar prominence. Right mandible: posterior edge of second marginal tooth nearly straight; inner layer of molar plate undeveloped, and notch at proximal end of molar plate obtuse.

**Geographical distribution.** Sumatra and Borneo.

## Taxonomic key

### Key 1. Key to the species of *Bulbitermes* based on the largest soldiers and largest workers

- 1 Soldier: antenna with 12 articles ..... 2
- Soldier: antenna with 13 to 14 articles ..... 3
- 2(1) Worker: antenna with 13 articles, second shorter than third, fourth and fifth almost equal in length. Left mandible of apical tooth shorter than first marginal tooth ..... *B. flavicans*
- Worker: antenna with 14 articles, second article much longer than third, fourth article the shortest. Apical and first marginal teeth of left mandible almost equal in length ..... *B. singaporiensis*

- 3(1) Soldier: antenna with 13 articles, fourth article the shortest. In dorsal view posterior margin weakly indented the middle. Worker: antenna with 14 articles, fourth article the shortest ..... *B. neopusillus*
- Soldier: antenna with 14 articles, third article the shortest, In dorsal view posterior margin nearly straight. Worker: antenna with 14 articles, third the shortest ..... *B. constrictus*

## Key 2. Key to the species of *Nasutitermes* based on the largest soldiers and largest workers

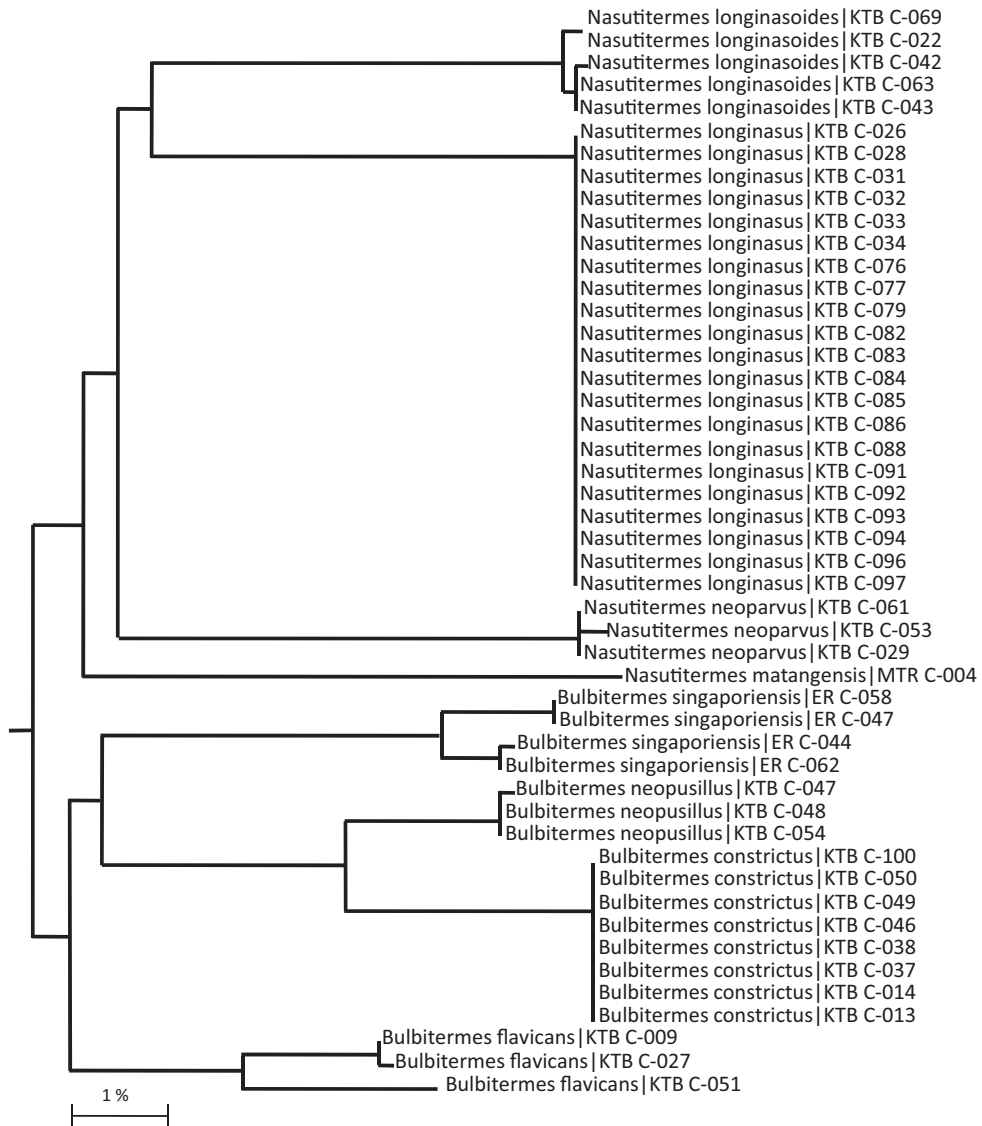
- 1 Soldier: antenna with 11 articles. [Worker: antenna with 12 articles.] ..... *N. neoparvus*
- Soldier: antenna with 13 articles ..... 2
- 2(1) Soldier: dimorphic. [The largest and smallest individuals differ markedly in size.] ..... *N. longinasus*
- Soldier: monomorphic ..... 3
- 3(2) Soldier: in dorsal view posterior margin of head capsule roundly convex in the middle, dorsal outline of head capsule (including rostrum) in profile nearly straight, maximum width of head capsule 1.23-1.32 mm. Worker: apical tooth of left mandible shorter than first marginal tooth ..... *N. longinasoides*
- Soldier: in dorsal view posterior margin of head capsule nearly straight in the middle, dorsal outline (including rostrum) in profile nearly straight, down-curved apically, maximum width of head capsule 1.37-1.50 mm. Worker: apical tooth of left mandible longer than first marginal tooth ..... *N. matangensis*

## Molecular barcode analysis

The study profile includes 48 COI sequences, representing eight putative species, as identified from the field using morphological characters. Of these taxa, there are four morphologically assigned to *Nasutitermes* and an additional four assigned to *Bulbitermes*. The number of specimens sequenced from each morphospecies ranged from 1 (a single individual) to 21, depending on specimen availability and sequencing success.

Using the built-in analysis workbench of BOLD, we built a Taxon ID tree using the NJ algorithm applied to a pair wise K2P distance matrix (Figure 25). This tree shows that *Nasutitermes* and *Bulbitermes* form monophyletic groups within the NJ analysis. Moreover, each morphospecies within each of these genera form monophyletic groups. No genera or morphospecies were paraphyletic with respect to each other. There is therefore a high degree of concordance between the morphological taxonomic characters used to sort species from a bifurcating key (Key 1, Key 2) and the molecular taxonomic characters used to sort species on a bifurcating tree (Figure 25).





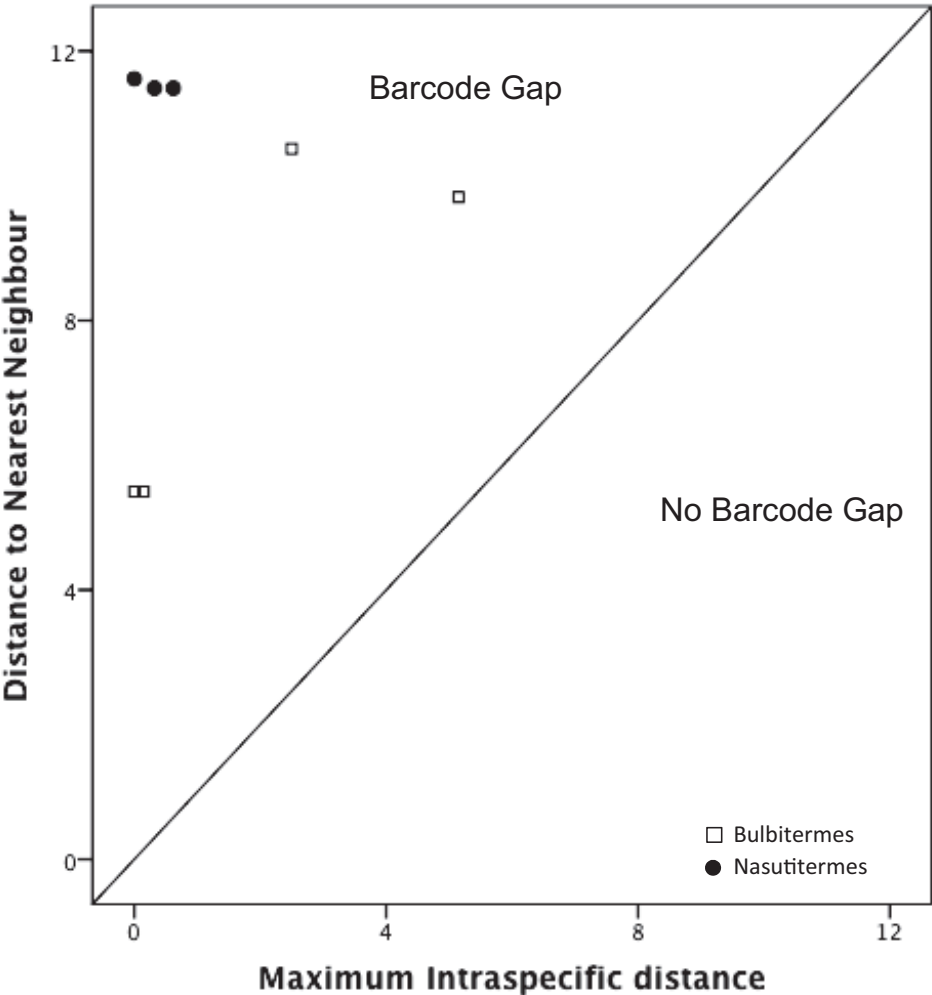
**Figure 25.** Neighbour-Joining analysis of K2P-corrected distances based on the analysis of 650 bp from the COI-5P marker locus in *Nasutitermes* spp. and *Bulbitermes* spp. collected from Sunda region.

Of the four *Bulbitermes* taxa examined, *B. constrictus* forms a sister group with *B. neopusillus*, which together form a sister group with *B. singaporiensis*. This complex is in turn a sister group to *B. flavicans*. Of the *Bulbitermes* taxa represented here, only *B. constrictus* is invariant in the barcode region across all eight specimens analyzed.

Of the four *Nasutitermes* taxa examined, *N. longinasus* forms a sister group with *N. longinasoides*, which together form a sister group with *N. neoparvus*. This three-species complex is in turn sister group to *N. matangensis*. Of the *Nasutitermes* taxa examined, only *N. longinasus* is invariant in the barcode region across all 21 specimens examined.

Levels of barcode variation within and between species showed a distinct barcode gap, whereby the mean interspecific divergence was significantly larger than the mean intraspecific divergence (0.09% vs. 11.86%;  $t = 93.98$ , d.f. = 586,  $P < 0.0001$ ; Table 1). Within genera, the intraspecific distance ranged from as low as 0% (fixed sequences) in *Bulbitermes constrictus* and *Nasutitermes longinasus*, to a high of 5.11% in *Bulbitermes flavicans*.

As expected the NN distance between species was always greater than the maximum intraspecific distance (Fig. 26). For no species was there an overlap in the range of maximum intraspecific distance and the distance to nearest neighbour.



**Figure 26.** Plot of maximum intraspecific divergence against nearest neighbour distance between species (*Bulbitermes* 4 spp. and *Nasutitermes* 4 spp.) as identified from morphological characters. All species fall above the 1:1 line, indicating the presence of a barcode gap.

**Table 1.** Genetic distance summary for barcode sequences generated from *Nasutitermes* and *Bulbitermes* from Sunda region.

Comparison	No. Comparisons	Genetic distance (%)		
		Minimum	Mean (S.E.)	Maximum
Within species	263	00	0.09 (0.03)	5.11
Within genera	325	5.42	11.86 (0.11)	16.01

**Discussion**

Our taxonomic study has two principle outcomes. First, we identify morphological characters that can be used to systematically identify *Nasutitermes* and *Bulbitermes* from the Sunda region of Southeast Asia. Second, we use these representative taxa to conduct a test case of DNA barcoding in termites. That is, we evaluate how well nucleotide sequence information from the COI barcode region of the mitochondrial genome can resolve species relationships through simple neighbour-joining analysis. We find that the field identification of our eight newly-collected species is possible based on morphological characters alone, and to this effect we present two new functional keys that correspond to each of two genera examined. This morphological classification is consistent with our molecular finding that *Nasutitermes* and *Bulbitermes* have statistically distinct COI profiles. A neighbour-joining tree based on aligned nucleotide sequence shows the complete set of sequenced specimens to cluster by species, and by genus. This clustering is perfect in the sense that no species or genus is mis-classified and no taxon is shown to be paraphyletic with respect to current taxonomy. This combined analysis therefore supports the notion that *Nasutitermes* and *Bulbitermes* are evolutionarily distinct, monophyletic genera – a result that substantiates their taxonomic separation by Emerson.

**Soldier of *Bulbitermes***

We find that the number of antennal articles is an easy character that can be used in the field to distinguish *B. constrictus* from *B. neopusillus*; 14 articles for the former and 13 articles for the later. Strongly constricted head-capsule behind antennal sockets also helps to separate these two species. Other species pairs are more difficult to distinguish on morphological criteria. For example, the head capsule is very similar between *B. constrictus* and *B. subulatus*, especially for specimens collected here from central Sumatra.

The development of our bifurcating key (Key 1) revealed several other criteria for distinguishing species pairs. Eleven antennal articles distinguish *B. flavicans* from other three species examined here. *B. flavicans* also has a head-capsule that is somewhat round and weakly constricted behind antennal sockets. Finally, there is atypical variation in the antennal segmentation pattern of *B. singaporiensis*; most specimens have 12 articles, but minorities have 13 articles. Haviland (1898) made this same observation of *Bulbitermes* from Singapore.

### **Soldier of *Nasutitermes***

We find that the width of the head capsule is an easy character that can be used to separate *N. matangensis* from other congeners from the region. Holmgren (1913) already noted the substantial variation in body size for this species (in that case, from Malacca, Malaysia), but subsequent authors (e.g. Ahmad 1965; Thapa 1981; Chhotani 1987; Gathorne-Hardy 2001) nonetheless use size to separate *N. matangensis* from its congeners. Other observations from our morphological analysis include: *N. neoparvus* separates from the other three species by having exactly eleven antennal articles. In addition, the somewhat rounded head capsule in dorsal view and scattered setae are important characters in recognizing the species. Dimorphic soldiers (the largest and smallest soldiers are markedly different in size) can be used to differentiate *N. longinasus* and *N. longinasoides*. Finally, Holmgren (1913) and Tho (1992) postulated that the presence of setae on or surrounding the nasus are a defining character for *N. longinasus*.

### **On identifying *Nasutitermes* and *Bulbitermes***

Generally, the soldier caste of *Nasutitermes* is monomorphic; it is rarely dimorphic. The soldier head capsule is, however, highly variable in size and shape, and without constriction behind antennal sockets. The rostrum of the *Nasutitermes* soldier caste is conical to cylindrical, and the antenna is with 11-14 articles. The pronotum is saddle-shaped, and legs relatively short with abdomen elongate. *Bulbitermes* was separated from *Nasutitermes* as a distinct new genus based on constrictions behind antennal sockets by Emerson (in Snyder 1949). However, any single characteristic peculiar to this genus has not been found; Emerson and subsequent authors were not able to show even a single characteristic separating it from *Nasutitermes*. Based on our morphological analysis, we retain the *Bulbitermes* genus. It may be defined by the following morphological conditions: soldier monomorphic; head capsule with a constriction behind the antennal sockets.

We also found many specimens from different morphospecies and habitats with the constrictions behind antennal sockets hardly visible, hence not *Bulbitermes*. While other characters also do not correspond with the *Nasutitermes*. Also not any single morphological character is prominent to erect them to a new genus.

### **Molecular taxonomy**

Our study shows that DNA barcoding holds promise for helping to solve termite taxonomic problems, with nearest neighbour distances far exceeding maximum intraspecific divergence (Fig. 26), at least for the specimens examined here. Even though our study includes only specimens from a narrow geographic and taxonomic range (two genera within a single subfamily), these observed values suggest that termites are generally amenable to mitochondrial gene barcoding, and that sequence information is

potentially useful for delineating species on a larger scale (e.g. Bergamashi et al. 2007). This finding is significant given the rapidly changing higher taxonomy that is currently affecting termite systematic classifications and phylogeny (Eggleton 2011; Engel et al. 2009). Barcode data may help to resolve species relationships within diverse clades (e.g. *Nasutitermes* with more than 250) for which global morphology-based taxonomic keys would be intractable.

## Acknowledgments

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# *Hospitalitermes krishnai*, a new nasute termite (Nasutitermitinae, Termitidae, Isoptera), from southern Sumatra, Indonesia

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## Abstract

A new species of nasute termite, *Hospitalitermes krishnai* **sp. n.**, is described from soldiers and workers discovered in Lampung Province, Sumatra. This species can be distinguished from other related *Hospitalitermes* species from Southeast Asia by the anterior part of head capsule that is much smaller than the posterior part, head capsule that is moderately constricted behind the antennal sockets, and relatively deep depression between the head and nasus and, finally, the short and robust nasus measuring less than half as long as head capsule. Moreover, in profile the nasus is slightly up-curved but slightly decurved at the apical tip. We name this new species after Professor Kumar Krishna in recognition of his life-long contributions to termite taxonomy, systematics and biology.

## Keywords

Nasutitermitinae, *Hospitalitermes*, nasute termite, new species, Sumatra

## Introduction

*Hospitalitermes* Holmgren is one of only a few termite genera, together with *Lacessitermes* and *Longipeditermes*, that forage in open-air processional columns (Tho 1992, Jones and Gathorne-Hardy 1995, Miura and Matsumoto 1998). These three genera are phylogenetically very closely related (Inward et al. 2007). *Hospitalitermes* has long been treated as a distinct genus within the nasute termites (Holmgren 1913), but morphological characters distinguishing *Hospitalitermes* from related genera are subtle (e.g. Tho 1992, Gathorne-Hardy 2001, Syaukani 2010). *Hospitalitermes bicolor* (Haviland), *H. ferrugineus* (John), *H. flaviventris* (Wasmann), *H. flavoantennaris* Oshima, *H. grassii* Ghidini, *H. hospitalis* (Haviland), *H. medioflavus* (Holmgren), *H. umbrinus* (Holmgren) and *H. seikii* Syaukani have all been collected from the island of Sumatra in Indonesia. In all of these species, the workers typically forage in the afternoon and evening *en masse*. They are conspicuous in the forests of Southeast Asia where their foraging parties can approach half a million individuals (Collins 1979). These foraging parties are composed of a minority of defensive nasute soldiers that protect a majority of workers. In this paper we describe *Hospitalitermes krishnai* sp. n. based on a series of specimens collected from southern Sumatra, Indonesia.

## Material and Methods

Specimens of *Hospitalitermes krishnai* sp. n. were collected from a processional column on the forest floor at Sumber Jaya, Kotabumi, Lampung Province, Sumatra on 18<sup>th</sup> September 2007. We photographed the head, body (in profile) and pronotum of the soldier caste (preserved in 80% ethanol) using a digital microscope (HFVH-8000, Keyence, Osaka). Further, we removed mandibles of the worker caste for closer examinations. We then examined these specimens for diagnostic characters on glass slides mounted with Euparal 3C 239 (Waldeck GmbH & Co. KG, Muenster). We photographed the specimens using a conventional digital camera (Coolpix 3340, Nikon, Tokyo) attached to a Nikon Eclipse E600 lense. From these images, we constructed multi-focused montages using Helicon Focus 4.03 Pro software (Helicon Soft Ltd, Kharkov). General morphological terminology used for describing soldiers and workers follows those of Tho (1992), Sands (1998) and Gathorne-Hardy (2001).

## Measurements

Measurements of the soldier body parts follow those in Roonwal and Chhotani (1989) and Tho (1992). Measurements were made for the soldier caste as follows: head length including nasus (HLN), head length to base of mandibles (HL), nasus length (NL), head width at point of constriction (HWC), maximum head width (HW), maximum

height of head excluding postmentum (HH), and length (PL) and width (PW) of pronotum. We also calculated the ratio of NL to HL.

## Systematics

Family Termitidae Latreille, 1802

Genus *Hospitalitermes* Holmgren, 1913

*Hospitalitermes krishnai* sp. n.

urn:lsid:zoobank.org:act:E6228361-6581-46F2-930D-863E7B438010

[http://species-id.net/wiki/Hospitalitermes\\_krishnai](http://species-id.net/wiki/Hospitalitermes_krishnai)

Figs 1–7

**Description. Alates.** Not available

**Soldier.** (Figs 1–4). Monomorphic. Head capsule entirely black (with indistinct spots behind antennal sockets); nasus with apical third lighter and basal two-thirds darker; antenna (except for the first segment) uniformly sepia brown to dark sepia brown, paler than head capsule. Pronotum in dorsal view slightly paler than or similar to head capsule in coloration. Abdominal tergites dark brown to blackish brown. Coxae and femora sepia brown to dark sepia brown; tibiae pale brown to brown. Head capsule in dorsal view moderately constricted behind antennal sockets, with anterior part excluding nasus extremely smaller than posterior part in size; median portion of its posterior margin nearly straight; dorsal outline (including nasus) in profile moderately concave (i.e., showing a depression). Nasus in dorsal view relatively short and robust, less than half as long as head capsule, in profile slightly up-curved but apical third feebly down-curved. Antenna with 14 segments; third segment longer than fourth; fourth and fifth nearly equal in length, the former slightly broader than the later; 6<sup>th</sup>–14<sup>th</sup> gradually decreasing in length. Pronotum in dorsal view with anterior margin very feebly indented in the middle and posterior margin roundly convex.

**Worker.** (Figs 5–6) Dimorphic. Head capsule dark brown to black. Epicranial suture brown. Fontanel brown to dark brown. Labrum yellowish to brown. Clypeus brown to blackish brown. Anticlypeus yellowish. Antenna sepia brown except for the first segment. Antenna consisting of 15 segments; third segment longer than fourth; fourth slightly shorter than or equal to fifth; 6<sup>th</sup>–15<sup>th</sup> gradually increasing in length. **Left mandible:** apical tooth clearly shorter than first marginal tooth; anterior edge of first marginal tooth distinctly longer than posterior edge; second marginal tooth absent, third marginal tooth smaller than first marginal tooth, but fairly protruding from cutting edge and separated from molar prominence by a distinct gap; fourth marginal tooth retracted, completely hiding behind molar prominence. **Right mandible:** first marginal tooth with anterior edge almost straight; second marginal tooth clearly recognized and separated from much larger first marginal tooth; posterior edge of second



**Table 1.** Measurements (in mm) for 20 soldiers of *Hospitalitermes krishnai* sp. n.

Character	Holotype	Range
Head length including nasus (HLN)	1.95	1.75-1.95
Head length measured to base of mandible (HL)	1.51	1.45-1.51
Nasus length (NL)	0.51	0.44-0.51
Nasus index = NL/HL	0.33	0.30-0.33
Head width at point of constriction (HWC)	0.85	0.78-0.86
Maximum head width (HW)	1.22	1.15-1.22
Maximum height of head excluding postmentum (HH)	0.95	0.82-0.95
Pronotum length (PL)	0.47	0.41-0.47
Pronotum width (PW)	0.80	0.75-0.80

Note: the holotype has the largest value in range for nearly all characters.

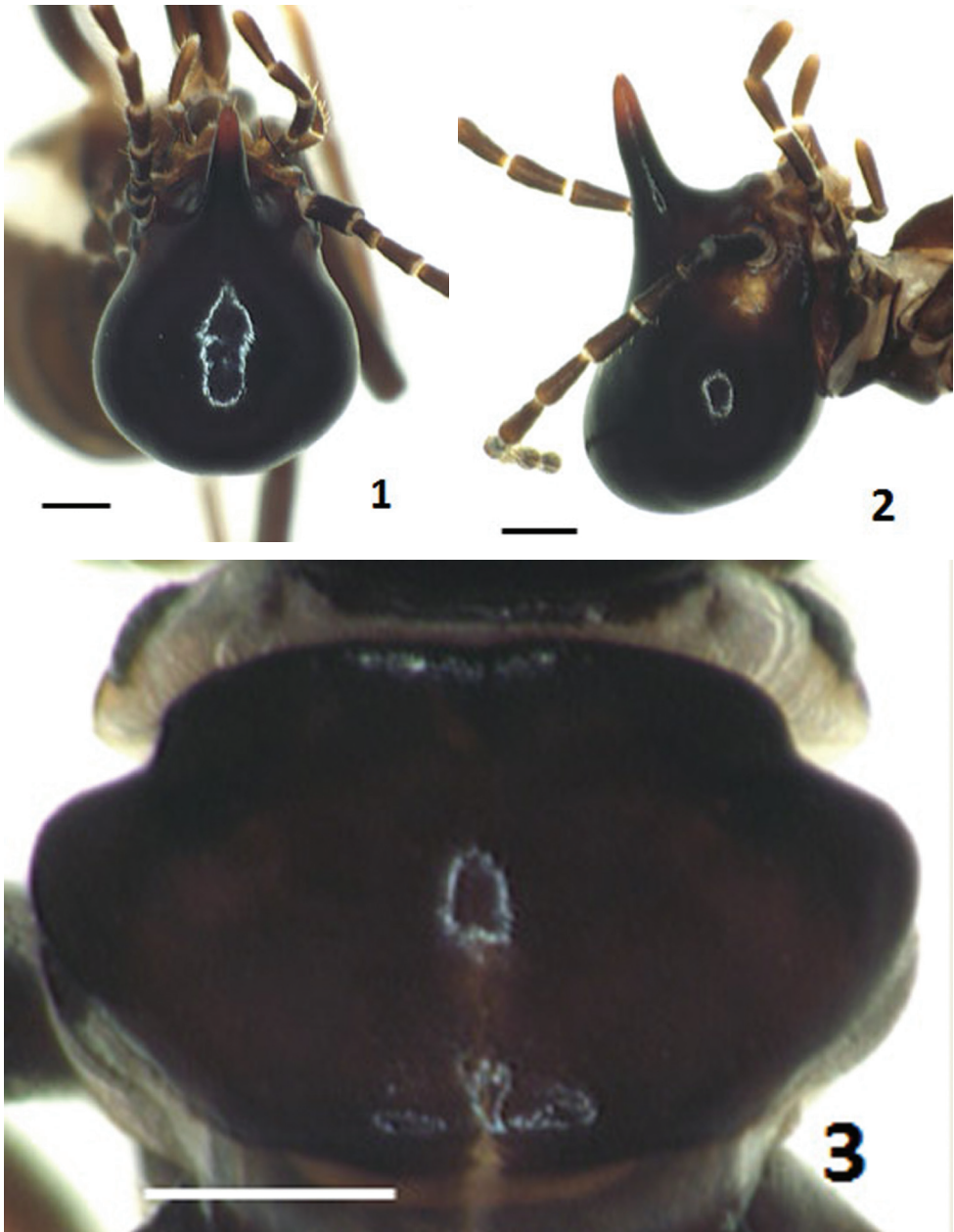
marginal tooth nearly straight; outline of molar plate slightly visible; cockroach notch of molar plate absent.

**Comparisons.** In the soldier caste, *H. krishnai* sp. n. differs from *H. birmanicus* Snyder both in the shape of the head capsule and nasus in dorsal view. The coloration of both antennae and tibiae (pale brown to dark sepia brown) distinguishes *H. krishnai* sp. n. from *H. umbrinus* (Haviland) and *H. diurnus* Kemner. In *H. krishnai* the nasus is less than half as long as the head capsule; this distinguishes it from *H. hospitalis* (Haviland), *H. medioflavus* (Holmgren), and *H. lividiceps* (Holmgren) in which the nasus is more than half as long as head capsule. Finally, *H. krishnai* is distinguished from *H. seikii* Syaukani by the gold-orange abdominal tergites in the latter species.

This species can be distinguished from other related *Hospitalitermes* from Southeast Asia by the anterior part of the head capsule that is much smaller than the posterior part, the head capsule that is constricted behind the antennal sockets, and the relatively deep depression between the head and nasus and, finally, the short and robust nasus measuring less than half as long as head capsule.

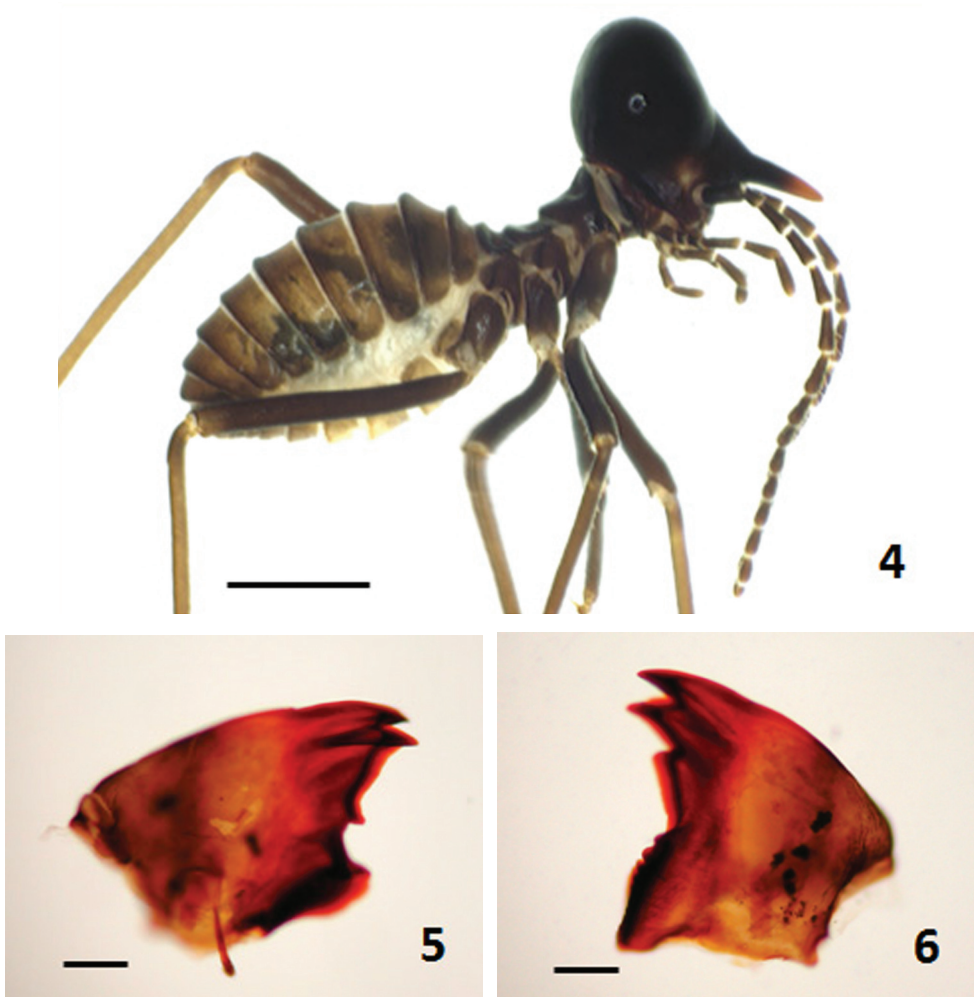
From the examination of thousands of specimens of *Hospitalitermes* from the Syaukani personal collection, as well as a number of type series at the Natural History Museum (London), we note that the pilosity cannot be used as a reliable character for identification since specimens from different *Hospitalitermes* colonies appear extremely variable in this character. We therefore do not consider pilosity here. Moreover, we think that similar variation in the concavity of the head capsule may occur in some related species (Chhotani 1997), and that soldier “eyes” described by Chhotani are actually just indistinct spots. Strictly, speaking *Hospitalitermes* soldiers do not have eyes.

**Material Examined.** Holotype: soldier collected in the afternoon from a mass processional column on the forest floor (very steep slope) in an undisturbed lowland/sub-montane rain forest (1.250 m in altitude), Sumber Jaya (4°47'16"S, 103°35'8"E), Kotabumi, Lampung Province, Sumatra. The nest was not located. Syaukani leg., 18 September, 2007. Colony code: SY-2007-LP-0092. The holotype is deposited at Museum Zoologicum Bogoriense, Cibinong, Indonesia. Paratypes (soldiers and workers from the same colony from which the holotype was collected) are deposited at Mu-



**Figures 1–3.** Soldiers of *H. krishnai* sp. n. Head in dorsal view **1**, head in profile **2**, and pronotum **3**. Scale bar: 0.3 mm **1, 2**, 0.2 mm **3**.

seum Zoologicum Bogoriense, Cibinong (Indonesia), the Natural History Museum, London (UK), Syiah Kuala University, Darussalam, Banda Aceh (Indonesia), the Kitakyushu Museum of Natural History and Human History (Japan), and the American Museum of Natural History, New York (USA).



**Figures 4–6.** *H. krishnai* sp. n. Soldier **4** and workers **5–6**. Habitus in profile **4**, left **5** and right **6** mandibles. Scale bar: 0.5 mm **4**, 0.1 mm **5–6**.

**Etymology.** This species is named after Professor Kumar Krishna who has made significant, life-long contributions to the knowledge of the taxonomy, systematics and biology of termites.

## Discussion

This study contributes to the knowledge of termite diversity in Sumatra, describing one new species of termite with above-ground processional foraging. From morphology it is difficult to separate the genus *Hospitalitermes* from the related *Lacessititermes* (also with processional foraging), but the presence of a notch on the molar plate of the





**Figure 7.** Soldiers and workers of *H. krishnai* sp. n are in processional column on forest floor. Workers are carrying food-balls and returning to the nest. Photo taken by Syaukani (2007).

worker right mandible in *Lacessititermes* is sufficient to distinguish the former from the later (Tho 1992, Gathorne-Hardy 2001, Syaukani 2008, 10) (*Hospitalitermes* lacks this notch). Our description of *H. krishnai* relies on colour, and while this character can be problematic for identification - for example, if color fades over the time - we also find that even type series stored for over a hundred years (e.g. *H. bicolor* that collected by Haviland in 1894), the color has remained adequate and suitable for recognizing the species. In our experience, a combination of colour and other morphological characters are important when identifying *Hospitalitermes* species. Indistinct spots behind antennal sockets of some species are not eyes. Soldiers of *Hospitalitermes* have no eyes.

*Hospitalitermes krishnai* sp. n. is notable because of its peculiar above-ground foraging. Furthermore it shows a distinct size dimorphism with large and small workers. This phenomenon, though rare among termites, has been previously noted for related species. For example, Tho (1992) reported a dimorphic worker caste in *H. hospitalis* from Peninsular Malaysia. Likewise Miura (2004) distinguished three types of worker (major, medium and small) in *H. medioflavus* based on material collected from Borneo. These examples may be interesting to understand the division of labour among workers in a colony. It is the evolution of morphologically distinct worker castes that is famously referred to as Darwin's "special difficulty" (Ratnieks et al. 2011).

We suspect there remain many undescribed species of *Hospitalitermes* in Sumatra. The diversity of previously undescribed termites in this region may stem from the island isolation and resulting high degree of animal endemism.

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# Family-group names for termites (Isoptera), redux

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## Abstract

Forty-eight family-group names are identified for insects among the Isoptera (termites), representing a nearly 19% increase since the last compilation less than 10 years ago. Accordingly, these names are newly catalogued, including various updates from the original summary. The name Reticulitermitidae is recognized as a *nomen nudum* while Caatingatermitinae is newly considered a *nomen invalidum*, and neither is available in zoological nomenclature. A catalogue of the suprafamilial names for Isoptera is appended. The name Xylophagodea is formally proposed for the Isoptera + Cryptocercidae clade.

## Keywords

Isoptera, termites, nomenclature, classification, family-group names, type genera

## Introduction

During the last 25 years numerous efforts have been undertaken to document family-group names for insects and to provide their correct authorship, date, type genus, combining stem, and availability or validity (e.g., Michener 1986; Wahl and Mason 1995; Menke 1997; Sabrosky 1999; Speidel and Naumann 2004; Engel 2005; Engel and Haas 2007; Menke et al. 2008; Miller 2009; Bouchard et al. 2011). Seven years ago such an exercise was completed for the termites (Engel and Krishna 2004a) and it is remarkable that the number of names has grown significantly for this small insect lineage, of approximately 3500 species, such that a full 19% of the names known today were not included in that original account. Accordingly, I provide an updated list, in order of priority, for all family-group names proposed for termites through to

the present day. The list is an updated and corrected version of that provided by Engel and Krishna (2004a), incorporating the various new names and edits of subsequent works (e.g., Engel and Krishna 2004b, 2007; Canello and DeSouza 2005; Engel et al. 2009). As in the earlier summary, all names are presented in their original forms, regardless of present day rank or suffix, with type genus and correct combining stem provided for each. Daggers (†) indicate names proposed for fossil taxa. The format generally follows that of Engel and Krishna (2004a).

In addition I have included here for the first time a summary of all names applied for suprafamilial groups of termites (i.e., names above the family-group ranks and not regulated by the ICZN).

### Catalog of Family-group names

1. **TERMITINA** Latreille, 1802: 293. Type genus: *Termes* Linnaeus, 1758. Combining stem: Termit–. Note: Latreille (1805, 1810) subsequently changed the name of his “famille” to Termitinae but the name was made first available in 1802 (ICZN 1999: Art. 11.7).
2. **CALOTERMITINAE** Froggatt, 1897: 516 [*recte* Kalotermitinae; in accordance with ICZN (1999) Art. 29.1 the name is automatically emended to Kalotermitinae Froggatt, 1897]. Type genus: *Kalotermes* Hagen, 1853 [*Calotermes* Hagen, 1858 is an unjustified emendation: *vide* Engel and Krishna 2001a; ICZN 2002]. Combining stem: Kalotermit–.
3. **GLYPTOTERMITINAE** Froggatt, 1897: 518. Type genus: *Glyptotermes* Froggatt, 1897. Combining stem: Glyptotermit–.
4. **RHINOTERMITINAE** Froggatt, 1897: 518. Type genus: *Rhinotermes* Hagen, 1858. Combining stem: Rhinotermit–.
5. **HETEROTERMITINAE** Froggatt, 1897: 550. Type genus: *Heterotermes* Froggatt, 1897. Combining stem: Heterotermit–.
6. **MASTOTERMITINAE** Desneux, 1904a: 284. Type genus: *Mastotermes* Froggatt, 1897. Combining stem: Mastotermit–.
7. **HODOTERMITINI** Desneux, 1904c: 284. Type genus: *Hodotermes* Hagen, 1853. Combining stem: Hodotermit–.
8. **STOLOTERMITINAE** Holmgren, 1910a: 285. Type genus: *Stolotermes* Hagen, 1858. Combining stem: Stolotermit–. Note: Stolotermitinae has often been included in an expanded Termopsidae for which the latter name has been used for the combined grouping despite the priority of the name based on *Stolotermes*. A petition was submitted (Engel et al. 2003; Engel and Krishna 2004c) and approved (ICZN 2005) reversing priority in favor of Termopsidae whenever *Termopsis* and *Stolotermes* are placed within the same family group. However, in the present classification (Engel et al. 2009 and table 1 herein) stolotermitines are segregated into their own family.
9. **LEUCOTERMITINAE** Holmgren, 1910a: 285. Type genus: *Leucotermes* Silvestri, 1901. Combining stem: Leucotermit–.

10. **COPTOTERMITINAE** Holmgren, 1910a: 285. Type genus: *Coptotermes* Wasmann, 1896. Combining stem: Coptotermi-. Note: Proposed again as new in Holmgren (1910b).
11. **SERRITERMITINAE** Holmgren, 1910a: 285. Type genus: *Serritermes* Wasmann, 1897. Combining stem: Serritermi-.
12. **TERMITOGETONINAE** Holmgren, 1910a: 286. Type genus: *Termitogeton* Desneux, 1904b. Combining stem: Termitogeton-.
13. **MICROCEROTERMITINAE** Holmgren, 1910b: 145. Type genus: *Microcerotermes* Silvestri, 1901. Combining stem: Microcerotermi-.
14. **EUTERMITINAE** Holmgren, 1910b: 146. Type genus: *Eutermes* Heer, 1849. Combining stem: Eutermi-. Note: Given the uncertainty in the application of the name *Eutermes*, and thereby the family-group name Eutermitinae, a petition to suppress proactively the name was submitted to the ICZN for consideration (Engel and Krishna 2005a) which, after discussion (Roisin 2005; Engel and Krishna 2005b), was not approved (ICZN 2007). The name is presently considered *incertae sedis*.
15. **TERMOPSINAE** Holmgren, 1911: 35. Type genus: *Termopsis* Heer, 1849. Combining stem: Termops-. Note: Refer to comments provided for Stolotermitinae (*vide supra*).
16. **PSAMMOTERMITINAE** Holmgren, 1911: 64. Type genus: *Psammotermes* Desneux, 1902. Combining stem: Psammotermi-.
17. **PSEUDOMICROTERTERMITINAE** Holmgren, 1912: 5. Type genus: *Pseudomicrotermes* Holmgren, 1912. Combining stem: Pseudomicrotermi-.
18. **FORAMINITERMITINAE** Holmgren, 1912: 5. Type genus: *Foraminitermes* Holmgren, 1912. Combining stem: Foraminitermi-.
19. **STYLOTERMITINAE** Holmgren and Holmgren, 1917: 141. Type genus: *Stylotermes* Holmgren and Holmgren, 1917. Combining stem: Stylotermi-.
20. †**PLIOTERMITINAE** Pongrácz 1917: 28. Type genus: †*Pliotermes* Pongrácz, 1917. Combining stem: Pliotermi-.
21. **ARRHINOTERMITINAE** Sjöstedt, 1926: 8. Type genus: *Arrhinotermes* Wasmann, 1902. Combining stem: Arrhinotermi-.
22. **ACANTHOTERMITINAE** Sjöstedt, 1926: 8. Type genus: *Acanthotermes* Sjöstedt, 1900. Combining stem: Acanthotermi-. Note: This name has priority over Macrotermi-; however, a petition was submitted to conserve the usage of Macrotermi- (Engel and Krishna 2001b) and was approved by the ICZN (2003). Macrotermi- is to be used whenever *Macrotermes* and *Acanthotermes* are placed into the same family-group taxon.
23. †**MIOTERMITINAE** Pongrácz, 1926: 29 [chart]. Type genus: †*Miotermes* Rosen, 1913. Combining stem: Miotermi-.
24. **MACROTERTERMITINAE** Kemner, 1934: 69. Type genus: *Macrotermes* Holmgren, 1909. Combining stem: Macrotermi-. Note: Refer to comments provided for Acanthotermitinae (*vide supra*).
25. **AMITERMITINAE** Kemner, 1934: 110. Type genus: *Amitermes* Silvestri, 1901. Combining stem: Amitermi-.



26. **MIRO-CAPRITERMITINAE** Kemner, 1934: 166. Type genus: *Mirocapritermes* Holmgren, 1914. Combining stem: Mirocapritermit–. Note: Although Kemner (1934) hyphenated the name in its original spelling, the ICZN (1999) does not allow hyphenation and the family-group name must be considered a single word.
27. **NASUTITERMITINAE** Hare, 1937. Type genus: *Nasutitermes* Dudley, 1890. Combining stem: Nasutitermit–.
28. †**ELECTRITERMITINAE** Emerson, 1942: 10. Type genus: †*Electrotermes* Rosen, 1913. Combining stem: Electrotermit–.
29. **POROTERMITINAE** Emerson, 1942: 10. Type genus: *Porotermes* Hagen, 1858. Combining stem: Porotermit–.
30. **APICOTERMITINAE** Grassé and Noirot, 1954 [1955]: 360. Type genus: *Apicotermes* Holmgren, 1912. Combining stem: Apicotermit–.
31. **ODONTOTERMITINI** Weidner, 1956: 82. Type genus: *Odontotermes* Holmgren, 1910a. Combining stem: Odontotermit–.
32. **CUBITERMITINI** Weidner, 1956: 99. Type genus: *Cubitermes* Wasmann, 1906. Combining stem: Cubitermit–.
33. **MIROTERMITINI** Weidner, 1956: 99. Type genus: *Mirotermes* Wasmann, 1897. Combining stem: Mirotermit–.
34. **CAPRITERMITINI** Weidner, 1956: 100. Type genus: *Capritermes* Wasmann, 1897. Combining stem: Capritermit–.
35. **INDOTERMITIDAE** Roonwal and Sen-Sarma *In* Roonwal, 1958: 81. Type genus: *Indotermes* Roonwal and Sen-Sarma *In* Roonwal, 1958. Stem: Indotermit–. Note: Proposed as new again in Roonwal and Sen-Sarma (1960).
36. †**CRETATERMITINAE** Emerson, 1967 [1968]: 278. Type genus: †*Cretatermes* Emerson, 1967 [1968]. Combining stem: Cretatermit–.
37. **PRORHINOTERMITINAE** Quennedey and Deligne, 1975: 265. Type genus: *Prorhinotermes* Silvestri, 1909. Combining stem: Prorhinotermit–.
38. †**LUTETIATERMITINAE** Schlüter, 1989: 61. Type genus: †*Lutetiatermes* Schlüter, 1989. Combining stem: Lutetiatermit–.
39. †**CARINATERMITINAE** Krishna and Grimaldi, 2000: 134. Type genus: †*Carinatermes* Krishna and Grimaldi, 2000. Combining stem: Carinatermit–.
40. †**ARCHEORHINOTERMITINAE** Krishna and Grimaldi, 2003: 2. Type genus: †*Archeorhinotermes* Krishna and Grimaldi, 2003. Combining stem: Archeorhinotermit–.
41. **RETICULITERMATIDAE** Szalanski, Austin, and Owen 2003: 1514, *nomen imperfectum* [recte Reticulitermitidae] *et nomen nudum*. Note: This name has appeared in several publications (e.g., Sobti et al. 2009) but has not been formally established. It would represent simply a junior synonym of Heterotermitinae.
42. **SYNTERMITINAE** Engel and Krishna, 2004a: 6. Type genus: *Syntermes* Holmgren, 1909. Combining stem: Syntermit–.
43. **SPHAEROTERMITINAE** Engel and Krishna, 2004a: 6. Type genus: *Sphaerotermes* Holmgren, 1912. Combining stem: Sphaerotermit–.

**Table 1.** Hierarchical and synonymic outline of termite classification (modified after Engel et al. 2009). *Nomina nuda* and *nomina invalida* omitted.

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Infraorder <b>Isoptera</b> Brullé, 1832
Family †Cratomastotermitidae Engel et al., 2009
Parvorder Euisoptera Engel et al., 2009
† <i>Cretatermitinae</i> Emerson, 1967 [1968]
† <i>Lutetiatermitinae</i> Schlüter, 1989
† <i>Carinatermitinae</i> Krishna & Grimaldi, 2000
Family Mastotermitidae Desneux, 1904a
= † <i>Pliotermitinae</i> Pongrácz, 1917
= † <i>Miotermitinae</i> Pongrácz, 1926
Family †Termopsidae Holmgren, 1911
Family Hodotermitidae Desneux, 1904c
Family Archotermopsidae Engel et al., 2009
Family Stolotermitidae Holmgren, 1910a
Subfamily Porotermitinae Emerson, 1942
Subfamily Stolotermitinae Holmgren, 1910a
Family Kalotermitidae Froggatt, 1897
= <i>Glyptotermitinae</i> Froggatt, 1897
= † <i>Electrotermitinae</i> Emerson, 1942
Nanorder Neoisoptera Engel et al., 2009
Family †Archeorhinotermitidae Krishna & Grimaldi, 2003
Family Stylotermitidae Holmgren & Holmgren, 1917
Family Rhinotermitidae Froggatt, 1897
Subfamily Coptotermitinae Holmgren, 1910a
= <i>Arrhinotermitinae</i> Sjöstedt, 1926
Subfamily Heterotermitinae Froggatt, 1897
= <i>Leucotermitinae</i> Holmgren, 1910a
Subfamily Prorhinotermitinae Quennedey & Deligne, 1975
Subfamily Psammotermitinae Holmgren, 1911
Subfamily Termitogetoninae Holmgren, 1910a
Subfamily Rhinotermitinae Froggatt, 1897
Family Serritermitidae Holmgren, 1910a
= <i>Glossotermitinae</i> Cancelli and DeSouza, 2005
Family Termitidae Latreille, 1802
Subfamily Apicotermitinae Grassé & Noirot, 1954 [1955]
= <i>Indotermitidae</i> Roonwal & Sen Sarma in Roonwal, 1958
Subfamily Foraminitermitinae Holmgren, 1912
= <i>Pseudomicrotermitinae</i> Holmgren, 1912
Subfamily Sphaerotermitinae Engel & Krishna, 2004a
Subfamily Macrotermitinae Kemner, 1934, nomen protectum [ICZN 2003]
= <i>Acanthotermitinae</i> Sjöstedt, 1926, nomen rejiciendum [ICZN 2003]
= <i>Odontotermitini</i> Weidner, 1956
Subfamily Syntermitinae Engel & Krishna, 2004a
= <i>Cornitermitinae</i> Ensaf et al., 2004, nomen nudum

Subfamily Nasutitermitinae Hare, 1937  
 Subfamily Cubitermitinae Weidner, 1956  
 Subfamily Termitinae Latreille, 1802  
     = *Microcerotermitinae* Holmgren, 1910b  
     = *Amitermitinae* Kemner, 1934  
     = *Mirocapritermitinae* Kemner, 1934  
     = *Mirotermitini* Weidner, 1956  
     = *Capritermitini* Weidner, 1956

*Incertae Sedis*

Eutermitinae Holmgren, 1910b

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44. **CORNITERMITINAE** Ensaf et al., 2004: 284, *nomen nudum*. Type genus: *Cornitermes* Wasmann, 1897. Combining stem: Cornitermit–.
45. **GLOSSOTERMITINAE** Cancellato and DeSouza, 2005: 35. Type genus: *Glossotermes* Emerson, 1950. Combining stem: Glossotermi–.
46. †**CAATINGATERMITINAE** Martins-Neto, Ribeiro-Júnior, and Prezoto, 2006: 127, *nomen invalidum*. Note: I consider this name to be unavailable as the type genus was not explicitly indicated. ICZN (1999) Art. 16.2 requires that after 1999 all new family-group names must have the type genus precisely identified, not implied through the formation of the name. Martins-Neto et al. (2006) nowhere mention the type genus for their new subfamily and include two genera and two species within their grouping. Accordingly, this name fails to meet all of the criteria for availability.
47. †**CRATOMASTOTERMITIDAE** Engel, Grimaldi, and Krishna, 2009: 9. Type genus: †*Cratomastotermes* Bechly, 2007. Combining stem: Cratomastotermi–.
48. **ARCHOTERMOPSIDAE** Engel, Grimaldi, and Krishna, 2009: 11. Type genus: *Archotermopsis* Desneux, 1904d. Combining stem: Archotermops–.

## Catalog of Names above the Family Group

Here I provide a brief checklist of those names applied to termites above the family-group category. While I have included those supraordinal names which combined termites within an expanded taxon alongside one other group of insects (e.g., Aetioptera Enderlein, 1909), I have not listed those older names which united Isoptera with what are today recognized as numerous other orders (e.g., Platyptera Packard, 1883, for Isoptera, Embiodea, Plecoptera, and Psocoptera). In older literature it is often challenging to determine at what rank a particular name was intended or to what categorical level such a name might be equivalent to today. When it has appeared that a name was intended as a family or category loosely equivalent to today's family group ranks, I have not included it here. For example, the 'Termitida' of Haeckel (1866) was as a family of his order Tocoptera, suborder Pseudoneuroptera, section Corrodentia, despite it having a termination reminiscent of that used in other litera-

ture as an ordinal, or other suprafamilial, suffix. Accordingly, I do not consider the Termitida of Haeckel (1866) to be the same as the Termitina or Termitida of Krausse (1906a, 1906b) and Krausse and Wolff (1919), since the former was clearly a family-group name [and thereby a *nomen translatum*, whether intentional or not, of Latreille's (1802) Termitina], while the latter two were explicitly employed as ordinal names. Lastly, despite the considerable biological significance of, and increasing reference in the literature to, the combined Isoptera + Cryptocercidae clade, a name has not formally been proposed for this lineage. Herein I offer the name Xylophagodea for this important biological grouping.

1. **Isopières** Brullé, 1832: 66 [Latinized by Brauer 1885].
2. **Orthoptera socialia** Gerstaecker, 1863: 40. Originally deemed a 'guild' or 'fraternity' ("Zunft", conceptually equivalent in his system to a suborder); equivalent to Isoptera.
3. **Socialia** Börner, 1904: 526. Originally deemed a suborder; equivalent to Isoptera of today [Note: Börner's 'Isoptera' included both Embiodea (as suborder Oligoneura Börner, 1904) and Isoptera (as Socialia *auctorum*)].
4. **Termiten** Krausse, 1906a: 116. Originally deemed an order; equivalent to Isoptera.
5. **Aetioptera** Enderlein, 1909: 171. Originally deemed a superorder; equivalent to Isoptera + Embiodea [as Embiidina].
6. **Cryptoclidoptera** Enderlein, 1909: 171. Originally deemed a suborder; equivalent to all Isoptera excluding Mastotermitidae.
7. **Hemiclidoptera** Enderlein, 1909: 172. Originally deemed a suborder; equivalent to Mastotermitidae.
8. **Termitida** Krausse and Wolff, 1919: 159 [*vide etiam* Rohdendorf 1977]. Equivalent to Isoptera, a form simultaneously used and preferred by the authors.
9. **Termitodea** Kevan, 1977: 12. Originally deemed a suborder; equivalent to Isoptera + Puknoblattinidea Kevan, 1977 [Note: The latter was simultaneously deemed an infraorder for "Puknoblattinidae Sellards, 1908", although Sellards (1908) never established a family-group for his genus *Puknoblattina*. In considering this genus as the sister group to Isoptera, Kevan (1977) was apparently following the notion of Tillyard (1936).].
10. **Termitidea** Kevan, 1977: 12. Originally deemed an infraorder; equivalent to Isoptera.
11. **Isopteroidea** Boudreaux, 1979: 217. Originally deemed a superorder; equivalent to Isoptera as it was the only included order.
12. **Afontanella** Myles, 1998: 334. Originally deemed a suborder; equivalent to Mastotermitidae, Termopsidae s.l., Hodotermitidae, and Kalotermitidae (obviously paraphyletic).
13. **Fontanella** Myles, 1998: 334. Originally deemed a suborder; equivalent to Rhinotermitidae, Serritermitidae, and Termitidae.
14. **Octatubula** Myles, 1998: 334. Originally deemed an infraorder; equivalent to Rhinotermitidae and Serritermitidae.

15. **Quadritubula** Myles, 1998: 334. Originally deemed an infraorder; equivalent to Termitidae.
16. **Euisoptera** Engel, Grimaldi, and Krishna, 2009: 3. Originally rankless; equivalent to all Isoptera exclusive of Cratomastotermitidae and Mastotermitidae.
17. **Neoisoptera** Engel, Grimaldi, and Krishna, 2009: 9. Originally rankless; equivalent to clade comprising Stylotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae.
18. **Xylophagodea**, herein. Originally rankless; equivalent to clade comprising Isoptera and Cryptocercidae.

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# Antennal cropping during colony foundation in termites

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## Abstract

The literature on pairing and mating behavior in termites indicates that a number of distal antennal segments in dealates of both sexes are often removed during colony foundation, with terms such as amputation, mutilation and cannibalism typically employed to report the phenomenon. Here we propose the use of the phrase ‘antennal cropping’ to describe the behavior, and assess naturally occurring levels of its occurrence by comparing the number of antennal segments in museum specimens of alates and dealates in 16 species of Australian termites (four families), supplemented by analyzing published data on *Coptotermes gestroi*. Dealates had significantly fewer antennal segments than alates in 14 of the 16 termite species, with both exceptions belonging to the family Termitidae. Levels of antennal cropping were not significantly different between the sexes but did vary by family. Dealates in the Kalotermitidae removed the most segments (41.3%) and those in the Termitidae removed the fewest (8.9%). We discuss the biological significance of this phylogenetically widespread termite behavior, and suggest that controlled antennal cropping is not only a normal part of their behavioral repertoire but also a key influence that changes the conduct and physiology of the royal pair during the initial stages of colony foundation.

## Keywords

mutilation, cannibalism, density effects, incipient colony

## Introduction

Several studies of colony foundation in termites note that the antennae of newly flown alates are typically undamaged, but the terminal antennal segments in both sexes

are removed during colony establishment (Heath 1903, Imms 1919, Mensa-Bonsu 1976, Hewitt et al. 1972, Costa-Leonardo and Barsotti 1998). The phenomenon has been described as amputation (Heath 1927), mutilation (Heath 1903), and ‘mild’ or ‘restrained’ cannibalism (Mensa-Bonsu 1976, LaFage and Nutting 1978), and in all documented examples the removal of the antennal segments occurred shortly after pair establishment. In *Zootermopsis* the behavior was observed after the nuptial cell was sealed (Heath 1927), three or four days after initial entry of the new pair (Heath 1903); it happened five to ten days after pairing in *Coptotermes havilandi* (now *C. gestroi* – Kirton and Brown 2005) (Costa-Leonardo and Barsotti 1998). The behavior may play a crucial role in the physiological and behavioral transitions that occur in imagoes during colony establishment (Hewitt et al. 1972), but is rarely quantified, Costa-Leonardo and Barsotti (1998) being a notable exception. In this study we used counts of antennal segments in museum specimens of alate and dealate Australian termites to begin characterizing the nature of ‘antennal cropping’, which we advocate as a more neutral term to describe the behavior. Our goals were to establish the phylogenetic extent of the behavior, to determine the precision of the act, and to describe the variation between sexes, among species, and among families.

## Methods

The Australian National Insect Collection (ANIC) at CSIRO Ecosystem Sciences, formerly CSIRO Entomology (Canberra, Australia), was systematically searched for termite species in which samples of both the alate and dealate stage were represented. Antennal segments of these stages were counted at 25× on a Wild M5A stereomicroscope (Meerbrugg, Switzerland), and included the scape, pedicel, and individual segments of the flagellum (= antennomeres or flagellomeres). Cropped antennae are easily distinguished from unaltered antennae as they typically have a melanized, healed wound at the distal tip. Because these are adult insects, wound healing occurs but there is no regeneration of lost segments. Data from the longer of the two antennae of each individual was used in the analysis. A dealate primary reproductive was included in the analysis only if it was collected with its mate or with colony members, or if it was physogastric, indicating that it was collected from an established colony. An individual was excluded from analysis if it exhibited any bodily damage resulting from the collection process. Individuals were sexed based on the shape of the terminal abdominal sternites (Weesner 1969). Sixteen species from ANIC were analyzed (see Table 1 for species names and sample sizes), representing the termite families Stolotermitidae (n = 2), Kalotermitidae (n = 7), Rhinotermitidae (n = 3), and Termitidae (n = 4) (classification of Engel et al. 2009).

We supplemented our data with that obtained from *Coptotermes gestroi* by Costa-Leonardo and Barsotti (1998: Table 4), who published antennal segment counts of

**Table 1.** The mean ( $\pm$  S.E.) number of of antennal segments in reproductives from 17 termite species. The t-tests are unpaired between alates and dealate.

Family	Length of antennae (# of segments)		Change in length of antennae		<i>t</i>	df	<i>p</i>
Species	Alates (n)	Dealates (n)	# of segments	%			
Stolotermitidae							
<i>Porotermes adamsoni</i>	16.3 ± 0.9 (9)	11.6 ± 1.1 (5)	-4.7	-32.1	8.784	12	<0.001
<i>Stolotermes victoriensis</i>	14.9 ± 1.8 (8)	10.2 ± 1.6 (12)	-4.7	-31.5	6.038	18	<0.001
Kalotermitidae							
<i>Neotermes papua</i>	18.5 ± 0.7 (2)	–		–			
<i>Neotermes insularis</i>	18.7 ± 1.3 (14)	11.8 ± 1.3 (12)	-6.9	-36.9	13.806	24	<0.001
<i>Ceratokalotermes spoliator</i>	13.2 ± 0.8 (9)	8.3 ± 1.2 (6)	-4.9	-33.3	9.316	13	<0.001
<i>Kalotermes convexus</i>	13.6 ± 1.0 (10)	7.8 ± 1.3 (15)	-5.8	-42.6	12.277	23	<0.001
<i>Glyptotermes brevicornis</i>	13.5 ± 0.8 (6)	8.4 ± 1.6 (14)	-5.1	-37.8	7.380	18	<0.001
<i>Cryptotermes secundus</i>	16.5 ± 1.4 (14)	8.5 ± 1.0 (12)	-8.0	-48.5	16.490	24	<0.001
<i>Bifiditermes condonensis</i>	17.7 ± 2.0 (9)	9.1 ± 1.7 (11)	-8.6	-48.6	10.372	18	<0.001
Rhinotermitidae							
<i>Heterotermes ferox</i>	16.9 ± 1.0 (10)	13.5 ± 2.1 (2)	-3.4	-20.1	3.792	10	0.004
<i>Schedorhinotermes actuosus</i>	18.8 ± 2.4 (12)	13.0 ± 2.3 (5)	-5.8	-30.9	4.533	15	<0.001
<i>Coptotermes gestroi</i>	20.2 ± 0.4 (80)	12.9 ± 0.2 (80)	-7.3	-36.1	15.541	158	<0.001
<i>Coptotermes lacteus</i>	18.4 ± 1.8 (16)	13.2 ± 0.5 (4)	-5.1	-27.9	5.585	18	<0.001
Termitidae							
<i>Microcerotermes turneri</i>	13.8 ± 0.4 (9)	12.7 ± 2.2 (18)	-1.1	-8.0	1.454	25	0.158
<i>Drepanotermes perniger</i>	15.6 ± 2.2 (11)	16.5 ± 1.7 (13)	0.8	+6.7	1.058	22	0.302
<i>Xylochomitermes occidualis</i>	14.9 ± 0.3 (14)	13.2 ± 1.2 (19)	-1.8	-11.4	5.548	31	<0.001
<i>Tumulitermes nastilis</i>	16.1 ± 1.0 (8)	12.2 ± 0.4 (5)	-3.9	-23.0	8.242	11	<0.001

alates and dealates without statistical analysis. As in our original data, we used data from the longer of the two antennae of *C. gestroi* individuals.

## Statistical analyses

The antennae lengths of the 17 species were analysed in a four factor Generalised Linear Model (GLM). The four factors used in analysis were species nested in families, families, sex, and wing status (alate or dealate). Planned posthoc pairwise comparisons were used to find differences between species and families; all comparisons were Tukey's-adjusted to account for potential errors. The posthoc comparisons were unnecessary for sex and status as there were only two levels in these factors. Interac-

tions between families, sex and wing status were also considered in the GLM. Finally, unpaired t-tests were performed on wing-status for each family.

Costa-Leonardo and Barsotti (1998) collected *Coptotermes gestroi* alates from two sources, the first from a tree stump, i.e. before the alates had flown, and the second from a swarm, i.e. during the mating flight but prior to pairing. We compared the antennal length of these alates to determine whether there was a difference between pre-flight and during-flight alates using a two-way ANOVA with source and sex as the factors. In addition Costa-Leonardo and Barsotti (1998) measured dealated, mated pairs of *Coptotermes gestroi* twice; the first was at nine months after colony initiation and the second 2 years after colony initiation. We compared the antennal length from these dealates to determine whether there was a difference over time using a two-way ANOVA with age and sex as the two factors.

Statistical analyses were performed using Systat v. 9.0 (1998).

## Results

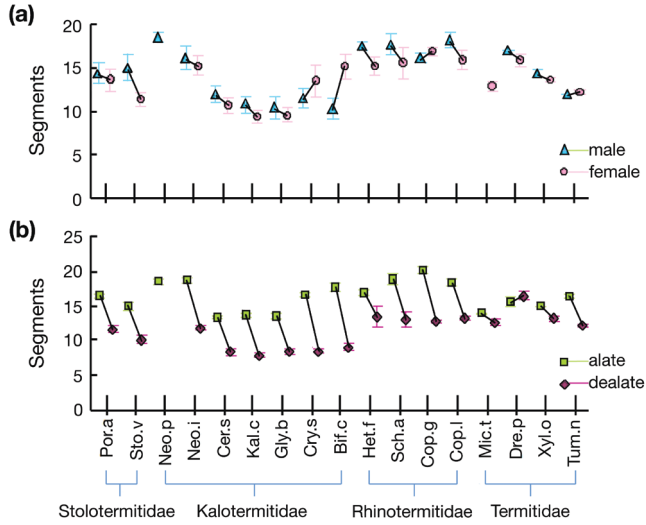
We documented a wide range of antennal lengths in the imaginal stage of termites (Table 1). Among alates, *Schedorhinotermes actuosus* had the highest number of antennal segments, around 19, and *Ceratokalotermes spoliator* had the fewest, with about 13. Among dealates segments were most numerous (around 16) in *Drepanotermes perniger*, and *Kalotermes convexus* had the fewest, with around eight.

Overall, the difference between the sexes was small, about one antennal segment, with overlapping standard errors; males had  $14.5 \pm 0.7$  antennal segments whereas females had  $13.5 \pm 0.6$ . However the difference between winged and wingless adults was substantial, about five antennal segments, with non-overlapping standard errors. Alates averaged  $16.3 \pm 0.5$  antennal segments, whereas dealates averaged  $11.4 \pm 0.6$  (all averaged across species; Fig. 1).

In the GLM analysis, significant differences were found between species (nested within families) ( $F_{12,379} = 8.151$ ;  $p < 0.001$ ), termite families ( $F_{3,379} = 25.586$ ;  $p < 0.001$ ), and wing status ( $F_{1,379} = 164.940$ ;  $p < 0.001$ ), but no significant differences between the sexes ( $F_{1,379} = 0.133$ ;  $p = 0.715$ ) (Table 2). The GLM analysis explained three quarters of the variation ( $r^2 = 0.757$ ). The mean differences in antennal length and Tukey-corrected posthoc pairwise comparisons between species are listed in Table 3. The general pattern is *Ceratokalotermes spoliator*, *Kalotermes convexus*, *Glyptotermes brevicornis* and *Cryptotermes secundus*, all in the Kalotermitidae, are different from *Schedorhinotermes actuosus*, *Coptotermes gestroi* and *Coptotermes lacteus* in the Rhinotermitidae, and *Microcerotermes turneri*, *Drepanotermes perniger* and *Tumulitermes nastilis* in the Termitidae. Differences between species therefore can be clustered into differences between families.

This pattern is also seen in the results of the GLM, as the  $F$  ratios suggest that the effect of family was about three times more important than the effect of species. In particular the Rhinotermitidae had longer antennae than the other families. Species





**Figure 1.** Average ( $\pm$  standard error) antenna length measured in number of antennal segments of 17 termite species for **a** male and females; and **b** alates and dealates. Species names abbreviated as in Table 3.

in the Termopsidae had  $13.3 \pm 1.3$  antennal segments, those in Kalotermitidae  $13.0 \pm 1.2$ , the Rhinotermitidae  $16.7 \pm 0.3$ , and the Termitidae  $14.4 \pm 0.6$ . The mean pairwise differences in antennal length between families, and the Tukey-corrected posthoc pairwise comparisons, were significantly different for Kalotermitidae  $\times$  Rhinotermitidae (mean difference 3.3,  $p < 0.001$ ), Kalotermitidae  $\times$  Termitidae (md 2.1,  $p = 0.002$ ) and Rhinotermitidae  $\times$  Termitidae (md 2.0,  $p = 0.004$ ); the remaining comparisons were not significant (Kalotermitidae  $\times$  Termopsidae md 1.2,  $p = 0.098$ ; Rhinotermitidae  $\times$  Termitidae md 1.2,  $p = 0.239$ ; Termitidae  $\times$  Termopsidae md 0.8,  $p = 0.688$ ).

The largest  $F$  ratio from the GLM was for wing status, which was about six times more important than family, and 20 times more important than species differences in determining antennae length. This is clear from the paired  $t$ -tests: 14 of the 16 possible alate vs. dealate comparisons were significant (Table 1, Fig. 1). The two species without a difference in alate and dealate antennal length were *Microcerotermes turneri* and *Drepanotermes perniger*, which both belong to the same branch of the Termitinae in the Termitidae, whereas *Xylochomitermes occidualis* lies in another branch of the Termitinae and *Tumulitermes nastilis* is in the Nasutitermitinae (Inwood et al. 2007, Legendre et al. 2008).

Only one interaction was significant: family  $\times$  wing status ( $F_{3,389} = 11.986$ ,  $p < 0.001$ ), showing that antennal cropping varies among families. This variation is clear in Fig. 2, with alates in Stolotermitidae, Kalotermitidae and Rhinotermitidae all losing five to seven antennal segments after dealation, whereas in Termitidae dealates lose perhaps two. Expressed as a percentage, kalotermids cropped on average the most antennal segments: Stolotermitidae 32.0%, Kalotermitidae 41.3%, Rhinotermitidae 28.8% and Termitidae 8.9%. The lack of an effect due to sex either as a main effect,

**Table 2.** The results of the generalised linear model run on antennal length.

Factor	Sum-of-Squares	df	Mean-Square	F-ratio	p
Species(Family)	499.010	12	41.584	8.151	0.000
Family	391.608	3	130.536	25.586	0.000
Sex	0.679	1	0.679	0.133	0.715
Wing status	841.514	1	841.514	164.940	0.000
Family × Sex	16.775	3	5.592	1.096	0.351
Family × Wing status	183.450	3	61.150	11.986	0.000
Sex × Wing status	0.140	1	0.140	0.027	0.868
Family × Sex × Wing status	4.612	3	1.537	0.301	0.824
Error	1933.631	379	5.102		

or in the interaction terms (Table 2) is clear from Figs. 1 and 2, with mostly small and inconsistent differences between males and females.

**Additional comparisons for *Coptotermes gestroi***

The mean antennal length for *Coptotermes gestroi* alates from the tree stump (i.e., prior to swarming) was  $20.7 \pm 0.7$  for males and  $19.8 \pm 1.1$  for females, and from the swarm it was  $19.2 \pm 0.9$  for males and  $21.0 \pm 0.6$  for females. There were no significant differences found either for alate source ( $F_{1,76} = 0.032$ ;  $p = 0.858$ ) or sex ( $F_{1,76} = 0.228$ ;  $p = 0.635$ ), and the interaction was not significant ( $F_{1,76} = 2.594$ ;  $p = 0.111$ ).

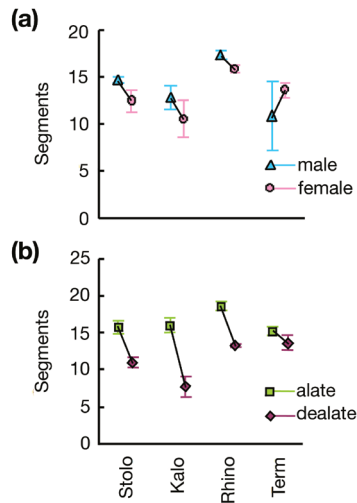
The mean antennal length for *Coptotermes gestroi* dealates at nine months after colony initiation was  $12.2 \pm 0.6$  for males and  $13.6 \pm 0.3$  for females, and from 2 years after colony initiation it was  $12.6 \pm 0.3$  for males and  $13.3 \pm 0.3$  for females. There were no significant differences found for age ( $F_{1,76} = 0.035$ ;  $p = 0.853$ ) but there was a significant difference for sex ( $F_{1,76} = 7.122$ ;  $p = 0.009$ ), as females had longer antennae than males, albeit only one segment longer; the interaction was not significant ( $F_{1,76} = 0.651$ ;  $p = 0.422$ ), indicating that the difference between the sexes did not change over time.

**Discussion**

Our data suggest that antennal cropping is a phylogenetically widespread, fairly precise behavior. There was a significant decrease in the number of antennal segments in dealates when compared to alates in termites from all families except two species of Termitidae. No more than half of the antenna was trimmed in any case, although our data may slightly underestimate differences since we used the longer of the two antennae in our analysis. There is some variation in both the number of segments in the right and left antennae of individuals (Costa-Leonardo and Soares 1997, Costa-Leonardo and Barsotti 1998), and among individuals within a species (Prestage et al. 1963). Our analysis sup-

**Table 3.** The matrix of pairwise mean differences in antennal length between species. Pairs that were significantly different in Tukey adjusted pairwise posthoc comparisons from the GLM posthoc are indicated as \*  $p < 0.05$ , †  $p < 0.01$ , ‡  $p < 0.001$ . Nb. *Neotermes papue* was excluded due to a lack of data. Abbreviations: Por.a = *Polytermes adamsoni*; Sto.v = *Stolotermes victoriensis*; Neo.i = *Neotermes insularis*; Cero.s = *Ceratokolotermes spoliator*; Kalo.c = *Kalotermes convexus*; Glypt.b = *Glyptotermes brevicornis*; Cry.s = *Cryptotermes secundus*; Bif.c = *Bifiditermes condonensis*; Het.f = *Heterotermes ferox*; Sch.a = *Schedorhinotermes actuosus*; Cop.g = *Coptotermes gestroi*; Cop.l = *Coptotermes lacteus*; Mic.t = *Microcerotermes turneri*; Dre.p = *Drepanotermes perniger*; Xyl.o = *Xylochomitermes occidualis*; Tum.n = *Tumulitermes nastilis*.

	Por.a	Sto.v	Neo.i	Cers	Kal.c	Gly.b	Crys	Bif.c	Het.f	Sch.a	Cop.g	Cop.l	Mic.t	Dre.p	Xyl.o
Sto.v	0.7														
Neo.i	1.1	1.8													
Cers	3.1	2.5	4.2‡												
Kal.c	3.3*	2.7	4.5‡	0.2											
Gly.b	3.1	2.4	4.2‡	0.0	0.3										
Crys	1.5	0.9	2.6†	1.6	1.8	1.6									
Bif.c	0.8	0.2	2.0	2.3	2.5	2.3	0.7								
Het.f	0.5	1.2	0.6	3.6	3.8	3.6	2.0	1.3							
Sch.a	2.2	2.9	1.1	5.3‡	5.5‡	5.3‡	3.7†	3.0	1.7						
Cop.g	2.5	3.2*	1.4	5.6‡	5.9‡	5.6‡	4.0‡	3.4‡	2.0	0.3					
Cop.l	1.9	2.6	0.8	5.0‡	5.2‡	5.0‡	3.4*	2.7	1.4	0.3	0.6				
Mic.t	2.0	2.7	0.9	5.1‡	5.3‡	5.1	3.5*	2.8	1.5	0.2	0.5	0.1			
Dre.p	1.8	2.5	0.7	5.0‡	5.2‡	4.9†	3.4*	2.7	1.3	0.4	0.7	0.1	0.		
Xyl.o	0.2	0.9	0.9	3.4	3.6	3.3	1.8	1.1	0.2	1.9	2.3*	1.6	1.8	1.6	
Tum.n	0.3	1.0	0.8	3.4†	3.7‡	3.4	1.8	1.1	0.2	1.9	2.2	1.6	1.7	1.5	0.0



**Figure 2.** Average ( $\pm$  standard error) antenna length measured in number of antennal segments of four termite families for **a** male and females; and **b** alates and delates. Abbreviations: Stolo = Stolotermitidae; Kalo = Kalotermitidae, Rhino = Rhinotermitidae; Term = Termitidae.

ports Costa-Leonardo and Barsotti's (1998) conclusion that antennal cropping occurs only during the early stages of colony formation in termites, and Hewitt et al.'s (1972) suggestion that it is a controlled process. We propose that antennal cropping is part of the normal behavioral repertoire during colony foundation in lower termites and at least some of the Termitidae. As such, terms such as amputation, mutilation and cannibalism should be avoided. We acknowledge that interactions between reproductives in polygynous colonies (a derived condition) may influence the extent of antennal cropping (Thorne 1984, Brandl et al. 2001), and that ageing, accidents, laboratory conditions, or aggression in other contexts may result in the wounding of antennae, legs, mouthparts, and wing pads (e.g., Williams 1959, Darlington 1988, Zimmerman 1983).

The sole description of the behavioral process leading to the loss of antennal segments is by Heath (1903) in *Zootermopsis*; this author indicates that the condition results from both self-cropping (autotilly) and from a reciprocal interaction between the sexes. He describes individuals that repeatedly bit off small portions of their own antennae, as well as members of a pair taking turns biting off the antennal tips of their partner. In the latter case, the antennae assumed a more or less 'stump-like condition' within a few hours. Heath (1903) could fathom no possible functional significance of the behavior, since it 'in no visible way affects their existence'. Later, Nel (1968), Hewitt et al (1972), and Watson et al. (1972) studied *Hodotermes mossambicus* and concluded that antennal cropping was a key element in the complex transition from the preflight group behavior exhibited by alates within a parent colony, to the paired behavior shown by post-flight dealates during colony initiation. The suite of coordinated behavioral changes in paired *H. mossambicus* include mating, oviposition and building behavior, aggression to intruders, and markedly increased levels of water consumption (Watson et al. 1972).

**Table 4.** The dual nature of antennal cropping: both partners are affected regardless of whether an individual crops its own or its partner's antennae.

	<b>Crop self</b>	<b>Crop partner</b>
<b>Effect on self</b>	Decreases self ability to detect environmental stimuli	Decreases tactile stimulation of self
<b>Effect on partner</b>	Decreases tactile stimulation of partner	Decreases partner's ability to detect environmental stimuli

Antennal cropping was proposed to play a key role in the transition to pair behavior by decreasing the amount of physical contact perceived by the male and female (Hewitt and Nel 1969, Hewitt et al. 1972). The logic was that if an individual's partner had stumpy antennae, then that individual would experience physical contact roughly equivalent to that of a solitary insect. Although Hewitt et al. (1972) demonstrated that it was the receipt of antennal stimulation on the body that was pivotal in the behavioral transitions of *H. mossambicus*, antennae are important in both transmitting and receiving information (Fraser and Nelson 1984). The loss of terminal antennal segments, then, likely results in a significant reduction in sensory input to the nervous system, the nature and extent of which would depend on the distribution and type of antennal receptors. Antennal sensillae in termites have been studied primarily in workers and soldiers, but in those developmental stages antennal sensillae of most types, including mechanoreceptors and chemoreceptors, increase in number or in length in the more distal segments (Prestage et al. 1963, Tarumingkeng et al. 1976, Yanagawa et al. 2009). If the same is true in alates, then the removal of the distal segments has potential to significantly reduce nervous input, with the loss of these signals affecting the endocrine system and, in turn, gene expression patterns (Gilbert 2005). Sensillae on the distal antennae of alates may be associated primarily with flight, mate finding, and mate evaluation, activities that occur only within the time frame prior to colony establishment. If so, these sensillae may be superfluous, and antennal cropping considered analogous to the shedding of wings: both behaviors remove a body part that no longer has functional significance. A detailed comparison of the sensillae in the proximal vs. distal halves of the antenna of alates would be of interest, because the proximal half of the antenna is required for successful colony foundation (Hewitt et al. 1972), and Richard (1969) noted that antennal cropping never reaches the level of the pedicel and its associated chordotonal organs.

The dual nature of the antenna as both transmitter and receiver dictates that regardless of whether a paired individual crops its own or its partner's antenna, both members of the pair are likely to be affected (Table 4). In its role as receiver, antennal cropping would decrease an individual's ability to detect environmental stimuli, including pheromones. In its role as transmitter, shorter antennae result in decreased tactile stimulation of the partner.

Antennal cropping has been recorded in several cockroach taxa, but its functional significance is unknown. Nymphs of *Blattella germanica* self-prune their antennae – the ends are nipped off just prior to molting (Campbell and Ross 1979). Although



first and second instars of *Cryptocercus punctulatus* almost always have intact antennae, cropped antennae can be found in third instars and are common in fourth instars (Nalepa 1990). Nymphs and adults of the myrmecophiles *Attaphila fungicola* and *A. bergi* usually have cropped antennae (Bolívar 1901, Brossut 1976); Wheeler (1900) was of the opinion that the host ants trimmed them for their guests, likening it to the human habit of cropping the ears and tails of dogs.

## Conclusion

Antennal cropping should be considered a key factor when studying changes in behavior and physiology during termite colony foundation, as density dependent effects result at least in part from sensory input mediated by the antennae in both crickets and locusts (Saeki 1966, Mordue 1977, Applebaum and Heifetz 1999). The role of antennal cropping, however, may vary with species or family, and interact with a number of additional stimuli in instigating the abrupt change from group to paired behavior. These stimuli may include exposure to the outside environment, wing use, wing loss (dealation), tandem behavior, and digging behavior. Regardless of the influence of these stimuli in shifting imagoes from group to paired behavior during colony initiation, however, the royal pair eventually re-acclimates to group living as their own offspring increase in number.

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# Webspinners in Early Eocene amber from western India (Insecta, Embiodea)

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## Abstract

The family Scelembiidae (Neoembiodea: Embiomorpha: Archembioidea) is recorded from Asia for the first time, based on two individuals preserved in Early Eocene amber from the Cambay Basin, western India. *Kumarembia hurleyi* Engel & Grimaldi, **gen. n. et sp. n.**, is described, figured, and distinguished from other archembioid genera. The genus shares male genitalic features with scelembiids, otherwise known from South America and Africa.

## Keywords

Polynoptera, Embioptera, Embiidina, Neoembiodea, Tertiary, taxonomy, India

## Introduction

Embiodea are one of the more infrequently encountered and investigated orders of insects. This is unfortunate given their remarkable morphological specializations, most of which relate to the production of and life within silken galleries. For example, the probasitarsus is greatly swollen and encompasses distinctive silk glands from which the galleries are spun. The wings are unique among the flying insects for their great flexibility, permitting individuals to move in reverse through their silken tunnels, but can be made more rigid by pumping haemolymph into distinctive ‘blood sinuses’, enabling them to gain temporary rigor and permit controlled flight. Females are apterous, while males can be either fully winged or shed their wings, much like termites. Even more fascinating is that where known, all species are gregarious, living in small colonies, much like their putative relatives among the Zoraptera.

The relationship of Embiodea to other orders has been problematic, much like everything pertaining to the phylogeny of webspinners. Among the numerous competing hypotheses, those with the greatest support are a relationship to the Phasmatoidea (e.g., Rähle 1970; Terry and Whiting 2005; Kjer et al. 2006; Ishiwata et al. 2011) or the Zoraptera (e.g., Engel and Grimaldi 2000; Grimaldi and Engel 2005; Yoshizawa 2007, 2011). Considerable work continues documenting the diversity of the order, with many hundreds of new species awaiting description (Ross 2000), and revising hypotheses of relationship based on this growing knowledge of the range of morphological variation observed across this fascinating group. Unfortunately, the fossil record has to date provided minimal insights toward clarifying systematic issues pertaining to embiodean evolution. This is because only nine definitive webspinner species are known from the fossil record (Table 1) and many of these are relatively modern, thereby relating more to questions of Tertiary biogeography than to higher-level branching patterns, many of which likely date from the Early Cretaceous or even Late Jurassic. Given this sparse record, any fossil webspinners are of considerable significance.

Herein we provide the description of a new genus and species of fossil webspinner based on two exceptionally well preserved individuals (Figs. 1, 2) recently recovered from Early Eocene amber of the Cambay Basin in western India. These are the first fossil webspinners from Asia (Table 1) and also the first records of their family, Scelembiidae, from the Oriental Region.



**Table 1.** Described fossil webspinners (updated from Engel and Grimaldi 2006). The fossil *Clothonopsis miocenica* Hong and Wang (1987) from the Miocene of China was originally described as a clothodid but is actually a bibionid fly (Zhang 1993).

Embiodea: Neoembiodea		
Teratembiiidae		
<i>Oligembia vetusta</i> Szumik, 1994	Miocene (Burdigalian)	Dominican Republic
Anisembiiidae		
<i>Poinarembia rota</i> Ross, 2003b	Miocene (Burdigalian)	Dominican Republic
<i>Glyphembia amERICA</i> Ross, 2003b	Miocene (Burdigalian)	Dominican Republic
<i>Glyphembia vetehae</i> (Szumik, 1998) Ross, 2003b	Miocene (Burdigalian)	Dominican Republic
“Embiidae”		
“ <i>Embia</i> ” <i>florissantensis</i> Cockerell, 1908*	Eocene-Oligocene	Colorado
<i>Electroembia antiqua</i> (Pictet, 1854) Ross, 1956	Eocene (Lutetian)	Baltic
Scelembiiidae		
<i>Kumarembia hurleyi</i> , gen. et sp. n.	Eocene (Ypresian)	India
Pachylembiidae: Sorellembiinae		
<i>Sorellembia estherae</i> Engel & Grimaldi, 2006	Cretaceous (Albian)	Myanmar
Notoligotomidae: Burmitembinae		
<i>Burmitembia venosa</i> Cockerell, 1919	Cretaceous (Albian)	Myanmar
*Incertae Sedis*		
Sinembiiidae		
<i>Sinembia rossi</i> Huang & Nel, 2009	Jurassic (Bathonian)	Inner Mongolia, China
<i>Juraembia ningchengensis</i> Huang & Nel, 2009	Jurassic (Bathonian)	Inner Mongolia, China

\* This species has been placed in the genus “*Lithembia*” by Ross (1984) but as noted by Engel and Grimaldi (2006) and Miller (2009) the generic name is a *nomen nudum* and so we have reverted to Cockerell’s original combination for our table. The species very likely does not belong to *Embia* and the two syntypes (UCM-4421 and YPM-26169) should be re-examined and critically revised (based on photographs of the specimens they would appear to have the primitive condition of basal vein branching as delimited by Szumik (1996) (Engel pers. obs.).

\*\* E.S. Ross (pers. comm. 2010) presently does not consider these to belong to Embiodea and, indeed, the presence of a distinct ovipositor, fully-winged females, absence of probasitarsal modifications (which is not swollen despite the assertion of the authors), absence of a radial blood sinus (indeed, from the figures provided, the presence of any blood sinuses seems to require confirmation), and cerci with three cercomeres exclude the species from the order. These species certainly require revision, as do all compressions presently assigned to Embiodea.

Material and methods

The age, origin, and biotic diversity of the Cambay amber are reviewed by Rust et al. (2010). Briefly, the amber occurs in rich concentrations within lignite mines in Gujarat State, western India. Its dating based on microfossils is earliest Eocene, ca. 50–52 Ma, just prior to complete suturing of India to the Asian continental plate. The amber was formed by trees in the Dipterocarpaceae, which are the dominant rainforest trees in Southeast Asia today. Specimens were prepared and preserved using the

methods described by Nascimbene and Silverstein (2000). Morphological terminology and abbreviations largely follow those of Ross (2000) and the general classification is modified from Ross (1970, 2001, 2003a, 2003b, 2006, 2007), Szumik (1996, 2004), Engel and Grimaldi (2006), Szumik et al. (2008), and Miller (2009). Measurements were made using an ocular micrometer on an Olympus SZX-12 stereomicroscope and photomicrographs prepared using a Nikon D1× digital camera attached to an Infinity K-2 long-distance microscope lens.

## Systematic Paleontology

### Family Scelembiidae Ross, 2001

<http://species-id.net/wiki/Scelembiidae>

**Diagnosis.** Mandibles depressed, with incisive teeth well differentiated from molar area. Wings without crossveins between  $MA_1$  and  $MA_2$ ;  $CuA$  frequently diffuse. Male 10T with a membranous area occupying base and center of sclerite; 10R and 10L connected by thin basal bar; 10RP<sub>2</sub> present, short, thumb-like; 10LP<sub>1</sub> a curved, apically-forked process; HP rectangular, centered; LC<sub>1</sub> with setae on apical area.

**Included genera.** *Ambonembia* Ross (= *Ischnosembia* Ross), *Biguembia* Szumik (= *Aphanembia* Ross), *Gibocercus* Szumik, *Kumarembia* Engel and Grimaldi gen. n., *Litosembia* Ross, *Malacosembia* Ross, *Navasiella* Davis, *Pararhagadochir* Davis, and *Rhagadochir* Enderlein (= *Scelembia* Ross) (Szumik 2004).

### *Kumarembia* Engel & Grimaldi, gen. n.

[urn:lsid:zoobank.org:act:F30F7AFB-D379-4F74-A76F-612169FD3B48](http://zoobank.org/act:F30F7AFB-D379-4F74-A76F-612169FD3B48)

<http://species-id.net/wiki/Kumarembia>

**Type species.** *Kumarembia hurleyi* Engel and Grimaldi, sp. n.

**Diagnosis. Male:** Head relatively slender, longer than wide, elongate oval (Fig. 3a), slightly narrowed posteriad; compound eyes well developed, prominent, emarginate at base of antenna, and less so on posterodorsal margin, setose, with stiff setae, some longer than diameter of facets, and most setae on outermost distal surface (Fig. 3b); ocelli absent; antennae long, with 17 articles (incomplete in holotype, number of articles based on paratype), articles apparently uniformly sclerotized and pigmented (apical articles not differently pigmented or unpigmented); lacinia entirely sclerotized, with two small apical teeth (Fig. 3b), remainder of maxilla generalized; mentum sclerotized, small, approximately one-third length of labium, without setae, tightly joined to submentum; submentum sclerotic, with four stiff, very fine setae, anterior margin straight (appearing to have medial hump owing to mentum), lateral

margins relatively straight and converging posteriorly toward base, margins meet before ventral margin of head capsule (Fig. 3b); ventral surface of head capsule, lateral to prementum, with eight (four pairs) fine, stiff, erect setae, head capsule otherwise with numerous decumbent setae, especially dorsally. Cervical area extensively membranous, especially ventrally. Pronotum longer than wide, well sclerotized and apparently pigmented, anterior margin straight, with prominent anterolateral corners, faintly constricted just posterior to anterior margin, posterior margin constricted, with rounded posterolateral corners, dorsally depressed just posterior to anterior margin (resulting in the anterior margin appearing somewhat lip-like), with thin, longitudinal, membranous “fracture” at midline (Fig. 3a). Wings large, mildly infumate; R reaching wing margin, straight apically (not procurved to terminate anteriorly); no c-r crossveins evident; Rs simple, terminating at wing apex (Fig. 4c), several r-rs crossveins present; single rs-ma<sub>1</sub> crossvein present shortly after origin of MA<sub>1</sub>; MA apically forked, MA<sub>1</sub> and MA<sub>2</sub> both reaching wing margin, without crossveins between them (Fig. 4c); MP simple, reaching to apical wing margin; CuA apparently joining MP apically. Protibia greatest width 0.33× length, silk-producing surface slightly concave (Fig. 4a); distal end with two minute, sclerotized, slightly-curved, spine-like setae on mesal surface (Fig. 4a); metafemur swollen; metabasitarsus (= metatarsomere I) elongate, without plantunlae (as in *Pararhagadochir*); metatarsomere II exceptionally short, without plantula; metadistitarsus (= metatarsomere III) elongate, nearly as long as combined lengths of metabasitarsus and metatarsomere II; pretarsal claws simple; arolium absent (Figs. 4a, 4b). Male terminalia asymmetrical; dorsally with left hemitergite (10L) relatively broad; right hemitergite (10R) relatively narrow, tapering posteriorly; hemitergites separated by membranous area, connected proximally by a thin sclerotic band (Fig. 4e); left tergal process (LP) sclerotized, short, curved, with forked apex, internal (caudad) hook longer than external (proximal) hook, both with tapered and pointed apices (Fig. 4e); right tergal caudal process (RP<sub>1</sub>) long, extending to LC<sub>1</sub>, apex with minute hook caudally and gentle lobe proximally; right tergal anterior process (RP<sub>2</sub>) present, short, thumb-like; ventrally with hypandrium (H) relatively large, broad, with rectangular hypandrial process (HP) positioned medially (Fig. 4d); cercomeres well sclerotized and uniformly covered by stiff, elongate setae in loose whorls (Fig. 4d); apical cercomeres (LC<sub>2</sub> and RC<sub>2</sub>) slightly longer than basal cercomeres (similar to *Archembia*); left basal cercomere (LC<sub>1</sub>) medially expanded and lobed (Fig. 4d), left cercal basipodite comprising a sclerotic flange fused to outer rim of LC<sub>1</sub> and without evidence of inner lobe or ring; right basal cercomere (RC<sub>1</sub>) well sclerotized throughout, cylindrical (Figs. 4d, 4e).

*Female*: Unknown.

**Etymology.** The new generic name is a combination of Kumar (honoring Dr. Kumar Krishna, faithful colleague and dear friend, as well as the world’s leading authority on the systematics of Isoptera), and *Embia*, type genus of and frequent stem for embiodeans. The name is feminine.

***Kumarembia hurleyi* Engel & Grimaldi, sp. n.**

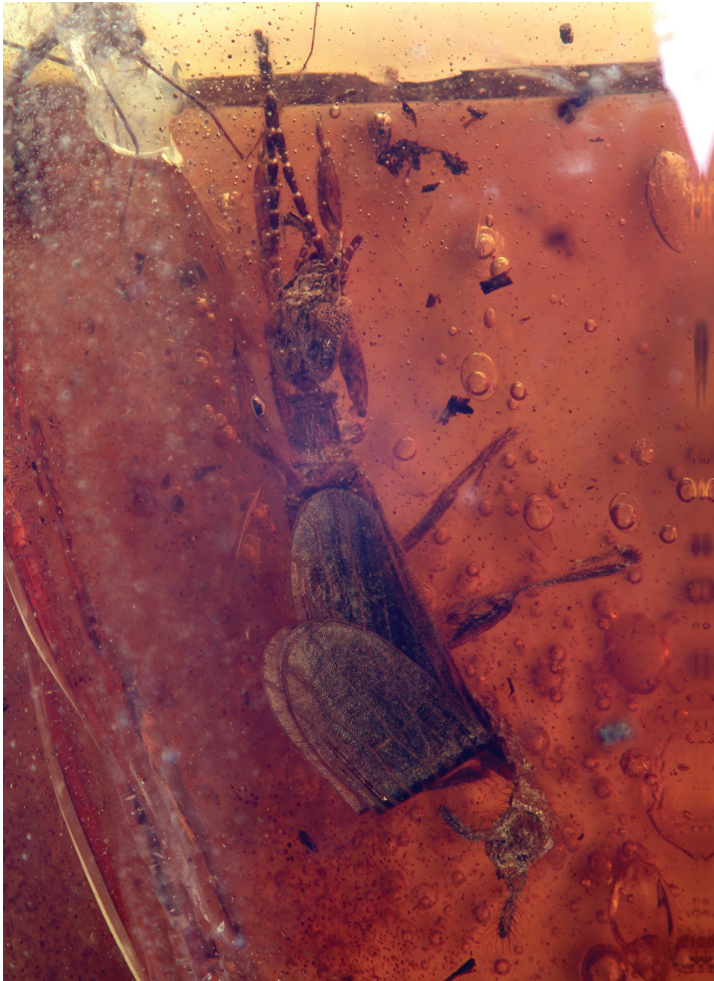
urn:lsid:zoobank.org:act:0124F7C1-BB06-4024-8C0A-3CFA053DD4CB

[http://species-id.net/wiki/Kumarembia\\_hurleyi](http://species-id.net/wiki/Kumarembia_hurleyi)

Figs 1–4

**Holotype.** ♂; AMNH Tad-261-A (Fig. 1), India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400'N, 73°4.532'E, 17–22 January 2010; to be deposited in the Birbal Sahni Institute of Paleobotany, Lucknow, India.

**Paratype.** ♂; AMNH Tad-253 (Fig. 2), India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene), 21°21.400'N, 73°4.532'E, 17–22 January 2010; in the Division of Invertebrate Zoology, American Museum of Natural History, New York.

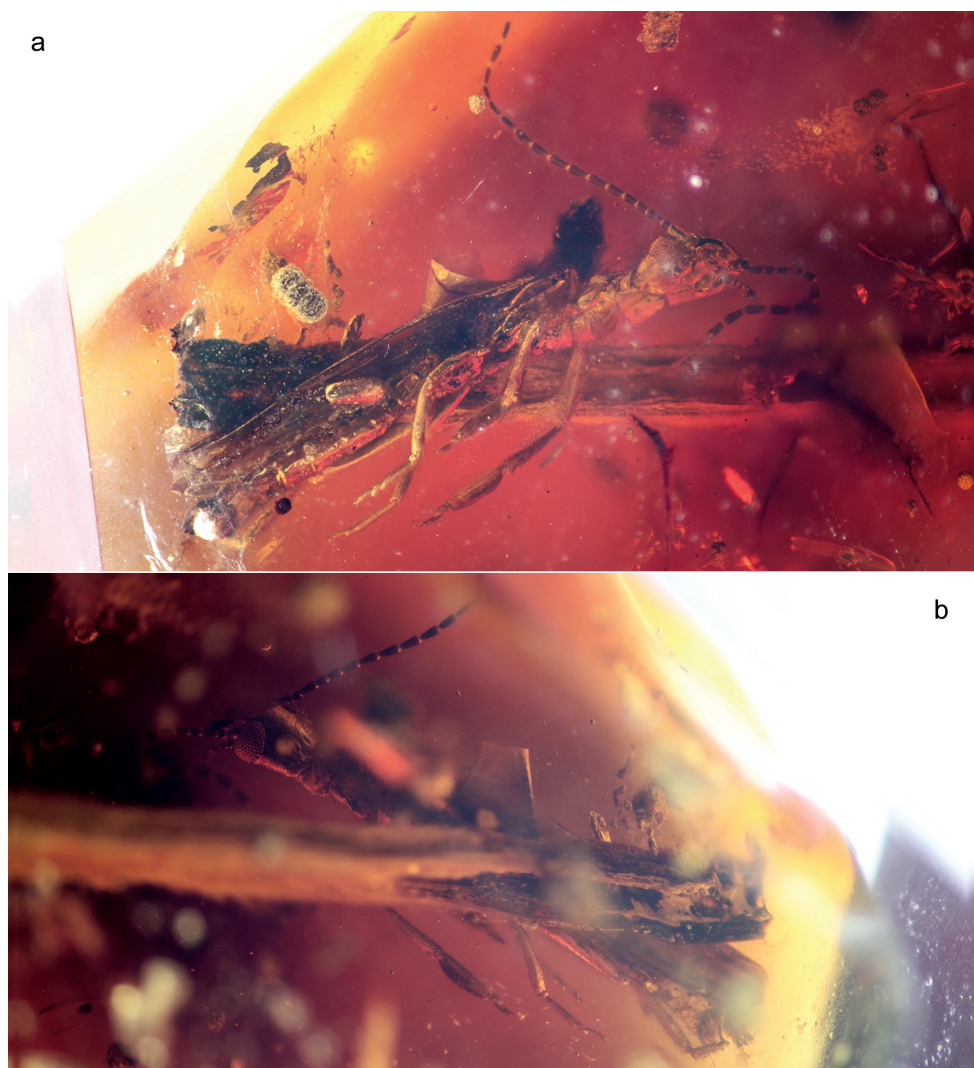


**Figure 1.** Photomicrograph of holotype male (Tad-261-A) of *Kumarembia hurleyi* Engel & Grimaldi, gen. et sp. n., in Early Eocene amber from western India. Total length of individual 5.3 mm.

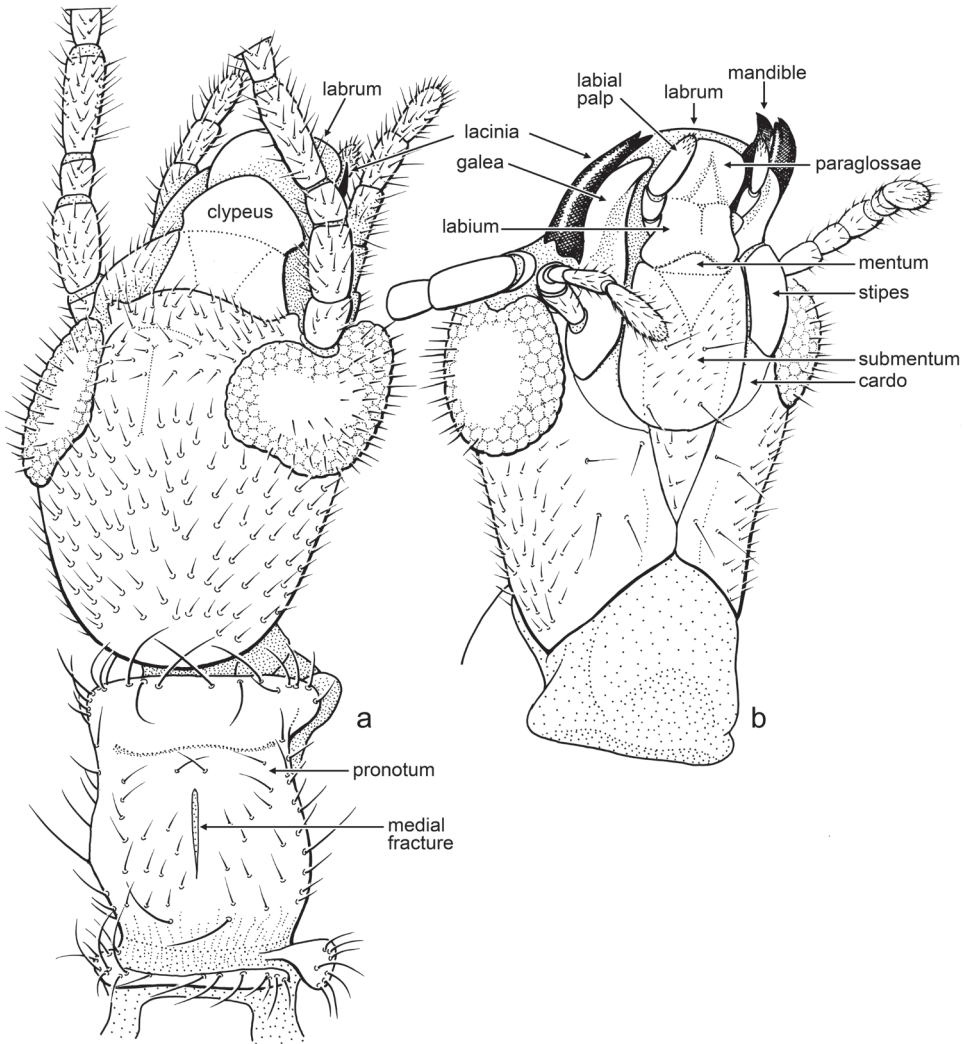


**Diagnosis.** As for the genus (*vide supra*).

**Description.** *Male*: Total length (excluding wings and antennae, as preserved) 5.3 mm; forewing length (estimated) 5.1 mm, width 1.1 mm; integument generally light brown except darker on head and antenna, finely imbricate and impunctate where evident (based on paratype, integument of holotype slightly wrinkled owing to apparent desiccation and shrinkage of individual). Head length (to apex of labrum) 1.1 mm, width (just posterior to compound eyes) 0.64 mm, head posterior to compound eyes longer than compound eye diameter, posterior border gently rounded, covered with



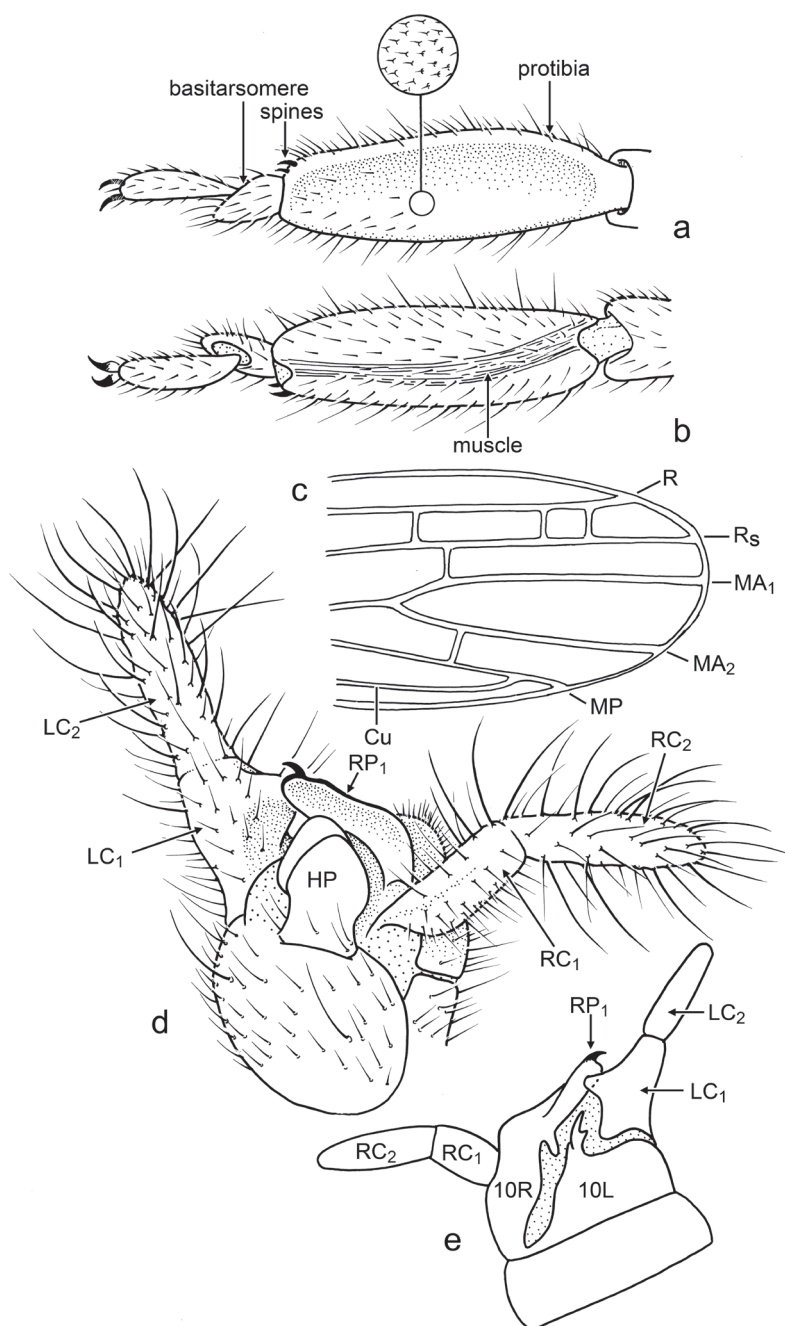
**Figure 2.** Photomicrographs of paratype male (Tad-253) of *Kumarembia hurleyi* Engel & Grimaldi, gen. et sp. n., in Early Eocene amber from western India. **A** Ventral aspect **B** Dorsal aspect. Total length of individual 5.2 mm.



**Figure 3.** Line drawings of *Kumarembia hurleyi* Engel & Grimaldi, gen. et sp. n. **A** Head of holotype, dorsal view **B** Head of paratype, ventral view. Head length (to apex of labrum) 1.1 mm.

numerous, short, prominent setae, longer ventrally (Fig. 3). Pronotum length 0.56 mm, width (medial) 0.40 mm, apparently with weak longitudinal strigae in posterior half, with abundant fine setae as follows: anterior margin with row of ~10 setae, medial pair cruciate, lateral to these an upright pair, and lateral to those three pairs medio-clinate setae; lateral margins with row ~8 erect setae of variable lengths; dorsal surface with two lateral rows of five short setae each; a short, anteromedial, cruciate pair, and longer posteromedial pair (Fig. 3). Wing membranes micronodulose and with numerous minute setae.  $LC_1$  length 0.28 mm, width at level of medial lobe 0.24 mm;  $LC_2$  length 0.36 mm;  $RC_1$  length 0.26 mm,  $RC_2$  length 0.35 mm.





**Figure 4.** Line drawings of *Kumarembia hurleyi* Engel & Grimaldi, gen. et sp. n. (a, b, and d to same scale). **A** Protarsus of holotype, dorsal view **B** Protarsus of holotype, ventral view **C** Forewing apex of holotype **D** Male genitalia of holotype, ventral view **E** Male genitalia of holotype, dorsal view. Refer to description for individual measurements.

*Female*: Unknown.

**Etymology.** The specific epithet is a patronym honoring Mr. Ailan Hurley-Echevarria for his diligent efforts in processing and screening amber, during which he personally found one of the two specimens.

## Discussion

The phylogeny of most webspinner lineages remain contentious and in a state of flux. More importantly, numerous undescribed genera and species are known in collections and will likely have a strong influence on any estimations of relationship. It is therefore challenging to make fine determinations of the closest relatives for the Cambay amber fossils. *Kumarembia* can be placed within the Archembioidea clade by the 10T with a membranous area occupying the base and center of the sclerite, 10R and 10L connected by a thin basal bar, and 10RP<sub>2</sub> present, short, and thumb-like. The genus can be placed within the Scelembiidae [= Group C of Szumik (2004); Group A = Archembidae s.str., Group B = Pachylembidae] by the rectangular and centered HP and the shape of 10LP<sub>1</sub> which is a curved process and apically forked (simple, curved, and externally laminate in Pachylembidae). This is quite significant given that other members of the clade occur in sub-Saharan Africa (Angola, Congo, Tanzania, Uganda) or in South America, particularly southern South America (e.g., Argentina, Bolivia, Brazil, and Peru, although *Pararhagadochir* is more widespread, extending as far north as Colombia and Venezuela). Accordingly, the discovery of a scelembiid in Cambay amber appears to represent one of the only Gondwanan elements of the fauna, while most other taxa show considerably different biogeographic affinities (Rust et al. 2010). As noted, relationships within Embioidea are contentious, with considerable cladistic inquiry revising phylogenetic hypotheses (e.g., Szumik 2004; Szumik et al. 2008; Klass and Ulbricht 2009). As these hypotheses of relationship continue to stabilize it will be interesting to explore further and refine the specific affinity of *K. cambayensis* with particular clades within Scelembiidae.

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# Phylogeny and classification of the Catantopidae at the tribal level (Orthoptera, Acridoidea)

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## Abstract

The grasshopper family Catantopidae is a well-known group, whose members include some of the most notorious agricultural pests. The existing classifications of the family are mostly utilitarian rather than being based on phylogenetic analysis and therefore unable to provide the stability desired for such an economically important group. In the present study, we present the first comprehensive phylogenetic analysis of the family based on morphology. By extensively sampling from the Chinese fauna, we included in the present analysis multiple representatives of each of the previously recognized tribes in the family. In total, we examined 94 genera represented by 240 species and evaluated 116 characters, including 84 for external morphology and 32 for male genitalia. The final matrix consists of 86 ingroup taxa and 88 characters. Our phylogenetic analyses resulted in a high resolution of the basal relationships of the family while showed considerable uncertainty about the relationships among some crown taxa. We further evaluated the usefulness of morphological characters in phylogeny reconstruction of the catantopids by examining character fit to the shortest trees found, and contrary to previous suggestions, our results suggest that genitalia characters are not as informative as external morphology in inferring higher-level relationship. We further suggest that earlier classification systems of grasshoppers in general and Catantopidae in particular most probably consist of many groups that are not natural due the heavy reliance on genitalia features and need to be revised in the light of future phylogenetic studies. Finally, we outlined a tentative classification scheme based on the results of our phylogenetic analysis.

## Keywords

Orthoptera, Acridoidea, Catantopidae, China, Phylogeny, Morphology, Systematics, Male Genitalia



*Zhiwei Liu would like to dedicate this paper to the honor of Professor Kumar Krishna for his friendship, kindness, professional encouragement, and the good times at the AMNH.*

## Introduction

Catantopidae (Acridoidea, Orthoptera) is a well-known grasshopper family; its members include some of the most notorious pests in agriculture, including *Schistocerca gregaria* (Forsköl), *Oxya* spp, and *Melanoplus* spp (Hill 1987). The family is by far the largest and the most diverse acridoid family, consisting of over 3000 species in about 640 genera mainly distributed in the tropical and subtropical areas of the world (Vickery and Kevan 1983).

The previous classifications of Acridoidea (Orthoptera) have been predominantly utilitarian; existing classifications of the superfamily almost entirely ignored phylogenetic relationships among taxa. Among the various classification systems or schemes of acridoids (Dirsh 1961, 1975, Harz 1975, Otte 1981, Yin 1982, Xia 1994, Li and Xia 2002) and several other classifications specifically proposed for the Catantopidae (Tinkham 1940, Mistshenko 1952, Harz 1975), there exist a great deal of disagreement concerning the classification within the family (Table 1), which cannot be easily settled because of the lack of phylogenetic studies. The most influential classification systems of Acridoidea at the present are still the one established by Dirsh (1956) and its modified versions (Dirsh 1961, 1975). The classifications by Dirsh are based on extensive comparative studies of the genitalia morphology of both sexes as well as other morphological characters, emphasizing especially the importance of the morphology of phallic complex and epiphallus in defining higher taxa. Several other authors also proposed their own classification for the Acridoidea (Rehn and Grant 1960, Uvarov 1966, Jago 1971, Vickery and Kevan 1983, Liu 1991). Otte (1981, 1984) adopted a compromised version of the various systems in his monographic treatment of North American grasshoppers. These classifications, although different, have one thing in common: all are entirely based on overall similarity and make little, if any, reference to phylogenetic relationship.

The need for a classification of the grasshoppers and locusts based on phylogeny, rather than based on overall similarity, is obvious. Yin (1982) pointed out the importance of distinguishing between plesiomorphic and derived features in the classification of the acridoids and paid special attention to the transformation series of antennae, wings, and stridulating apparatuses and tympanum. However, Yin's classification of Acridoidea based on his studies of the Chinese members of the group was not based on phylogenetic analysis and his circumscriptions of higher-rank taxa were often based on characters that obviously have been obtained through convergent evolution. Key and Colless (1993) attempted to conduct a cladistic (and phenetic) analysis of the subfamily Catantopinae from Australia. They coded 104 male external characters for 166 genera and conducted a series of analyses from typical phenetic approaches to cladistic

**Table 1.** Classification systems of the Catantopid fauna from China

Tinkham (1940)	Misshenko (1952)	Dirsh (1961), Uvarov (1966)	Harz (1975)	Dirsh (1975)	Yin (1982)	Xia (1994)	Otte (1981), Eades et al (2011) <sup>1</sup>
Cyrtacanthacrinae	Catantopinae	Acrididae	Catantopidae	Hemicarididae Hemiacridinae	Oedipodidae	Catantopidae	Acrididae
	Conophymatini	Hemiacaridinae		Conophyminae Spathosterninae Leptacrinae Catantopidae	Conophyminae Spathosterninae	Conophyminae	Conophyminae Spathosterninae Leptacrinae
Spathosternini Leptacri Caryandae			Spathosterninae				
	Dericorythini	Dericorythinae	Dericorythinae	Dericorythinae	Dericorythinae	Dericorythinae	(Dericorythidae)
Oxyae	Oxyini	Oxyinae	Oxyinae	Oxyinae	Oxyinae	Oxyinae	Oxyinae
Catantopini	Catantopini	Catantopinae	Catantopinae	Catantopinae	Catantopinae	Catantopinae	Catantopinae
Calliptamini	Calliptamini	Calliptaminae	Calliptaminae	Calliptaminae	Calliptaminae	Calliptaminae	Calliptaminae
Eyprepocnemini	Eyprepocnemidini	Eyprepocneminae	Eyprepocneminae	Eyprepocneminae	Eyprepocneminae	Eyprepocneminae	Eyprepocnemidinae
Cyrtacanthacridini	Cyrtacanthacridini	Cyrtacanthacridinae	Cyrtacanthacridinae	Cyrtacanthacridinae	Cyrtacanthacridinae	Cyrtacanthacridinae	Cyrtacanthacridinae
Coptacrae	Coptacriini	Coptacrinae		Coptacrinae	Coptacrinae	Coptacrinae	Coptacridinae
Podisminae	Podismini			Podisminae	Podisminae	Podisminae	Podismini
	Tropidopolini	Tropidopolinae	Tropidopolinae	Tropidopolinae			Tropidopolinae
Tristrini	Tristrini					Tristrinae	(Tristiridae)
	Hieroglyphini					Hieroglyphinae	Hieroglyphinae
Trauliae	Traulini						
Oxyrrhepini					Habrocneminae	Habrocneminae	Habrocneminae
Xenacanthippi						Melanoplinae	Melanoplodinae
Tauchirae						Acrididae	Acridinae
Incolacri						Leptacrinae	
	Egnatiinae	Egnatiidae	Egnatiinae	Egnatiinae	Egnatiinae	Egnatiinae	Egnatiinae
			Acrididae		Gomphoceridae	Gomphoceridae	Gomphocerinae

1. Additional subfamilies of Acrididae: Cpiocerinae, Eremogryllinae, Euryphyminae, Leptysminae, Marellinae, Oedipodinae, Ommatolampinae, Pauliniinae, Protolabinae, Rhytidochrotinae, Teratodinae

methods as implemented in PAUP (version not mentioned). The results of this particular study showed almost no resolution of relationships or useful clustering except for a few ‘low-level groups’. The authors consequently did not even bother to present the cladograms and resolved to ‘develop a classification by traditional non-quantitative methods’.

There has been an increased interest in recent years in the phylogenetic relationship of orthopteroid insects in general (Flook and Rowell 1997a, 1997b, 1998, 1999; Flook et al 2000, Rowell and Flook 1998, Yin et al. 2003) and the acridoids in particular (Amedegnato et al. 2003, Chapco et al 2001, Litzenberger and Chapco 2001, 2003, Ren et al. 2002, Xi and Zheng 1997, Xu et al. 2003, Xu and Zheng 1999, 2002; Zheng and Qiao 1998). Most of these recent studies are based on molecular data with relatively limited taxon sampling; the few morphology-based studies either targeted at lower level relationship (e.g., within genus, Xu et al. 2003, but see Song and Wenzel 2007) or are characterized by sporadic taxon sampling (Ren et. al 2002, Xu and Zheng 1999, 2002; Zheng and Qiao 1998). Therefore, the potential of morphology in resolving higher-level phylogeny within Orthoptera and Acridoidea has not been fully explored.

This lack of higher-level phylogenetic study of Catantopidae leads to a lack of stability in the classification within the family (Table 1), which is unusual for such a well-known and economically important group. In this paper, we present the first comprehensive phylogenetic analysis of the family Catantopidae based on morphology by sampling extensively from the Chinese fauna. Our purpose is to (1) conduct an exploratory phylogenetic analysis of the phylogenetic relationship within the family represented by the Chinese members, (2) provide an objective evaluation of the usefulness of morphological characters in phylogeny reconstruction of the acridoids in general and the catantopids in particular, and (3) provide a general framework for taxon sampling in future studies of acridoid phylogeny on a global basis.

## Materials and methods

### I. Monophyly

The name Catantopidae, or its original form Catantopinae as subfamily, has had a long history of divergent usages (Key and Colles 1993). The modern definition of Catantopidae took after the name of Cyrtacanthacrinae (Tinkham 1940, Roberts 1941) and was subsequently assigned subfamily status as Catantopinae by Mistshenko (1952). The latter author further assigned the members of the subfamily in the fauna of the former Soviet Union and adjacent countries into thirteen tribes, and considered Egnatiinae as a separate group from the Catantopinae. Mistshenko (1952) was mostly accepted by later authors, including Dirsh (1961), Uvarov (1966), and Harz (1975). Dirsh (1975) later divided Mistshenko’s Catantopinae into two families, Hemiacrididae and Catantopidae, and included Egnatiinae in the family Catantopidae. Yin (1982) also

divided Mistshenko's Catantopinae into two families, Acrididae and Oedipodidae, but treated Egnatiidae as a separate family. Xia (1994) included in the family Catantopidae some of the subfamilies of Oedipodidae in Yin's system and raised most of the tribes in Mistshenko's system to subfamilies. The Xia System has been adopted for the recent monographic treatment of the Chinese fauna of Catantopidae (Li and Xia 2002). The classification scheme used by Otte (1981, 1984) in his monographic treatments of the grasshoppers of North America north of the Gulf of Panama, although unexplained, is obviously completely utilitarian without reference to phylogenetic relationship among groups. The Otte classification was later expanded and adopted by the author in his multi-volume catalog of the orthopteran insects of the world (Otte 1994a, 1994b, 1994c, 1995a, 1995b), which in turn has been eventually published as a searchable online database, the Orthoptera Species File (Eades et al 2011). While the Orthoptera Species File database is tremendously useful for taxonomic purposes, species groups defined by earlier classification systems were often used in phylogenetic studies on Acrididae / Acridoidea at levels of tribe and above (Litzenberger and Chapco 2003; Song and Wenzel 2007). A comparison of catantopid classification systems by various authors is given in Table 1.

Catantopidae in our view is readily defined by the unmistakable synapomorphy of having a distinct prosternal process between the forecoxae. Although some species of Pamphagidae and Pyrgomorphidae have a lamellate process on the prosternum, the process in these species is on the anterior margin of the prosternum and is obviously an independently evolved feature not homologous to the prosternal process between the forecoxae observed in Catantopidae. Nonetheless, as shown in Table 1, there was considerable disagreement among earlier authors about the definition of Catantopidae, which obviously arose from the fact that earlier acridologists defined higher-level taxa on basis of overall similarities, instead of on synapomorphies. Our interpretation of Catantopidae in the present paper, as defined by the presence of prosternal process between the forecoxae, is in accordance with Catantopinae of Roberts (1941) and Mistshenko (1952) and Catantopidae of Harz (1975) and is equivalent to the "Spine-breasted Acrididae" as keyed out in Otte (1981). Throughout the paper, we consistently use the name Catantopidae except when discussing its treatment by various previous authors. In the latter case, they were referred to as were originally treated by these authors, such as Catantopinae or Catantopini. The same rule is also consistently applied to other taxa, e.g. Egnatiidae.

## **II. Taxa Sampling and Sources of Specimens**

About 327 species in 96 genera of Catantopidae (*sensu* Mistshenko 1952) are known from China, with representatives from both the Palearctic (21.44%) and the Oriental regions (79.56%) (adjusted according to Huang and Chen (1999)). The Chinese fauna of catantopids represents 15% of world genera of the family (data from Vickery and Kevan, 1983) and all of the tribes recognized by Mistshenko (1952) or subfamilies by

Dirsh (1975). In this study, we examined a total of 2,536 specimens representing 240 species in 94 genera, accounting for 73% and 98% of the total number of species and genera known from the country, respectively. Of the 94 examined genera, 84 genera were included in our phylogenetic analysis while the other eight were excluded (Appendix 1). The reasons for the exclusion are: 1) type specimens were not available for examination and no other specimen of these genera had been collected since the original publications, such as *Tzacris* Tinkham and *Chapacris* Tinkham; 2) only females were then discovered, such as *Liaopodisma* Zheng. In addition, we also left out several genera that were described after the data collection stage of this study, such as *Caryandoides* (Liu and Li 1995, Özdikmen 2009) and *Tectiacris* (Wei and Zheng 2005). The final inclusion of taxa represented all of the tribes recognized by Mistshenko (1952) and subfamilies by Dirsh (1975).

The majority of the study materials of the present project were provided by the following institutions (curators in parentheses):

Entomological Museum, Shaanxi Normal University, Xi'an, Shaanxi Province (Shengquan Xu)

Entomological Museum, Zhongshan University, Guangzhou, Guangdong (Geqiao Liang)

Entomological Museum, Research Institute of Entomology, Chinese Academy of Sciences, Shanghai (Kailing Xia)

Entomological Museum, Beijing Institute of Zoology, Chinese Academy of Sciences, Beijing (Chunmei Huang)

Zoological Museum, Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining, Qinghai (Xiangchu Yin)

### III. Selection of outgroups

Because of the lack of phylogenetic analysis of Acridoidea at levels above subfamily, we had to rely on previous systematic studies on Acridoidea for outgroup selection. All existing classifications of Acridoidea treated Catantopinae, Egnatiinae, Acridinae, and Oedipodinae as being closer to each other than they are to Pyrmorphinae and Pamphaginae (Roberts 1941, Mistshenko 1952, Dirsh 1956, 1961, 1975; Yin 1982, Xia 1994). Dirsh (1961, 1975) suggested that Egnatiinae was closer to Catantopinae than any other subfamily of his Catantopidae because Egnatiinae possesses a Comstock-Kellogg gland, which is otherwise believed to occur only in Catantopinae. Furthermore, Egnatiinae and Catantopinae share similar folds and sculpture in the internal surface of foregut, which are different from those of Oedipodinae. Stebaev et al. (1984) also agreed on a close relationship between Egnatiinae and Catantopinae on basis of cytogenetical, taxonomical and ecological data, but considered the Egnatiinae as a tribe within Catantopinae. Many contemporary acridologists are in agreement about a close relationship between Egnatiinae and Catantopinae (e.g., David Hollis, pers. comm.). Because of the close relationship

between Egnatiidae and Catantopidae, very likely as sister clades, and the lack in Egnatiidae of the obvious catantopid synapomorphy of having a prosternal process between the forecoxae, the family Egnatiidae represented by the two genera *Egnatius* Stal and *Egnatioides* Voss, was used as outgroup for the phylogenetic analysis of Catantopidae relationships.

#### **IV. Specimen study and character coding**

Terms and abbreviations used in the present study followed B.-Bienko and Mistshenko (1952) for external morphology and Dirsh (1956, 1961, 1975) for genitalia structures.

Specimens for the study were selected in the following order of priority: 1) type specimens, 2) specimens determined by the author of the taxon, and 3) specimens determined by experts of the taxon. All characters were coded from direct observation of specimens, except in a few instances where characters of a species were coded based on illustrations and descriptions from monographs or reviews (Willemse 1956, 1957; B.-Bienko and Mistshenko 1951, Mistshenko 1952, Hollis 1975).

External morphology was surveyed before specimens were dissected for examination of genitalia characters. When available, multiple individuals were examined for each species and multiple species for each genus. For polymorphism at species level, we took an approach similar to, but much more restricted than, the “majority state rule” proposed by Wiens (1995). We generally avoided characters that are polymorphic at species level, and only in very few cases, coded species in question as the predominant state when the other state(s) was rare (presence rate < 15%). In a few cases when character polymorphism occurred at generic level, the characters in question were initially coded as missing for the genus, but were eventually abandoned and not included in the analysis. Some of the characters with three or more states were treated prior to the cladistic analysis as ordered or additive characters, *i.e.*, the transformation series was hypothesized to be 0-1-2 and so on. This was done only when it was possible to order the states unambiguously, *e.g.*, for measurement ratios, and ordered characters are indicated in Appendix 1. In a few cases, one of the states of a main character was more finely subdivided into one or two subsidiary character(s). Taxa with other states of the main character were coded as having state unknown (character not applicable) in the subsidiary character. This commonly used method has been referred to as ‘state-unknown coding’ (Nordlander et al. 1996). The method may give incorrect lengths for some trees when there is homoplasy in the main character and different subsidiary states are ancestral for the different clades having the subdivided state of the main character (Maddison 1993). It has been suggested to use step matrices to represent main/subsidiary character systems exactly (Maddison and Maddison 1992), but this will slow down calculations considerably and is especially impractical for relatively large matrixes like ours. In the present study, therefore, we consistently used state-unknown coding for main/subsidiary character systems and weighted all main and subsidiary



characters equally. More detailed discussion about the application of the method is found in Nordlander et al. (1996).

The final matrix contained 87 terminals, including outgroup and 86 catantopid genera in the ingroup, and 88 characters, of which 79 were phylogeny-informative and the other nine were autapomorphies (Appendix 2-3). The autapomorphic characters were excluded from the final cladistic analyses and not counted when calculating tree length, CI, or RI. Nonetheless, they were kept in the matrix for their taxonomic values and potential use in future phylogenetic studies involving the included taxa.

## **V. Phylogenetic Analysis**

PAUP version 4.0 beta10 (Swofford 2003) was used for phylogenetic analyses. The large number of taxa and characters included in this study did not allow the use of exact searching algorithms. Therefore, we used a combination of several ‘shortcut’ approaches. We first used PAUPRat (Sikes and Lewis 2001) to generate batch files for maximum parsimony analysis within PAUP using the Parsimony Ratchet method described by Nixon (1999). We performed 30 repetitions of the Parsimony Ratchet analysis, with 200 iterations per run as suggested by Sikes and Lewis (2001), giving a total of 6,000 iterations. The single shortest tree from each of the 6,000 iterations were then loaded into computer memory for comparison and only the shortest trees over all iterations were kept and duplicates of trees were removed. Because these overall shortest trees were each only the single best tree retained from a particular iteration, they each were probably one of the many possible equally most parsimonious trees or one of the less than most parsimonious trees that actually exist for the dataset. Therefore, these trees were further subjected to TBR branch swapping in order to find out all possible trees of equal or shorter length. To ensure that we find the best trees, we also analyzed our dataset in NONA 2.0 (Goloboff 1999a), a program said to be much faster than competitors like PAUP (Goloboff 1999b). For NONA analyses, we started with MULT\*50 (randomize order of taxa, create a weighted Wagner tree, swap using TBR, and with 50 replications) and then swapped the shortest trees from MULT analysis using Max\*, which is equal to PAUP’s TBR swapping. NONA was also used for calculation of Bremer Support values (/decay index) for branches (Bremer 1994) while PAUP was used for diagnosis of apomorphic characters supporting each branch. TNT (Goloboff et al. 2011), a program that implemented the tree search methods of NONA as well as additional search methods, including sectorial search, tree drifting, and tree fusing (Goloboff 1999b), was also used for Parsimony Ratchet analysis of the dataset with options comparable to afore-described NONA analysis. The other so-called “New Technology” searching techniques were also used with default options of the software, but were not extensively explored because our dataset was not too large and thus further aggressive approximation was not considered necessary.

## Results

### I. Character Analysis

We examined a total of 116 characters, including 84 characters of external morphology and 32 characters of male genitalia morphology. Twenty-eight characters were excluded from our analysis either because they were too variable across examined species of a genus to reach a generic consensus or because they were continuous and discrete coding of character states was impossible. In addition, characters of body color patterns, although important for identification of some species of the family, were found to be too variable, both among individuals of species and among species of genera, to be of much use in resolving phylogenetic relationships within Catantopidae and were therefore excluded from the present study. The eighty-eight characters included in the final character matrix consist of 71 external morphological characters and 17 genitalia characters (Appendix 2). Character fit on the shortest trees, as expressed by the consistency index (CI) and retention index (RI), was lower for characters of male genitalia morphology in comparison to characters of external morphology (Table 2).

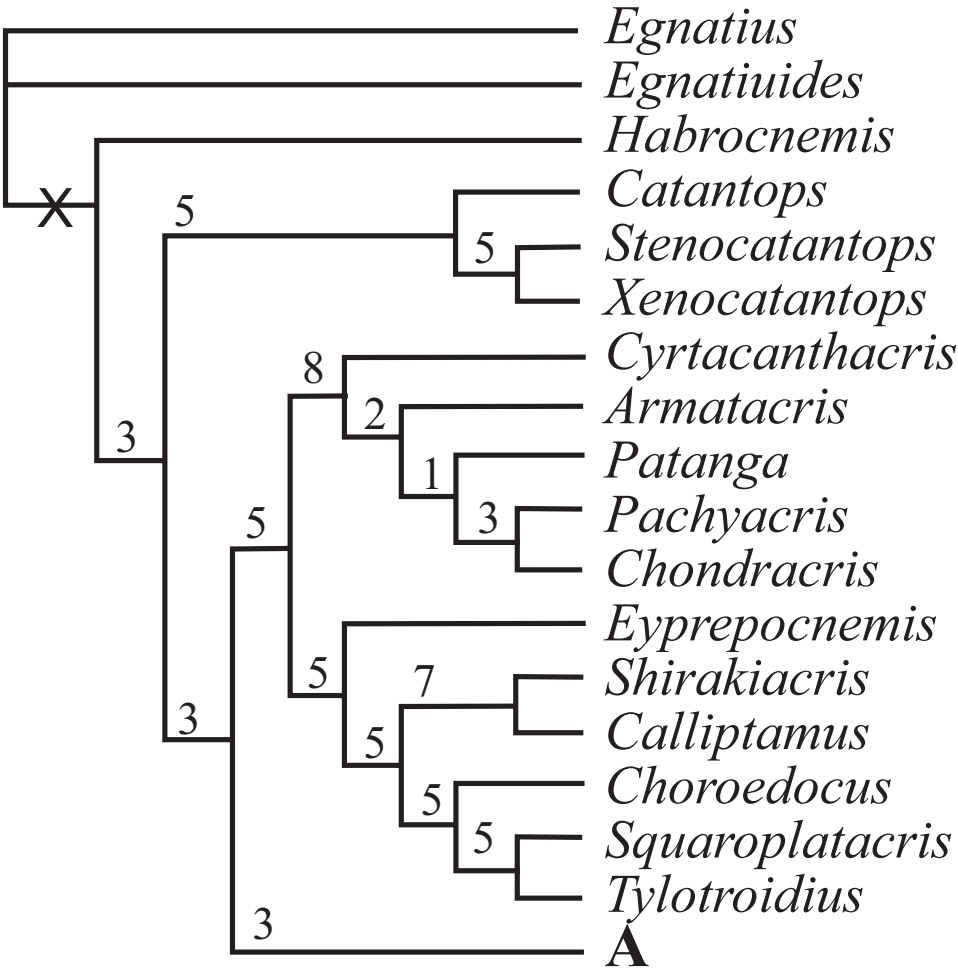
### II. Phylogenetic Analyses

Using maximum parsimony analysis with Nixon's ratchet method, we found in thirteen of our 30 replications and 218 of the 6,000 iterations a tree with the shortest length of 688 steps ( $L=688$ ,  $CI = 0.17$ ,  $RI = 0.55$ ). With duplicate trees deleted, the final number of the shortest trees was 204; subsequent swapping of these optimal trees using TBR did not find shorter trees, but found a total of 22,354 equally most parsimonious trees. Figs. 1–2 and Fig. 3 show the strict consensus tree with Bremer Support for completely resolved branches and the 50% majority consensus tree with percentage of branches appearing in all shortest trees summarized, respectively.

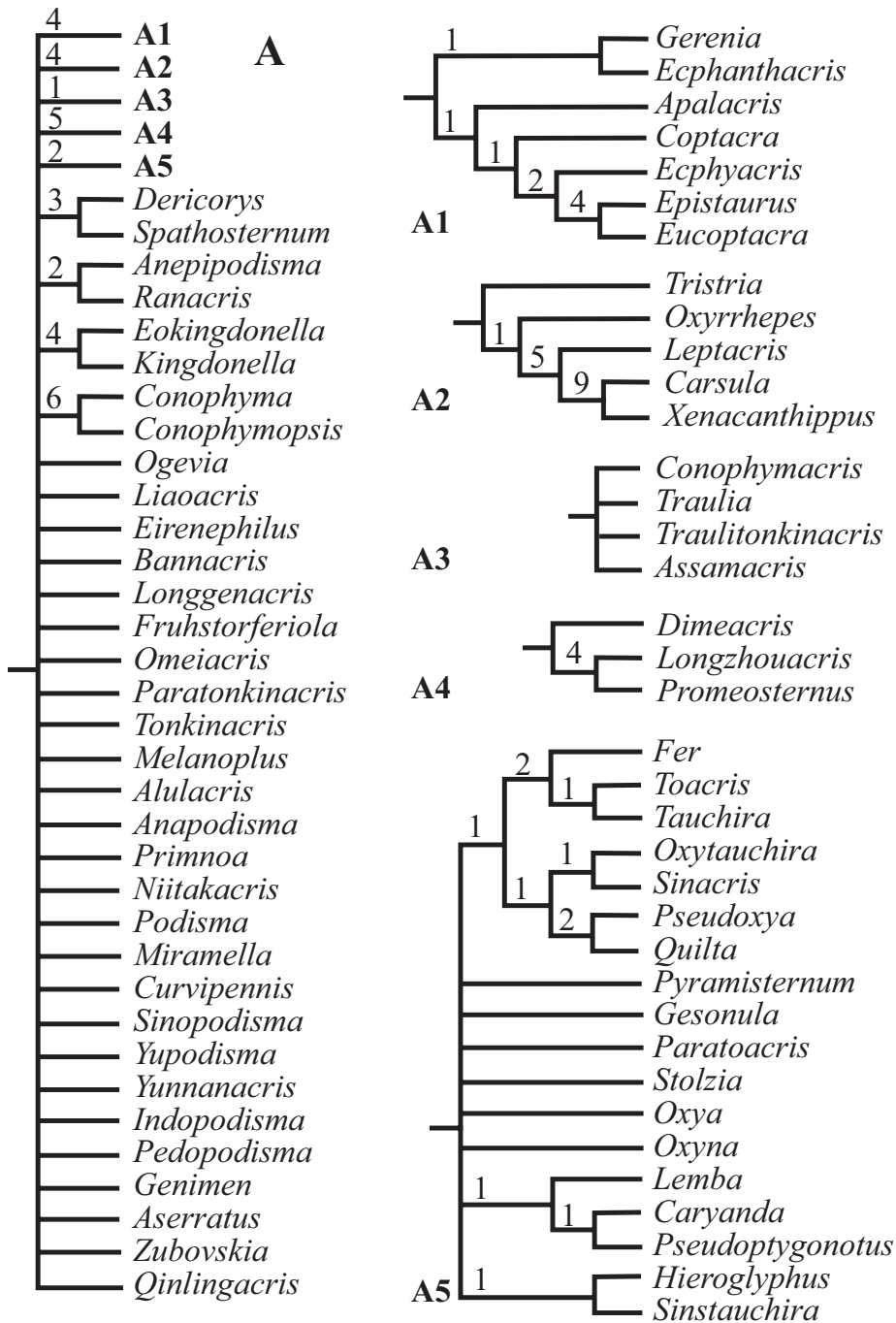
Searching with NONA 2.0 (Hold=10,000–30,000, Mult\*50, and Max\*) did not find trees shorter than those found with PAUP 4.0 using parsimony ratchet method. Although we were always able to find trees of the shortest length in a few minutes with NONA, our searches invariably resulted in only about 50 trees with MAX\*, even when we increased the number of trees to be held in memory to 30,000. Further swapping using SSWAP\*2 and MSWAP\*2 apparently would take a long time (3.2GHZ CPU frequency and 1G RAM) and were terminated after a few hours. Comparison of the NONA trees with PAUP trees showed that they were a (small) subset of the trees we found using ratchet method in PAUP. Searching with TNT, either ratchet method or other new technology methods, did not result in shorter trees.

**Table 2.** Fit on shortest trees of different categories of characters, as expressed by the consistency index (CI) and retention index (RI) (n = number of characters; autapomorphis excluded).

Character Category	n	CI	RI
<b>External Morphology</b>	<b>63</b>	<b>0.19</b>	<b>0.58</b>
Body shape	1	0.25	0.63
Head	10	0.17	0.54
Mesosoma	29	0.20	0.66
Metasoma	23	0.20	0.45
<b>Male Genitalia</b>	<b>16</b>	<b>0.12</b>	<b>0.49</b>



**Figure 1.** Strict consensus tree of the 22,355 found shortest trees using Parsimony Ratchet method in PAUP 4.0 beta10 (30 repetitions and 200 iterations per run, followed by TBR swapping). Above each resolved branch is the Bremer Support value (/decay index) for the branch estimated using NONA2.0. Only the completely resolved basal part is shown.



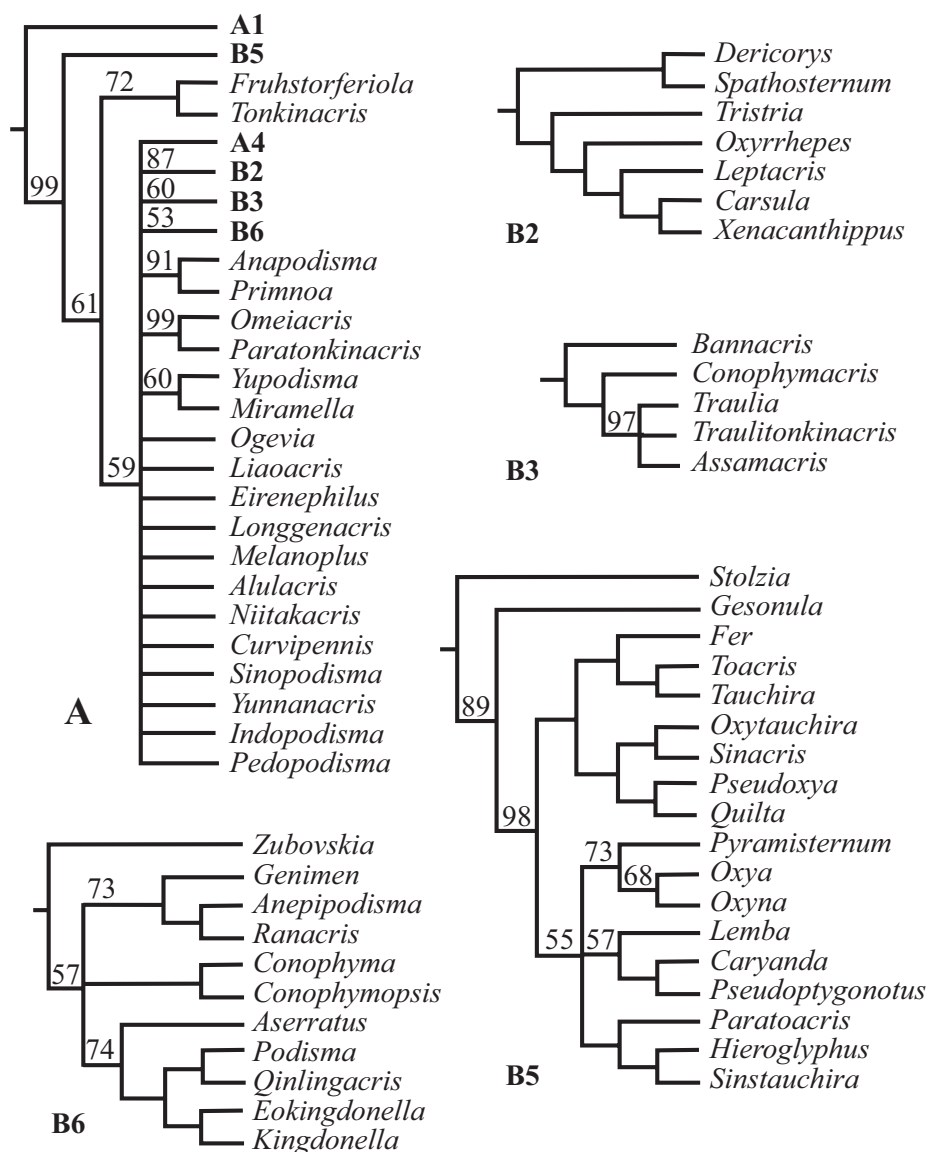
**Figure 2.** Strict consensus tree of the 22,355 found shortest trees using Parsimony Ratchet method in PAUP 4.0 beta10 (30 repetitions and 200 iterations per run, followed by TBR swapping). Shown in the figure is the expansion of Clade A of Figure 1. Several completely resolved clades are further expanded as **A1, A2, A3, A4** and **A5** respectively.

### III. Phylogenetic Relationship

Although the number of shortest trees found by our cladistic analyses is huge, the phylogenetic relationship among genera at the base of the cladogram was well resolved, and all basal clades were also relatively well supported with Bremer Support values ranging mostly from 3 to 8 (Fig. 1). The majority of genera, 71 out of 88, fell into the monophyletic Clade A (Fig. 1), which is a polytomy consisting of several relatively well-supported monophyletic clades (Fig. 2: A, A1–5; clade A3 is only supported by a Bremer Support value of 1) as well as a number of unresolved genera / pairs of genera (Fig. 2: A). When a 50% majority consensus tree was calculated, better resolution within Clade A is achieved (Fig. 3, A, B2–B6). In comparison to the strict consensus tree, a sister relationship between A1 and the rest of the clade is supported by 99% of all shortest trees (Fig. 3: A), and A5 (Fig. 2: A5) is supported as the sister clade of the clade consisting of the rest of the genera with improved within-clade resolution (Fig. 3: B5), and (*Fruhstorferiola* + *Tonkinacris*) becomes the sister clade to the clade including all members of Clade A except clade A1 and B5 (Fig. 3:A). This terminal clade, while supported by 59% of all shortest trees, form a polytomy consisting of several monophyletic, relatively well resolved clades, 12 distinct genera, and three genera pairs. In addition, there is also an increased resolution at the base of Clade A -- B2 consists of A2 and (*Dericorys* + *Spathosternum*) (Fig. 3: B2), B3 includes A3 and *Bannacris*, and an additional clade is resolved (Fig. 3: B6).

### IV. Discussion

Male genital morphology received special attention from Dirsh (1956, 1961, and 1975) when the author established his classification of acridoids. In fact, the various versions of Dirsh classification depended heavily on the male genitalia morphology, and the practice has greatly influenced later systematists of grasshoppers and other orthopteran insects (Hollis 1975, Yin 1982, Ronderos and Cigliano 1991, Xia 1994, Zheng and Xia 1998). Our result showed that character fit on the shortest trees, as expressed by the consistency index (CI) and retention index (RI), was actually lower for characters of male genitalia morphology in comparison to external morphology characters (Table 2), suggesting that genital characters are not as phylogeny informative as previously thought, at least at higher level, and earlier classification systems of grasshoppers in general and Catantopidae in particular probably include many groups that are not natural due to the heavy reliance on genital features. Eberhard (1985) argued that the species-specific diagnostibility of male genitalia is a reflection of both the rate and extent to which they diverge, and any structure so useful taxonomically must have evolved rapidly. In fact, a recent study showed that morphologically very similar species of *Melanoplus* grasshoppers differ in the shape of the male genitalia and this is probably due to extremely rapid speciation caused by glacial cycles during the Pleistocene glaciations (Knowles and Otte 2000). The rapid evolution of male genitalia morphology is considered to be caused by strong sexual selection on the male imposed by the females (Eberhard 19985, Knowles



**Figure 3.** Majority (50% and above) consensus tree of the 22,355 found shortest trees using Parsimony Ratchet method in PAUP 4.0 beta10. The basal part of the majority consensus tree is completely resolved and is the same as in Figure 1, and the figure shows only the phylogenetic relationship within Clade **A** as resolved by MJ consensus tree. The clades better resolved in comparison with strict consensus tree are further expanded as **B2**, **B3**, and **B5**. **B5** is the same as **A5** of Figure 2, but with better internal resolution. **B2** is **A2** plus (Dericorys, Spathosternum) at the base, and **B3** is **A3** plus Bannacris added at base and has higher internal resolution. **B6** consists of several pairs of genera unresolved in the strict consensus tree. **A1** and **A4** are each completely resolved and remain the same as in Figure 1, and are thus not expanded here in. More differences between strict and MJ consensus trees are found in the basal part of Clade **A** (cf. Figure 2: **A**). Number above each branch is frequency of occurrence of a particular branch among all 22,354 found shortest trees, and branches not indicated with a number have 100% occurrence.

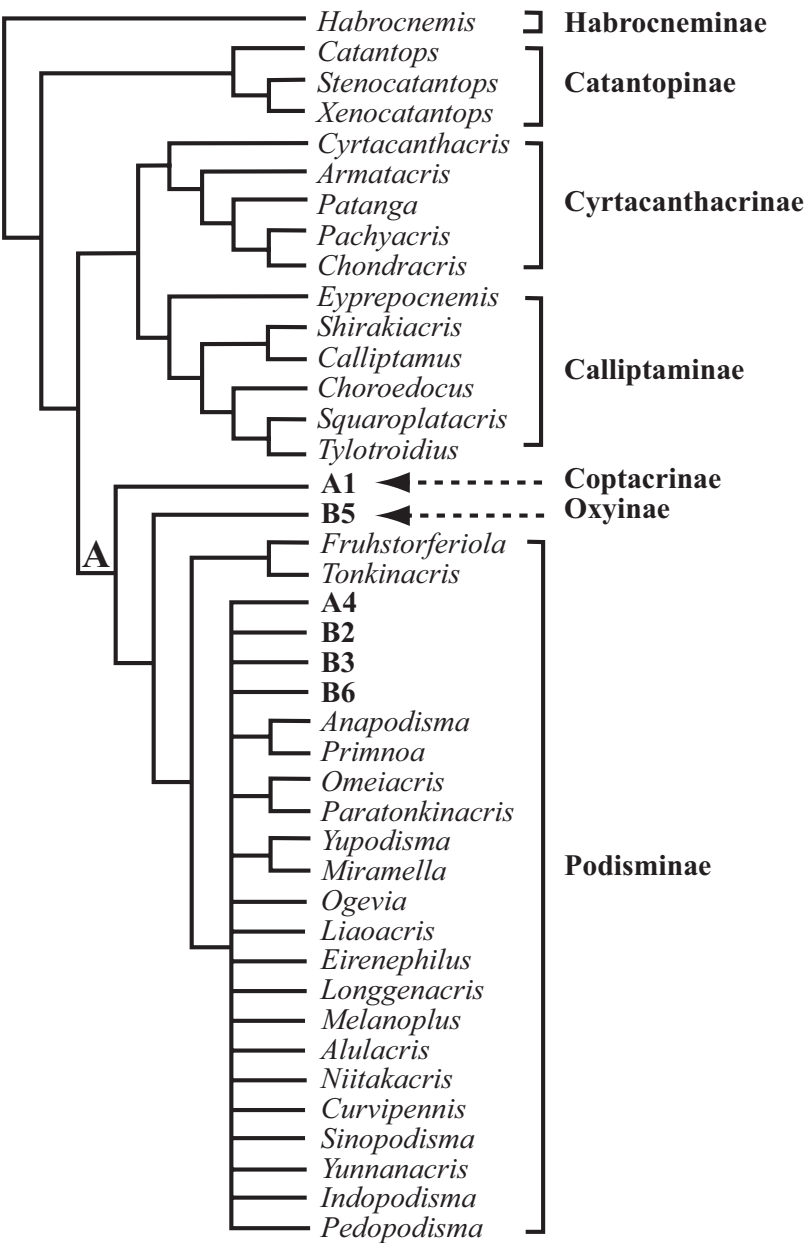


and Otte 2000). Regardless of the mechanism, male genital features, while very useful in species identification, show high degree of homoplasy and are therefore of limited value in phylogenetic studies, especially at higher levels. Consequently earlier classifications of acridoids as well as Catantopidae need to be revised critically in the light of phylogenetic analyses based on a broad range of characters.

An earlier attempt to study the phylogenetic relation within Catantopidae from Australia found almost no resolution, especially at the base (Key and Colless 1993), which is strikingly different from the results of our study where the phylogenetic relationship was reasonably resolved, especially at the base. Key and Colless (1993) was able to assemble an impressive dataset consisted of 166 terminals and 104 characters, but unfortunately provided otherwise very limited information about their dataset, which prevents us from interpreting exactly why there is such a big difference between their results and ours. Several factors might have contributed to this. For example, their study is based on males only. While male characteristics are frequently the only useful features for species identification, especially for closely related species, males of different grasshopper species may have been subjected to sexual selection and developed convergent similarities similar to what we have discussed earlier about male genital characteristics. In addition, the authors only used Neighbor-joining and Wagner parsimony without further branch swapping in their analyses, and it is thus very unlikely that what the authors found were the shortest trees. It would be of interest to request from the authors their dataset and reanalyze it using the currently available computation power that is far more superior than it was almost two decades ago. Computation power is especially relevant for analyzing dataset of their size.

Rowell and Flook (1998) presented a phylogenetic tree for the Acridoidea based on the mitochondrial DNA sequences 12S and 16S. They found support for several catantopid clades, *i.e.*, Oxyinae, Podisminae+Melanoplinae, and Coptacridinae. In addition, their study also supported as monophyletic the clade consisting of Cyrtacanthacridinae, Calliptaminae, Catantopinae *s. str.*, and Eyprepocnemidinae. These clades are mostly supported by the present study except the monophyly of (Cyrtacanthacridinae + Calliptaminae + Catantopinae *s.s.* + Eyprepocnemidinae). While a sister relationship between Cyrtacanthacridinae and Calliptaminae is supported by the present study, Catantopinae is supported as a monophyletic basal clade in the family cladogram and *Eyprepocnemis* as a member of Calliptaminae (Fig. 4).

Rowell and Flook (1998) also suggested that the Acridoidea ‘seems to be the product of a single explosive radiation’ because they were unable to find a resolution at the sub-family level for the basal acridoids. However, this conclusion, according to the authors, is based on a ‘preliminary analysis’, for which the method was not described, and therefore has to be treated with caution. Meanwhile, the result of the study may be biased simply because of the used genes being inadequate with regard to the divergence level and evolution rate of the study group. According to Simon et al. (1994), the mitochondrial rRNA genes of 12S and 16S are considered to be mostly useful at the population level where highly variable sites have not yet experienced multiple substitutions and at deep levels of divergence where the more conserved sites of these genes supply useful phylogenetic



**Figure 4.** A possible scheme classification of Catantopidae from China based on parsimony phylogenetic analysis of 86 genera and 79 phylogeny-informative morphological characters. Details of Coptacridae and Oxyinae are found in Figure 2 (Clade **A1** Coptacridae and **A5** Oxyinae) and Figure 3 (**B5** Oxyinae). Podisminae is further divided into six tribes, of which five are supported as monophyletic by the 50% majority consensus tree of all shortest trees found while the other ‘tribe’ Melanoplini is suggested as a ‘sink’ to temporarily keep the genera that do not belong to any of the supported clades. The Fruhstorferiolini is the most basal tribe consisting of Fruhstorferiola and Tonkinacris, while details of Melanoplini are found in Figure 2 (**A4**: Promeosternini) and Figure 3 (**B2** Dericorythini, **B3** Traulini, **B6** Podismini).

information. At intermediate levels of divergence, however, the relatively variable sites probably have experienced multiple substitutions that may obscure phylogenetic signals. In addition, the rates and patterns of evolution of mitochondrial rRNA genes can vary greatly among taxa (Simon et al. 1994, and references therein). The particular analysis of Rowell and Flook (1998) of Acridoidea based on these two genes might just deal with this ‘intermediate level of divergence’ for the Orthoptera. It would be interesting to reanalyze their dataset to resolve the phylogenetic relationship at various levels with in the superfamily, e.g., to include all their major lineages, but include only a few of their sampled species for each of these lineages, or alternatively, analyze each of these major lineages with all their sampled species included. Unfortunately, the article provided neither the sequences nor genbank accession numbers for the sequences.

To our knowledge, the present study is the most comprehensive of its kind to study the higher level phylogeny of orthopteran insects in terms of the number of taxa sampled and characters examined and coded. Through this study we were able to demonstrate that the external morphology of orthopteran insects can be a very useful source for assessing higher-level phylogeny. For example, the study provided complete resolution for the basal relationships of the Catantopidae (Fig. 1), Nonetheless, our dataset were unable to provide an unambiguous solution for the relationships within the largest terminal clade that comprise 80% of all sampled genera in this study (Figs. 2, 3). It is generally accepted that phylogenetic hypotheses basing on as many independent lines of evidence as possible have the highest explanation value (Nixon and Carpenter 1996a). Combining morphological and molecular data should be the direction for future phylogenetic studies of orthopteran insects including Catantopidae. In addition, our study sampled only taxa from China, which was necessary due to the lack of resources, and future phylogenetic studies of Catantopidae should include representative taxa from other areas of the world.

## V. Classification of Chinese Catantopidae

Based on the strict consensus tree and the 50% Majority-rule consensus of the 22,355 shortest trees, we hereby outline a scheme for the classification for the family Catantopidae from China. As we discussed above, a comprehensive phylogenetic study based on a more inclusive taxon sampling from all regions of the world and including both morphology and molecular sequences is needed for highly resolving the phylogenetic relationship within the family, especially with regard to the relationship between and within the subfamilies Coptacridinae, Oxyinae, and especially Podisminae (see below). Therefore, the purpose of our outline is to serve as a basis for further studies, rather than as formal classification.

According to this scheme, the Chinese Catantopidae can be classified into seven subfamilies: Habrocneminae, Catantopinae, Cyrtacanthacrinae, Calliptaminae, Coptacridinae, Oxyinae, and Podisminae (Fig. 4). Among the seven recognized subfamilies, Habrocneminae, Catantopinae, Cyrtacanthacrinae, and Calliptaminae are unambiguously supported as monophyletic clades, and the relationship of each to the rest

of the family are completely resolved (Fig. 1, Fig. 4). Coptacridinae and Oxyinae, although each relatively well supported as monophyletic clade, are part of a crown clade that is highly unresolved in terms of within clade relationship (Clade A, Fig. 2). The monophyly of Podisminae, and the resolution of its relationship with Coptacridinae and Oxyinae are only supported by the 50% Majority-rule consensus, which is considered as a compromised solution in phylogenetic systematics (Nixon and Carpenter 1996b). Our analyses also identified within the subfamily Podisminae five monophyletic clades (Fig. 4), which may be treated as tribes: Fruhstorferiolini, Promeosternini, Dericorythini, Traulini, and Podismini. Finally, the rest of the genera within Podisminae are temporarily lumped together in the tribe 'Melanoplina' for convenience until further phylogenetic information becomes available.

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## Appendix I

**List of sampled taxa** († outgroups. \*indicates genus not included in the final analysis. All ingroup genera are listed alphabetically).

Genus	Species	Examined specimens	
		♂	♀
<i>Egnatius</i> Voss.†			
	<i>apicalis</i> Stål	10	5
<i>Egnatioides</i> Liu†			
	<i>xinjiangensis</i> Liu	6	4
<i>Arcyptera</i> Serv. †*			
	<i>coreona</i> Shiraki	4	4
	<i>fusca fusca</i> (Pall.)	4	4
<i>Epacromius</i> Uv. †*			
	<i>tergestinus</i> (Charp.)		
<i>Alulacris</i> Zheng			
	<i>shilingensis</i> (Cheng)	11	8
<i>Anapodisma</i> Dov.-Zap.			
	<i>miramae</i> Dov.-Zap.	10	8
	<i>rufipenna</i> Zheng		2
<i>Anepipodisma</i> Huang			
	<i>punctata</i> Huang	1	1
<i>Apalacris</i> Walker			
	<i>hyaline</i> Walker	6	5
	<i>nigrogeniculata</i> Bi	5	5
	<i>tonkinensis</i> Ramme		1
	<i>varicornis</i> Walker	5	5
	<i>viridis</i> Huang et Xia	1	
	<i>xizangensis</i> Bi	14	11
<i>Armatacris</i> Yin			
	<i>xishanensis</i> Yin	1	5
<i>Assamacris</i> Uv.			
	<i>curticerca</i> ( Huang )	1	
	<i>longicerca</i> ( Huang )	6	12
<i>Bannacris</i> Zheng			
	<i>punctonotus</i> Zheng	2	2
<i>Calliptamus</i> Serv.			
	<i>abbreviatus</i> Ikonn.	15	10
	<i>barbarus</i> (Costa.)	15	10

Genus	Species	Examined specimens	
		♂	♀
	<i>coelesyriensis</i> (G.-T.)	7	2
	<i>italicus</i> (L.)	15	10
	<i>turanicus</i> Tarb.	7	15
<i>Carsula</i> Stal			
	<i>brachycerca</i> Huang et Xia		1
	<i>brachyptera</i> Huang et Xia	2	1
	<i>yunnana</i> Zheng		1
<i>Caryanda</i> Stal			
	<i>bambusa</i> Liu et Yin	3	3
	<i>bidentata</i> Zheng et Liang		1
	<i>elegans</i> Bol.	15	15
	<i>glauca</i> You	6	5
	<i>gracilis</i> Liu et Yin	2	10
	<i>hunana</i> Liu et Yin	2	3
	<i>methiola</i> Chang		1
	<i>nigrovittata</i> Lian et Zheng	4	3
	<i>omeiensis</i> Cheng		1
	<i>pieli</i> Chang	4	5
	<i>quadrata</i> Bi et Jin	1	1
	<i>vittata</i> Li et Jin	4	5
<i>Catantops</i> Schaum			
	<i>pinguis</i> (Stal)	10	7
	<i>simlae</i> Dirsh	2	2
<i>Chondracris</i> Uv.			
	<i>rosea brunneri</i> Uv.	6	8
	<i>rosea</i> (De Geer)	10	10
<i>Choroedocus</i> I. Bol.			
	<i>capensis</i> (Thunb.)	11	10
	<i>robusta</i> (Serv.)	13	10
	<i>violaceipes</i> Miller	15	10
<i>Conophyma</i> Zub.			
	<i>almasyi almasyi</i> Kuthy	10	10
	<i>zhaosuensis</i> Uv.	2	1
<i>Conophymacris</i> Will.			
	<i>chinensis</i> Chang	10	10
	<i>szechwanensis</i> Chang	10	10
	<i>viridis</i> Zheng	10	10
	<i>yunnanensis</i> Zheng	2	2

Genus	Species	Examined specimens	
		♂	♀
<i>Conophymopsis</i> Huang			
	<i>labrispinus</i> Huang	10	10
	<i>linguspinus</i> Huang	6	8
<i>Coptacra</i> Stal			
	<i>hainanensis</i> Tink.		1
	<i>tonkinensis</i> Will.	2	3
<i>Cuvipennis</i> Huang			
	<i>wixiensis</i> Huang	10	10
<i>Cyrtacanthacris</i> Walk			
	<i>tatarica</i> L.	10	7
<i>Dericorys</i> Serv.			
	<i>annulata roseipennis</i> (Redt.)	1	
	<i>tibialis</i> (Pall.)		
<i>Dimeacris</i> Niu et Zheng			
	<i>prasina</i> Niu et Zheng	2	2
<i>Ecphanthacris</i> Tink.			
	<i>mirabilis</i> Tink.	4	3
<i>Ecphymacris</i> Bi			
	<i>lofaoshana</i> (Tink.)	2	5
<i>Eirenephilus</i> Ikonn.			
	<i>longipennis</i> (Shir.)	10	7
<i>Epistaurus</i> I. Bol.			
	<i>aberrans</i> r.-W.	10	10
	<i>meridionalis</i> Bi	15	12
<i>Eucoptacra</i> I. Bol.			
	<i>binghami</i> Uv.	4	2
	<i>kwangtungensis</i> Tink.	10	11
	<i>motuoensis</i> Yin	5	6
	<i>praemorsa</i> Stal	5	5
<i>Eyprepocnemis</i> Fieb.			
	<i>hoktuensis</i> Shiraki	2	6
	<i>perbrevipennis</i> Bi et Xia		2
<i>Fer</i> I. Bol.			
	<i>bimaculatus</i> You et Li	4	4
	<i>nonmaculatus</i> Zheng		1
	<i>yunnensis</i> Huang et Xia	2	2

Genus	Species	Examined specimens	
		♂	♀
<i>Fruhstorferiola</i> Will.			
	<i>huangshanensis</i> Bi et Xia	6	11
	<i>huayinensis</i> Bi et Xia	3	3
	<i>kulinga</i> (Chang)	10	10
	<i>omei</i> (Rehn et Rehn)	1	5
	<i>tonkinensis</i> Will.	10	10
	<i>viridifemorata</i> (Caud.)	12	8
<i>Genimen</i> I.-Bol.			
	<i>burmanum</i> Ramme		1
	<i>yunnanensis</i> Zheng	7	4
<i>Gerenia</i> Stal			
	<i>intermedia</i> Br.-W.	1	1
<i>Gesonula</i> Uv.			
	<i>mundata</i> zemaensis Cheng	3	3
	<i>punctifrons</i> Stal	8	6
<i>Habrocnemis</i> Uv.			
	<i>sinensis</i> Uv.	1	4
<i>Hieroglyphus</i> Krauss.			
	<i>annuliconis</i> (Shir.)	10	5
	<i>banian</i> (Fabr.)	13	7
	<i>concolor</i> (Walk.)		1
	<i>tonkinensis</i> I.-Bol.	10	3
<i>Indopodisma</i> Dov.-Zap.			
	<i>kingdoni</i> (Uv.)	7	10
<i>Kingdonella</i> Uv.			
	<i>hanburyi</i> Uv.	15	3
	<i>kozlovi</i> Mistsh.	14	13
	<i>nigrofemora</i> Yin	2	2
	<i>nigrotibia</i> Zheng		1
	<i>parvula</i> Yin	5	8
	<i>pienbaensis</i> zheng	1	1
	<i>qinghaiensis</i> Zheng		2
	<i>rivuna</i> Huang	3	1
<i>Lemba</i> Huang			
	<i>bituberculata</i> Yin et Liu	2	7
	<i>daguanensis</i> Huang	1	
	<i>viridatibia</i> Niu et Zheng	2	2



Genus	Species	Examined specimens	
		♂	♀
	<i>yunnana</i> Ma et Zheng	1	
	<i>zhengi</i> Li	2	
<i>Leptacris</i> Walk.			
	<i>taeniata</i> (Stal)	3	4
	<i>vittata</i> (Fabr.)	8	7
<i>Liaoacris</i> Zheng			
	<i>ochropterus</i> Zheng	2	4
<i>Longgenacris</i> You et Li			
	<i>maculacorina</i> You et Li	2	2
<i>Longzhouacris</i> You et Bi			
	<i>hainanensis</i> Zheng et Liang	4	5
	<i>jinxiuensis</i> Li et Jin	14	8
	<i>rufipennis</i> You et Bi	9	8
<i>Melanoplus</i> Stal			
	<i>frigidus</i> (Boh.)	4	7
<i>Miramella</i> Dov.-Zap.			
	<i>sinensis</i> Chang	2	1
	<i>solitaria</i> (Ikonn.)	5	3
<i>Niitakacris</i> Tinkham			
	<i>goganzanensis</i> Tink.	4	5
	<i>rosaeceanum</i> (Shir)	8	1
<i>Emeiacris</i> Zheng			
	<i>maculata</i> Zheng	2	2
<i>Ognevia</i> Ikonn.			
	<i>sergii</i> Ikonn.	2	1
<i>Oxya</i> Saerv.			
	<i>adentata</i> Will.	10	10
	<i>agavisa</i> Tsai	14	10
	<i>anagavisa</i> Bi	11	9
	<i>chinensis</i> (Thunb.)	12	10
	<i>hainanensis</i> Bi	11	10
	<i>intricata</i> (Stål)	10	10
	<i>ningpoensis</i> Chang	13	13
	<i>tinkhami</i> Uv.	13	12
	<i>velox</i> (Fabr.)	6	3
	<i>yunnana</i> Bi	8	10

Genus	Species	Examined specimens	
		♂	♀
<i>Oxyina</i> Hollis			
	<i>sinobidentata</i> (Hollis)	13	14
<i>Oxyrrhypes</i> Srtal			
	<i>cantonensis</i> Tink.	5	11
	<i>obtuse</i> (De Haan)		
	<i>quadripunctata</i> Will.		
<i>Oxytauchira</i> Ramme			
	<i>brachyptera</i> zheng	1	1
	<i>elegans</i> Zheng et Liang	2	
<i>Pachyacris</i> Uv.			
	<i>vinosa</i> (Walk.)	3	3
<i>Paratoacris</i> Li et Jin			
	<i>reticulipennis</i> Li et Jin	4	3
<i>Patanga</i> Uv.			
	<i>apicerca</i> Huang	1	1
	<i>humilis</i> Bi	12	10
	<i>japonica</i> (I.-Bol.)	10	7
	<i>succincta</i> (Johan.)	6	5
<i>Pedopodisma</i> Zheng			
	<i>emeiimensis</i> (Yin)	3	3
	<i>huangshana</i> Huang	1	1
	<i>protrucula</i> Zheng	4	4
	<i>shennongjiana</i> Huang	1	1
	<i>tsinlingensis</i> (Chang)	2	2
<i>Podisma</i> Berthold			
	<i>aberrans</i> Ikonn.	4	3
	<i>pedestris</i> (L.)	3	5
<i>Prumna</i> Motschulsky			
	<i>arctica</i> Zhang et Jin	10	12
	<i>cavicerca</i> Zhang	3	3
	<i>jingpohu</i> Huang	1	3
	<i>primnoa</i> F.-W.	10	10
	<i>primnoides</i> (Ikonn.)	3	
	<i>wuchangensis</i> Huang	1	1
<i>Promesosternus</i> Yin			
	<i>himalayicus</i> Yin	1	
	<i>vittatus</i> Yin		1

Genus	Species	Examined specimens	
		♂	♀
<i>Pseudopterygionotus</i> Zheng			
	<i>gunshensis</i> Zheng et al		1
	<i>kunmingensis</i> Cheng	7	6
<i>Pseudoxya</i> Yin et Liu			
	<i>diminuta</i> (Walk.)	15	15
<i>Pyramisternum</i> Huang			
	<i>herbaceum</i> Huang	1	1
<i>Qinlingacris</i> Yin et Chou			
	<i>elaeodes</i> Yin et Chou	3	4
	<i>taibaiensis</i> Yin et Chou	3	4
<i>Quilta</i> Stal			
	<i>oryzae</i> Uv.	7	8
<i>Shirakiacris</i> Dirsh			
	<i>brachyptera</i> Zheng	13	10
	<i>shiraki</i> (I.-Bol.)	15	8
	<i>yunkweiensis</i> (Chang)	9	6
<i>Sinacris</i> Tinkham			
	<i>longipennis</i> Liang	1	1
	<i>oreophilus</i> Tink.	1	1
<i>Sinopodisma</i> Chang			
	<i>bidenta</i> Liang	1	4
	<i>formosana</i> (Shir.)	5	4
	<i>houshana</i> Huang	2	2
	<i>huangshana</i> Huang		1
	<i>jiulianshana</i> Huang	2	2
	<i>kawakamii</i> (Shir.)	1	2
	<i>kelloggii</i> (Chang)	10	10
	<i>kodamae</i> (Shir.)	1	2
	<i>lofaoshana</i> (Tink.)	11	19
	<i>pieli</i> (Chang)	10	8
	<i>quzhouensis</i> Zheng	10	10
	<i>rostellcerca</i> Zheng et Liang	8	10
	<i>shiraki</i> (Tink.)	3	2
	<i>spinocerca</i> Zheng et Liang	1	2
	<i>splendida</i> (Tink.)	2	3
	<i>tsai</i> (Chang)	13	15
	<i>yingdensis</i> Liang	7	4

Genus	Species	Examined specimens	
		♂	♀
<i>Sinstauchira</i> Zheng			
	<i>gressitti</i> (Tink.)	1	1
	<i>pui</i> Liang et Zheng	11	11
	<i>ruficornis</i> Huang	10	10
	<i>yunnansis</i> Zheng	1	1
<i>Spathosternum</i> Krauss			
	<i>prasiniiferum</i> (Walk.)	15	13
<i>Squaroplatacris</i> Liang et Zheng			
	<i>elegans</i> Zheng et Cao	4	3
	<i>violatibialis</i> Liang		1
<i>Stenocatantops</i> Dirsh			
	<i>splendens</i> (Thunb.)	15	10
<i>Stolzia</i> Will.			
	<i>hainanensis</i> (Tink.)	1	1
	<i>jianfengensis</i> Zheng et Liang	1	1
<i>Tauchira</i> Stal			
	<i>damingshana</i> Zheng	1	1
<i>Toacris</i> Tink.			
	<i>shaloshanensis</i> Tink.	1	1
	<i>yaoshanensis</i> Tink.	1	1
<i>Tonkinacris</i> Carl.			
	<i>decoratus</i> Carl.	1	1
	<i>meridionalis</i> Li	4	4
	<i>sinensis</i> Chang	10	8
<i>Traulia</i> Stal			
	<i>lofaoshana</i> Tink.	4	2
	<i>minuta</i> Huang et Xia	5	5
	<i>nigrotibialis</i> Bi	3	3
	<i>orientalis</i> Ramme	4	3
	<i>szetshuanensis</i> Ramme.	7	4
	<i>orchotibialis</i> Liang et Zheng	1	1
	<i>ornate</i> Shir.	4	4
	<i>tonknensis</i> C. Bol.	3	3
<i>Tristria</i> Stal			
	<i>palvinata</i> Uv.	1	1
	<i>pisciform</i> (Serv.)	1	

Genus	Species	Examined specimens	
		♂	♀
<i>Tylotropidius</i> Stal			
	sp.	2	3
	<i>yunnanensis</i> Zheng et Liang Ge-qiu	2	5
<i>Xenacanthippus</i> Mill.			
	<i>hainanensis</i> Tink.	4	1
<i>Xenocatantops</i> Dirsh			
	<i>brachycerus</i> (Will.)	10	8
	<i>humilis</i> (Serv.)	15	10
<i>Yunnanacris</i> Chang			
	<i>yunnaneus</i> (Ramme)	10	10
<i>Yupodisma</i> Zhang et Xia			
	<i>rufipennis</i> Zhang et Xia	2	2
<i>Zubovskia</i> Dov.-Zap.			
	<i>koeppeni</i> (Zub.)	4	3
	<i>parvula</i> (Ikonn.)	8	10
	<i>planicaudata</i> Zhang et Jin	5	3
	<i>striata</i> Huang	10	10

## Appendix 2.

### Character list

1. Shape of body: (0) stout, ratio of body length to width equal at most 4; (1) moderate; ratio of body length to width is between 4–8; (2) elongated and cylindrical, ratio of body length to width is at least 8. (ordered)

#### I. Head

2. Obliquity of frons in profile: (0) not oblique, forming with vertex an right angle; (1) oblique, forming with vertex an acute angle of over 40°; (2) strongly oblique, forming with vertex an very acute angle less than 40°. (ordered)

3. Shape of fastigium in dorsal view: (0) normal, not strongly projected anteriorly, the distance from anterior margin of eyes to the apex of fastigium equal or less than the horizontal diameter of eye; (1) strongly projected anteriorly, the distance from anterior margin of eyes to the apex of fastigium obviously greater than the horizontal diameter of eye (Fig. 5).

4. Transverse groove at base of fastigium: (0) absent; (1) present and fine, not interrupting lateral carinae of vertex. (2) present and distinct, cutting through lateral carinae of vertex (Fig. 6). (ordered)

5. Interorbital distance of vertex: (0) obviously wider than the width of the frontal costa between antennae; (1) almost as broad as the frontal costa between antennae; (2) obviously narrower than the frontal costa between antennae. (ordered)

6. Foveola: (0) distinct; (1) absent or not perceptible.

7. Frontal costa between antennae: (0) not obviously projected; (1) obviously projected forward.

8. Shape of eye: (0) long oval, vertical diameter of eye greater than 1.3 times its horizontal diameter; (1) oval, vertical diameter of eye equal to or less than its horizontal diameter.

9. Size of eye: (0) large, vertical height greater than 1.3 times length of subocular groove; (1) small, vertical height less than 1.2 times length of subocular groove.

10. Shape of antennae: (0) filiform; (1) sword-shaped, width of basal segments greater than length.

11. Length of male antennae: (0) short, tip distinctly not reaching to base of hind femur; (1) long, tip distinctly reaching to or beyond base of hind femur.

#### II. Mesosoma

12. Convexity of median posterior margin of pronotum: (0) smoothly round or broadly angular; (1) projected into a right or acute angle.

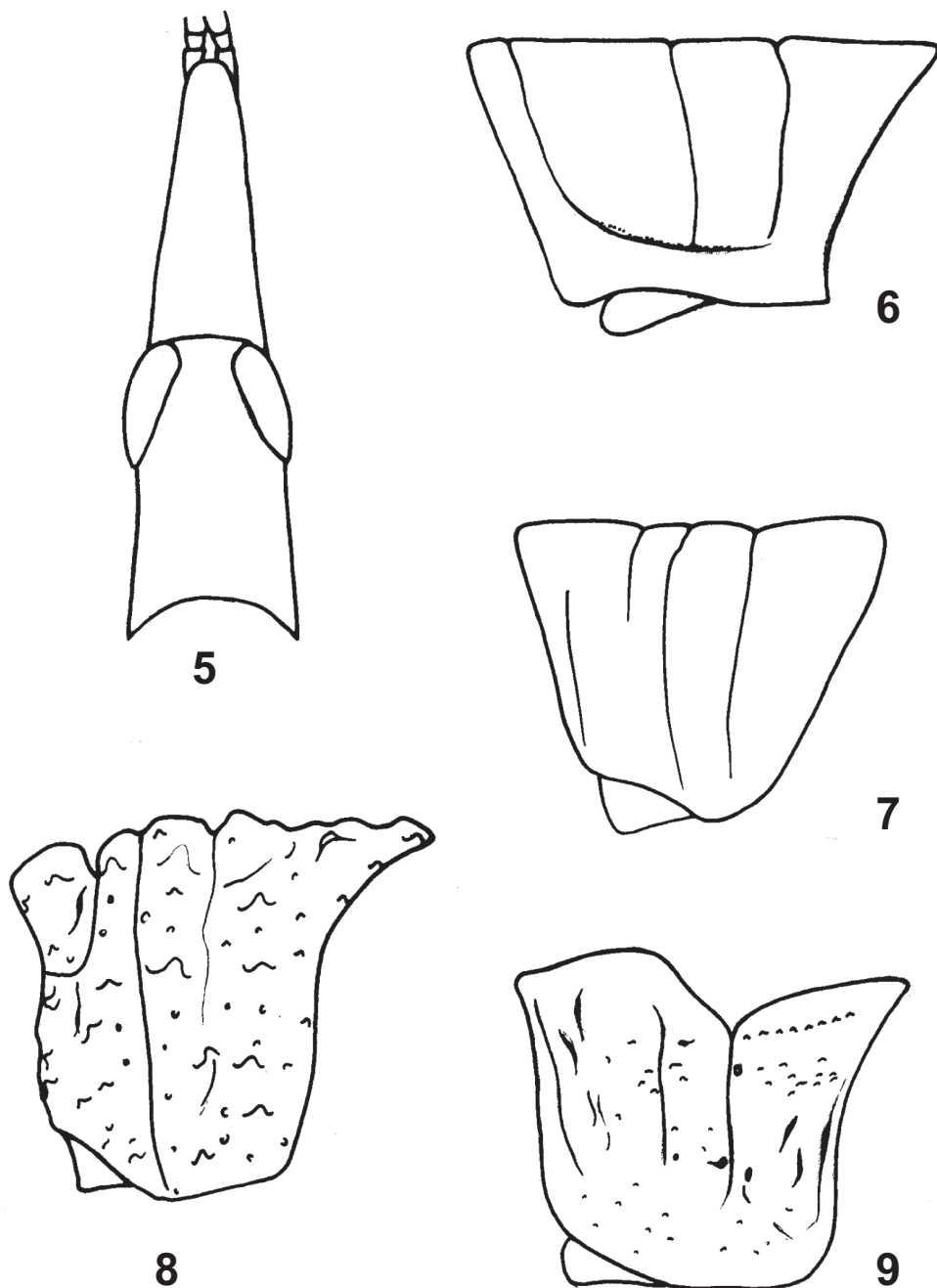
13. Concavity of median posterior margin of pronotum: (0) not concave; (1) broadly concave (Fig. 12); (2) distinctly concave, forming a triangle (Fig. 11). (ordered)

14. Longitudinal margins of dorsal surface of pronotum: (0) constricted in the middle; (1) parallel.

15. Surface of pronotum: (0) smooth to finely sculptured; (1) coarsely granulate, irregularly carinulate, or tuberculate (Fig. 8).

16. Median carina on prozona of pronotum: (0) flat; (1) distinctly elevated and roundly pectinate (Fig. 9).





**Figures 5–9.** Head and pronotum: **5–6** *Carsula brachyptera* Huang et Xia, female: head and pronotum, dorsal view and lateral view, respectively; **7** *Yunnanacris yunaeus* (Ramme), pronotum, lateral view; **8** *Ephanthacris mirabilis* Tinkham, male, pronotum, lateral view; **9** *Dericorys roseipennis* (Redt.), male, pronotum, lateral view.

17. Distinctness of median carina on pronotum: (0) distinct, from almost complete to complete; (1) barely discernible to absent.

18. Median carina on pronotum in lateral view: (0) straight; (1) strongly elevated medially, forming a distinct round ridge (Fig. 10).

19. Incision on median carina of pronotum by principal sulcus: (0) shallow to indistinct; (1) very deep (Fig. 8).

20. Presence of additional incisions of median carina of pronotum by minor transverse carina(e): (0) absent; (1) present.

21. Ratio of length of prozona to length of metazona of pronotum measured along median carina: (0) 1.0–1.2; (1) 1.5–2.0; (2) more than 2.3. (ordered)

22. Lateral carinae on pronotum: (0) absent or slightly elevated, distinctly not reaching to posterior margin of pronotum; (1) distinctly elevated, complete or nearly so.

23. Ventral posterior angle of lateral lob of pronotum: (0) broadly round (Fig. 7); (1) roundly angular to angular (Fig. 6, 10).

24. Posterior margin of lateral lob of pronotum: (0) not concave to slightly arched; (1) strongly concave.

25. Shape of prosternal process: (0) conical (Fig. 16); (1) cylindrical (Fig. 17); (2) transverse and lobular (Fig. 20, 21); (3) mushroom-shaped (Fig. 18, 19).

26. (25:0) Apical part of cone-shaped prosternal process: (0) straight; (1) strongly bent posteriorly.

27. (25:1) Apical part of cylindrical prosternal process: 0 straight or slightly bent posteriorly; (1) strongly bent posteriorly, almost reaching anterior margin of mesosternum, (2) compressed laterally and flat apically.

28. (25:2) Ventral margin of lobular prosternal process: (0) truncate or slightly serrated (Fig. 21); (1) with 2–3 apically rounded, triangular processes (Fig. 20); (2) medially projected into a large triangle; (3) triangular as state 2 and turned anteriorly (Fig. 22, 23).

29. Anterior border of mesosternum: (0) straight or slightly arched; (1) broadly projected in the middle (Fig. 13).

30. Shape of mesosternal interspace: (0) wide, as long as or less than width; (1) elongate, length at least 1.3 times its narrowest width; (2) very reduced, lateral margins partly or completely contiguous. (ordered)

31. Contact of lateral lobes of metasternum medially: (0) separated; (1) contiguous.

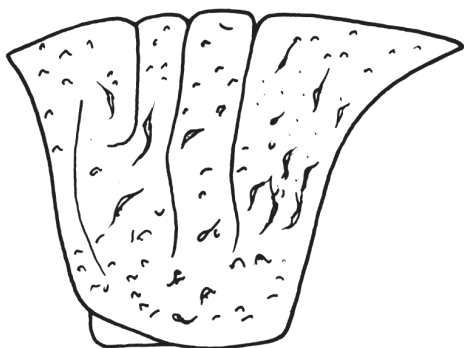
32. Inner posterior corners of lateral lobes of mesosternum: (0) obtusely round or angularly round; (1) right angular to acutely angular.

33. Relative length of dorsal and ventral basal lobe of hind femur: (0) dorsal lobe as long as ventral lobe; (1) dorsal lobe longer than ventral lobe.

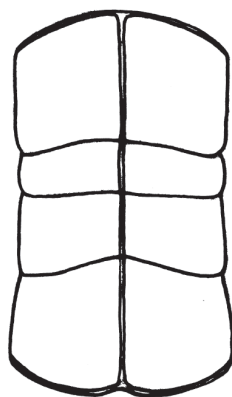
34. Shape of ventral genicular lobe of hind femur: (0) round or roundly angular distally; (1) spined distally.

35. Shape of dorsal genicular lobe of hind femur: (0) round distally; (1) spined distally.

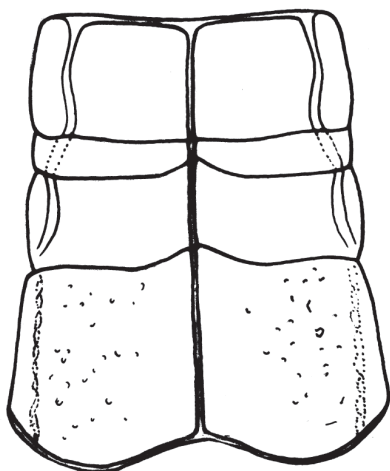
36. Serration of dorsal carina of hind femur: (0) absent, smooth; (1) present, finely serrated.



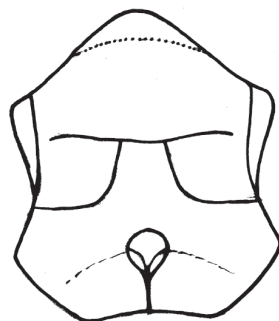
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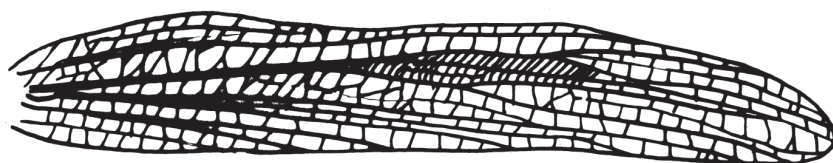
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12



13



14

**Figures 10–14.** Thorax: **10** *Chondracris rosae rosae* (De Geer), male, pronotum, lateral view; **11** *Caryanda elegans* I–Bol., male, pronotum, dorsal view; **12** *Niitakacris rosaceanum* (Shiraki), male, pronotum, dorsal view; **13** *Longzhouacris hainanensis* Zheng et Liang, male, mesosternum and metasternum, ventral view; **14** *Tauchira damingshana* Zheng, female, elytron.

37. Shape of distal end of dorsal carina of hind femur: (0) round or slightly broadly angular; (1) spined, acutely pointed, or narrowly obtuse-angular.

38. Outer apical spine on hind tibia: (0) absent; (1) present.

39. Number of spines on outer margin of hind tibia: (0) 5–6; (1) 8–10; (2) over 12. (ordered)

40. Distance between 1<sup>st</sup> and 2<sup>nd</sup> spines of inner spine series on hind tibia: (0) as long as any other inter-spine distance; (1) longer than any other inter-spine distance.

41. Distal half of hind tibia: (0) not obviously broaden toward apex, without obvious edges running through the spines; (1) broadened toward apex, with distinct outer and inner edges running through the spines; (2) strongly broadened toward apex, with sharp outer and inner edges running through the spines. (ordered)

42. Size of male tegmina: (0) developed, at least in contact with each other above abdomen; (1) abbreviated, lobate, and lateral, not in contact above abdomen, but reaching to posterior margin of metanotum; (2) rudimentary, not reaching to posterior margin of metanotum; (3) absent. (ordered)

43. Distal margin of tegmina: (0) round; (1) obliquely truncated.

44. Cells of distal part of tegmina: (0) rectangular or irregular; (1) oblique.

45. Radial cells in the middle of tegmina: (0) with irregular cross-veins; (1) with parallel cross-veins (Fig. 14).

### **III. Metasoma**

46. Development of tympanal organ: (0) developed, distinct; (1) vestigial with just discernible opening, or absent.

47. Presence of tubercle on sides of apical field of male supra-anal plate: (0) absent, (1) present.

48. Presence of transverse groove on apical field of male supra-anal plate: (0) absent, (1) present.

49. Presence of transverse ridge on middle field of male supra-anal plate: (0) absent, (1) present (Fig. 25).

50. Presence of tubercle on sides of middle field of male supra-anal plate: (0) absent, (1) present.

51. Presence of transverse groove on middle field of male supra-anal plate in male: (0) absent, (1) present.

52. Presence of hair tufts on last sternum of abdomen: (0) absent; (1) present.

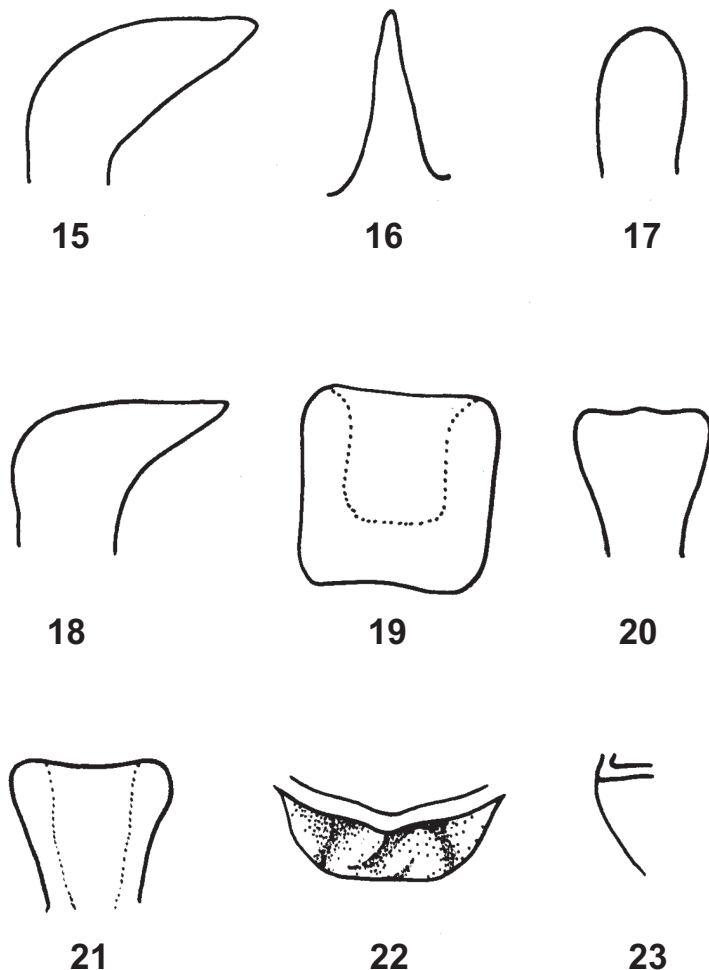
53. Presence and size of furcula: (0) absent; (1) present and small (Fig. 26); (2) present, and large and long (Fig. 28–30). (ordered)

54. Basal field of male supra-anal plate: (0) smooth without tubercles near lateral margins; (1) with two digitiform tubercles near lateral margins (Fig. 28).

55. Shape of male supra-anal plate: (0) triangular; (1) rectangular or trapezoid; (2) scutate.

56. Shape of male cerci: (0) conical; (1) compressed laterally.

57. (55:0) Length of conical cerci in male: (0) short; (1) long.

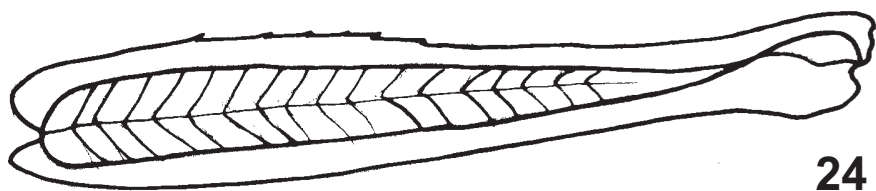


**Figures 15–23.** Prosternal process: **15** *Cyrtacanthacris tatarica* L., male lateral view; **16** *Caryanda elegans* I–Bol., male lateral view; **17** *Calliptamus barbarus* (Costa), male lateral view; **18–19** *Tristria pulvinata* Uv., male lateral view and ventral view respectively; **20** *Sinistauchira yunnana* Zheng, male rear view; **21** *Spathosternum prasiniferum* (Walk), male front view; **22–23** *Conophymopsis labrispinus* Huang, male ventral view, and lateral view respectively (from Huang 1983).

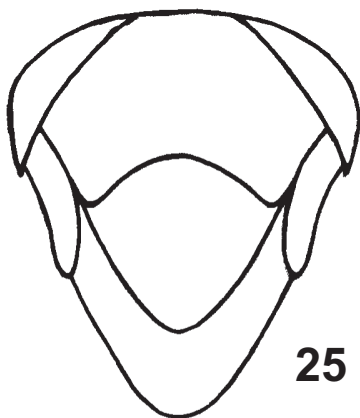
58. Curvature of male cerci: (0) straight; (1) curved inward posteriorly (Fig. 28); (2) curved upward posteriorly; (3) curved downward posteriorly.

59. Apex of cerci in males: (0) pointed; (1) round (Fig. 34); (2) truncated (Fig. 31); (3) bifurcated (Fig. 29); (4) dentate (Fig. 35). (ordered)

60. Shape of male cerci in lateral view: (0) strongly tapering toward apex, width at apical part less than at middle; (1) broadened toward apex, width at apical part slightly greater than at middle (Fig. 32, 33); (2) strongly broadened toward apex, width at apical part much greater than at middle (Fig. 35). (ordered)



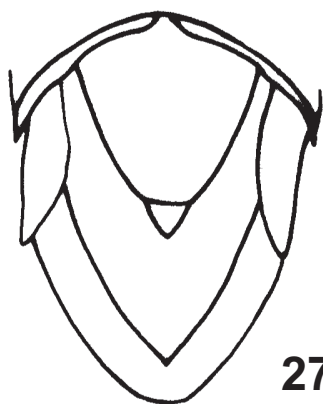
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26



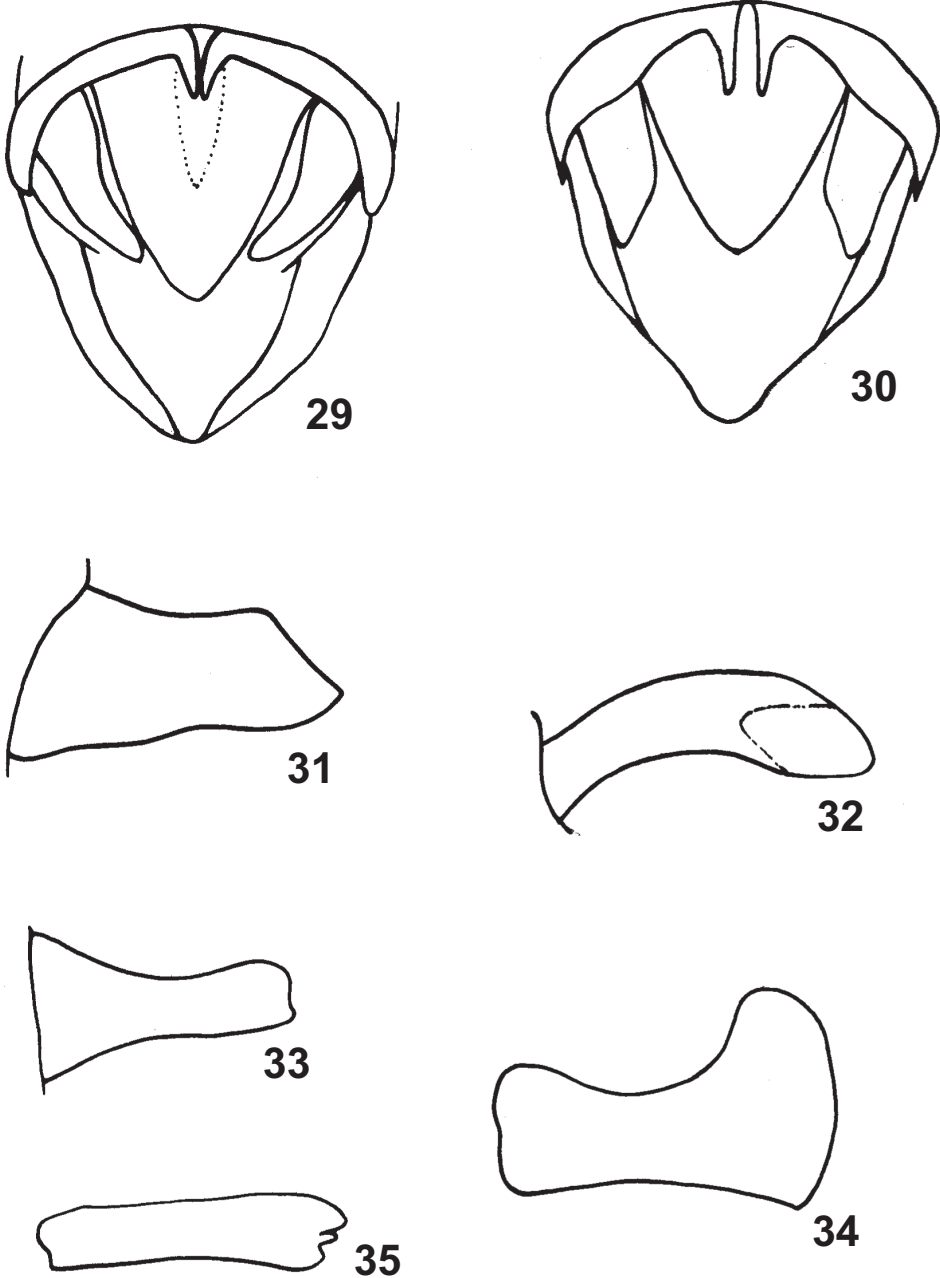
27



28

**Figures 24–28.** 24 *Dericorys roseipennis* (Redt.), male, hind femur, lateral view; 25–28 End of male abdomen in dorsal view: 25 *Dericorys roseipennis* (Redt.); 26 *Ecphanthacris mirabiis* Tinkham; 27 *Spathosternum prasiniferum* (Walk); 28 *Anapodisma miramae* Dov.–Zap.





**Figures 29–35.** 29–30 End of male abdomen in dorsal view: **29** *Niitakacris rosaceanum* (Shiraki); **30** *Indopodisma kingdoni* (Uv.); **31–34** Cercus in lateral view: **31** *Indopodisma kingdoni* (Uv.); **32** *Squaroplatocris elegans* Zheng et Cao; **33** *Sinopodisma tsaii* (Chang); **34** *Fruhstorferiola omei* (Rehn et Rehn); **35** *Calliptamus barbarus* (Costa).

61. Shape of male subgenital plate in ventral view: (0) very short, length equal to or less than basal width; (1) long, length greater than basal width, but not more than 1.5 times; (2) strongly elongated, more than twice basal width (Fig. 38). (ordered)

62. Shape of posterior part of male subgenital plate in ventral view: (0) conical; (1) trapezoid.

63. (61:0) Compression of posteriorly conical subgenital plate in males in ventral view: (0) not compressed; (1) compressed laterally.

64. Shape of male subgenital plate in dorsal view: (0) strongly tapering toward apex, end pointed or blunt; (1) gradually tapering toward apex, end round or concave; (2) not tapering, sometimes even slightly broaden, toward the apex, end truncated. (ordered)

65. Presence of tubercle at apex of male subgenital plate: (0) absent; (1) present and short (Fig. 29, 30); (2) present and much prolonged, forming prominent pointed projection. (ordered)

66. Posterior margin of female subgenital plate in ventral view: (0) triangularly projected posteriorly in the middle; (1) straight or broadly rounded.

67. Presence of lateral teeth on posterior margin of female subgenital plate in ventral view: (0) absent; (1) present.

68. Shape of dorsal valves of ovipositors in profile: (0) stout, less than 3 times as long as broad when in a position coalesced with ventral valves; (1) slender, more than 3.5 times as long as broad when in a position coalesced with ventral valves.

69. Serration of dorsal external margin of dorsal ovipositor valves: (0) smooth or weakly serrated; (1) distinctly serrated.

70. Presence of a notch on apex of dorsal external margin of dorsal valves of ovipositor: (0) absent; (1) distinctly present.

71. Apex of dorsal valves of ovipositor: (0) not bidentate; (1) bidentate.

#### **IV. Male genitalia**

Details of the male genitalia morphology are explained in Figures 43-53. Terminology for genital structures follow Dirsh (1956). Acronyms used in description of the listed genital characters are:

Ac: arc of cingulum (of phallic complex)

A: ancora (of epiphallus)

Ap: apical valves of penis (of phallic complex)

Anp: anterior projection (of epiphallus)

Apd: apodeme (phallic complex)

B: bridge (of epiphallus)

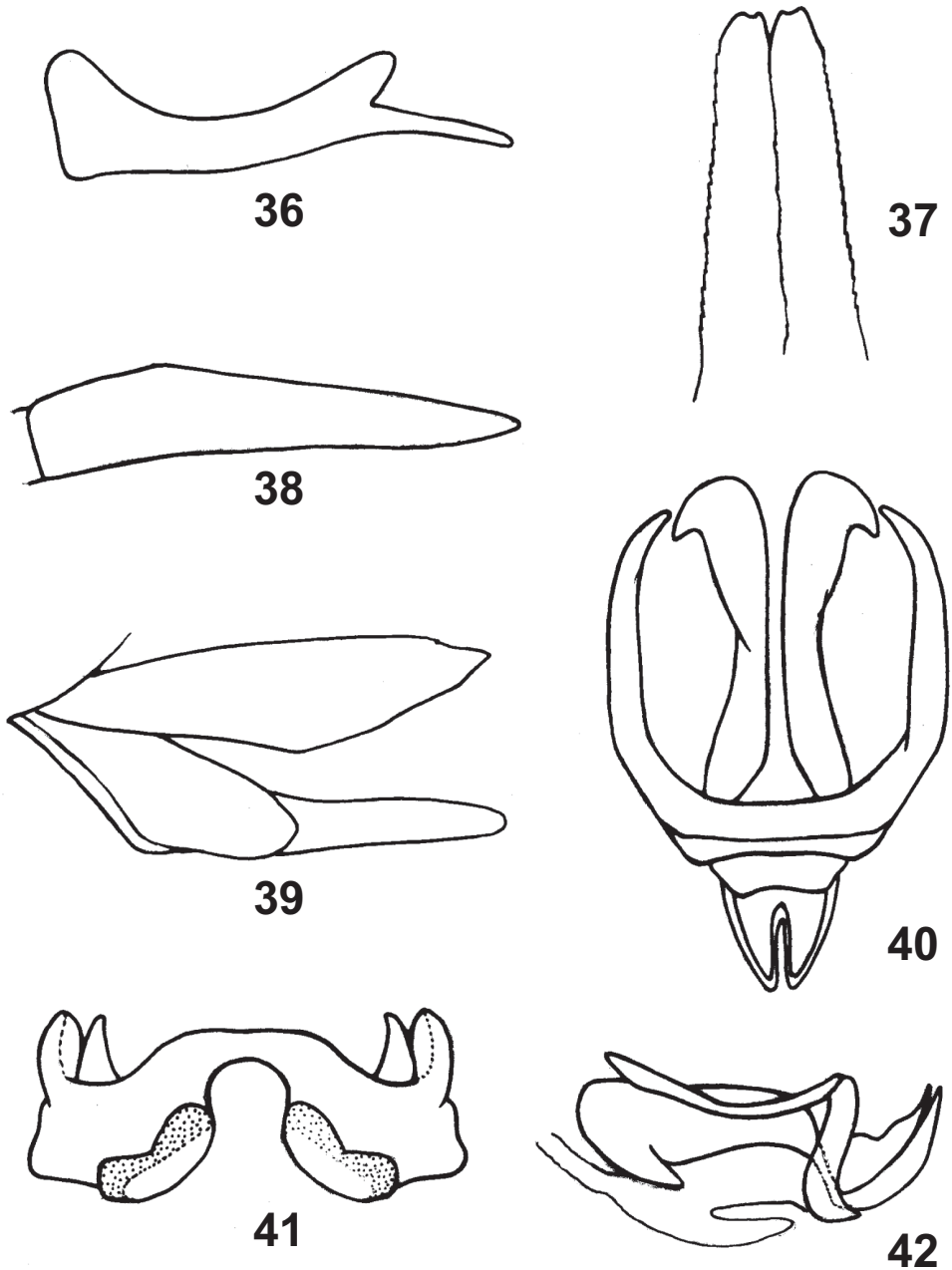
Bp: basal valves of penis (of phallic complex)

Cv: valves of cingulum (of phallic complex)

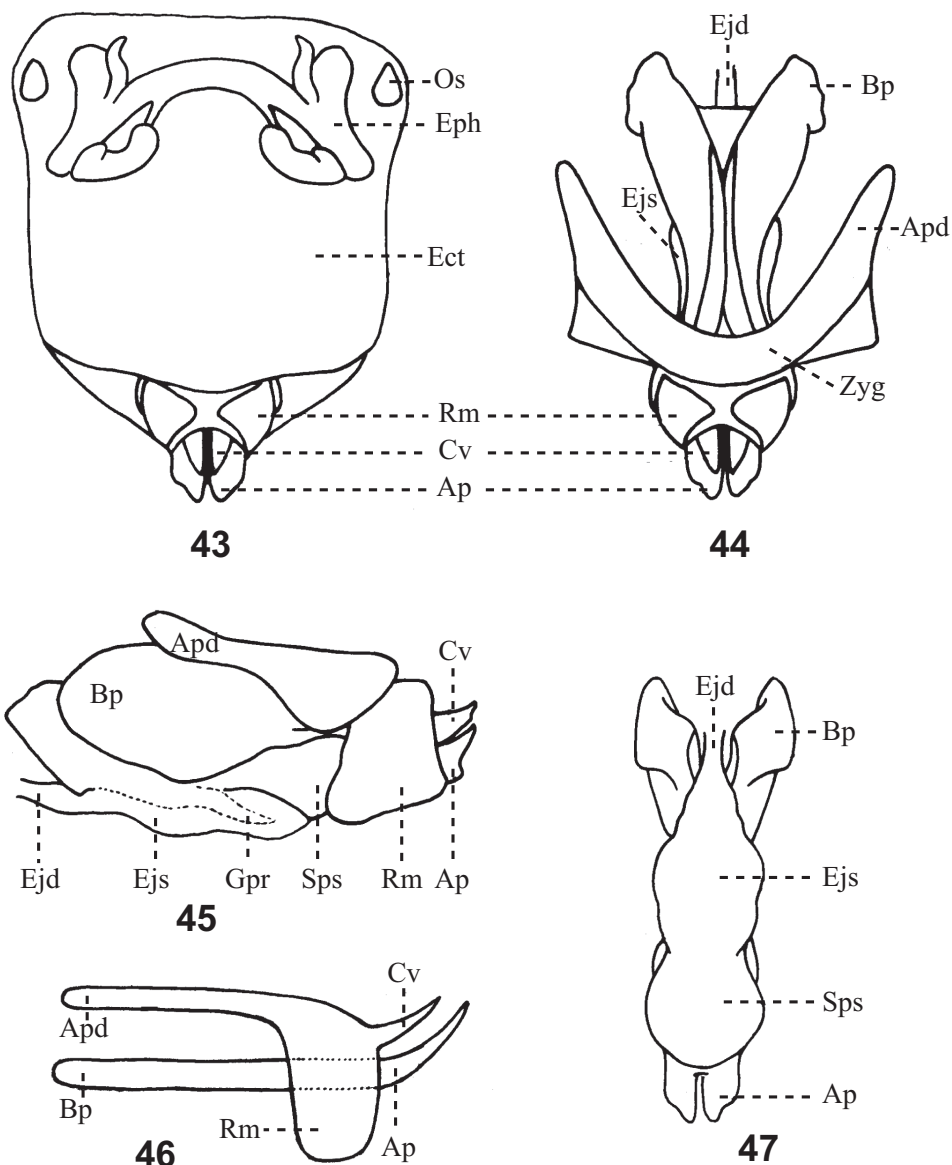
L: lophus (of epiphallus)

Rm: rami of cingulum (of phallic complex).

72. Rami of cingulum (Rm) of phallic complex: (0) undeveloped, narrowly sclerotized; (1) developed, broadly sclerotized (Fig. 45).



**Figures 36–42.** **36.** *Assamacris longicerca* (Huang), cercus, male, lateral view; **37** *Anapodisma miramae* Dov.–Zap., upper ovipositor valve of female, dorsal view; **38** *Leptacris vittata* (Fabr.), subgenital plate of male, lateral view; **39** *Longzhouacris hainanensis* Zheng et Liang, ovipositor, lateral view. **40–42** *Egnatius apicalis* Stål **40**: phallic organ of male, dorsal view **41** epiphallus dorsal view and **42** phallic organ, lateral view.



**Figures 43–47.** General morphology of phallic complex. Terminology and abbreviations used in the figures follow Dirsh (1956). **43** Whole phallic complex, dorsal view; **44** Phallic organ (phallic complex with epiphallus removed) dorsal view; **45** Phallic organ lateral view; **46** Penis and cingulum of simple form lateral view; **47** Phallic organ with zygoma apodemes and rami removed ventral view. Abbreviations: **Ap** – apical valves of penis, **Apd** – apodemes, **Bp** – basal valves of penis, **Cv** – valves of cingulum and **Rm** – rami of cingulum **Zyg** – zygoma. Additional abbreviations for characters not coded: **Ect** – ectophallus **Ejd** – ejaculatory duct, **Ejs** – ejaculatory sac, **Eph** – epiphallus, **Gpr** – gonopore process, **Os** – oval sclerite of epiphallus, **Sps** – spermatophore sac.

73. Length of the apodemes (Apd): (0) far from reaching to apex of the basal valves of penis (Bp); (1) reaching to apex of basal valves of penis; (2) reaching beyond apex of the basal valves of penis. (ordered)

74. Shape of apodemes (Apd) (dorsal view): (0) slender, more than 7 times as long as broad; (1) stout, less than 6 times as long as broad.

75. Prominence of arc of cingulum (Ac): (0) well developed and large; (1) weak, but perceptible; (2) absent. (ordered)

76. Bp and apical valves of penis (Ap): (0) connected by strongly sclerotized flexure (Fx) (Fig. 53); (1) separated, being connected by membrane.

77. Apex of Ap (in profile): (0) distinctly bent upward (Figs. 42); (1) straight; (2) distinctly bent sideward.

78. Length of the valves of cingulum (Cv): (0) very long, apex distinctly reaching beyond apex of Ap (Fig. 42); (1) long, apex reaching to or almost to apex of Ap; (2) reduced, apex reaching at most to middle of Ap; (3) completely absent. (ordered)

79. Shape of epiphallus: (0) bridge-shaped (Fig. 41); (1) shield-shaped (Fig. 49).

80. Integrity of epiphallus: (0) complete, not divided (Fig. 41); (1) longitudinally divided into two parts along midline, connected by membrane (Figs. 49).

81. Bridge of epiphallus in dorsal view in relation to width of lateral plate (width of plate refers to its width at ancora without including the latter): (0) broad; width in the middle broader than 1/2 of, but narrower than width of lateral plate (Fig. 49); (1) narrow; width in the middle narrower than half of the width of lateral plate (Fig. 41); (2) absent (Fig. 50). (ordered)

82. Presence of ancorae (A) and its size in relation to width of bridge of epiphallus: (0) developed, distinctly projected, longer than 1/2 of width of bridge (Fig. 41); (1) small, obviously less than 1/2 of width of bridge; (2) absent. (Ordered)

83. Development of lophi (L): (0) well developed, large; (1) undeveloped, small but perceptible; (2) absent. (ordered)

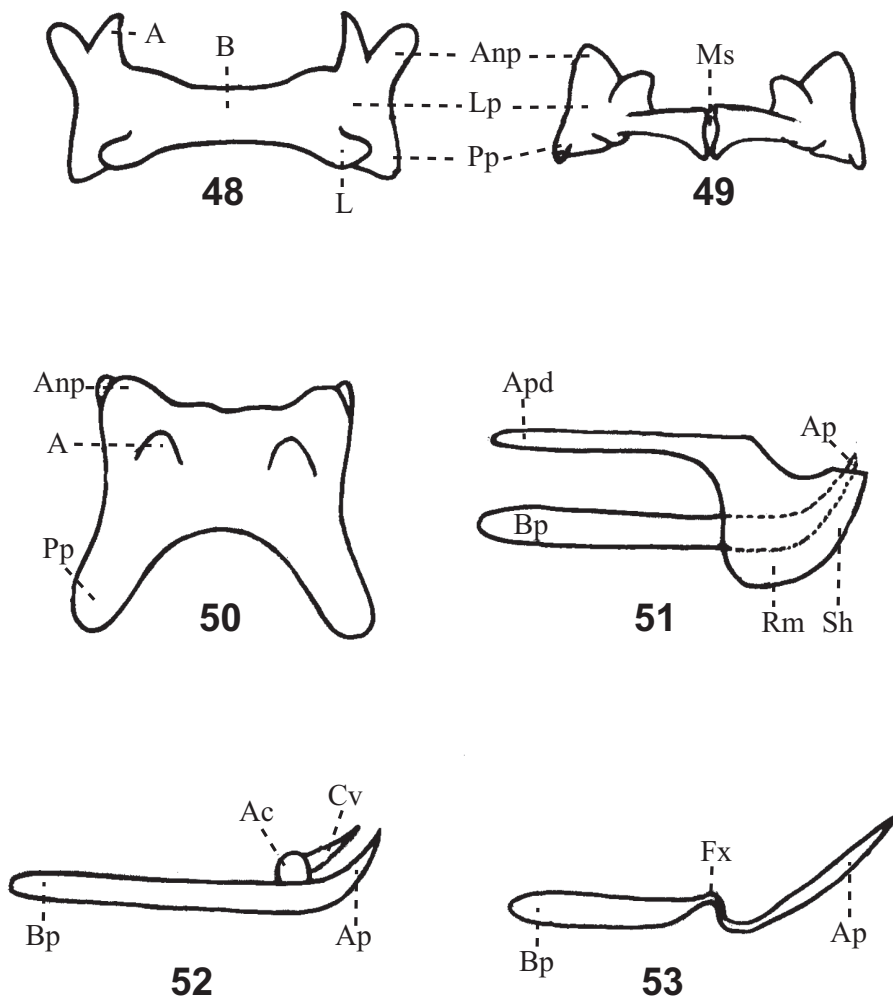
84. Shape of lophi: (0) lobiform with 2 or 3 lobes (Fig. 41); (1) lobiform with only one lobe.

85. Shape of anterior projections of epiphallus (Anp): (0) distinctly projected (Fig. 41); (1) slightly projected.

86. Posterior projections of epiphallus (Pp): (0) not or slightly projected; (1) distinctly projected.

87. Apex of ancorae: (0) pointed, (1) bluntly round; (2) truncated.

88. Length of Bp relative to Ap: (0) Bp more than 1.5 times length of Ap; (1) Bp as long as Ap (Fig. 42); (2) Bp less than 0.8 times length of Ap. (ordered).



**Figures 48–53.** Variations of phallic complex: **48–50** Variation of epiphallus in dorsal view; **51.** Penis with sheath formed from cingulum and exposed apex of penis; **52** Penis with arch of cingulum and valve derived from it; **53** Valve of penis with flexure. Abbreviations: **A** – ancora of epiphallus, **Ac** – arc of cingulum of phallic complex, **Anp** – anterior projections of epiphallus, **Ap** – apical valves of penis of phallic complex, **Apd** – apodeme of phallic complex, **B** – bridge of epiphallus, **Bp** – basal valves of penis of phallic complex, **Cv** – valves of cingulum of phallic complex, **Fx** – flexure **L** – lophi of epiphallus, **Ms** – median slit of epiphallus, **Pp** – posterior projections of epiphallus, **Rm** – rami of cingulum and **Sh** – sheath



Appendix 3.

Character Matrix (Taxa in bold are outgroups).

CHARACTERS									
TAXA	1	11	21	31	41	51	61	71	81
<i>Egnatius</i>	1100000002	0000000001	0000-----00	0000000010	0000000000	0000000000	0000000000	0010000100	10000000
<i>Egnatinides</i>	1100000002	0000000001	0000-----00	0000000010	0000000000	0000000000	0000000000	0010000100	10000000
<i>Alulacris</i>	0000110100	0101001000	-01000--11	00000001010	0100000000	101001-010	0000100010	1000001100	00000100
<i>Anapodisma</i>	0000110100	1011001000	200000--11	00000001010	01000001000	1021000000	0000100110	1000011100	11000002
<i>Aneipodisma</i>	0000000000	0011101000	200000--11	0000000000	03---10000	10100001000	0000000000	0111000100	01001100
<i>Apalacris</i>	0001-00000	---1000000	001000--11	0000011010	0010000000	10000010-0	0000000010	011-000001	00010100
<i>Armatacris</i>	0000110000	0100000000	001001--10	1100010010	0000001000	101101-100	2000000000	0101001100	11011101
<i>Aserratus</i>	0000010000	0001001000	101000--10	0000001010	03---00000	1010000100	0000000010	0020101100	00000100
<i>Assamacris</i>	0000011100	1101100000	101000--11	0000011010	0000000000	1010200031	0000000110	0111000000	00000000
<i>Bannacris</i>	0000210000	1101000000	101000--11	0000001010	0000000000	1010000200	0000100010	0001000100	10000000
<i>Calliptamus</i>	1100110000	010100000-	01001-0-11	0000011010	0000000000	100001-141	0000000000	011100-110	112--110
<i>Carsula</i>	2212000011	0101000000	10103---12	1000000120	1000100000	111001-000	1000000110	0111010101	020101-1
<i>Caryanda</i>	0001010000	---100-000	-01000---0	1001001110	1100000000	1110000000	00000--010	00-10000101	01000-1-
<i>Catanops</i>	0000210000	0101000000	00101-0-10	1000011010	0000000000	10-0000111	0000000000	00--000000	10000000
<i>Chondracris</i>	0000010000	0021100100	001001--10	0100010010	0000001000	100001-100	1000000000	01110000100	11010011
<i>Choroedocus</i>	0000010000	0101000000	1010111-10	0000011020	0000000000	101001-112	0000000000	0-01000000	-000110-
<i>Conophryma</i>	0000010000	0001001000	211000--11	0000000110	03---100--	-0-011-0-0	000-000000	0000211300	00010010
<i>Conophrymacris</i>	0001010000	0101000000	111000--11	0000001110	0100000000	1000200311	00000-1010	0000000-00	00000000
<i>Conophrymopsis</i>	0000010110	0001000000	20102--311	0000000110	03---10000	1020100000	0000000000	001021-300	10010110
<i>Coptacra</i>	0002100000	0021100000	001000--11	0000011010	0010000000	1020000100	0000000000	0110000101	00000100
<i>Curvipennis</i>	0000110000	0001101000	100000--11	0000001010	0100000000	10100000010	0000000010	01100001000	10000101
<i>Cyrtacanthacris</i>	0000110000	0100000000	0010111-10	0100010000	00000001000	1010000000	1000000000	0101000200	120101-1
<i>Dimeacris</i>	0002010000	1001000000	200000--11	1000000000	0100000000	1110101000	0000000000	0001010100	00010100
<i>Deritocorys</i>	0100000000	0101110001	000000--10	0010010120	0000000010	00000001010	0000000001	0101011100	00010010

CHARACTERS									
TAXA	1	11	21	31	41	51	61	71	81
<i>Ephanthacris</i>	0102000010	1021100110	001000--11	0000011010	0010000000	1010000000	0000000000	0100100100	00001100
<i>Echpyacris</i>	0102100000	0021100000	001000--11	0000011010	0011000000	1010000100	00000--010	0110000101	00000100
<i>Eirenephilus</i>	0000010110	0101101000	000000--11	00000001010	0000000000	1010000000	0000100010	0011010100	00000100
<i>Emeiacris</i>	0000010000	0101001000	101000--11	0000000010	0000000001	00100001010	0000100010	0101011100	00010100
<i>Eokingdonella</i>	0000010110	0001001000	111000--11	0000000010	03---00001	00200001000	0000000010	0-----0000	-----
<i>Epistaurus</i>	0102200000	0101000001	001000--11	0000011010	0011000000	1020100-00	0000000000	00100001001	00000000
<i>Eucoptacra</i>	0102200000	0021000000	000000--11	0000011010	0011000000	1020000--0	0000000010	00-1000001	0000--00
<i>Eyprepocnemis</i>	0000010000	0101000000	-0101-0-10	0000011010	0000000000	1010000000	0000000000	011-000-00	10010100
<i>Fer</i>	0001010000	0101001000	10101-0-10	0001001110	1000100000	1110000000	0000000010	0100000301	01000110
<i>Fruhstorferiola</i>	0000110000	0101001000	001000--10	0000001010	0000000000	1010000012	00001-1010	01--00--00	00000100
<i>Genimen</i>	0000210100	1001001001	200000--11	1000000010	03---00000	10-0000000	0000000000	0110000300	00010100
<i>Gerenia</i>	1000000000	0021000000	001000--11	0000011010	0011000000	1010000000	0000000010	0100100200	11101100
<i>Gesonula</i>	0000-10000	0101001000	001001--11	1001001111	2000100000	11-0000-00	0000000010	01000-0101	00000100
<i>Habrocnemis</i>	1000000000	0101100000	10001-0-10	0000011010	0100000010	002001-000	0000000000	0101000101	20000000
<i>Hieroglyphus</i>	0001010000	1101001000	101000--10	1000001110	-000101000	11-0-001--	00000000-0	01010-1001	0000-000
<i>Indopodisma</i>	0000210000	0001001000	100000--11	0000001010	0200000000	102001-020	0000100010	0000111100	00000020
<i>Kingdonella</i>	1100010010	0--100-00-	110000--11	0000000010	03---10001	00-00010-0	0000000010	012--11100	11001100
<i>Lemba</i>	0001010000	0101000000	101000--10	0011001110	1000000000	1110000000	1001010010	0120100101	00000001
<i>Leptacris</i>	2202000001	0101000000	101000--12	1000000120	0000100000	10100001000	2010000000	0000011100	10100-02
<i>Litaoacris</i>	0000010100	0101001000	000000--11	0000000010	0000000000	10100001000	0000000010	0001011100	01000100
<i>Longgenacris</i>	0000110000	0101001000	101000--11	0000001010	0000000000	101001-010	0000100000	0000101100	10010101
<i>Longzhouacris</i>	0001110000	1101101000	10-000--01	1000011010	0100000000	11101000000	00000-1110	0001010100	10011101
<i>Melanoplus</i>	0000110100	0101001000	-00000--11	0000000010	0000000000	102001-010	0000100000	0100011100	00000100
<i>Miramella</i>	0000010110	1101001000	100000--11	0000000010	0-00000--	-0200000000	0000200010	10-0101100	0100000-
<i>Nitidacris</i>	0000110000	0011001000	100000--11	0000001010	0100000000	1020000010	0000000010	0000111100	00000110
<i>Ognevia</i>	0000010110	0101000000	001000--11	0000000010	0000000000	1010000000	0000100010	0-----0000	-----
<i>Oxya</i>	0001-10000	0101001000	-01000--10	1001001110	20000000--	-1000000-0	00000--010	0100000-01	020000--

CHARACTERS

TAXA	1	11	21	31	41	51	61	71	81
<i>Oxyura</i>	0001110000	0101001000	101000--10	1001000110	2000000000	11000000--0	0000000010	0---00--01	0000000-
<i>Oxyrrhypes</i>	2000000000	0101000000	001000--12	0000010120	0000000001	00100--100	1000000000	0---011100	00-10-01
<i>Oxytauchina</i>	0000010000	010100-000	10102--110	0001001110	1000000000	1110000000	0000010010	0100001101	00000100
<i>Pachyactris</i>	0000-00000	0101100100	001000--10	1100011010	00011001000	1000000100	1000000000	0111000100	11010011
<i>Paratocaris</i>	0001010000	0101001000	101000--10	1001001010	1000000000	1110000000	0000000010	0100000001	00000000
<i>Paratonkinacris</i>	0000010010	110100100-	101000--11	0000000010	0000000001	0010000310	0000100010	0-----	-----
<i>Patanga</i>	00001110000	0100000000	0010111-10	11000110010	0000001000	100001-0-0	1000000010	01--000100	01010011
<i>Pedopodisma</i>	00001110000	0001000100-	-01000--10	000000-010	0200000000	1010000--0	0000100010	0100-1-100	01000100
<i>Podisma</i>	0000210110	0101000000	001000--1-	0000000010	0-00000000	1020201000	0000000010	0121110100	01000100
<i>Primnoa</i>	00001110110	-011001000	201000--11	000000-010	010000--00	1010--0-0	01-20000-0	0021014200	11010102
<i>Promecosternus</i>	0001010000	1101101000	101000--00	1000010000	010-000001	0020100111	0000000100	0000010100	00011110
<i>Pseudoxya</i>	0000210000	0101001000	101000--10	0011001110	2000000000	1110000000	0000000010	0100001101	01000010
<i>Pseudopterygnotus</i>	0000010000	0001000000	201000--10	0000000110	1100100000	1110200000	00000-1010	0100010101	00000011
<i>Pyramisternum</i>	0001110000	0101001000	10102--210	0001000110	1000000000	1100000000	0000000010	0-----	-----
<i>Quilta</i>	2000010000	0101001000	101101--00	0011101110	2000000010	0110000000	10010-1000	01110001001	020100-0
<i>Qinlingacris</i>	0000010110	0001000000	001000--11	0000000010	03---00000	10200001000	0000000010	002000-100	01000100
<i>Ranacris</i>	0000000000	0001100000	200000--11	0000011010	03---00000	1010000000	000000---	-----	-----
<i>Shirakiacris</i>	0000010000	010100000-	01001-0-10	1000011010	0000000000	100001-111	00000-1000	01110001000	10010100
<i>Sinacris</i>	0000010000	0101001000	10102--110	0001001110	1000000000	1100000000	0000010010	0010001101	01001100
<i>Sinopodisma</i>	0000-10000	0001001000	101000--10	0000001010	0100000000	10100001--	0000100010	0000-1-100	00000-00
<i>Sirstauchina</i>	0002-10000	0101001000	10102--010	1000001110	1000100000	11-0000000	0000000010	0100000001	00001000
<i>Spabosternum</i>	0000010000	0101000001	01002--010	1000000110	0000100100	1010001000	0000000000	0110011000	01101121
<i>Squaroplatiacris</i>	0000010000	0101000000	01101-0-10	1000001020	0000000000	101001-111	0000010000	0011000100	00001000
<i>Stenocatantops</i>	0000210000	0101000000	00001-0-10	1000011010	0000000000	1000000110	1000000000	0100000100	10000000
<i>Stolzia</i>	0000210000	-010101000	001000--11	0001001110	0000001000	1110000000	0000000010	0-----0--01	00000-1-
<i>Tauchina</i>	0001010000	0101001000	10102--110	0001001010	1000100000	1110000000	0000000010	0100000101	01001100
<i>Toacris</i>	0002010000	0101001000	10101-0-10	1001001010	1000100000	1110000000	0000000010	0101000101	00000100

CHARACTERS										
TAXA	1	11	21	31	41	51	61	71	81	
<i>Tonkinacris</i>	0000210000	1101001000	-01000--10	0000001010	0000000000	10100-----0	0000100010	01000010100	00000100	
<i>Traulia</i>	0000001000	-1010000000	101000--1-	0000011010	0-000000000	10-00000--	00000000-0	01--000001	00000100	
<i>Tristria</i>	2000001000	0101000000	11103--1-12	0000000120	0000000000	10200000100	1001000000	01010001100	00000000	
<i>Traulitonkinacris</i>	0000001100	1101001000	101000--10	0000011010	1000000001	001021-031	0000000010	0-----	-----	
<i>Tylotropidius</i>	0000001000	0101000000	01101-2-10	1000011020	0000000000	1010200000	0000000000	00110000100	10001001	
<i>Xenacanthippus</i>	22120100001	0101001000	20101-0-12	1000000110	0000000010	0010000000	2010000010	0011210200	120100-2	
<i>Xenocatantops</i>	0000210100	0100000000	00101-0-10	0000011010	0000000000	1010000010	0000000000	0110000000	100000-0	
<i>Yupodisma</i>	0000001010	0001001000	101000--11	0000001010	0100000001	0021000000	0000100010	1001001100	00000001	
<i>Yunnanacris</i>	0000210000	0001001000	100000--11	0000001010	0100000000	1010000010	0000100010	0000111100	01000101	
<i>Zubovskia</i>	0000110000	0001001000	20-000--11	0000000010	03---1---00	10-00000010	0000-00010	1000111100	01000100	



# ***Osmia* species (Hymenoptera, Megachilidae) from the southeastern United States with modified facial hairs: taxonomy, host plants, and conservation status**

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**§** [urn:lsid:zoobank.org:author:AD099E58-A69A-4C05-8E8E-2CC367FF3CA0](https://zoobank.org/urn:lsid:zoobank.org:author:AD099E58-A69A-4C05-8E8E-2CC367FF3CA0)

**||** [urn:lsid:zoobank.org:author:80DCC2BA-6D2D-449B-83DA-08BB71DBE589](https://zoobank.org/urn:lsid:zoobank.org:author:80DCC2BA-6D2D-449B-83DA-08BB71DBE589)

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[urn:lsid:zoobank.org:pub:8DBFAD71-1C0C-4B82-8C06-1BCEAD9D85C6](https://zoobank.org/pub:8DBFAD71-1C0C-4B82-8C06-1BCEAD9D85C6)

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## **Abstract**

We describe females and males of *Osmia* (*Melanosmia*) *calaminthae* **sp. n.**, an apparent floral specialist on *Calamintha ashei* (Lamiaceae), and provide observations on the behavior of female bees on flowers of this plant. We also provide diagnostic information for *Osmia* (*Diceratosmia*) *conjunctoides* Robertson, **stat. n.**, and synonymize *O. (Diceratosmia) subfasciata miamiensis* Mitchell with *O. conjunctoides* **syn. n.** Females of both *O. calaminthae* and *O. conjunctoides* are unique among North American *Osmia* for having short, erect, simple facial hairs, which are apparent adaptations for collecting pollen from nototribic flowers. *Osmia calaminthae* is currently only known from sandy scrub at four nearby sites in the southern Lake Wales Ridge in Highlands County, Florida, USA, while *O. conjunctoides* is known from limited but widespread sites in the southeastern USA. We discuss the conservation status of both species based on known or speculated floral associates and distributions.



**Keywords**

Bee, Apoidea, Megachilinae, Osmiini, *Melanosmia*, *Osmia calaminthae*, *Osmia conjunctoides*, Lamiaceae, *Calamintha ashei*, oligolecty

**Introduction**

The genus *Osmia* in North America comprises about 150 described species (Ascher and Pickering 2011) that are usually metallic green or blue, sometimes brilliantly so. The 30 species recorded east of the Mississippi River prior to this contribution have been relatively well studied taxonomically (Sandhouse 1939, Mitchell 1962), and the internet houses freely available matrix-based and dichotomous keys to the species (Arduser 2009, Griswold et al. 2010, Andrus et al. 2010). As in many other bee genera, the species diversity in eastern North America is depauperate compared to west of the Mississippi River. Nonetheless, there remain many areas in eastern North America that would benefit from increased study and collection effort. In particular, Florida and other states in the southeastern United States appear to house a number of interesting bee endemics, and new state records continue to be documented from this region (Hall and Ascher 2010).

Herein we describe one such find, *Osmia* (*Melanosmia*) *calaminthae* sp. n., known only from Highlands County, Florida, in sandy scrub at the southern end of the Lake Wales Ridge. This habitat houses many Florida endemic plants and animals, including bees (Deyrup et al. 2002). *Osmia calaminthae* is apparently a floral specialist on *Calamintha ashei* (Weath.) Shinnery (Lamiaceae), Ashe's Calamint (Figs 1, 4; also known as Ashe's Savory), a threatened woody mint found in sand pine/scrub habitat in the Florida central highlands and southeastern Georgia (Coile 2000). The new species was discovered by Deyrup et al. (2002) during surveys of the Archbold Biological Station. During subsequent searches by J. S. Ascher, H. G. Hall, and colleagues, including photographer T. Lethbridge, numerous females and a few males were found visiting the host plant in late morning at the Placid Lakes Development southwest of the town of Lake Placid (N27.250, W81.389). At this site the host plant grows commonly in sand scrub, much of which occurs in vacant lots within a partially completed housing subdivision.

*Osmia calaminthae* females have modified hairs on the face that readily distinguish the species from similar species of *Osmia* (see Diagnosis, below). Modified facial hairs for collecting pollen from nototribic flowers occur rarely in scattered species across multiple bee families (e.g., Müller 1996, Ayala and Griswold 2005, Michener 2007). In *O. calaminthae*, the hairs on the frons, clypeus, and scape are uniformly short, erect, and simple, and apparently function to trap pollen when the female enters the corolla and her head contacts the anthers of this flower (Figs 2, 3, 5–7). The pollen accumulates to form a conspicuous mass and evidently remains on the face of the bee for an extended time during foraging bouts (as opposed to being immediately transferred

to the metasomal scopa), as evidenced by conspicuous loads adhering to the face of approximately one-fourth of the female specimens examined. Interestingly, another *Osmia* that is also found in the southeastern United States, *Osmia (Diceratosmia) conjunctoides* Robertson, new status, has nearly identical hairs on the frons and clypeus of females (Fig. 8). *Osmia (Diceratosmia) subfasciata miamiensis* Mitchell, 1962, was described as a subspecies but is herein distinguished from typical *O. subfasciata subfasciata* Cresson and newly synonymized under *O. conjunctoides*. Specimens and floral records are scarce for *O. conjunctoides* (Pascarella 2008); only one examined specimen has an associated floral record, *Crotalaria pumila* Ortega (Fabaceae), which limits our interpretation of floral associations for this bee.

It is the honor of MGR and JSA to dedicate this paper to Kumar Krishna in celebration of his lifelong achievements in the study of Isoptera. Both authors are grateful to Kumar and Valerie Krishna for the kindness and generosity shown to them during their respective tenures at the American Museum of Natural History.

## Methods

The morphological terminology follows that proposed by Michener (2007) and Harris (1979). Mandibular teeth are numbered from ventral-most tooth to dorsal-most tooth. Thus, the ventral-most tooth is the first tooth and the next ventral-most tooth is the second. In the species treated herein, between the second and dorsal-most tooth is a smaller, slightly more interior, cutting edge extended from the dorsal-most tooth, here called the third tooth. The dorsal-most tooth is the fourth tooth.

The following morphological abbreviations are used: flagellar segment (F), metasomal tergum (T), metasomal sternum (S), and ocellar diameter (OD). Measurements are given for the holotype specimen, with the observed range from other specimens following in parentheses.

Bee specimens were examined and measured using a Leica MZ12 dissection microscope and ocular micrometer. Pollen grains were slide mounted in silicone oil and examined using a Nikon E200 compound microscope. Photomicrographs of pinned specimens were taken using a Keyence VHX-500F Digital Imaging System.

The following abbreviations are used for specimen repositories, with individuals associated with those repositories following in parentheses:

**Champaign** – Illinois Natural History Survey, Champaign IL (D. Dmitriev)

**New York** – American Museum of Natural History, New York NY (J. S. Ascher, J. G. Rozen, Jr.)

**Gainesville** – Florida State Collection of Arthropods, Gainesville FL (J. Wiley)

**Lake Placid** – Archbold Biological Station, Lake Placid FL (M. Deyrup)

**Logan** – USDA-ARS Bee Biology and Systematics Laboratory, Logan UT (T. Griswold, H. Ikerd)

**Orlando** – University of Central Florida, Orlando FL (S. M. Fullerton, S. Kelly)

**Raleigh** – North Carolina State University, Raleigh NC (R. Blinn)

**Washington, D.C.** – United States National Museum of Natural History, Washington D.C. (S. G. Brady, B. Harris)

## Taxonomy

***Osmia (Melanosmia) calaminthae*, Rightmyer, Ascher & Griswold, sp. n.**

urn:lsid:zoobank.org:act:DB373E46-E362-4108-8AD5-52DE1598A8FD

[http://species-id.net/wiki/Osmia\\_calaminthae](http://species-id.net/wiki/Osmia_calaminthae)

Figs 2, 3, 5–7, 9–26

*Osmia* sp.; Deyrup et al. 2002: 99.

**Diagnosis.** Females of *O. calaminthae* are most similar to *O. (Melanosmia) albiventris* Cresson and *O. (Melanosmia) cordata* Robertson, sharing with those species the white hairs of the body (including scopa) and four-toothed mandible with the outer and condylar ridges parallel (Figs 13, 14). Unlike those species, *O. calaminthae* has specialized hairs on the face (including clypeus and frons) that are extremely short, evenly spaced, simple, and stout (Figs 5, 6; longer and finer in *O. albiventris* and *O. cordata*). In addition, the punctures of the head and mesosoma are large and deeply impressed in *O. calaminthae*, the hairs on the posterior surface of the foretarsal segments are relatively long, the wings are heavily infuscate, the rugose sculpturing of the dorsal propodeal triangle is strongly impressed and well differentiated from the ventral area of shagreened integument (Fig. 15), and the hairs on the lateral dorsal surface of T1 are dense and long, much more so than on remaining metasomal terga (Figs 9, 10; T1 hairs not conspicuously longer and denser than those on other metasomal terga in *O. albiventris* and *O. cordata*). *Osmia (Melanosmia) sandhouseae* Mitchell is a superficially similar species found sympatrically in Florida and is known to visit *Calamintha* in March (Deyrup et al. 2002); however, in that species the outer and condylar ridges of the mandible converge apically (parallel in *O. calaminthae*) and the hairs of the clypeus and frons are long and fine.

Males of *O. calaminthae* are distinguished from many other *Osmia* by the relatively slender, pointed teeth of T7 (basally about one-fourth the width of the midapical emargination; Fig. 22). Among the *Osmia* with such slender teeth on T7, *O. calaminthae* is extremely similar to *O. cordata* due to the white hairs on the metasomal terga (including laterally on T6) and S4 (Fig. 24), and by the hairs on the apical margin of S4 that are longer medially than laterally. *Osmia calaminthae* can be separated from *O. cordata* by the deep and large punctures on the frons and vertex. Males of *O. sandhouseae* Mitchell are superficially similar; however, in that species the punctures on the upper gena are extremely large and deep, much more so than on the vertex, while in *O. calaminthae* the punctures of the upper gena and vertex are subequal in size.



**Figures 1–3.** 1 Flowers of *Calamintha ashei* (Weath.) Shinnery (Lamiaceae) 2–3 *Osmia calaminthae*, sp. n., visiting flowers of *C. ashei* at Lake Placid, Highlands County, Florida. Photographs by T. Lethbridge.





**Figure 4.** Habitus illustration of *Calamintha ashei*, the only known floral host of *Osmia calaminthae* sp. n. Illustration by M. Deyrup.

**Description. Female.** Figs 5–7, 9–16. Total length: ca. 11 mm (10–11 mm); Forewing length: 7 mm (6–7 mm); distance between lateral ocellus and preoccipital margin 0.6 mm (0.5–0.6 mm); distance of lateral ocellus to compound eye 0.6 mm.

**Color:** Dark blue (mesosoma sometimes with integument slightly paler blue), except with brown integument on mouthparts, labrum, mandible, apical edge of clypeus, antenna, legs distal to trochanters, apical margins of metasomal terga, and metasomal sterna. Wings strongly infusate.

**Pubescence:** Hairs entirely white to pale golden except darker golden on mouthparts and distally on legs, brown on wings; hairs conspicuous on mesosoma and T1

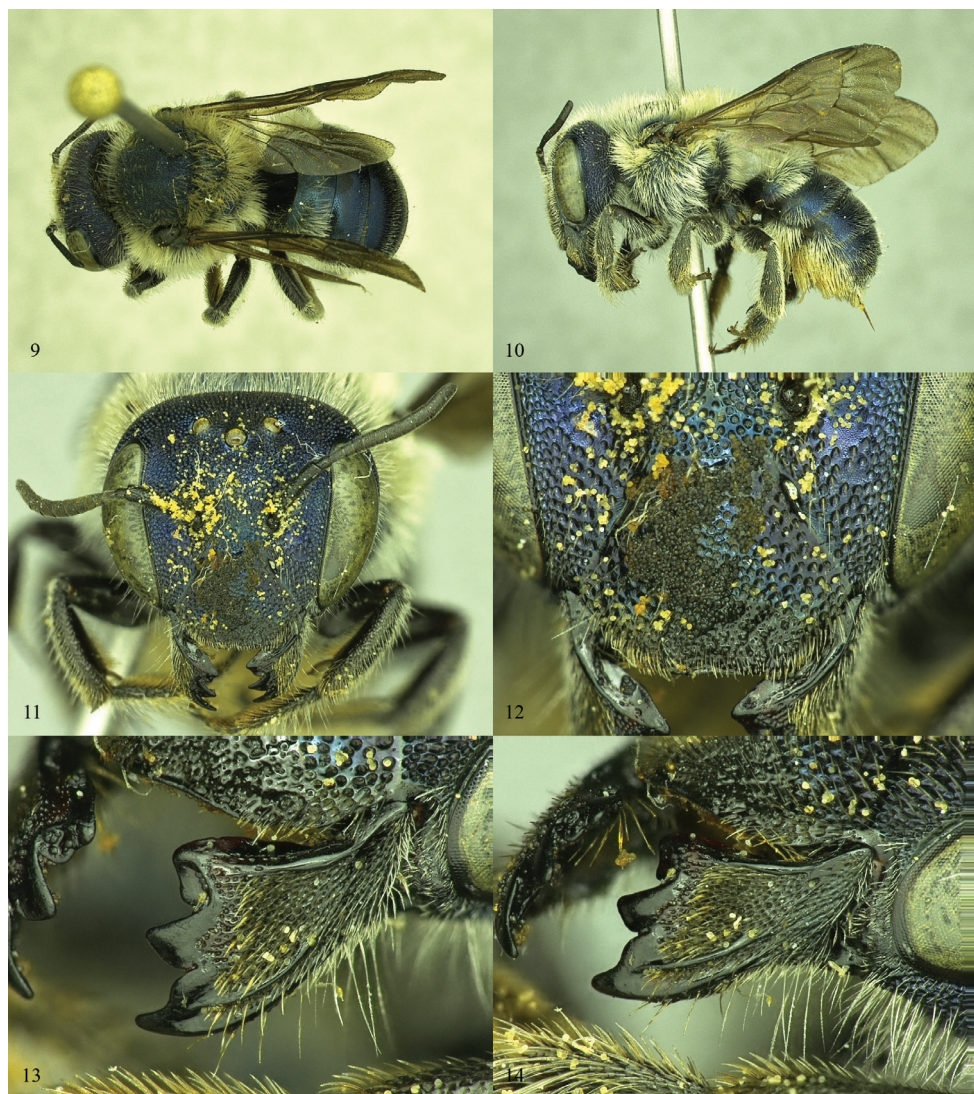


**Figures 5–8.** Oblique view of female *Osmia* heads **5, 6** *Osmia calaminthae*, holotype specimen **6** Close up of clypeus and paraocular area **7** *Osmia calaminthae*, paratype specimen, showing pollen mass on face **8** *Osmia conjunctoides* (holotype specimen of *O. subfasciata miamiensis*).



so as to obscure underlying blue integument, but inconspicuous on distal terga. Galea and basal two labial palpal segments with hairs on lateral margins straight, 0.2–0.5 OD in length. Labrum with long hairs arranged in two curved, transverse rows, along subapical margin and at approximate midpoint (hairs slightly more scattered along row at midpoint), with additional fringe of shorter hairs at apical margin. Clypeus below apical margin with lateral tuft of pale golden, medially directed hairs (often hidden by clypeal margin). Head with short, stout, simple, erect hairs evenly spaced on face (Figs 5, 6), scape, and pedicel, these hairs denser and appressed on outer surface of mandible, longer and relatively sparse on ventral margin of mandible, vertex, and posteriorly on gena. Hypostomal area with straight, minutely branched hairs evenly distributed across area, 2.0–3.0 OD in length. Mesosoma (excluding legs and wings) and laterally on T1 covered with dense, long, minutely branched, white hairs (Figs 9, 10); remainder of metasomal terga with hairs conspicuously shorter and sparser than hairs on mesosoma and T1. Legs with hairs on outer surfaces white, on forefemur and foretibia relatively slender and minutely branched, on foretarsal segments long (ca. 3.0 OD in length), slightly stouter, and simple; on midleg outer surface entirely minutely branched; on hindleg outer surface mostly minutely branched except basitarsus with hairs appressed, simple, and relatively stout. Legs with hairs on inner surfaces of fore- and midfemora and fore- and midtibiae white, minutely branched, and relatively sparse, with some shining areas lacking hairs; inner surface of hindfemur with denser, minutely branched white hairs, of hind tibia with very dense, short, white, subappressed hairs; inner surfaces of all tarsal segments with hairs dense, golden, stout, and simple. Wing membranes with short, dense, evenly distributed, simple hairs. Scopa white to pale golden.

*Punctuation:* Head and mesosoma with punctures nearly contiguous, round, and strongly impressed except as follows: labrum mostly impunctate; clypeus with impunctate midapical truncation about half length of F1; clypeus immediately adjacent to apical impunctate truncation and next to compound eye with punctures relatively small and dense (Fig. 12); paraocular area with punctures separated by up to two puncture diameters; clypeus, vertex, and mesoscutum immediately posterior to median longitudinal sulcus with punctures separated by up to one puncture diameter; mesepisternum in upper anterior corner with punctures relatively small, ventrally with punctures separated by up to one puncture diameter; hypostomal area, pronotum, propodeum, and legs with punctures shallowly impressed, sometimes elongated into oval shape; tegula with punctures minute, dense at margins and sparse medially (separated by up to four or five puncture diameters); metanotum, metepisternum, and lateral and posterior surfaces of propodeum with background integument moderately granulose and relatively dull; propodeal triangle with dorsal third strongly, deeply areolate to lineate, lower two thirds granulose grading to shining, glabrous area along lower lateral margin (Fig. 15). T1 anterior and dorsal surfaces, and T2–T3 shining, T4–T6 moderately shagreened, T1 medially on disc with small punctures separated by up to a puncture diameter, grading to slightly larger and denser punctures on more posterior terga, T1–T5 apical impunctate bands relatively



**Figures 9–14.** *Osmia calaminthae*, holotype female **9** Dorsal habitus **10** Lateral habitus **11** Face **12** Close up of clypeus and paraocular area **13** Mandible, showing the shape and placement of teeth **14** Mandible, showing outer and condylar ridges and overall shape.

narrow laterally, ca. one puncture diameter in length, medially with impunctate bands widened, up to four puncture diameters in length (or even longer at exact midpoint).

*Structure:* Labial palpus four-segmented, second labial palpal segment ca. one-fourth longer than basal-most segment. Mandible with outer and condylar ridges of subequal thickness or with condylar ridge slightly thicker, parallel along length (Fig. 14); apical margin with four teeth, third separated from second and fourth by carina, margin of third tooth forming distinct V-shape with adjacent margin of second and

weakly curved U-shape with adjacent margin of fourth, third tooth weakly set back from second and fourth (Fig. 13); inner, ventral margin of mandible lacking distinct tooth, very weakly diverging away from condylar ridge basally; mandible apically widened (1.5 times wider than median width), first tooth length subequal to that of other teeth or very slightly longer, second tooth located about half way between first and fourth teeth (Fig. 13). Clypeus with apical margin forming anteriorly produced truncation, linear or weakly concave along truncation and forming ca. 130 degree angle with lateral apical margin of clypeus. F1 one-third longer than F2 length or slightly more, remaining apical flagellar segments gradually increasing in length such that F10 ca. one-fourth longer than F1 length. Vertex behind lateral ocellus 2.5–3.0 OD in length. Genal width subequal to that of compound eye in lateral view. Preoccipital margin rounded, not carinate. Hypostomal carina moderately high, highest at about midpoint of hypostomal area posterior to angle, not forming triangular projection at this point but forming distinct, semicircular projection, tapering to low carina or near obsolescence at angle. Malus forming pointed apical spine, this spine more or less a narrowed continuation of nearby edge of velum. Foretarsal segments excluding basitarsal and apical-most segments with lobes moderately swollen, anterior lobes slightly longer than posterior. Midtarsal segments with anterior and posterior lobes of equal width, weakly swollen; hind tarsal segments not swollen. Hind tibial spurs more or less straight on basal three-fourths, with outer spur moderately curved at apical tip and inner spur slightly less strongly curved apically, outer spur about a fifth to a sixth shorter than inner. Hind basitarsus with lateral margins of outer surface parallel.

**Male.** Figs 17–26. Total length: ca. 10 mm; Forewing length: 6 mm; length of lateral ocellus to preoccipital margin 0.4 mm; length of lateral ocellus to compound eye 0.5 mm.

**Color:** Head and mesosoma pale blue, metasoma dark blue, except with brown integument on mouthparts, labrum, mandible, apical edge of clypeus, antenna, legs distal to trochanters, S5–S8, and apical margins of all metasomal terga and S1–S4. Wings moderately infusate, except along leading edge of forewing more strongly infusate.

**Pubescence:** White, minutely branched hairs on body except golden to pale golden, stouter hairs on inner surfaces of tarsi. Labrum sparsely covered with hairs on apical half and with hairs forming short fringe at apical margin. S2 with hairs at apical third relatively long (ca. 3.0 OD). S3 with dense, posteriorly directed hairs forming semicircular fringe along entire emargination (hairs ca. 1.5 OD in length throughout) (Fig. 23). S4 sparsely covered with white, medio-posteriorly directed, distally wavy hairs, these hairs not interrupted medially on S4, distinctly longer at midapical truncation than laterally on apical margin of disc. S6 midapical truncation sparsely covered with short, white hairs.

**Punctuation:** Head with punctures ovate to circular, contiguous or nearly so and deeply impressed except as follows: labrum mostly impunctate on basal half; clypeus with impunctate area immediately next to anterior tentorial pit and impunctate band along apical margin about one-fourth length of F1 and slightly swollen on median third (Fig. 20); disc of clypeus and interantennal area with punctures small and ovate;





**Figures 15–20.** 15, 16 *Osmia calaminthae*, females 15 Propodeal triangle of paratype specimen 16 T1–T3 of holotype specimen 17–20 *Osmia calaminthae*, male paratype 17 Dorsal habitus 18 Lateral habitus 19 Face 20 Mandibles

hypostomal area anteriorly near angle with punctures weakly, shallowly impressed. Mesosoma with punctures round, nearly contiguous and deeply impressed except as follows: tegula with punctures minute, sparser medially, separated by up to eight puncture diameters; metepisternum with punctures more irregular and with impunctate area near anterior margin and sometimes medially across sclerite; pronotum and lateral and posterior surfaces of propodeum strongly shagreened, with very weakly, shallowly impressed punctures; metanotum with punctures distinct but smaller than on

mesoscutum and separated by about a puncture diameter; propodeal triangle strongly lineolate to reticulate on dorsal half and shagreened on lower half, sometimes with weakly shining areas laterally near ventral margin (Fig. 21); legs with inner surfaces of trochanters, femora, and tibiae (except hind tibia) shining, with scattered smaller punctures. T1 with anterior surface weakly shagreened, shining; metasomal terga with dorsal surfaces very weakly shagreened, shining. Metasomal terga with punctures small and well impressed (slightly less impressed on T5–T7). T1–T4 dorsal surfaces with punctures separated between 0.5 and 2.0 puncture diameters; apical impunctate margins medially ca. 3.0–4.0 puncture diameters in length, laterally as little as 1.0 puncture diameter. T5–T6 with punctures less distinct, separated by ca. 1.0 puncture diameter medially; T5 with apical impunctate margin medially ca. 3.0 puncture diameters in length. S1–S3 with punctures moderately impressed, ovate. S4 with integument punctate basally, grading to shagreened and papillate at bases of hairs apically. S5–S6 shagreened.

*Structure:* Mandible with outer and condylar ridges converging apically; with two teeth, upper and lower teeth nearly the same width and length; inner margins of upper and lower teeth forming nearly 90 degree angle; upper tooth with inner and dorsal margins forming ca. 45–60 degree angle; inner, ventral margin of mandible weakly diverging away from condylar ridge basally. Clypeus apical margin lacking distinct apical truncation, medially very weakly concave, laterally with weakly tuberculate swelling. Flagellar segments subequal in length, except F1 about three-fourths length of F2 and F11 slightly longer than other segments. Vertex behind lateral ocellus 1.5 OD in length or slightly longer. Genal width ca. three-fourths that of compound eye in lateral view or slightly wider. Preoccipital margin rounded, not carinate. Hypostomal carina relatively shallow, about the same height along length of head, gradually tapering to near obsolescence at angle, not forming distinct tooth. Malus forming small but distinct, pointed apical spine. Foretarsal segments excluding basitarsal and apical-most segments with anterior lobes very slightly more swollen than posterior. Mid- and hind tarsal segments not swollen. Hind tibial spurs relatively stout, very weakly curved along length, outer spur slightly shorter than inner. Hind basitarsus with lateral margins of outer surface subparallel, with very small tooth on inner margin about one-fourth from apical margin along length. T6 midapically with moderate emargination, forming one-half of circle in outline or nearly so (Fig. 22); T6 lateroapical margin smoothly, weakly convex, not forming distinct tooth or forming very weak lateral tooth. T7 midapically strongly emarginate, forming semicircle about as wide as deep (slightly smaller than 1.0 OD in width), with spines on either side of emargination slender, about one-fourth as wide as emargination width (Fig. 22). S2 evenly convex, covering most of S3 (in one specimen with weak emargination at midapex). S3 with midapical emargination strongly semicircular, about as wide and long (half entire width of sternum, 1.5 OD in length or slightly more, measuring only apical margin of sternum and not including basal fringe of hairs; Fig. 23). S4 midapically with wide, poorly defined truncation (about third width of entire sternum). S6 with midapical truncation ca. one-fifth width of sternum, truncation as wide as long, apical margin of truncation distinctly emargin-





**Figures 21–26.** *Osmia calaminthae*, male paratypes **21** Propodeal triangle **22** T6 and T7 **23** S3 and S4, dorsal view **24** S3 and S4, oblique view **25** Genital capsule, dorsal view **26** Genital capsule, lateral view.

ate. Gonoforceps narrowed apical to subapical bend, weakly pointed at apical tip in dorsal view (Fig. 25), more or less straight along length in lateral view (Fig. 26).

**Distribution.** Known only from Highlands County, Florida.

**Holotype female.** “USA: FL [Florida]: Highlands Co. Lake Placid, 18 March 2002, J. S. Ascher, ex: *Calamintha asheil*/HOLOTYPE ♀ *Osmia calaminthae* Rightmyer, Ascher, Griswold [red label]” (NEW YORK). The type locality is southwest of the town of Lake Placid in an area of the subdivision of Placid Lakes Development that still includes many vacant lots: N27.2502, W81.3898.



**Paratypes. USA: FLORIDA, Highlands Co.,** Lake Placid, 18 March 2002, *Calamintha ashei*, J. S. Ascher (4♀, NEW YORK; 1♀, LOGAN), Archbold Biological Station, 28 March 1988, *Satureja ashei*, A. Warneke (1♀, LAKE PLACID), 29 March 2000, *C. ashei*, M. Deyrup (1♀, LAKE PLACID), 10 April 2001, *C. ashei*, M. Deyrup (1♀, LAKE PLACID), 18 April 1983, H. L. Dozier (1♀, GAINESVILLE), 25 April 1983, *Lupinus diffusus*, A. Schreffler (1♀, GAINESVILLE), Archbold Biological Station, Junction roads 40 & 36 Rosemary Bald, 27 March 2001, *C. ashei*, M. Deyrup (2♀, LAKE PLACID); Lake Wales Ridge Wildlife and Environmental Area, Gould Road Preserve, N27.13657, W08132495, 15 March 2009, *Ceratiola* scrub, Townes and bowl traps, M. & N. Deyrup, A. May, H. Otte (4♀, LAKE PLACID; 1♀, LOGAN); Lake Wales Ridge Wildlife and Environmental Area, Holmes Avenue Preserve, N27.28097 W081.31862, 24 April 2009, *C. ashei*, M. Deyrup (1♀, LAKE PLACID); Placid Lakes, 8 April 2001, *C. ashei*, Florida scrub habitat, M. Deyrup (3♀, LAKE PLACID); Placid Lakes Development, 16 March 2002, *C. ashei*, sand pine scrub habitat, M. Deyrup (3♀, GAINESVILLE; 4♀, LAKE PLACID; 1♀, LOGAN), 29 March 2007, *C. ashei*, M. Deyrup (2♀, LAKE PLACID), 30 March 2009, *C. ashei*, J. S. Ascher, D. Webber (3♀, 2♂, NEW YORK), 31 March 2009, *C. ashei*, J. S. Ascher, D. Webber (8♀, NEW YORK), 3 April 2006, *C. ashei*, J. S. Ascher, C. Dong (4♀, NEW YORK), 4 April 2006 (8♀, NEW YORK; 1♀, LOGAN).

**Additional records.** Four females were collected by H. G. Hall at the type locality on 31 March and others were observed and photographed there by T. Lethbridge on 31 March and 2 Apr 2010 (Figs 1–3; additional photos and informative captions here: <http://bugguide.net/node/view/394002/bgimage>).

**Etymology.** The name “calaminthae” is Latin, referring to mint, and is derived from the name of its presumed pollen host plant.

***Osmia (Diceratosmia) conjunctoides* Robertson, stat. n.**

[http://species-id.net/wiki/Osmia\\_conjunctoides](http://species-id.net/wiki/Osmia_conjunctoides)

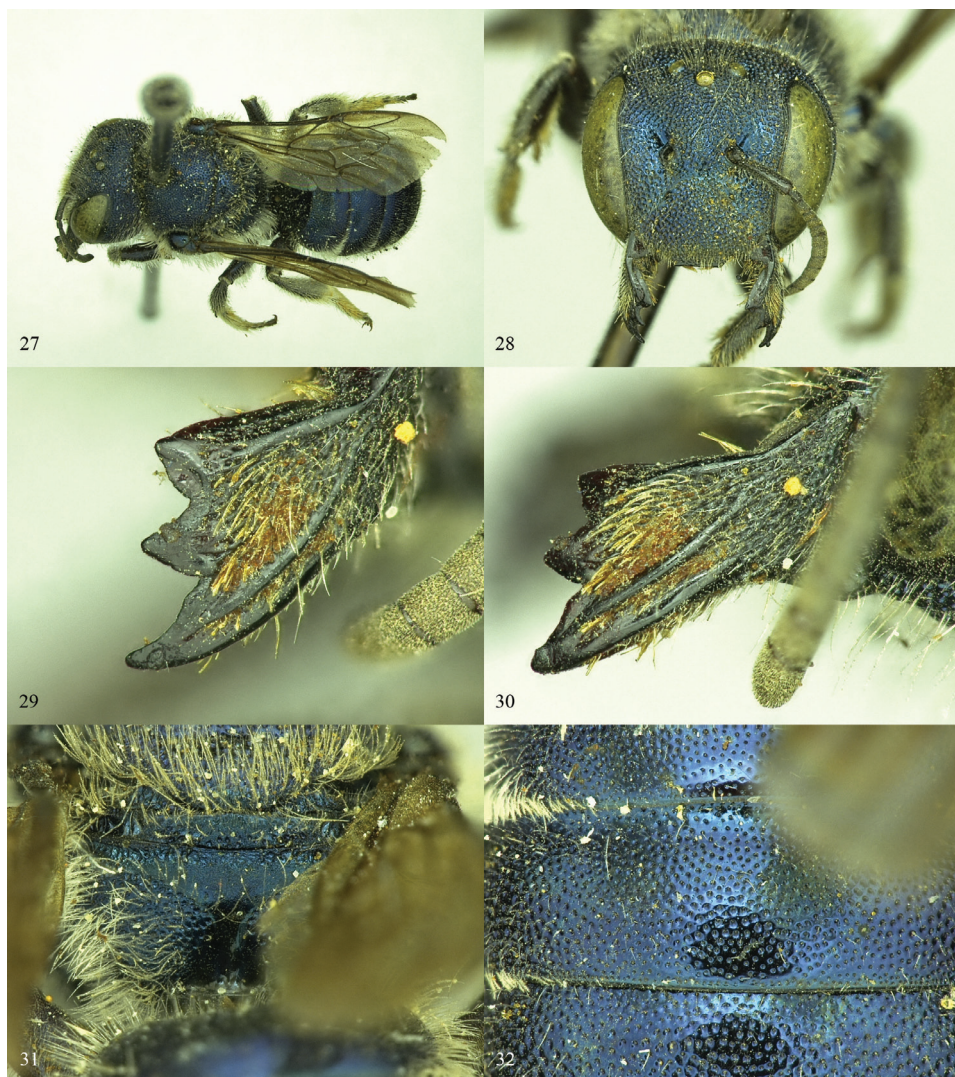
Figs 8, 27–32

*Osmia conjunctoides* Robertson 1893: 276; Sandhouse 1939: 140 [synonymy with *O. subfasciata*]; Mitchell, 1962:83 [synonymy with *O. subfasciata subfasciata*]; LaBerge (in Webb) 1980: 118 [lectotype designation].

*Diceratosmia subfasciata conjunctoides* (Robertson); Michener 1949: 264 [diagnosis].

*Osmia (Diceratosmia) subfasciata miamiensis* Mitchell 1962: 84. syn. n.

**Diagnosis.** Females of this species are distinguished from all other *Diceratosmia*, including typical *Osmia (Diceratosmia) subfasciata*, by the nearly uniformly short, straight to slightly hooked hairs on the clypeus and slightly longer hairs on the frons (Fig. 8). *Osmia conjunctoides* is also distinguished from *O. subfasciata* by the scopal hairs: in *O. conjunctoides*, the apical tips of the hairs on S2 and S3 are weakly tapered, while in *O. subfasciata* the hairs are blunt, widened and slightly rounded at their apical tips. The form of clypeal hairs in the female is very similar to that of *O. (Melanosmia) calamin-*



**Figures 27–32.** *Osmia conjunctoides* (female holotype of *O. subfasciata miamiensis*) **27** Dorsal view. **28** Face **29** Mandible, showing the shape and placement of teeth **30** Mandible, showing outer and condylar ridges and overall shape **31** Propodeal triangle **32** T1–T3.

*thae*; however, in that species the punctures of the metasomal terga are not so large (compare Figs 16 and 32), there is no carinate ridge on the hind coxa, the parapsidal line is punctiform, and the metasomal terga (especially T1 and T2) lack the distinct, short, dense, pale, apicolateral hair bands characteristic of subgenus *Diceratosmia* (in *O. calaminthae* T1 has dense, pale hairs, but these hairs are long and contrast with the short, sparse hairs on T2).

Males of *O. conjunctoides* are extremely similar to *O. (Diceratosmia) subfasciata*. Finding reliable characters to distinguish the two species is made problematic by the

availability of only seven male specimens of *O. conjunctoides*. This material suffices to permit the two species to be differentiated by the following characters: In *O. conjunctoides*, the mesoscutum is more finely and densely punctate than in *O. subfasciata* (*O. conjunctoides* with ca. 16 punctures between parapsidal line and midline, these punctures distinctly smaller than those on the scutellum; *O. subfasciata* with ca. 11 punctures between parapsidal line and midline, these punctures about the same size as those on the scutellum). In dorsal view, T1 of *O. conjunctoides* is less concave along its anterior margin, while in *O. subfasciata* the anterior margin is strongly curved, forming anterolaterally rounded corners. In addition, *O. conjunctoides* is usually a slightly larger bee than *O. subfasciata* (6–7 mm vs. 8–9 mm); all examined *O. conjunctoides* from Florida and Georgia are dark blue, while all examined *O. subfasciata* from throughout its range are a paler greenish blue; however, the male specimen of *O. conjunctoides* from Mississippi is greenish blue, similar to *O. subfasciata*. In *O. conjunctoides*, the lower propodeal triangle tends to be weakly shagreened throughout, while in *O. subfasciata* the lower propodeal triangle tends to be shining. In addition, T6 of *O. conjunctoides* has an apical, upturned flange that is longer than in examined specimens of *O. subfasciata* (ca. 2.0 adjacent puncture diameters in the former versus 1.0 adjacent puncture diameters in the latter).

**Material examined.** **USA: FLORIDA, Citrus Co.**, Inverness, Robertson [1♂, NEW YORK], 17 February 1891 [1♂, Champaign (holotype of *O. conjunctoides*)]; **Highlands Co.**, Highlands Hammock State Park, 14 April 1968, malaise trap, H. V. Weems Jr. [1♀, GAINESVILLE]; **Hillsborough Co.**, Lutz, 17 March 1926, Krautwurm [1♀, LOGAN]; **Liberty Co.**, Torreya Ravine, 15 April 1938, F. E. Lutz (1♀, NEW YORK); **Miami-Dade Co.**, Cape Florida, 15 February 1925, *Crotalaria*, S. Graenicher [1♀, WASHINGTON DC (holotype of *O. subfasciata miamiensis*)]; Miami Beach, 8 February 1917, Graenicher [1♂, RALEIGH (allotype of *O. subfasciata miamiensis*)]; **Seminole Co.**, Lower Wekiva River Preserve State Park, Burn Zone LW-10, S39 T19S R29E, LLP-Turkey Oak, P. Russell, S. Fullerton, 6 February 2001, blue pan trap (1♂, ORLANDO), 19 February 2001, yellow pan trap (1♂, ORLANDO), blue pan trap (1♂, LOGAN); **GEORGIA, St. Catherines Island**, 16–22 April 1983, Rozen, Favreau, Stupakoff (1♀, NEW YORK); **MISSISSIPPI, Forrest Co.**, Hattiesburg, 12 March 1944, C. D. Michener (1♂, NEW YORK), 6 April 1944 (1♀, NEW YORK).

**Comments.** Graenicher (1930) provides brief collecting notes on this species, under the name *O. subfasciata*: “This species occurs in the sand dunes at Miami Beach and on Biscayne Key (across the Bay southeast of Miami), and visits the flowers of *Crotalaria pumila*. Dates of capture: February 8, 15, and March 17.”

Michener (1949: 264) considered a male specimen of *O. conjunctoides* from northern peninsular Florida to intergrade with the typical *O. subfasciata* in features of T6 and T7 (although not in color). However, he was apparently unaware of the distinct facial and scopal hair features distinguishing females of *O. conjunctoides* from *O. subfasciata*. Specimens of *O. conjunctoides* that we have examined from northern peninsular Florida as well as Mississippi and Georgia are consistent with those from southern Florida in these diagnostic features of the females as well as in the finer punctures of the male mesoscutum. Although *O. conjunctoides* and *O. subfasciata sensu stricto* are extremely similar in the male S4, we do not agree



with the historic placements of this bee as a subspecies or synonym of *O. subfasciata* due to the consistent differences in male punctuation and female clypeal and scopal hairs.

According to Mitchell (1962: 84), two additional female paratype specimens of *O. subfasciata miamiensis* exist in Raleigh with the same label data as the male allotype. Pascarella (2008) also recorded the species from “Charlotte Harbor,” possibly based on distributional records found in Michener (1949), but we have not been able to confirm this record. Until we have access to further material, *O. conjunctoides* is provisionally considered to range from southern Florida north to Georgia and Mississippi, while we can confirm the presence of typical *O. subfasciata* from northeastern Mexico and southeastern California southeast to Alabama and South Carolina, and northeast to Illinois and New Jersey.

## Natural history and conservation status

### *Osmia calaminthae*

As indicated by its specific epithet, *O. calaminthae* appears to be closely associated with the woody mint *Calamintha ashei* (Figs 1, 4). Individual plants of this species may persist for at least a decade, possibly considerably longer. The flowering period is primarily from mid-March through mid-April; there can be variation in flowering phenology within this main blooming period among individuals growing in close proximity. Individual mature plants present hundreds of flowers over a period of several weeks. For flower visitors, *C. ashei* provides a dependable annual resource, even when the population of mature plants is small; as few as 20–30 plants may produce thousands of flowers each season.

Flowers have a corolla about 7 mm long, strongly protected against nectar-robbers by a stiff calyx that subsequently functions as a seed capsule (Figs 1, 4). There is almost no evidence of nectar robbing. Pollen is produced by four anthers whose filaments lie along the fused upper petals. Anthers are arranged in two rows, approximately marking the corners of a square (Fig. 1). In late morning and early afternoon when the anthers open, visiting female *O. calaminthae* rapidly bob their heads three to four times upon entering a flower (Figs 2, 3). This behavior, unusual in bees, might be associated with dislodging pollen, although this remains to be investigated. Pollen grains scraped from the head of one paratype specimen of *O. calaminthae* were found to be consistent with those described for *Calamintha*: three ridges were observed in lateral view, suggesting a hexacolpate condition (Trudel and Morton 1991). The behavior exhibited by *O. calaminthae* has not been observed in 23 other species of bees that visit flowers of *C. ashei* (Deyrup et al. 2002). Approximately one-fourth of the examined females had a large quantity of pollen trapped on the clypeus, supraclypeal area, frons, and scape (i.e., with pollen masses conspicuously visible to the naked eye, similar to Fig. 7). The large pollen load on the face suggests that females of *O. calaminthae* do not immediately groom the pollen back to the scopa when foraging between flowers. Such large pollen masses may even indicate that females are able to use the modified hairs on the face, in addition to the metasomal scopa which also contained pollen, to transport pollen to the nest; however, this was not directly observed and should be investigated in the future.

Flowers of *C. ashei* are also visited by flies in the family Bombyliidae: *Bombylius* spp., *Systoechus solitus* (Walker), *Geron* sp. and *Toxophora* sp., as well as a member of the Syrphidae: *Copestylum florida* (Hull). The occurrence of numerous alternative potential pollinators adds some resilience to a pollination system that includes a rare plant and an apparently specialized bee. The only species of visitor that occurs in large enough numbers to be suspected of being a disruptive competitor in some patches of *C. ashei* is the European Honey Bee, *Apis mellifera* Linnaeus.

The known distribution and natural history of *O. calaminthae* suggest that it may be among the most geographically restricted and host specific bees in eastern North America. It is possible that *O. calaminthae* has wider geographic and host plant ranges than now known, as there has never been a comprehensive attempt to survey the bees of Florida, or to document their hosts. There are, however, biogeographic factors that could explain narrow geographic and host ranges for this species.

*Osmia calaminthae* is known from Florida scrub habitat on the southern half of the Lake Wales Ridge. Florida scrub is a unique shrub community found on ridges and knolls of wind-deposited silica sand. Vegetation consists of small, sclerophyllous oaks and a variety of other shrubs and small trees. The low and open structure of the habitat is maintained by occasional fires. For a more complete description of Florida scrub, see Myers (1990). An important sub-category of Florida scrub habitat is the “scrub rosemary bald.” Scrub Rosemary, *Ceratiola ericoides* Michx. (also known as Sandhill- or Florida-Rosemary, or Sand Heath), is an aberrant member of the Ericaceae that occurs on the most highly drained scrub sites, often forming nearly pure stands of bushes that grow to be about 1.5 m high, with patches of bare sand between the clumps of *Ce. ericoides* (Johnson 1982). *Calamintha ashei* and several other narrowly distributed Florida scrub specialist plants seem to need bare sand patches in scrub rosemary balds, although some of these plants can move into areas of bare sand caused by human disturbance. Several of the plants found in rosemary balds have host-specific insects, including *C. ashei*, which is the host of the plant bug *Keltonia clinopodii* Kelton (Miridae) (Kelton 1966). Palynological evidence shows that *Ceratiola* barrens were much more widespread in south Florida at various times during the last 40,000 years (Delcourt and Delcourt 1981, Trapnell et al. 2007).

The Lake Wales Ridge, especially its southern half where *O. calaminthae* occurs, is the area with the largest number of Florida scrub specialist arthropods and plants, and has the only concentration of scrub specialists not found elsewhere in Florida (Deyrup 1990). This is probably due to the large size of the Lake Wales Ridge, its relative antiquity (over one million years), its southern position, and its uneven topography, which may affect fire frequency (Deyrup 1990). About 90 species of Florida scrub specialist arthropods are known from the Lake Wales Ridge, although many of these also occur in scrub areas elsewhere in Florida (Deyrup 2011, unpublished list). *Calamintha ashei* is largely restricted to the Lake Wales Ridge (Turner et al. 2006). Another spring-blooming woody mint, *Conradina brevifolia* Shinnery, has a similar floral structure, although it is yet to be associated with *O. calaminthae*. *Conradina brevifolia* is largely restricted to a small area on the Lake Wales Ridge (Turner et al. 2006).

*Osmia calaminthae* is currently known from only four sites within an area about 20 km long and 2 km wide on the Lake Wales Ridge. Archbold Biological Station is a private research station on the southern end of the Lake Wales Ridge where natural habitats have been protected since 1941. Two other protected sites are Lake Wales Ridge Wildlife and Environmental Areas managed by the Florida Fish and Wildlife Conservation Commission. One of these areas, Gould Road Preserve, has a large population of *C. ashei* and apparently a substantial population of *O. calaminthae*, but the site is unfenced and subject to pesticide drift from adjacent orange groves. The other protected site, Holmes Avenue Preserve, also has a large population of *C. ashei*, but is similarly unfenced, includes a large number of small, unacquired private parcels, and is subject to destructive use by off-road vehicles. There are over 20 Florida scrub preserves on the Lake Wales Ridge, but many of these lack large populations of *C. ashei*. The majority of *O. calaminthae* records are from scattered undeveloped lots in Placid Lakes, a platted subdivision south of the town of Lake Placid; this collection area is unprotected.

The nest site of *O. calaminthae* is unknown, but nest sites are less likely to be a limiting factor for this species than a scarcity of floral hosts and habitat. If nests are in dead wood, fires that remove most dead wood could affect populations of *O. calaminthae*.

Considering all the factors discussed above, attention should be given to the conservation needs of this recently discovered bee. The type locality of this species, where most known individuals have been observed, photographed, and collected, is a site with many vacant lots within a subdivision. Future full residential development at this site would threaten much of the known habitat of this species. *Osmia calaminthae*, remains, however, an extremely poorly known insect. It has a short flight period, and is therefore easily overlooked. It could be more abundant and widespread than it appears at present. Surveys of additional potential habitat, i.e., areas of sand scrub where the host plant occurs, are urgently needed to better assess whether the few known sites are critical habitat for the species or if it is more widely distributed but under recorded.

### ***Osmia conjunctoides***

Unfortunately, *O. conjunctoides* has been too rarely collected to allow for more than a few speculative comments on its conservation status; none of the authors have seen this bee in life. Only one examined specimen, the holotype of *O. subfasciata miamiensis*, has a recorded host plant associated with it (*Crotalaria pumila* Ortega); thus, it is not possible to say if the species is restricted in its plant host use. However, the presence of nearly uniformly short, erect hairs on the face of females is rare among *Osmia* in North America; in fact, this particular facial hair morphology is only known from *O. conjunctoides* and *O. calaminthae*. It is therefore reasonable to suspect that *O. conjunctoides* is associated with a restricted set of floral host species or with a particular floral morphology. At least six other *Osmia* from North America have facial hair modifications suggestive of pollen collection from nototribic flowers (V. H. Gonzalez, Griswold, & Rightmyer, unpublished data); the hairs on these bees either form a basket of stiff, proclinate hairs on the vertex and frons, or are cork-screw shaped on the clypeus and frons. Although the



hair morphology is not identical, the placement of the modified hairs on the clypeus and frons appears to be associated with pollen collection from nototribic flowers in both Old and New World *Osmia*, usually from the family Lamiaceae (although polylecty with preference for both Lamiaceae and Fabaceae has been documented; Müller 1996) or Scrophulariaceae.

A strong association of *O. conjunctoides* with *Crotalaria pumila* is tenuous. This legume has anthers that are enclosed in a narrow passageway in the keel, and it is not yet known if a bee collecting pollen or nectar would contact the anthers of this plant with her head. However, in alfalfa (*Medicago sativa* Linnaeus), another plant in the family Fabaceae (albeit an unusual one), the act of pollination changes the placement of the anthers from a ventral position to a more dorsal one (i.e., “tripping” the flower, causing the staminal column to snap upward toward the banner petal; Pitts-Singer and Cane 2011). Indeed, for *M. sativa*, *Megachile rotundata* (Fabricius) is preferred over honey bees for managed pollination due to its tolerance for being struck repeatedly on the head by the anthers of this flower. Thus, although *Crotalaria* is not likely the main host plant of *O. conjunctoides*, it cannot be ruled out until field observations have taken place. It is also unknown if the distribution of *Cr. pumila* has any predictive value for the distribution of *O. conjunctoides*. However, as it is the only floral information available to us for *O. conjunctoides* we provide a few comments on the natural history of this plant species and a related species within the same genus. *Crotalaria pumila* occurs in beach dunes and coastal pinelands along the Atlantic Coast from Brevard County south (Taylor 1998). Although much of this range has been heavily developed or overrun by exotic plants, patches of native habitat can be found in a series of coastal preserves, the largest of which are Jonathan Dickinson State Park, Hobe Sound National Wildlife Preserve, and Merritt Island National Wildlife Preserve. Cape Florida, where the holotype of *O. subfasciata miamiensis* was collected, might still have a protected population of this species within Bill Baggs Cape Florida State Park. St. Catherines Island is a National Historic Landmark and is also a protected area. *Crotalaria rotundifolia* Walter ex J. F. Gmel. might also be a potential plant to investigate when searching for further specimens of *O. conjunctoides*; *Cr. rotundifolia* is more widespread in Florida, and inland populations are dependent upon fire. The most recently collected specimens were from a burn zone in Seminole County. Thus, open, frequently burned or disturbed areas (i.e., Brooksville Ridge in Citrus and Levy Counties) are potential habitat.

Until further individuals of *O. conjunctoides* have been located and studied, the conservation status of this species will remain unclear. It is potentially an endangered species, considering the massive scale of destruction and alteration of most of its presumed coastal habitat. The decrease of fire frequency in many inland areas of the southeastern United States may also be a factor in this species’ conservation status, although the species has yet to be associated with a fire-dependent plant.

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# Descriptions of Mature Larvae of the Bee Tribe Emphorini and Its Subtribes (Hymenoptera, Apidae, Apinae)

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## Abstract

A description of the mature larvae of the bee tribe Emphorini based on representatives of six genera is presented herein. The two included subtribes, Ancyloscelidina and Emphorina, are also characterized and distinguished from one another primarily by their mandibular anatomy. The anatomy of abdominal segments 9 and 10 is investigated and appears to have distinctive features that distinguish the larvae of the tribe from those of related apine tribes.

## Keywords

Emphorini, Emphorina, Ancyloscelidina, larva, last larval instar

## Introduction

A recent study of the immature stages of the Exomalopsini (Rozen in press) presented a preliminary tribal key based on last larval instars to the non-cleptoparasitic apine taxa whose larvae were available, exclusive of the corbiculate tribes. It revealed that the last stage larva of *Ancyloscelis apiformis* (Fabricius) was in certain ways remarkably different from those of other Emphorini. To investigate these differences the present paper describes the tribe based on its mature larvae and then offers a larval description of *Ancyloscelis* (based primarily on *A. apiformis*), the only genus in the subtribe Ancyloscelidina, and compares it with a characterization of mature larvae of the sub-

tribe Emphorina as listed in Table 1. Although Roig-Alsina and Michener (1993) first proposed the subtribe Ancyloscelina for *Ancyloscelis*, the tribal name was corrected as Ancyloscelidina and validated by Engel and Michener in Engel (2005). These are the only two subtribes of the Emphorini (Michener 2007).

With great pleasure I dedicate this study to Drs. Kumar and Valerie Krishna, long-term associates and currently next-door office neighbors, whom I have known for nearly a half century. May their good humor and scholarship prevail long into the future!

Aspects of the biology of *Ancyloscelis apiformis* were described by Torchio (1974), Michener (1974), and Rozen (1984), and more recently Gonzalez et al. (2007) treated the biology of *Ancyloscelis* aff. *apiformis*. Previous descriptions of immature stages were listed by McGinley (1989).

In the study of larval Exomalopsini, the highly sclerotized mandibular morphology revealed considerable structural variation; this variation was not reflected in the surrounding mouthparts, presumably because of their soft, non-sclerotized anatomy. A preliminary survey of emphorine larval mandibles from the earlier study revealed mandibular variation as remarkable as that of the Exomalopsini, thus prompting the current study.

## Methods and terminology

For clearing, larvae were boiled in an aqueous solution of sodium hydroxide, stained with Chlorazol Black E, and then submerged in glycerin on well slides for study and storage. Specimens to be examined with a Hitachi S-4700 scanning electron microscope (SEM) were critical-point dried and then coated with gold/palladium. Microphotographs of Figs. 1–3 were taken with a Microptics-USA photographic system equipped with an Infinity Photo-Optic K-2 lens system. Microphotographs of mandibles were taken with a Cannon PowerShot SD880 IS handheld to the ocular of a Zeiss compound microscope. Fig. 12 was rendered with a Carl Zeiss LSM 710 confocal microscope.

Table 1 gives the full name and authorship of all species treated herein.

For descriptions of mandibles, the right mandible is used and assumed to have its long axis horizontal making the upper surface dorsal, lower surface ventral, and inner surface the adoral surface. As explained in Rozen (in press), the cusp is defined as an adoral extension of the apical mandibular edge that forms the upper boundary of the apical concavity. It seems well represented in the Emphorina but greatly modified in Ancyloscelidina because of the blade-like thinness of the mandibular apex and the coarse serrations of the dorsal apical edge (Figs. 12, 21, 22). The ventrally projecting tubercle-like structure and surrounding uneven surface (Figs. 12, 21) near the basal boundary of the apical concavity is likely a derived modification of the cusp.

To determine the foramen-to-head-width index of mature larvae, the maximum transverse width of the foramen was divided by the maximum transverse head width. This is a measure of the degree of constriction of the posterior edge of the head capsule relative to the lateral expansion of the parietals.

**Table 1.** Taxa of the Emphorini whose mature larvae were examined for current study, with source of material and other information

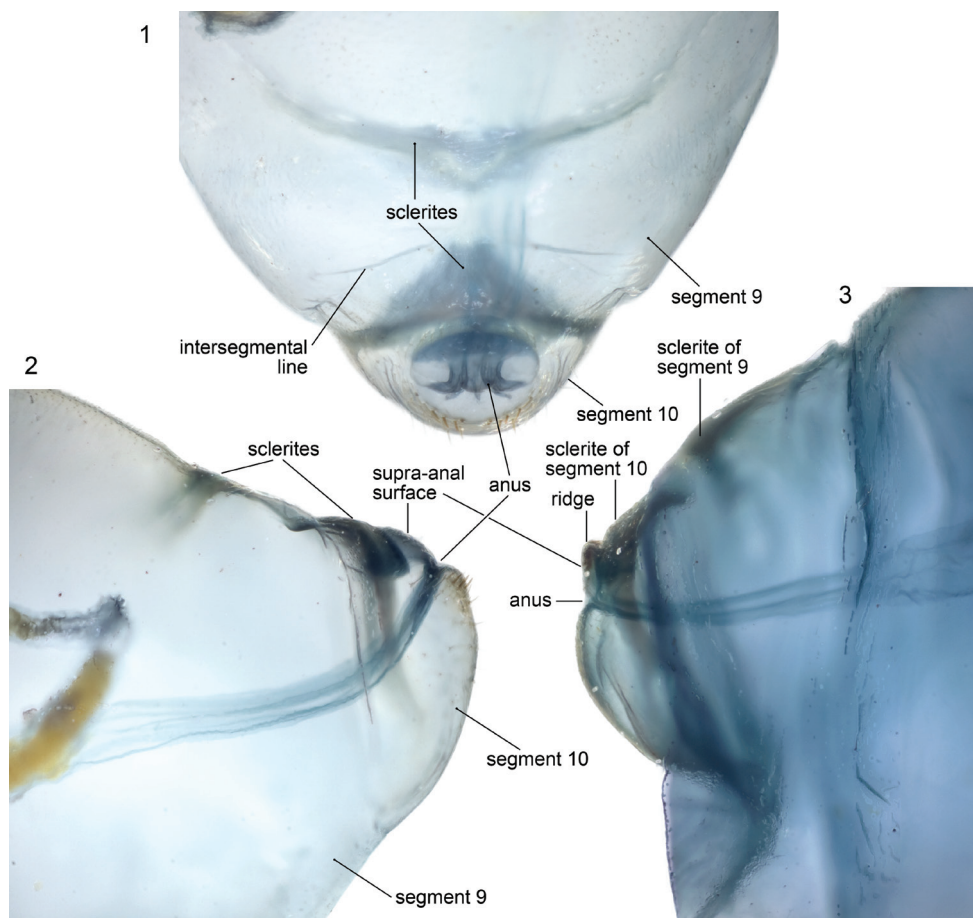
<b>EMPHORINI</b>	
<b>Ancylloscelidina:</b>	
<i>Ancylloscelis apiformis</i> (Fabricius)	KU and AMNH collections
<b>Emphorina:</b>	
<i>Diadasia</i> ( <i>Diadasia</i> ) <i>enavata</i> (Cresson)	Michener, 1953; AMNH collection
<i>D.</i> ( <i>Dasiapis</i> ) <i>olivacea</i> (Cresson)	AMNH collection
<i>D.</i> ( <i>Coquillettapis</i> ) <i>rinconis</i> Cockerell	"
<i>D.</i> ( <i>Coquillettapis</i> ) <i>vallicola</i> Timberlake	"
<i>Diadasina</i> ( <i>Diadasina</i> ) sp.	"
<i>Melitoma grisella</i> (Cockerell & Porter)	"
<i>M. marginella</i> (Cresson)	"
<i>M. segmentaria</i> (Fabricius)	"
<i>Ptilothrix bombiformis</i> (Cresson)	Michener, 1953; AMNH collection
<i>P.</i> near <i>sumichrasti</i> (Cresson)	AMNH collection
<i>P. tricolor</i> (Friese)	"
<i>Toromelissa nemaglossa</i> (Toro & Ruz)	"

## Anatomy of Abdominal Apex

This section explores the anatomy of abdominal segments 9 and 10 of the emphorine last larval instar because certain features found there have been overlooked. Although this study is based primarily on the predefecating larva of *Melitoma grisella* (Cockerell and Porter) and *Diadasia rinconis* Cockerell, these features are evident on all emphorine larvae examined. Abdominal segments 9 and 10 each has a scarcely visible dorsal sclerotized area that is nearly unpigmented. However, when a specimen is cleared and stained with Chlorazol Black E, the sclerite of abdominal segment 9 is visible (although poorly delineated) as a narrow, transverse, somewhat impressed (compare with surrounding integument) dark band (Figs. 1, 2) tapering at both ends and stretching across the segment somewhat more than halfway to the segment's posterior edge. Although its anterior margin is gently curved, its posterior margin is broadly V-shaped and points toward the following segment.

The stained transverse sclerite (also not sharply delineated) of abdominal segment 10 rings much of the segment but fades ventrally. Its anterior margin approaches the preceding segment at mid line, so that the sclerites of abdominal segments 9 and 10 point toward one another suggesting that they function together. The dorsal part of the posterior edge of the sclerite on segment 10 bends outward forming a shallow groove in front of it. The abdominal apex lies beyond this sclerite, and the anus (Figs. 1, 11, 16, 17) is a transverse slit, positioned a short distance posterior to the sclerite. The surface of the abdominal apex between anus and sclerite projects beyond the sclerite as the raised, verrucose supra-anal surface (Figs. 11, 16, 17) with its dorsal edge forming a semicircle from one side of the anus to the other when viewed from behind (Figs. 11, 16, 17). This edge often becomes carinate on postdefecating specimens creating a ridge circling the anus from above (Figs. 11,





**Figures 1–3.** Microphotographs of terminal abdominal segments of cleared, stained emphorine larvae. **1,** *Melitoma grisella*, predefecating, dorsal and lateral views **3** *Diadasia rinconis*, postdefecating, lateral view.

16). The area below the anus is planar, defined as a semicircle by the conspicuous setae at the border in the case of *Melitoma grisella* (Figs. 1, 2, 17); in other species that area is less well-defined. Hence, the dorsal view of the abdominal apex is an oval, traversed by the anus (Fig. 1).

The dorsal sclerites of abdominal segments 9 and 10 and the position of the anus with projecting, verrucose surface, all ringed by fine setae, suggest that these structures function together for some purpose currently not understood. One can speculate that these modifications support fecal deposition or perhaps deposition of some substance on the cell wall to safeguard the bee from water loss or parasites. Instead, these features might relate in some way to locomotion, for how does such an elongate larva move around in the cell while it feeds and defecates? Careful observations of living specimens during this stadium will likely lead to an explanation.

## Mature larva of Emphorini

**Diagnosis:** The best way to distinguish larval emphorines from those of other apid tribes is with the characters indicated in the preliminary tribal key based on last larval instars to the non-cleptoparasitic apine taxa (Rozen, in press). The presence of fine to moderate setae on abdominal segment 10 is a feature restricted to the Emphorini and to the exomalopsine genus *Eremapis* among the Apidae, but *Eremapis* lacks the sclerites of abdominal segments 9 and 10. Unlike other emphorines, *Toromelissa nemaglossa* (Toro and Ruz), known from Chile, has only a pair of setae on the outer surface of its mandible, although like other emphorine taxa it does possess numerous scattered fine setiform sensilla on abdominal segment 10 as well as a spiculate mandibular corium. No other bee larva is known to possess this combination of characters. The following is based on mature larvae of species listed in Table 1, which also indicates the sources of preserved specimens.

**Head** (Figs. 5, 8, 9, 13): Integument of head capsule with scattered, small sensilla, many of which are clearly setiform; epipharyngeal surface spiculate but with different patterns of distribution; mandibular corium nonspiculate, except clearly spiculate in *Toromelissa* and in some *Diadasia*. Integument pigmentation variable; mandible pigmented apically but far less so basally, with pigmented area usually defined by sharp line of separation (Figs. 24, 26, 28, 30, 32, 34); hypopharyngeal groove distinct.

Head (Figs. 6, 7) moderately to very small relative to elongate body (Figs. 6, 7); width of foramen magnum compared to head width as follows: *Ancyloscelis* 0.73; *Diadasia* 0.66–0.70; *Diadasina* 0.67; *Melitoma* 0.65–0.72; *Ptilothrix* 0.71; *Toromelissa* 0.71; bridge between posterior tentorial pits well developed; rest of tentorium normally robust for cocoon-spinning larva (even though not all spin cocoons). Center of anterior tentorial pit much closer to anterior mandibular articulation than to outer ring of antenna in frontal view (Figs. 9, 13; ATP = anterior tentorial pit), so that lateral segment (between anterior tentorial pit and anterior mandibular articulation) of epistomal ridge extremely short; posterior tentorial pit (i.e., junction point of postoccipital ridge, hypostomal ridge, and tentorial bridge) in normal position, deeply recessed; all internal head ridges strongly developed; coronal ridge extending to, or nearly to, middle of epistomal ridge in frontal view; median section of epistomal ridge more or less well developed; dorsomedial portion of postoccipital ridge nearly straight (not bending forward) as viewed from above; hypostomal ridge without distinct dorsal ramus. Parietal bands faintly evident as integumental scars. Antennal prominence non-extant; antennal papilla moderate to large in size, always longer than basal diameter, conical in shape, apically bearing 6 or more (in some cases many more) sensilla. Apex of labrum at most shallowly emarginated in frontal view (Figs. 9, 13); apical front surface of labrum with pair of low, forward-projecting, sensilla-bearing lobes (Figs. 5, 8, 9, 13); transverse labral sclerite absent.

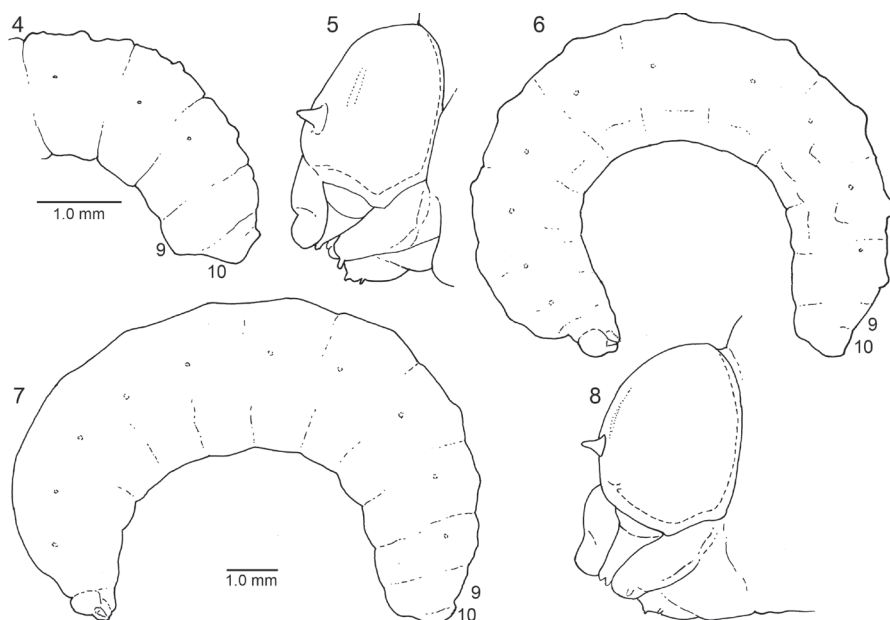
Mandible with two apical teeth but on postdefecating forms mandible sometimes appearing to have single tooth because of wear; outer surface of mandible with 8 or more small to large setae at mid length, except *Toromelissa* with only a pair of setae; other mandibular features varying considerably between subtribes: see subtribal descriptions,

below. Labiomaxillary region moderately weakly projecting in lateral view (Figs. 5, 8) for cocoon spinning larva. Maxilla with apex bent adorally, bearing palpus subapically; galea not evident; cardo and stipes sclerotized but in some cases unpigmented; articulating arm of stipital sclerite evident; maxillary palpus well developed, about twice as long as labial palpus but shorter and more slender than antennal papilla. Labium clearly divided into prementum and postmentum; prementum moderately small in frontal view; premental sclerite weakly evident; labial palpus about as long as basal diameter. Salivary opening on apex of prementum, transverse with strongly (*Diadasina*, *Melitoma*, *Ptilothrix*) to weakly (*Ancyloscelis*, *Toromelissa*) projecting lips that vary in width; lips consisting of tapering elongate filaments (Fig. 15). Except in *Ancyloscelis*, hypopharynx abruptly elevated behind articulating arms of stipes, high, sometimes densely covered with coarse spicules, other times with fewer, finer spicules; hypopharyngeal groove present.

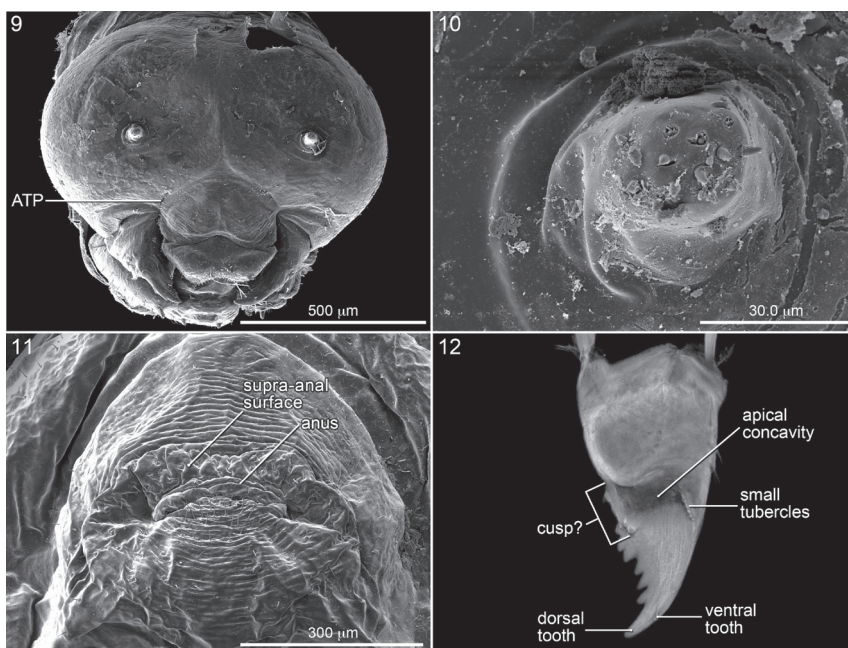
**Body:** Integument without general body setae, but abdominal segment 10 with fine to moderately conspicuous setae found especially around anus (a few setae may also be found dorsally on posterior part of segment 9); ventral surfaces of all segments with most species spiculate except for segment 10. Body form of predefecating larva (Fig. 6) unusually elongate, linear, parallel-sided; extent of expression of inter- and intrasegmental lines variable on predefecating larva (partly determined by amount of food ingested), on postdefecating larva often evident; dorsal body tubercles usually absent but see Remarks, below; dorsal tubercles absent on abdominal segment 9; abdominal segment 9 on pre- and postdefecating forms produced ventrally as seen in lateral view (Figs 4, 6, 7); abdominal segment 10 positioned dorsally on 9 in lateral view (Figs. 4, 6, 7); anus positioned close to dorsal surface on segment 10 (Figs. 2, 3); on postdefecating larvae, dorsal surface of segment 10 traversed by groove extending from one side of anus to other side, its posterior edge ending as strong transverse ridge above anus. Spiracles (Figs. 4, 6, 7) small to moderate sized, usually inconspicuous, subequal in size throughout, not surrounded by well defined sclerites, and not on tubercles; peritreme present; atrium projecting beyond body wall, with distinct rim, globose; atrial wall smooth, without ridges or spines, moderately thick; primary tracheal opening with collar; subatrium consisting of about 12 chambers; subatrial chambers decreasing in outside diameter from body surface inward. Males to extent known (but unknown in case of *Ancyloscelis apiformis*) with single median scar on apex of ventral protuberance of abdominal segment 9; females presumably lacking scars.

**Remarks:** Although dorsal body tubercles are generally absent on mature larvae, earlier instars and even on early stages of last larval instars have paired tubercles on most body segments rising from the middle of each segment for abdominal segments 9 and 10. (These tubercles should not to be confused with the middorsal tubercles of immature Megachilidae, which are intersegmental in position, Rozen and Hall (2011) figs. 85, 86.)

Each tubercle is small but often rises sharply with its front-to-back measurement about the same as the lateral measurement (i.e., tubercle non-transverse). Tubercles are uniquely positioned for bee larvae: those of each segment tend to be contiguous, lying close to the body midline. On some species they appear to be a single median bimodal tubercle.



**Figures 4-8.** 4-5. Diagrams of mature larva of *Ancyloscelis apiformis*, lateral view 4 Posterior part of abdomen of predefecating form 5 Head. 6-8. Diagrams of last larval instar of *Diadasia rinconis*, lateral view 6 Predefecating form 7 Postdefecating form 8 Head, lateral view; Figs. 6 and 7 to same scale.



**Figures 9-12.** 9-11. SEM micrographs of last larval instar of *Ancyloscelis apiformis*. 9 Head, frontal view 10 Antenna with many sensilla 11 Abdominal segment 10, posterior view. 12. Confocal micrograph of mandible of same, ventral view.

### Mature Larva of Subtribe Ancyloscelidina

**Description:** *Head* (Figs. 5, 9): Epipharyngeal surface with patch of short but abundant spicules covering most of anterior surface on each side; mandibular corium nonspiculate. Integument unpigmented except for mandibular apices and mandibular points of articulation with head capsule; hypopharyngeal groove faintly pigmented.

Mandibular apex uniformly pale tan, with sharp line demarking tan apex from nearly pigmentless basal part of mandible as seen in dorsal view (Fig. 22, though value contrast generally not as great as in mandible of Emphorina). Entire mandibular apex rotated and flattened, blade-like, so that coarsely serrated dorsal edge directed adorally, forming very broad, ventrally directed apical concavity (Fig. 12); dorsal apical tooth elongate, gradually narrowing to acute point directed adorally (mandible appearing rapacious) (Figs. 12, 22); ventral apical tooth greatly reduced, scarcely noticeable (Figs. 12, 21, 22); ventral edge of apical concavity sharply defined by fine ridge, which toward base bears short series of small tubercles (Fig. 12, 21); dorsal apical edge of concavity broadening slightly toward base and bearing large, ventrally projecting tubercle and uneven surface at its base (Fig. 12); these elements presumably homologue of mandibular cusp. Cardio and stipes sclerotized but unpigmented. Prementum moderately small in frontal view. Salivary lips weakly projecting, only about one-half as wide as distance between bases of labial palpi. Hypopharynx well behind apices of articulating arms of stipes, low, questionably bilobed, faintly spiculate on both sides.

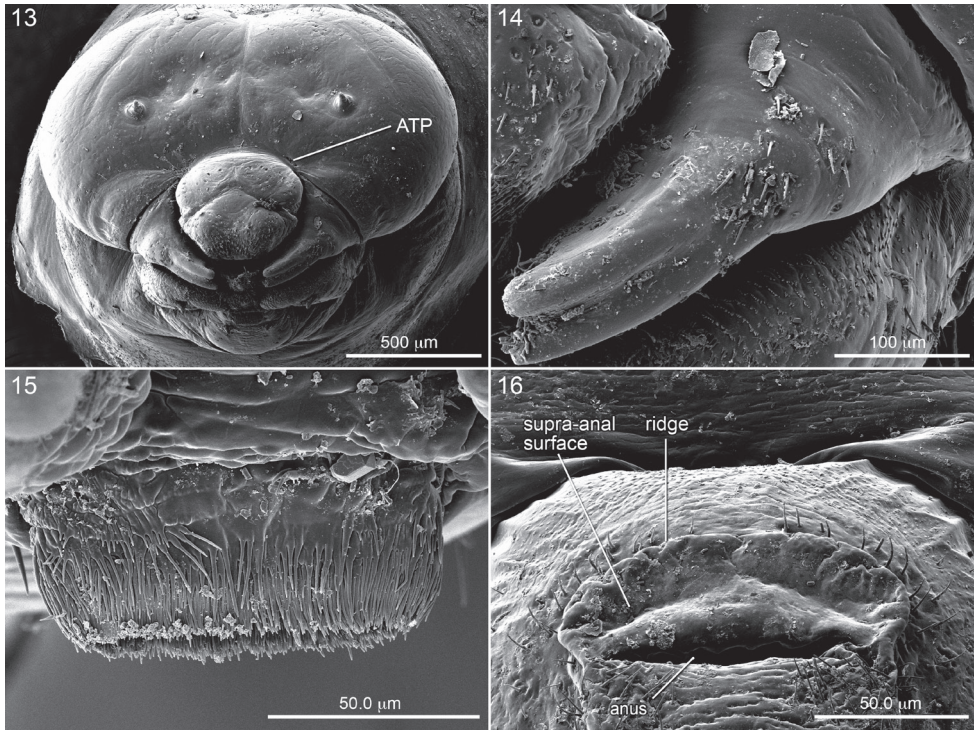
*Material examined:* 3 postdefecating larva: Trinidad: Maracas Valley, II-24-1966, III-01-1966 (F.D. Bennett, J.G. Rozen); 1 predefecating larva: same except III-08-1968 (J.G. and B.L. Rozen); 4 predefecating, 1 postdefecating larvae: Colombia: Valle del Cauca: Cali I-10-1972 (C.D. Michener).

### Mature Larva of Subtribe Emphorina

**Description:** *Head* (Figs. 8, 13): Apicolateral angles of epipharyngeal surface angles with restricted swollen protuberances well separated from one another, each of which is densely covered with short spicules; mandibular corium nonspiculate, except clearly spiculate in *Toromelissa nemaglossa* and in some *Diadasia*. Integumental sclerotized areas, especially internal head ridges and sclerotized mouthparts, tending to be more pigmented than those of Ancyloscelidina.

Apical part of mandible (including mandibular apex and all of cuspal area) very darkly pigmented, almost black; line separating pigmented and nonpigmented parts sharply defined as seen in dorsal (Figs. 24, 26, 28, 30, 32, 34) or ventral view. Mandibular apex usually with two apical teeth; dorsal tooth larger, ventral tooth slightly smaller (except approximately equal in *Diadasia*, Fig. 27, and in some species such as *Diadasia olivacea*, Fig. 25, ventral tooth longer than dorsal one);



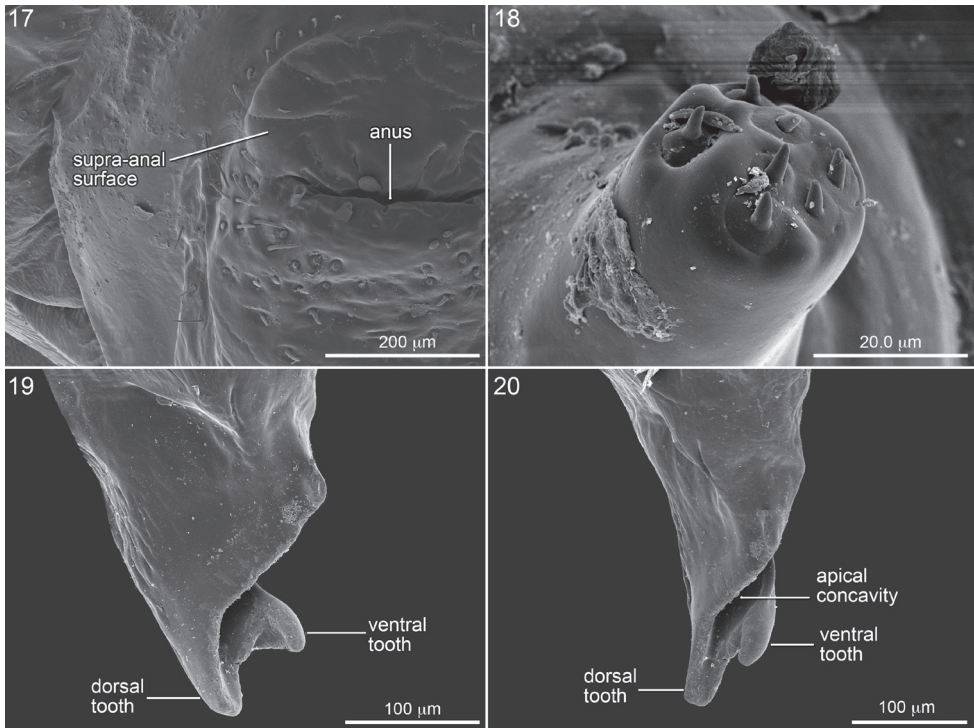


**Figures 13–16.** SEM micrographs of postdefecating larva of *Diadasia rinconis*. **13** Head, frontal view **14** Left mandible, showing setae on outer surface **15** Salivary lips, from above **16** Upper part of segment 10, posterior view.

dorsal apical mandibular edge without teeth; ventral mandibular tooth and ventral edge of mandibular apex twisted adorally forming elongate oblique apical concavity (Fig. 20) on adoral apical surface in conjunction with strongly produced dorsal apical edge (Fig. 20); when viewed dorsally (Figs. 19, 34) ventral tooth appearing more curved than dorsal tooth; adoral surface of cusp thick toward mandibular base; leading cuspal edge linear, rounded (*Ptilothrix*), or narrowly planar (*Melitoma*, *Diadasia*), without distinct spines, sometimes irregularly roughened or minutely pebbled (e.g., *Diadasia enavata*, Fig. 24). Prementum moderately small to moderately wide in frontal view. Salivary lips weakly to strongly projecting; width one-half as wide, to as wide, as distance between bases of labial palpi. Hypopharynx well behind apices of articulating arms of stipes, often dorsally projecting, in some cases bilobed, spiculate on dorsal surface.

*Material examined:* *Diadasia enavata*: 10+ larvae, all stages: USA: Washington: Yakima Co.: S of Granger, IX-5-1993 (E. Miliczky). *D. olivacea*: 3 predefecating last larval instars: USA: Arizona: Cochise Co.: Southwestern Research Station, 5 mi S of Portal, IX-7-1773 (J.G. Rozen, M. Favreau). *D. rinconis*: 10+ larvae, all stages: USA: Arizona: Pima Co.: Arizona-Sonora Desert Museum, V-9-1987 (J.G. Rozen, S.L. Buchmann); 10+ mature larvae: same except: Catalina State Park, V-8-1990 (S.L. Bu-

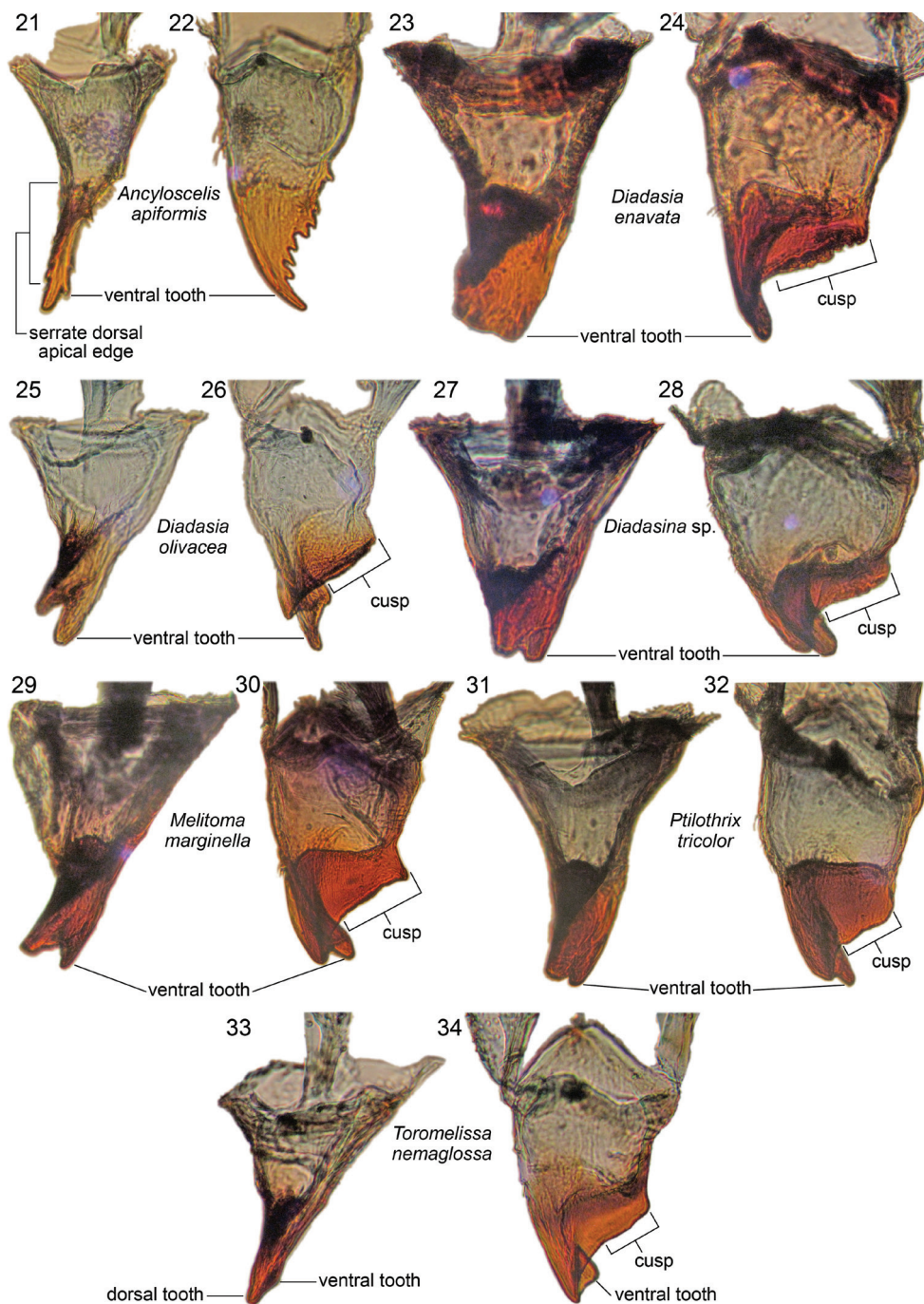




**Figure 17–20.** SEM micrographs of mature larva of *Melitoma grisella*. **17** Left side of abdominal segment 10, posterior view **18** Antenna **19** Mandible, dorsal view, and **20** inner view.

chmann). *D. vallicola*: 10+ late stage larvae: USA: California: Riverside Co.: 18 mi W of Bythe, V-2-1991 (J.G. Rozen). *Diadasina* sp. 2 postdefecating larvae: Argentina: Chaco Prov.: Capitan Solari, I-31-2006 (J. Straka). *Melitoma grisella*: 10+ various larval instars: USA: Nebraska: Keith Co.: Cedar Point Biological Station, VII-20-1988 (J.G. Rozen). *M. marginella*: 1 postdefecating larva: Mexico: Jalisco: Chemela, XI-7-1986 (J.G. Rozen). *M. segmentaria*: 5 mature larvae: Trinidad: Nariva Swamp, X-12-1965 (F.D. Bennett). *Ptilothrix bombiformis*: 2 cast larval skins: USA: Maryland: Prince George Co.: Greenbelt, IX-21, 22-1986 (B. Norden). *P. near sumichrasti*: 3 mature larvae: USA: Arizona: Cochise Co.: 8 mi NE of Portal, VIII-18–24- 990 (J.G. Rozen, J. Krieger). *P. tricolor*: 2 postdefecating larvae: Argentina: Tucumán Prov.: 11 km NW of Cadillal, XII-4-1993 (J.G. Rozen). *Toromelissa nemaglossa*: 10+ larvae of all stages: Chile: Atacama Region(III): Huasco Prov. 37 km W of Domeyko, XI11-11-2000 (J.G. Rozen).

**Remarks:** In *Diadasia enavata* (and perhaps in some other species in that genus) the ventral apical mandibular tooth appears missing (Michener, 1953: Figs. 209, 210). Examination of an early stage last larval instar (Fig. 23) shows that it clearly present, but in postdefecating forms it is worn away leaving the mandible with a broad, obliquely truncate apex, bearing a large, adorally directed apical concavity.



**Figures 21–34.** Right mandibles of mature larvae of Emphorini, showing inner view and dorsal view of each representative, as labeled.

## Conclusions and discussion

Because all taxa whose immatures were examined in this study possessed most if not all features of abdominal segments 9 and 10 described above, this character complex strongly supports the relationship of *Ancyloscelis* with the Emphorina, despite the very different mandibles of the two groups.

Except for mandibular morphology, there is a strong similarity among not only larval Ancyloscelidina, as represented by *Ancyloscelis apiformis*, and larvae of Emphorina, but also larvae of Exomalopsini (Rozen, in press) and Tetrapediini (Rozen, et al., 2006). These similarities include: body shape (protruding venter on abdominal segment 9, dorsally positioned anus, and paired low or virtually absent dorsal body tubercles); spiracle morphology; and head features (excluding mandible morphology).

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# Brachyceran Diptera (Insecta) in Cretaceous ambers, Part IV, Significant New Orthorrhaphous Taxa

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## Abstract

Thirteen species of basal Brachycera (11 described as new) are reported, belonging to nine families and three infraorders. They are preserved in amber from the Early Cretaceous (Neocomian) of Lebanon, Albion of northern Spain, upper Albion to lower Cenomanian of northern Myanmar, and Late Cretaceous of New Jersey USA (Turonian) and Alberta, Canada (Campanian). Taxa are as follows, with significance as noted: In Stratiomyomorpha: Stratiomyidae (*Cretaceogaster pygmaeus* Teskey [2 new specimens in Canadian amber], *Lysistrata emerita* Grimaldi & Arillo, **gen. et sp. n.** [stem-group species of the family in Spanish amber]), and Xylomyidae (*Cretoxyia azari* Grimaldi & Cumming, **gen. et sp. n.** [in Lebanese amber], and an undescribed species from Spain). In Tabanomorpha: Tabanidae (*Cratotabanus newjerseyensis* Grimaldi, **sp. n.**, in New Jersey amber). In Muscomorpha: Acroceridae (*Schlingeromyia minuta* Grimaldi & Hauser, **gen. et sp. n.** and *Burmacyrtus rusmithi* Grimaldi & Hauser **gen. et sp. n.**, in Burmese amber, the only definitive species of the family from the Cretaceous); Mythicomyiidae (*Microburmyia analvena* Grimaldi & Cumming **gen. et sp. n.** and *M. veanalvena* Grimaldi & Cumming, **sp. n.**, stem-group species of the family, both in Burmese amber); Apsilocephalidae or near (therevoid family-group) (*Kumaromyia burmitica* Grimaldi & Hauser, **gen. et sp. n.**



[in Burmese amber]]; Apystomyiidae (*Hilarimorphites burmanica* Grimaldi & Cumming, **sp. n.** [in Burmese amber], whose closest relatives are from the Late Jurassic of Kazakhstan, the Late Cretaceous of New Jersey, and Recent of California). Lastly, two species belonging to families incertae sedis, both in Burmese amber: Tethepomyiidae (*Tethepomyia zigrasi* Grimaldi & Arillo **sp. n.**, the aculeate ovicapt of which indicates this family was probably parasitoidal and related to Eremochaetidae); and unplaced to family is *Myanmyia asteiformia* Grimaldi, **gen. et sp. n.**, a minute fly with highly reduced venation. These new taxa significantly expand the Mesozoic fossil record of rare and phylogenetically significant taxa of lower Brachycera.

### Keywords

amber, fossils, flies, Lebanon, Myanmar, New Jersey, Spain

## Introduction

This is the fourth paper in a series devoted to the Cretaceous record of brachyceran flies preserved in amber, the original work being a treatment of orthorrhaphans and Cyclorrhapha (Grimaldi and Cumming 1999), and the second and third being treatments of the enigmatic families Tethepomyiidae (Grimaldi and Arillo 2008) and Chimeromyiidae (Grimaldi et al. 2009). The present paper deals specifically with additional records and taxa of orthorrhaphan (“basal”) Brachycera, while separate papers will deal with the empidoids and Cyclorrhapha. Rhagionidae will also require separate study, given their confusing Mesozoic diversity and relationships. Updates to the original 1999 monograph are necessary since additional Brachycera have been uncovered in all of the major Cretaceous amber deposits dealt with then (i.e., New Jersey, western Canada, Lebanon), but, most importantly, diverse Brachycera have been discovered in amber from the Early Cretaceous (Albian) of northern Spain (Alonso et al. 2000; Delclòs et al. 2007; Peñalver and Delclòs 2010) and the Late Albian to Early Cenomanian of northern Myanmar (Grimaldi et al. 2002; Cruikshank and Ko 2003).

## Materials and methods

Specimens were prepared according to the protocols described in Nascimbene and Silverstein (2000) and, for the Spanish amber, in Corral et al. (1999). After rough pieces were screened for inclusions, preliminary preparation to view the inclusion was done by grinding and polishing one or more flat surfaces onto the piece using emory papers of decreasing grit sizes on a wet flat lapidary wheel. Then each piece was embedded in epoxy under vacuum in order to impregnate cracks within the amber, which improved transparency and strengthened the piece for trimming (using a water-fed diamond saw with a very thin blade) and more grinding and polishing. Eventually, depending on the size and number of inclusions, the preparations were several millimeters in thickness, such that it could be mounted between a microscope slide and coverslip using a drop of glycerin on each of the two opposing surfaces. The inclusions were examined with

a stereomicroscope and with compound microscopy at 40 – 400× using both reflected and transmitted light.

**Collection repositories of specimens are the following:**

- AMNH** American Museum of Natural History, Entomology Section, New York.  
**AZ** Azar Collection, presently housed in Musée national d'Histoire naturelle, Paris.  
**KU** University of Kansas Division of Entomology, Natural History Museum, Lawrence.  
**MCNA** Museo de Ciencias Naturales, Álava, Spain.  
**NHML** Natural History Museum, London.  
**RTMP** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

It is a pleasure for the senior author to dedicate this paper to Kumar Krishna, world authority on the Isoptera, close colleague and friend.

**Infraorder Stratiomyomorpha**

This lineage comprises three living families, the Xylomyiidae (cosmopolitan; approximately 134 species in four genera), Stratiomyidae (cosmopolitan; 2651 species in 375 genera as of the year 2000 [Woodley 2001]), and Pantophthalmidae (Neotropical; approximately 20 species of very large flies in two genera). Xylomyiids and stratiomyiids are closely related based on the shortened vein  $R_1$ ,  $R_s$  branching off of  $R$  distally, and the stem of  $R_s$  very short, as well as the larval cuticle with calcareous “warts” and pupariation taking place within the last larval cuticle. Pantophthalmids appear to be the sister group to the other two families (Sinclair et al. 1994; Yeates 2002; Wiegmann et al. 2011). Pantophthalmids have no fossil record, and the other two families have very limited Mesozoic fossil records, reviewed below. A fourth family of the infraorder is the extinct Zhangsolvidae, originally erected by Nagatomi and Yang (1998) for *Zhangsolva cupressa* from the Early Cretaceous Laiyang Formation in China (Zhang et al. 1993). The original description of *Zhangsolva* included obvious errors, and the antenna probably has no more than eight flagellomeres (the groundplan of Brachycera); some artifacts were also reported as venational features in the original report. There are two well preserved zhangsolvid species in Early Cretaceous limestone from the Crato Formation of Brazil, *C. macrorrhyncha* (Mazzarolo and Amorim, 2000), and *Cratomyoides cretacicus* Wilkommen (in Martill et al. 2007). Both of these species have a long, jutting proboscis and a venation very similar to that *Zhangsolva*; *Cratomyoides* is separated from *Cratomyia* on the basis of minor features and probably should be synonymized with the latter genus. Based on the long proboscis, hovering-type of venation, and phylogenetic position, the three species of Zhangsolvidae probably fed from flowers (Grimaldi and Engel 2005).

## Family Stratiomyidae

### Genus *Cretaceogaster*

<http://species-id.net/wiki/Cretaceogaster>

*Cretaceogaster* Teskey 1971: 1660. Type species: *C. pygmaeus* Teskey 1971: 1660; Woodley 1986 (redescription, placement); Grimaldi and Cumming 1999: 17–19 (redescription, new specimens).

*Cretaceogaster pygmaeus* Teskey 1971: 1660.

**Remarks.** We were able to study two additional specimens of this very primitive genus of stratiomyid, both in Canadian amber collected by Ted Pike from Grassy Lake, Alberta (Campanian) (Pike 1995), housed in the RTMP.

RTMP 96.9.1117: Amber is a typical clear, dark yellow with reddish flow lines; it also contains a small spider. The piece is a cylindrical runnel  $12 \times 4 \times 2$  mm, with the fly preserved near the middle, which was embedded in epoxy at the AMNH and trimmed to  $9 \times 13 \times 4$  mm (including epoxy) for better observation. The fly is laterally very flattened, especially the thorax, and is a male (though details of the genitalia are not observable). Unfortunately, the apex of the mid tibia cannot be observed in detail, so the apparent absence of tibial spurs is uncertain. Wing is slightly distended in length, but otherwise the venation is very similar to *C. pygmaeus*.

RTMP 96.9.1230: Fly is also preserved in a cylindrical runnel of amber,  $7 \times 3$  (diam.) mm, and embedded in epoxy for careful trimming. The fly is lying at the rounded end of the runnel, with its dorsal surface against the surface of the flow. The thorax is partly decayed and wing venation is obscured. The antenna and mouthparts are visible in ventral view. Specimen is a male, but its genitalic details are also not observable. Mid tibia appears to have a small apical spur, contrary to the original description of the species but in agreement with Woodley (1986: 380).

### *Lysistrata* Grimaldi & Arillo, gen. n.

urn:lsid:zoobank.org:act:C038F6C9-1BFF-49D2-A756-A6235259B6A9

<http://species-id.net/wiki/Lysistrata>

**Diagnosis.** Antennal flagellum submoniliform, with approximately 7 short flagellomeres tapered in width apicad; articulation between basal 3 flagellomeres faint. Protibia lacking spurs; mesotibia with two short apical spurs (c. 50  $\mu$ m length). Metatibia probably with one pair of short apical spurs. Vein Rs branches from  $R_1$  in the distal third of vein R. Stem of  $R_{4+5}$  straight,  $R_4$  curved basally, long and subparallel to  $R_5$ . Cell d long and narrow, length approximately 3.5 $\times$  the width; cell  $m_3$  absent.

**Type species.** *Lysistrata emerita*, sp. n., by present designation.

**Etymology.** From the Greek, Λυσιστράτη, meaning “army disbander”, after the comedy by Aristophanes and in reference to the common name for Stratiomyidae, or “soldier flies”. Feminine.

**Discussion.** *Lysistrata* is clearly within the Stratiomyomorpha, and appears closely allied with Stratiomyidae on the basis of the radial branching. The presence of two minute spurs on the mesotibia, and probably a short pair on the metatibia is indicative of either Stratiomyidae or Xylomyidae. A few Recent stratiomyids have a minute apical spur on the mesotibia, whereas xylomyids have either a 0–2–2 or 0–2–1 tibial spur formula. Pantophthalmids have one or two spurs on the mesotibia only, but are distinct from the other two families by the longer branches of  $R_1$  and  $R_s$ .

The Recent and primitive genus *Parhadrestia* James (consisting of two species from Chile) shares some similarities with *Lysistrata*, both of them possessing a long  $R_4$  vein curved only at the base and with the main branch only slightly divergent from  $R_5$ . The genus *Montsecia* Mostovski, 1999, preserved as a compression in Early Cretaceous (Barremian) limestone of Montsec, Lérida Province, Spain (originally and incorrectly placed in the subfamily Beridinae) also has the fork of  $R_4+R_5$  quite long. This long fork may be a plesiomorphic feature, seen for example in Rhagionidae and Spaniidae.

*Lysistrata* differs plesiomorphically from *Parhadrestia* by the following: antenna multi-articulate; wing longer, narrower;  $R_{2+3}$  slightly longer and gradually sloped to C; apex of  $R_{2+3}$  not close to the apex of  $R_1$ ;  $R_5$  and  $M_1$  slightly divergent instead of parallel;  $M_1$ ,  $M_2$ , and  $CuA_1$  not as divergent (a condition shared with *Montsecia*); cell d much longer, its length approximately 3× the width (vs. 2× the width in *Montsecia* and 1.5× the width in *Parhadrestia*; in most Recent stratiomyids cell d is quite small);  $CuA_2$  more sloped toward CuP (e.g., apex of cell cup acute, instead of truncate [similar to *Montsecia*], although an acute cell cup is considered apomorphic by Woodley [2001]). In *Montsecia* the base of M is weak, whereas it is well developed in *Lysistrata*. *Lysistrata* has two apomorphic features: small female abdominal segments 6 and 7, which telescope within the proximal ones (in the basal Recent subfamilies Parhadrestiinae, Chiromyzinae and Beridinae segments 6 and 7 are large [Woodley 2001]); also, vein  $M_3$  is lost. Loss of this vein occurs in all Parhadrestiinae and Pachygastrinae, and is frequently absent in Chiromyzinae and Beridinae (Woodley 2001). Absence of  $M_3$  may actually be a ground-plan feature of Stratiomyidae.

The oldest fossil stratiomyiid is *Montsecia martinezdelclosi* Mostovski (1999), from the same outcrop that yielded several larvae believed to be stratiomyiids (Whalley and Jarzembowski 1985). According to Mostovski (1999), several undescribed stratiomyiids are known from Jurassic and Cretaceous outcrops of Kazakhstan and Russia, although none has as yet been described. *Gigantoberis liaoningensis*, described as a stratiomyiid by Huang and Lin (2007) from the Early Cretaceous of Lianoning, China, was shown by Zhang (2009) not to belong to this family, which Huang acknowledges (pers. comm. to AA, 2010). The only other Cretaceous stratiomyiids are *Cretaceogaster pygmaeus* (Teskey 1971; Grimaldi and Cumming 1999; herein *vide supra*), an incomplete and undescribed species in Turonian-aged amber from New Jersey USA (Grimaldi and Cumming 1999), and the very well-preserved *Lysistrata emerita*, described below and which is very basal in the family. Diverse

stratiomyiids belonging to modern subfamilies and genera, including undescribed species, occur in shales and amber from the Tertiary and were summarized in Evenhuis (1994).

***Lysistrata emerita* Grimaldi & Arillo, sp. n.**

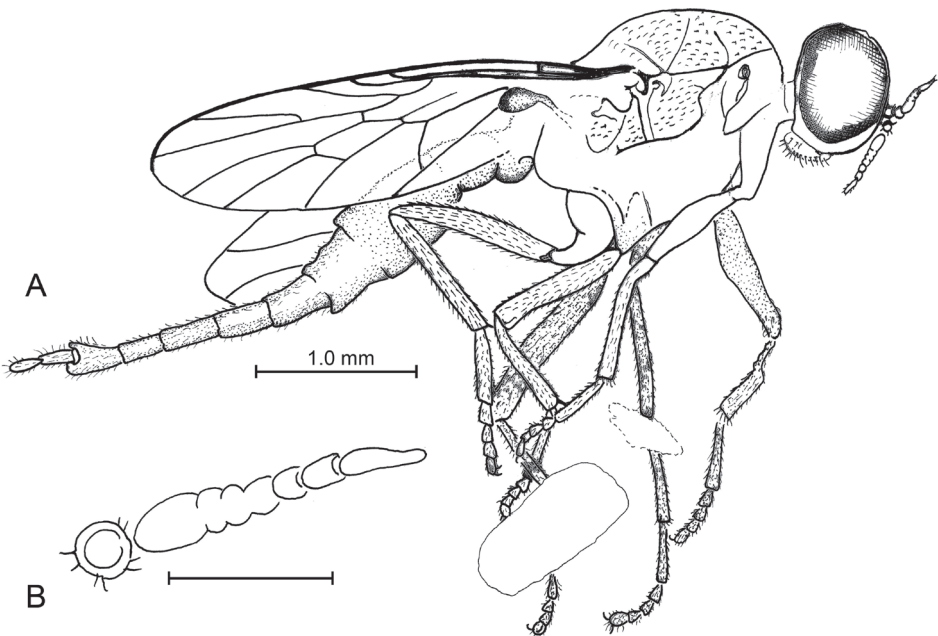
urn:lsid:zoobank.org:act:FD339789-7504-41CB-832A-23238FC6675A

[http://species-id.net/wiki/Lysistrata\\_emerita](http://species-id.net/wiki/Lysistrata_emerita)

Fig. 1

**Diagnosis.** As for the genus.

**Description.** Body length 5.75 mm. Head length 0.60 mm. Specimen well preserved, but only visible in lateral view. Head slight distorted, with right antenna slightly separated from base. Eyes bare, large, covering most of head; facets not differentiated. Ocellar triangle not visible. Antenna submoniliform, with approximately 7 short flagellomeres tapered in width distad (articulations between 3 basal flagellomeres faint, number of articles difficult to discern); length of antenna approximately equal to length of head; length of flagellum 3× that of scape + pedicel combined. Distal flagellomere distinctly longer and narrower than more basal ones. Palpi reduced, segmentation not discernable; labellum well developed. Thorax: Mesonotum short and compact, finely pilose dorsally, without macrosetae. Scutellum without spines. Surface of notum slightly metallic and foveolate. All legs preserved; protibia lacking spurs; mesotibia with two apical spurs (50



**Figure 1. a, b** *Lysistrata emerita* Grimaldi & Arillo, gen. et sp. n. (Stratiomyidae) in Albian amber from Spain. Holotype, MCNA 12698 **a** lateral view **b** Antenna (scale bar 0.25 mm).

µm long); probably one short apical spur on metatibiae. Length of hind basitarsomere equal to that of tarsomeres 2–5. Wing length 3.05 mm, width 0.75 mm; hyaline, vein Sc straight, length approximately  $0.45\times$  wing length, complete. Lengths of costal section of wing between apices of  $R_{2+3}$  and  $R_1$  equal to that between  $R_1$  and Sc.  $R_{2+3}$  arising distant from r-m.  $R_{4+5}$  straight,  $R_4$  curved at base, long and subparallel to  $R_5$ . Veins  $M_1$  and  $M_2$  separated at discal cell. Cell  $m_3$  absent, vein  $M_3$  either absent or fused to  $CuA_1$ . Abdomen elongate; basal 4 or 5 segments large and wide; apical 5 segments narrow and telescoping. Cercus composed of 2 segments, basal segment longer than apical one.

**Type.** Holotype, female, MCNA 12698, SPAIN: Alava, Peñacerrada I (Moraza), Escucha Formation, Lower Cretaceous (Albian). Deposited in MCNA. Specimen is well preserved in a clear piece of amber  $10 \times 7 \times 1.5$  mm, partially missing the left side of the thorax and the left wing; the amber is embedded in epoxy  $15 \times 13 \times 2$  mm. An empidoid fly (Microphorinae) is present as a syninclusion.

**Etymology.** From the Latin noun, *Emeritus*, a name given to retired Roman soldiers, used here in reference to this long-retired (i.e., extinct) species.

## Family Xylomyiidae

### *Cretoxyla* Grimaldi & Cumming, gen. n.

urn:lsid:zoobank.org:act:EB99B611-9DD4-4B20-A808-02847EC2188D

<http://species-id.net/wiki/Cretoxyla>

**Diagnosis.** Antenna thick, greatest width (in middle)  $0.25\times$  total length, with apparently 7 flagellomeres; protibia without apical spur; most distinctive features are in venation, which distinguishes this genus from other Mesozoic xylomyids by: vein M (separating cells br and bm) weak; cell  $m_3$  very small, width and length approximately half that of cell d (these are of equivalent size in other xylomyids, or  $m_3$  is slightly smaller), and, very distinctively, vein  $R_{2+3}$  is uniquely lost.

**Type species.** *Cretoxyla azari* sp. n., by present designation.

**Etymology.** From *Cretaceous*, and *Xylomyiidae*.

**Discussion.** The closed wing cell  $m_3$  is a feature also seen in some Xylophagidae. *Cretoxyla*, however, apomorphically has no protibial spur (as in Stratiomyomorpha) and plesiomorphically does not have a reduced alula (a greatly reduced alula occurs in the Xylophagidae). The extent of vein C, particularly whether it extends only to the apex of  $M_1$  or  $M_2$  (Woodley 1986: 1377), unfortunately cannot be checked since the apical quarter of the wing is lost. Vein C is definitely not circumambient. Other features that are important for xylomyid relationships that cannot be observed in the incomplete fossil are the number of palpal segments (1 vs. 2), presence of denticles on the ventral surface of the hind femur (e.g., *Solva* Walker), and various male and female genitalic structures.

The oldest fossil record of Xylomyiidae is *?Xylomyia* [sic] *shcherbakovi* Mostovski from the Upper Jurassic (Karabastau Formation) of Kazakhstan (Mostovski 1999). Zhang and Zhang (1993) indicated that *Mesosolva* Hong and *Prosolva* Hong, also



described as xylomyids from the Upper Jurassic of China, belong in another lower brachyceran family. Undescribed Cretaceous xylomyids are from the Upper Cretaceous amber of Siberia (Zherikhin and Sukacheva 1973), and an incomplete specimen of an undescribed species in Spanish amber (*vide infra*), so *Cretoxyla* is the oldest Cretaceous xylomyid (Early Cretaceous, Neocomian). Tertiary fossil xylomyids are *Solva inornata* Melander, 1949 and *Xylomya moratula* Cockerell, 1914 in late Eocene shale from Florissant, Colorado; and *Solva nana* Loew, 1850 in mid-Eocene Baltic amber.

***Cretoxyla azari* Grimaldi & Cumming, sp. n.**

urn:lsid:zoobank.org:act:0B1DC31D-17E2-4756-BDB2-E24C5E066E05

[http://species-id.net/wiki/Cretoxyla\\_azari](http://species-id.net/wiki/Cretoxyla_azari)

Fig. 2

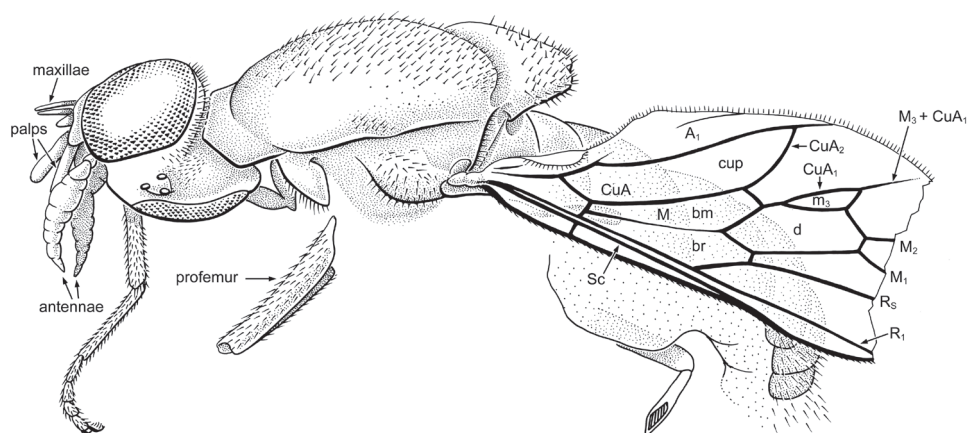
**Diagnosis.** As for genus.

**Description.** *Head:* Largely preserved, visible in oblique dorsal and ventral views. Head slightly flattened dorsoventrally, wider than deep, but exact proportions unclear since head seems somewhat distorted. Eyes large, bare, facets not differentiated; dorsal margins of eyes widely separated, by distance approximately 3× width of ocellar triangle. Gena/postocciptut with fine pilosity; frons bare. Antenna large and thick; length equal to length of head, thickest portion of antenna near middle (width 0.25 × length of antenna). Flagellomeres difficult to discern, apparently 7, all but distal 2 are wider than long; flagellomere “2” [which may be 2 flagellomeres – if sulcus is present it is very obscure] twice the length of other flagellomeres; apical flagellomere small and conical. Mouthparts slightly prognathous, elements separated but difficult to discern; pair of stiff, stylate maxillae apparent, other elements probably include a labrum or hypopharynx, the labium and/or palps (segmentation of possible palps cannot be discerned).

*Thorax:* Pronotum fairly large, collar-like; mesonotum large, relatively flat; mesonotum, apical 2/3 of mesoscutellum, and anepimeron with homogeneous vestiture of fine, stiff setulae, each setula having a slightly raised, papilla-like base; row of such setulae just above wing base. Only fore leg preserved sufficiently; without spines or spurs even at apex of tibia. Empodium pulvilliform. Halter slender. *Wing:* Distal quarter lost at surface of amber. Sc complete, meeting C slightly beyond level of crossvein r-m. Vein h in line with short m-cu. Vein R<sub>1</sub> straight. Vein R<sub>2+3</sub> lost. Cells br and bm virtually equal in size, bisected by weak vein M. Cell m<sub>3</sub> spindle-shaped, very small, approximately half the length and width of discal cell; vein M<sub>3</sub>+CuA<sub>1</sub> incomplete (not reaching wing margin) and long, length only slightly less than length of cell m<sub>3</sub>. Cell cup very large, considerably thicker than and extended well beyond apical levels of cells br and bm. Vein A<sub>1</sub> complete, A<sub>2</sub> not apparent; alula present, but not particularly large.

*Abdomen:* Poorly preserved, genitalia lost.

**Type.** Holotype, sex unknown, Lebanon (Early Cretaceous, Neocomian): “Hammana/Mdeiru, Aptien inférieur,” in Azar Collection no. 391, temporarily deposited in Musée National d’histoire Naturelle, Paris. The specimen is partially preserved, missing



**Figure 2.** *Cretoxyla azari* Grimaldi & Cumming, gen. et sp. n. (Xylomyidae) in Early Cretaceous amber from Lebanon. Holotype, AZ391. Body length (as preserved) 3.6 mm.

the right side of the body, most of the legs, and the right wing at the surface of the amber. It is mounted in a shallow glass well in Canada balsam on a glass slide.

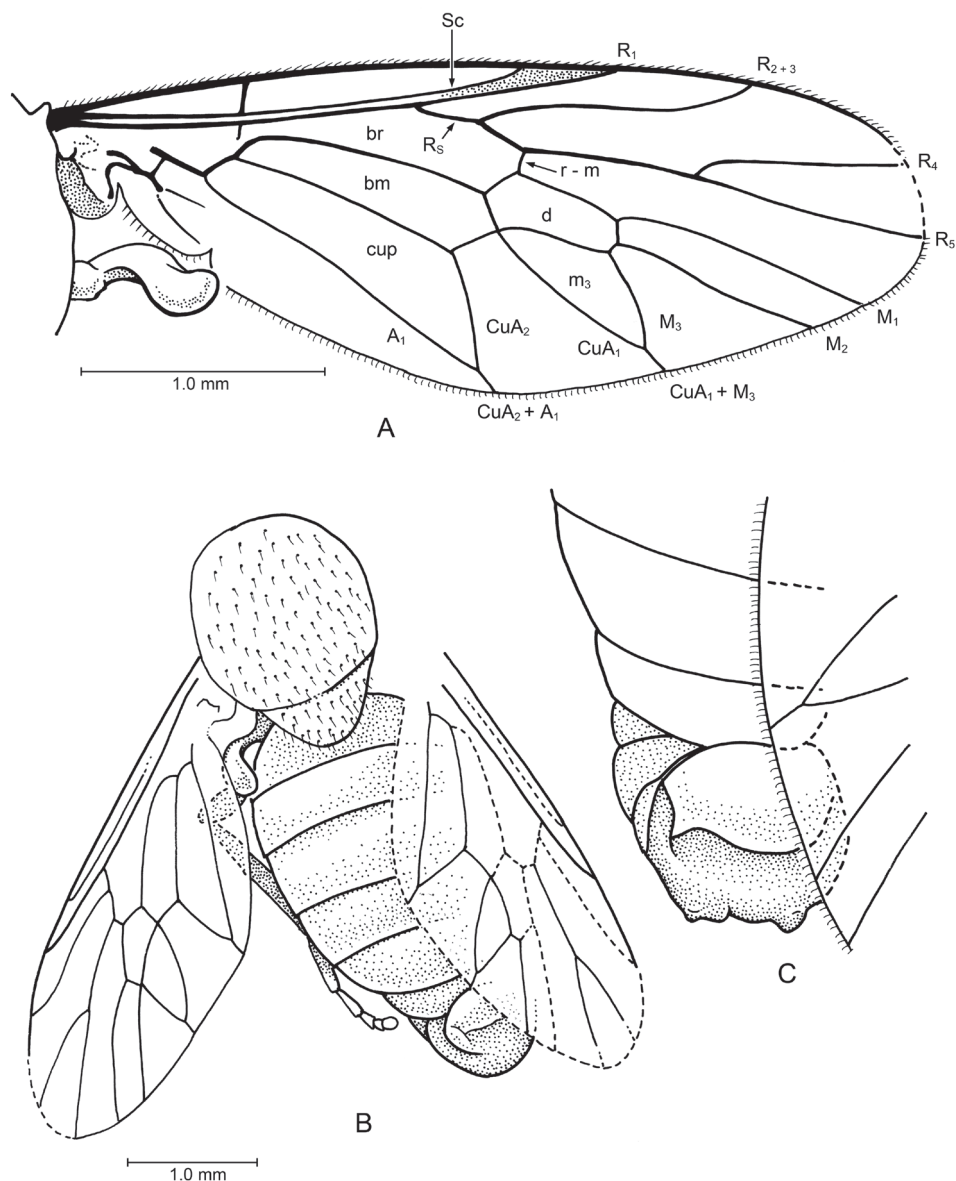
**Etymology.** Patronym, for Dany Azar, for his extensive contributions to the paleontology of Lebanese amber.

### **Xylomyidae(?) genus indet.**

Fig. 3

**Description.** *Head:* Lost. *Thorax:* Partially preserved, relatively broad (width of mesonotum equal to length, 1.40 mm), mesoscutellum of moderate size. Notum foveolate and scutellum covered only with numerous fine setulae, no macrosetae. Left wing 3.57 mm long, it and halter entirely preserved; right wing partially preserved. Vein C ends either at apex of  $R_4$  or  $R_5$ ; Sc long, meets C beyond midpoint of wing length, approximately at same level as crossvein r-m.  $R_1$  parallel and very close to Sc, with slightly sclerotized, pterostigmatic membrane where they diverge slightly at apex. Base of  $R_s$  (before fork of  $R_{2+3}$  and  $R_{4+5}$ ) short,  $R_s$  connected to  $R_1$  quite distad, at 0.42 complete length of wing. Veins  $R_4$  and  $R_5$  forked, branches of fork relatively straight (not curved), with  $R_5$  distinctively ending at apex of wing rather than below it. Cell d small, distinctively short (length  $2.5 \times$  greatest width); closed cells  $m_3$  and cup present, cell  $m_3$  triangular, short branches of  $M_3 + CuA_1$  and  $A_1 + CuA_2$  present. Alula relatively small. Halter relatively short and stout. *LEG:* [Presumably] hind leg without macrosetae on it; presence of an empodium difficult to discern, but pulvilli well developed. *Abdomen:* Relatively broad, ending short of wing apex.

**Specimen.** MCNA 8833, Spain: Álava: Peñacerrada I, Escucha Formation, Lower Cretaceous (Albian). Specimen lacks a head, and the thorax and abdomen are only partially preserved.



**Figure 3.** ?Xylomyidae sp. in Albian amber from Spain. MCNA 8833.

**Discussion.** Because of the incomplete preservation, a precise diagnosis and family placement of the specimen is not possible, so we did not provide a name and formal description. There are genera of lower Brachycera in several families that have a venation similar to this fossil, including the closed cell  $m_3$ . A distinctive feature of the fossil is vein  $R_5$  ending at the apex of the wing. This is rarely seen in the lower Brachycera, occurring, for example, in Xylomyiidae and *Apsilocephala* Kröber, 1914 (*Apsilocephali-*

dae). Unlike *Apsilocephala*, which has the branches of  $R_4$  and  $R_5$  curved, these branches in the fossil are straight. Also, *Apsilocephala* and most therevids usually have a longer, more slender abdomen (although see *Kumaromyia*, *vide infra*), and usually have bristle-like setae on the mesonotum. These features, plus the short branch of  $R_s$  and its distal connection to  $R_1$  indicate that the fossil is in the Stratiomyomorpha, not the Asiloidea.

## Infraorder Tabanomorpha

### Family Tabanidae

#### Genus *Cratotabanus*

<http://species-id.net/wiki/Cratotabanus>

*Cratotabanus* Martins-Neto and Santos, 1994: 291. Type species: *C. stenomyomorphus* Martins-Neto and Santos, 1994. Crato Formation (Aptian), Early Cretaceous of Brazil.

**Diagnosis.** *Cratotabanus* is distinguished from modern tabanids by veins  $M_1$ ,  $M_2$ , and  $M_3$  long, with lengths of  $M_1$  approximately the same as that of cell d (vs.  $0.5 - 0.7 \times$  length of cell d in Recent Tabanidae);  $R_5$  only slightly deviated from the path of vein  $R_{4+5}$  (in most Recent tabanids, excepting *Chrysops* Meigen 1803,  $R_5$  curved strongly downward). Distinguished from some Cretaceous Tabanidae, as follows: *Eotabanoid* Mostovski et al. 2003 and Yixian Formation genera with longer  $R_1$  (reaching well past level of apex of cell d); fork of  $R_{4+5}$  in *Eotabanoid*, *Palaepangonius* Ren, 1998, and *Eopangonius* Ren 1998 much longer (about equal in length to vein  $M_1$ ).

#### *Cratotabanus newjerseyensis* Grimaldi, sp. n.

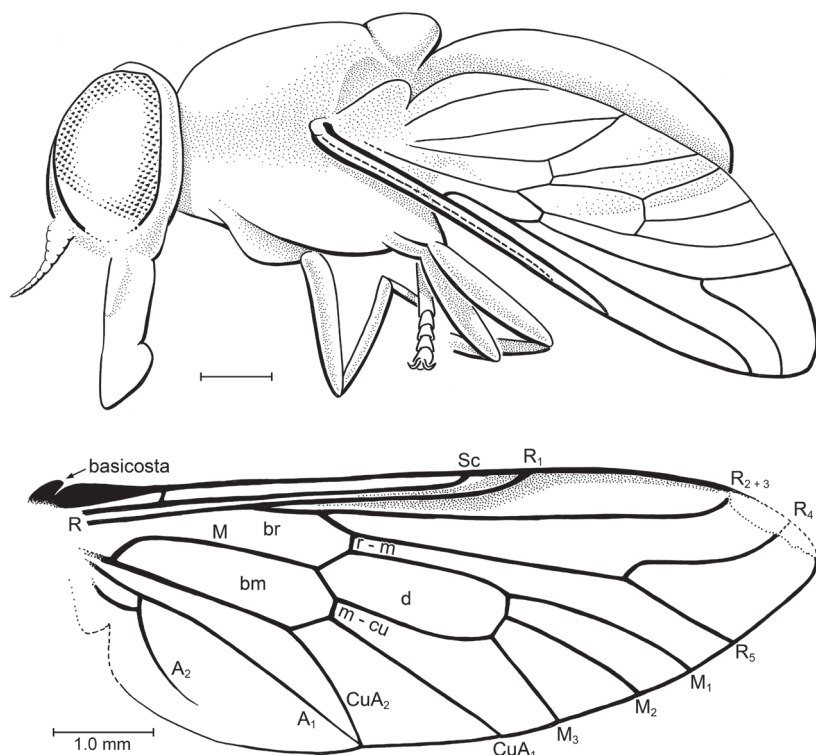
urn:lsid:zoobank.org:act:B8FD8A73-669D-44EB-B923-464378B6AB94

[http://species-id.net/wiki/Cratotabanus\\_newjerseyensis](http://species-id.net/wiki/Cratotabanus_newjerseyensis)

Fig. 4

**Diagnosis.** Venation differs from congener by *C. stenomyomorphus* having vein  $R_4$  not strongly upcurved (vs. strongly upcurved) and  $R_5$  slightly downcurved (vs. nearly in line with  $R_{4+5}$ ).

**Description.** AMNH NJ-1862 (holotype): Body length 1.0 cm, wing length 8.0 mm. Most of left lateral view and some of dorsal, right lateral, and frontal view of face observable. Specimen apparently female. *Head:* Eyes bare, large, not dichoptic, no differentiation of facets nor apparent color patterns. Details of frons and face not entirely observable (e.g., presence of frontal callus and subcallus unlikely; development of ocelli not discernable). Antenna with scape and pedicel not observable but apparently short (not projected); flagellomere I apically narrowed to  $0.5 \times$  basal width, with 3 faint annuli; remaining 6 flagellomeres stylate, tapered apicad, articles of approximately equal



**Figure 4.** *Cratotabanus newjerseyensis* Grimaldi, sp. n. (Tabanidae) in Turonian amber from New Jersey, USA. Above: Lateral view of holotype, AMNH 1862. (scale 1.0 mm). Below: Wing of paratype, AMNH NJ1081.

lengths [best seen in frontal view]. Proboscis robust, palps barely discernable (but apparently short, length  $0.4 \times$  that of proboscis), labellum well developed; entire proboscis fairly long, length =  $0.75 \times$  depth of head. *Thorax*: Standard proportions for Tabanidae; legs without discernable spurs (although apices of hind tibiae not observable). Metathoracic spiracle also not observable [e.g., presence of postspiracular scale]. *Wing*: Completely hyaline, no patterning. Base of  $R_{2-5}$  nearly perpendicular to  $R_1$ , not at a sharp, acute angle. Fork of  $R_{4-5}$  widely divergent and encompassing entire wing tip, base of  $R_4$  perpendicular to  $R_5$ , then strongly and concavely curved to meet C; base of  $R_4$  without a small appendix.  $M_1$ ,  $M_2$ ,  $M_3$  nearly parallel;  $M_3$  and  $CuA_1$  convergent (not parallel);  $CuA_1$  and  $A_1$  meeting just before wing margin.  $A_2$  extended nearly to wing margin; alula very large. *Abdomen*: Details (e.g., segmentation of cerci) not observable.

*Specimen*. AMNH NJ-1081 (paratype): Thorax + abdomen length 8.2 mm, wing length 8.5 mm (from base of basicosta to wing tip). Wing: Basicosta present as a thick, scale-like lobe at base of vein C. C thickened proximally, circumambient. Short cross-vein h present, where costal thickening is narrowed. Sc long,  $0.6 \times$  length of wing, straight and parallel to vein C. Veins R and base of  $R_1$  also straight, parallel, and close to Sc; apices of Sc and  $R_1$  diverging apically. Dark, heavily sclerotized pterostigma cov-

ers and surrounds  $R_1$ , vein C, and extends to tip of  $R_{2+3}$ .  $R_{2+3}$  straight, turned slightly upward at apex. Stem of  $R_4$  and  $R_5$  straight, base of  $R_4$  nearly perpendicular to this stem, then curved upward and meeting C anterior to tip of wing;  $R_5$  nearly in line with stem of  $R_4+R_5$ . Cell d large, length ca.  $2.7 \times$  the width; with veins  $M_1$ ,  $M_2$  and  $M_3$  each deriving directly from apical wall of cell. M veins slightly divergent, long;  $M_1$  slightly longer than cell d,  $M_3$  ca.  $0.6 \times$  length of cell d. Crossveins r-m and m-cu in line with each other. Veins  $CuA_2$  and  $A_1$  meet slightly before wing margin, forming long, complete cua cell with very short vein  $CuA_2+A_1$ . Vein  $A_2$  well developed, concave to  $A_1$ , evanescent apically; anal lobe and anal cell well developed. Alula present but partially obscure. Abdomen: Short, broad, tergites short, typical of tabanids.

**Types.** Holotype (sex unknown), AMNH NJ-1862, New Jersey (USA): Middlesex Co., Sayreville, White Oaks [Old Crossman's] pits (Turonian), collected by Stephen Swolensky. Observation of the fly was optimized by embedding the amber in epoxy under vacuum and trimming very close to surfaces of the fly, but the specimen is not well preserved, being occluded with a reddish, crazed layer over most of the body and by similar internal fractures in the piece, as well as by a suspension of fine particles in the amber. Piece is irregular in shape,  $10 \times 13$  mm in largest dimensions. Study of the specimen might benefit from microtomography.

Paratype (sex unknown), AMNH NJ-1081, in Late Cretaceous (Turonian) amber from Crossman's Pits, Sayreville, New Jersey. Fly is partially preserved: besides the entire right wing and a very small portion of left wing, only the dorsal surfaces of the abdomen and thorax remain; the head and legs are entirely lost. The amber piece is triangular and approximately  $19 \times 8 \times 5$  mm, embedded in epoxy but trimmed and polished so as to expose a dorsal view of the fly. The amber itself is light yellow and turbid, with a thick suspension of organic particles that obscures much of the fly. AMNH NJ-1081 differs from NJ-1862 by the following minor venational details:  $R_1$  slightly longer,  $R_s$  branches from  $R_1$  at a more acute angle, proximal end of cell d slightly more shallow V-shaped;  $A_2$  slightly shorter. Both specimens are also very similar in body shape and size.

**Etymology.** "from New Jersey," in reference to provenance.

**Discussion.** These are the only tabanids known to be preserved in Cretaceous amber. Other tabanids in amber are from the Miocene of the Dominican Republic and the Eocene Baltic amber (Evenhuis 1994).

Ren (1998) described three genera of putative, compression-fossilized tabanids with long proboscides from the Early Cretaceous Yixian Formation of China. Grimaldi (1999) discussed the characters on which his assignment was made, and concluded that these fossils may not be tabanids. For example, features of *Palaepangonius eupterus* Ren that are inconsistent with Tabanidae are the short, upturned  $R_{2+3}$ , very long veins  $R_4$  and  $R_5$  (half this length and much more divergent in true Tabanidae), and veins  $A_1$  and  $CuA_2$  that do not fuse but meet the wing margin independently (Fig. 4c). These do appear to be tabanomorphs, but may be stem-group taxa to Recent Tabanidae, Athericidae, Pelecorhynchidae, and possibly even Rhagionidae (some fossil rhagionids had long, piercing mouthparts). Another early compression fossil, *Baissomyia redita*, from the Early Cretaceous Zaza Formation of Russia, was attributed to the Tabanidae



essentially on the basis of body shape and styletiform mouthparts (Mostovski et al. 2003), since the antennae and most of the wing (and, thus, most features defining the family) were not preserved. *Eotabanoid lordi*, from the Early Cretaceous of England, is probably a tabanid, but it too plesiomorphically has long  $R_4$  and  $R_5$  veins, which are nearly symmetrical (in true tabanids  $R_4$  is typically much more curved) (Mostovski et al. 2003) (Fig. 4c). Besides the specimens in New Jersey amber described herein, the only other definitive Tabanidae from the Cretaceous is *Cratotabanus stenomyomorphus* from the Aptian-aged Crato limestone of Brazil (Martins-Neto and Kucera-Santos 1994). Venation of *C. stenomyomorphus* and *C. newjerseyensis* are extremely similar. Another species of the genus from the Crato Formation is as yet undescribed (Martins-Neto 2003). Diverse Tabanidae occur in Tertiary rocks and amber (summarized by Evenhuis, 1994), but generic assignments of those species described prior to 1950 need to be assessed. Cretaceous fossils assigned to the Tabanidae include the following:

*Baissomyia redita* Mostovski, Jarzembowski & Coram, 2003: Zaza Formation, Baissa, Transbaikalia, Russia.

*Eotabanoid lordi* Mostovski, Jarzembowski & Coram, 2003: Durlston Formation (Berriasian), Purbeck Group, Dorset UK.

*"Allomyia"* [sensu Ren] *ruderalis* Ren, 1998: Yixian Formation, China.

*Eopangonius pletus* Ren, 1998: Yixian Formation, China.

*Palaepangonius eupterus* Ren, 1998: Yixian Formation, China.

*Cratotabanus stenomyomorphus* Martins-Neto & Santos, 1994: Crato Formation (Aptian), Ceara, Brazil.

*"Cratotabanus* sp. n.": Crato Formation (Aptian), Ceara, Brazil (in Martins-Neto 2003: pg. 31, ex: Grimaldi 1990).

*Cratotabanus newjerseyensis* sp.n.: Raritan Formation amber (Turonian), New Jersey, USA (herein).

## Infraorder Muscomorpha

### Superfamily Nemestrinoidea

#### Family Acroceridae

Acroceridae has been hypothesized to be closely related either to the family Nemestrinidae (Woodley 1989), or as the basal family of the Heterodactyla with the Nemestrinidae as the basal family of the Muscomorpha (Yeates 2002). Both of these families have larvae that are ectoparasitoids on other terrestrial arthropods (in the case of Acroceridae, on spiders). Relationships presented in Wiegmann et al. (2011) are extremely unusual, with Nemestrinidae close to the Tabanomorpha and Acroceridae close to Stratiomyomorpha. Nemestrinidae

<sup>1</sup> *Allomyia* Ren, 1998 is a junior primary homonym of *Allomyia*, Banks 1916 (Trichoptera) and requires a replacement name. See the thorough and very entertaining discussion by O'Hara (2011) on homonym-chasing by cyber-nomenclaturists and the extravagant case of *Allomyia*.

in particular is an ancient lineage with a distinctive wing venation, the oldest of which are Early Jurassic, and they were quite diverse by the Late Jurassic (Evenhuis 1994). An equivalent age of Acroceridae is very plausible, but Bayesian estimates of divergence between the Acroceridae and Nemestrinidae in the Triassic (Winterton et al. 2007) are almost certainly too old. The two new Burmese amber genera described below are very significant records for the family since these are the only acrocerids known from the Cretaceous, and also the best-preserved Mesozoic ones. The only other Mesozoic species of an acrocerid is from the Late Jurassic sediments of Karatau (Ussatchov 1968; Mostovski 1998), *Archocyrtus gibbosus* Ussatchev (*Juracyrtus kovalevi* Nartshuk 1996, from the same outcrops, is very similar and may even be conspecific [Hauser and Winterton 2007]). There are five acrocerid species preserved in Eocene Baltic amber. In the monophyletic subfamily Philopotinae (Winterton et al. 2007) are *Archacterphis hennigi* Hauser and Winterton 2007 (closely related to the African genus *Africaterphis* Schlinger 1968), *Eulonchiella eocenica* Meunier 1912 (which is closely related to the Recent South African genus *Thyllis* Erichson 1840), and *Prophilopota succini* Hennig 1966. Other Baltic amber species are *Glaesoncodes completinervis* Hennig 1968 and *Villalites electrica* Hennig 1966. *Ogcodes exotica*, in Miocene Dominican amber, is closely related to several Asian species of the genus (Grimaldi 1995).

***Schlingeromyia* Grimaldi & Hauser, gen. n.**

urn:lsid:zoobank.org:act: A659E121-9307-4454-B910-A586A82613E4

<http://species-id.net/wiki/Schlingeromyia>

**Diagnosis.** A minute, distinctive acrocerid with medial margins of male eyes contiguous above and below antennae, hind and ventral margins of eye strongly emarginate; antennae minute, in middle of head; proboscis vestigial; eyes bare, thorax with very sparse, fine setulae; postpronotal lobes of moderate size, slightly protruding; abdomen devoid of microtrichia and glabrous (possibly reflective). Mediolobus (i.e., “pulvilli-form empodium”) and pulvilli pad-like. Venation distinct: All veins sclerotized, none faint; C ends at apex of  $R_{4+5}$ ; Sc short;  $R_1$  and  $R_s$  fork at ca.  $0.4\times$  length of wing; cells br and bm continuous, not bisected (vein M extremely faint or lost from this area); two closed radial cells ( $r_{4+5}$  and d), plus cell  $m_3$  present;  $R_{4+5}$  ends near apex of wing, without an apical fork of  $R_4-R_5$  encompassing apex of wing.

**Type species.** *S. minuta*, sp. n., by present designation.

**Etymology.** Patronym in honor of Evert Schlinger, Emeritus Professor of entomology at the University of California, Berkeley, who has devoted his career to the study of Acroceridae and who also has been a very generous patron of systematic entomology. Feminine, following the Greek *myia*, for fly.

**Discussion.** This is a very distinctive, minute acrocerid – in body size quite the opposite of its generic namesake – which is unique for the venation, genitalia, and virtually bare body. Most acrocerids have long, fine pile on the thorax and abdomen, and many have it on the eyes and calypters. Vein Sc is very short in the fossil, and cells br and bm are contiguous. In addition, apparent retention of freely articulated gonostyli

in the male genitalia appears to be a significant feature of the genus, since loss of articulated gonostyli through fusion with the gonocoxites is considered an apomorphy of the remainder of the family (Sinclair et al. 1994). The broad, pad-like structure between the pulvilli, called the empodium in homeodactylous flies, is actually a median outgrowth of the pulvilli as based on the detailed but overlooked work of Röder (1986). The true empodium is a bristle-like distal extension of the unguitractor plate. Thus, we are calling the pad-like empodium a mediolobus. Presence of a true (setiform) empodium is considered a synapomorphy of the Heterodactyla (Woodly 1989; Yeates 2002).

Winterton et al. (2007) recently analyzed acrocerid relationships based on sequences, and concluded that the subfamily Acrocerinae is diphyletic, and the subfamilies Panopinae and Philopotinae are monophyletic. Philopotines are particularly distinctive for the hump-backed notum and postpronotal lobes that are so enlarged as to form a collar dorsally over the cervical region. Although the Baltic amber *Archaeoterphis hennigi* superficially resembles *Schlingeromyia* in small body size and eye shape (Hauser and Winterton, 2007), the relatively complete venation of the latter, structure of male genitalia, and pretarsal structure indicate a much more basal position for the Burmese amber species. Relationships of *Schlingeromyia* to any Recent generic-group or subfamily is obscure and may reflect a stem-group position.

***Schlingeromyia minuta* Grimaldi & Hauser, sp. n.**

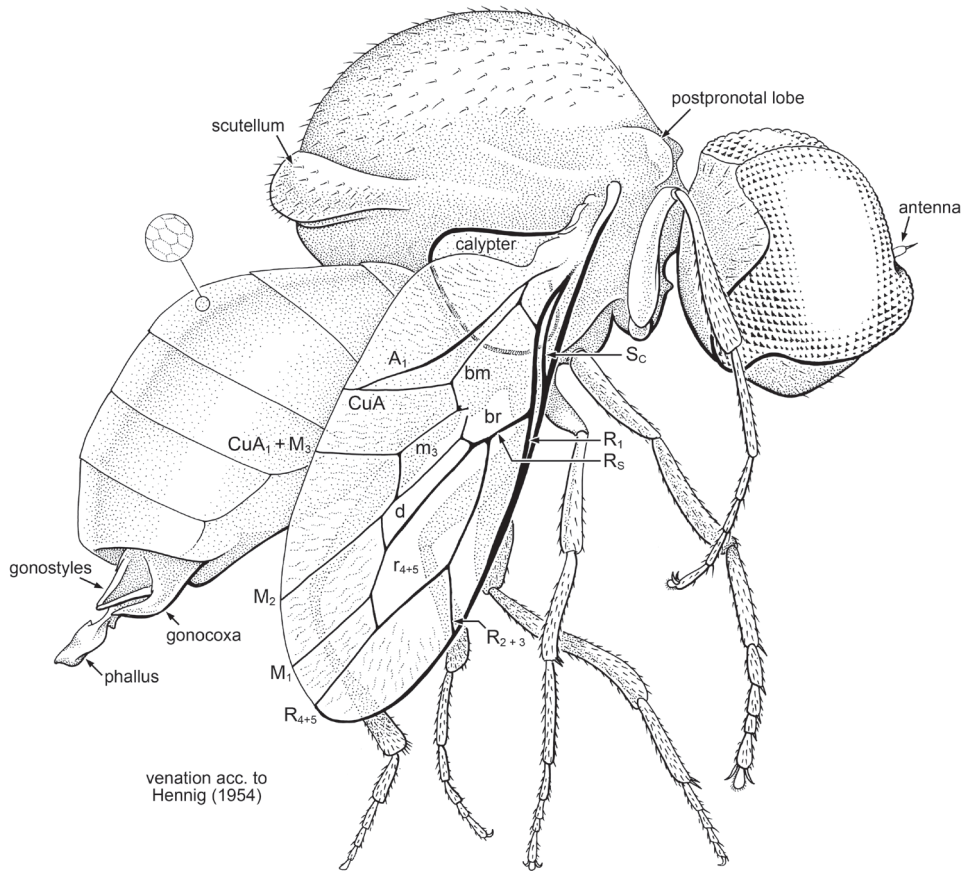
urn:lsid:zoobank.org:act:4881BDDC-D10C-47FE-91B1-5BA12EBE2B64

[http://species-id.net/wiki/Schlingeromyia\\_minuta](http://species-id.net/wiki/Schlingeromyia_minuta)

Fig. 5

**Diagnosis.** As for the genus.

**Description.** Body length 3.0 mm, wing length 2.1 mm. *Head:* Large, spherical. Eyes very large, occupying most of head capsule. Eyes bare, without interfacetal setulae; no dorso-ventral or frontal differentiation of facets. Entire mesal margins of eyes above antennae are contiguous, portion of mesal eye margin below antenna also contiguous. Posterior margin of eye strongly emarginate; ventral margin of eye slightly less so. Antenna minute, length approximately equal to diameter of 2–3 eye facets; consists of small oval pedicel and minute apical style. Mouthparts vestigial. Postociput with scattered, fine setulae. *Thorax:* Scutum strongly arched, very large, length of (meso)thorax 1.25 mm (nearly half the body length). Scutellum small. Position of cervical region near ventral surface of thorax. Pair of well-developed postpronotal lobes dorsal to cervical region, posterior surface of lobe slightly concave. Scutum with sparse, short setulae; scutellum with slightly thicker setulae. Legs slender, mesotibia with short pair of apical spurs; apices of tarsomeres with pair of short, thick setae. Length of basitarsomere approximately equal to that of remaining, distal tarsomeres; hind tibia expanded in width apically to approximately twice the proximal width. Pretarsus with claws large; mediolobus and pulvilli large, pad-like. Wing short and slender, length 2.10 mm, greatest width 0.75 mm; membrane with fine, faint pleating/wrinkling over



**Figure 5.** *Schlingeromyia minuta* Grimaldi & Hauser, gen. et sp. n. (Acroceridae) in latest Albian – early Cenomanian amber from Myanmar. Holotype, AMNH Bu332a. Body length 3.0 mm. Terminology for wing venation after Hennig (1954).

apical and posterior regions, but not in closed cells [best seen in oblique views]. Calypter large, ovoid, greatest diameter 0.58 mm. All veins sclerotized, none faint. C ends at apex of  $R_{4+5}$ ; Sc short, meets C slightly distal to level of where  $R_1$  and  $R_s$  fork.  $R_1$  and  $R_s$  fork at ca.  $0.4 \times$  length of wing; stem of  $R_s$  short, approximately  $0.2 \times$  total length of  $R_s$ .  $R_s$  surrounds large  $r_{4+5}$  cell, near middle of which  $R_{2+3}$  branches off to meet C. Vein  $R_{4+5}$  branches off of apex of cell  $r_{4+5}$ , apex meets C slightly posterior to wing apex;  $M_1$  also short, branching subapically off of cell  $r_{4+5}$ . Tip of wing not encompassed by an apical fork of  $R_4-R_5$ . Cell d bounded by  $M_1$  and  $M_2$ ; slender (ca.  $0.3 \times$  thickness of cell  $r_{4+5}$ ). Cell  $m_3$  slender, trapezoidal, with proximal end slightly opened. Cells br and bm continuous, not bisected (vein M extremely faint or lost from this area).  $A_1$  slender, meeting CuA shortly before wing margin.  $A_2$  not apparent; anal lobe of wing well developed. Calypter large, hemispherical, greatest diameter  $0.25 \times$  length of wing. *Abdomen*: Smaller than thorax, with six tergites visible (tergite I small, tI and tII virtu-

ally obscured in dorsal view under postnotum). Tergites entirely bare of microtrichia and setulae; glabrous [probably reflective], with cuticular microsculpture of minute hexagonal cells present. Spiracles not visible near lateral margins of tergites [in pleural membrane?]. Tergites VII–VIII apparently small [not discernable]. Two pairs of male genitalic appendages present: slender dorsal pair (probably gonostyli), thicker ventral pair (gonocoxites), plus terminal, central, membranous appendage, the phallus.

**Type.** Holotype, Male, AMNH Bu332a, in Burmese amber. Paratype, AMNH Bu332b, in same piece of amber. Both specimens are entirely preserved, though slightly obscured by debris and a few small fractures. The specimens occur in a runnel-shaped piece of dark but transparent amber, 16 × 7 mm, which has been embedded in epoxy. The piece also contains 1 Coleoptera, 1 Hymenoptera (Serpitidae), and 6 other Diptera (Cecidomyiidae, Empidoidea), as well as twisted strands of spider webs. Interestingly, acrocerids are parasitoids of spiders.

**Etymology.** Latin, adjective, in reference to the very small size of the species.

***Burmacyrtus* Grimaldi & Hauser, gen. n**

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<http://species-id.net/wiki/Burmacyrtus>

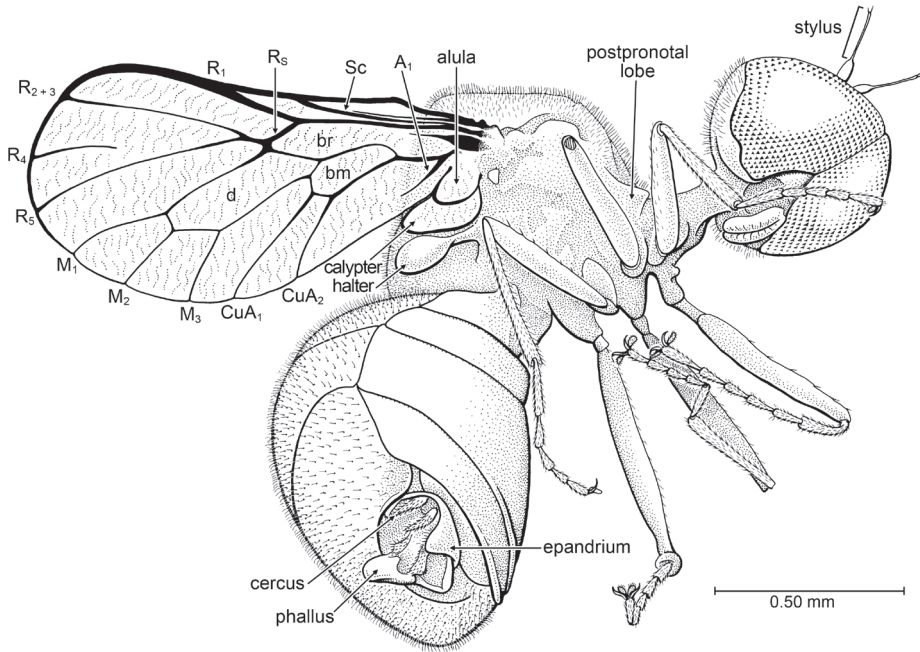
**Diagnosis.** A small, primitive acrocerid in Burmese amber easily separated from *Schlingeromyia* based on the well developed mouthparts; long, fine antennal stylus; dense, fine pilosity on thorax and abdominal tergites; absence of a mediolobus on the pretarsus; absence of tibial spurs; wing apex rounded; and by the venation: Vein C circumambient, cells br and bm completely separated, absence of cells  $r_{4+5}$  and  $m_3$ , presence of a very large cell d, vein  $R_4$  present but vestigial (not connected to  $R_5$ ), veins  $CuA_1$  and  $CuA_2$  each present, vein  $A_1$  vestigial (cell cup not present).

**Type species.** *B. rusmithi* sp. n., by present designation.

**Etymology.** Combination derived from Burma (the pre-junta name for Myanmar) and *Cyrtus*, nominal genus of Cyrtidae, a formerly used name of Acroceridae.

**Discussion.** Derived acrocerid features that *Burmacyrtus* shares with *Schlingeromyia* and Recent acrocerids are the following: spherical head with large, holoptic eyes in male; apex of antennal flagellum with simple stylus; presence of a distinct cervical region; wing membrane with fine wrinkling and devoid of microtrichia; and with a large calypter. Apomorphic features in *Burmacyrtus* that are lacking in *Schlingeromyia* are fine, dense pilosity; a broadly rounded wing apex; long, fine stylus; and lack (loss) of a mediolobus. The wing shape of *Burmacyrtus* is similar to that of some Recent acrocerine genera such as *Turbopsebius* Schlinger, 1972, but the latter genus has cell  $r_{4+5}$  present, veins  $CuA_1+M_3$  fused, and a complete vein  $A_1$ , among other features. Like *Schlingeromyia*, *Burmacyrtus* is also very basal in the Acroceridae. Some of the derived features in wing venation of the two species in Burmese amber may be due to the very small body size.





**Figure 6.** *Burmacyrtus rusmithi* Grimaldi & Hauser, gen. et sp. n. (Acroceridae) in Burmese amber. Holotype AMNH Bu-RS1.

***Burmacyrtus rusmithi* Grimaldi & Hauser, sp. n.**

urn:lsid:zoobank.org:act:17FA87A4-457F-4BB0-AC59-03ECEBF4CAA4

[http://species-id.net/wiki/Burmacyrtus\\_rusmithi](http://species-id.net/wiki/Burmacyrtus_rusmithi)

Fig. 6

**Diagnosis.** As for genus.

**Description.** Wing length approximately 1.4 mm, body length approximately 2.0 mm. *Head:* Rounded, spherical. Male eyes bare of setulae, frontally holoptic [dorsum of head not visible], occupying most of head capsule, ventromesal margins of eyes diverging around clypeus; facets in ventral portion of eye not differentiated in size; posteroventral margin of eye with shallow emargination. Basal portion of flagellum small, ovoid; stylus long and very slender, length c. 2 × that of basal portion; apex of stylus with pair of minute setulae. Labellum well developed; palps not evident. Postocciput with dense, fine pilosity. *Thorax:* Cervical region elongate, but not comprised of elongate postpronotal lobe (which protrudes slightly from anterior surface of scutum); cervical region connected anteroventrally to thorax. Thorax deep. Dorsal surface of mesoscutum and scutellum with dense, fine pilosity. Legs slender, metafemur longest; without spines, bristle, or tibial spurs; tibial and tarsal setulae not in regular rows. Apical portions of tibiae not distinctly broadened. Pretarsal claws large; pulvilli large, mediolobus absent [if setiform empodium present, not visible]. Wing short, with broadly rounded apex and narrow base; surface



devoid of microtrichia, with fine wrinkling throughout. Vein C circumambient, though thinner past apex of  $M_1$ ; small hump in C midway along length of Sc. Sc complete, length ca.  $0.4 \times$  that of wing (a thin, faint, incomplete, and apparently spurious vein runs parallel and very close to Sc). Vein  $R_1$  short, length approximately  $0.5 \times$  length of stem of R;  $R_1$  and C thickened where they meet. Stem of Rs short, length approximately  $0.5 \times$  that of  $R_1$ ; Rs and where it meets M thickened.  $R_4$ – $R_5$  apparently a vestigial fork ( $R_4$  incomplete, not connected to  $R_5$ ). Cells  $r_{4+5}$  and  $m_3$  absent; cell d present, large; length of cell d  $0.3 \times$  that of wing. Cells br and bm present, separated by well developed basal portion of M. Veins  $M_1$ ,  $M_2$ ,  $M_3$  present, originating from apex of cell d. Veins  $CuA_1$  and  $CuA_2$  present, originating from apex of cell bm. Vein A present, but short and vestigial (cell cup absent). Alula and calypter well developed, each with fine wrinkling; calypter approximately  $2 \times$  diameter of alula. Halter apparently dark. *Abdomen*: larger than thorax; sternites well developed, glabrous, without setulae or punctures. Tergites large, with dense, fine pilosity; each setula situated in minute puncture. Male genitalia: epandrium well developed, shallow; cerci slender and apically pointed; everted, distal portion of phallus bulbous; subapical portion flanked by pair of flat, setulose lobes. Spiracles not visible.

**Type.** Holotype, Male, AMNH Bu-RS1, in Burmese amber. The holotype is in excellent condition, though only the ventral and lateral portions are visible (the dorsal surface is obscured by the depth and curvature of the amber). The amber is clear yellow and the fly lies on an internal surface plane that contains bubbles and stellate trichomes. The original piece was drop-shaped,  $10 \times 16$  mm, and contained a small spider, cecidomyiid midge, and berothid lacewing. These inclusions were separated from the fly.

**Etymology.** Patronym, for Dr. R.D.A. (Ru) Smith, who generously donated the specimen to the AMNH from his personal collection.

## Superfamily Asiloidea

### Family Mythicomyiidae

#### *Microburmyia* Grimaldi & Cumming, gen. n.

urn:lsid:zoobank.org:act:7C83B2CC-BD8F-4BDA-A19D-E61110619770

<http://species-id.net/wiki/Microburmyia>

**Diagnosis.**  $R_1$  long, apex reaching to  $2/3$  length of wing;  $R_1$  branching off of the stem of R quite distad,  $R_{2+3}$  long, branching off of Rs in the distal half of the wing; cells br and bm large, length nearly half that of wing;  $M_{1+2}$  forked; vein  $A_1$  either incomplete or absent. Mesoscutum strongly arched; it and abdominal tergites devoid of bristle-like setae or long pilosity; apical tibial spurs lacking. Body size minute, ca. 1.0 mm in length.

**Type species.** *M. analvena*, sp. n. By present designation

**Etymology.** Derived from *micro-* (L.), minute; *-burm-*, Burma; and *-myia* (Gr.), fly, in reference to the minute body size and provenance of this brachyceran. Feminine.

**Discussion.** The family placement of the two new species in this genus is not entirely certain, particularly since in mythicomyiids vein  $R_{2+3}$  is typically short and its

apex fused with  $R_1$ . The genus is placed in the Mythicomysiidae since the venation bears a resemblance to the Baltic amber genus *Carmenlectra* Evenhuis (Evenhuis 2002), though differing from that Baltic amber genus by  $R_1$  branching off of the stem of R quite distad (vs. near the base of the wing),  $R_{2+3}$  branching off of Rs in the distal half of the wing (vs. in the basal half), and by crossveins r-m and cu-m being in line (vs. stepped). Other features of *Microburmyia* that are consistent with mythicomysiids are the strongly arched scutum, structure of apical antennal articles (with minute stylus in *M. analvena*, ovoid first flagellomere in *M. veanalvena*), incomplete Sc vein, palpi minute or absent, and the minute body size. *Microburmyia* is plesiomorphic with respect to all other known mythicomysiids (cf., Evenhuis 2002).

Mythicomysiidae are traditionally (e.g., Hall 1981) and phylogenetically (e.g., Yeates 1994; Woodley 1989; Woodley et al. 2009) placed as the sister group to the Bombyliidae s.s., often classified as a subfamily, but also as a separate family (e.g., Evenhuis 2002). There is strong morphological and molecular support for Bombyliidae + Mythicomysiidae being the sister group to the rest of Asiloidea (Woodley 1989; Yeates 2002; Wiegmann et al. 2011) or the sister group to the rest of Asiloidea and Eremoneura (Sinclair et al. 1994; Trautwein et al. 2010). With the exception of an unforked  $R_{4+5}$  and short or vestigial anal vein in *Microburmyia*, it is very interesting that its venation is intermediate between that of the Hilarimorphidae and the more specialized venation of mythicomysiines. This would lend support to the hypothesis that Hilarimorphidae is the sister group to the Bombyliidae (Woodley 1989; Yeates 1994; Woodley et al. 2009). Another hypothesis places the Hilarimorphidae (sometimes including the enigmatic and monotypic genus *Apystomyia* Melander 1950) as the sister group to the Eremoneura (Yeates, 2002) (see also discussion under Apystomyidae, *vide infra*). Oddly, the recent total-evidence phylogeny of flies placed the Hilarimorphidae (excluding *Apystomyia*) as sister group to the Acroceridae (Wiegmann et al. 2011), for which there is very limited molecular and no morphological support, although this result does suggest a position of Hilarimorphidae distant from Eremoneura.

Lastly, it is interesting to note that the fossil record of Bombyliidae s.s., exclusive of mythicomysiines, is entirely Tertiary. Bombyliidae is a large, cosmopolitan family (ca. 4,500 species) of flies that are most diverse in xeric ecosystems, where they are important pollinators of herbaceous plants. Their fossil record in sedimentary matrices and in amber (Baltic, Dominican) is quite diverse for North America and Europe (Evenhuis 1994), suggesting that the bombyliids s.s. radiated rapidly in the early Tertiary.

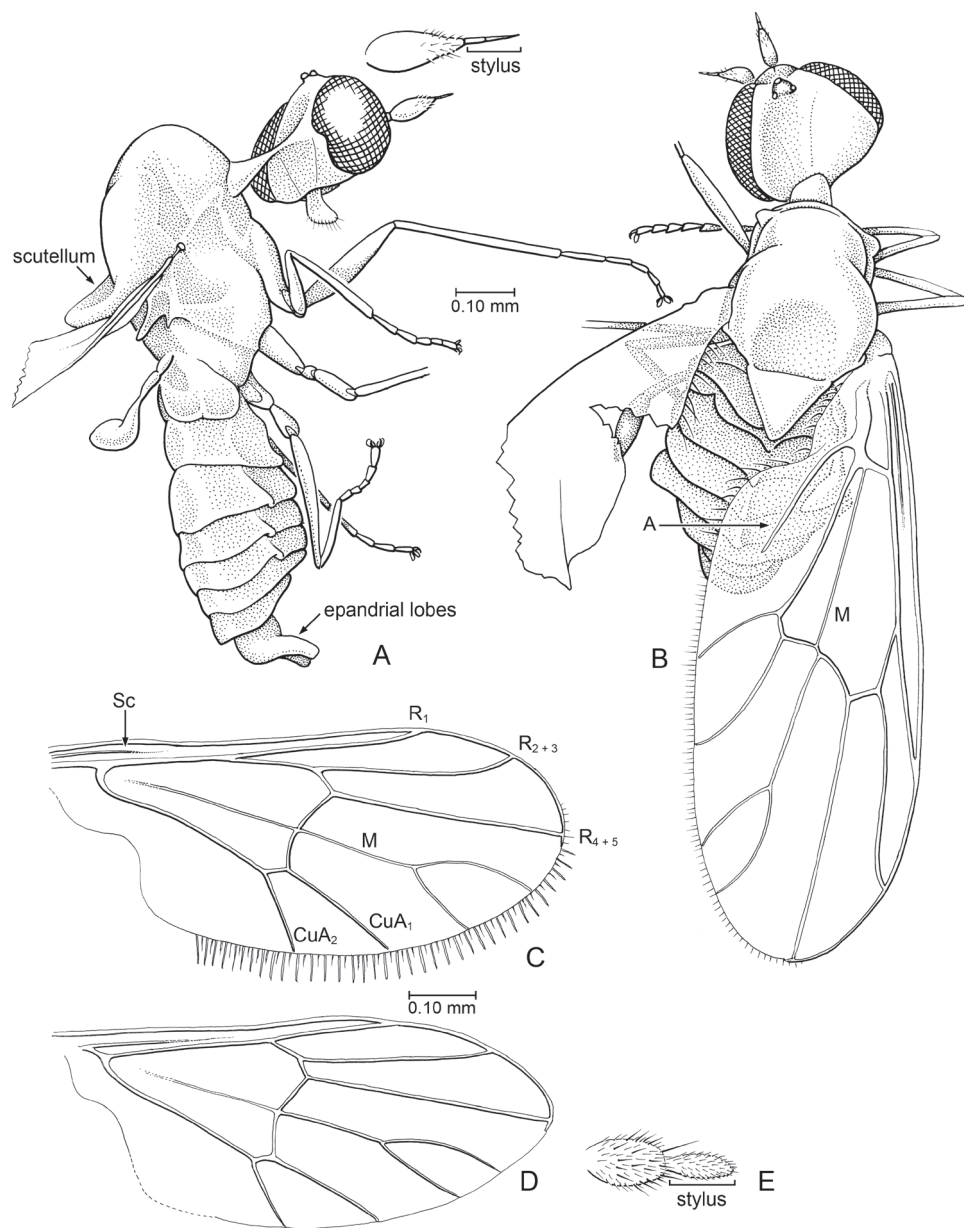
***Microburmyia analvena* Grimaldi & Cumming, sp. n.**

urn:lsid:zoobank.org:act:E64C24A4-F610-4034-AC24-D65721D5BEF5

[http://species-id.net/wiki/Microburmyia\\_analvena](http://species-id.net/wiki/Microburmyia_analvena)

Fig. 7a, b

**Diagnosis.** Distinguished from *M. veanalvena* sp. n. (below) by longer wing; presence of an anal vein; fringe of fine (vs. thick) setae on posterior wing margin; antennal style very fine, with very small article between it and basal flagellomere.



**Figure 7.** *Microburmyia* Grimaldi & Cumming, gen. n. (Bombyliidae: Mythicomyiinae), in Burmese amber **a, b** *M. analvena* Grimaldi and Cumming sp. n. Holotype, KU-Bu079 (**a** lateral view, with detail of antenna **b** dorsal view, as preserved) **c – e** *M. venanalvena* Grimaldi and Cumming, sp. n., Holotype AMNH Bu1552 **c, d** left and right wings, showing variation in vein proportions. **e**, antenna.

**Description.** A minute fly, body length c. 1.1 mm, thorax length 0.5 mm, wing length 1.15 mm. *Head:* Short, somewhat flattened anteroposteriad. Cervical region long. Eyes bare, large, well separated; no dorsoventral differentiation of facets; with small, shal-

low emargination on posterior margin. Proboscis short [palps not visible]. Antenna with basal flagellomere drop-shaped, with sparse setulae; apical style  $0.6 \times$  length of basal flagellomere, very thin, with two articles. Three ocelli present. Postoccipt expansive, concave. *Thorax*: Mesoscutum dorsally arched, devoid of setae or setulae; thorax deep in lateral view; mesoscutellum triangular in shape (nearly equilateral), posterior end tilted upward. Coxae of moderate size; legs slender; devoid of setae, tibiae without apical spurs. Pretarsus with large pulvilli; empodium probably setiform. Halter with slender stem, large knob. Wing long, length slightly greater than length of body, wing  $L/W = 2.72$ . Costa either without spinules or spinules minute; C reaching slightly beyond apex of  $R_{4+5}$ . Posterior margin of wing with fringe of short, fine setae, including alula (setae longer in this area). Vein Sc with apex apparently evanescent, not reaching C.  $R-R_1$  nearly straight;  $R_{2+3}$   $2.0 \times$  length of  $R_1$ ;  $R_{4+5}$  straight, ends at apex of wing; proximal portion of  $R_{4+5}$  joined to r-m to form distal margin of cell br. Cells br and bm large, br is  $0.33 \times$  length of wing,  $W/L$  cell br =  $0.3$ ; cell bm narrower and shorter. Base of M straight, with short apical fork. Crossvein bm-cu slightly shorter than r-m, not in line with each other.  $CuA_1$  and  $CuA_2$  short, curved slightly toward each other. Vein  $A_1$  present, incomplete (reaching to  $0.6 \times$  distance between vein base and wing margin), apex of vein blunt, not evanescent. Anal lobe and alula small. *Abdomen*: Short,  $1.3 \times$  length of mesothorax, apparently devoid of setae and setulae. Tergites I – V with shallow, median keel; epandrium with pair of large ventral lobes.

**Type.** Holotype, male: Myanmar: Kachin (northern Myanmar), in Burmese amber, KU Bu079 (Univ. Kansas, Division of Entomology, Natural History Museum). The amber piece containing the holotype is a very transparent, deep amber color,  $14 \times 7 \times 5$  mm, which also contains 2 scelionid wasps. The minute holotype is at the surface of a fractured corner.

**Etymology.** in reference to the presence of an anal vein (i.e., the Latin noun *vena*), albeit incomplete.

***Microburmyia veanalvena* Grimaldi & Cumming, sp. n.**

urn:lsid:zoobank.org:act:440657CB-BAD8-4D35-8F8A-1D03B5752FB0

[http://species-id.net/wiki/Microburmyia\\_veanalvena](http://species-id.net/wiki/Microburmyia_veanalvena)

Fig. 7c-e

**Diagnosis.** cf. *M. analvena* (above), distinguished by the absence of an anal vein; posterior fringe of setae long, thick; basal flagellomere and style setulose, style with one article, oval.

**Description.** A minute fly, wing length 0.85 mm. *Head*: Short, somewhat flattened anteroposteriad. Cervical region with connection anteroventrally on thorax; not visible dorsally. Eyes bare, large, well separated; no dorsoventral differentiation of facets [presence of emargination on posterior margin not visible]. Proboscis short [palps not visible]. Antenna with basal flagellomere ovoid, having dense setulae (longer apicad); apical style  $0.6 \times$  length of basal flagellomere, thick (nearly  $0.5 \times$  thickness of basal flagellomere), one articulated, setulose. Three ocelli present. Postoccipt expansive, concave. *Thorax*: Mesoscutum dorsally arched, devoid of setae

or setulae; thorax deep in lateral view; mesoscutellum triangular in shape (nearly equilateral). Legs slender; devoid of setae, tibiae without apical spurs. Pretarsus with large pulvilli; empodium probably setiform. Halter with slender stem, large knob. Wing  $W/L = 0.43$ . Costa either without spinules or spinules minute; C reaching slightly beyond apex of  $R_{4+5}$ . Posterior margin of wing with fringe of long, thick setae (visible only on left wing), but margin of alula bare. Vein Sc extremely faint, evanescent.  $R-R_1$  nearly straight;  $R_{2+3}$   $2.0 \times$  length of  $R_1$ ;  $R_{4+5}$  straight, ends at apex of wing; proximal portion of  $R_{4+5}$  joined to r-m to form distal margin of cell br. Cells br and bm large, br is  $0.42 \times$  length of wing,  $W/L$  cell br = 0.27; cell bm slightly narrower and shorter. Base of M straight, with short apical fork. Length crossvein bm-cu approximately equal to that of r-m, in line with each other.  $CuA_1$  and  $CuA_2$  short, straight and diverging. Vein  $A_1$  absent. Anal lobe differentiated, alula small. *Abdomen*: Very broad anteriorly, devoid of setae and setulae on tergites. Tergites I – V apparently without shallow, median keel [difficult to discern with preservation]; epandrium with 5–6 long, thick setae on posterior surface, length of setae approximately equal to length of epandrium.

**Type.** Holotype, Male: Myanmar: Kachin (northern Myanmar), latest Albian to earliest Cenomanian. AMNH Bu1552. Specimen is displayed with wings and legs outspread, but body is only moderately well preserved, with some details obscured beneath layer of deep reddishness. Dorsal view is better than ventral view.

**Etymology.** *ve-* (Latin prefix meaning without), anal vein (L., *vena*), in reference to this venational character.

**Discussion.** It could be argued that these two species might warrant separate genera, based on the differences of antennae, wing fringe, epandrial setae, and proportions of the wing. However, other than the presence/absence of the anal vein, the wing venation is very similar between the two species.

### Therevidae family group

This asiloid group includes the Recent families Therevidae (cosmopolitan; 1,063 described species), the Scenopinidae (cosmopolitan, approximately 420 described species), the monotypic family Evocoidae from Chile (Yeates et al. 2003, 2006), and the small, relict family Apsilocephalidae. Species in the group are most diverse in and largely adapted to dry habitats. Apsilocephalidae is comprised of *Apsilocephala* Kröber (one extant and several undescribed ones species from western North America, plus two fossil species [see below]), *Burmapsilocephala* Gaimari & Mostovski, 2000 (one species in Burmese amber), *Clesthentia* White (two species, from Tasmania), and *Kaurimymia* Winterton and Irwin (one species, from New Zealand) (Yeates et al. 2003; Winterton and Irwin 2008). Monophyly of the family group is not disputed, though hypotheses of relationships among the four families differ slightly (Yeates 2002; Yeates et al. 2003; Wiegmann et al. 2011), and the possibility exists that Therevidae is paraphyletic with respect to Scenopinidae (Woodley 1989; Yeates et al. 2007).

**Family Apsilocephalidae, or near*****Kumaromyia* Grimaldi & Hauser, gen. n.**

urn:lsid:zoobank.org:act:08C3574B-22B5-4654-99CE-3DE0488EDBA2

<http://species-id.net/wiki/Kumaromyia>

**Diagnosis.** Body stout, abdomen short (length about equal to that of thorax); eyes large, bare; antenna with 3 flagellomeres, second article and third (style) minute; palp one-segmented; legs and thorax with bristle-like setae, no pilosity except for postocipital region; hind coxa with small knob on anterior surface; thickness of metatarsi equal that of metatibial base; wing with C ending between apices of  $R_5$  and  $M_1$ , apex of  $R_5$  ending slightly subapically;  $R_4$  and  $R_5$  divergent, not parallel for any part of their lengths, base of  $R_4$  not perpendicular to stem of  $R_{4+5}$  and  $R_5$ .

**Etymology.** Patronym in honor of a great colleague and friend to the senior author, Prof. Kumar Krishna. Appropriately, *Kumaromyia* (as presently known) is preserved in amber from Burma, a place of significance in Kumar's early years.

**Type species.** *K. burmitica*, sp. n., by present designation.

**Discussion.** *Psilocephala electrella* Cockerell, 1920, is a similar species preserved in Burmese amber, but *Kumaromyia burmitica* has a smaller body size (wing width 0.75 mm, vs. 1.5 mm in holotype of *electrella*), and differs venationally, specifically with the apex of  $R_5$  meeting C preapically (vs. slightly postapically in *electrella*),  $M_1$  and  $M_2$  nearly parallel (distinctly divergent in *electrella*), and apex of  $M_3$  distinctly curved to meet apex of  $CuA_1$  at the wing margin (vs. straight in *electrella*). The holotype and unique specimen of *electrella* (NHML In. 20148) is shown in an excellent photograph in Gaimari and Mostovski (2000: fig. 1), and it was examined by the senior author in 2004. It is very partial, with most of the specimen lost (just portions of the scutum and abdomen, two legs and most of both wings remain), so it is very difficult to determine if the two species may be congeneric.

***Kumaromyia burmitica* Grimaldi & Hauser, sp. n.**

urn:lsid:zoobank.org:act:96FE6FDB-D380-47A8-8EDB-2FE979761B72

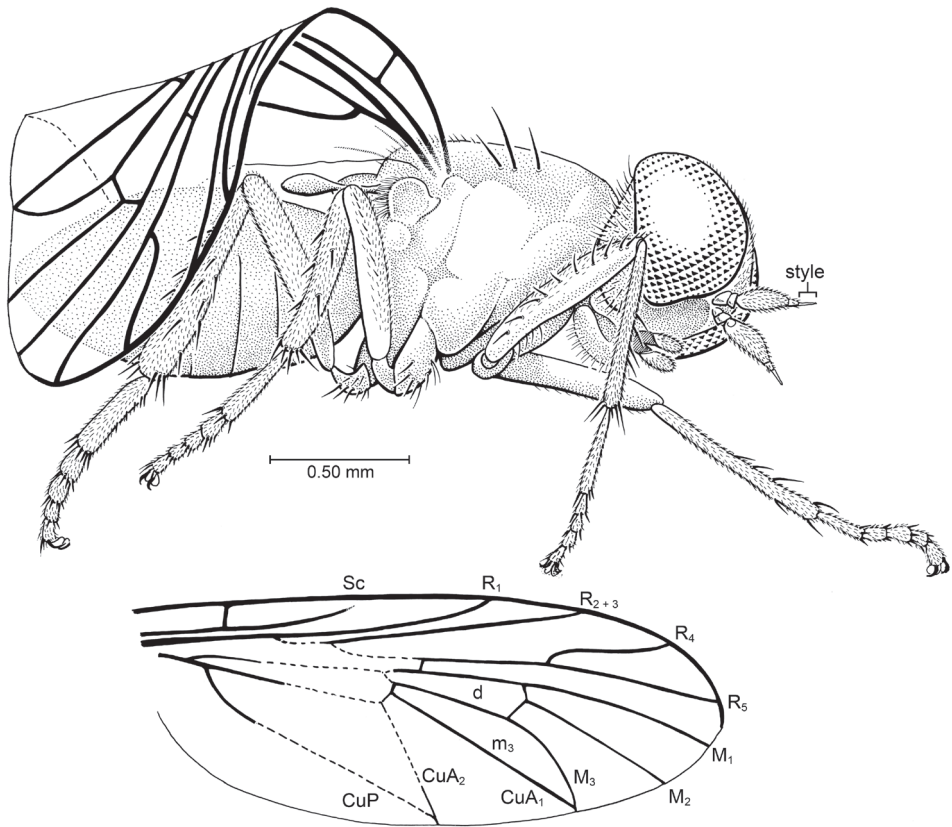
[http://species-id.net/wiki/Kumaromyia\\_burmitica](http://species-id.net/wiki/Kumaromyia_burmitica)

Fig. 8

**Diagnosis.** As for the genus.

**Description.** Small fly, total body length ca. 2.70 mm, thorax length 1.0 mm, wing length (estimated) 2.50 mm. *Head:* Large, with large eyes. Eyes bare, hemispherical in lateral view (posterior margin flat), no dorsoventral differentiation of facets; inner margins of eyes parallel, separated by distance approximately equal to width between antennal bases. Frons slightly convex, not protruding anteriorly; with numerous fine setulae, without calli. Face ("subcranial cavity") depressed, dark (sclerotized?), glabrous. Antennal scape and pedicel small, approximately equal in size, devoid of thick setae; basal flagellomere largest antennomere, drop-shaped, with dense setulae (no setae); api-





**Figure 8.** *Kumaromyia burmitica* Grimaldi & Hauser, gen. et sp. n. (Therevoid family group: ?Apsilopcephalidae), in Burmese amber. Right lateral habitus of holotype AMNH Bu131, as preserved. Below: wing, partially reconstructed.

cal two antennomeres (including apical style) small, fine, with style slightly longer than penultimate antennal article. Maxilla with bases (cardostipites) sclerotized and partially fused, palp 1-segmented. Labellum slightly larger than palps. Postgena well developed, with numerous fine setae (pilosity). *Thorax*: Deep in lateral view, pleura apparently devoid of fine or bristle-like setae; scutum with at least 8 pairs of setae [dorsal view, including scutellum, obscured]. Scutum with 3 pairs of notopleurals and 5 pairs in supralar region and some setulae; no cervical/postcervical setae. *Legs*: With thick, stiff setae, primarily on tibiae; fore tibia slender, hind tibia thickest. Fore leg: femur with lateral row of ca. 10 fine setae, tibia with anterior row of 4–5 setae, 4 pre-apical setae. Mid leg: Femur apparently devoid of setae, tibia with 3 evenly-spaced setae on dorsal surface, 2 more ventrad, 4 apically. Hind leg: Coxa with small knob on ventral surface [best seen in left coxa]; femur devoid of setae, tibia with dorsal row of 3–4 setae, lateral row of 3 setae, ventral row of 3–4 setae. Basitarsomere on each leg equal in length to (or slightly longer than) combined length of distal tarsomeres. Each tarsomere with ca. 4 short, stiff setae on rim of distal end. Pretarsus with pair of large pulvilli, empodium setiform.

**Wing:** Large, length nearly equal to that of body. Crossvein h long (space between Sc and C deep); Sc long, length approximately  $\frac{1}{2}$  that of wing and slightly shorter than length of R<sub>1</sub>; apex of Sc apparently incomplete (not meeting C). Apices of Sc and R<sub>1</sub> without pterostigma surrounding apices. Fork of R and Rs deep, proximal to level of vein h. R<sub>2+3</sub> straight, without apical curve. Fork of R<sub>4+5</sub> not widely divergent; R<sub>5</sub> in line with stem of R<sub>4+5</sub>, apex of R<sub>5</sub> ending very near apex of wing (not posterior to it); R<sub>4</sub> slightly curved, distinctly shorter than R<sub>5</sub>. Cell d slender, greatest width  $<0.25 \times$  length. Veins M<sub>1</sub> and M<sub>2</sub> slightly divergent, M<sub>2</sub> and M<sub>3</sub> very divergent, all M veins attached to apex of cell d. Apex of M<sub>3</sub> meeting apex of CuA<sub>1</sub> at wing margin. ABDOMEN: Short, only slightly longer than thorax; details (e.g., sternites, genitalia) not observable.

**Type.** Holotype, female, AMNH Bu131: Myanmar: Kachin State, near Myitkyina (mid-Cretaceous: Late Albian – Cenomanian). Specimen is complete, but the right wing (the only one observable) is folded, and most of the dorsal view is obscured, compromising a complete reconstruction of the venation (fig.8). The fly is complete, though slightly compressed and with a slight coating of particulate matter over some areas. Its left side is lying on a rough surface of the amber, which obscures that view. The piece also contains some twisted strands of spider webbing.

**Etymology.** In reference to the country of origin.

**Discussion.** There is little question this fossil belongs to the therevid group, albeit unusually small (within the range in body size of some apsilocephalids and a few genera of Phycinae, such as *Efflatouniella* Kröber, 1927). Therevid-group features include the antennal structure, bristle-like setae on the scutum and on the legs, the small knob on the hind coxa, as well as the venation. Unlike most Therevidae, *Kumaromyia* lacks any pruinosity and pilosity (except for the postgena), although Xestomyzinae and Agaphotinae are also robust and have sparse pilosity. *Kumaromyia* lacks any thick setae that typically encircle the scape and/or pedicel subapically in Therevidae. Also, *Kumaromyia* has R<sub>4</sub> and R<sub>5</sub> above the wing tip, whereas in Therevidae these are above and below the wing tip, respectively. Unlike Apsilocephalidae, *Kumaromyia* has a one-segmented palp, vs. two-segmented in Apsilocephalidae, where the basal segment is distinctively thin and long (oddly, palp segmentation and structure was not described for *Kaurimyia*). The antennal stylus and stout body in *Kumaromyia* is much more similar to that of *Clethentia*, as the stylus in *Apsilcephala*, *Kaurimyia*, and even *Burmapsilcephala* is long and thin. It is quite possible that *Kumaromyia* is a stem-group taxon for the therevid-family group, not necessarily belonging within Apsilocephalidae or Therevidae.

Fossil Therevidae are scarce, with only five definitive species known, all from the Tertiary. Hauser (2007) and Hauser and Irwin (2005) revised the fossil species:

*Ambradolon grimaldii* Metz and Irwin 2000: Early Miocene Dominican Republic amber  
*Arctogephyra agilis* (Meunier 1908): mid-Eocene Baltic amber  
*Dasystethos hoffeinsi* Hauser 2007: mid-Eocene Baltic amber  
*Kroeberiella pinguis* (Loew 1850): mid-Eocene Baltic amber  
*Palaeophrocera scudderi* (Cockerell 1909): uppermost Eocene, Florissant, Colorado, USA  
 Fossil Apsilocephalidae range from the Cretaceous to early Tertiary:

*Apsilocephala pusilla* (Hennig 1967): mid-Eocene Baltic amber

*Apsilocephala vagabunda* (Cockerell 1927): uppermost Eocene, Florissant, Colorado, USA

*Burmapsilocephala cockerelli* Gaimari and Mostovski 2000: mid-Cretaceous Burmese amber  
Undescribed sp.: Early Cretaceous amber, Wealden, UK (Chandler 2010: plate 32, fig. 2).

The position of *Psilocephala electrella* Cockerell 1920 within the therevoid group is uncertain.

## Families Incertae sedis

### Family Apystomyiidae

This family contains the sole Recent species *Apystomyia elinguis* Melander, 1950, from California, one of the world's most relict and intriguing flies, with a dramatic history of systematic interpretation. Traditionally, *Apystomyia* has been placed in the Bombyliidae (e.g., Hall 1981), and then was hypothesized to be the sister group to the Eremoneura (Wiegmann et al. 1993). It has been placed in the Hilarimorphidae (Yeates 1994), as well as allied to the Therevidae (Sinclair et al. 1994). Nagatomi and Liu (1994) concluded that the male and female terminalia differ markedly from Hilarimorphidae, with the female terminalia similar to those of the Cyclorrhapha, and they erected the Apystomyiidae for this species. Soon thereafter, Nagatomi (1996) indicated that *Apystomyia* is allied to the proratine Scenopinidae. More recently, Yeates (2002), in his morphological analysis of basal Brachycera relationships, hypothesized the Hilarimorphidae (including *Apystomyia*) as being the sister group to the Eremoneura. However, Trautwein et al. (2010) considered *Apystomyia* to be the sister group to the Cyclorrhapha based on molecular evidence. Lastly, the comprehensive total-evidence study by Wiegmann et al. (2011) proposed a sister-group relationship of *Apystomyia* to the Cyclorrhapha, separate from Hilarimorphidae (which was placed near Bombyliidae).

### Genus *Hilarimorphites*

*Hilarimorphites* Grimaldi & Cumming, 1999: 21. Type species: *H. yeatesi* Grimaldi and Cumming. By original designation.

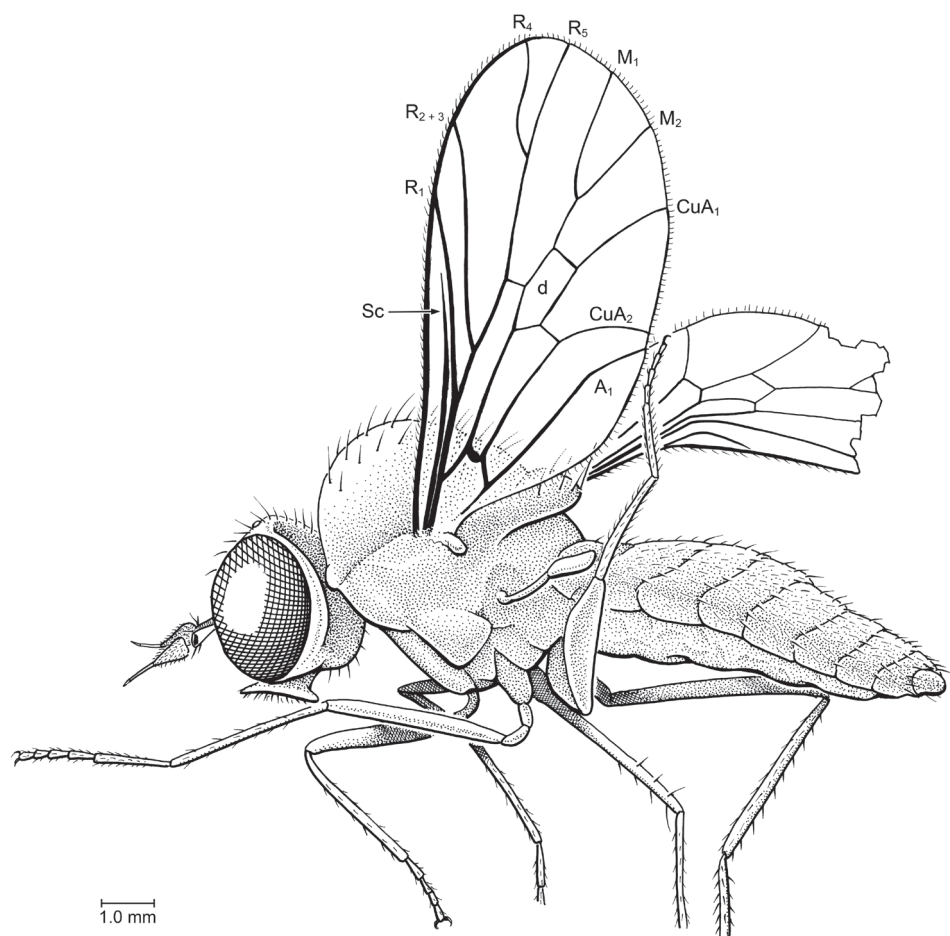
#### *Hilarimorphites burmanica* Grimaldi & Cumming, sp. n.

urn:lsid:zoobank.org:act:BAEACD0A-8879-4761-95DB-4AF8297CADA0

[http://species-id.net/wiki/Hilarimorphites\\_burmanica](http://species-id.net/wiki/Hilarimorphites_burmanica)

Fig. 9

**Diagnosis.** Distinguished from the 4 other species in the genus (known only in New Jersey amber) by venation: vein C ending just slightly beyond apex of  $R_4$  (not



**Figure 9.** *Hilarimorphites burmanica* Grimaldi & Cumming, sp. n. (Apystomyiidae) in Burmese amber, as preserved. Holotype, AMNH 098.

at apex of  $R_5$ ); Sc long, distally incomplete (more so than in *H. superba* Grimaldi and Cumming 1999, the only other species with this trait); veins  $CuA_2$  and  $A_1$  not joined before meeting wing margin (anal cell open distally). Distinguished from *Apystomimus* by the larger (normal-sized) wings, with an open cup (anal) cell. Also, basal flagellomere is more elongate and triangular in *H. burmanica*, and the antennal stylus longer than in the other species of *Hilarimorphites*.

**Description.** Based on a virtually complete, well-preserved female. Body length (excluding antennae) 1.40 mm; thorax length 0.50 mm; wing length 0.95 mm. *Head:* Antenna with first flagellomere an elongate triangle in lateral view; apical antennal article(s) form a thin style, with possibly a minute apical article. Eyes large, glabrous. Frons with sparse, scattered setae. Proboscis with broad, flat labellum (palps not vis-

ible). *Thorax*: Notum dome-shaped, with sparse, fine, stiff setae; scutellum with 2 pairs of erect setae. Legs very slender, of moderate length, without distinctive spines or tibial spurs. *Wing*: typical of *Hilarimorphites*, except as given in diagnosis above [also, anal lobe may be less developed than in other species, but this area slightly folded under and obscured]. Halter of moderate length, knob slender. *Abdomen*: Slender, tergites unmodified, cerci and genitalia not fully visible.

**Type.** Holotype female, AMNH Bu-098, in amber from Myanmar: Kachin, Tanai Village (on Ledo Rd. ca. 105 km Myitkyna). Amber is a deep, clear yellow,  $15 \times 10 \times 5$  mm, and was embedded in epoxy and trimmed to a wedge shape in order to maximize a full lateral view of the fly and its venation. The piece also contains a male chironomid and a thrips (Thysanoptera).

**Etymology.** From Burma (Myanmar).

**Discussion.** *Hilarimorphites* was known only from Turonian-aged amber of central New Jersey, USA, and besides the new species in Burmese amber a very similar taxon is also now known from the Upper Jurassic of Kazakhstan. Mostovski (1999) described *Apystomimus zaitzevi*, preserved as a compression from the Karabastau Formation (Upper Jurassic) of the famous Karatau-Mikhailova Lagerstätte. That well-preserved specimen has a venation indistinguishable from that of *Hilarimorphites* Grimaldi & Cumming, 1999. *Apystomimus* differs from that genus by having small, brachypterous wings (ca.  $0.5 \times$  length of the body) and very long cerci (nearly  $0.5 \times$  length of wing; *Hilarimorphites* has very small cerci typical of lower Brachycera). Since these are autapomorphic features of *Apystomimus*, it could be appropriate to synonymize one of the genera (although *Apystomimus* is more aptly named, *Hilarimorphites* has date precedence by two months). *Hilarimorphites* was originally placed in the Hilarimorphidae, and Mostovski placed *Apystomimus* in Asilomorpha family-incertae sedis (but near the extant genus *Apystomyia*). Recent *Hilarimorpha* lack the discal cell, they have the cup cell closed, and lack a well-developed anal lobe while retaining a vestige of the anal vein, so the venation of the fossils is far more easily derived from *Apystomyia*. Thus, we agree that *Hilarimorphites* and *Apystomima* should both be classified in Apystomyiidae. The wing of *Hilarimorphites* differs from that of *Apystomyia* by the following: slightly shorter  $R_1$  and  $R_{2+3}$  veins; fork of  $R_4+R_5$  less divergent, the branches slightly longer; cells br and bm significantly larger; cell cup significantly larger, with veins  $CuA_2$  and  $CuP$  meeting just before or at the wing margin, or not all (vs.  $CuA_2+CuP$  with a long stem in *Apystomyia*); anal lobe of wing not protruding; and cell d much shorter, its length ca.  $3 \times$  the width in *Hilarimorphites* (vs.  $5 \times$  the width in *Apystomyia*).

*Hilarimorphites burmanica* is intermediate in age between the previously known fossils, and greatly extends the geographic range. An extinct clade or grade of Apystomyiidae occurred minimally throughout Laurasia from the Upper Jurassic to the Upper Cretaceous, which is an age that is consistent with its hypothesized sister-group relationship near Eremoneura (Grimaldi and Cumming, 1999; Grimaldi and Engel, 2005; Wiegmann et al., 2011). Oddly, there are no other fossils as yet known of the family, not even from prolific and diverse Tertiary deposits like Baltic amber.

## Family Tethepomyiidae

**Diagnosis.** Small flies 1.5 mm in total body length, with venation and other features of the wing reduced. Vein  $CuA_1$ - $CuA_2$  comprised of short fork; vein M simple; vein A either absent or reduced to vestige at base of wings. Eyes very large, extensively holoptic in males. Cervical region long, head well separated from thorax; mesonotum compact, scutellum very short.

This is a highly specialized family of Diptera known only in amber from the Cretaceous of New Jersey, USA (Grimaldi and Cumming, 1999), Spain (Grimaldi and Arillo 2008), and now Myanmar (herein), comprised of two genera, *Tethepomyia* Grimaldi & Cumming and *Tethepomima* Grimaldi & Arillo. Discovery of the female of a new species in Burmese amber reveals the oviscapt to be a highly specialized, aculeus-type possibly used for parasitizing insect hosts. A few structures of tethepomyiids are similar to that of the Cretaceous brachyceran family Eremochaetidae (Ussatchev 1968; Kovalev 1986, 1989; Ren and Guo 1995; Mostovski 1997), which are discussed by (Grimaldi and Arillo, 2008: p. 264). The aculeate oviscapt is now known to be another shared similarity (below). Either the highly reduced venation of tethepomyiids is a result of miniaturization, or these two families are unrelated and share remarkably convergent features. Tethepomyiidae were originally considered to possibly be nematoceran (Grimaldi and Cumming 1999), but we are including the family in this report since the oviscapt reveals a likely close relationship with Eremochaetidae, which are definitive Brachycera.

### Genus *Tethepomyia*

<http://species-id.net/wiki/Tethepomyia>

*Tethepomyia* Grimaldi and Cumming 1999: 6. By original designation.

**Diagnosis** (emended). Distinguished from *Tethepomima* by the following: Most or all of antennal flagellum lost; mesonotum bare, devoid of setae or setulae; apical tibial spurs absent; costal vein incomplete, not reaching to apex of Rs; costal spinules and fringe of fine setae on posterior margin of wing lost; alula and anal lobe lost; veins  $R_{2+3}$  and  $R_{4+5}$  lost (Rs simple, unbranched), crossvein r-m lost.

**Type species.** *T. thauma* Grimaldi and Cumming 1999: 6. By original designation.

### *Tethepomyia zigrasi* Grimaldi & Arillo, sp. n.

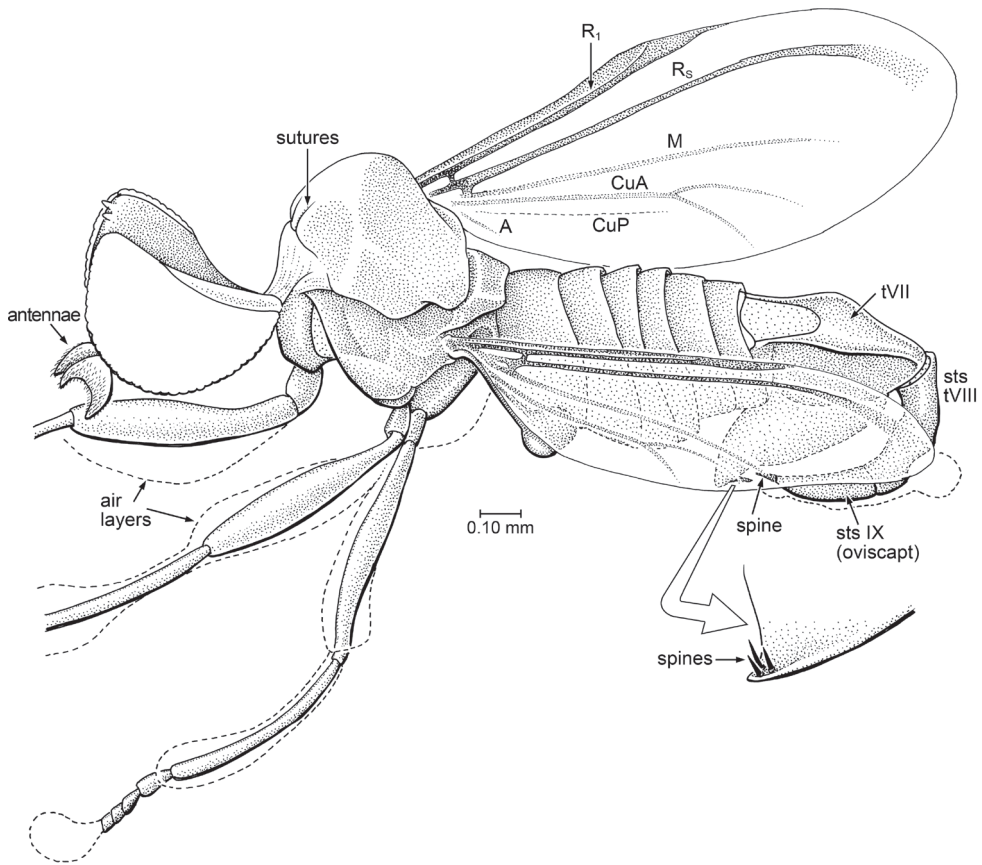
urn:lsid:zoobank.org:act:1D051ABF-34FA-461F-8583-F3E6CB322FCF

[http://species-id.net/wiki/Tethepomyia\\_zigrasi](http://species-id.net/wiki/Tethepomyia_zigrasi)

Fig. 10

**Diagnosis.** Distinguished from the other two species of the genus, which are known only from males (*T. thauma* Grimaldi and Cumming: New Jersey amber; and *T. buruhandi* Grimaldi and Arillo: Spanish amber), by the following: thickened costal and





**Figure 10.** *Tethepomyia zigراسi* Grimaldi & Arillo, sp. n. (Tethepomyiidae) in Burmese amber, also showing ventral detail of distal portion of abdomen. Private collection of James Zigras. sts: syntergosternite.

*Rs* veins, bases of *M* and *Cu* complete; dorsoventral differentiation of eye facets (in female, undoubtedly more differentiated in males); U-shaped basal flagellomere large, pedicel small, indistinct. Known only from female.

**Description.** Body length (tip of basal flagellomere to posterior-most surface of tergite VIII) 2.15 mm. **HEAD:** Hemispherical in female; eyes very large, covering most of head, only small strip of gena exposed [view of face and frons not visible]. Dorsal eyes facets approximately 0.5× diameter of ventral facet; eye completely bare, no interfacetal setulae. No setae apparent on gena or frons. Ocelli possibly on small tubercles – small, digitate lobes in this area [but details obscure]. Antenna with large, crescent-shaped basal flagellomere; pedicel apparently small [indistinct]. Proboscis and palps not visible [ventral surface of head covered with bubble]. Posterior surface of head evenly and shallowly concave. Cervical region long; head not adpressed to pronotum.

**Thorax:** Small and short, *L* = 0.55 mm, with scutum arched, posterior half long and sloped; scutum and scutellum devoid of acrostichals or setae. Scutellum short, length

ca.  $0.20 \times$  that of scutum; posterior margin flat and slightly concave, not acute. Legs bare, devoid of setae or setulae; with femora slightly swollen in middle. Fore and mid coxae adjacent, hind tibia with coxal-trochanteral articulation facing anteriorly (hind legs apparently held forward). Tibiae long and slender (slightly shorter than respective femur). Metatibia slightly bowed, as if to fit tightly against ventral surface of femur. Tarsi short, with basitarsomere only slightly longer than tarsomere 2 [most tarsomeres obscured by layer of air]. Halter long; knob large, length of stem approximately  $2.2 \times$  greatest diameter of knob; stem without setae. Forewing with reduced venation; veins extremely light (particularly M and Cu); microtrichia of forewing either absent or so microscopic as to not be visible; no costal spinules or fringe of fine setulae on posterior margin of wing. Vein C short, extended to only ca.  $0.6 \times$  length of wing, sclerotized, swollen towards apex; apex of  $R_1$  fused with swollen portion of C. Rs thick, width slightly increased apically; vein incomplete, not reaching wing margin/tip. Vein M faint, complete, tip evanescent and not reaching wing margin. Vein CuA faint, with short fork  $CuA_1$ – $CuA_2$  (length of fork  $0.7 \times$  length of stem); branches of fork curved towards anal region. What appears as deep fold ( $CuP$ ?) parallel and posterior to stem of CuA. Faint, short vein A at base of posterior portion of wing; anal lobe and alula not present.

**Abdomen:** Tergites and sternites well developed, sclerotized; segments I – VI short (I longest), tergite VII long, sclerotized, length approximately equal to that of tII through tVI, with deeply incised membranous region basally, dorsal and lateral surfaces concave. Sternite VII very large, lobe-like, suspended beneath abdomen; apex pointed, bearing three short, sharp spines. Base of tVII apparently articulating with apex of tVI; tVII+VIII formed into a curved, sclerotized, sharp ovipositor-like structure, with a small, sharp, sclerotized spine at tip. Spine at tip of abdomen/oviscapt (sts IX) apparently interdigitating between three spines of sVII.

**Type.** Holotype, Female: Myanmar, Kachin State, Early Cenomanian. Specimen is in excellent condition and is in the private collection of James Zigras.

**Etymology.** Patronym for James Zigras, for allowing preparation and study of this remarkable specimen.

**Discussion.** *Tethepomyia zigrasi* sp. n. appears to be a sister group to *T. buruhandi* + *thauga*, from Spanish and New Jersey ambers, respectively. *Tethepomyia zigrasi* retains the bases of M, Rs, and Cu, which the other two species have lost. It shares with *buruhandi* and *thauga* many losses: of the antennal stylus, tibial spurs, crossvein r-m, veins  $R_{2+3}$  and  $R_{4+5}$ , costal vestiture, fringe of marginal setulae on the wing, as well as the reduction of vein C.

With little question the oviscapt of *T. zigrasi* is a hypodermic-like (“aculeus”) structure, probably used for injecting its eggs into hosts. It was probably a parasitoid. An oviscapt of similar specialization has sporadically evolved in Diptera. It occurs in a few Phoridae (e.g., *Apocephalus*), all Pipunculidae, and within the Schizophora in some Conopidae (e.g., *Stylogaster*), most Tephritoidea, all Cryptochaetidae, and probably other families. The trait appears to have evolved most often in parasitoid groups (all those listed above except tephritoids). Most tephritoids inject their eggs into fruits or stems, though a few (like Pyrgotidae) are parasitoids. Fine structure of the injecting

ovisclapt reveals its convergent development: what is labelled as the “ovipositor” in Pipunculidae (Hardy, 1989: pg 747) is probably a sclerotized, spine-like derivative of the cercus. In Cryptochaetidae the syringe-like ovisclapt is sternite VIII; in Tephritoidea the ovisclapt is a telescoping structure composed of segments 7–9. Interestingly, *Tethepomyia* has a suite of other convergent features similar to those of parasitoid families. Like Pipunculidae, Tethepomyiidae possess large eyes; like Pipunculidae and Cryptochaetidae the family has large pulvilli; and like Cryptochaetidae the basal flagellomere is enlarged and the arista minute to lost. These are probably functionally correlated features.

## Unplaced to Family

### *Myanmyia* Grimaldi, gen. n.

urn:lsid:zoobank.org:act:7090815B-8878-487D-9980-78581DB36111

<http://species-id.net/wiki/Myanmyia>

**Diagnosis.** Distinctive small flies (body length less than 1.5 mm) with antennal stylus arista-like and terminal, having a single article; face without ptilinal suture; median margins of eyes very close on frons; maxillary palpus two-segmented; mesonotum with dorsocentral and scutellar setae; wing venation highly reduced, with  $R_{2+3}$  and  $R_{4+5}$  each unbranched, M unbranched and evanescent at both ends, Cu simple; female with pair of long, digitate, unsegmented cerci.

**Etymology.** From Myanmar, country of origin, and *-myia*, a common suffix referring to the feminine Greek word for fly.

**Type species.** *M. asteiformia* sp. n. By present designation.

**Discussion.** This is a perplexing little fly. Chaetotaxy of the thorax, the wing venation, and even body shape are strikingly similar to acalyptrate flies in the Asteiidae. Convergent wing features of the two groups include short  $R_1$  and  $R_{2+3}$  veins; a straight  $R_{4+5}$  that meets the tip of the wing, and even microtrichia that are arranged in rows. However, *Myanmyia* is not even a cyclorrhaphan, by virtue of the terminal (versus dorsal) arista-like stylus, lack of a ptilinum, and presence of two-segmented (vs. 1-segmented) palpi. With the exception of a few very basal Recent and extinct Platypetidae, almost all other Cyclorrhapha have a dorsal arista. Two-segmented palpi exclude *Myanmyia* from the Eremoneura (the apparent basal segment of the two segmented palpi seen in some Phoridae is probably a palpifer [Cumming and Wood 2009]). While some empidoids (e.g., Cretaceous *Nemedina* genus-group species [Grimaldi and Cumming 1999]) have short R veins and faint M and Cu veins, the branching pattern for these flies differs significantly at the base from that of *Myanmyia*.

***Myanmyia asteiformia* Grimaldi, sp. n.**

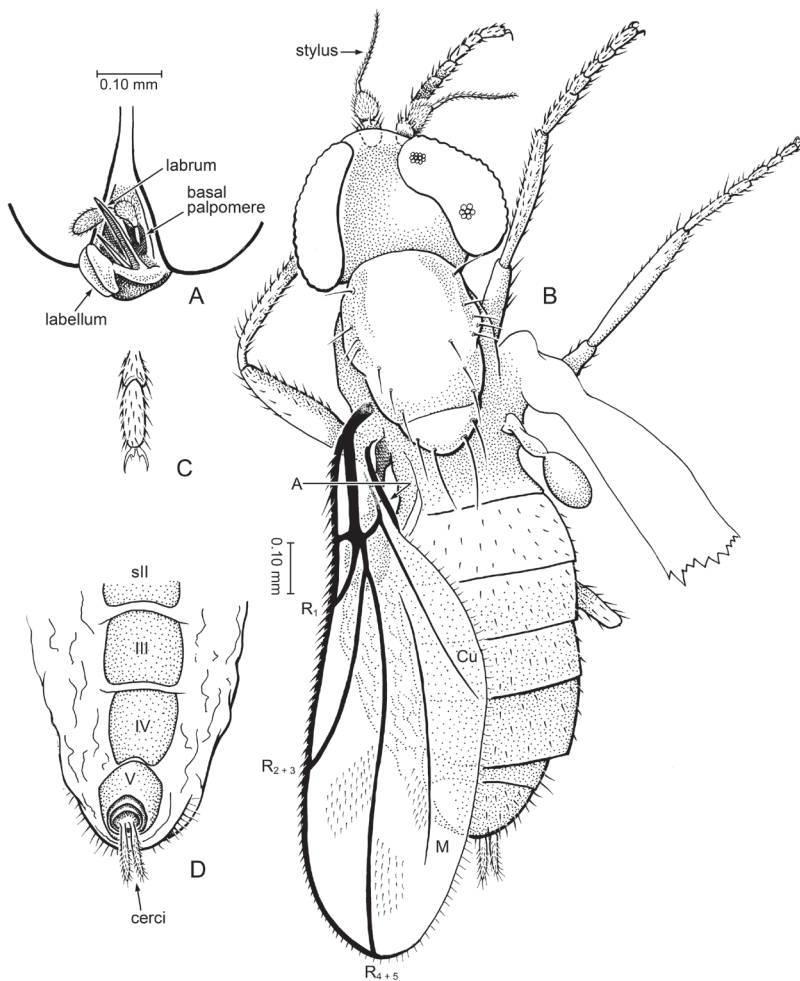
urn:lsid:zoobank.org:act:3BD4F73D-375A-4B7F-8637-5449BC695495

[http://species-id.net/wiki/Myanmyia\\_asteiformia](http://species-id.net/wiki/Myanmyia_asteiformia)

Fig. 11

**Diagnosis.** As for genus.

**Description.** Body size small, length 1.35 mm (excluding antennae and cerci), slender. Wing length 1.05 mm. *Head:* Slightly wider than thorax [possibly preservational, as head is slightly compressed]. Antenna with cup-like pedicel, distal edge rimmed with fine, stiff setae; basal flagellomere drop-shaped, width approximately equal to length; arista-



**Figure 11. a-d** *Myanmyia asteiformia* Grimaldi, gen. et sp. n. (unplaced to family), in Burmese amber (holotype, AMNH Bu1616) **a** Anteroventral detail of head **b** dorsal habitus, as preserved **c** pretarsus. **d** apex of abdomen, ventral view.

like stylus terminal, setulose, 1-articled (no small basal articles), length approximately  $3 \times$  length of basal flagellomere. Eyes large (occupying virtually entire lateral surface of head), bare, with slight dorsoventral differentiation of facets (dorsal facets ca.  $2 \times$  diameter of ventral ones); inner margins of eyes (on frons) very close, width of separation equal to ca. 3 facet diameters. Ptilinal suture absent. Maxillary palp 2-segmented, with apical segment clavate and basal segment slender. Labrum long, very slender; hypopharynx (?) stylet-like; labellum small. Gena very shallow or barely developed (not apparent). Postociput broad, concave. *Thorax*: Slender, with the following dorsal setae (*per side*): 1 postpronotal, 4 supra-alar/notopleurals, 3 postsutural dorsocentrals (posterior one largest), 2 pairs scutellars [pleura not visible]. Legs of moderate length, setulose, without distinctive spines/spurs. Pretarsus with claws well developed, but no pulvilli. Wing: Long, slender,  $W/L = 0.33$ ; membrane microtrichia arranged in oblique rows (between R veins) and longitudinal rows (portions of space between  $R_{4+5}$  and M). Vein C slightly beyond apex of  $R_{4+5}$ , no humeral or subcostal breaks; with long, sparse spinules. Sc short, very faint [best seen when tilting specimen]. Base of vein R thick,  $R_1$  short (length  $0.3 \times$  length of wing);  $R_{2+3}$  unbranched, meeting C at  $\frac{2}{3}$  the length of wing.  $R_{4+5}$  straight, extended to tip of wing, unbranched. Vein M simple, unbranched, very lightly sclerotized; both ends evanescent. Sc. Vein A thick, heavily sclerotized strip along alular edge of wing. Anal lobe and alula not developed. Halter: with large, darkened knob, stem approximately same length as knob or slightly longer. *Abdomen*: Tergites I–VII well developed, with sparse setulae, without macrosetae; sternites II, III, IV large, bare; segment V is tubular; VI, VII ring-like; terminal segment bearing pair of long, finger-like, one-segmented cerci. Presence/absence of abdominal muscle plaques not visible.

**Type.** Holotype, female, AMNH Bu1616, in amber from northern Myanmar: Kachin State, Tanai Village, 105 km NW Myitkyina. The holotype is the sole inclusion in a clear amber-colored piece  $9 \times 6 \times 2$  mm. Ventral surface of the thorax and the abdomen are compressed, and a crack through the thorax obscures some details. The left wing of the unique specimen is well preserved, but venation is optimally observed by tilting and observing the piece at various oblique angles. Right wing is twisted, but in oblique view additional details of venation are visible.

**Etymology.** L., for like, and *Asteia* (type genus of the Asteiidae, a family of Schizophoran flies) and Latin *-formia*, meaning like, in reference to the similarity of the unrelated two taxa in body shape, size, and wing venation.

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